New Mexico Register / Volume XXX, Issue 19 / October 15, 2019

STATE GAME COMMISSION MEETING AND RULE MAKING NOTICE

The New Mexico State Game Commission ("Commission") has scheduled a regular meeting and rule hearing for Thursday November 21, 2019, beginning at 9:00 a.m. at the New Mexico Department of Game and Fish office, 1615 W. College Blvd., Roswell, NM 88201, to hear and consider action as appropriate on the following: presentation of proposed changes to the Bear and Cougar rule.

Synopsis:

The proposal is to adopt a new Bear and Cougar rule, 19.31.11 NMAC, which will become effective April 1, 2020. The current Bear and Cougar rule is set to expire on March 31, 2019.

The proposed new rule includes: 1) changing the start date for the bear general weapon type season to September 25 in Bear Management Zones 10, 12, and 13, and extending the closing date to December 15 in Zones 10 and 12, and November 30 in Zone 13; 2) grouping the Barker and Colin Neblett Wildlife Management Area (Hunt Code BER-1-104) and Valle Vidal (Hunt Code BER-1-105) draw licenses as a single license and including the Urraca Wildlife Management Area in the areas open to hunting with that license; 3) no longer allowing traps and foot snares as a method of sport harvest for cougar; 4) adjusting cougar harvest limits to align with recent data and management objectives; 5) moving Game Management Unit 25 from Cougar Management Zone J to Cougar Management Zone L; and 6) no longer allowing an additional two tags for cougar license holders who have successfully filled their original two tags. A full text of changes will be available on the Department's website at: www.wildlife.state.nm.us.

Interested persons may submit comments on the proposed changes to the Bear and Cougar rule at: DGF-Bear-Cougar-Rules@state.nm.us, or individuals may submit written comments to the physical address below. Comments are due by 5:00 p.m. on November 19, 2019. The final proposed rule will be voted on by the Commission during a public meeting on November 21, 2019. Interested persons may also provide data, views or arguments, orally or in writing, at the public rule hearing to be held on November 21, 2019.

Full copies of text of the proposed new rule, technical information related to proposed rule changes, and the agenda can be obtained from the Office of the Director, New Mexico Department of Game and Fish, 1 Wildlife Way, Santa Fe, New Mexico 87507, or from the Department's website at www.wildlife.state.nm.us/commission/proposals-under-consideration/. This agenda is subject to change up to 72 hours prior to the meeting. Please contact the Director's Office at (505) 476-8000, or the Department's website at www.wildlife.state.nm.us for updated information.

If you are an individual with a disability who is in need of a reader, amplifier, qualified sign language interpreter, or any other form of auxiliary aid or service to attend or participate in the hearing or meeting, please contact the Department at (505) 476-8000 at least one week prior to the meeting or as soon as possible. Public documents, including the agenda and minutes, can be provided in various accessible formats. Please contact the Department at 505-476-8000 if a summary or other type of accessible format is needed.

Legal authority for this rulemaking can be found in the General Powers and Duties of the State Game Commission 17-1-14, et seq. NMSA 1978; Commission's Power to establish rules and regulations 17-1-26, et seq. NMSA 1978.

EXHIBIT

1

Clean Copy - Initial Proposed Rule

TITLE 19 NATURAL RESOURCES AND WILDLIFE
CHAPTER 31 HUNTING AND FISHING
PART 11 BEAR AND COUGAR

19.31.11.1 ISSUING AGENCY: New Mexico department of game and fish.
[19.31.11.1 NMAC - Rp, 19.31.11.1 NMAC, 4/1/2020]

19.31.11.2 SCOPE: Sportspersons interested in bear and cougar management and hunting. Additional requirements may be found in Chapter 17 NMSA 1978 and Title 19 NMAC.
[19.31.11.2 NMAC - Rp, 19.31.11.2 NMAC, 4/1/2020]

19.31.11.3 STATUTORY AUTHORITY: 17-1-14 and 17-1-26 NMSA 1978 provide that the New Mexico state game commission has the authority to establish rules and regulations that it may deem necessary to carry out the purpose of Chapter 17 NMSA 1978 and all other acts pertaining to protected mammals, birds, and fish.
[19.31.11.3 NMAC - Rp, 19.31.11.3 NMAC, 4/1/2020]

19.31.11.4 DURATION: April 1, 2020 through March 31, 2024.
[19.31.11.4 NMAC - Rp, 19.31.11.4 NMAC, 4/1/2020]

19.31.11.5 EFFECTIVE DATE: April 1, 2020, unless a later date is cited at the end of a section.
[19.31.11.5 NMAC - Rp, 19.31.11.5 NMAC, 4/1/2020]

19.31.11.6 OBJECTIVE: Establishing open hunting seasons and regulation, rules and procedures governing the distribution and issuance of bear and cougar licenses by the department.
[19.31.11.6 NMAC - Rp, 19.31.11.6 NMAC, 4/1/2020]

19.31.11.7 DEFINITIONS:

A. **"Bear entry permit"** shall mean a permit awarded through a public drawing which entitles the holder of an over-the-counter bear license to hunt in a limited entry area during season dates established in rule.

B. **"Bear zones"** shall define hunt areas consisting of one or more game management units as described in 19.30.4 NMAC.

C. **"Cougar zones"** shall define hunt areas consisting of one or more game management units as described in 19.30.4 NMAC.

D. **"Department"** shall mean the New Mexico department of game and fish.

E. **"Director"** shall mean the director of the New Mexico department of game and fish.

F. **"Game management unit" or "GMU"** shall mean those areas as described in 19.30.4 NMAC.

G. **"Wildlife management areas" or "WMAs"** shall mean those areas as described in 19.34.5 NMAC.

[19.31.11.7 NMAC - Rp, 19.31.11.7 NMAC, 4/1/2020]

19.31.11.8 ADJUSTMENT OF LICENSES, PERMITS AND HARVEST LIMITS:

A. The director, with verbal concurrence of the chairperson or their designee, may adjust the number of licenses, permits or harvest limits, up or down by no more than twenty percent within a bear zone or cougar zone, to address critical department management needs, significant changes in population levels or habitat availability. This adjustment may be applied for bear and cougar within the specified zones to any or all of: the specific hunt codes; total harvest limits; or female harvest sub-limits.

B. The director, with verbal concurrence of the chairperson or their designee, may take management actions independent of seasons and restrictions, harvest limits or female sub-limits for population management, or to address critical situations including ungulate population protection, depredation, human health and safety or other wildlife management issues. The decision to take management actions pursuant to this subsection shall be reported to the commission.

[19.31.11.8 NMAC - Rp, 19.31.11.8 NMAC, 4/1/2020]

19.31.11.9 BEAR AND COUGAR LICENSE APPLICATION REQUIREMENTS AND RESTRICTIONS:

EXHIBIT
2

A. Bear entry hunt: It shall be unlawful to hunt bear in designated wildlife management areas or other specifically designated special entry hunt areas without having a valid bear entry permit and a valid bear license in the hunter's possession or as otherwise allowed by game commission rule. Bear entry hunters shall be allowed to hunt in any other open bear zone provided they have a valid bear license.

B. Mandatory cougar identification course: All persons shall complete the mandatory cougar identification course offered on the department's website prior to purchasing a cougar license.
[19.31.11.9 NMAC - Rp, 19.31.11.9 NMAC, 4/1/2020]

19.31.11.10 BEAR AND COUGAR ZONE CLOSURES, BAG LIMITS AND AREA CLOSURES:

A. Zone closures: Bear and cougar may be hunted or taken only in zones designated as open on the department hotline or website. Zones will close within 72 hours of when the reported number of bears or cougars harvested is within ten percent of the total limit or female sub-limit for that zone, whichever occurs first.

B. Bag limit: The bag limit for bear is one; the bag limit for cougar is two. It is unlawful to kill a bear sow with cub(s) or any bear cub less than one year old, or to kill a spotted cougar kitten or any female cougar accompanied by spotted kitten(s).

C. Areas closed to bear and cougar hunting: Limited entry hunt areas listed in 19.31.11 NMAC are closed to over-the-counter bear hunters who do not possess an entry permit. Cougar hunting in these areas is allowed only by licensed deer or elk hunters in possession of a valid cougar license in the E.S. Barker, Colin Neblett, Humphries, Marquez, Sargent, and Urraca WMAs, and the Valle Vidal. Deer or elk hunters choosing to hunt cougar under this provision may not use dogs, may only hunt in open cougar zones, and must adhere to the weapon type restriction and season dates as specified by their deer or elk licenses. Cougar hunting is closed in the Florida mountains hunt area during any open Persian ibex season, except by legal Persian ibex hunters in possession of a valid cougar license. Persian ibex hunters may only hunt cougar if the cougar zone is open, and must adhere to the weapon type restrictions and season dates as specified by their Persian ibex license.
[19.31.11.10 NMAC - Rp, 19.31.11.10 NMAC, 4/1/2020]

19.31.11.11 BEAR HUNTING SEASONS:

A. Over-the-counter bear hunts for the 2020-21 through 2023-24 seasons: The following table lists bear zones, open GMUs, weapon type restrictions, season dates, total harvest limits, and female harvest sub-limits.

Bear zone	open GMUs or areas	bow only	any big game sporting arms	2020-21 total limit (female)	2021-22 total limit (female)	2022-23 total limit (female)	2023-24 total limit (female)
1	4, 5, 6, 7, 51, 52	9/1 - 24	9/25 - 11/15	158 (63)	158 (63)	158 (63)	158 (63)
2	2	9/1 - 24	9/25 - 11/15	15 (6)	15 (6)	15 (6)	15 (6)
3	49, 50, 53	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	65 (26)	65 (26)	65 (26)	65 (26)
4	45, 46, 48	9/1 - 24	8/16 - 8/31 and 9/25 - 11/30	109 (43)	109 (43)	109 (43)	109 (43)
5	54, 55	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	92 (37)	92 (37)	92 (37)	92 (37)
6	39, 40, 41, 42, 43, 47, 59	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	33 (13)	33 (13)	33 (13)	33 (13)
7	56, 57, 58	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	35 (14)	35 (14)	35 (14)	35 (14)
8	8	9/1 - 24	10/15 - 11/15	11 (4)	11 (4)	11 (4)	11 (4)
9	9, 10	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	36 (14)	36 (14)	36 (14)	36 (14)
10	12, 13, 15, 16, 17, 18, 20, 21, 22, 23, 24, 26, 27	9/1 - 24	9/25 - 12/15	146 (58)	146 (58)	146 (58)	146 (58)
11	37, 38	9/1 - 24	8/16 - 8/31 and 9/25 - 11/30	36 (14)	36 (14)	36 (14)	36 (14)
12	34	9/1 - 24	9/25 - 12/15	33 (13)	33 (13)	33 (13)	33 (13)

13	36	9/1 - 24	9/25 - 11/30	16 (6)	16 (6)	16 (6)	16 (6)
14	14	9/1 - 24	10/15 - 11/15	19 (7)	19 (7)	19 (7)	19 (7)

B. **Entry hunts for the 2020-21 through 2023-24 seasons** shall be as indicated below, listing the open areas, hunt dates, hunt codes, and number of permits.

open GMUs or areas	2020-2021 hunt dates	2021-2022 hunt dates	2022-2023 hunt dates	2023-2024 hunt dates	hunt code	licenses
2, **youth only**	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-100	5
4: Sargent WMA only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-101	10
4: Humphries WMA only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-102	5
9: Marquez WMA only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-103	5
54:55: Uracca, E.S. Barker, and Colin Neblett WMAs, and Valle Vidal	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-104	32
55: Valle Vidal	4/15-5/20	4/15-5/20	4/15-5/20	4/15-5/20	BER-1-105	20
57: Sugarite Canyon State Park/ bow only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-2-106	5

[19.31.11.11 NMAC - Rp, 19.31.11.11 NMAC, 4/1/2020]

19.31.11.12 COUGAR HUNTING SEASONS:

A. Over-the-counter cougar hunting season shall be from April 1 through March 31, or until the total harvest limit or female sub-limit, whichever comes first, is met in any given cougar zone.

B. The following table lists cougar zones, open GMUs, total harvest limits and female harvest sub-limits for the 2020-21 to 2023-24 seasons.

zone	open GMUs or areas	2020-21 total limit (female)	2021-22 total limit (female)	2022-23 total limit (female)	2023-24 total limit (female)
A	2, 7	42 (13)	42 (13)	42 (13)	42 (13)
B	5, 6, 50, 51	25 (8)	25 (8)	25 (8)	25 (8)
C	43, 45, 46, 48, 49, 53	57 (17)	57 (17)	57 (17)	57 (17)
D	41, 42, 47,59	15 (5)	15 (5)	15 (5)	15 (5)
E	9, 10	43 (13)	43 (13)	43 (13)	43 (13)
G	13, 17	50 (15)	50 (15)	50 (15)	50 (15)
H	18, 19, 20	29 (9)	29 (9)	29 (9)	29 (9)
I	36, 37, 38	24 (7)	24 (7)	24 (7)	24 (7)
J	15, 16, 21	84 (25)	84 (25)	84 (25)	84 (25)
K	22, 23, 24	45 (14)	45 (14)	45 (14)	45 (14)
L	25, 26, 27	19 (6)	19 (6)	19 (6)	19 (6)
M	31, 32, 33, 39, 40	25 (7)	25 (7)	25 (7)	25 (7)
N	4, 52	13 (4)	13 (4)	13 (4)	13 (4)
O	12	17 (5)	17 (5)	17 (5)	17 (5)
P	56, 57, 58	14 (7)	14 (7)	14 (7)	14 (7)
Q	28, 29, 30, 34	35 (11)	35 (11)	35 (11)	35 (11)
R	54, 55	26 (8)	26 (8)	26 (8)	26 (8)
S	8, 14	17 (5)	17 (5)	17 (5)	17 (5)

[19.31.11.12 NMAC - Rp, 19.31.11.12 NMAC, 4/1/2020]

HISTORY OF 19.31.11 NMAC:

Pre-NMAC History: The material in this part was derived from that previously filed with the state records center and archives under:

Regulation No. 482, Establishing Seasons on Deer, Bear, Turkey, Elk, Antelope, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, and Barbary Sheep, filed 5/31/1967;
Regulation No. 487, Establishing 1967 Seasons on Javelina and Barbary Sheep, filed 12/15/1967;
Regulation No. 489, Establishing Turkey Seasons for the Spring of 1968, filed 3/1/1968;
Regulation No. 491, Establishing Big Game Seasons for 1968 for Jicarilla Reservation, filed 3/1/1968;

Regulation No. 492, Establishing Seasons on Deer, Bear, Turkey, Elk, Antelope, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, and Barbary Sheep, filed 6/6/1968;
Regulation No. 495, Establishing a Season on Bighorn Sheep, filed 10/2/1968;
Regulation No. 496, Establishing an Elk Season in the Tres Piedras Area, Elk Area P-6, filed 12/11/1968;
Regulation No. 502, Establishing Turkey Seasons for the Spring Of 1969, filed 3/5/1969;
Regulation No. 503, Establishing 1969 Deer Seasons for Bowhunting Only and Big Game Seasons for the Jicarilla Indian Reservation, filed 3/5/1969;
Regulation 504, Establishing Seasons on Deer, Bear, Turkey, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, and Barbary Sheep, filed 6/4/1969;
Regulation No. 507, Establishing a Season on Bighorn Sheep, filed 8/26/1969;
Regulation No. 512, Establishing Turkey Season for the Spring Of 1970, filed 2/20/1970;
Regulation No. 513, Establishing Deer Season for Bowhunting Only in Sandia State Game Refuge, filed 2/20/1970;
Regulation No. 514, Establishing Seasons on Deer, Bear, Turkey, Elk, Antelope, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Barbary Sheep and Bighorn Sheep, filed 6/9/1970;
Regulation No 520, Establishing Turkey Seasons for the Spring of 1971, filed 3/9/1971;
Regulation No. 522, Establishing 1971 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 3/9/1971;
Regulation No. 523, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Elk, Antelope, Barbary Sheep and Bighorn Sheep, filed 6/9/1971;
Regulation No. 531, Establishing a Season on Javelina, filed 12/17/1971;
Regulation No. 532, Establishing Turkey Seasons for the Spring of 1972, filed 3/20/1972;
Regulation No. 534, Establishing 1972 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 3/20/1972;
Regulation No. 536, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, Elk, Antelope, Barbary Sheep and Bighorn Sheep, filed 6/26/1972;
Regulation No. 542, Establishing a Season on Javelina, filed 12/1/1972;
Regulation No. 545, Establishing Turkey Seasons for the Spring Of 1973, filed 2/26/1973;
Regulation No. 546, Establishing 1973 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 2/26/1973;
Regulation No. 547, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, Elk, Antelope, Barbary Sheep and Bighorn Sheep, and Javelina, filed 5/31/1973;
Regulation No. 554, Establishing Special Turkey Seasons for the Spring of 1974, filed 3/4/1974;
Regulation No. 556, Establishing 1974 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 3/14/1974;
Regulation No. 558, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex, filed 5/29/1974;
Regulation No. 565, Establishing Special Turkey Seasons for the Spring of 1975, filed 3/24/1975;
Regulation No. 567, Establishing 1975 Seasons on Deer, Bear, and Turkey on the Jicarilla Apache and Navajo Indian Reservations and on Elk on the Jicarilla Apache Indian Reservation, filed 3/24/1975;
Regulation No. 568, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 6/25/1975;
Regulation No. 573, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/23/1976;
Regulation No. 583, Establishing Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/11/1977;
Regulation No. 590, Establishing Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/15/1978;
Regulation No. 596, Establishing Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/23/1979;
Regulation No. 603, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1980 through March 31, 1981, filed 2/22/1980;
Regulation No. 609, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1981 through March 31, 1982, filed 3/17/1981;
Regulation No. 614, Establishing Open Seasons on Deer, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1982 through March 31, 1983, filed 3/10/1982;

Regulation No. 622, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1983 through March 31, 1984, filed 3/9/1983;
Regulation No. 628, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1984 through March 31, 1985, filed 4/2/1984;
Regulation No. 634, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1985 Through March 31, 1986, filed 4/18/1985;
Regulation No. 640, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1986 through March 31, 1987, filed 3/25/1986;
Regulation No. 645, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1987 through March 31, 1988, filed 2/12/1987;
Regulation No. 653, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1988 through March 31, 1989, filed 12/18/1987;
Regulation No. 663, Establishing Opening Spring Turkey for the Period April 1, 1989 through March 31, 1990, filed 3/28/1989;
Regulation No. 664, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1989 through March 31, 1990, filed 3/20/1989;
Regulation No. 674, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1990 through March 31, 1991, filed 11/21/1989;
Regulation No. 683, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex for the Period April 1, 1991 through March 31, 1992, filed 2/8/1991;
Regulation No. 689, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex for the Period April 1, 1992 through March 31, 1993, filed 3/4/1992;
Regulation No. 700, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex for the Period April 1, 1993 through March 31, 1995, filed 3/11/1993.

History of Repealed Material:
19.31.8 NMAC, Big Game, filed 3/1/2001 - duration expired 3/31/2003.
19.31.8 NMAC, Big Game and Turkey, filed 3/3/2003 - duration expired 3/31/2005.
19.31.8 NMAC, Big Game and Turkey, filed 12/15/2004 - duration expired 3/31/2007.
19.31.11 NMAC, Bear and Cougar, filed 12/1/2006 - duration expired 3/31/2009.
19.31.11 NMAC, Bear and Cougar, filed 3/13/2009 - duration expired 3/31/2011.
19.31.11 NMAC, Bear and Cougar, filed 2/22/2011 - duration expired 3/31/2016.
19.31.11 NMAC, Bear and Cougar, filed 2/29/2016 - duration expired 3/31/2020.

Initial Proposed Rule

TITLE 19 NATURAL RESOURCES AND WILDLIFE
CHAPTER 31 HUNTING AND FISHING
PART 11 BEAR AND COUGAR

19.31.11.1 ISSUING AGENCY: New Mexico ~~D~~department of ~~G~~game and ~~F~~fish.
[19.31.11.1 NMAC - Rp, 19.31.11.1 NMAC, 4-1-2020]

19.31.11.2 SCOPE: Sportspersons interested in bear and cougar management and hunting. Additional requirements may be found in Chapter 17~~,~~ NMSA 1978, and ~~Chapters 30, 31, 32 and 33 of~~ Title 19 NMAC.
[19.31.11.2 NMAC - Rp, 19.31.11.2 NMAC, 4-1-2020]

19.31.11.3 STATUTORY AUTHORITY: 17-1-14 and 17-1-26 NMSA 1978 provide that the New Mexico state game commission has the authority to establish rules and regulations that it may deem necessary to carry out the purpose of Chapter 17 NMSA 1978 and all other acts pertaining to protected mammals, birds, and fish.
[19.31.11.3 NMAC - Rp, 19.31.11.3 NMAC, 4-1-2020]

19.31.11.4 DURATION: April 1, ~~2016~~2020 through March 31, ~~2020~~2024.
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[19.31.11.5 NMAC - Rp, 19.31.11.5 NMAC, 4-1-2020]

19.31.11.6 OBJECTIVE: Establishing open hunting seasons and regulation, rules and procedures governing the distribution and issuance of bear and cougar licenses by the department.
[19.31.11.6 NMAC - Rp, 19.31.11.6 NMAC, 4-1-2020]

19.31.11.7 DEFINITIONS:

~~**A.** **“Arrows”** shall mean only those arrows or bolts having broadheads with steel cutting edges.~~

~~**B.** **“Baiting”** shall mean the placing, exposing, depositing, distributing, or scattering of any salt, grain, scent or other feed on or over areas where hunters are attempting to take bear or cougar.~~

~~C~~A. **“Bear entry ~~hunt~~permit”** shall mean a permit awarded through a public drawing which ~~the valid official document awarded through a public drawing for hunting bear. This valid official permit shal~~l entitles the holder of ~~a~~ an over-the-counter bear license to hunt ~~where hunter numbers are limited by rule~~ in a limited entry area during season dates established in rule.

~~**D.** **“Bear license”** shall mean a valid official document that is issued or approved by the director that each person hunting bear in New Mexico must have or obtain prior to hunting.~~

~~E~~B. **“Bear zones”** shall define hunt areas consisting of one or more game management units as ~~documented~~ described in ~~the state game commission’s rule~~ 19.30.4 NMAC.

~~**F.** **“Bow”** shall mean compound, recurve, or long bow. Sights on bows shall not project light, however, illuminated pins/reticles and scopes of any magnification are allowed.~~

~~**G.** **“Cougar license”** shall mean a valid official document that is issued or approved by the director that each person hunting cougar in New Mexico must have or obtain prior to hunting.~~

~~H~~C. **“Cougar zones”** shall define hunt areas consisting of one or more game management units as ~~documented~~ described in ~~the state game commission’s rule~~ 19.30.4 NMAC.

~~**I.** **“Crossbow”** shall mean a device with a bow limb or band of flexible material attached horizontally to a stock and has a mechanism to hold the string in a cocked position. Sights on crossbows shall not project light, however, illuminated pins/reticles and scopes of any magnification are allowed.~~

~~J~~D. **“Department”** shall mean the New Mexico department of game and fish.

~~K~~E. **“Director”** shall mean the director of the New Mexico department of game and fish.

~~**L.** **“Foot snare”** shall mean a wire or cable with a single closing device set to capture a cougar by the foot.~~

~~M~~F. **“Game management units” or “GMUs”** shall mean those areas as described in ~~the state game commission’s rule~~ 19.30.4 NMAC.

~~**N.** **“Hunter designee”** shall mean a person given a written statement by the properly licensed hunter who lawfully killed and possessed the bear or cougar. A written statement consists of: the kind and number of bear and cougar, the date and game management unit of where the bear or cougar was lawfully taken, the hunter’s name,~~

~~address, and license number under which the bear or cougar was lawfully killed, and the date and place where the written statement was given.~~

~~**O.** **"License year"** shall mean the period from April 1 through March 31.~~

~~**P.** **"Modern firearms"** shall mean center-fire firearms, not to include any fully automatic firearms. Legal shotguns shall be only those shotguns capable of being fired from the shoulder.~~

~~**Q.** **"Muzzle-loader" or "muzzle-loading firearms"** shall mean those rifles and shotguns in which the charge and projectile are loaded through the muzzle. Only blackpowder, Pyrodex or equivalent blackpowder substitute may be used. Use of smokeless powder is prohibited. Legal muzzle-loader shotguns shall be only those shotguns capable of being fired from the shoulder.~~

~~**R.** **"Trap"** shall mean a spring actuated device designed to capture a cougar by the foot.~~

~~**S.** **"Unlimited"** shall mean there is no set limit on the number of permits or licenses established for the described hunt areas.~~

~~**T.** **"Website"** shall refer to accessing the department's internet address.~~

~~U~~G. **"Wildlife management areas" or "WMAs"** shall mean those areas as described in ~~the state game commission's rule~~ 19.34.5 NMAC.
[19.31.11.7 NMAC - Rp, 19.31.11.7 NMAC, 4-1-2020]

19.31.11.8 ADJUSTMENT OF LICENSES, PERMITS~~, AUTHORIZATIONS~~, AND HARVEST LIMITS:

A. The director, with verbal concurrence of the ~~chairman~~chairperson or ~~his~~their designee, may adjust the number of licenses, permits or harvest limits, up or down by no more than twenty percent within ~~the GMU,~~ a bear zone or cougar zone, to address critical department management needs, significant changes in population levels or habitat availability. This adjustment may be applied for bear and cougar within the specified zones to any or all of: the specific hunt codes; total harvest limits; or female harvest sub-limits.~~, or sustainable total mortality, for bear and cougar~~. ~~The director, with verbal concurrence of the chairman or his designee, may also modify the season dates and manner and method of take, to facilitate target removals or embedded quotas for cougars and bears in specific areas or zones for ungulate protection, or conflict minimization in densely populated residential areas.~~

B. The director, with verbal concurrence of the ~~chairman~~chairperson or ~~his~~their designee, may take management actions independent of seasons and restrictions, harvest limits or female sub-limits for population management, or to address critical situations including ungulate population protection, depredation, ~~and~~ human health and safety or other wildlife management issues. The decision to take management actions pursuant to this subsection shall be reported to the commission ~~within 48 hours~~.

~~**C.** The previous year's harvest data and management implications shall be presented to the commission at a regularly scheduled state game commission meeting by August of each year. The results of this annual review shall be made available to the public at least 30 days prior to presentation at a regularly scheduled and noticed commission meeting.~~
[19.31.11.8 NMAC - Rp, 19.31.11.8 NMAC, 4-1-2020]

19.31.11.9 BEAR AND COUGAR LICENSE APPLICATION REQUIREMENTS AND RESTRICTIONS:

~~**A.** **One license per year:** It shall be unlawful for anyone to hold more than one permit or license for bear or cougar during the current license year unless otherwise allowed by rule.~~

~~**B.** **Validity of license or permit:** All bear entry permits or licenses shall be valid only for specified dates, eligibility requirements or restrictions, legal sporting arms, bag limit and area specified by the hunt code printed on the permit or license. Over-the-counter bear licenses shall be valid only for specified dates, eligibility requirements or restrictions, legal sporting arms, bag limit and area specified by rule or regulation. Over-the-counter cougar licenses shall be valid only with concurrent possession of a cougar identification course completion number as described in Subsection G of 19.31.11.9 NMAC and for specified dates, eligibility requirements or restrictions, legal sporting arms, bag limit and area specified by rule or regulation~~.

~~D~~A. **Bear entry hunt:** It shall be unlawful to hunt bear in designated wildlife management areas or other specifically designated special entry hunt areas without having a valid bear entry permit and a valid bear license in the hunter's possession or as otherwise allowed by ~~Subsection O of 19.31.11.10~~ game commission rule. Bear entry hunters shall be allowed to hunt in any other open ~~bear hunt~~ bear zone provided they have a valid bear license. ~~No more than one person may apply under each application number for bear entry permits.~~

~~**E.** **License purchase:** Cougar hunters must purchase a cougar license at least two days prior to hunting cougar. Bear hunters must purchase a bear license at least two days prior to hunting bear.~~

~~**F.** **Youth only (YO) hunts:** It shall be unlawful for anyone to participate in youth only (YO) hunts except as allowed by 19.31.3.11 NMAC.~~

~~G~~B. **Mandatory cougar identification course:** All persons shall complete ~~It shall be unlawful to hunt cougars without carrying a department issued alpha-numeric number which shall be proof of successful completion of~~ the mandatory cougar identification course ~~as~~ offered on the department's website prior to purchasing a cougar license.
[19.31.11.9 NMAC - Rp, 19.31.11.9 NMAC, 4-1-2020]

19.31.11.10 BEAR AND COUGAR ZONE CLOSURES, BAG LIMITS AND AREA CLOSURES ~~MANNER AND METHOD REQUIREMENTS AND RESTRICTIONS~~:

A. **~~Season and hours~~ Zone closures:** Bear and cougar may be hunted or taken ~~only during open seasons and only during the period from one-half hour before sunrise to one-half hour after sunset and~~ only in zones ~~or areas~~ designated as open on the department hotline or website. ~~Twenty-four hours prior to hunting bear or cougar, every hunter or hunter's designee must call the toll free number designated by the department or access the department's website to determine if their desired hunt zone is open. Failure to call or check prior to hunting is unlawful~~. ~~Cougar and bear seasons in each zone~~ Zones will close within 72 hours of when the reported number of bears or cougars ~~or bears~~ harvested is within ten percent of the total limit or female sub-limit~~, or ten percent of the sustainable mortality limit~~ for that zone, whichever occurs first.

B. **Bag limit:** ~~It is unlawful for any person to hunt for or take more than one bear or two cougars during a current license year unless otherwise provided by regulation. Holders of a valid cougar license who have harvested two cougars under their license may request authorization from the department to take an additional two cougars in the same license year in any cougar management zone that has not closed in at least two of the past three years. Additional take may be requested once the bag limit for the previous authorization has been met.~~ The bag limit for bear is one; the bag limit for cougar is two. It is unlawful to kill a bear sow with cub(s) or any bear cub less than one year old, or to kill a spotted cougar kitten or any female cougar accompanied by spotted kitten(s).

~~**(1)** It shall be unlawful to kill a female bear accompanied by cub(s), or any cub less than one year old.~~

~~**(2)** It shall be unlawful to kill a female cougar accompanied by spotted kitten(s), or any spotted kitten.~~

~~**C.** **Proof of sex of bear or cougar:** It shall be unlawful for anyone to transport or possess the pelt (even if the pelt is attached to the carcass) of a bear or cougar without proof of sex. External genitalia of any bear or cougar killed shall remain attached to the pelt and be readily visible until the pelt has been inspected and pelt-tagged by a department official.~~

~~**D.** **Bear and cougar pelt tagging requirements:**~~

~~**(1)** Any bear or cougar killed shall be tagged with a pelt tag furnished free of charge by the department.~~

~~**(2)** The hunter who kills the bear or cougar or the hunter's designee must present the unfrozen skull and pelt to a department official for tooth removal and pelt tagging within five calendar days from the date of harvest before the pelt can be processed by a taxidermist, or before taking the pelt out of New Mexico, whichever comes first.~~

~~**(3)** Any hunter who appoints a designee to present the skull and pelt for pelt tagging is required to contact a conservation officer prior to having the pelt inspected and tagged.~~

~~**(4)** The pelt tag shall remain attached until the pelt is tanned.~~

~~**(5)** The skull of the bear or cougar must remain unfrozen with the mouth fixed open for removal of a premolar tooth by a department official.~~

~~**(6)** Licensed bear or cougar hunters who provide false or fraudulent information regarding the required information including, but not limited to, sex, date, or location of harvest shall be assessed 20 revocation points pursuant to 19.31.2 NMAC.~~

~~**E.** **Seizure:** Any conservation officer or other officer authorized to enforce game laws and regulations shall seize the carcasses or pelts of bear or cougar that are improperly tagged, presented for pelt tagging without proof of sex attached or without presenting the skull along with the pelt.~~

~~**F.** **Use of dogs in hunting:** Dogs may be used only to hunt bear and cougar during specific open seasons unless otherwise restricted. It shall be unlawful to:~~

~~**(1)** hunt for or pursue bear or cougar with dog(s) in any WMA as described in 19.34.5 NMAC except as provided by regulation;~~

~~(2) hunt for or pursue bear or cougar during September bow seasons statewide except as otherwise allowed by rule;~~

~~(3) release dogs with the intent of pursuing or hunting bear or cougar or to pursue or hold bear or cougar, outside of legal shooting hours or during closed seasons, it shall be unlawful to pursue a bear or cougar with dog(s) for dog training purposes;~~

~~(4) pursue bear or cougar with dog(s) without the licensed hunter, who intends to kill or who kills the bear or cougar, present continuously from the initial release of any dog(s).~~

~~**G. Use of baits or scents:** It shall be unlawful for anyone to take or attempt to take any bear or cougar by use of baits or scents as defined in 19.31.10.7 NMAC. Scent masking agents on one's person are allowed.~~

~~**H. Live animals:** It shall be unlawful to use live animals as a blind or decoy in taking or attempting to take any bear or cougar.~~

~~**I. Use of calling devices:** It shall be unlawful to use any electrically or mechanically recorded calling device in taking or attempting to take any bear, such calling devices are allowed for taking cougar.~~

~~**J. Killing out-of-season:** It shall be unlawful to kill any bear or cougar out of their respective hunting seasons.~~

~~**K. Bullets:** It shall be unlawful to take or attempt to take bear or cougar by the use of tracer ammunition or any ammunition loaded with full metal jacketed bullets that does not expand or mushroom. Soft-nosed or hollow-pointed bullets may be used in hunting or taking bear or cougar.~~

~~**L. Drugs and explosives:** It shall be unlawful to use any form of drug on an arrow or use arrows driven by explosives.~~

~~**M. Legal weapon types** for bear and cougar are as follows: any center-fire rifle; any center-fire handgun; shotguns not smaller than 28 gauge, firing a single slug; muzzle-loading rifles; bows and arrows; and crossbows and bolts. The Sandia ranger district portion of the Cibola national forest in zone 4 shall be open for hunting with crossbow and bow only.~~

~~N~~C. Areas closed to bear and cougar hunting: ~~The following areas shall remain closed to bear and cougar hunting, except as permitted by regulation: Sugarite Canyon state park; Rio Grande wild and scenic river area, including the Taos Valley overlook; all wildlife management areas including the Water Canyon and Marquez WMAs in GMU 9 (Marquez is open only to hunters with valid bear entry permit and bear hunting license); the Valle Vidal area; and sub-unit 6B (Valles Caldera national preserve).~~ Limited entry hunt areas listed in 19.31.11 NMAC are closed to over-the-counter bear hunters who do not possess an entry permit. Cougar hunting in these areas is allowed only by ~~legal~~ licensed deer or elk hunters in possession of a valid cougar license in the E.S. Barker, Colin Neblett, Humphries, Marquez, Sargent, and Urraca WMAs, and the Valle Vidal ~~and Greenwood areas~~. Deer or elk hunters choosing to hunt cougar under this provision may not use dogs, may only hunt in open cougar zones, and must adhere to the weapon type restriction and season dates as specified by their deer or elk licenses. ~~Dogs are not allowed~~. Cougar hunting is closed in the Florida mountains hunt area during any open Persian ibex season, except by legal Persian ibex hunters in possession of a valid cougar license. Persian ibex hunters ~~choosing to hunt cougar under this provision~~ may only hunt cougar if the cougar zone is open, and must adhere to the weapon type restrictions and season dates as specified by their Persian ibex license.

~~**O. Use of traps and foot snares:** Hunters with a valid cougar license may use traps or foot snares to harvest cougars on state trust land, or private deeded land with written permission from the landowner. Neck snares are not permitted. Restrictions for cougar take using traps or foot snares shall follow the regulations on methods, trap specification, trap inspection, and cougar removal as defined in 19.32.2.10 NMAC Manner and Method of Take, and 19.32.2.11 NMAC Trap Inspection and Furbearer Removal. Foot snares shall be prohibited in GMU 27 and those portions of GMU 26 designated by the United States fish and wildlife service as critical habitat for jaguar.~~

~~**P.** Any take of cougar on public land, other than state trust lands, by the use of traps or snares shall be unlawful unless authorized by the director.~~

~~**Q.** It shall be unlawful to attach any collar or electronic tracking device to any bear or cougar except as expressly permitted by the department.~~

[19.31.11.10 NMAC - Rp, 19.31.11.10 NMAC, 4-1-2020]

19.31.11.11 BEAR HUNTING SEASONS:

A. Over-the-counter bear hunts for the ~~2016-17~~ 2020-21 through ~~2019-20~~ 2023-24 ~~hunt~~ seasons: The following table lists bear zones, open GMUs ~~or areas within zones~~, weapon type restrictions, season dates, total harvest limits, and female harvest sub-limits.

Bear zone	open GMUs or areas	bow only	any legal ~~weapon~~ big game sporting arms	~~2016-17~~ 2020-21 total limit (female)	~~2016-17~~ 2021-22 total limit (female)	~~2016-17~~ 2022-23 total limit (female)	~~2019-20~~ 2023-24 total limit (female)
1	4, 5, 6, 7, 51, 52	9/1 - 24	9/25 - 11/15	158 (63)	158 (63)	158 (63)	158 (63)
2	2	9/1 - 24	9/25 - 11/15	15 (6)	15 (6)	15 (6)	15 (6)
3	49, 50 ~~and~~, 53	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	65 (26)	65 (26)	65 (26)	65 (26)
4	45, 46, ~~and~~, 48	9/1 - 24	8/16 - 8/31 and 9/25 - 11/30	109 (43)	109 (43)	109 (43)	109 (43)
5	54 ~~and~~, 55	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	92 (37)	92 (37)	92 (37)	92 (37)
6	39, 40, 41, 42, 43, 47 ~~and~~, 59	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	33 (13)	33 (13)	33 (13)	33 (13)
7	56, 57 ~~and~~, 58	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	35 (14)	35 (14)	35 (14)	35 (14)
8	8	9/1 - 24	10/15 - 11/15	11 (4)	11 (4)	11 (4)	11 (4)
9	9 ~~and~~, 10	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	36 (14)	36 (14)	36 (14)	36 (14)
10	12, 13, 15, 16, 17, 18, 20, 21, 22, 23, 24, 26~~, and~~, 27	9/1 - 24	~~8/16 - 8/31 and~~ ~~9/25 - 11/30~~ 9/25 – 12/15	146 (58)	146 (58)	146 (58)	146 (58)
11	37 ~~and~~, 38	9/1 - 24	8/16 - 8/31 and 9/25 - 11/30	36 (14)	36 (14)	36 (14)	36 (14)
12	34	9/1 - 24	~~8/16 - 8/31 and~~ ~~9/25 - 11/30~~ 9/25 – 12/15	33 (13)	33 (13)	33 (13)	33 (13)
13	36	9/1 - 24	~~8/16 - 8/31 and~~ ~~9/25 - 11/15~~ 9/25 – 11/30	16 (6)	16 (6)	16 (6)	16 (6)
14	14	9/1 - 24	10/15 - 11/15	19 (7)	19 (7)	19 (7)	19 (7)

B. Entry hunts for the ~~2016-17~~2020-21 through ~~2019-20~~2023-24 ~~hunting~~ seasons shall be as indicated below, listing the open areas, hunt dates, hunt codes, and number of ~~licenses permits.~~ ~~, and bag limit~~.

~~open GMUs or areas~~	~~hunt start~~	~~hunt end~~	~~hunt code~~	~~licenses~~	~~bag limit~~
~~2, YO~~	~~8/1~~	~~8/31~~	~~BER-1-100~~	~~5~~	~~1 bear~~
~~4: Sargent WMA only~~	~~8/1~~	~~8/31~~	~~BER-1-101~~	~~10~~	~~1 bear~~
~~4: Humphries WMA only~~	~~8/1~~	~~8/31~~	~~BER-1-102~~	~~5~~	~~1 bear~~
~~9: Marquez WMA only~~	~~8/1~~	~~8/31~~	~~BER-1-103~~	~~5~~	~~1 bear~~
~~54/55: E.S. Barker-Colin Neblett WMAs~~	~~8/1~~	~~8/31~~	~~BER-1-104~~	~~12~~	~~1 bear~~
~~55: Valle Vidal and Greenwood areas~~	~~8/1~~	~~8/31~~	~~BER-1-105~~	~~20~~	~~1 bear~~
~~55: Valle Vidal and Greenwood areas~~	~~4/15~~	~~5/20~~	~~BER-1-106~~	~~20~~	~~1 bear~~
~~57: Sugarite Canyon State Park/ bow only~~	~~8/1~~	~~8/31~~	~~BER-2-107~~	~~5~~	~~1 bear~~

open GMUs or areas	2020-2021 hunt dates	2021-2022 hunt dates	2022-2023 hunt dates	2023-2024 hunt dates	hunt code	licenses
2, youth only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-100	5
4: Sargent WMA only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-101	10
4: Humphries WMA only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-102	5
9: Marquez WMA only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-103	5
54,55: Urraca, E.S. Barker, and Colin Neblett WMAs, and Valle Vidal	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-104	32

55: Valle Vidal	4/15-5/20	4/15-5/20	4/15-5/20	4/15-5/20	BER-1-105	20
57: Sugarite Canyon State Park/ bow only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-2-106	5

~~**C.** Bear hunting is closed in the Valle Vidal and Greenwood areas except by legal Valle Vidal and Greenwood area elk hunters or successful applicants for bear entry hunts BER-1-105 and BER-1-106. Dogs are permitted for the BER-1-105 and BER-1-106. Valle Vidal and Greenwood area elk hunters choosing to hunt bears under this provision must adhere to the weapon type restriction and season dates specified by their elk license.~~

~~**D.** Bears taken from the Sargent and William A. Humphries WMAs in zone 1, Elliot Barker/Colin Neblett WMAs and Valle Vidal and Greenwood areas in zone 5, Sugarite Canyon state park in zone 7, or Marquez WMA in zone 8 shall count towards the harvest limit in those zones.~~

[19.31.11.11 NMAC - Rp, 19.31.11.11 NMAC, 4-1-2020]

19.31.11.12 COUGAR HUNTING SEASONS:

A. Over-the-counter cougar hunting season shall be from April 1 through March 31, or until the total ~~mortality~~ harvest limit~~,~~ or female sub-limit, whichever comes first, is met in any given cougar ~~management~~ zone.

~~**B.** Cougar trapping and foot snaring season on state trust land and private deeded land shall be from November 1 through March 31, or until the total mortality limit, or female sub-limit, whichever comes first, is met in any given cougar management zone.~~

~~C~~B. The following table lists cougar zones, open GMUs ~~or areas within zones, weapon type restrictions,~~ ~~season dates~~, total harvest limits and female harvest sub-limits for the ~~2016-2020~~2020-21 to 2023-24 seasons.

~~zone~~	~~open GMUs or areas~~	~~2016-17 total limits (female)~~	~~2017-18 total limits (female)~~	~~2018-19 total limits (female)~~	~~2019-20 total limits (female)~~
~~A~~	~~2 and 7~~	~~42 (13)~~	~~42 (13)~~	~~42 (13)~~	~~42 (13)~~
~~B~~	~~5, 50, and 51~~	~~28 (8)~~	~~28 (8)~~	~~28 (8)~~	~~28 (8)~~
~~C~~	~~43, 45, 46, 48, 49, 53~~	~~85 (43)~~	~~85 (43)~~	~~85 (43)~~	~~85 (43)~~
~~D~~	~~41, 42, 47 and 59~~	~~23 (12)~~	~~23 (12)~~	~~23 (12)~~	~~23 (12)~~
~~E~~	~~9 and 10~~	~~50 (15)~~	~~50 (15)~~	~~50 (15)~~	~~50 (15)~~
~~F~~	~~6~~	~~46 (23)~~	~~46 (23)~~	~~46 (23)~~	~~46 (23)~~
~~G~~	~~13, and 17~~	~~73 (37)~~	~~73 (37)~~	~~73 (37)~~	~~73 (37)~~
~~H~~	~~18, 19 and 20~~	~~37(16)~~	~~37(16)~~	~~37(16)~~	~~37(16)~~
~~I~~	~~36, 37, and 38~~	~~24 (7)~~	~~24 (7)~~	~~24 (7)~~	~~24 (7)~~
~~J~~	~~15, 16, 21, and 25~~	~~89 (27)~~	~~89 (27)~~	~~89 (27)~~	~~89 (27)~~
~~K~~	~~22, 23, and 24~~	~~66 (33)~~	~~66 (33)~~	~~66 (33)~~	~~66 (33)~~
~~L~~	~~26 and 27~~	~~19 (10)~~	~~19 (10)~~	~~19 (10)~~	~~19 (10)~~
~~M~~	~~31, 32, 33, 39, and 40~~	~~31 (9)~~	~~31 (9)~~	~~31 (9)~~	~~31 (9)~~
~~N~~	~~4 and 52~~	~~15 (5)~~	~~15 (5)~~	~~15 (5)~~	~~15 (5)~~
~~O~~	~~12~~	~~21 (6)~~	~~21 (6)~~	~~21 (6)~~	~~21 (6)~~
~~P~~	~~56, 57, and 58~~	~~14 (7)~~	~~14 (7)~~	~~14 (7)~~	~~14 (7)~~
~~Q~~	~~28, 29, 30, and 34~~	~~35 (11)~~	~~35 (11)~~	~~35 (11)~~	~~35 (11)~~
~~R~~	~~54 and 55~~	~~26 (8)~~	~~26 (8)~~	~~26 (8)~~	~~26 (8)~~
~~S~~	~~8 and 14~~	~~25 (13)~~	~~25 (13)~~	~~25 (13)~~	~~25 (13)~~

zone	open GMUs or areas	2020-21 total limit (female)	2021-22 total limit (female)	2022-23 total limit (female)	2023-24 total limit (female)
A	2, 7	42 (13)	42 (13)	42 (13)	42 (13)
B	5, 6, 50, 51	25 (8)	25 (8)	25 (8)	25 (8)
C	43, 45, 46, 48, 49, 53	57 (17)	57 (17)	57 (17)	57 (17)
D	41, 42, 47, 59	15 (5)	15 (5)	15 (5)	15 (5)
E	9, 10	43 (13)	43 (13)	43 (13)	43 (13)
G	13, 17	50 (15)	50 (15)	50 (15)	50 (15)
H	18, 19, 20	29 (9)	29 (9)	29 (9)	29 (9)
I	36, 37, 38	24 (7)	24 (7)	24 (7)	24 (7)
J	15, 16, 21	84 (25)	84 (25)	84 (25)	84 (25)

K	22, 23, 24	45 (14)	45 (14)	45 (14)	45 (14)
L	25, 26, 27	19 (6)	19 (6)	19 (6)	19 (6)
M	31, 32, 33, 39, 40	25 (7)	25 (7)	25 (7)	25 (7)
N	4, 52	13 (4)	13 (4)	13 (4)	13 (4)
O	12	17 (5)	17 (5)	17 (5)	17 (5)
P	56, 57, 58	14 (7)	14 (7)	14 (7)	14 (7)
Q	28, 29, 30, 34	35 (11)	35 (11)	35 (11)	35 (11)
R	54, 55	26 (8)	26 (8)	26 (8)	26 (8)
S	8, 14	17 (5)	17 (5)	17 (5)	17 (5)

[19.31.11.12 NMAC - Rp, 19.31.11.12 NMAC, 4-1-2020]

~~**19.31.11.13 PROCEDURES FOR CONDUCTING COUGAR DEPREDATION CONTROL IN OCCUPIED BIGHORN SHEEP RANGES:**~~

~~**A.** The department shall investigate all bighorn sheep deaths to determine if cougar depredation has occurred. To determine cougar depredation, a field examination and a standardized necropsy of the dead bighorn sheep shall be completed by a department employee or contractor.~~

~~**B.** Should it be determined that a depredation has occurred, the following procedures will be used.~~

~~**(1)** The department will make an evaluation of the following: viability of the statewide bighorn population, review of long-term and recent data on the local population (or meta-population), review of data on recent predation, alternative management options such as habitat manipulation or transplants, feasibility of taking the offending animal(s), effects on the predator population, and feasibility of having a positive effect on the local bighorn population.~~

~~**(2)** The wildlife management division and the appropriate area operations office will be contacted.~~

~~**(3)** A permit for the taking of each depredating cougar(s) will be issued to the local district wildlife officer. Physical possession of the permit is not required to initiate action.~~

~~**(4)** A decision to hound hunt or snare will be based on evidence at the kill site.~~

~~**(5)** If the bighorn sheep kill is fresh enough that the cougar may return or is likely to still be in the immediate area, the department will attempt to get a hound-hunter or trapper to begin kill the cougar(s) the same day the bighorn carcass is discovered.~~

~~**(6)** The size of the hunted area will be determined from the sex and, in some cases, number of cougars (i.e. female with kittens) involved in the bighorn kill.~~

~~**(7)** Where possible, cougar feces shall be taken at the scene of the depredation and tissue samples from the cougar killed by the hunter(s) will be collected. Deoxyribonucleic acid (DNA) testing will be performed to determine if the scat and tissue samples are from the same cougar.~~

~~[19.31.11.13 NMAC - Rp, 19.31.11.15 NMAC, 4-1-2020]~~

~~**19.31.11.14 DURATION OF DEPREDATION CONTROL PROGRAMS:** The duration of the special permit to take depredating cougars shall be for no more than six weeks from the onset to the end of the measures taken. An evaluation and justification for extension of the permit shall be written before measures will continue beyond six weeks.~~

~~[19.31.11.14 NMAC - Rp, 19.31.11.16 NMAC, 4-1-2020]~~

~~**19.31.11.15 PROCEDURES FOR CONDUCTING PREVENTIVE COUGAR CONTROL IN BIGHORN SHEEP RANGES:**~~

~~**A.** The New Mexico department of game and fish may conduct preventive cougar control within bighorn sheep ranges.~~

~~**B.** The total number of cougars removed per license year from any zone containing bighorn ranges will not exceed the sustainable mortality limit for that zone unless approved pursuant to 19.31.11.8 NMAC.~~

~~**C.** The department will obtain the services of houndsmen or trappers either from the department's depredation list or through private contract.~~

~~**D.** A decision to hunt with hounds or to use snares will be made by the department.~~

~~**E.** All cougars taken for preventive control will be reported to the department.~~

~~**F.** The department will provide a program evaluation update to the commission no later than December biennially beginning in December 2010.~~

~~[19.31.11.15 NMAC - Rp, 19.31.11.17 NMAC, 4-1-2020]~~

HISTORY OF 19.31.11 NMAC:
Pre-NMAC History: The material in this part was derived from that previously filed with the state records center and archives under:
Regulation No. 482, Establishing Seasons on Deer, Bear, Turkey, Elk, Antelope, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, and Barbary Sheep, filed 5/31/1967;
Regulation No. 487, Establishing 1967 Seasons on Javelina and Barbary Sheep, filed 12/15/1967;
Regulation No. 489, Establishing Turkey Seasons for the Spring of 1968, filed 3/1/1968;
Regulation No. 491, Establishing Big Game Seasons for 1968 for Jicarilla Reservation, filed 3/1/1968;
Regulation No. 492, Establishing Seasons on Deer, Bear, Turkey, Elk, Antelope, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, and Barbary Sheep, filed 6/6/1968;
Regulation No. 495, Establishing a Season on Bighorn Sheep, filed 10/2/1968;
Regulation No. 496, Establishing an Elk Season in the Tres Piedras Area, Elk Area P-6, filed 12/11/1968;
Regulation No. 502, Establishing Turkey Seasons for the Spring Of 1969, filed 3/5/1969;
Regulation No. 503, Establishing 1969 Deer Seasons for Bowhunting Only and Big Game Seasons for the Jicarilla Indian Reservation, filed 3/5/1969;
Regulation 504, Establishing Seasons on Deer, Bear, Turkey, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, and Barbary Sheep, filed 6/4/1969;
Regulation No. 507, Establishing a Season on Bighorn Sheep, filed 8/26/1969;
Regulation No. 512, Establishing Turkey Season for the Spring Of 1970, filed 2/20/1970;
Regulation No. 513, Establishing Deer Season for Bowhunting Only in Sandia State Game Refuge, filed 2/20/1970;
Regulation No. 514, Establishing Seasons on Deer, Bear, Turkey, Elk, Antelope, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Barbary Sheep and Bighorn Sheep, filed 6/9/1970;
Regulation No 520, Establishing Turkey Seasons for the Spring of 1971, filed 3/9/1971;
Regulation No. 522, Establishing 1971 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 3/9/1971;
Regulation No. 523, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Elk, Antelope, Barbary Sheep and Bighorn Sheep, filed 6/9/1971;
Regulation No. 531, Establishing a Season on Javelina, filed 12/17/1971;
Regulation No. 532, Establishing Turkey Seasons for the Spring of 1972, filed 3/20/1972;
Regulation No. 534, Establishing 1972 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 3/20/1972;
Regulation No. 536, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, Elk, Antelope, Barbary Sheep and Bighorn Sheep, filed 6/26/1972;
Regulation No. 542, Establishing a Season on Javelina, filed 12/1/1972;
Regulation No. 545, Establishing Turkey Seasons for the Spring Of 1973, filed 2/26/1973;
Regulation No. 546, Establishing 1973 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 2/26/1973;
Regulation No. 547, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, Elk, Antelope, Barbary Sheep and Bighorn Sheep, and Javelina, filed 5/31/1973;
Regulation No. 554, Establishing Special Turkey Seasons for the Spring of 1974, filed 3/4/1974;
Regulation No. 556, Establishing 1974 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 3/14/1974;
Regulation No. 558, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex, filed 5/29/1974;
Regulation No. 565, Establishing Special Turkey Seasons for the Spring of 1975, filed 3/24/1975;
Regulation No. 567, Establishing 1975 Seasons on Deer, Bear, and Turkey on the Jicarilla Apache and Navajo Indian Reservations and on Elk on the Jicarilla Apache Indian Reservation, filed 3/24/1975;
Regulation No. 568, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 6/25/1975;
Regulation No. 573, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/23/1976;
Regulation No. 583, Establishing Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/11/1977;

Regulation No. 590, Establishing Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/15/1978;
Regulation No. 596, Establishing Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/23/1979;
Regulation No. 603, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1980 through March 31, 1981, filed 2/22/1980;
Regulation No. 609, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1981 through March 31, 1982, filed 3/17/1981;
Regulation No. 614, Establishing Open Seasons on Deer, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1982 through March 31, 1983, filed 3/10/1982;
Regulation No. 622, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1983 through March 31, 1984, filed 3/9/1983;
Regulation No. 628, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1984 through March 31, 1985, filed 4/2/1984;
Regulation No. 634, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1985 Through March 31, 1986, filed 4/18/1985;
Regulation No. 640, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1986 through March 31, 1987, filed 3/25/1986;
Regulation No. 645, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1987 through March 31, 1988, filed 2/12/1987;
Regulation No. 653, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1988 through March 31, 1989, filed 12/18/1987;
Regulation No. 663, Establishing Opening Spring Turkey for the Period April 1, 1989 through March 31, 1990, filed 3/28/1989;
Regulation No. 664, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1989 through March 31, 1990, filed 3/20/1989;
Regulation No. 674, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1990 through March 31, 1991, filed 11/21/1989;
Regulation No. 683, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex for the Period April 1, 1991 through March 31, 1992, filed 2/8/1991;
Regulation No. 689, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex for the Period April 1, 1992 through March 31, 1993, filed 3/4/1992;
Regulation No. 700, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex for the Period April 1, 1993 through March 31, 1995, filed 3/11/1993.

History of Repealed Material:
19.31.8 NMAC, Big Game, filed 3/1/2001 - duration expired 3/31/2003.
19.31.8 NMAC, Big Game and Turkey, filed 3/3/2003 - duration expired 3/31/2005.
19.31.8 NMAC, Big Game and Turkey, filed 12/15/2004 - duration expired 3/31/2007.
19.31.11 NMAC, Bear and Cougar, filed 12/1/2006 - duration expired 3/31/2009.
19.31.11 NMAC, Bear and Cougar, filed 3/13/2009 - duration expired 3/31/2011.
19.31.11 NMAC, Bear and Cougar, filed 2/22/2011 - duration expired 3/31/2016.
19.31.11 NMAC, Bear and Cougar, filed 2/29/2016 - duration expired 3/31/2020.

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Final Adopted Rule

TITLE 19 NATURAL RESOURCES AND WILDLIFE
CHAPTER 31 HUNTING AND FISHING
PART 11 BEAR AND COUGAR

19.31.11.1 ISSUING AGENCY: New Mexico department of game and fish.
[19.31.11.1 NMAC - Rp, 19.31.11.1 NMAC, 4/1/2020]

19.31.11.2 SCOPE: Sportspersons interested in bear and cougar management and hunting. Additional requirements may be found in Chapter 17 NMSA 1978 and Title 19 NMAC.
[19.31.11.2 NMAC - Rp, 19.31.11.2 NMAC, 4/1/2020]

19.31.11.3 STATUTORY AUTHORITY: 17-1-14 and 17-1-26 NMSA 1978 provide that the New Mexico state game commission has the authority to establish rules and regulations that it may deem necessary to carry out the purpose of Chapter 17 NMSA 1978 and all other acts pertaining to protected mammals, birds, and fish.
[19.31.11.3 NMAC - Rp, 19.31.11.3 NMAC, 4/1/2020]

19.31.11.4 DURATION: April 1, 2020 through March 31, 2024.
[19.31.11.4 NMAC - Rp, 19.31.11.4 NMAC, 4/1/2020]

19.31.11.5 EFFECTIVE DATE: April 1, 2020, unless a later date is cited at the end of a section.
[19.31.11.5 NMAC - Rp, 19.31.11.5 NMAC, 4/1/2020]

19.31.11.6 OBJECTIVE: Establishing open hunting seasons and regulation, rules and procedures governing the distribution and issuance of bear and cougar licenses by the department.
[19.31.11.6 NMAC - Rp, 19.31.11.6 NMAC, 4/1/2020]

19.31.11.7 DEFINITIONS:

A. **"Bear entry permit"** shall mean a permit awarded through a public drawing which entitles the holder of an over-the-counter bear license to hunt in a limited entry area during season dates established in rule.

B. **"Bear zones"** shall define hunt areas consisting of one or more game management units as described in 19.30.4 NMAC.

C. **"Cougar zones"** shall define hunt areas consisting of one or more game management units as described in 19.30.4 NMAC.

D. **"Department"** shall mean the New Mexico department of game and fish.

E. **"Director"** shall mean the director of the New Mexico department of game and fish.

F. **"Game management unit" or "GMU"** shall mean those areas as described in 19.30.4 NMAC.

G. **"Wildlife management areas" or "WMAs"** shall mean those areas as described in 19.34.5 NMAC.

[19.31.11.7 NMAC - Rp, 19.31.11.7 NMAC, 4/1/2020]

19.31.11.8 ADJUSTMENT OF LICENSES, PERMITS AND HARVEST LIMITS:

A. The director, with verbal concurrence of the chairperson or their designee, may adjust the number of licenses, permits or harvest limits, up or down by no more than twenty percent within a bear zone or cougar zone, to address critical department management needs, significant changes in population levels or habitat availability. This adjustment may be applied for bear and cougar within the specified zones to any or all of: the specific hunt codes; total harvest limits; or female harvest sub-limits.

B. The director, with verbal concurrence of the chairperson or their designee, may take management actions independent of seasons and restrictions, harvest limits or female sub-limits for population management, or to address critical situations including ungulate population protection, depredation, human health and safety or other wildlife management issues. The decision to take management actions pursuant to this subsection shall be reported to the commission.

[19.31.11.8 NMAC - Rp, 19.31.11.8 NMAC, 4/1/2020]

19.31.11.9 BEAR AND COUGAR LICENSE APPLICATION REQUIREMENTS AND RESTRICTIONS:

A. Bear entry hunt: It shall be unlawful to hunt bear in designated wildlife management areas or other specifically designated special entry hunt areas without having a valid bear entry permit and a valid bear license in the hunter's possession or as otherwise allowed by game commission rule. Bear entry hunters shall be allowed to hunt in any other open bear zone provided they have a valid bear license.

B. Mandatory cougar identification course: All persons shall complete the mandatory cougar identification course offered on the department's website prior to purchasing a cougar license.
[19.31.11.9 NMAC - Rp, 19.31.11.9 NMAC, 4/1/2020]

19.31.11.10 BEAR AND COUGAR ZONE CLOSURES, BAG LIMITS AND AREA CLOSURES:

A. Zone closures: Bear and cougar may be hunted or taken only in zones designated as open on the department hotline or website. Zones will close within 72 hours of when the reported number of bears or cougars harvested is within ten percent of the total limit or female sub-limit for that zone, whichever occurs first.

B. Bag limit: The bag limit for bear is one; the bag limit for cougar is two. It is unlawful to kill a bear sow with cub(s) or any bear cub less than one year old, or to kill a spotted cougar kitten or any female cougar accompanied by spotted kitten(s).

C. Areas closed to bear and cougar hunting: Limited entry hunt areas listed in 19.31.11 NMAC are closed to over-the-counter bear hunters who do not possess an entry permit. Cougar hunting in these areas is allowed only by licensed deer or elk hunters in possession of a valid cougar license in the E.S. Barker, Colin Neblett, Humphries, Marquez, Sargent, and Urraca WMAs, and the Valle Vidal. Deer or elk hunters choosing to hunt cougar under this provision may not use dogs, may only hunt in open cougar zones, and must adhere to the weapon type restriction and season dates as specified by their deer or elk licenses. Cougar hunting is closed in the Florida mountains hunt area during any open Persian ibex season, except by legal Persian ibex hunters in possession of a valid cougar license. Persian ibex hunters may only hunt cougar if the cougar zone is open, and must adhere to the weapon type restrictions and season dates as specified by their Persian ibex license.
[19.31.11.10 NMAC - Rp, 19.31.11.10 NMAC, 4/1/2020]

19.31.11.11 BEAR HUNTING SEASONS:

A. Over-the-counter bear hunts for the 2020-21 through 2023-24 seasons: The following table lists bear zones, open GMUs, weapon type restrictions, season dates, total harvest limits, and female harvest sub-limits.

Bear zone	open GMUs or areas	bow only	any big game sporting arms	2020-21 total limit (female)	2021-22 total limit (female)	2022-23 total limit (female)	2023-24 total limit (female)
1	4, 5, 6, 7, 51, 52	9/1 - 24	9/25 - 11/15	158 (63)	158 (63)	158 (63)	158 (63)
2	2	9/1 - 24	9/25 - 11/15	15 (6)	15 (6)	15 (6)	15 (6)
3	49, 50, 53	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	65 (26)	65 (26)	65 (26)	65 (26)
4	45, 46, 48	9/1 - 24	8/16 - 8/31 and 9/25 - 11/30	109 (43)	109 (43)	109 (43)	109 (43)
5	54, 55	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	92 (37)	92 (37)	92 (37)	92 (37)
6	39, 40, 41, 42, 43, 47, 59	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	33 (13)	33 (13)	33 (13)	33 (13)
7	56, 57, 58	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	35 (14)	35 (14)	35 (14)	35 (14)
8	8	9/1 - 24	10/15 - 11/15	11 (4)	11 (4)	11 (4)	11 (4)
9	9, 10	9/1 - 24	8/16 - 8/31 and 9/25 - 11/15	36 (14)	36 (14)	36 (14)	36 (14)
10	12, 13, 15, 16, 17, 18, 20, 21, 22, 23, 24, 26, 27	9/1 - 24	9/25 - 12/15	146 (58)	146 (58)	146 (58)	146 (58)
11	37, 38	9/1 - 24	8/16 - 8/31 and 9/25 - 11/30	36 (14)	36 (14)	36 (14)	36 (14)
12	34	9/1 - 24	9/25 - 12/15	33 (13)	33 (13)	33 (13)	33 (13)

13	36	9/1 - 24	9/25 - 11/30	16 (6)	16 (6)	16 (6)	16 (6)
14	14	9/1 - 24	10/15 - 11/15	19 (7)	19 (7)	19 (7)	19 (7)

B. **Entry hunts for the 2020-21 through 2023-24 seasons** shall be as indicated below, listing the open areas, hunt dates, hunt codes, and number of permits.

open GMUs or areas	2020-2021 hunt dates	2021-2022 hunt dates	2022-2023 hunt dates	2023-2024 hunt dates	hunt code	licenses
2, **youth only**	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-100	5
4: Sargent WMA only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-101	10
4: Humphries WMA only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-102	5
9: Marquez WMA only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-103	5
54:55: Uracca, E.S. Barker, and Colin Neblett WMAs, and Valle Vidal	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-1-104	32
55: Valle Vidal	4/15-5/20	4/15-5/20	4/15-5/20	4/15-5/20	BER-1-105	20
57: Sugarite Canyon State Park/ bow only	8/1-8/31	8/1-8/31	8/1-8/31	8/1-8/31	BER-2-106	5

[19.31.11.11 NMAC - Rp, 19.31.11.11 NMAC, 4/1/2020]

19.31.11.12 COUGAR HUNTING SEASONS:

A. Over-the-counter cougar hunting season shall be from April 1 through March 31, or until the total harvest limit or female sub-limit, whichever comes first, is met in any given cougar zone.

B. The following table lists cougar zones, open GMUs, total harvest limits and female harvest sub-limits for the 2020-21 to 2023-24 seasons.

zone	open GMUs or areas	2020-21 total limit (female)	2021-22 total limit (female)	2022-23 total limit (female)	2023-24 total limit (female)
A	2, 7	42 (13)	42 (13)	42 (13)	42 (13)
B	5, 6, 50, 51	25 (8)	25 (8)	25 (8)	25 (8)
C	43, 45, 46, 48, 49, 53	57 (17)	57 (17)	57 (17)	57 (17)
D	41, 42, 47,59	15 (5)	15 (5)	15 (5)	15 (5)
E	9, 10	43 (13)	43 (13)	43 (13)	43 (13)
G	13, 17	50 (15)	50 (15)	50 (15)	50 (15)
H	18, 19, 20	29 (9)	29 (9)	29 (9)	29 (9)
I	36, 37, 38	24 (7)	24 (7)	24 (7)	24 (7)
J	15, 16, 21	84 (25)	84 (25)	84 (25)	84 (25)
K	22, 23, 24	45 (14)	45 (14)	45 (14)	45 (14)
L	25, 26, 27	19 (6)	19 (6)	19 (6)	19 (6)
M	31, 32, 33, 39, 40	25 (7)	25 (7)	25 (7)	25 (7)
N	4, 52	13 (4)	13 (4)	13 (4)	13 (4)
O	12	17 (5)	17 (5)	17 (5)	17 (5)
P	56, 57, 58	14 (7)	14 (7)	14 (7)	14 (7)
Q	28, 29, 30, 34	35 (11)	35 (11)	35 (11)	35 (11)
R	54, 55	26 (8)	26 (8)	26 (8)	26 (8)
S	8, 14	17 (5)	17 (5)	17 (5)	17 (5)

[19.31.11.12 NMAC - Rp, 19.31.11.12 NMAC, 4/1/2020]

HISTORY OF 19.31.11 NMAC:

Pre-NMAC History: The material in this part was derived from that previously filed with the state records center and archives under:
Regulation No. 482, Establishing Seasons on Deer, Bear, Turkey, Elk, Antelope, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, and Barbary Sheep, filed 5/31/1967;
Regulation No. 487, Establishing 1967 Seasons on Javelina and Barbary Sheep, filed 12/15/1967;
Regulation No. 489, Establishing Turkey Seasons for the Spring of 1968, filed 3/1/1968;
Regulation No. 491, Establishing Big Game Seasons for 1968 for Jicarilla Reservation, filed 3/1/1968;

Regulation No. 492, Establishing Seasons on Deer, Bear, Turkey, Elk, Antelope, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, and Barbary Sheep, filed 6/6/1968;
Regulation No. 495, Establishing a Season on Bighorn Sheep, filed 10/2/1968;
Regulation No. 496, Establishing an Elk Season in the Tres Piedras Area, Elk Area P-6, filed 12/11/1968;
Regulation No. 502, Establishing Turkey Seasons for the Spring Of 1969, filed 3/5/1969;
Regulation No. 503, Establishing 1969 Deer Seasons for Bowhunting Only and Big Game Seasons for the Jicarilla Indian Reservation, filed 3/5/1969;
Regulation 504, Establishing Seasons on Deer, Bear, Turkey, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, and Barbary Sheep, filed 6/4/1969;
Regulation No. 507, Establishing a Season on Bighorn Sheep, filed 8/26/1969;
Regulation No. 512, Establishing Turkey Season for the Spring Of 1970, filed 2/20/1970;
Regulation No. 513, Establishing Deer Season for Bowhunting Only in Sandia State Game Refuge, filed 2/20/1970;
Regulation No. 514, Establishing Seasons on Deer, Bear, Turkey, Elk, Antelope, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Barbary Sheep and Bighorn Sheep, filed 6/9/1970;
Regulation No 520, Establishing Turkey Seasons for the Spring of 1971, filed 3/9/1971;
Regulation No. 522, Establishing 1971 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 3/9/1971;
Regulation No. 523, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Elk, Antelope, Barbary Sheep and Bighorn Sheep, filed 6/9/1971;
Regulation No. 531, Establishing a Season on Javelina, filed 12/17/1971;
Regulation No. 532, Establishing Turkey Seasons for the Spring of 1972, filed 3/20/1972;
Regulation No. 534, Establishing 1972 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 3/20/1972;
Regulation No. 536, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, Elk, Antelope, Barbary Sheep and Bighorn Sheep, filed 6/26/1972;
Regulation No. 542, Establishing a Season on Javelina, filed 12/1/1972;
Regulation No. 545, Establishing Turkey Seasons for the Spring Of 1973, filed 2/26/1973;
Regulation No. 546, Establishing 1973 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 2/26/1973;
Regulation No. 547, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, Elk, Antelope, Barbary Sheep and Bighorn Sheep, and Javelina, filed 5/31/1973;
Regulation No. 554, Establishing Special Turkey Seasons for the Spring of 1974, filed 3/4/1974;
Regulation No. 556, Establishing 1974 Seasons on Deer, Bear, Turkey, and Elk on the Jicarilla Apache Indian Reservation, filed 3/14/1974;
Regulation No. 558, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex, filed 5/29/1974;
Regulation No. 565, Establishing Special Turkey Seasons for the Spring of 1975, filed 3/24/1975;
Regulation No. 567, Establishing 1975 Seasons on Deer, Bear, and Turkey on the Jicarilla Apache and Navajo Indian Reservations and on Elk on the Jicarilla Apache Indian Reservation, filed 3/24/1975;
Regulation No. 568, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Chickaree and Tassel-Eared Squirrel, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 6/25/1975;
Regulation No. 573, Establishing Seasons on Deer, Turkey, Bear, Cougar, Dusky Grouse, Tassel-Eared and Chickaree Squirrel, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/23/1976;
Regulation No. 583, Establishing Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/11/1977;
Regulation No. 590, Establishing Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/15/1978;
Regulation No. 596, Establishing Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex, filed 2/23/1979;
Regulation No. 603, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1980 through March 31, 1981, filed 2/22/1980;
Regulation No. 609, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1981 through March 31, 1982, filed 3/17/1981;
Regulation No. 614, Establishing Open Seasons on Deer, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1982 through March 31, 1983, filed 3/10/1982;

Regulation No. 622, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1983 through March 31, 1984, filed 3/9/1983;
Regulation No. 628, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1984 through March 31, 1985, filed 4/2/1984;
Regulation No. 634, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1985 Through March 31, 1986, filed 4/18/1985;
Regulation No. 640, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1986 through March 31, 1987, filed 3/25/1986;
Regulation No. 645, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1987 through March 31, 1988, filed 2/12/1987;
Regulation No. 653, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1988 through March 31, 1989, filed 12/18/1987;
Regulation No. 663, Establishing Opening Spring Turkey for the Period April 1, 1989 through March 31, 1990, filed 3/28/1989;
Regulation No. 664, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1989 through March 31, 1990, filed 3/20/1989;
Regulation No. 674, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx and Ibex for the Period April 1, 1990 through March 31, 1991, filed 11/21/1989;
Regulation No. 683, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex for the Period April 1, 1991 through March 31, 1992, filed 2/8/1991;
Regulation No. 689, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex for the Period April 1, 1992 through March 31, 1993, filed 3/4/1992;
Regulation No. 700, Establishing Open Seasons on Deer, Turkey, Bear, Cougar, Elk, Antelope, Barbary Sheep, Bighorn Sheep, Javelina, Oryx, and Ibex for the Period April 1, 1993 through March 31, 1995, filed 3/11/1993.

History of Repealed Material:
19.31.8 NMAC, Big Game, filed 3/1/2001 - duration expired 3/31/2003.
19.31.8 NMAC, Big Game and Turkey, filed 3/3/2003 - duration expired 3/31/2005.
19.31.8 NMAC, Big Game and Turkey, filed 12/15/2004 - duration expired 3/31/2007.
19.31.11 NMAC, Bear and Cougar, filed 12/1/2006 - duration expired 3/31/2009.
19.31.11 NMAC, Bear and Cougar, filed 3/13/2009 - duration expired 3/31/2011.
19.31.11 NMAC, Bear and Cougar, filed 2/22/2011 - duration expired 3/31/2016.
19.31.11 NMAC, Bear and Cougar, filed 2/29/2016 - duration expired 3/31/2020.

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2019 DEC -3 PM 4: 51

NMAC
Transmittal Form

NEW MEXICO
Commission of Public Records
at the State Records Center and Archives
Your Access to Public Information

Volume: XXX **Issue:** 23 **Publication date:** Dec. 17, 2019 **Number of pages:** 5 **(ALD Use Only) Sequence No.**

Issuing agency name and address: New Mexico Department of Game and Fish

Agency DFA code: 516

Contact person's name: Elise Goldstein

Phone number: 505-476-8032

E-mail address: Elise.Goldstein@state.nm.us

(ALD Use Only) Most recent filing date:

Type of rule action:

New ☑ **Amendment** ☐ **Repeal** ☐ **Emergency** ☐ **Renumber** ☐

Title number: 19 **Title name:** Natural Resources and Wildlife

Chapter number: 31 **Chapter name:** Hunting and Fishing

Part number: 11 **Part name:** Bear and Cougar

Amendment description (If filing an amendment):

Amendment's NMAC citation (If filing an amendment):

Are there any materials incorporated by reference?

Yes ☐ **No** ☒

Please list attachments or Internet sites if applicable.

If materials are attached, has copyright permission been received? **Yes** ☐ **No** ☐ **Public domain** ☐

Specific statutory or other authority authorizing rulemaking:

Sections 17-1-14, et seq. NMSA 1978; Sections 17-1-26, et seq. NMSA 1978

Notice date(s): Oct. 15, 2019

Hearing date(s): Nov.21, 2019

Rule adoption date: Nov. 21, 2019

Rule effective date: April 1, 2020

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2019 DEC -3 PM 4: 51

Concise Explanatory Statement For Rulemaking Adoption:

Findings required for rulemaking adoption:

Findings MUST include:

- **Reasons for adopting rule, including any findings otherwise required by law of the agency, and a summary of any independent analysis done by the agency;**
- **Reasons for any change between the published proposed rule and the final rule; and**
- **Reasons for not accepting substantive arguments made through public comment.**

The rulemaking was undertaken to adopt a new Bear and Cougar rule, 19.31.11 NMAC, which will become effective April 1, 2020. The current Bear and Cougar rule will expire on March 31, 2020.

The new rule includes: 1) changing the start date for the bear general weapon type season to September 25 in Bear Management Zones 10, 12, and 13, and extending the closing date to December 15 in Zones 10 and 12, and November 30 in Zone 13; 2) grouping the Barker and Colin Neblett Wildlife Management Area (Hunt Code BER-1-104) and Valle Vidal (Hunt Code BER-1-105) draw licenses as a single license and including the Urraca Wildlife Management Area in the areas open to hunting with that license; 3) no longer allowing traps and foot snares as a method of sport harvest for cougar; 4) adjusting cougar harvest limits to align with recent data and management objectives; 5) moving Game Management Unit 25 from Cougar Management Zone J to Cougar Management Zone L; and 6) no longer allowing an additional two tags for cougar license holders who have successfully filled their original two tags. A full text of changes is available on the Department's website at: www.wildlife.state.nm.us

There have been no changes between the published proposed rule and the final rule. A wide array of public comments were submitted. To view public comments, please visit www.wildlife.state.nm.us/commission/meeting-agendas/ and click on the Hearing Archive tab. It was not possible to incorporate all of the comments into the final rule as many of the comments were mutually exclusive. The resulting rule was based on what was best for the resource and overall hunter satisfaction.

Issuing authority (If delegated, authority letter must be on file with ALD):

Name:

Michael B. Sloane

Check if authority has been delegated ☐

Title:

Director

Signature: (BLACK ink only)

Date signed: 11/27/19

Bear and Cougar Rule Development 19.31.11 NMAC

November 21, 2019
Bear and Cougar Rule
Roswell, NM

Wildlife Management Division

EXHIBIT
3

Bear Comments

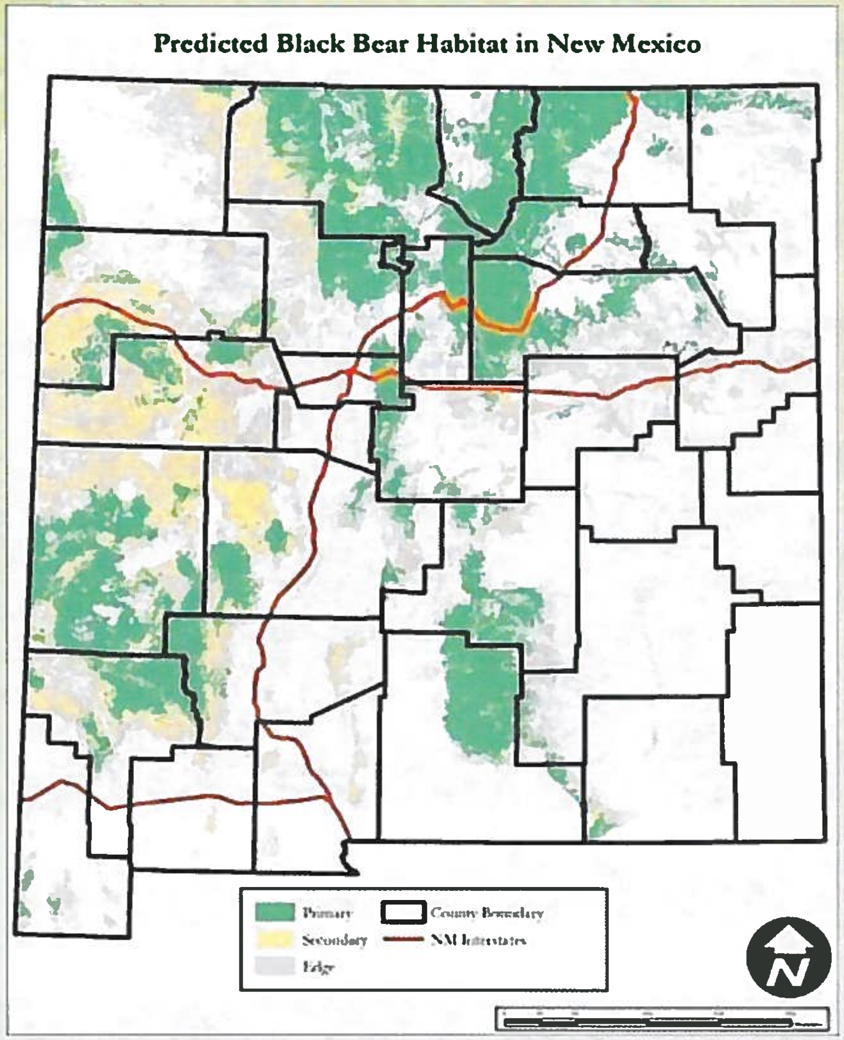
- As of November 19, 2019: 277 comments
- The proposals most commonly commented upon were:
    - No change in bear harvest limits
    - Change the start and end date in BMZs 10, 12, and 13

Bear Proposals

- Not proposing changes to bear harvest limits
- Propose changing the season start and end dates for BMZs 10, 12 and 13
- Include Urraca in August draw hunts in NE

Habitat Model

Primary habitat = 54,793 km²
(18% of NM)



Predicted Black Bear Habitat in New Mexico

Population Information

Mountain Range	Costello et al. (2001) Density Estimates (bears/100 km^2)	Gould et al. Density Estimate (bears/100 km^2)
Northern Sangre de Cristo	17.0	21.9*
Southern Sangre de Cristo	17.0	19.7*
Sandia	13.2	18.4†
Northern Sacramento	17.0	20.1†
Southern Sacramento	17.0	16.5*

†Gould et al. 2016, *Gould et al. 2018

Bear Harvest

Year	Sport Harvest (females)	Max Allowable Harvest	Depredation	Other	Total	# of Zones Closed
2016-17	438 (154)	804	50	13	501	4
2017-18	483 (178)	804	85	56	624	5
2018-19	496 (188)	804	68	36	600	3
AVG	**472** **(173)**	**804**	**68**	**35**	**575**	**4**

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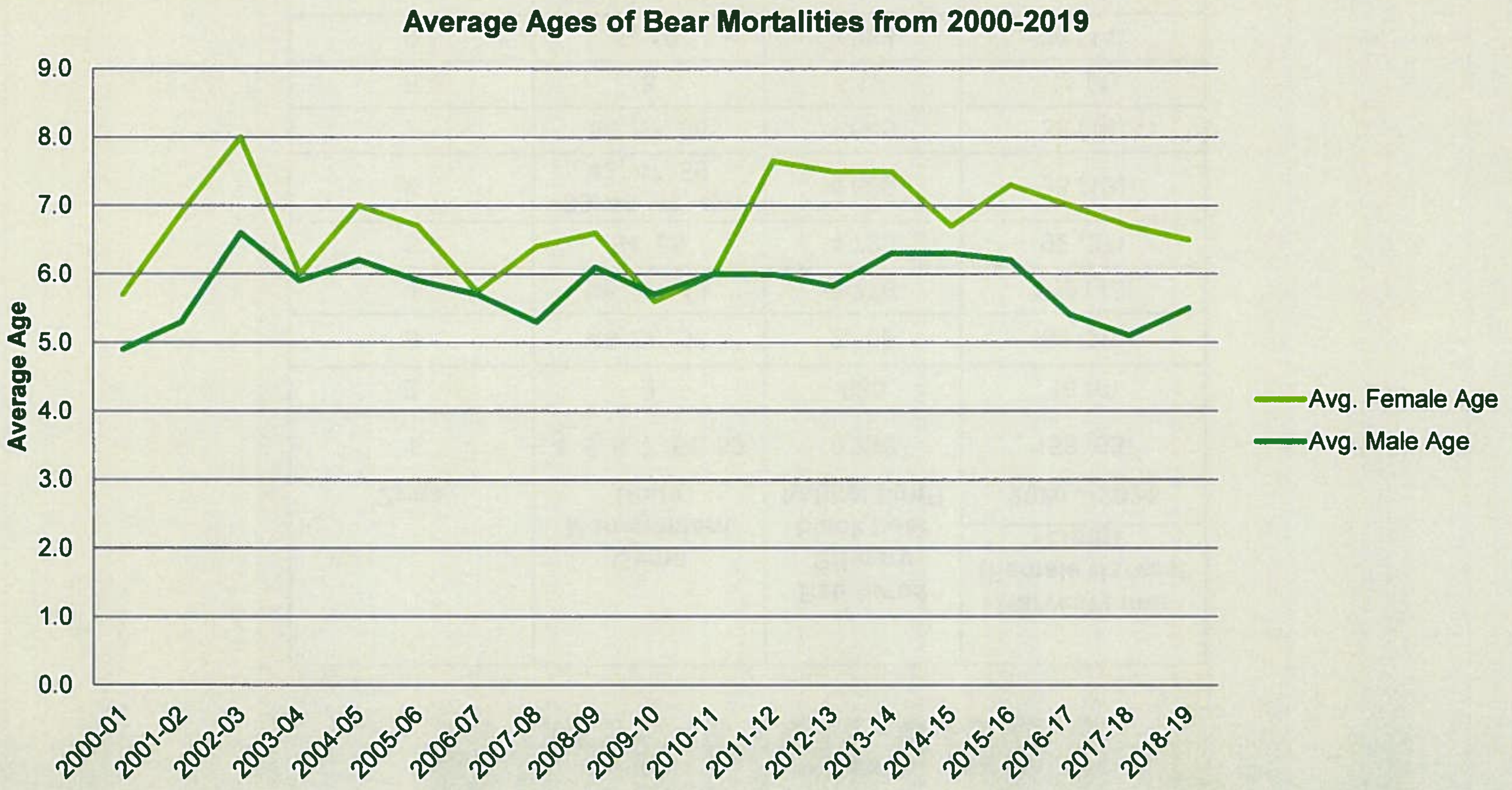
Bear Age at Mortality



Bear Harvest

Zone	Game Management Units	Estimated Primary black bear habitat (km²)	Harvest Limit (Female Harvest Limit)
			2020 – 2024
1	4, 5, 6, 7, 51, 52	9,296	158 (63)
2	2	880	15 (6)
3	49, 50, 53	2,109	65 (26)
4	45, 46, 48	5,778	109 (43)
5	54, 55	4,723	92 (37)
6	39, 40, 41, 42, 43, 47, 59	4,689	33 (13)
7	56, 57, 58	1,645	35 (14)
8	8	719	11 (4)
9	9, 10	2,963	36 (14)
10	12, 13, 15, 16, 17, 18, 20, 21, 22, 23, 24, 26, 27	15,488	146 (58)
11	37, 38	1,811	36 (14)
12	34	2,428	33 (13)
13	36	1,184	16 (6)
14	14	1,267	19 (7)
Totals		**54,793**	**804 (318)**

Cougar Comments

- As of November 19, 2019: 277 comments
- The proposals most commonly commented upon were:
  - No longer allow foothold traps and foot snares as a method of take for sport harvest of cougars
  - Reduce cougar harvest limits in certain zones

Cougar Proposals

- No longer allow traps as a method for sport harvest
- Harvest limit adjustments to align with data
- Adjust Cougar Management Zone L and J; combine B and F

Cougar: Proposal

Manner and Method Requirements and Restrictions 19.31.11.10 NMAC

- No longer allow traps and foot snares for sport harvest on private and state trust land
    - Infrequently used method of take
        - 2016 – 2017: 4 trapped (300)
        - 2017 – 2018: 20 trapped (292)
        - 2018 – 2019: 13 trapped(409)

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Cougar Harvest

Year	Sport Harvest (females)	Max Allowable Harvest	Depredation	Other	Total	# of Zones Closed
2016-17	244 (90)	749	21	35	300	2
2017-18	238 (93)	749	20	34	292	5
2018-19	344 (117)	740	25	40	409	4
AVG	**275 (100)**	**746**	**22**	**35**	**331**	**4**

Cougar Sport Harvest Limits

- Adjustments to harvest limits for zones based on findings from recent NMDGF research and new findings in the literature

Wildlife Management Division

Cougar Sport Harvest Limits

CMZ	Current Total Limit (Female Sub-limit)	Harvest Limit Proposal	Proposed Total Limit (Female Sub-limit)	Additional Proposals
A	42 (13)	No Change	42 (13)	
B	28 (9)	Change*	25 (8)**	Combined with CMZ F
C	84 (42)	Change	57 (17)	
D	23 (11)	Change	15 (5)	
E	50 (15)	Change	42 (13)	
F	46 (23)	Add to CMZ B	Added to CMZ B	Added to CMZ B
G	73 (37)	Change	50 (15)	
H	42 (21)	Change	29 (9)	
I	24 (7)	No Change	24 (7)	
J	89 (27)	Change*	84 (25)	GMU 25 removed
K	66 (33)	Change	45 (14)	
L	19 (10)	Change*	19 (6)	GMU 25 added
M	31 (9)	Change	25 (7)	
N	15 (5)	Change	13 (4)	
O	21 (6)	Change	17 (5)	
P	14 (7)	No Change	14 (7)	
Q	35 (11)	No Change	35 (11)	
R	26 (8)	No Change	26 (8)	
S	25 (13)	Change	17 (5)	

*CMZ boundary adjustments; ** Limits set based upon research conducted in CMZ B and F

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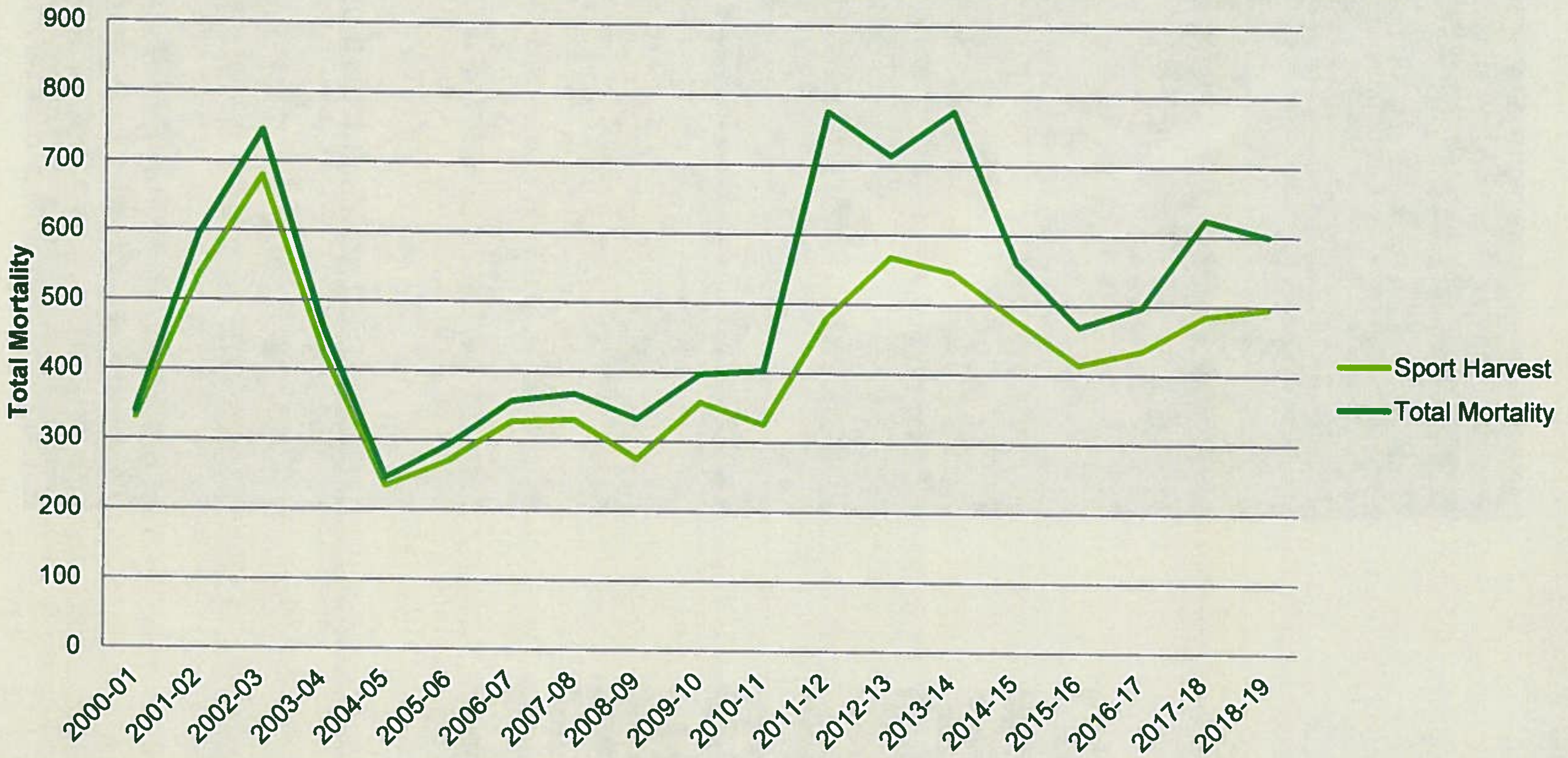
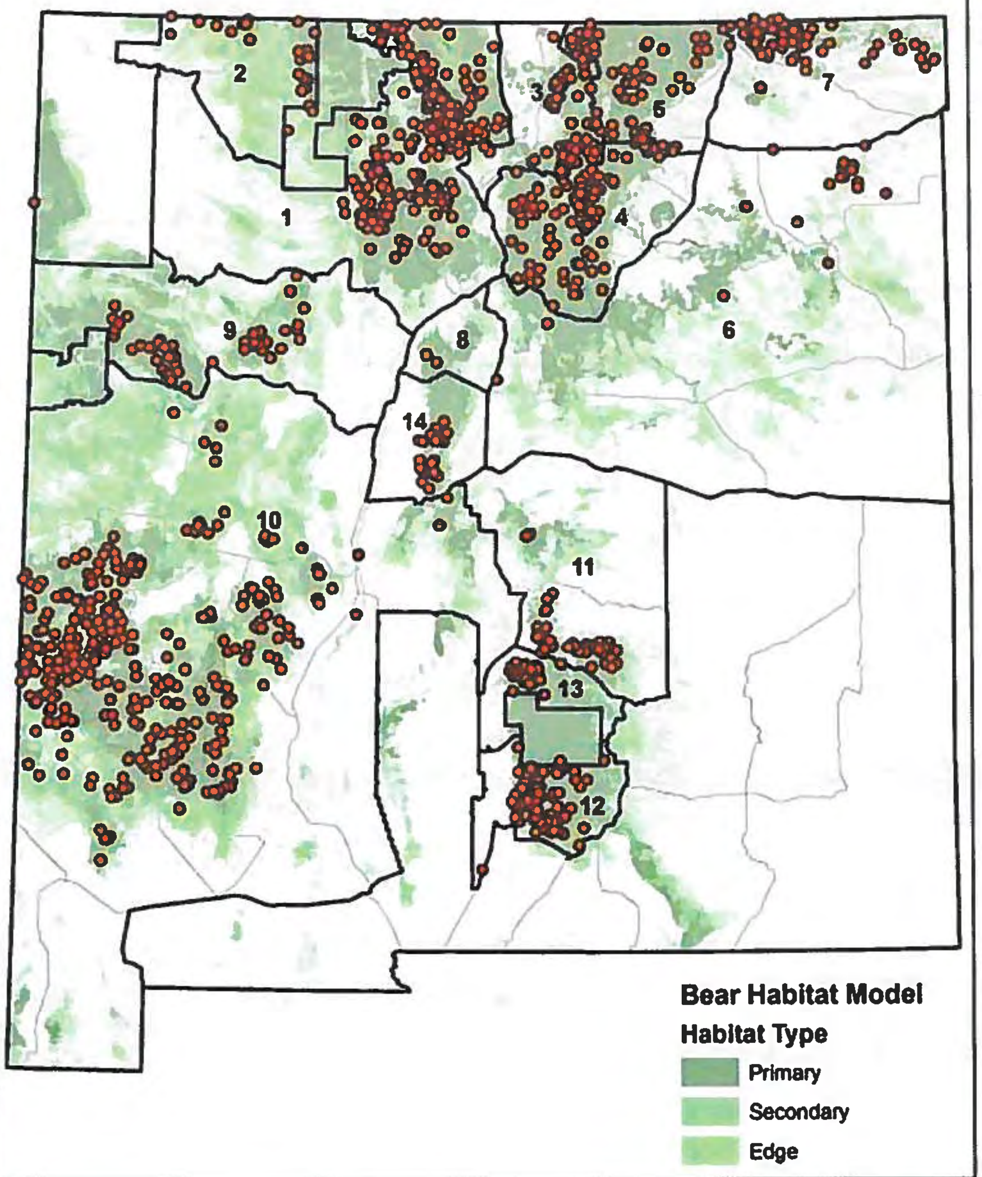
QUESTIONS

Bear Harvest



Black Bear Mortality and Sport Harvest in New Mexico, 2000-2019

Bear Harvest 2016 - 2019



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Bear – Catch Per Unit Effort


Catch Per Unit Effort for Black Bear Harvested 2000 - 2018

Bear Harvest Limits

BMZ	*Max*	2016 Actual	2017 Actual	2018 Actual
1	*158*	**138**	**70**	**121**
2	*15*	**7**	**16**	**5**
3	*65*	**27**	**42**	**26**
4	*109*	**21**	**39**	**50**
5	*92*	**21**	**30**	**21**
6	*33*	**4**	**11**	**5**
7	*35*	**31**	**31**	**30**
8	*11*	**0**	**0**	**2**
9	*36*	**18**	**16**	**20**
10	*146*	**98**	**154**	**143**
11	*36*	**17**	**22**	**21**
12	*33*	**30**	**30**	**32**
13	*16*	**16**	**13**	**13**
14	*19*	**10**	**12**	**7**

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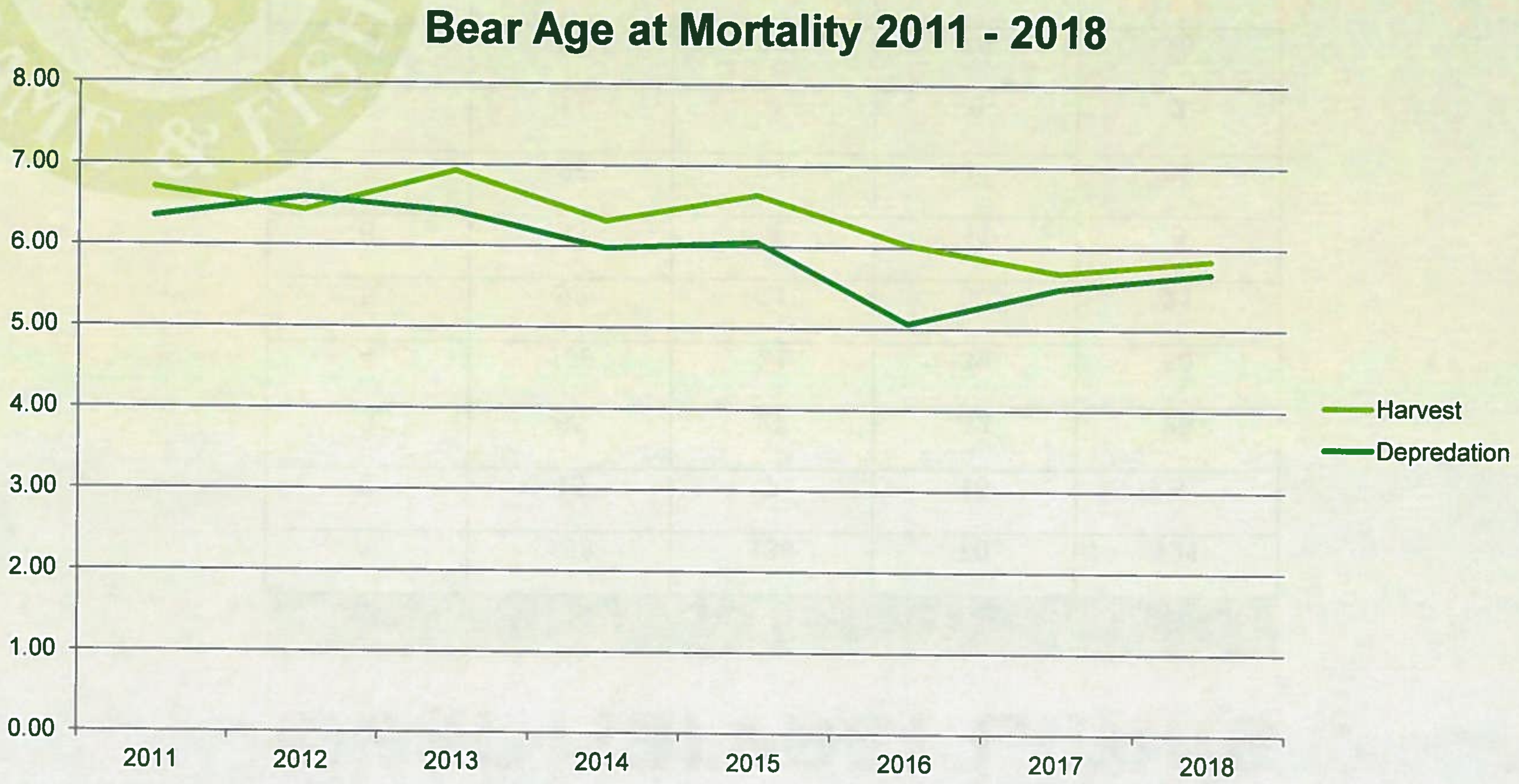
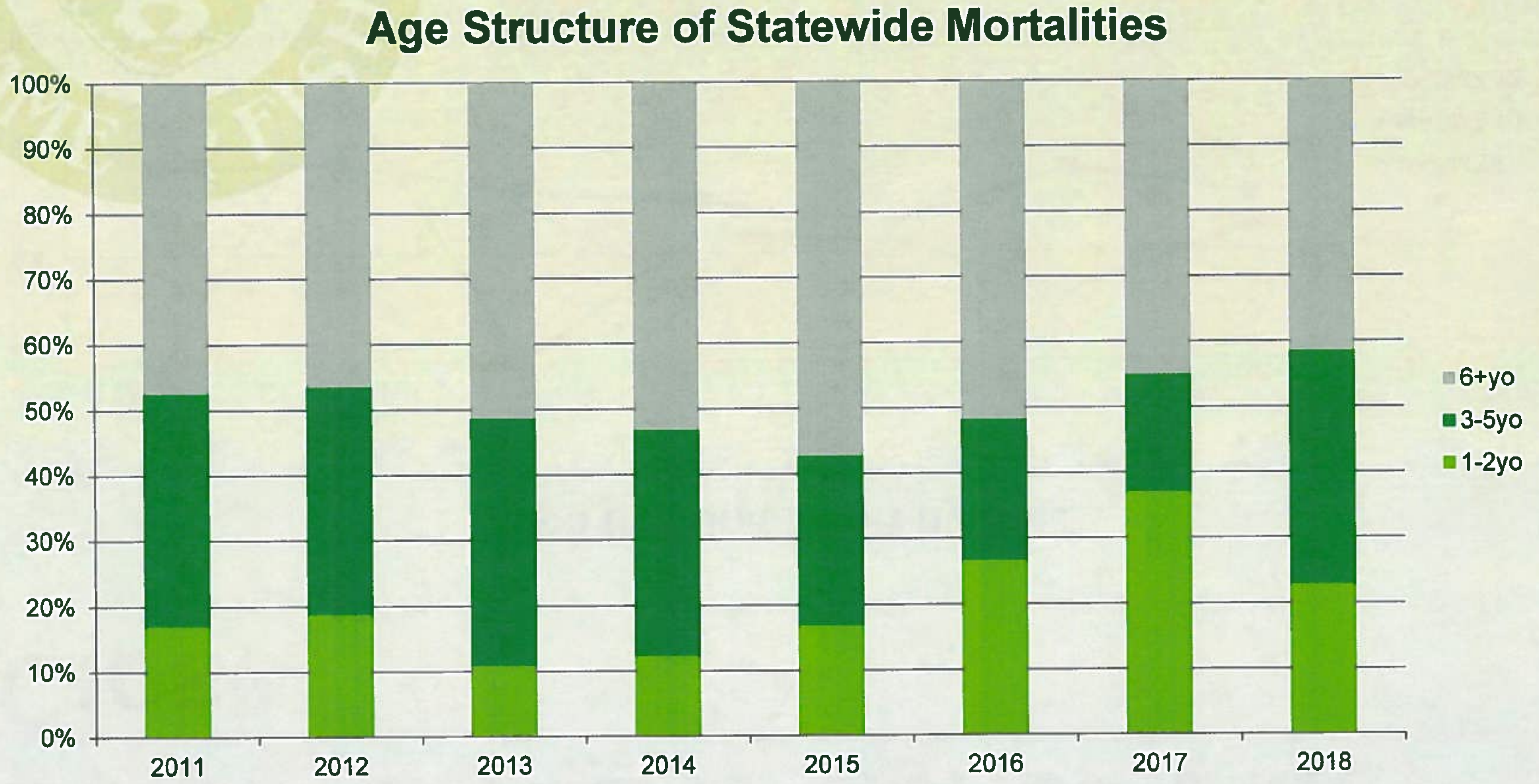
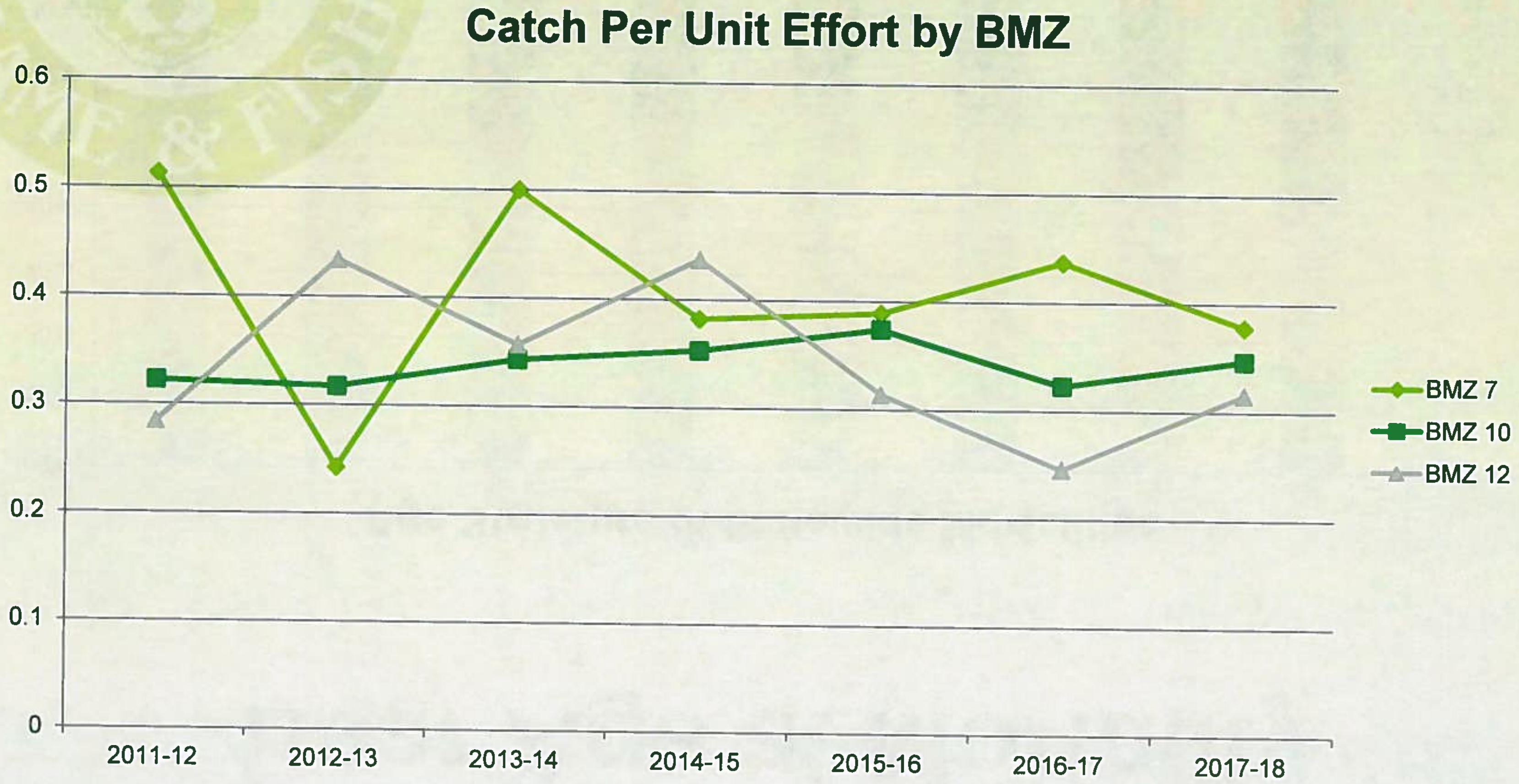
Bear Age at Mortality


Bear Age at Mortality 2011 - 2018

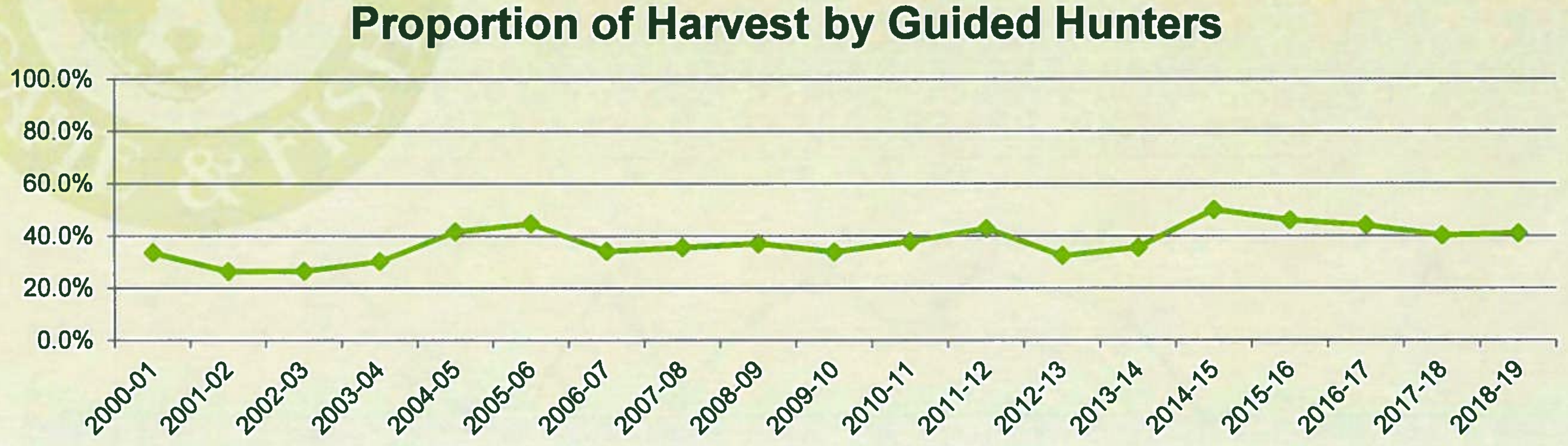
Bear Age at Mortality

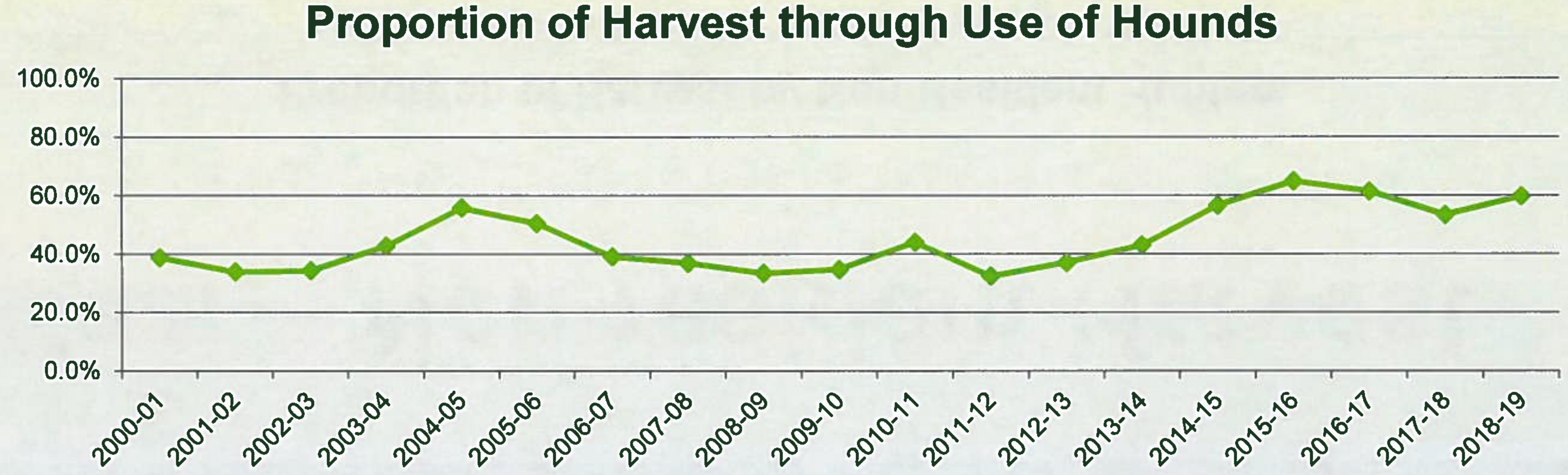

Age Structure of Statewide Mortalities

Bear – CPUE in Zones that Close



Bear – Guided and/or with dogs

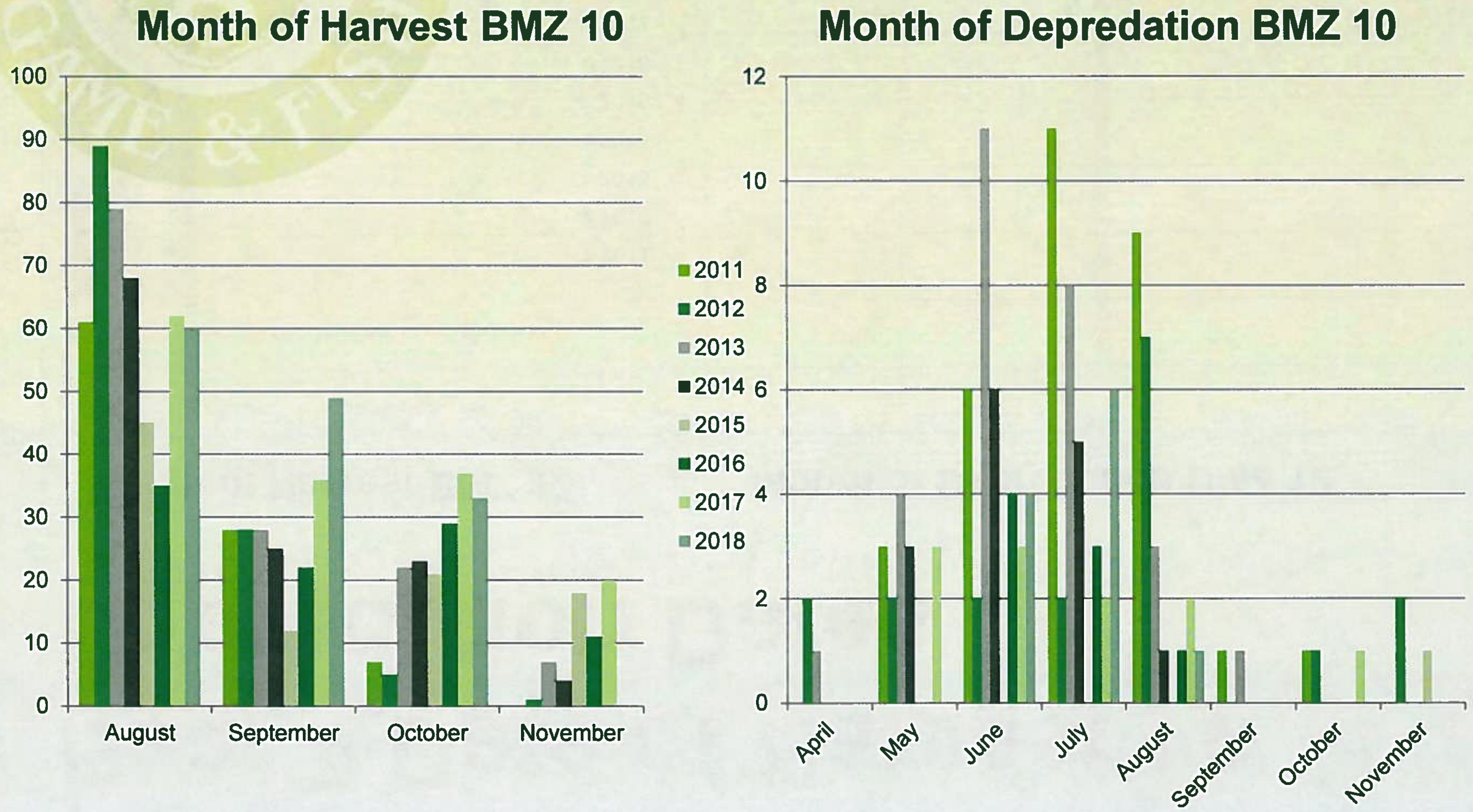

Proportion of Harvest by Guided Hunters


Proportion of Harvest through Use of Hounds

Bear – Non-resident Harvest

Proportion of Harvest by Non-Resident Hunters

Bear – Harvest Dates vs Depredation Dates



Month of Harvest BMZ 10

Month of Depredation BMZ 10

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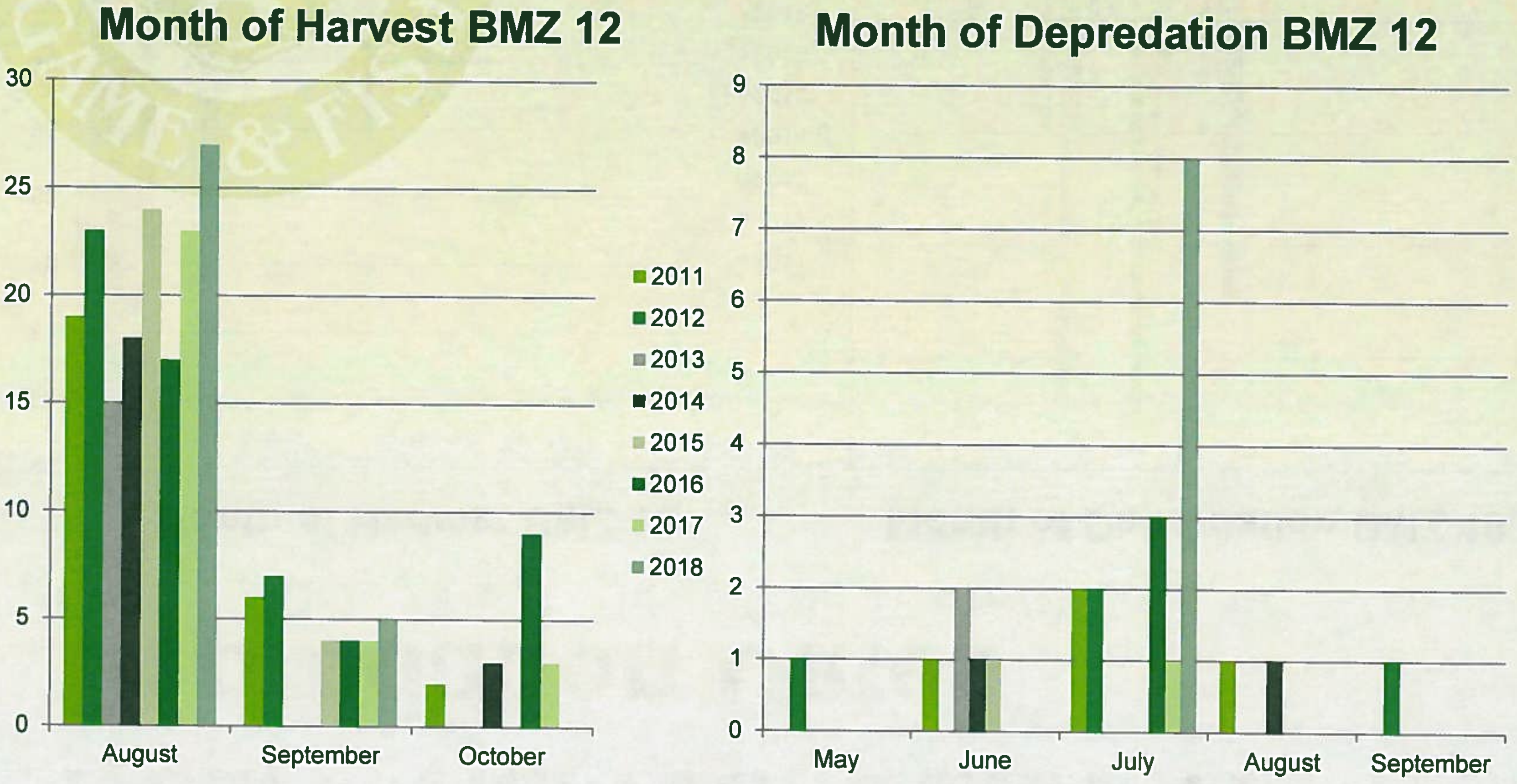
Bear – Date of Harvest vs Depredation Dates

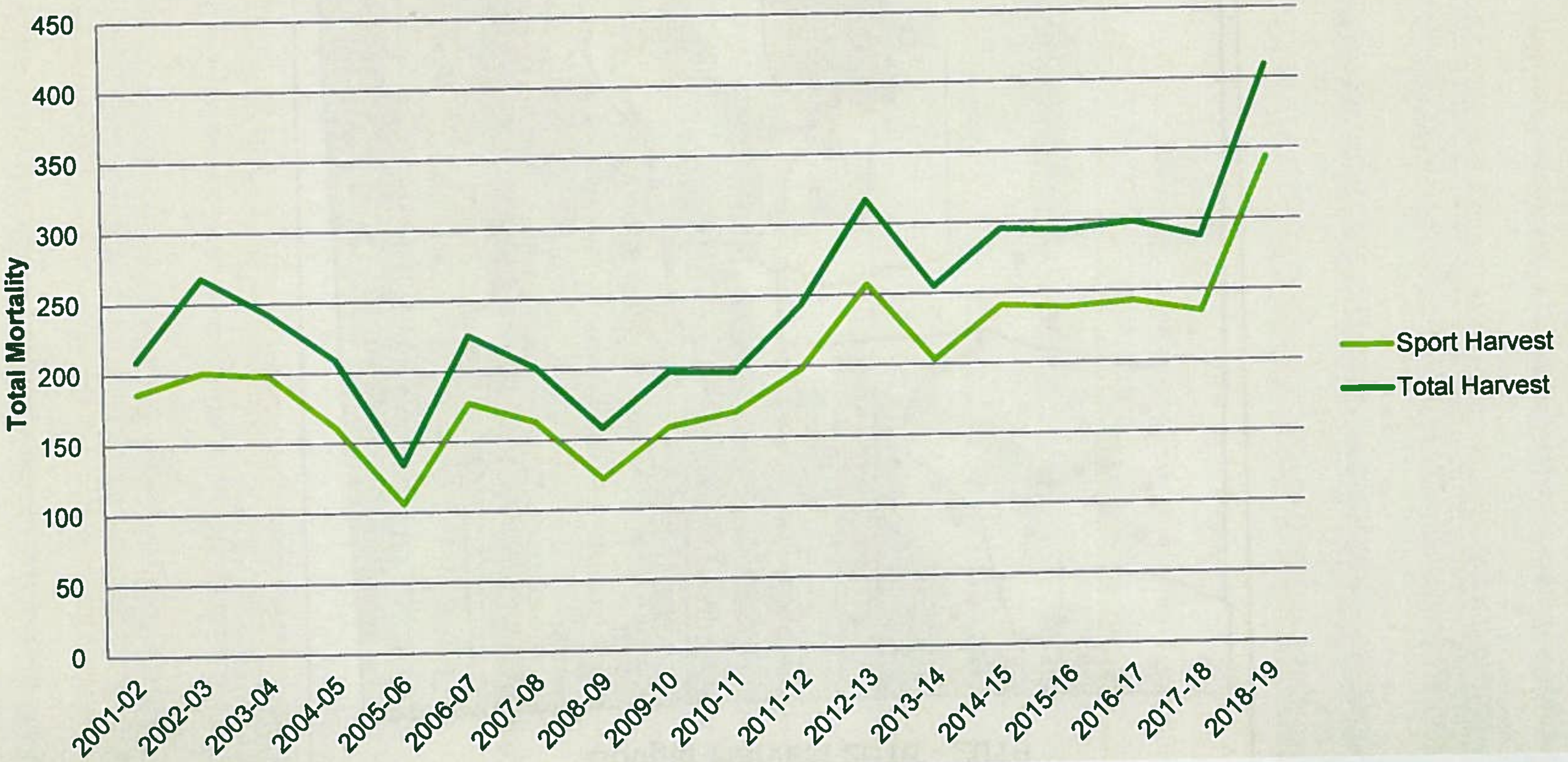


Month of Harvest BMZ 12

Month of Depredation BMZ 12

Cougar Harvest

Total Mortality and Sport Harvest of Cougars in New Mexico, 2001 - 2019



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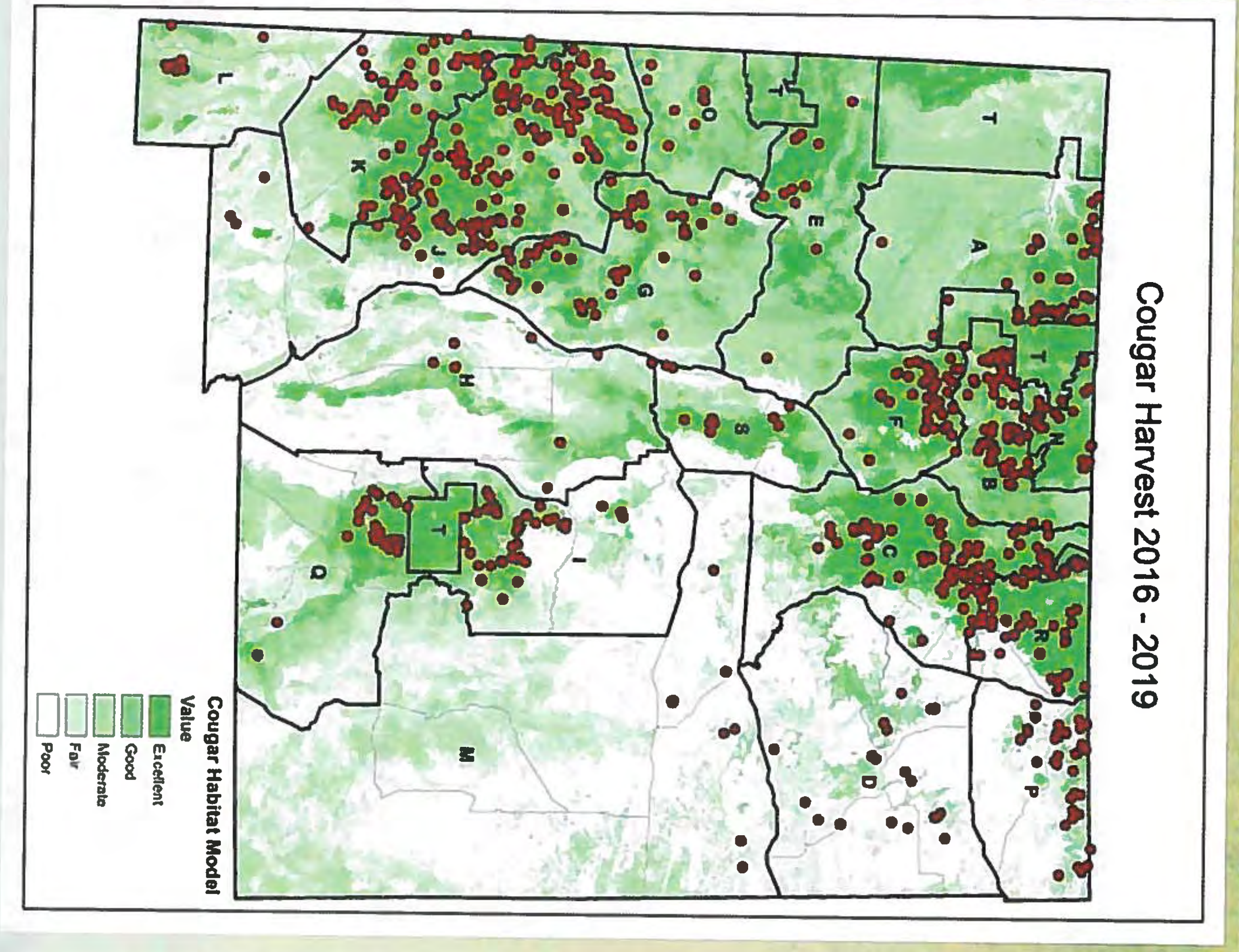
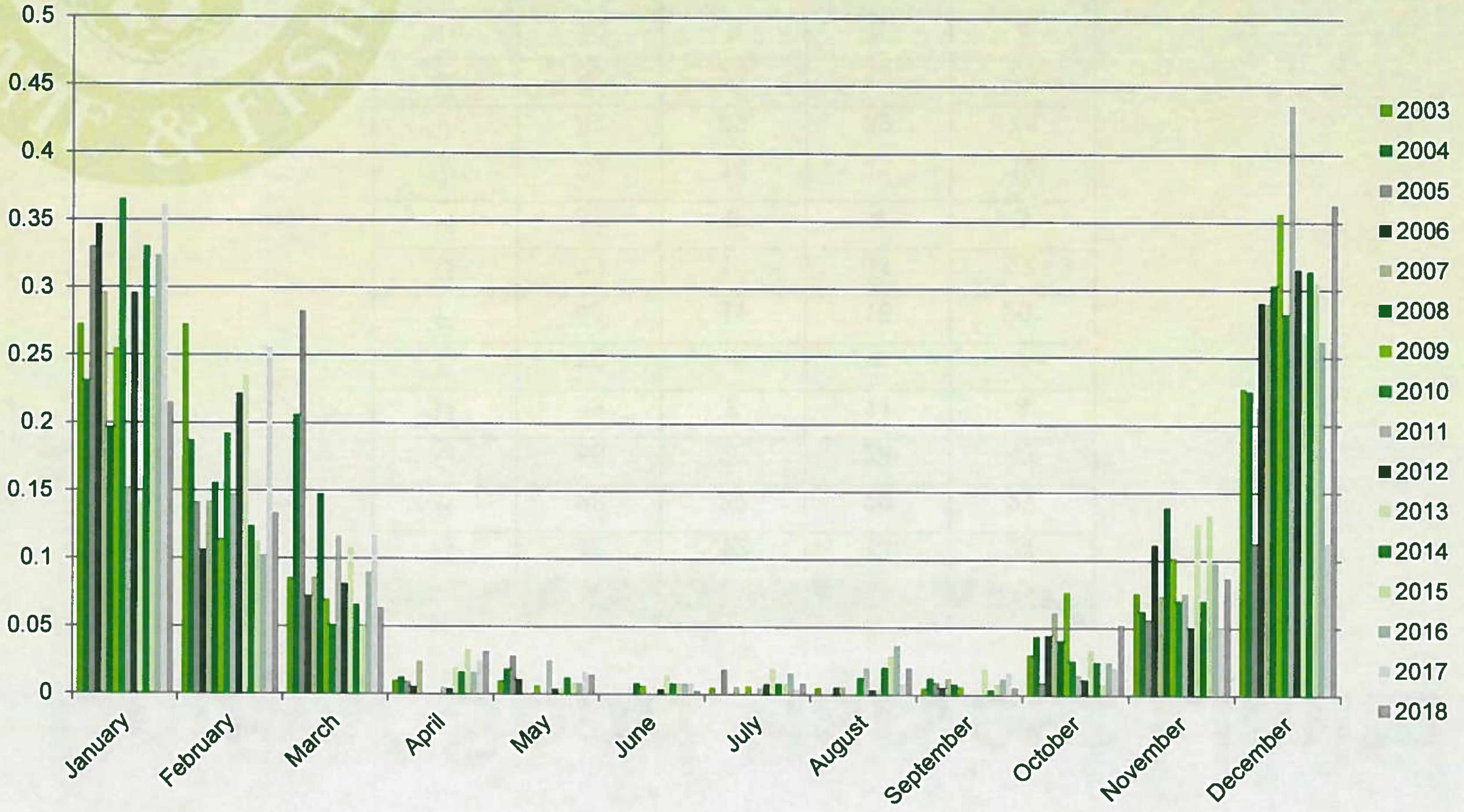

Cougar Harvest 2016 - 2019

Cougar Sport Harvest Limits

	Max	**2016**	**2017**	**2018**
A	*42*	**12**	**14**	**21**
B	*28*	**22**	**20**	**27**
C	*85*	**25**	**24**	**47**
D	*23*	**5**	**11**	**8**
E	*50*	**1**	**3**	**7**
F	*46*	**11**	**16**	**20***
G	*73*	**13**	**11**	**27**
H	*37*	**0**	**4**	**3**
I	*24*	**14**	**11**	**19**
J	*89*	**49**	**39**	**74**
K	*66*	**24**	**25**	**25**
L	*19*	**5**	**3**	**4**
M	*31*	**2**	**4**	**4**
N	*15*	**10**	**10**	**10**
O	*21*	**5**	**1**	**5**
P	*14*	**13**	**15**	**13**
Q	*35*	**13**	**7**	**9**
R	*26*	**16**	**17**	**17**
S	*25*	**4**	**3**	**4**

*2018 CMZ F limit was reduced to 37

Cougar Harvest by Month



Harvest by Month 2003-2018

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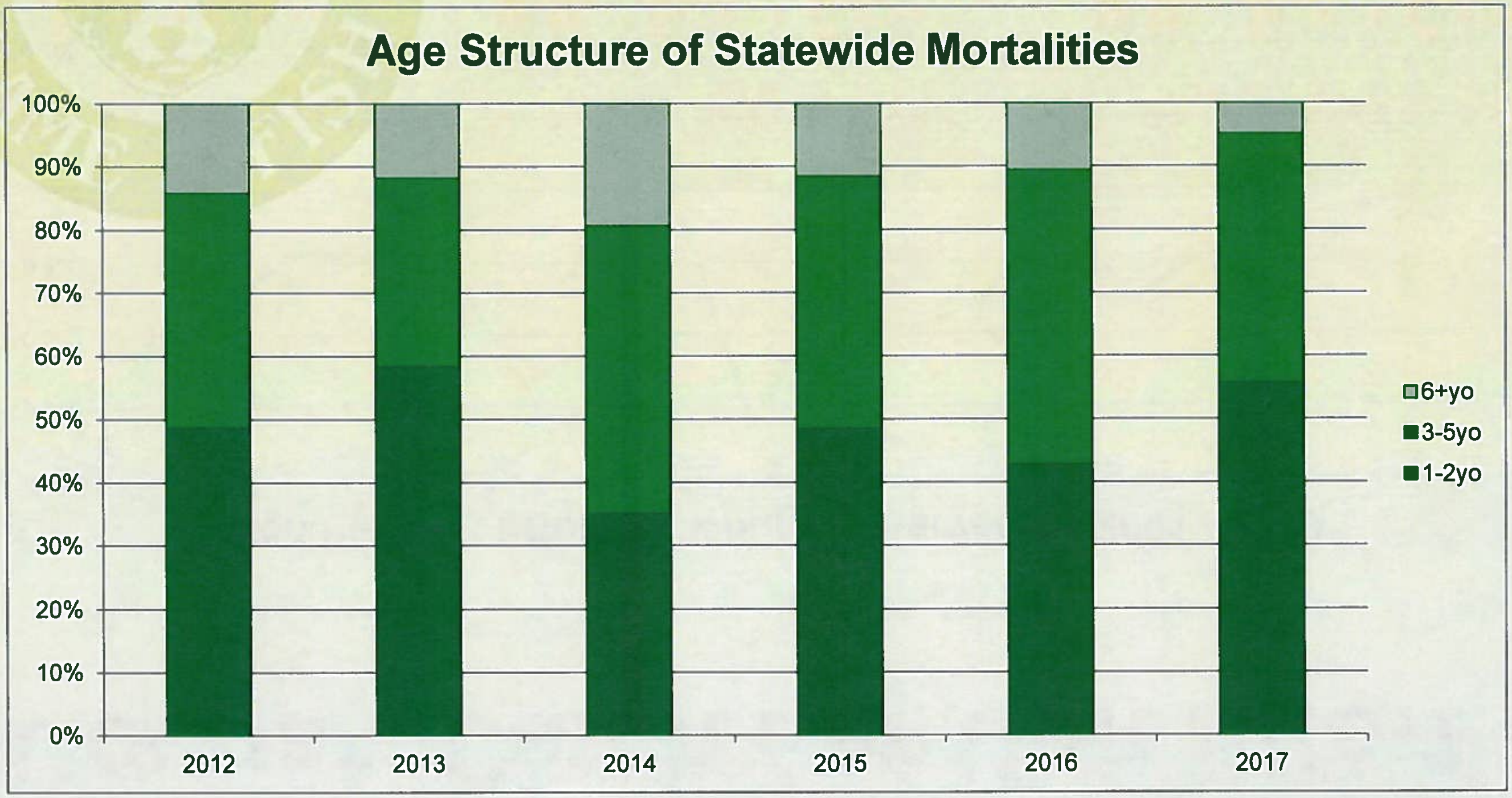
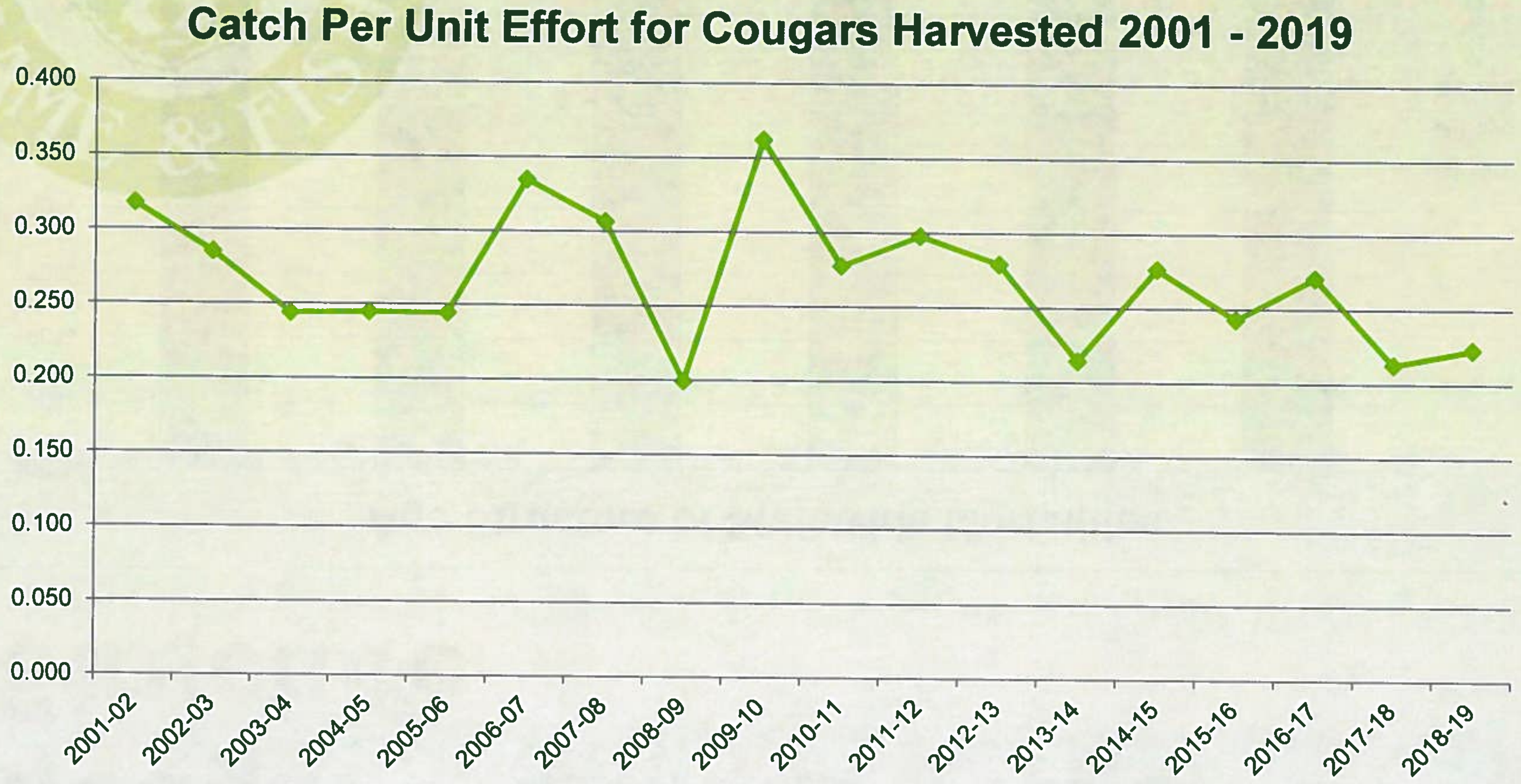
Cougar Population Age Structure

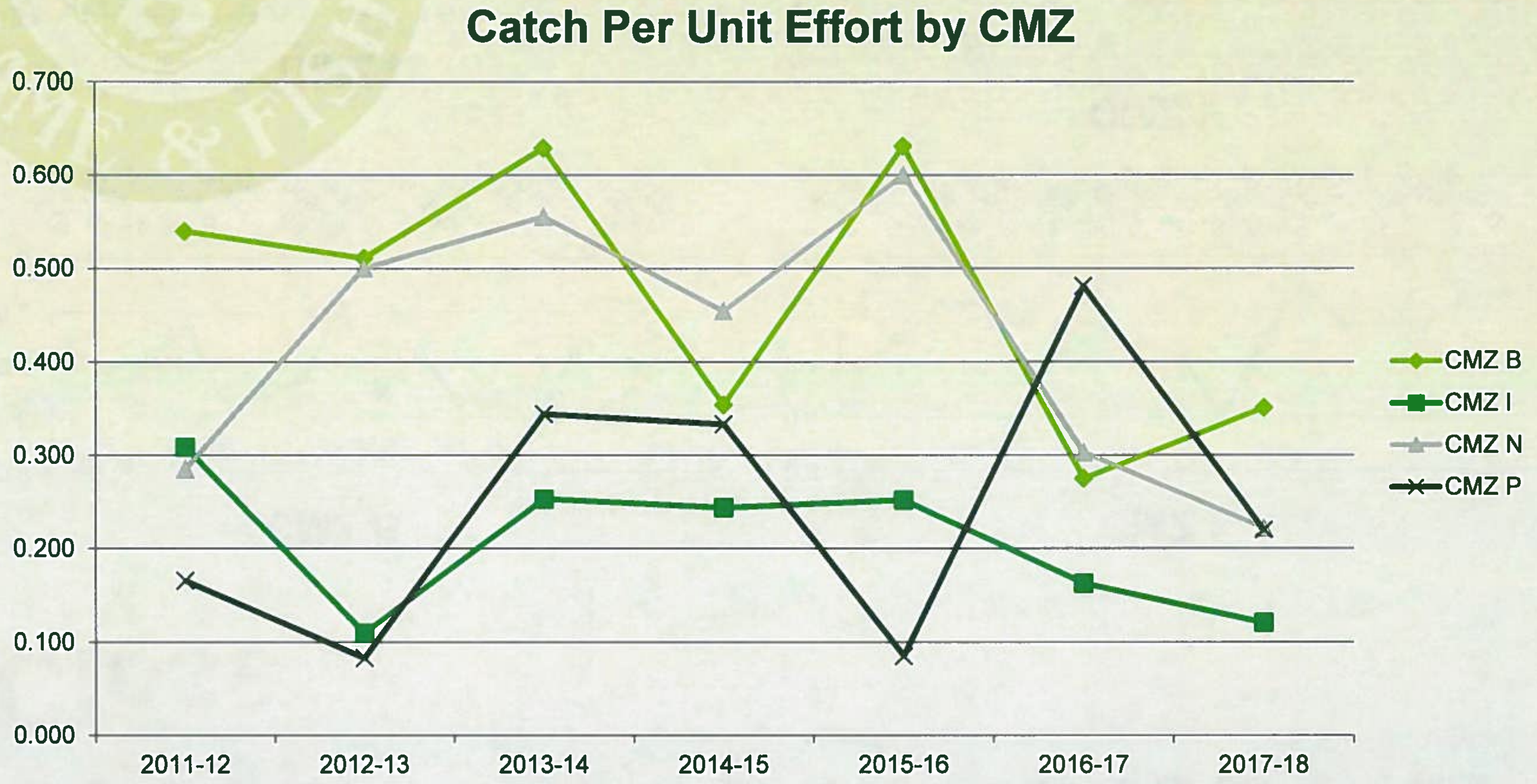

Age Structure of Statewide Mortalities

Cougar: Catch Per Unit Effort



Catch Per Unit Effort for Cougars Harvested 2001 - 2019

Cougar – CPUE in Zones that Close

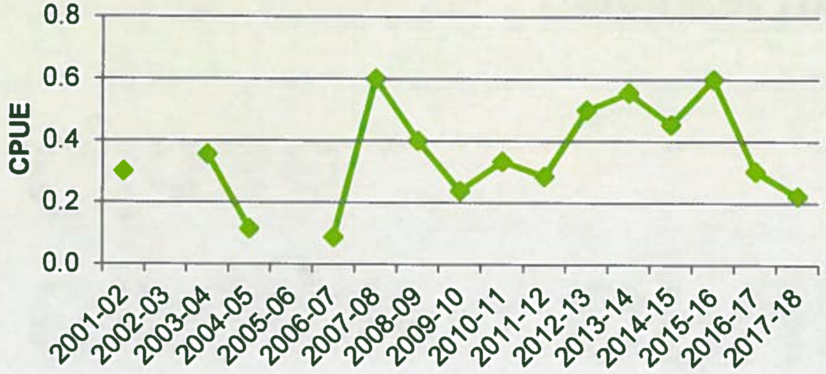


Cougar – CPUE in Zones that Close

CMZ B

CMZ I

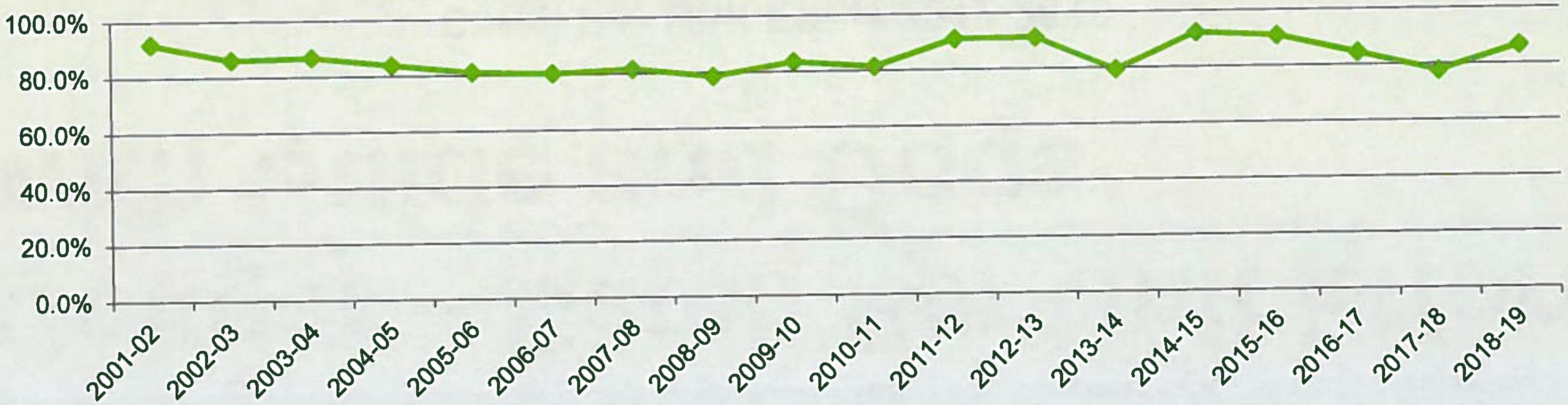
CMZ N



CMZ P

Cougar – Guided and/or with dogs


Proportion of Harvest by Guided Hunters 2001 - 2019


Proportion of Harvest through use of Hounds 2001 - 2019

Cougar – Catch Per Unit Effort with Guide and Dogs

Catch Per Unit Effort 2012-2019

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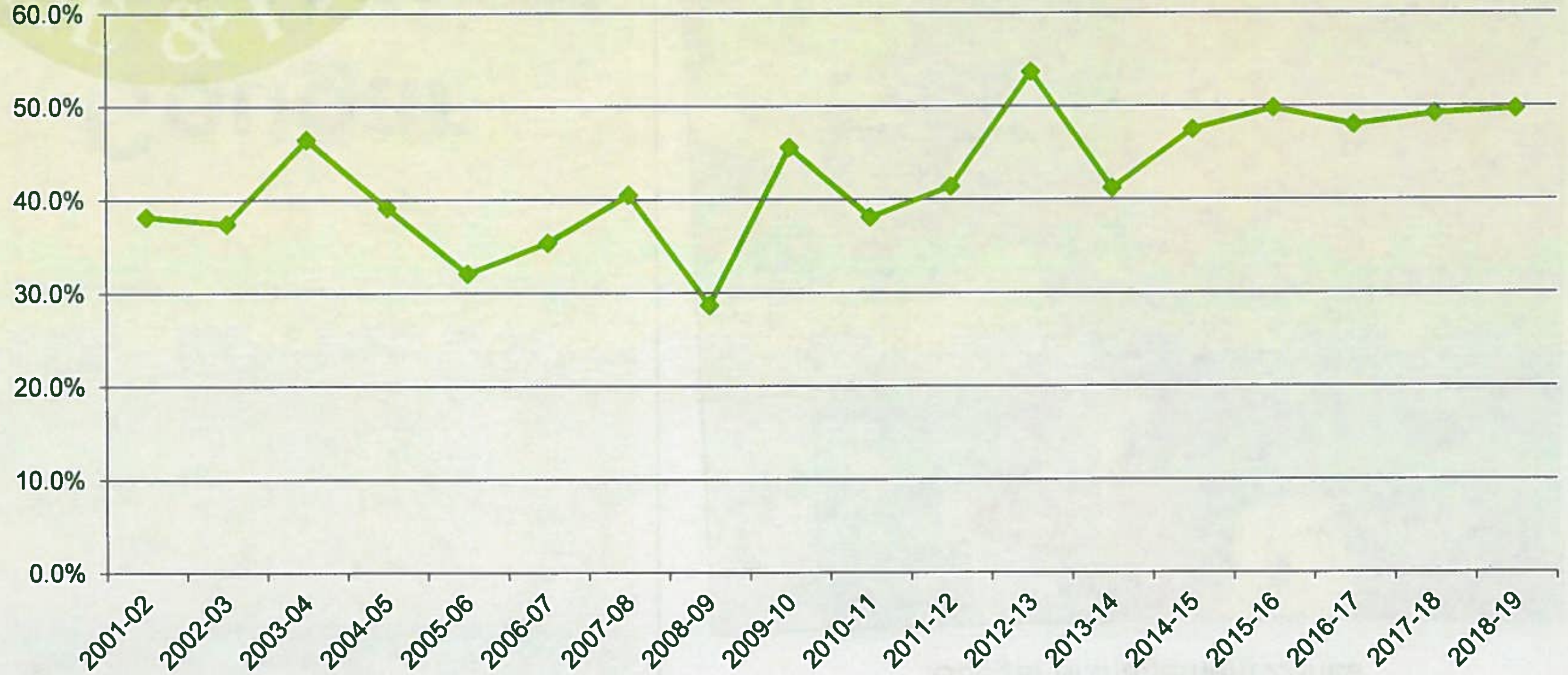
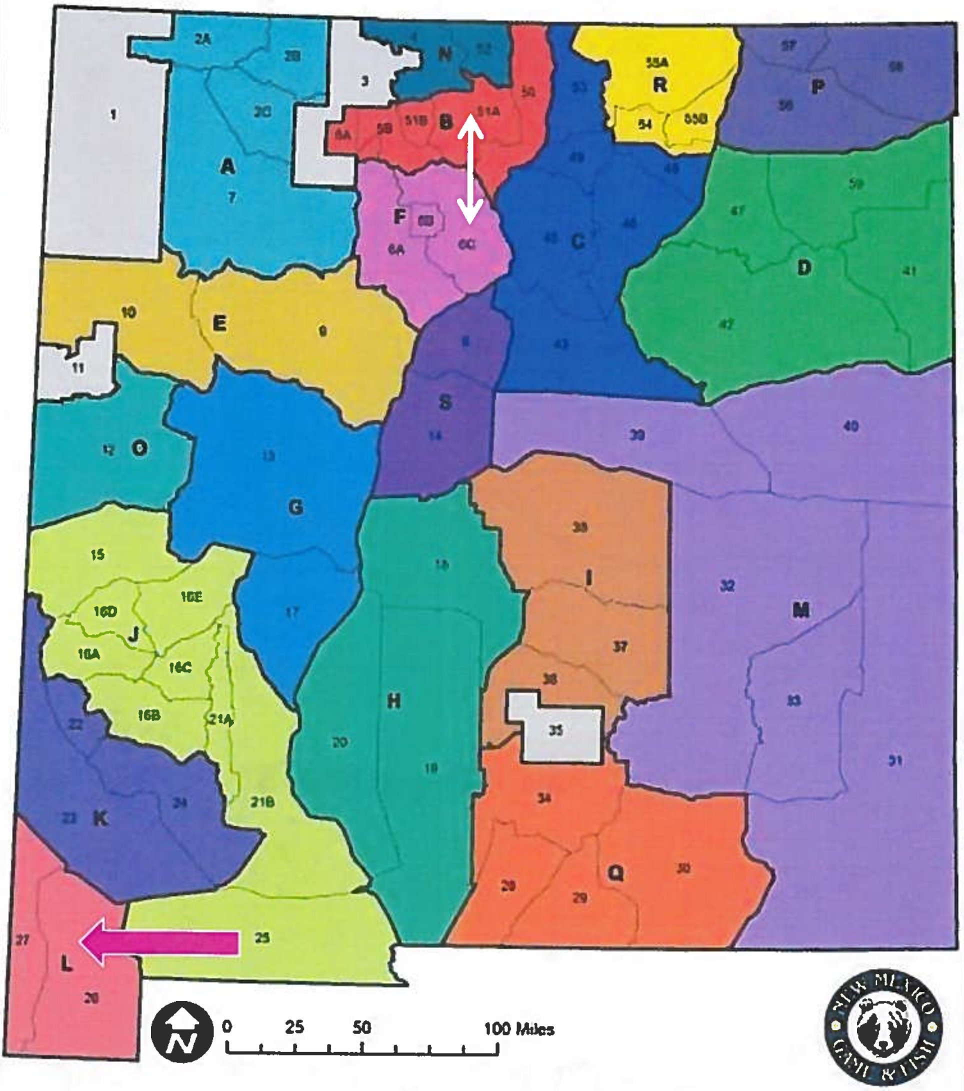
Cougar – Harvest by Non-Residents


Proportion of Harvest by Non-resident Hunters 2001 - 2019

Cougar Management Zone Boundaries

Cougar Management Zones



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Cougar Sport Harvest Limits

- No recommendation to increase maximum allowable harvest
- Harvest has been below the statewide harvest limit for the past 8 years
- Current harvest limits set 8 years ago
    - Recent data and user-group input suggest densities used to set those limits may be too high
- We are considering adjustments in some zones that will decrease limit

Cougar – Harvest both tags or additional tags

	2016	2017	2018
Harvested 2	13	22	23
Harvested > 2	2	1	4

Cougar Sport Harvest Limits

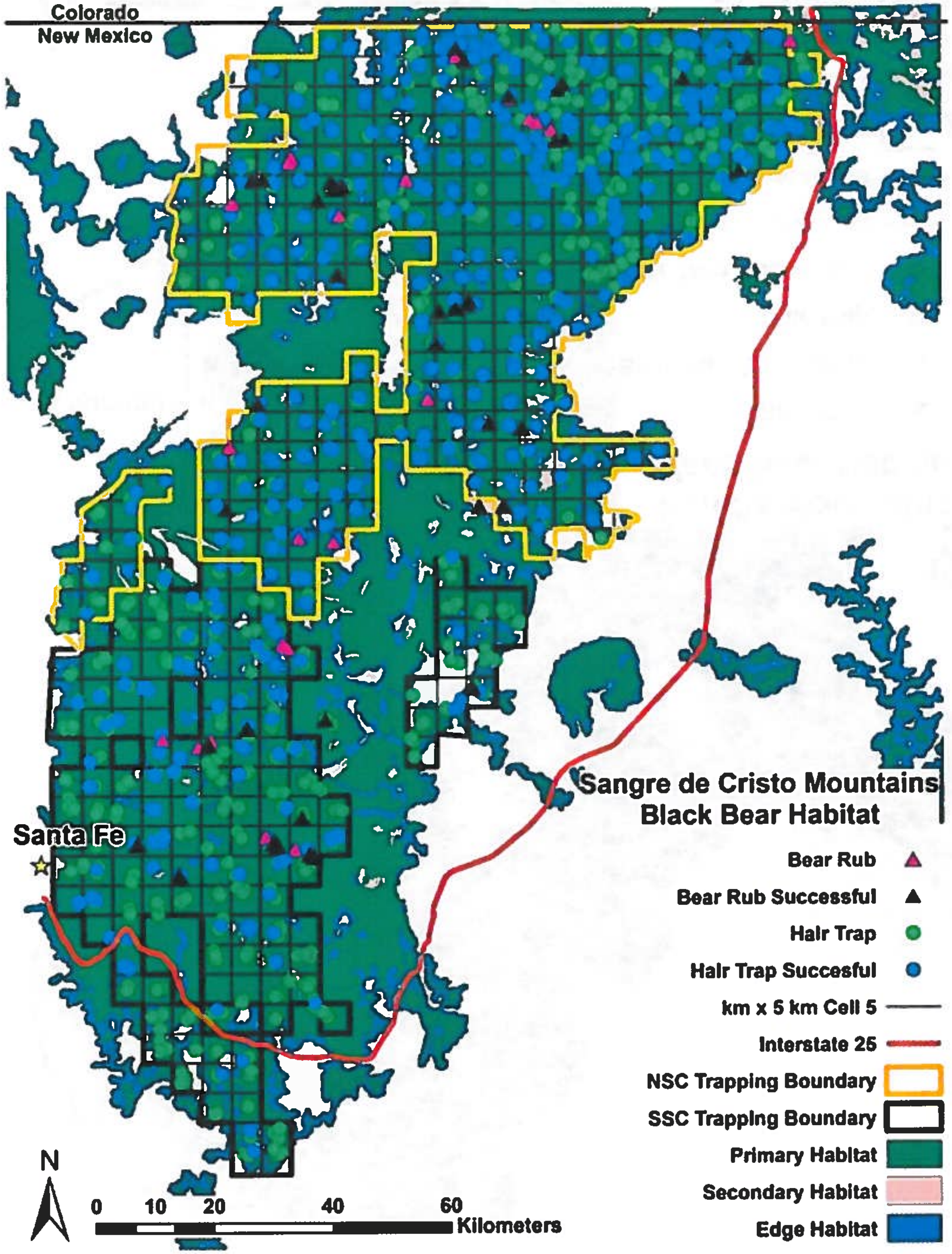
CMZ	Current Total Limit (Female Sub-limit)	Harvest Limit Proposal	Proposed Total Limit (Female Sub-limit)	Additional Proposals
A	42 (13)	No Change	42 (13)	
B	28 (9)	TBD	TBD	Combine with CMZ F
C	84 (42)	Change	57 (17)	
D	23 (11)	Change	15 (5)	
E	50 (15)	Change	42 (13)	
F	46 (23)	TBD	TBD	Combine with CMZ B
G	73 (37)	Change	50 (15)	
H	42 (21)	Change	29 (9)	
I	24 (7)	No Change	24 (7)	
J	89 (27)	Change*	84 (25)	GMU 25 moved to CMZ L
K	66 (33)	Change	45 (14)	
L	19 (10)	Change*	19 (6)	GMU 25 added
M	31 (9)	Change	25 (7)	
N	15 (5)	TBD	TBD	
O	21 (6)	Change	17 (5)	
P	14 (7)	No Change	14 (7)	
Q	34 (11)	No Change	34 (11)	
R	26 (8)	No Change	26 (8)	
S	25 (13)	Change	17 (5)	

*Change reflects the change in harvest limit as a result of added/subtracted GMU

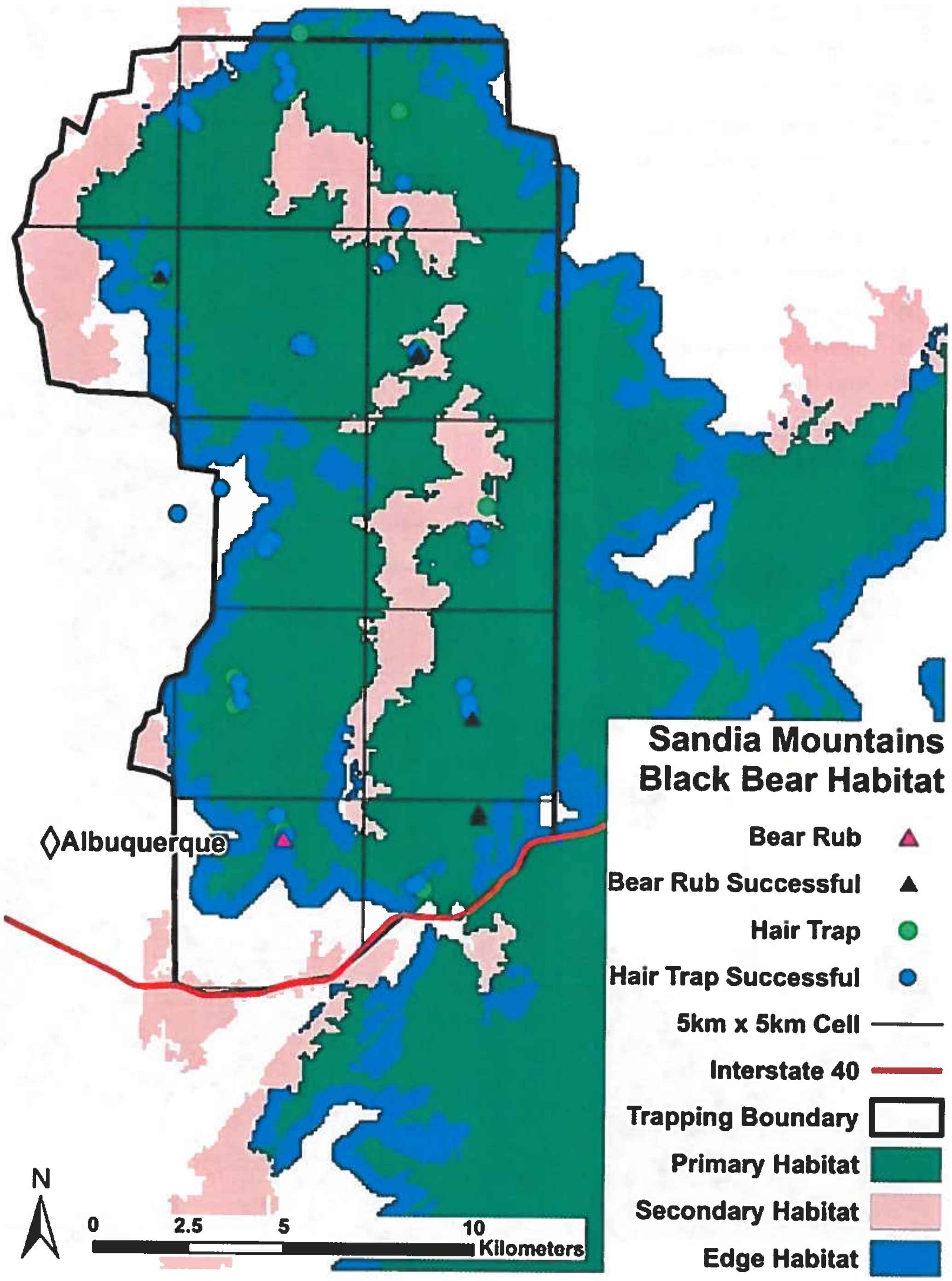
Rule Development Timeline

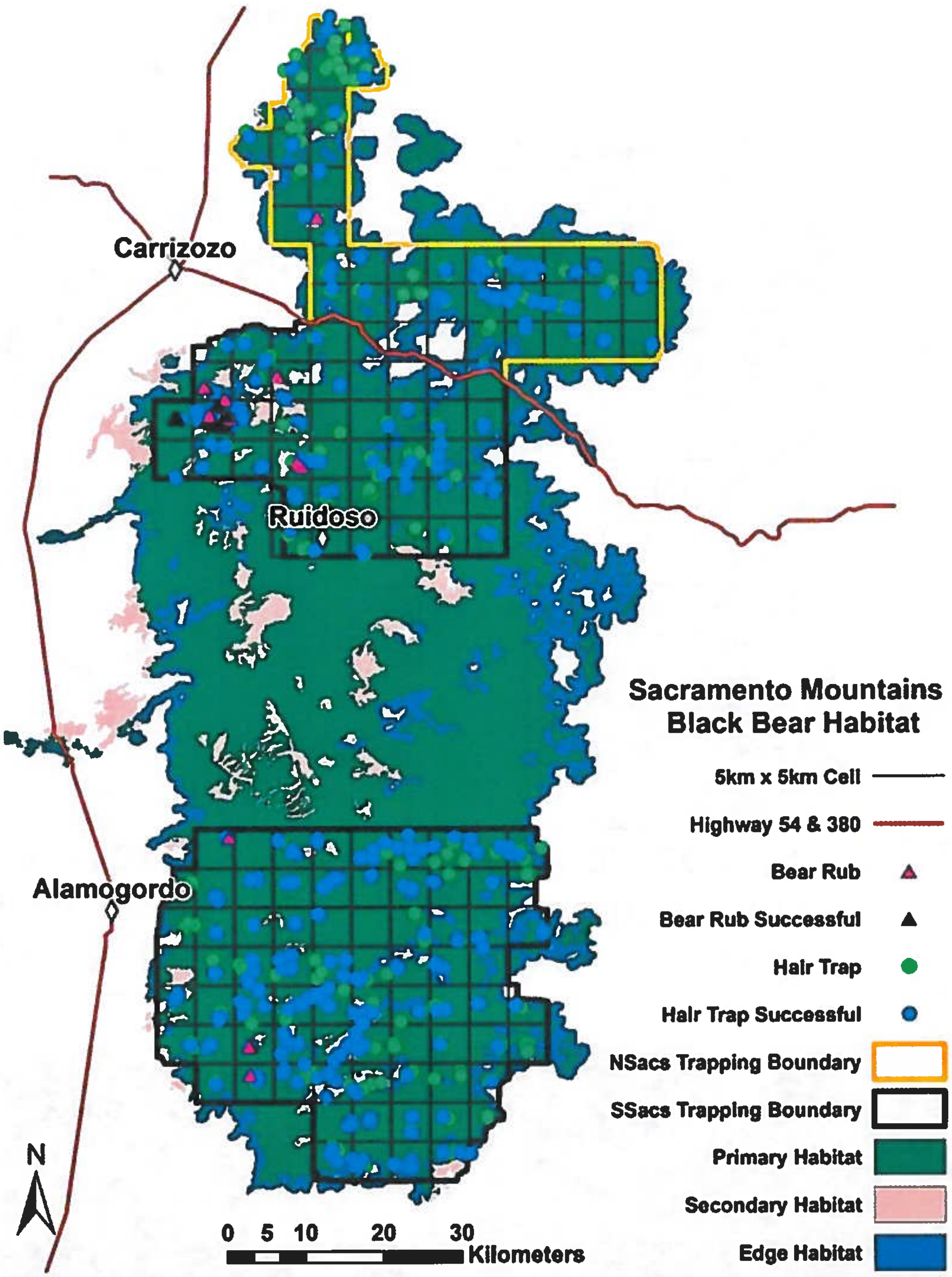
- **July, August, & September** – present at SGC meetings
- **July** – Initial NMDGF ideas posted on the website
- **August** – Public meetings throughout the state
- **Early October** - Final NMDGF proposed rule posted on the website
- **November 21st** – Act on rule

Wildlife Management Division

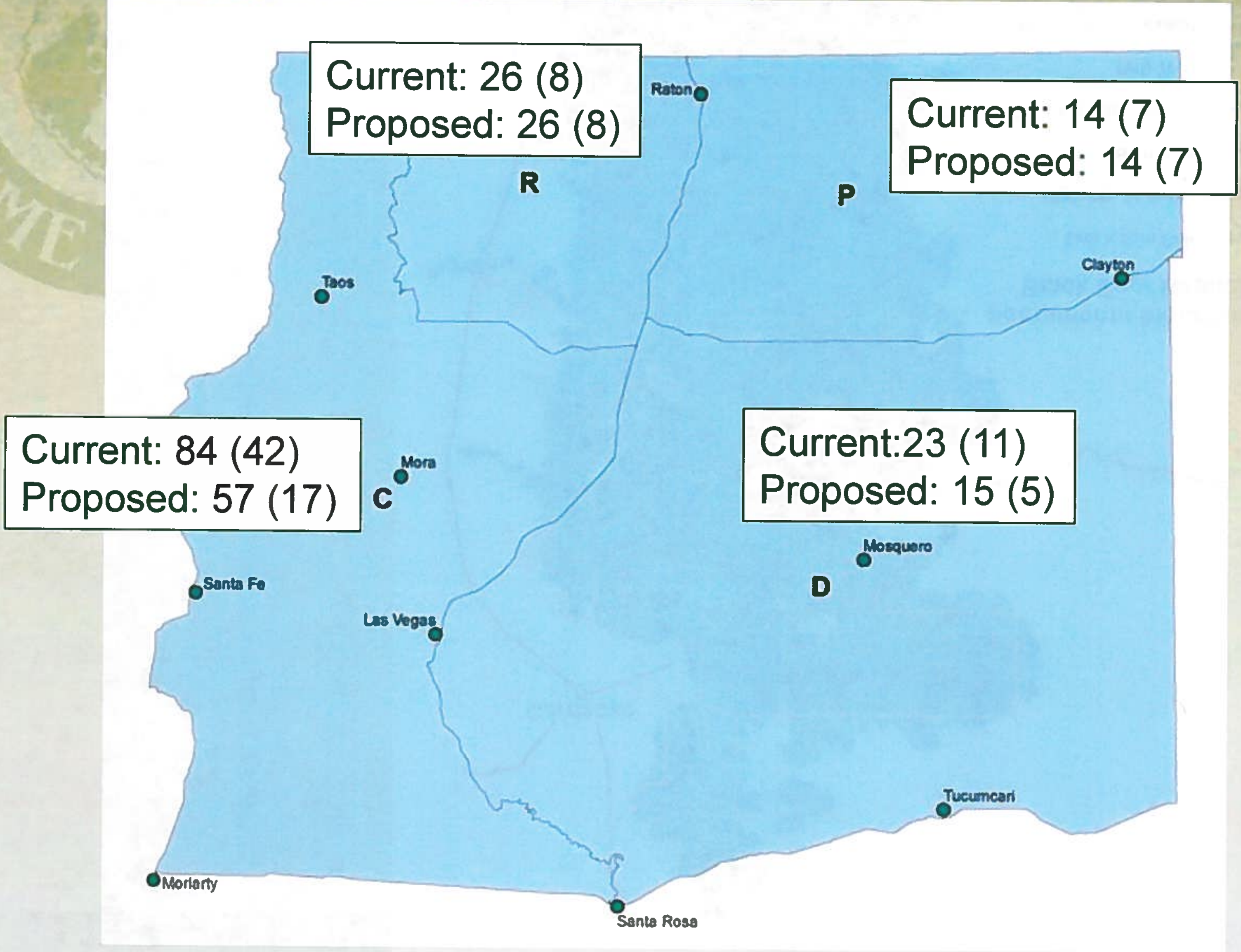


Sangre de Cristo Mountains
Black Bear Habitat
Colorado
New Mexico
Santa Fe
N
0
10
20
40
60
Kilometers
Bear Rub 🔺
Bear Rub Successful ▲
Hair Trap ●
Hair Trap Successful ●
km x 5 km Cell 5
Interstate 25
NSC Trapping Boundary
SSC Trapping Boundary
Primary Habitat
Secondary Habitat
Edge Habitat


Sandia Mountains
Black Bear Habitat
Bear Rub
Bear Rub Successful
Hair Trap
Hair Trap Successful
5km x 5km Cell
Interstate 40
Trapping Boundary
Primary Habitat
Secondary Habitat
Edge Habitat
Albuquerque
N
0
2.5
5
10
Kilometers


Carrizozo
Ruidoso
Alamogordo
N
0 5 10 20 30 Kilometers
Sacramento Mountains
Black Bear Habitat
5km x 5km Cell
Highway 54 & 380
Bear Rub
Bear Rub Successful
Hair Trap
Hair Trap Successful
NSacs Trapping Boundary
SSacs Trapping Boundary
Primary Habitat
Secondary Habitat
Edge Habitat

Cougar Sport Harvest Limits



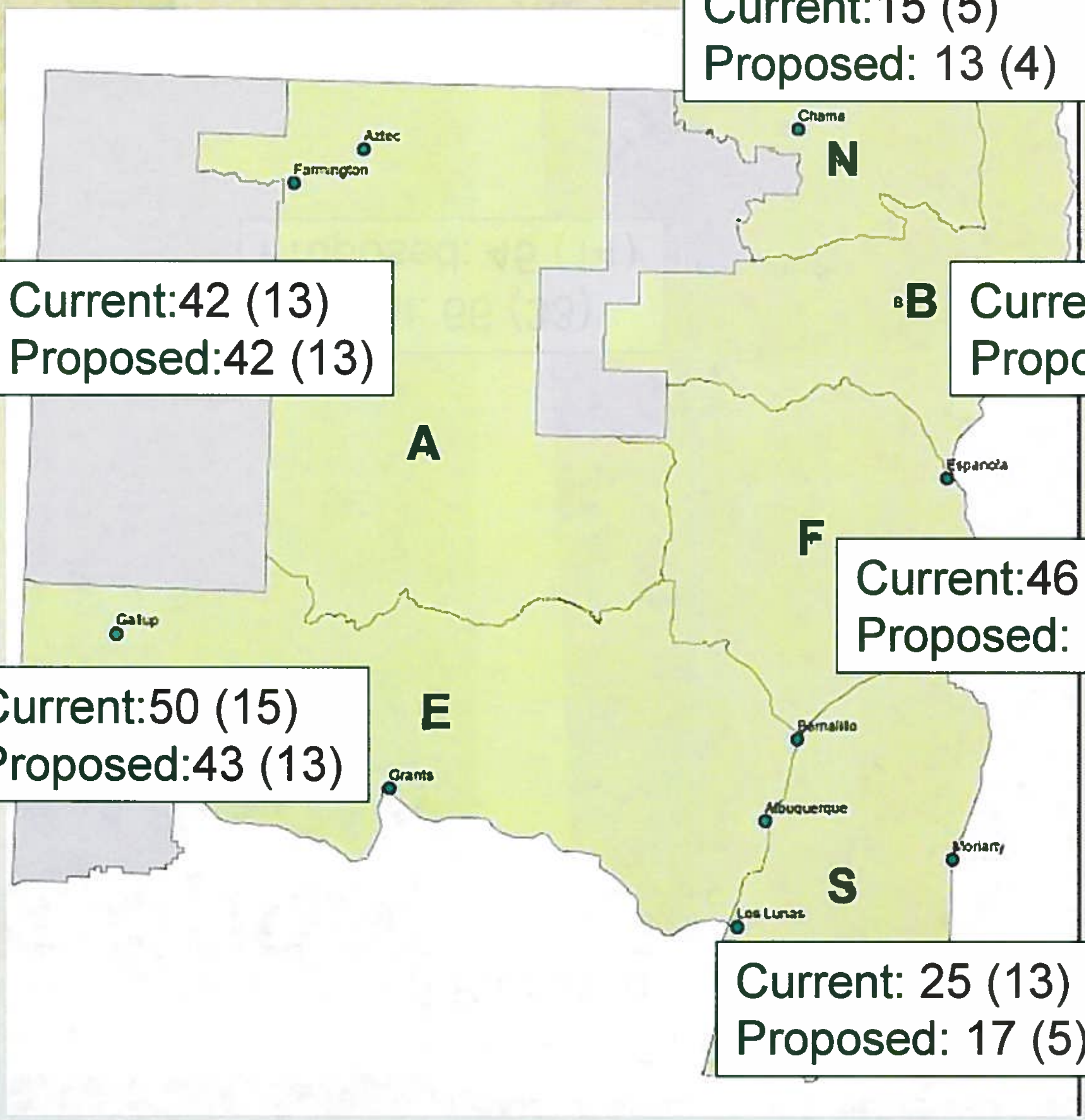
Current: 26 (8)
Proposed: 26 (8)

Current: 14 (7)
Proposed: 14 (7)

Current: 84 (42)
Proposed: 57 (17)

Current:23 (11)
Proposed: 15 (5)

Cougar Sport Harvest Limits



Current:15 (5)
Proposed: 13 (4)

Current:42 (13)
Proposed:42 (13)

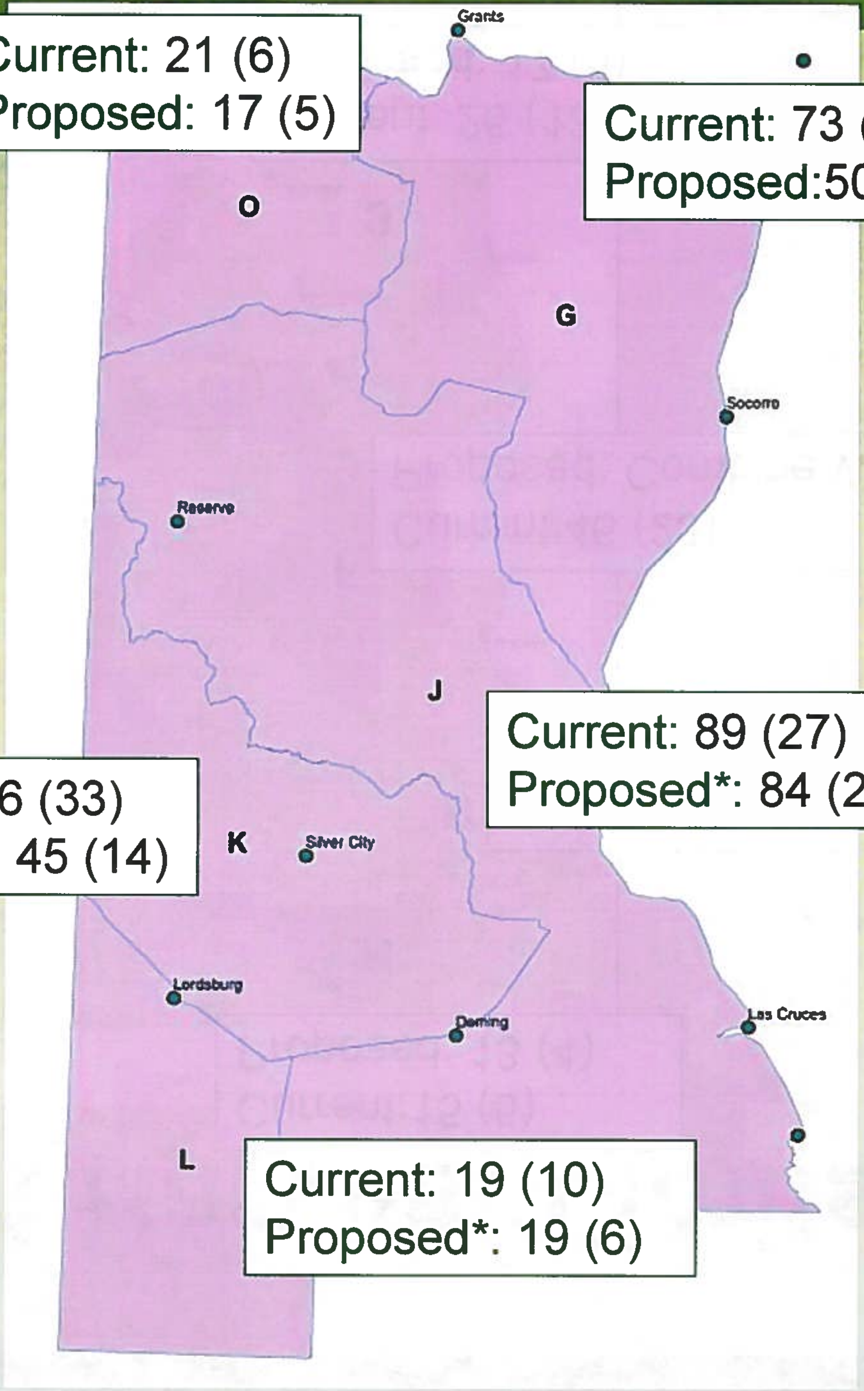
Current:28 (9)
Proposed: 25 (8)

Current:46 (23)
Proposed: Combine With B

Current:50 (15)
Proposed:43 (13)

Current: 25 (13)
Proposed: 17 (5)

Cougar Sport Harvest Limits



Current: 21 (6)
Proposed: 17 (5)

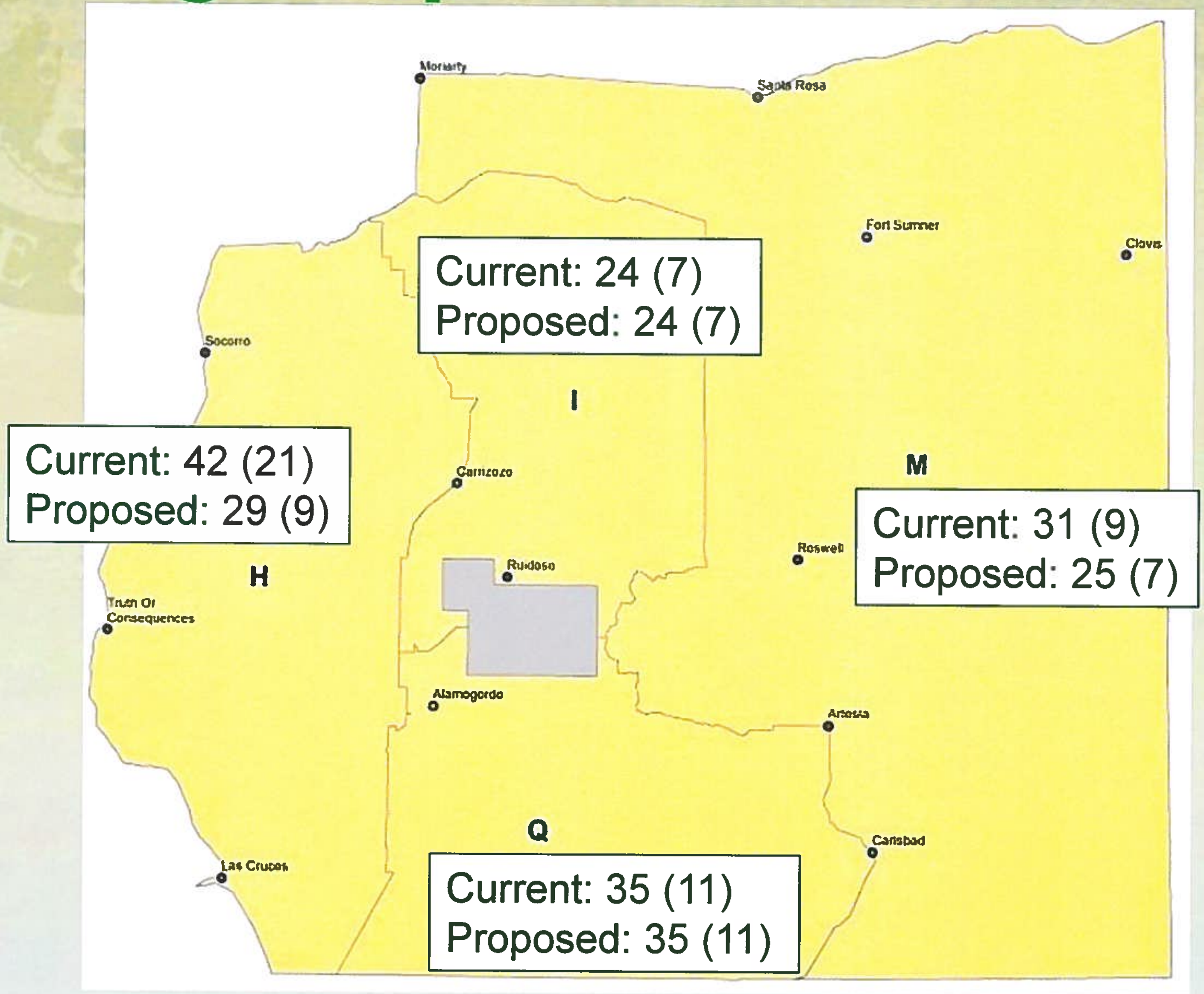
Current: 73 (37)
Proposed:50 (15)

Current: 89 (27)
Proposed*: 84 (25)

Current: 66 (33)
Proposed: 45 (14)

Current: 19 (10)
Proposed*: 19 (6)

Cougar Sport Harvest Limits



Current: 24 (7)
Proposed: 24 (7)

Current: 42 (21)
Proposed: 29 (9)

Current: 31 (9)
Proposed: 25 (7)

Current: 35 (11)
Proposed: 35 (11)

Wildlife Management Division

NMDGF
BEAR & COUGAR ROLE
DEVELOPMENT 2019
- TECHNICAL INFORMATION -

EXHIBIT
5

Experimental Evaluation of Population Trend and Harvest Composition in a Wyoming Cougar Population
Author(s): Charles R. Anderson, Jr. and Frederick G. Lindzey
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Experimental evaluation of population trend and harvest composition in a Wyoming cougar population

Charles R. Anderson, Jr. and Frederick G. Lindzey

Abstract Cougar (*Puma concolor*) management has been hindered by inability to identify population trends. We documented changes in sex and age of harvested cougars during an experimentally induced reduction in population size and subsequent recovery to better understand the relationship between sex–age composition and population trend in exploited populations. The cougar population in the Snowy Range, southeast Wyoming, was reduced by increased harvest (treatment phase) from 58 independent cougars (>1 year old) (90% CI=36–81) in the autumn of 1998 to 20 by the spring of 2000 (mean exploitation rate=43%) and then increased to 46 by spring 2003 following 3 years of reduced harvests (mean exploitation rate=18%). Pretreatment harvest composition was 63% subadults (1.0–2.5 years old), 23% adult males, and 14% adult females (2 seasons; *n*=22). A reduction in subadult harvest, an initial increase followed by a reduction in adult male harvest, and a steady increase in adult female harvest characterized harvest composition trends during the treatment phase. Harvest composition was similar at high and low densities when harvest was light, but proportion of harvested subadult males increased at low density as they replaced adult males removed during the treatment period (high harvest). While sex ratio of harvested cougars alone appears of limited value in identifying population change, when combined with age class the 2 appear to provide an index to population change. Composition of the harvest can be applied to adaptively manage cougar populations where adequate sex and age data are collected from harvested animals.

Key words adaptive management, cougar, exploitation, population trend, *Puma concolor*, sex–age composition

Several authors have noted the need for reliable techniques to adequately monitor cougar population changes (e.g., Shaw 1981, Lindzey 1991, Anderson et al. 1992, Riley 1998). While populations have been monitored with long-term, intensive capture efforts over relatively small areas (Ashman et al. 1983, Anderson et al. 1992, Ross and Jalkotzy 1992, Lindzey et al 1994, Logan and Sweanor 2001), reliable and affordable techniques to monitor population trends for large-scale management programs remain elusive.

Cougar management traditionally has employed harvest levels to achieve specific population objectives with little understanding of the quantitative effect that differing harvest levels have on cougar population demographics. Sex and age classes of cougars exhibit different and relatively predictable movement patterns (Barnhurst 1986). These differences, in turn, presumably expose each group to differing risks of being harvested. This concept has been applied to managing black bear (*Ursus americanus*) populations in many western states

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(Garshelis 1990). Barnhurst (1986) investigated the vulnerability of cougars to sport hunting as a step toward understanding how to interpret harvest data. He proposed that vulnerability to harvest would be related to the frequency at which differing sex- and age-class cougars cross roads because cougars are generally hunted using trailing hounds, typically from roads or trails. The vulnerability index he developed from road-crossing frequencies suggested that transient males were most vulnerable, followed by resident males, transient females, resident females both without young and with young >6 months old, and finally resident females with young ≤6 months old.

Conceptually, the likelihood of a specific sex or age class of cougar being harvested would reflect its relative abundance in the population multiplied by its relative vulnerability. The least-vulnerable individuals should become prominent in the harvest only after the population had been reduced in size by removal of more vulnerable cougars. Our objective was to test the hypothesis that sex and age composition of the harvest would vary predictably with population size in a cougar population primarily hunted using hounds.

Study areas

Experimental population

The Snowy Range, located in southeast Wyoming about 30 km west of Laramie, was a 2,760-km^2 timbered region including a 2,170-km^2 portion of the Medicine Bow National Forest surrounded by private, Bureau of Land Management, and state-owned lands. This terminal mountain range was surrounded by sagebrush (*Artemisia tridentata*) grasslands except on the southern end, where it was connected to contiguous habitat by a 14-km-wide segment of the Medicine Bow Mountains. Cougars occupied about 1,700 km^2 of this area during winter. Wyoming State Highway 230 on the west, United States Interstate 80 on the north, the Laramie River and Sand Creek drainages on the east, and Colorado highways 125 and 127 on the south bounded the Snowy Range. The area was topographically diverse, ranging in elevation from about 2,100 m in the valleys to 3,652 m at Medicine Bow Peak. Vegetation communities were dominated by sagebrush grasslands in the peripheral valleys; lodgepole pine (*Pinus contorta*) stands with interspersed quaking aspen (*Populus tremuloides*), Rocky Mountain juniper (*Juniperus scopulorum*), and limber pine (*Pinus flexilis*) at mid-elevations; and Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) forests with occasional limber pine at higher elevations (Alexander et al. 1986). Understory dominants in the mid- and high-elevation communities included huckleberry (*Vaccinium scoparium*), buffalo berry (*Shepherdia canadensis*), serviceberry (*Amelanchier alnifolia*), snowberry (*Symphoricarpos* spp.), and common juniper (*J. communis*). Riparian areas were composed primarily of willow (*Salix* spp.) with interspersed narrowleaf cottonwood (*P. angustifolia*) at low elevations.

Abundant roads provided good access to most cougar habitat in the Snowy Range. Annual harvest was relatively constant during the 5 years before our study, ranging from 9-12 cougars.

Comparison population

The northern portion of the Laramie Range included an isolated mountain range near the cities of Casper and Wheatland in southeast Wyoming and encompassed 2,960 km^2 of timbered habitat. Elevation ranged from 1,620 m in the eastern valleys to 3,132 m at Laramie Peak. Ponderosa pine (*P. ponderosa*) stands dominated low to mid elevations, with lodgepole pine common at mid to high elevations. Low-elevation, nonforested regions and interspersed meadows were vegetated by grasses, forbs, and shrubs. Riparian areas consisted primarily of willow with occasional aspen pockets. Other forest species occurring at low levels included limber pine, subalpine fir, Douglas-fir (*Pseudotsuga menziesii*), and Engelmann spruce.

Annual harvest in Laramie Peak averaged 11 cougars during the 5-year period before harvest treatment, ranging from 7-16 cougars per year. The Wyoming Game and Fish Department changed its management objective from sustained harvest of a stable to increasing population to reducing the population through increased harvest in 1996 and increased harvest quotas from 10 to 34 for the next 7 seasons. Regional Wyoming Game and Fish Department personnel believed the Laramie Peak cougar population was at a relatively high density prior to 1996 based on increased cougar sightings, depredation incidents, and hunter interviews.

Methods

We trailed cougars using hounds and immobilized them upon capture with a mixture of 5 mg/kg

Telazol® (Aveco Co., Inc., Cherry Hill, N.J.) and 1 mg/kg xylazine hydrochloride delivered in a hypodermic dart fired from a CO_2 pistol; we reversed the effects of xylazine hydrochloride using yohimbine hydrochloride (0.15 mg/kg). We tagged independent cougars (>1 year old and solitary) with standard VHF radiocollars (Model 9D, warranty battery life=3 years) and dependent young with 22-g ear-tag transmitters (Model 7PN, warranty battery life=295 days; Advanced Telemetry Systems, Inc., Isanti, Minn.); we equipped transmitters with mortality-sensing options. We also attached a uniquely numbered ear tag to all captured cougars. We recorded sex, age, weight, and morphometric measurements at capture. We estimated age (juvenile <1 year, subadult 1-2.5 years, adult ≥3 years) from tooth wear, canine ridge eruption, spotting progression, and evidence of previous lactation for females (Shaw 1979, Ashman et al. 1983, Lindzey et al. 1989, Laundre et al. 2000) or known birth date for cougars born to radiocollared females based on female denning behavior. We located radiotagged cougars weekly from fixed-wing aircraft between December 1997 and May 2001 and once per month from June 2001-April 2003.

We used radiotelemetry to identify female denning behavior (consecutive locations at the same location), timing of family breakup, and emigration of subadults. We assumed emigration when an individual dispersed from its mother, had not yet exhibited territorial behavior, and we were no longer able to detect its radio signal. We estimated age of juveniles of unknown birth date by applying the growth-curve models developed in the Northern Great Basin (Laundre and Hernandez 2002) after adjusting them for differences detected when comparing model estimates to size of known-age juveniles in the Snowy Range (C. R. Anderson, unpublished data).

Experimental design

We manipulated size of the Snowy Range cougar population using regulated hunter harvest to reduce and then allow recovery of the population; all cougars harvested during the study except 2 were taken using hounds. The cougar-hunting season was open from 1 September-31 March, but most cougar harvest did not occur until mid-November, when snow conditions were adequate for tracking cougars using trained hounds; >90% of cougars harvested in Wyoming were taken using hounds (Wyoming Game and Fish Department 2003). Annual harvest levels were regulated by a quota system in which the season was closed if the quota was met before 31 March. Young (<1 year old) cougars and females with young at side were legally protected from harvest. We concurrently monitored sex and age composition of the population and the harvest and annually tested predictions of harvest composition based on abundance of sex- and age-class cougars in the population and their relative harvest vulnerability (Barnhurst 1986). We predicted that harvest composition would be predominantly subadults (possibly more females) during the pretreatment year (high density, low harvest), shift to adult males during the first year of treatment (from high to moderate density, high harvest), shift from adult males to adult females during the second treatment year (from moderate to low density, high harvest), and return to subadults during the post-treatment period (increasing population, low harvest) where the subadult segment would initially consist primarily of males and eventually consist primarily of females as the population approached pretreatment levels. We examined annual changes in harvest composition of adult males, adult females, and subadults using the Fisher's exact test; we applied 1-tailed tests to compare the first 4 seasons where changes were predicted and 2-tailed tests to examine the recovery period when composition was not expected to change greatly. We also examined the relationship between proportion of adults in the female harvest and estimated harvest rate using simple linear regression analysis, expecting adult female harvest composition to increase with harvest level.

We then compared harvest composition documented in the Snowy Range to that observed in Laramie Peak. Although we did not monitor density in this area, it represented a geographic population (i.e., occupied cougar habitat surrounded by inhospitable, unoccupied landscapes) similar to the Snowy Range, contained a similar amount of cougar habitat, had adequate hunter access to facilitate population reduction, and the population was exposed to harvest levels similar to those we applied in the Snowy Range before and during the treatment period. We assumed that harvest composition from this area would show similar trends to those documented in the Snowy Range if harvest composition changed predictably with population size in harvested populations. We tested for differences in annual harvest composition between populations using the Fisher's exact test (2-tailed). We also determined ages from counts of cementum annuli of harvested adult females in both populations to determine whether age of adult females declined as the population declined following high harvest levels.

Age-class estimates

We assigned harvested and captured cougars to age class based on tooth wear, presence or absence of a canine ridge, evidence of spots or foreleg bars, evidence of previous lactation if female (Anderson and Lindzey 2000), and counts of bands in the cementum of premolars removed from harvested cougars. We first gave priority to evidence of previous lactation in females (subadult: nipples white and ~4-6 mm wide; adult: nipples dark or mottled and ~8-10 mm wide), followed by annuli age (subadult = 1-2 yr), canine ridge eruption (absent = subadult), and finally foreleg bars (dark = subadult or young adult) and spots (present = subadult or young adult). To evaluate reliability of our aging techniques, we compared ages estimated from counts of cementum bands to ages estimated with the other criteria for those cougars that were captured and later harvested.

Population estimates

During the first winter (Dec 1997-Apr 1998), we conducted intensive capture efforts in 2 regions of the Snowy Range to obtain an initial density estimate and to create a marked sample for subsequent mark-recapture efforts. We captured cougars in a 439-km^2 area in the southeast region and a 382-km^2 area in the west-central region of the Snowy Range; 90% of cougar harvests in the Snowy Range came from these primarily public land areas (Wyoming Game and Fish Department mountain lion harvest data base, Lander, Wyo.). We estimated density for the 2 areas by summing number of cougars marked and tracks of known, unmarked cougars. We included unmarked cougars only if track characteristics (identified as male or female via planter pad width and stride length; Fjelline and Mansfield 1988) and number and size of young accompanying a female suggested a unique individual and when tracks were located outside traditional use areas of radiocollared cougars identified from previous telemetry locations. The initial density estimates from the 2 areas were then applied to the remainder of cougar habitat in the Snowy Range to estimate population size for the study area. Cougar habitat was delineated using elevations and topography used by radiocollared cougars February-April, 1998.

We applied the Lincoln-Peterson estimator (Pollock et al. 1990) to calculate annual, pre-hunting-season (autumn) population estimates of independent cougars. Post-hunting-season (spring) population estimates were pre-season estimates minus harvest removals and estimated natural mortality from our marked sample. We attempted to meet assumptions of the technique by modifying our sampling design and using information from radiotagged cougars. We addressed geographic closure by recapturing during late autumn and winter months when emigration and immigration were least likely (Ross and Jalkotzy 1992). We addressed the demographic closure assumption by adjusting for deaths based on records from radiocollared cougars and by considering young cougars in our marked sample independent at the mean age family groups became loosely associated (prior to dispersal), and thus available for recapture (e.g., harvest), by the beginning of the recapture period (15 Nov, average date of sufficient snow for hunting). Because cougar captures relied heavily on adequate snow conditions for tracking that varied temporally and spatially, maintaining equal capture effort throughout the study area was not possible and reduced our ability to assure equal capture probabilities across cougars. To minimize potential biases from capture heterogeneity and provide sufficient time to sample the entire study area, we treated the entire winter sampling period (15 Nov-31 Mar) as a single capture effort and counted each individual detected only once in the recapture sample regardless of the number of times they were actually detected. Because captured cougars remained ear-tagged throughout the study but transmitter failures occasionally occurred, we assumed individuals that had established territories prior to transmitter failure and that had been monitored until the previous summer were still in the population and available during the following winter recapture period; on 10 of 12 occasions where transmitters failed, marked residents were subsequently recaptured or harvested.

The capture sample was independent, radiotagged cougars in the population at the beginning of the recapture sampling period (15 Nov) during both treatment and recovery periods. The recapture sample was cougars harvested by hunters during the hunting seasons of the treatment periods, but, because harvests were intentionally reduced during the recovery period (winters of 2000-2001, 2001-2002, and 2002-2003), we augmented the recapture sample by hunting the study area after hunters had finished. During our hunting we tagged and released unmarked cougars, recorded marked cougars recaptured, and recorded presence of individual, unmarked cougars (defined earlier) we were unable to capture. We included cougars marked in the population prior to 15 November each year in our initial capture sample and those captured from 15 November-31 March in our recapture sample. We recorded capture effort as number of hunter days for successful hunters (no data for unsuccessful hunters) and number of days spent tracking and capturing cougars by study personnel. Post-season population estimates were pre-season estimates minus harvest and mortality from other causes estimated from our marked sample during the recapture period. We estimated 90% confidence intervals around pre-season population estimates following Pollock et al. (1990). We estimated autumn sex and age composition of the population by adding unmarked cougars harvested during that year's hunting season to our sample of marked cougars.

Results

We tagged 16 independent and 13 dependent male and 17 independent and 15 dependent female cougars between December 1997 and February 2002. Twenty-one marked, independent cougars were harvested during the treatment and recovery phases of the project, and 9 marked cougars (5 adult males, 4 adult females) were alive at the end of the study. Cougar ages estimated using cementum annuli counts were in agreement with other aging criteria in 14 of 18 comparisons and within 1 year for 3 others (Anderson 2003). We noted that ages of dependent young of known birth date in the Snowy Range were consistently underestimated ($\bar{x}$ = 1.47 mo, SD = 1.26, n = 13) using the Northern Great Basin growth-curve models (Laundre and Hernandez 2002) and therefore added the mean difference to estimate ages for litters of unknown birth date.

Dependent cougars became independent at an average age of 14 months (range = 11-17 months, n = 7); 2 litters became independent following the death of their mother at 14 and 17 months old (1 natural, 1 harvest). Association among family members became progressively looser over the month before independence. Thus, to account for recruitment in our recapture sample, we included marked dependent young as subadults if they were 13 months of age by 15 November each season. Emigration occurred between April and September for 8 of 9 emigrants monitored; 1 subadult male emigrated during January.

Population estimates

We tagged 18 cougars in the study area and identified 6 others from tracks after 60 days of trapping and tracking in the southeast and 45 days in the west-central section of the Snowy Range during winter 1997-1998. We estimated independent cougar density at 3.42/100 km^2 in the southeast (15 cougars/439 km^2 × 100) and 2.35/100 km^2 in the west-central region (9 cougars/383 km^2 × 100). Cougar habitat in the Snowy Range during this period, estimated from characteristics of habitat used by marked cougars February-April 1998, was 1,720 km^2. We estimated 50 independent cougars in the Snowy Range in spring 1998 (45-55 depending on the density estimate applied). A harvest quota of 25 was then set for the next 2 hunting seasons (treatment; 1998-1999 and 1999-2000) to elicit the desired (about 50%) reduction in the Snowy Range cougar population.

Harvests were 25 and 17 cougars for the 2 treatment seasons, resulting in an estimated population of 20 independent cougars by spring 2000 (Table 1). Harvest quotas were then reduced to 6-8 cougars per season to facilitate population recov-

Table 1. Pre (autumn) and post-harvest (spring) cougar population estimates[a] from the Snowy Range, Wyoming, USA, autumn 1998–spring 2003. Note population decline following 2 years of high harvest and population increase following 3 years of light harvest.

Season	n_1	n_2	m_2	$\hat{n}_{pre}$ (90% CI)	No. harvested	% natural mortality	$\hat{n}_{post}$
1998/99	15	25	6	58 (36–81)	25	11	30
1999/00	19	17	8	39 (28–50)	17	9	20
2000/01	15	21	9	34 (26–42)	8	0	26
2001/02	15	25	10	37 (29–44)	6	0	31
2002/03	11	39	7	59 (42–76)	8	9	46

[a] $\hat{n}_{pre} = [(n_1 + 1)(n_2 + 1) / (m_2 + 1)] - 1$, where n_1 = number marked and released in first sample, n_2 = number captured in second sample, and m_2 = number captured in second sample that were marked from first sample. $\hat{n}_{post} = (\hat{n}_{pre} - \text{harvest}) - [(\%\ \text{natural mortality})(\hat{n}_{pre} - \text{harvest})]$.

ery. The population increased to an estimated 46 independent cougars by spring 2003 (Table 1). The number of hunter-days totaled 47 and 79 during the 2-year treatment period and 27, 50, and 21 days during the 3-year recovery period; high hunter effort during the second treatment year and the second recovery year were due to excessive time spent hunting by an individual hunter each year (30 and 36 days, respectively). We spent 60, 54, and 68 days tracking and marking cougars to augment the recapture sample during the recovery phase.

Cougar harvest composition in response to manipulation

Cougar harvest ($n=22$) composition during the pretreatment period was composed primarily of subadults (36% F, 27% M) followed by adult males (23%) and finally adult females (14%; Figure 1). As harvest levels increased and the population declined in size, there was an initial increase (40%) followed by a decrease (24%) in proportion of adult males in the harvest and a consistent increase in the proportion of adult females (14 to 24 to 41%). Subadult harvest declined from the pretreatment period (from 63 to 36%) but was consistent during the treatment period (35%) and was primarily composed of females (28 and 29%). Subadult cougars again dominated the harvest after harvest quotas were reduced, but subadult male composition was relatively higher than during pretreatment and treatment periods until the third year of recovery when the population returned to pretreatment levels. Annual harvest composition among adult males, adult females, and subadults differed significantly ($P \leq 0.034$) from the pretreatment period through the first year post-treatment and was similar ($P \geq 0.664$) during the 3-year recovery phase.

We compared harvest records from Laramie Peak, the comparison population, to harvest records from the Snowy Range including the first 3 years of harvest (harvest levels below quota) in Laramie Peak and 2 years of harvest treatment and the first year post-treatment in the Snowy Range. During the 3-year period, harvest declined and pri-

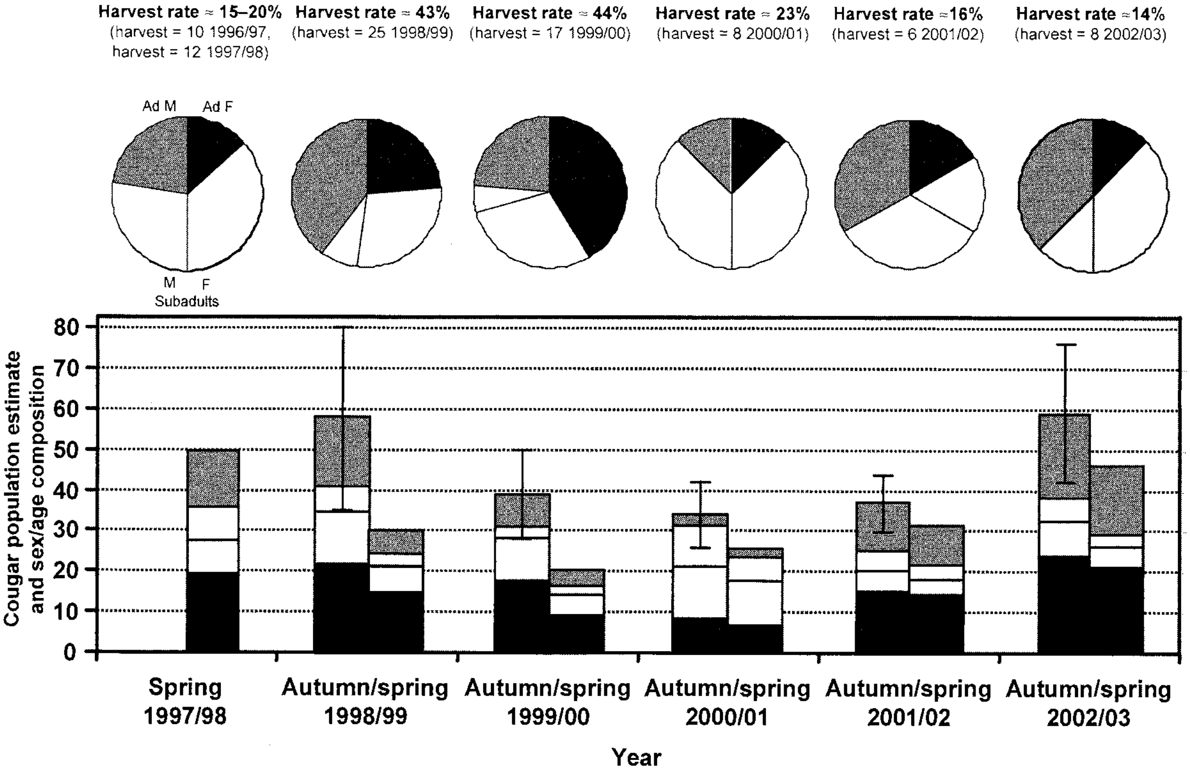

Figure 1. Sex–age composition of cougar harvest (pie charts) from the Snowy Range, Wyoming, relative to population change through increased (1998–2000) and reduced (2000–2003) harvest levels (order of sex–age classes in bar graphs follow pie charts). Harvest composition and rate prior to 1999 represent harvest years 1996–1997 and 1997–1998 combined (first column). The population estimate for spring 1998 was determined from mountain lion density detected from capture and tracking efforts during winter 1997–1998; subsequent population estimates were derived using mark–recapture methods. Error bars represent 90% confidence intervals. Number of cougars known to be in the population each spring were 22, 12, 15, 18, 20, and 34, respectively.

marily consisted of adult males initially, followed by adult females, and finally subadults in both populations (Figure 2); annual harvest composition was similar between populations ($P \geq 0.217$). Mean annuli age of adult females declined following the first treatment year from 6–8 years old to 3–4 years old the second year in both populations. Unlike the Snowy Range, unrestricted harvests continued in Laramie Peak for the next 4 years, resulting in annual oscillations in harvest level and harvests of primarily subadults (Figure 2); adult females averaged 4.3 years of age during this period.

Characteristics of female cougar harvest

We noted that proportion of adults in the female harvest increased with harvest rate, ranging from 20% with a 21% harvest rate to 58% with a harvest rate of about 44% (Figure 1), but this relationship was not statistically significant ($r^2=0.40, F_{1,6}=3.32$, $P=0.13$). Sixteen adult and 19 subadult females were harvested (total harvest = 64) in the Snowy Range during the 2-year treatment and 3-year post-treatment periods. Of 8 marked adult females harvested, 4 were without young, 3 had young at the time, and we suspect the last female may have had young when harvested because we had seen kitten tracks with her 2 months earlier. All harvested females with young were taken during the treatment period (>40% harvest rate).

Discussion

The Snowy Range cougar population recovered in numbers after 2 years of intensive harvest (~43% of independent cougars) followed by 3 years of light harvest (~18% of independent cougars). Recovery of the population was facilitated by immigration of males and recruitment of females from within the population as found in other recovering cougar populations (Lindzey et al. 1992, Logan and Sweanor 2001). Composition of the harvest from pretreatment through the 2 years of heavy harvest supported our predictions based on predicted relative vulnerability of the various sex and age classes. The most vulnerable classes were harvested until their reduced abundance in the population

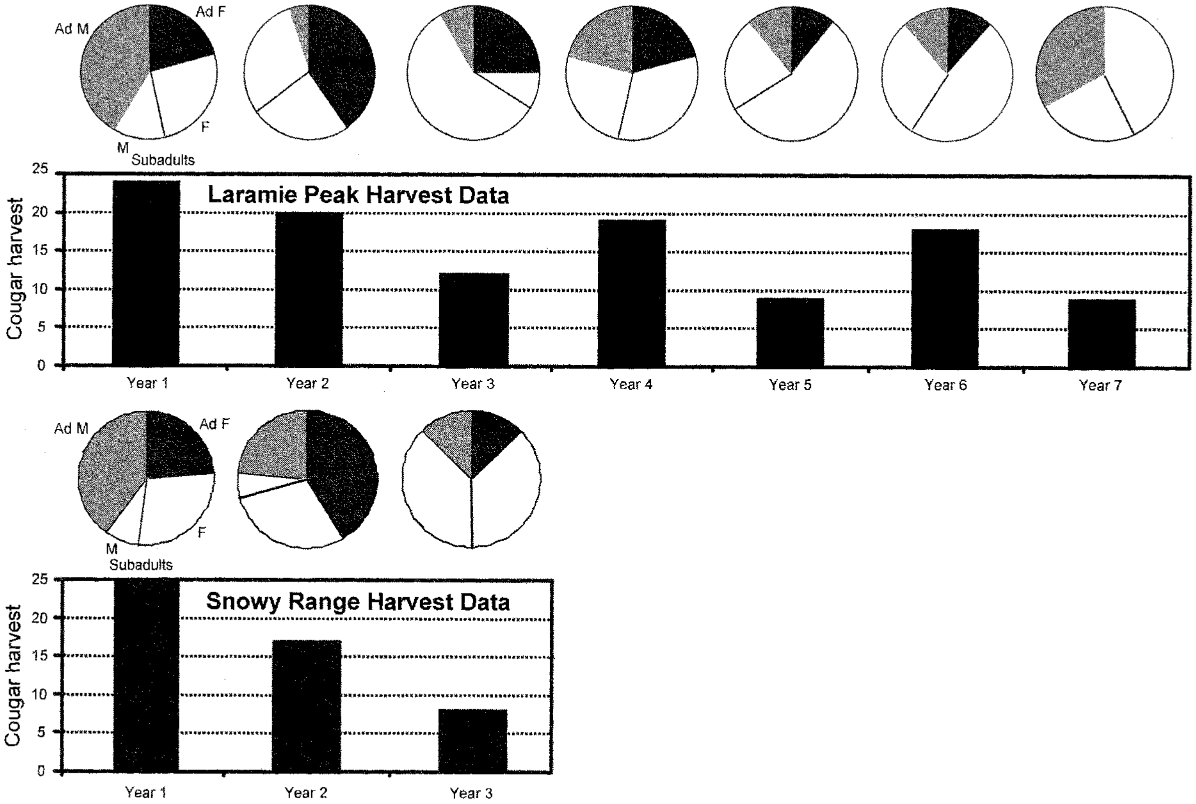

Figure 2. Comparison of total harvests (bar graphs) and harvest composition (sex–age class; pie charts) from Laramie Peak and the Snowy Range in southeast Wyoming. Cougar harvest quotas were not met, except in the Snowy Range during years 1 and 3. Note similarities in harvest levels and composition between populations exposed to similar harvest treatments.

exposed the next most vulnerable class, terminating in a harvest dominated by adult females (Figure 1). The increase in adult females in the harvests coincided with a decrease in size of this hunted population, suggesting that proportion of adult females in harvests may be a useful indicator of trends in other hunted cougar populations. The similarity of composition trends in the Snowy Range and Laramie Peak populations during the initial years of intensive harvest suggests that the intensive harvest in the Laramie Peak population had achieved its goal of reducing population size in this area. Decline in average age of harvested females in both populations further suggested that harvests had similar effects on the 2 populations.

While factors other than composition of hunted cougar populations (e.g., weather patterns, changes in legal access) can influence harvest level, none should result in adult females dominating the harvest if they are not proportionately the most abundant sex or age class present in the population. Experienced cougar hunters often can differentiate males and females from track size, presence of scrapes, or body characteristics if the cougar is seen, but selective hunters tend to harvest males. Further, our experience suggests that hunters tend to be most selective when competition for available cougars is low. When demand exceeds harvest quotas, competition among hunters appears to result in less-selective hunting, and harvest should reflect the relative abundance or vulnerability of sex and age classes. Snow conditions also can affect hunting success (>90% of cougars harvested in Wyoming are hunted using hounds and most require snow cover), but this should influence harvest rate, not the relative vulnerability of the sex and age classes. Access, influenced by weather events or land-ownership patterns, can create ephemeral or more permanent refuges within cougar management areas. In these situations harvests may be maintained by adjacent, unavailable adult females providing young females for the harvest (e.g., Figure 2). We identified areas of suitable cougar habitat in the Laramie Peak area that received no cougar harvest and apparently were functioning as refuges. The similar abundance of subadult females in the pretreatment Snowy Range harvest and post-treatment harvests from Laramie Peak illustrates the contribution of refuges to maintaining harvests and underscores the need to monitor harvest composition over a number of years before drawing inferences about trend in the population from harvest composition. Subadult females in the pretreatment Snowy Range harvest reflected their relative abundance and vulnerability to harvest, while their dominance in later harvests from Laramie Peak apparently reflected their abundance in the portion of the area accessible to hunters. Examination of composition of earlier harvests should help identify whether the harvest reflects a lightly hunted population or one that has been reduced with harvests being supported by young produced by adjacent, unavailable adult females. Prior harvests in the Laramie Peak area were composed of progressively more adult females, suggesting the population had been reduced in size.

Management implications

Cougar managers typically have used harvest level and occasionally sub-quotas typically aimed at protecting females to achieve population objectives, although both imply knowledge of population size. While observations suggest that cougar populations can sustain harvest rates of up to 20-30% (Ashman et al. 1983, Ross and Jalkotzy 1992), the effect of harvests on populations will differ depending on sex and age of cougars removed. Harvest of males, the cohort most easily replaced by immigration, and subadult females, which can be quickly replaced by female young produced in the population, will have less impact on the population than harvest of adult females, which are more difficult to replace. Adult females that die are most often replaced by the population's female progeny and less often by immigrating subadults because most female progeny are philopatric (Lindzey et al. 1989,

Duggin Wroe's dog, Luna, corners male cougar number 610. Photo by Hall Sawyer.

Anderson et al. 1992, Logan and Sweanor 2001).

Monitoring levels of adult females in cougar harvests to index the effect the harvest is having on the population is intuitive. Sensitivity analyses by Martorello and Beausoleil (2003) suggest that cougar populations are most sensitive to survival of this sex and age class. Adult females provide the resiliency in a population that allows it to respond to loss of members. This approach will work well in an adaptive management framework, where harvest composition goals are set to achieve specific population objectives. Hunting programs can simply be modified until harvest composition indicates that desired population and recreation objectives are being met. The proportion of adult females in the Snowy Range harvest when the more vulnerable sex and age classes had been removed and the population was beginning to decline was about 25%, while the population appeared to sustain a harvest composed of 10-15% adult females (Figure 1). The 25% estimate came from a single experiment and should be used with caution in other programs because cougar populations more isolated than the Snowy Range or that contain more refuge areas may respond differently to similar harvest rates of adult females. Also, because harvest from a single management area in a single year may be too small to support inferences, and harvest level may vary because of weather events, combining years or adjacent management areas for analyses may be appropriate.

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Literature cited

ALEXANDER, R. R., G. R. HOFFMAN, AND J. M. WIRSING. 1986. Forest vegetation of the Medicine Bow National Forest in southeastern Wyoming: a habitat type classification. United States Department of Agriculture Forest Service Research Paper RM-271, Rocky Mountain Range Experiment Station, Fort Collins, Colorado, USA.

ANDERSON, A. E., D. C. BOWDEN, AND D. M. KATTNER. 1992. The puma on the Uncompahgre Plateau, Colorado. Colorado Division of Wildlife Technical Publication No. 40, Fort Collins, USA.

ANDERSON, C. R., JR. 2003. Cougar ecology, management, and population genetics in Wyoming. Dissertation, University of Wyoming, Laramie, USA.

ANDERSON, C. R., JR., AND F. G. LINDZEY. 2000. A photographic guide to estimating cougar age classes. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, USA.

ASHMAN, D. L., G. C. CHRISTENSEN, M. L. HESS, G. K. TSUKAMOTO, AND M. S. WICKERSHAM. 1983. The mountain lion in Nevada. Nevada Department of Wildlife, Federal Aid in Wildlife Restoration Project W-48-15, Final Report.

BARNHURST, D. 1986. Vulnerability of cougars to hunting. Thesis, Utah State University, Logan, USA.

FJELLINE, D. P., AND T. M. MANSFIELD. 1988. Method to standardize the procedure for measuring mountain lion tracks. Pages 49-51 *in* R. H. Smith, editor. Proceedings of the Third Mountain Lion Workshop. Arizona Game and Fish Department, Phoenix, USA.

GARSHELIS, D. L. 1990. Monitoring effects of harvest on black bear populations in North America: a review and evaluation of techniques. Proceedings of the Eastern Workshop of Black Bear Research and Management 10: 120-144.

LAUNDRE, J. W., AND L. HERNANDEZ. 2002. Growth curve models and age estimation of young cougars in the Northern Great Basin. Journal of Wildlife Management 66: 849-859.

LAUNDRE, J. W., L. HERNANDEZ, D. STREUBEL, K. ALTENDORF, AND C. L. GONZALEZ. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28: 963-966.

LINDZEY, F. G. 1991. Needs for mountain lion research and special management studies. Pages 86-94 *in* C. E. Braun, editor. Mountain lion-human interactions symposium. Colorado Division of Wildlife, 24-26 April 1991, Denver, USA.

LINDZEY, F. G., B. B. ACKERMAN, D. BARNHURST, T. BECKER, T. P. HEMKER, S. P. LAING, C. MECHAM, W. D. VAN SICKLE. 1989. Boulder-Escalante cougar project, Final Report. Utah Division of Wildlife Research, Salt Lake City, USA.

LINDZEY, F. G., W. D. VAN SICKLE, B. B. ACKERMAN, D. BARNHURST, T. P. HEMKER, S. P. LAING. 1994. Cougar population dynamics in southern Utah. Journal of Wildlife Management 58: 619-624.

LINDZEY, F. G., W. D. VAN SICKLE, S. P. LAING, AND C. S. MECHAM. 1992. Cougar population response to manipulation in southern Utah. Wildlife Society Bulletin 20: 224-227.

LOGAN, K. A., AND L. L. SWEANOR. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

MARTORELLO, D. A., AND R. A. BEAUSOLEIL. 2003. Characteristics of cougar harvest with and without the use of dogs. Pages 129-135 *in* S. A. Becker, D. D. Bjornlie, F. G. Lindzey, and D. S. Moody, editors. Proceedings of the Seventh Mountain Lion Workshop, May 15-17, 2003. Wyoming Game and Fish Department, Lander, USA.

POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments.

Wildlife Monograph No. 107.

RILEY, S. J. 1998. Integration of environmental, biological, and human dimensions for management of mountain lions. Dissertation, Cornell University, Ithaca, New York, USA.

ROSS, P. I., AND M. G. JALKOTZY. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417–426.

SHAW, H. G. 1979. Mountain lion field guide. Arizona Game and Fish Department Special Report No. 9, Phoenix, USA.

SHAW, H. G. 1981. Comparison of mountain lion predation on cattle on two study areas in Arizona. Pages 306–316 *in* L. Nelson and J. M. Peek editors. Proceedings of the Wildlife Livestock Relationships Symposium. University of Idaho Forest, Wildlife, and Range Experiment Station, Moscow, USA.

WYOMING GAME AND FISH DEPARTMENT. 2003. Annual mountain lion mortality summary harvest year 2002. Trophy Game Section, Lander, Wyoming, USA.

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Associate editor: *Crête*

Non-Invasive DNA-Based Black Bear Density Estimates in Colorado – 2009.

Jerry A. Apker, Paul Lukacs, John Broderick, Brian Dreher, Julie Mao, Allen Vitt

ABSTRACT We estimated black bear (*Ursus americanus*) density in two survey areas in Colorado. The southeast survey area (SESA) (575 km^2) is located northwest of Trinidad, Colorado, and the northwest survey area (NWSA) (500 km^2) is located southwest of Glenwood Springs, Colorado. Each survey area represents high quality black bear habitat. Surveys were conducted from late June through early August of 2009. Scent baits were used to attract bears to hair snag stations and natural rub trees adapted for hair snagging were used to non-invasively collect hair samples from which DNA could be extracted and genetically analyzed. Tissue samples from black bear mortalities and also from conflict bears handled in the vicinity of the survey areas were also a source of DNA for analysis. All samples of adequate quality were genotyped using 7 microsatellite loci and gender identified using the ZFX/ZFY gender marker method to identify unique individuals within the survey areas. We used several different mark-recapture analysis methods and applied assumed home range data from Idaho and New Mexico to calculate a range of possible densities. Applying the most robust mark-recapture methods, our analysis suggests that there are 45-50 bears/100 km^2 in the NWSA. In the SESA our analysis indicates 44-85 bears/100 km^2. Analysis challenges and key assumptions are discussed.

We conducted surveys to non-invasively collect DNA samples of black bears in two survey areas of Colorado. Both survey areas were selected because they are considered high quality black bear habitat and are in relatively close proximity to high human-bear conflict areas. One survey area was located near the Spanish Peaks, northwest of Trinidad (SESA) (Fig. 1) in Game Management Unit (GMU) 85, Data Analysis Unit (DAU) B-9. The other was near Divide Creek, southwest of Glenwood Springs (NWSA) (Fig. 2) in GMUs 42 and 43, DAUs B-11 and B-17. The SESA was 575 km^2 and the NWSA was 500 km^2 in size.

With minor modification survey protocols followed those described by Kendall (K. Kendall, USGS, personal comm. 2009) for research being conducted on grizzly (*Ursus arctos*) and black bears in northwestern Montana and previously by Mowat and Strobeck (2000) and Woods et al. (1999). We modified the survey protocols by using a smaller grid area of 25 km^2 (~9.5 square miles per grid) in order to accommodate a survey focused solely on black bears which have smaller home range areas than grizzlies. The smaller grid area provides increased opportunity for all bears within the survey area to have opportunity to encounter one or more snag stations. The survey areas ultimately were configured to their final shape and size in order to include bear habitat typical of the high quality habitat in the DAUs they are located and also to avoid human development (or potential human conflicts).

Table 1. Vegetation composition in survey areas based on CDOW GIS Basinwide layers, in broad categories.

Vegetation types	NWSA % composition	SESA % composition
Aspen dominant	40%	4%
Conifer (not ponderosa pine)	21%	21%
Ponderosa Pine	-	33%
Conifer/Aspen Mix	10%	6%
Gambel Oak	10%	17%
Berry/Mesic Mtn. Shrub	8%	-
Sagebrush	3%	-
Pinyon-Juniper Mix	1%	6%
Dryland/Irrigated Agri.	<1%	2%
Alpine/Subalpine (grass, forb, or shrub)	2%	1%
Riparian	1%	1%
Other	4%	9%

Vegetation types were grouped into broad categories and differed between the two survey areas (Table 1). Ponderosa pine and ponderosa affiliations with gambel oak or aspen was a significant component of plant communities in the SESA, but absent from the NWSA. Oakbrush and serviceberry were avoided and aspen stands or mixed aspen/conifer types were selected for when formulating the grid area in the NWSA. While oakbrush and serviceberry are important black bear habitat types in fall season, they were not deemed as important for a survey conducted in the summer on the NWSA. In contrast, the SESA included oakbrush habitats (although serviceberry was not present in the SESA). The SESA also included more open meadow grassland areas and dryland and irrigated agriculture lands which were not found in the NWSA.

We collected hair from late June through early August. Snag stations were baited mainly with decomposed, liquefied fish (mung) soaked burlap and drizzled on logs, Anise oil soaked burlap strips, decomposed deer roadkill-soaked burlap strips. Some stations were baited with portions of road kill deer or elk. Hair collections occurred every 5-7 days on average ($\bar{x} = 6$ days, range 2-10 days) for up to 9 repeated collection sessions.

We collected tissue or hair samples from black bears handled due to human conflicts during the course of summer and fall. We also collected tissue samples from other bear mortalities such as road kills, second strike bear, or hunter harvest documented by the Division of Wildlife (DOW). We submitted these additional samples from GMUs within or surrounding the survey area for genetic analyses. NW GMUs for these additional samples included 33, 34, 42, 43, 45, 47, 421, 444, 471, and 521. SE GMUs for these additional samples included 83, 861, 84, 85, 851, and 140.

Results

A total of 1,103 snagged hair samples were submitted to the lab for analysis; 457 from the NWSA and 646 from the SESA. An additional 259 samples (161 from NW GMUs, 98 from SE GMUs) were submitted from harvest mortality, non-harvest mortality, or euthanized conflict bear; these are called “known bear” samples. Wildlife Genetics International conducted the genetic analysis under the direction of Dr. David Paetkau, president and geneticist. We have attached the genetic analysis report to this report. Laboratory protocols exceeded DOW specified quality controls and Dr. Paetkau independently, and at no charge to DOW, took additional steps to conduct more detailed analyses and to safeguard against false identifications of unique individuals.

The genetic analysis resulted in identification of 117 unique bears in the NWSA and 149 unique bears in the SESA. We documented a surprisingly low number of recapture events (Table 2). We reconstructed the capture histories for all identified individuals.

Table 2. Summarized capture history by site and ‘x’ week.

Number of times detected	NWSA		SESA	
	Individuals	% of total	Individuals	% of total
1	82	70%	113	75%
2	19	16%	18	12%
3	13	11%	10	7%
4	2	2%	4	3%
5	0	-	4	3%
6	1	1%	0	-
Total	117		149	
Recaptured in Harvest or other	6	-	4	-

In general, the frequency of capturing new individuals declined over time (Table 3). Declining numbers of new individuals is expected in capture-recapture sampling, but other factors may have contributed to the decline. Bears may become attenuated to the bait material or bears may be beginning hyperphagic movement to lower elevation mast production areas. Bait attenuation might result when bears detected no novel scents and having previously explored baits used at one or more snag stations were no longer driven to investigate the scent further. We attempted to mitigate bait attenuation by using different bait material at different snag stations over time. Although, not all snag stations had different baits over the course of the survey.

Table 3. Summary of captures of new female and total individuals by week.

Week #	NWSA				SESA			
	Date Start	Date End	New Female N	New Total N	Date Start	Date End	New Female N	New Total N
0	6-9	6-12	5	9				-
1	6-16	6-18	9	23	6-22	6-26	18	31
2	6-23	6-27	12	22	6-29	7-3	8	25
3	6-26	7-1	9	16	7-6	7-10	9	20
4	7-2	7-8	3	8	7-13	7-17	5	13
5	7-9	7-14	7	9	7-20	7-24	9	17
6	7-15	7-22	5	14	7-27	7-31	10	17
7	7-22	7-28	3	10	8-3	8-7	6	13
8	7-28	7-31	3	6	8-10	8-14	4	13
Sum			56	117			69	149

Movements by bears to lower elevation mast production areas would be expected later in the summer to early fall as bears entered hyperphagia. This could result in less frequent detection of new bears as they moved out of the survey area in later survey collection sessions. This should have been most notable in the NWSA since its grid layout avoided substantial oakbrush/serviceberry vegetation complexes, although it could have been offset by the earlier end date of the NWSA survey. While the NWSA survey efforts were concluded prior to the expected time in which bears would enter hyperphagia, it might be possible that movements toward lower elevations occurred earlier than we predicted.

Density

We analyzed the encounter data using three different mark-recapture analysis methods (Table 4); spatially-explicit mark-recapture (Bochers and Efford 2008), maximum likelihood mark-recapture (Otis et al. 1978), and a jackknife mark-recapture (Burnham and Overton 1979).

> Spatially explicit method. This method uses the distance between captures to estimate the average center of activity and area used by a bear. With sufficient recapture events this method would provide a strong representation of the size area that bears are moving within during our sampling time frame. The paucity of recaptures we have to work with severely weakens this analysis. Because there are so few recapture events we are not confident that they are representative of the actual area of use by bears in either survey location. Although this estimation method suffers from the low number of recaptures in 2009 it can be applied across multiple years which increases sample sizes and increases the power of the analysis. This estimation method results in density estimates of 47 bears/100 km^2 in the NWSA and 44 bears/100 km^2 in the SESA.

The following two estimation methods attempt to account for the effect of enticing bears that may be on the periphery of the survey area into snag stations. In any survey of this nature there will be some individuals whose home areas overlap the outer boundary of the survey area. Presumably, these bears may be enticed to hair snag stations by the scent baits. Since their home areas extend beyond the outer edge of the survey area, there must be some accounting for the larger geographic area of impact when calculating an estimated density. The mechanism for doing this is to apply an estimated home area at each snag station point. The estimated home area is derived from projecting an area with ½ the radius of an assumed home area. The outer perimeter of this projection is then used to compute an estimation of the amount of area actually surveyed. The estimated population size from the mark-recapture analysis is then divided by the estimated survey area to arrive at the density.

The assumed home area values used for our analysis were estimates from Idaho research (Beecham and Rohlman 1994) and the mean annual primary home area found in the northern study area (NSA) in New Mexico (Costello et al. 2001). In both cases we used home ranges estimated for males and females. In the Idaho research, home areas were presented in a range so we applied a small and large home area size to yield a range of density here as well. The primary home area in New Mexico doesn't include the long distance movements that bears occasionally embark upon, but subsequently return from (Costello et al. 2001, Baruch-Mordo personal comm. 2009). Ultimately we selected Idaho and New Mexico home area values due to the similarity in our raw density (minimum individuals per total grid area) and Idaho density results, and similarity of New Mexico NSA habitat to Colorado survey area habitats.

Home area data from Colorado studies were not used for several reasons; the Black Mesa study (Beck 1991) estimated annual ranges from relatively infrequent VHF locations per individual bear and consequently computed an extremely wide range of home area sizes (although the mean values fell within the range of values we applied). Data from the more recent Roaring Fork valley investigations were not used because all tracked bears were captured within towns and represent potentially biased home areas as "conflict" bears. In addition the principle investigator was out of the country and unavailable to update home area sizes reported from 2007 data.

Maximum likelihood method. This method estimates the number of bears available to be detected in each survey. We then applied the assumed home area values to the estimated population size to calculate density. This method assumes that there is no difference in detection probability among individuals (except by sex which can be analyzed separately). This assumption is known to result in estimates biased low when compared to known densities. This analysis method yields an estimated density range of 28-32 bears/100 km^2 in the NWSA and 54-59 bears/100 km^2 in the SESA.

Jackknife method. This method applies home areas in the same manner as the maximum likelihood method. This method does assume that there is variation in the detection probability among individual bears, but doesn't presume any specific cause for the variation. This assumption seems reasonable. This analysis method results in an estimated density range of 45-50 bears/100 km^2 in the NWSA and 78-85 bears/100 km^2 in the SESA.

Table 4. Estimated black bear densities derived from hair snag mark recapture analysis. Results are from three methods; spatially explicit model, maximum likelihood model, and the jackknife model. The maximum likelihood and jackknife models apply assumed home range areas from New Mexico, northern study area (Costello et al. 2001) and Idaho (Beecham and Rohlman 1994). The Idaho home areas presented a range of values, therefore we applied a small home area value and a large home area value in our analyses.

Spatially Explicit Capture-Recapture

Combined Gender Density		Bears/ha	SE	Bears/sq. mile	SE
NWSA		0.0047	0.0007	1.22	0.18
SESA		0.0044	0.0006	1.14	0.16
Density by Gender					
NWSA	Female	0.0026	0.0006	0.67	.016
	Male	0.0022	0.0005	0.57	0.13
	Total	0.0048	0.0008	1.24	0.20
SESA	Female	0.0025	0.0005	0.65	0.13
	Male	0.0021	0.0004	0.54	0.10
	Total	0.0046	0.0006	1.19	0.17

Maximum Likelihood Capture-Recapture

				Small Home Area (ID)			Large Home Area (ID)			NM Home Area		
		N	SE	Area	Bears/sq. mile	SE	Area	Bears/sq. mile	SE	Area	Bears/sq. mile	SE
NWSA	Female	80	9.48	202	0.40	0.05	212	0.38	0.04	205	0.39	0.05
	Male	117	19.06	278	0.42	0.07	337	0.35	0.06	343	.034	0.06
	Total	197	21.29		0.82	0.08		0.73	0.07		.073	0.07
SESA	Female	276	46.94	298	0.93	0.16	309	0.89	0.15	294	0.94	0.16
	Male	231	29.37	387	0.60	0.08	455	0.51	0.06	457	0.51	0.06
	Total	507	55.37		1.52	0.17		1.40	0.17		1.44	0.17

Jackknife Capture-Recapture

				Small Home Area (ID)			Large Home Area (ID)			NM Home Area		
		N	SE	Area	Bears/sq. mile	SE	Area	Bears/sq. mile	SE	Area	Bears/sq. mile	SE
NWSA	Female	140	25.08	202	0.69	0.12	212	0.66	0.12	205	0.68	0.12
	Male	168	27.24	278	0.60	0.10	337	0.50	0.08	343	0.49	0.08
	Total	308	37.03		1.30	0.16		1.16	0.14		1.17	0.15
SESA	Female	358	35.98	298	1.20	0.12	309	1.16	0.12	294	1.22	0.12
	Male	390	36.76	387	1.01	0.09	455	0.86	0.08	457	0.85	0.08
	Total	748	51.44		2.21	0.15		2.02	0.14		2.07	0.15

Ideally at least two of the methods would produce similar estimates and thus we could have confidence in selecting results with most relevance for management. Unfortunately, substantial differences exist between the estimates for each method. Future results will help us draw more meaningful conclusions and inferences. In the interim, managers should consider that our results may have potential biases in capture probability between age classes and genders and could also be influenced by our assumed home area sizes. Although preliminary and considering the various assumptions in the different methods we place most confidence in the estimates produced by the spatially explicit and jackknife methods which yield densities of between 45-50 bears/100 km^2 in the NWSA and between 44-85 bears/100 km^2 in the SESA.

In order to place our results into context, we examined black bear density estimates from certain studies in different States and Provinces, representing different habitat types (Table 5). Although there is little doubt that the method of density estimation along with size of the study area plays a role in density estimates, we attempted to minimize disparity by selecting reports from, in most cases, mark-recapture surveys. However, three are derived from minimum individual animal reconstructions (Colorado – Beck 1991, Utah – UDWR 2000, and Colorado – Baldwin and Bender 2007). We also excluded extremely small study areas with the exception of island habitats (Washington – Lindzey 1977 and Wisconsin – Belant et al. 2005), where populations would be closed and allow for more accurate enumeration. We included the Nevada – Tahoe Basin urban estimate (Beckmann and Berger 22003) due to the extreme influence of a highly rich food source. In general, black bear densities are greater in areas of greater quality and abundant forage.

Table 5. Reported black bear densities from research, analysis, or management reports in diverse locations and habitat types. Bullet ●, indicates results of this study.

Location	Source	Per 100 km^2
Washington	Lindzey 1977	112 – 149
Nevada – Tahoe Basin (urban)	Beckmann and Berger 2003	120
●Colorado – SESA	Apker et al. 2010 unpublished	44 – 85
Wisconsin	Belant et al. 2005	50 – 64
Idaho	Beecham and Rohlman 1994	31 – 77
●Colorado – NWSA	Apker et al. 2010 unpublished	47 – 50
Idaho	Beecham 1980	43 – 47
Alberta	Kemp 1976	38
Montana	Jonkel and Cowan 1971	38
Colorado – Uncompahgre	Beck 1995 Fed Aid Rpt	36
Idaho	Rohlman 1989	34
Arizona	LeCount 1982	33
Nevada – Sierra Range	Goodrich 1990	20 – 40
Arizona	Waddel and Brown 1984	27.8
Colorado – BMSA	Beck 1991	17.9
New Mexico	Costello et al. 2001	9.4 – 17
Colorado – Middle Park	Beck 1997 Fed Aid Rpt	8.1
Utah	Utah Division of Wildlife Resources 2000	7.7
Arizona	LeCount 1987	6
Wyoming	Grogan and Lindzey 1999	2.1 – 3.0
Colorado - RMNP	Baldwin and Bender 2007	1.35

Application of this particular survey methodology (scent bait hair snag station) commonly results in a bias against small black bears (D. Moody, WY G&F, personal comm. 2009, K. Kendall, USGS personal comm. 2009). Given that the first year results show relatively high bear densities, bear home range areas in our survey locations may be smaller or more overlapping than we first considered and consequently we potentially missed bears because snag stations didn't occur in some bear home areas within the overall survey area. The hair collection methodology definitely misses most cubs, due to both their size and behavior. To a lesser extent the negative bias extends to sub-adults and females but the extent of bias isn't known.

A second consideration for interpreting the results is the influence of our assumed home area. We used assumed home areas in two of the mark recapture analyses in order to consider the potential "impact area" from which we were actually surveying bears. The home area values we used were annual home areas. We presume that these home areas are likely to be larger than the area that bears are using in the relatively short period that hair is being collected. We offset this potential error somewhat by including opportunity for recapture to include fall hunter harvest periods when bears will have had opportunity to use more expansive portions of their home areas.

Another consideration is that cementum age data on large numbers of harvested bears in Colorado, statewide, as well as in the vicinity of these two survey areas shows a relatively young mean and median age structure for

Colorado bear populations. Cementum age structure derived from hunter harvest is almost always biased younger than the actual population. Yet comparing Colorado's harvest age composition results to hunter harvest results in other states has indicated that Colorado appears to have a younger average age at harvest. If this is reflective of the actual population then a larger than expected portion of bears on both survey areas may be highly mobile animals, yet to settle into an established home area. Consequently, the potential "impact area" may be much larger than that represented by even large home areas and the resulting density of bears would be lower than our results show. This could also explain the relatively low number of recapture events during hair snag collection sessions. It does not, however, explain why there were relatively few hair snag bears 'recaptured' in hunter harvest.

Gender

Hair snare captures and known bear captures were slightly male biased (53% and 56% respectively). The "known bear" group of samples is derived mostly from hunter harvest. Genetic gender identification of this group closely matches the identification of gender reported for hunter harvest in the 3 DAUs in which the survey areas (56.7% male). In fact, out of 256 unique genotypes identified from the known bear captures group only 4 bears identified as male at the mandatory check were, based on genetic analysis, found to be females.

The small difference between mortality based samples (56%) and hair snag population based samples (53%) could be due to normal variation in sample collection or could be attributed to a slight tendency of hunters to select for larger bears which tend to be males more frequently than females. Likewise, the slight male bias in the hair snag sample may be due to normal variation in sample collection or could be due to the previously discussed bias against smaller bears, which tend to be females and young bears.

Conclusion

Our results are among the highest black bear densities reported in the Rocky Mountains, but are not inconsistent with other densities derived from mark-recapture methods in most other highly productive mast producing habitats. Although the small recapture sample sizes, especially the independent known bear (mortality based recaptures), influence confidence in our computed densities, future replication of the surveys will increase sample size and power and therefore increase the confidence of our estimates.

With that in mind, we have replicated both survey areas in 2010 and have begun sending samples to the laboratory for analysis. It is our plan that the NWSA is concluded and a new survey site will be selected and should be conducted for two years. The SESA is an area in a DAU in which some experimental management is planned. Therefore, we propose to continue with surveys in this area through 2013 to test if bear population trend can be detected. After 2013 we propose to close the SESA and move to another site.

We suggest that at least two survey areas should be continuously operated in Colorado until representative densities derived from two consecutive years of survey data are obtained for each black bear DAU. Conducting surveys in this manner will support and bolster black bear DAU plan development which has begun this year. Results from surveys can be applied to habitat and population models and ongoing monitoring in experimental management strategies.

Literature Cited

Baldwin, R.A. and L.C. Bender. 2007. Population demographics, habitat utilization, critical habitats, and condition of black bears in Rocky Mountain National Park. Rocky Mountain National Park, Estes Park, Colorado. 244pp.

Beck, T.D. 1991. Black bears of west-central Colorado. Colorado Division of Wildlife Report Number 39. 86pp.

Beck, T.D. 1995. Development of black bear inventory techniques. Colorado Division of Wildlife. Wildlife Research Report. Federal Aid Project W-153-R-8, Job Progress Report. 11pp.

Beck, T.D. 1997. Development of black bear inventory techniques. Colorado Division of Wildlife. Wildlife Research Report. Federal Aid Project W-153-R-10, Final Report. 11pp.

Beckmann, J.P. and J. Berger. 2003. Using black bears to test ideal-free distribution models experimentally. Journal of Mammalogy 84:594-606.

Beecham, J.J. 1980. Population characteristics, denning, and growth patterns of black bears in Idaho. Ph.D. Dissertation. University of Montana, Missoula. 101pp.

Beecham, J.J. and J. Rohlman. 1994. A shadow in the forest: Idaho's black bear. The University of Idaho Press, Idaho, 245pp.

Belant, J.L., J.F. Van Stappen, and D. Paetkau. 2005. American black bear population size and genetic diversity at Apostle Island National Lakeshore. Ursus 16:85-92.

Borchers, D.L. and Efford, M.G. 2008. Spatially explicit maximum likelihood methods for capture{recapture studies. Biometrics 64, 377-385.

Burnham, K.P., and W.S. Overton. 1979. Robust Estimation of Population Size When Capture Probabilities Vary Among Animals. Ecology 60:927-936

Costello, C.M., D.E. Jones, K.A. Green Hammond, R.M. Inman, K.H. Inman, B.C. Thompson, R.A. Deitner, H.B. Quigley. 2001. A study of black bear ecology in New Mexico with models for population dynamics and habitat suitability. Final Report Federal Aid in Wildlife Restoration Project W-131-R. 197 pp.

Goodrich, J.M. 1990. Ecology, conservation, and management of two western Great Basin black bear populations. MS Thesis. University of Nevada, Reno.

Grogan, R.G. and F.G. Lindzey. 1999. Estimating the population size of a low-density black bear population using capture-resight. Ursus 11:117-122.

Jonkel, C.J. and I.McT. Cowan. 1971. The balck bear in the spruce-fir forest. Wildlife Monographs 27.

Kemp, G.A. 1972. Black bear population dynamics at Cold Lake, Alberta, 1968-70. International Conference on Bear Management and Research 3:191-197.

LeCount, A. L. 1982. Characteristics of a central Arizona black bear population. Journal of Wildlife Management 47:861-868.

LeCount, A. L. 1987. Causes of black bear cub mortality. International Conference on Bear Research and Management 7:71-82.

Lindzey, F.G. 1977. Population characteristics of black bears on an island in Washington. Journal of Wildlife Management 41:408-412.

Mowat, G. and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. Journal of Wildlife Management 64:183-193.

Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62.

Rohlman, J. A. 1989. Black bear ecology near Priest Lake, Idaho. M.S. Thesis, University of Idaho, Moscow. 76pp.

Utah Division of Wildlife Resources. 2000. Utah black bear management plan. 70pp.

Waddel, T. E. and D. E. Brown. 1984. Exploitation of two subpopulations of black bears in an isolated mountain range. Journal of Wildlife Management 48:933-938.

Woods, J.G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free ranging black and brown bears. Wildlife Society Bulletin 27:616-627.

Figure 1. Southeast survey area (SESA) and snag points.

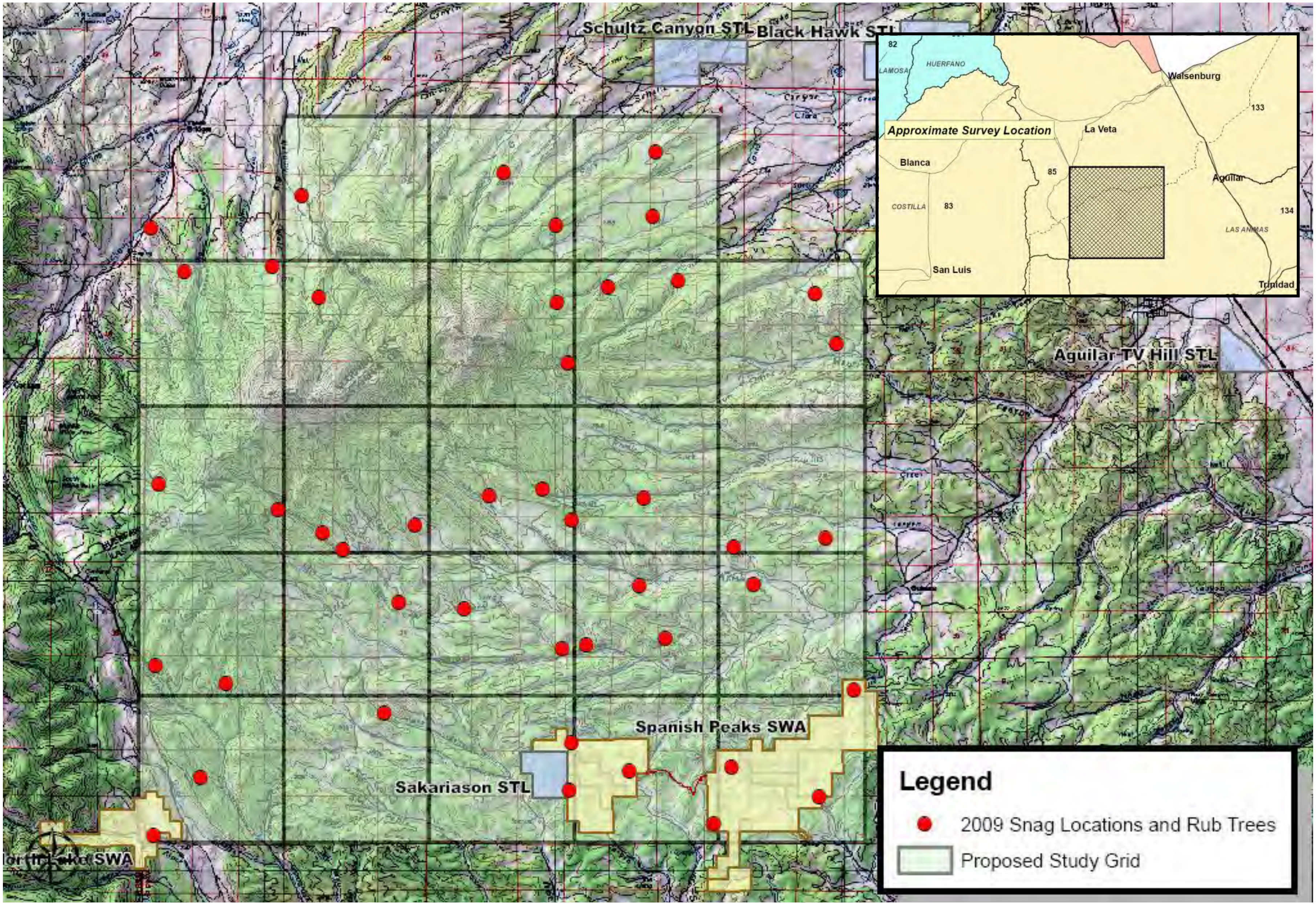
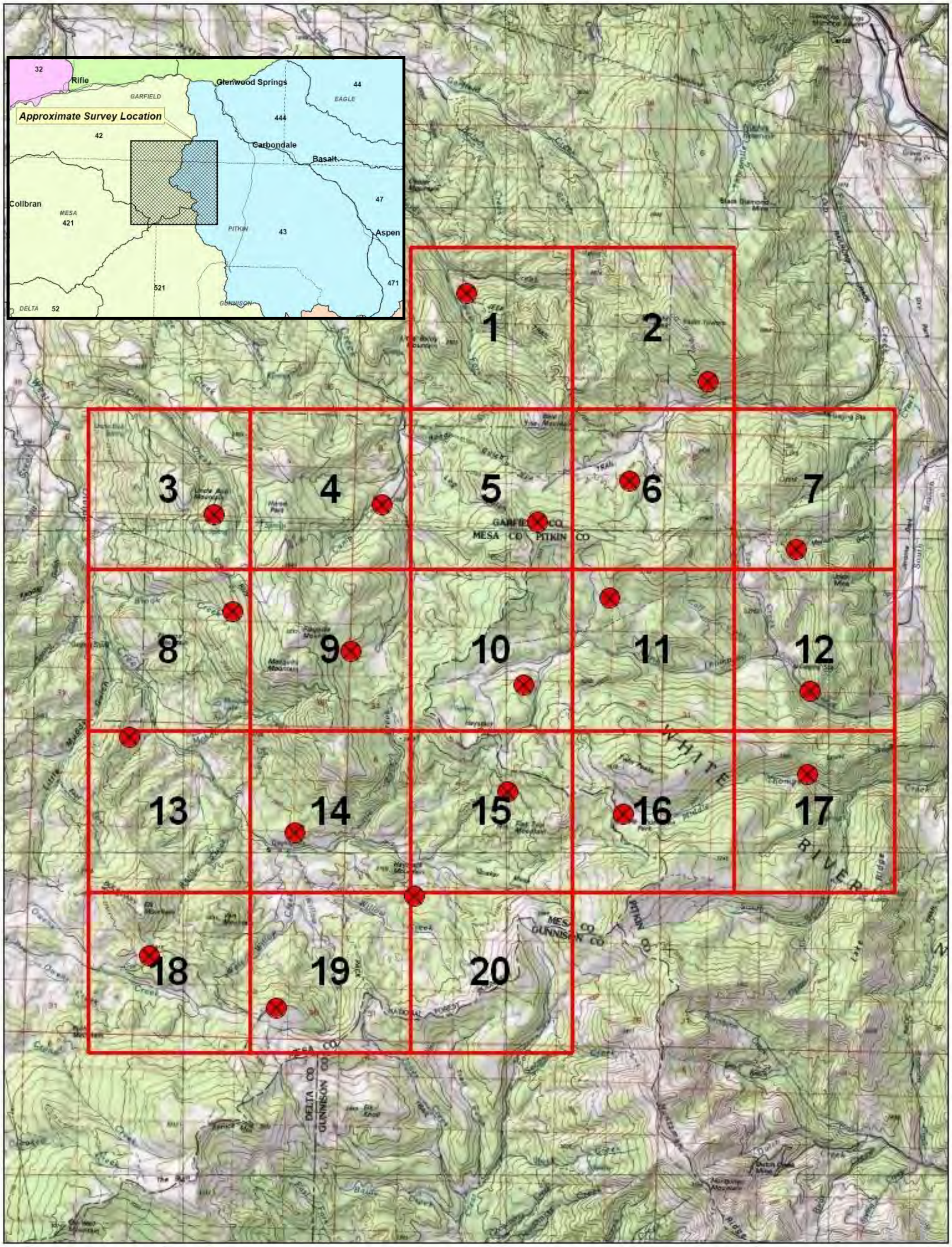


Figure 2. Northwest survey area (NWSA) and snag points.



Wildlife Genetics International

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June 9, 2010

Jerry Apker and Brian Dreher
Colorado Division of Wildlife
0722 South Road 1 East
Monte Vista, CO 81144

Re: WGI project g0805 Colorado BB

Dear Sirs:

I have enclosed genetic results for 1,362 black bear hair and extracted DNA samples that we received from you on January 21st, 2010. The results are presented in the attached MS Excel workbook in which one spreadsheet lists field, extraction and genetic data for each sample, while a second sheet summarizes information by individual. The following notes should provide the information needed to understand and defend this project, but feel free to contact us for further detail on any aspect of this project.

Sample Classification Summary

Of the 259 samples from known bears, 256 produced complete genotypes suitable for individual identification, including all 210 of your DNA extracts. The 1,103 hair samples from snares were classified as follows:

Xspecies (0%): 5 samples that did not look like bear hair

Xinadequate (22%): 241 samples that lacked suitable material for extraction

Xmixed (1%): 12 samples that appeared to contain DNA from > 1 bear

Xbomb (13%): 139 samples that failed during genetic analysis

sample (64%): 706 samples with complete genotypes for 7 microsatellite markers (plus gender) that were assigned individual ID

The 706 good snare samples were assigned to 266 individuals, while the 256 successful ‘known’ samples were assigned to 256 individuals.

Database Issues

We noted the following discrepancies between database records and information on sample envelopes:

Samples NW0512 – NW0519 show a trap site of 04_01 in your spreadsheet versus trap site 09 on the envelopes.

Sample SE0312 shows a trap site of SE15A-4 in your spreadsheet versus trap site 21A on the envelope.

The following discrepancies were noted between the collection dates indicated in your spreadsheet and those on the sample envelopes:

Sample ID	Date in Spreadsheet	Date on Envelope
SE0490 – SE0500	8/6/2009	7/30/2009
SE0510 – SE0514	8/6/2009	7/30/2009
SE0538	8/3/2009	8/10/2009
NW0668	7/13/2009	7/12/2009
985121006936833	7/5/2009	7/7/2009
4452666771	8/29/2009	12/18/2009
NW0571 & NW0572	6/27/2009	6/26/2009
985121009462869	9/9/2009	9/11/2009
985121009094047	8/29/2009	12/18/2009

The following discrepancies were noted between the barb numbers indicated in your spreadsheet and those on the sample envelopes:

Sample ID	Barb # in Spreadsheet	Barb # on Envelope
SE0352	122	120
SE0607	73	74
SE0608	74	73
NW0626	132	134
NW0671	48	47

DNA Extraction

In dialogue with you, and with reference to preliminary results, we decided to exclude samples from the extraction process if they contained no guard hairs with roots and < 5 underfur (*Xinadequate*) or if their appearance was inconsistent with that of bear hair (*Xspecies*; mostly coarse ungulate hair or banded hair). We noted a disproportionate number of inadequate samples from the SE region (32%), as compared to the NW region (7%).

DNA was extracted using QIAGEN's DNeasy Tissue kits, and following the manufacturer's instructions (for details search http://www.qiagen.com/). We aimed to use 10 guard hair roots (see '#G' column) where available. When underfurs were used, the number recorded (see '#U' column) was an estimate because entire clumps of whole underfur were extracted rather than clipping individual roots. An estimate of the amount of the leftover hair (see 'Left' column) was made using three classes: no guard hairs (C); 1–4 guard hairs (B); and > 4 guard hairs (A).

Sample quality was very good, with a mean of 4.8 guard hairs per extracted sample. Many of the samples from known bears had shorter hairs that we typically see, although this did not appear to affect results. If possible, however, we would prefer longer hairs, as these tend to have larger roots and are easier to work with. Alternatively, a piece of footpad the size of a lentil is the best sample material from dead bears, both for ease of handling and data quality.

Marker Selection

Marker selection turned out to be more involved than we envisioned, as we struggled to find markers with the 75% to 80% heterozygosity that we expect in large black bear populations. We initially screened 12 markers that had worked well in previous black bears projects from Utah, Idaho, Texas and Wyoming. These markers were tested on 30 known bears, after which we identified 6 markers (*G10J*, *G10L*, *G10B*, *G1D*, *G10H*, and *G10M*) with mean $H_E = 0.76$ to use for analysis of individual identity. We decided to add a gender marker to this 6-locus system, providing a further reduction in match probability of ~ 50%.

After analyzing ~200 samples we became concerned that there were more pairs of highly similar genotypes than expected, suggesting a higher than anticipated match probability. We also began to fully appreciate the large number of individuals that you had sampled, which creates a challenge since the number of false matches between individuals scales with the square of this number. We therefore tested another 8 microsatellite markers on 29 or 30 individuals, and identified a 7th marker (*G1A*) to use in the analysis of individual identity. This marker had the largest observed number of alleles of the 14 candidate markers (20 minus the 6 already in use) based our sample at the time of 29–30 individuals. The remainder of the analysis of individual identity was therefore conducted with 8 markers, including 7 microsatellites and a gender marker.

Unfortunately, with the benefit of hindsight (Table 1) we can see that *G1A* was not as variable as our original marker selection data had suggested, and that it would have been better to use *G10U* as the 8th marker. Despite the large number of alleles at *G1A*, allele 192 occurs at such high frequency (> 70% in the NW study area) that the marker contributes little to individual identification. I recommend that future projects in this region replace *G1A* with *G10U*, and continue to use 7 microsatellites, plus a gender marker.

Table 1. Summary of marker variability. The first 7 markers, and a gender marker, were run on every sample for the purpose of individual identification. *G10U* was subsequently run on 1 sample per individual to further differentiate pairs whose genotypes were so similar as to be candidates for genotyping error.

Locus	*N*	H_E	H_O	*A*
G10J	512	0.79	0.80	10
G10L	512	0.81	0.81	12
G10B	512	0.73	0.68	7
G1D	512	0.78	0.73	7
G10H	512	0.75	0.73	10
G10M	512	0.75	0.73	7
G1A	512	0.49	0.46	7
7-Locus Mean		0.73	0.70	8.6
G10C	30	0.30	0.33	3
G10P	30	0.16	0.17	4
MU23	30	0.56	0.53	5
MU59	30	0.59	0.63	6
G10X	30	0.64	0.50	5
REN145P07	29	0.66	0.52	5
MSUT2	29	0.59	0.55	4
CPH9	30	0.51	0.60	3
CXX110	30	0.65	0.63	5
CXX20	30	0.65	0.63	5
MU51	30	0.46	0.43	2
MU50	29	0.13	0.14	2
G10U	86	0.70	0.65	8
20-Locus Mean		0.59	0.56	5.9

Microsatellite Analysis

While the marker selection was not straightforward, the analysis of individual identity went smoothly once the markers were selected. This analysis started with a first pass of all 8 markers (including gender). After first pass, we culled 10 mixed samples (*Xmixed*) and 119 samples that had produced high-confidence genotype scores[1] for < 4 of 8 markers. This culling step is central to the efficiency and accuracy of our process, eliminating the samples with the lowest success rate and the highest rate of genotyping error (Paetkau 2003).

---

[1] We use a combination of objective (peak height) and subjective (appearance) criteria to classify genotype scores. Low-confidence scores are identified by removing the leading digit from the allele score, and should be treated as equivalent to missing data.

The first pass was followed by a cleanup phase in which we re-analyzed data points that were weak or difficult to read the first time. In some cases multiple rounds of re-analysis were used to confirm weak data points. Another 21 samples were excluded following cleanup, but the remaining 962 samples had complete, high-confidence scores for the 8 markers that we were analyzing.

The last phase of analysis was error-checking, following our published protocol of selective data re-analysis (Paetkau 2003). Through a combination of reviewing the original results for data entry errors, and re-analyzing obvious candidates for amplification error, we found 12 errors in the new data. We normally encounter errors in about 2–3% of remotely collected hair samples (Paetkau 2003), so the number of errors detected in this project was below average at ~ 1.25%. Rates of amplification error vary with sample quality, suggesting higher than average sample quality in the current project.

After correcting these 12 errors, there were 4 1MM-pairs (pairs that matched at 7 of 8 markers) and 24 2MM-pairs remaining in the file, as well as 6 3MM-pairs that fit the pattern expected of ‘allelic dropout’ (ADO; the only type of error that is expected to affect 3 markers in a single sample). With this total of 34 pairs that were candidates for error-checking, we decided to analyze *G10U* on each pair (1 sample per genotype) to reduce the number of similar pairs prior to the formal process of confirmation through re-analysis.

After adding the *G10U* results there were 2 1MM-pairs, 5 2MM-pairs, and 2 ADO-style 3MM-pairs left in the file, each of which was then confirmed by re-analyzing the mismatching markers (twice for the 1MM-pairs). Extensive testing with blind control samples has shown that this protocol effectively prevents the identification of false individuals through genotyping error (Kendall *et al.* 2009).

Notes on the Gender Analysis

We originally indicated that the amelogenin marker would be used for gender analysis, and we started the analysis using that marker. However, the decision to add *G1A* to the analysis created a size overlap conflict with amelogenin, prompting us to switch to a newer ZFX/ZFY gender marker. This marker is functionally equivalent to amelogenin, using a single pair of primers to amplify a segment of DNA that occurs on the ‘pseudoautosomal’ portion of the sex chromosomes, but with different lengths on the X- and Y-chromososmes.

Some of your samples arrived with ‘known’ gender from the field, but we included these samples in the gender analysis since we were already setup with an 8-locus marker system for the rest of the project. There were 4 cases where successful known samples were identified as male in your spreadsheet but then produced female gender results. We analyzed each of these samples at least twice for gender, including at least one analysis with the amelogenin marker. Given the reproducibility of the results, and the concordance between markers, we believe that these 4 animals are indeed female. Gender results for these bears are highlighted in yellow in the results file.

A final note on the gender results is that they come with an expected error rate of ~ 0.001 unless they have been replicated. When more than one sample is identified per individual, then the entire genotype has been replicated between samples. A subset of samples (~ 1 in 30) were also replicated by being re-run as positive control samples. However, in many cases there was only 1 sample identified from a given individual, and there was no field data to confirm the gender, and in such cases there is no method short of wholesale data replication for detecting the approximately 1 in 1000 animals with inaccurate gender data.

Notes on the Success Rate

Of the 706 successful snare samples, 274 were extracted from samples that did not meet the original quality threshold of 3 guard hairs. Success rate, expressed as the proportion of extracted samples that were analyzed successfully, was higher than we typically see, at 80% for the SE region, 85% for the NW region, and 99% for known bears. We expect remotely snared samples to have a lower success rate than samples from bears that have been physically handled, but I was interested in the difference between study areas, and so looked at that in more detail.

While there was an obvious difference between study areas in terms of extraction rate, among the samples that were collected in June and July the success rate for the SE study area was only 2–3% lower than for the NW study area. In both areas the extraction rate and the success rate were lower in July than in June. Where the study areas differed more significantly was that August collections were only made in the SE, and the success rate for August was substantially lower than for either June or July. This decline in sample quality as the season advances has been noted in other studies, and we presume that it relates to the ease with which hair can be pulled at different times of year. In studies that continue into the fall, and even into winter in places like Florida, sample quality continues to decline until spring.

Identification of Individuals

Once the genotypes were completed and checked for errors, we defined individuals for each unique genotype, taking ID numbers from the first sample to be assigned to a given individual. This information is cross-referenced in the "Individual" column of the "Samples" worksheet, and the "List of Samples" column of the "Individuals" worksheet.

The 706 hair snare samples with good genotypes were assigned to 266 individuals (117 NW, 149 SE), with no individuals caught in both study areas. Unsurprisingly, the 256 known samples were assigned to 256 different bears, including 10 'recaptures' of bears identified from hair snare samples. In each case where a snared bear was matched to a known bear, the gender results were the same, and the snare capture event preceded the physical 'capture' event. Both the hair snare captures and the known bears were slightly male-biased (53% and 56% male, respectively).

Marker Power

The 6-locus marker system that we started the project with (the first 6 rows of Table 1) have a respectable H_E of 0.77, in keeping with our recommendation for 6-locus marker systems (Paetkau 2003). Each individual that we identified in this project had a unique genotype for these 6 markers, so the addition of a gender marker and *G1A* to the analysis had no practical influence on the individual identifications.

Calculated match probabilities vary by orders of magnitude depending on what assumptions are made about the degree of relatedness among the individuals sampled. For example, in the current file the sibling match probability for the 7 microsatellite markers at which all samples were typed was 2×10^{-3} whereas the match probability for unrelated individuals was 1×10^{-7} (both of these values should be multiplied by approximately 0.5, which is the match probability for gender, independent of degree of relatedness). The disparity between these values renders them unhelpful for assessing the actual risk that we sampled any pair of individuals with the same 8-locus genotype.

An alternative to calculated match probabilities is to extrapolate from an observed mismatch distribution (Paetkau 2003). Experience with data from known individuals has shown that this approach provides a more precise estimate of the risk of false matches. For example, had we analyzed the 256 known bears in this dataset using just the first 4 markers in Table 1 — reducing the number of markers to the point where some false matches will occur — extrapolation from the observed mismatch distribution would have provided a reasonable prediction of the number of false matches (Fig. 1).

While each of the 256 'known' bears had a unique 8-locus genotype, we would like an estimate of the risk of false matches in the rest of the dataset, either between pairs of snared bears, or between snared bears and known bears. For this exploration I used the 7 markers that I am recommending for continued use, allowing us to confirm that those 7 markers have an appropriately low match probability. The 7-locus mismatch distribution included 5 1MM-pairs (Fig. 2), which is enough to convince us that an 8th marker is called for, but not so many as to call into question the current results.

My conclusion is that the marker system used in this project left little chance for false matches between individuals, but I encourage you to look for evidence of errors as you compare the genetic results to your field data. For example, if we have placed an animal at implausibly distant points within a short period of time, the samples in question should be analyzed at additional markers to confirm the match.

Fig. 1. Distribution of genotype similarity for 256 known bears using data from just 4 markers. This example illustrates how extrapolation from an observed mismatch distribution can accurately predict the number of pairs of animals with identical genotypes (3 in this example).

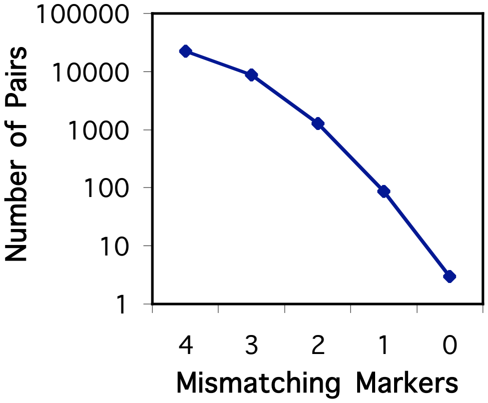
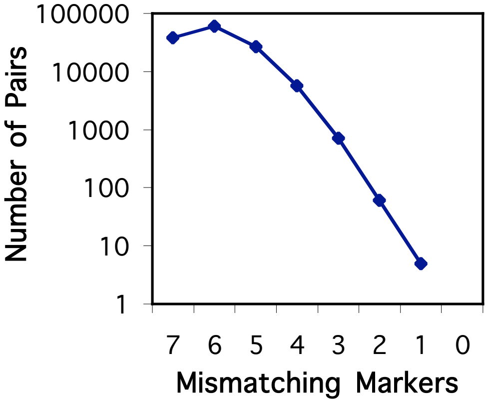


Fig. 2. Actual mismatch distribution for 512 individuals in the attached results file, based on the 7 markers (including gender) that we recommend to continue using (i.e. without *G1A*). Extrapolation suggests < 1 pair of individuals with identical genotypes were sampled. Adding *G10U* to future analyses would further reduce the match probability.

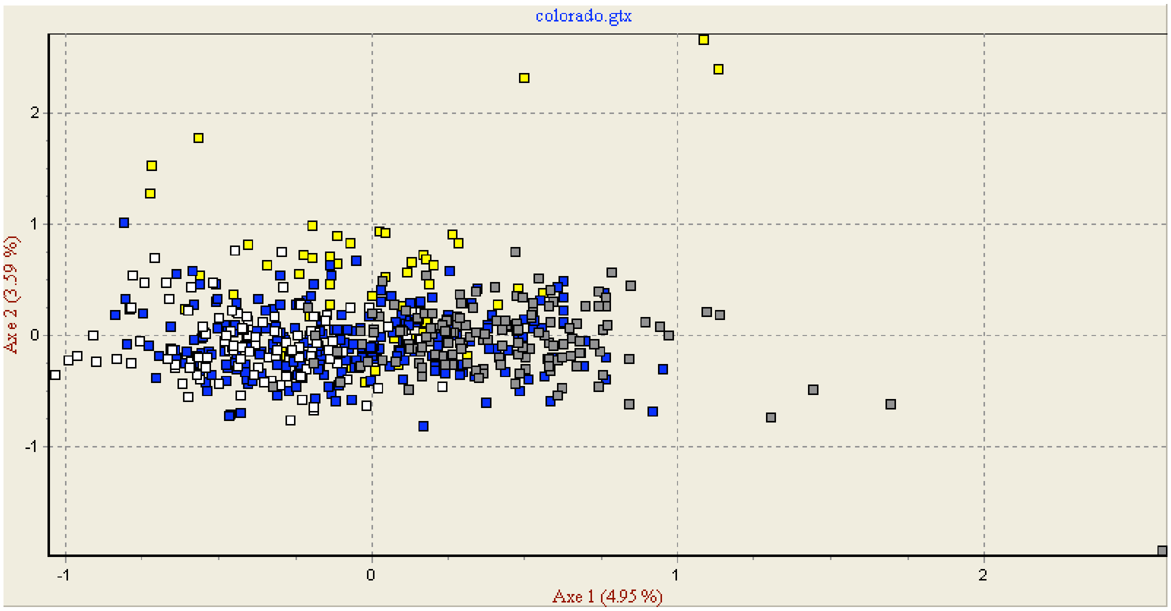


Population Clustering

I realize that we were unlikely to have sampled any grizzly bears, or immigrants from genetically distinctive populations, but it is always worthwhile to check a dataset like this in a clustering program to see if any individuals stand out for any reason (e.g. genotyping error). I was also interested in the distinctiveness of your two study areas, although I don't know their locations. I therefore performed a quick clustering analysis in the program Genetix, which performs a principle components-style treatment on individual genotypes. Out of personal interest, I included reference data from a similar project in Utah.

While the clusters produced for the SE and NW study areas were not superimposed, as would be expected if they were genetically homogeneous, the degree of differentiation between areas appeared slight (Fig. 3). There was one particular outlier that I looked at in detail, including reviewing genotyping runs, but this appeared to be a simple case of an individual with a rare genotype, as are often encountered when clustering analysis is based on so few markers.

Fig. 3. Results from the first two dimensions of a factorial correspondence analysis (program Genetix) based on 6-locus microsatellite data from NW (white), SE (grey), and 'known' (blue) study groups, as well as comparative data from an unknown population in Utah. Data for *G1A* were not available from Utah, so this marker was not included in the analysis. I could find no explanation for the outlier at bottom right, other than it had some rare alleles in its genotype; an analysis based on more markers would be required to conduct a serious investigation of individual origins.



Various and Sundries

It is my intention to communicate these documents in electronic form only, but I'd be happy to send hardcopies through the post if you need them. An invoice for US $43,550 accompanies these results, with unit prices taken from the contract (including the $5 discount for samples that you extracted). We did not charge you for a customs invoice that we received because you declared a commercial value of $200 on the shipment, but please enter a nominal value of $1 on future shipments. Unless you tell me otherwise, I'll count on you to get the invoice to the appropriate desk for processing.

While there were unusual administrative demands associated with the lead up to this project, and unexpected complexities at the marker selection phase, the high sample quality, large sample size, and straightforward nature of the work alleviated any initial concerns about the financial viability of the project. Now that we have dealt with many one-off complexities, any opportunity for involvement with your future studies would be more than welcome.

We understand that you would like any unused hair returned to you. Please let us know the contact name and address for where you would like the hair sent, as well as a courier account to which shipping charges can be billed. Note that we are also willing to archive your leftover materials under appropriate conditions for 5 years, as long as there is a prospect for continuing work; we often refer to such archived material when error-checking new data against old, or when adding data in the context of population genetics or parentage analysis.

Please keep us in mind when distributing reports relating to this work; we are always interested to learn more about the projects that we have worked on.

Thank you for your patronage, and please feel free to call with any questions or concerns.

Yours sincerely,

David Paetkau, Ph.D.
President

encl.: g0805 Results.xls; g0805 Invoice.pdf.

THE
MOUNTAIN
LION
IN
NEVADA

STATE OF NEVADA

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0-4101

THE MOUNTAIN LION IN NEVADA

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NEVADA DEPARTMENT OF WILDLIFE

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1983

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INTRODUCTION

The mountain lion (Felis concolor) is one of the most intriguing large game species in Nevada and the controversies surrounding this great cat have often become embroiled in a battle between fact and fiction, love and hate, and conservation and exploitation.

In its simplist interpretation the lion has been merely laying claim to the land it has freely roamed since the Pleistocene epoch. The recent invasion of its realm by the modern American and his livestock, followed by the bounty hunter, the fur hunter, and the sport hunter, contradicted that claim and resulted in a reduction of Nevada's mountain lion populations, as well as a conflict in ideologies among the people of the state. Hopefully, now, in a more enlightened period, we may, in some way, find a means of compromising the forces which have been working against the mountain lion's survival. In order to do this a basic understanding of the lion's life history is required so identified conflicts can be resolved or mitigated. If the myths are separated from the facts, and people are willing to try and resolve their differences, then a management plan which will provide for sustained mountain lion populations can be implemented.

In March 1972, the Nevada Department of Wildlife initiated a study of the mountain lion as a part of the Ruby-Butte deer project (Papez 1976) in eastern Nevada. The objective was to determine the status of lion populations within this highly valuable deer area and evaluate them in relation to deer populations. Within two years this objective was changed to: a) establish population estimates of mountain lions by mountain range or management area statewide, b) establish basic habitat requirements, 3) establish a harvest management program. From that period on, increased emphasis was placed upon lion capture and marking with the more sophisticated telemetry devices which were being manufactured. This program involved lion monitoring from both land and air and was instrumental in expanding our life history data base as well as providing an approach toward estimating the annual population status of key mountain ranges. The findings which resulted from this study were then utilized in formulating an approach toward estimating statewide lion populations.

In doing this, the Department was essentially moving toward the development and implementation of a Unit Harvest Management scheme. This management approach was a direct result of pressures arising from three distinct groups of people, all of whom had different interests:

1. The livestock industry which wanted stringent predator control.
2. The professional mountain lion guide who wanted the freedom of taking clients where he desired, with minimum restrictions in season length, harvest, or area of hunt.
3. The protectionist who basically wanted no harvest of the mountain lion.

The role of the Department of Wildlife was, therefore, one of attempting to develop a plan which satisfied most interests as well as meeting the legislative mandate of preserving viable mountain lion populations for the future. In the latter years of the study, while developing a Unit Management approach, Department personnel throughout the state were assigned to pertinent jobs in their local areas, the study areas, or both.

ACKNOWLEDGMENTS

Dave Ashman was the principal investigator assigned to the mountain lion study during most of its ten year duration. A rough draft, which was partially used in the preparation of this manuscript, was written by Dave prior to his resignation from the Department in 1982.

Personnel from the United States Fish and Wildlife Service cooperated in this study from its initiation by providing experienced lion hunters with trained hounds and much of the necessary equipment. The late Dick Hall, a U.S. Fish and Wildlife Service lion hunter in Nevada from 1956-79, unselfishly provided a vast storehouse of knowledge, time and experience during the first 7 years of the study. Jim Buhler and Richard Holcomb, also government lion hunters, provided able assistance in capturing lions during the last 3 years of study.

Many Department of Wildlife employees assisted in the field work, some of which was done under the most adverse winter conditions. A listing of them would include almost the entire Game Division staff and most of the Regional game personnel, all of whom willingly assisted in study design, equipment procurement, and endless hours of field work. Allan Flock, Jim Jeffress and Gregg Tanner provided help beyond the normal call of duty.

Dave Beatty of Telonics, Inc. was instrumental in designing and manufacturing the telemetry equipment which was used so successfully during the later years of the study. A phone call to Dave saved many a day when there were equipment crises.

Glen C. Christensen was responsible for data analysis, rewriting and editing of this manuscript. In doing so he drew freely upon the talents of George Tsukamoto, Mike Hess and Mike Wickersham of the Nevada Department of Wildlife and Harley Shaw of the Arizona Game and Fish Department.

DESCRIPTION OF THE STUDY AREAS

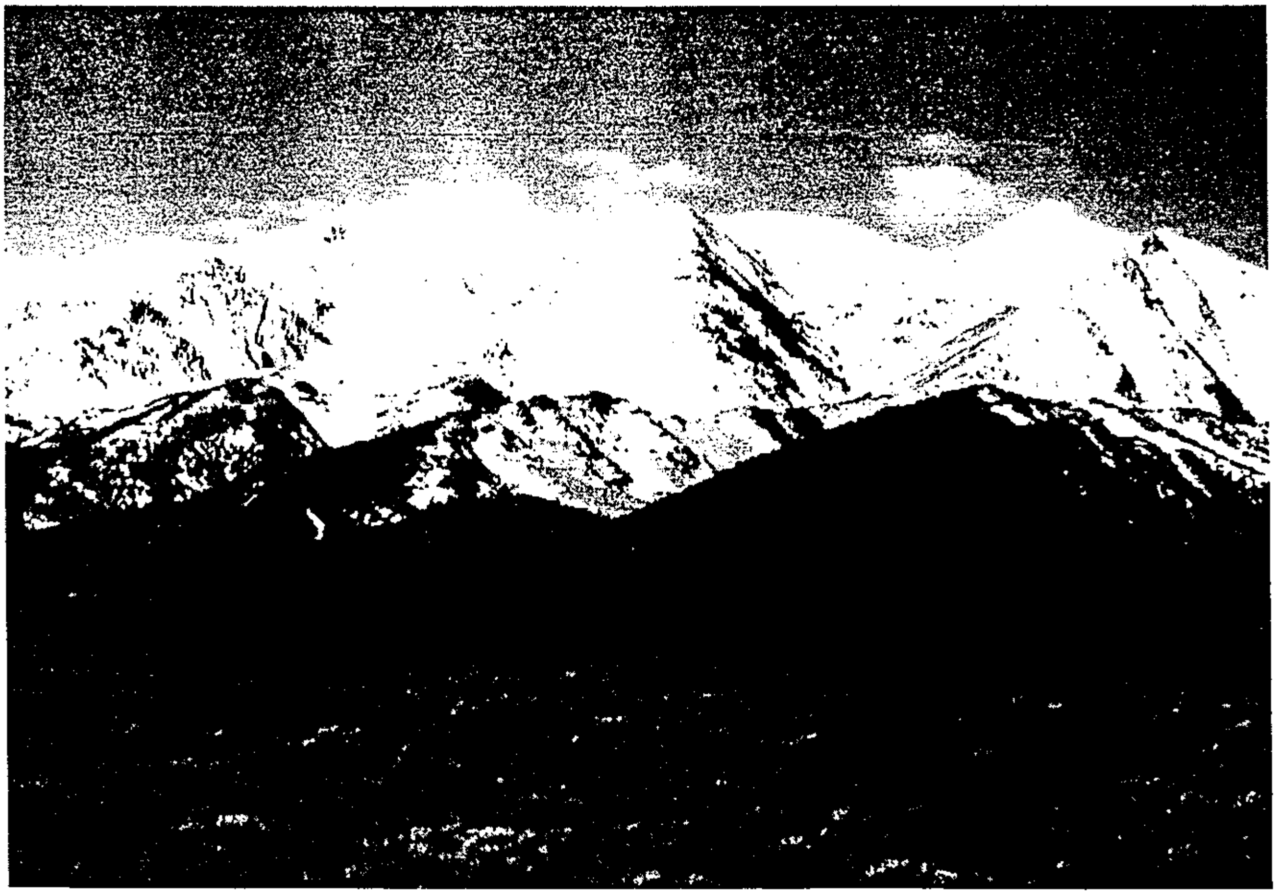
Location

The principle study areas were located in the Ruby Mountains (eastern Nevada) and in the Monitor Range (central Nevada). Additional, but less extensive work was conducted in the following ranges: Schell Creek, Cherry Creek-Egan, Spruce, White Pine, Toana, Maverick Springs, Snake, Jarbidge and Antelope-Fish Creek, all of them being grouped in Northeastern and Central Nevada (Figure 1).

RUBY MOUNTAINS--The Ruby Mountains are composed of three distinct divisions: the East Humboldt Range, Ruby and South Ruby (Figure 2). The East Humboldt Range, which comprises the northern portion, is located north of Secret Pass and south of Wells encompassing an area of 221 square miles. This division embraces extensive summer range for both mule deer (Odocoileus hemionus) and lions. Winter range is limited due to deep snow which forces the deer to migrate considerable distances south and east (Papez 1976).

The Ruby division, located between Secret Pass and Harrison Pass, is the largest unit and contains 362 square miles of mule deer and mountain lion summer and winter range.

The South Ruby division is primarily winter range for mule deer and lions, although some fair to good summer range is present on the west slopes between Harrison Pass and Overland Pass. This area embraces 270 square miles, but generally lacks good water distrubution and high quality deer habitat.



South Ruby Mountain Range Lion Habitat

The entire Ruby study area encompasses approximately 853 square miles. The northern third of the Ruby Range and the majority of East Humboldt Range are composed of intermixed private and public lands.

MONITOR RANGE--The Monitor Range extends 97 miles north to south between the general vicinity of Eureka and Tonopah, Nevada. Most of the field work was conducted on the northern 25 miles of the range, primarily from Dobbin summit north, which included an area of 335 square miles (Figure 3), nearly all of which is on public lands.

General Characteristics of the Environment

Detailed descriptions of the topography, soil, climate and vegetation, which are applicable to the study areas, are presented in the Nevada Department of Wildlife publication titled "The Ruby-Butte Deer Herd" (Papez 1976). Generally, these descriptions also apply to mountain lion habitat throughout the state, with some local modifications, which are well covered by Billings (1951).

In brief, the physiographic characteristics are typical of the Great Basin. The mountains and valleys trend in a north-south direction with elevations ranging from 5,500 feet in the valleys to heights of 9,000-11,000 feet for the mountain peaks. The exceptional Wheeler Peak, in the Snake Range, crests at over 13,000 feet.

Monitor Range Lion Habitat

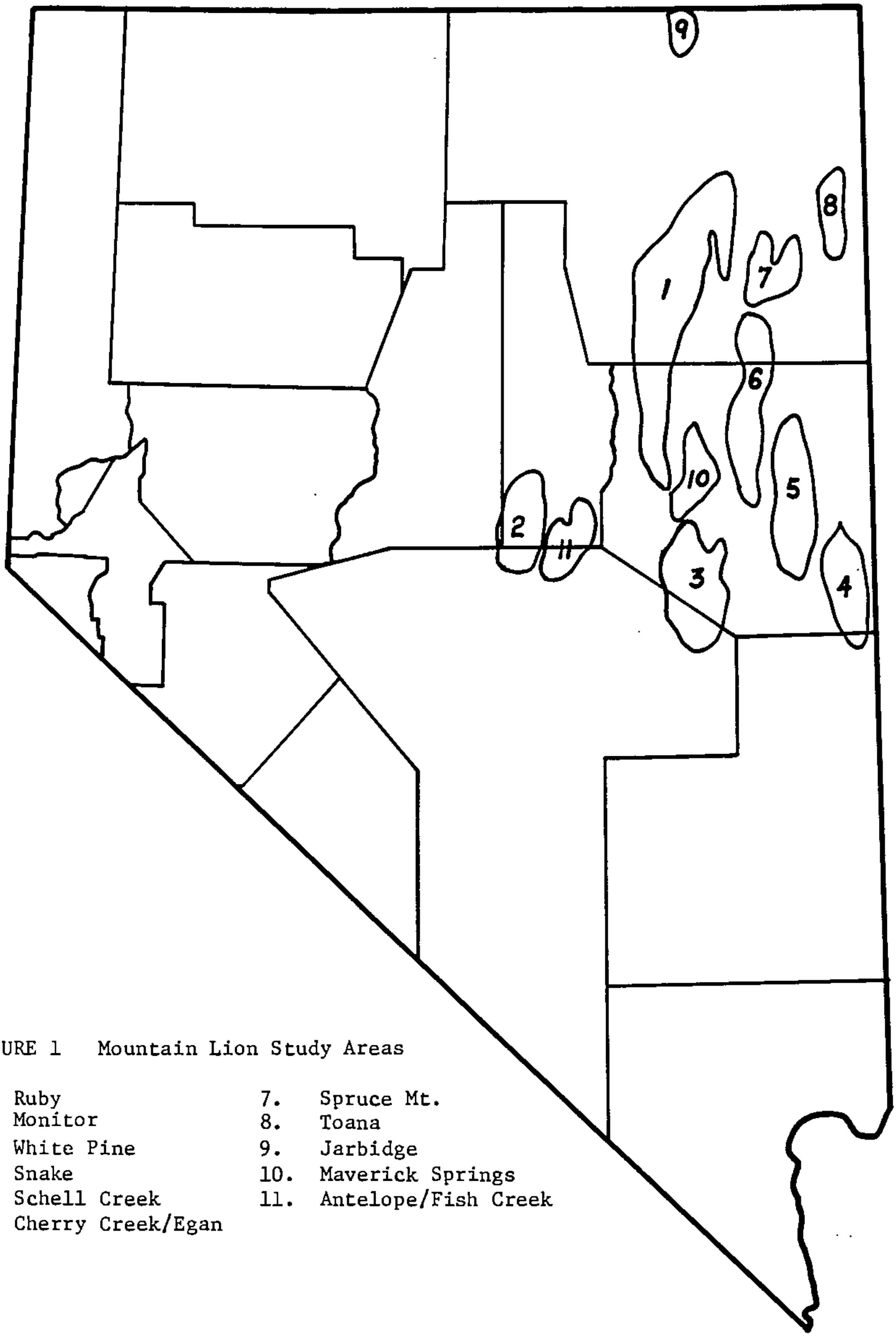


FIGURE 1   Mountain Lion Study Areas

1. Ruby
2. Monitor
3. White Pine
4. Snake
5. Schell Creek
6. Cherry Creek/Egan
7. Spruce Mt.
8. Toana
9. Jarbidge
10. Maverick Springs
11. Antelope/Fish Creek

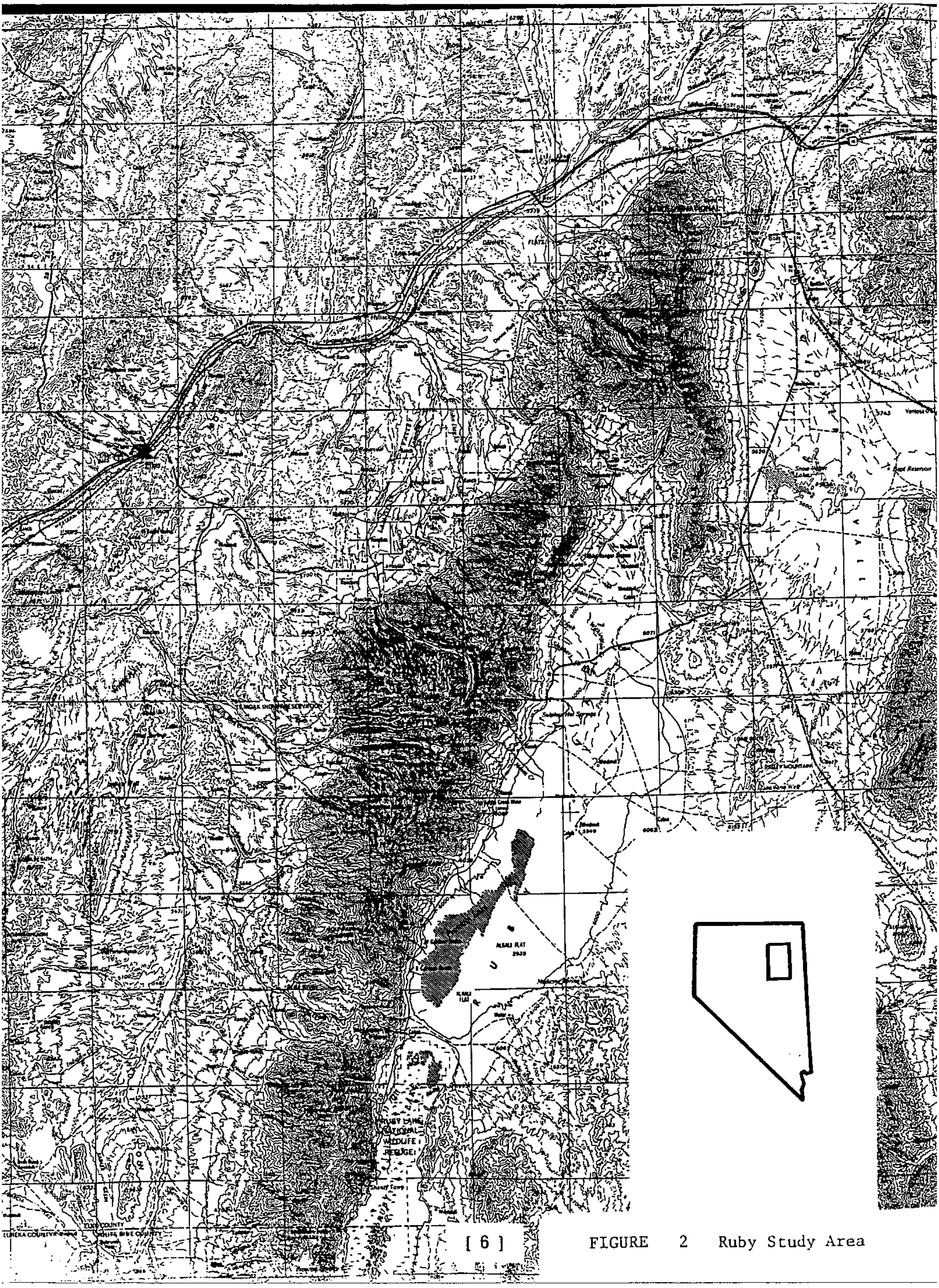


FIGURE 2 Ruby Study Area

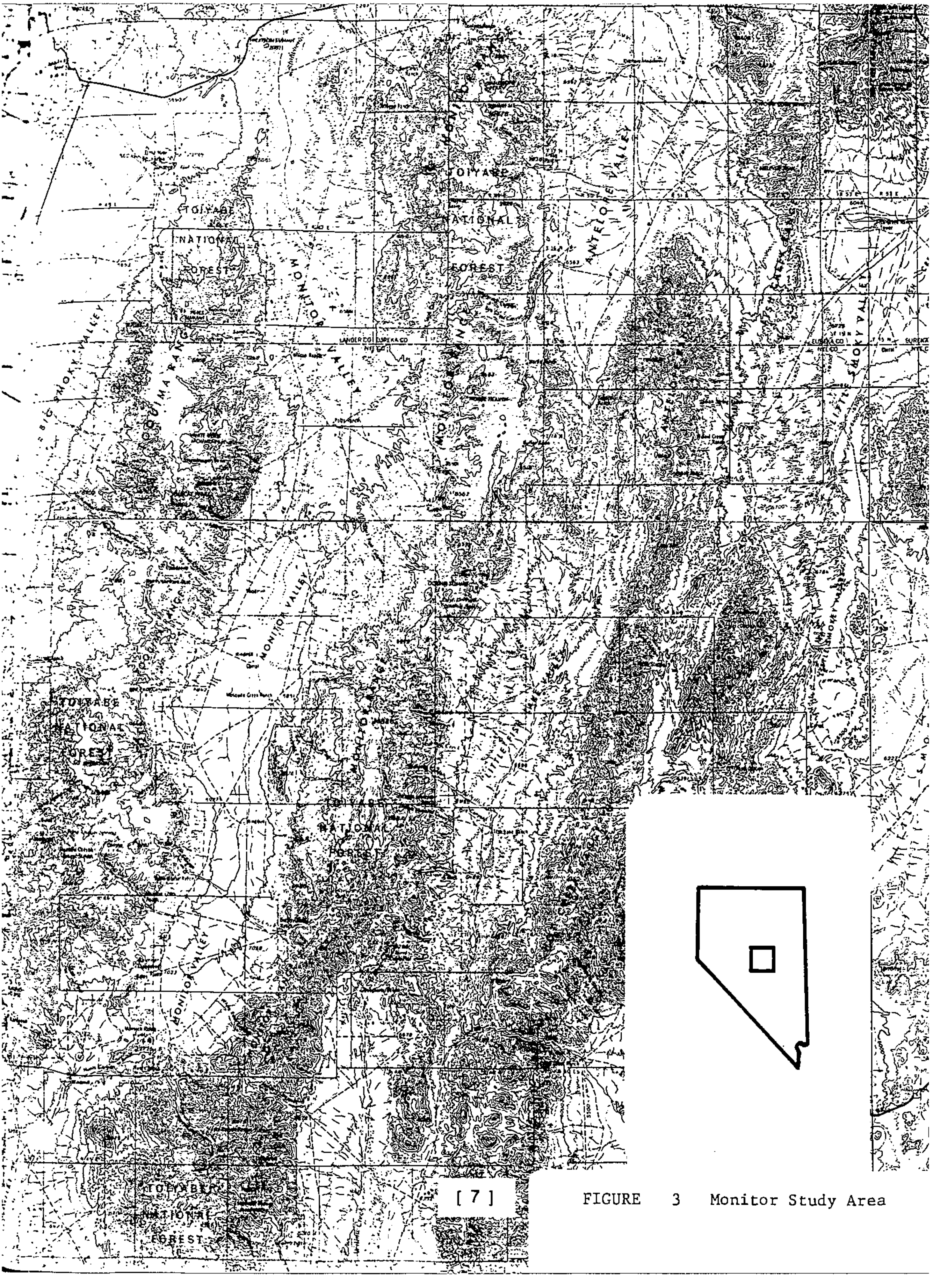


FIGURE 3 Monitor Study Area

The climate is typically one of hot, dry summers and cold, wet winters. Maximum precipitation occurs in late winter and early spring and varies considerably by site, being 13-15 inches annually at elevations above 7,500 feet in the study area. Temperatures vary dramatically over a 24-hour period and it is not unusual to record a 50°F spread between the morning low and the afternoon high. Similarly, there is also a great variation between the winter lows and summer highs, such as a -43°F minimum and 107°F maximum recorded in Elko, Nevada. The wide ranging temperatures are a feature of the Great Basin area which makes it prudent for one to carry a down sleeping bag the year around.

The vegetation is typified by a Sagebrush Zone which dominates the valley floors and the lower foothills. Big sage (Artemisia tridentata) is the major species. Big sage and black sage (Artemisia nova) are also well represented in the other vegetational zones which occur in the study area. At the lower elevations of the deer summer range, which would also demark the mountain lion ranges, big sage is associated with bitterbrush (Purshia tridentata) and rabbitbrush (Chrysothamnus vicidiflorus).

On the foothills above the sagebrush zone, but below 7,500 feet, a belt of Pinyon-Juniper (Pinus monophylla - Juniperus osteosperma) becomes the dominant type. This pygmy forest is a very important transitional zone for deer as they move through it from their summer and winter ranges. The major understory plants are sagebrush, bitterbrush, rabbitbrush and serviceberry (Amalanchier alnifolia). Pinyon-Juniper is not significantly present in the Ruby Mountains north of Harrison pass; however, in the Monitor study area it is the dominant vegetation at the lower elevations.

Elevations above 7,500 feet to 9,500 feet are characterized by mountain brush. This summer range is an extremely important zone for deer, and consequently mountain lions, and is dominated by quaking aspen (Populus tremuloides), mountain mahogany (Cercocarpus ledifolius), snowbrush (Ceonothus velutinus), chokecherry (Prunus virginianus), willow (Salix spp.) and wild rose (Rosa spp.).

Along the crests of the mountains at elevations above 9,500 feet, the Alpine-Subalpine forest is found. Limber pine (Pinus flexilus), whitebark pine (Pinus albicaulis) and occasionally white fir (Abies concolor) and bristlecone pine (Pinus aristata) are the dominant trees. Prominent understory species are snowbrush, dwarf juniper (Juniperous communis) and bearberry (Arctostaphylos uva-ursi).

METHODS

Harvest data, which included U.S. Fish and Wildlife Service depredation removal and the Nevada Department of Wildlife sport harvest records, were reviewed to identify mountain ranges throughout the state that contained lion populations. Sight records, of lions or their tracks, obtained by professional government lion hunters, sport hunters and guides, and Department personnel were used to augment harvest data in compiling distribution maps. All records were plotted on 1/250,000 topographic maps and the area of occupied lion habitat was delineated and square miles computed.

The primary methods used for obtaining data was through lion capture, marking and recapture, and from radio-telemetry monitoring. The majority of the capture efforts were conducted during winter months when the ground was covered with snow and tracks could be located by driving roads, snowmobiling or on foot. Once fresh tracks were found, trained hounds owned by government hunters would be started and followed until a successful capture was made or the hounds had to be pulled off the trail due to severe weather, darkness, exhaustion or other reasons. Once a lion was cornered, its weight was estimated and the proper drug dosages prepared for tranquilizing. During the first six years of the study the drugs Sernylan (Phencyclidine hydrochloride) and Sparine (Promazine hydrochloride) were used in combination, with a ratio of 1-3 parts Sparine to 1 part Sernylan, depending on the dart syringe capacity (1.5-3.0 cc). These drugs were used at a rate of 0.1 cc per each 20 pounds of body weight. During the last 4 years of the study the drug Ketaset/Vetalar (Ketamine hydrochloride) was used with considerable success, although the volume required (1 cc per 20 pounds) did present some difficulties because occasionally not all of the drug was absorbed by the muscle. All drugs were manufactured by Park, Davis & Company, Detroit, Michigan. All Cap-Chur syringes, powder charges and guns were supplied through Palmer Chemical and Equipment Company, Douglasville, Georgia.

After immobilization each animal was sexed, weighed and aged. Any injuries, other abnormalities and ectoparasites were recorded. Females were checked for indications of pregnancy, estrus or nursing. Tooth replacement, amount of stain and wear, and a measurement of the upper canines from the gum line to the tips of the labial side of the tooth were recorded for selected lions. During subsequent recapture or harvest any changes were noted. Numbered metal ear tags were placed on some lions early in the study but due to losses were discontinued in favor of numbered rope collars. Once the telemetry program gained momentum radio collars were used. Following data collection and marking the lion was placed in a protected location and allowed to recover.

During the period of 1973-75 lions were instrumented with low frequency radio collars (31 MHz) manufactured by Thomas Owens, Sacramento, California. These collars were either solar powered or a combination solar/nickel cadmium battery units with a life expectancy of less than 6 months. A variety of receiving equipment was used to locate and monitor the radioed lions, but none of it was entirely satisfactory.

During late 1977 more reliable radio collars were obtained from Telonics, Inc., of Mesa, Arizona. These units were of a higher frequency (159 MHz) and were entirely operated by lithium batteries with a theoretical life of up to 44 months. The receiving unit (Telonics Model TR-2) had a direct frequency reading and self-contained rechargeable power pack. Searches and monitoring were conducted from small aircraft and from the ground. Aerial reception varied from 2-50 miles and ground reception from 0.5-20 miles. Some radio collars incorporated a motion sensing device (mercury switch) where non-movement after 5 hours caused an increase in pulse rate (mortality mode) and this feature proved to be very helpful.

FINDINGS

The Mountain Lion

The mountain lion, locally called the cougar, puma, panther or just plain lion, is endemic to Nevada. It is the largest of the unspotted cats in the United States and the sexes are colored alike. The color of adults is tawny or greyish above and whitish below with dark brown on the tip of the long tail, backs of ears and sides of nose. The young are spotted with blackish-brown on a pale fawn ground color. Males are larger than females.

Ninety-seven lions were captured and marked between March 1972 and February 1982 (Table 1). Three of these were captured in western Nevada and 94 from the primary study areas in central and eastern Nevada. The sex and age composition was 57 males and 40 females of which 46 were classified as adults, 16 as subadults and 35 as kittens (see age section for classification criteria).

Fifty-two of the 97 lions were captured and recaptured 116 times and located 695 times through radio telemetry monitoring (Table 2). Many hours and miles were logged in tracking lions on foot which further added to the knowledge of a particular animal. Daily, monthly and seasonal movements were determined for several lions. This monitoring effort made it possible to gain insight on many of the life history subjects presented in this section. Additional information was obtained through the examination of lions killed (for depredations or by sport harvest) during the course of the study.

Distribution

Since mountain lions are adaptable to a great variety of environmental conditions, they are able to occupy most of the mountain ranges in Nevada and are found from the hot southern deserts to the coldest extremes of the northeastern mountains. A generalized distribution map which depicts the probable extent of the mountain lion's range, when considering habitat types and prey base as well as documented lion occurrence, is presented in Figure 4. Based on this map it is estimated that there are 27,811 square miles of mountain lion habitat in Nevada.

Reproduction

Breeding Age -- The average estimated age of first conception for nine female lions which were examined was 29 months, with a range of 22-40 months. Using a 90-day gestation period (Asdell 1964) the average age for giving first birth was 32 months. Eaton and Velander (1977) found that 4 captive females in Washington state had first birth between 26.5-30 months of age. They also reported that the earliest record of a lion giving birth was 21 months.

No data for sexual maturity of male lions was obtained during this study.

TABLE 1. MOUNTAIN LIONS CAPTURED IN NEVADA, 1972-82.

Lion No.	Sex	Estimated Age at Capture	Age Group*	Weight (lbs.)	Date Captured
1	M	7 years	A	147	3-17-72
2	F	18-20 months	SA	95	4-4-72
3	M	18-20 months	SA	--	4-8-72
4	F	6 years	A	--	4-14-72
5	M	20-24 months	SA	123	5-2-72
6	M	6 years	A	--	12-17-73
7	M	2 years	A	144	11-22-75
8	F	3 years	A	105	1-9-73
9	M	7 months	K	55	1-9-73
10	M	18-20 months	SA	--	1-17-73
11	F	16-18 months	SA	79	12-12-75
12	F	18-20 months	SA	--	1-17-73
13	F	18-20 months	SA	105	1-17-73
14	F	4 years	A	95	1-29-73
15	M	5 years	A	152	5-8-73
16	M	20-24 months	SA	--	12-4-73
17	M	18-20 months	SA	128	1-8-74
18	M	7 months	K	55	1-24-74
19	M	7 months	K	50	2-8-74
20	M	7 months	K	53	2-8-74
21	F	4 years	A	110	2-2-74
22	M	4 months	K	35	2-1-74
23	F	4 months	K	30	2-2-74
24	F	4 months	K	28	2-2-74
25	M	5 months	K	42	2-6-74
26	M	5 months	K	42	2-6-74
27	M	15-16 months	K	122	1-28-75
28	M	15-16 months	K	118	1-28-75
29	F	9 years	A	115	1-29-75
30	M	5 months	K	39	1-29-75
31	M	5 months	K	40	1-30-75
32	F	15-16 months	K	--	2-19-75
33	F	17-19 months	SA	--	2-21-75
34	M	2 years	A	130	4-1-75
35	M	6 years	A	155	4-11-75
36	F	13-14 months	K	71	11-21-75
37	F	16-18 months	SA	91	12-18-75
38	F	16-18 months	SA	93	12-18-75
39	M	16-18 months	SA	115	12-19-75
40	F	18-22 months	SA	--	1-7-76
41	F	5 years	A	84	1-8-76
42	M	2 months	K	23	1-11-76
43	M	15-16 months	K	123	1-6-76
44	F	2 years	A	88	1-11-77
45	M	3 years	A	133	1-14-77
46	M	17-19 months	SA	140	1-21-77
47	F	15-16 months	K	81	1-12-78
48	M	15-16 months	K	100	1-13-81
49	F	20-24 months	SA	85	1-23-78
50	M	10+ years	A	145	1-24-78
51	M	8-9 years	A	--	1-25-78
52	M	3 months	K	--	2-2-78
53	F	14-15 months	K	78	2-18-78

TABLE 1. MOUNTAIN LIONS CAPTURED IN NEVADA, 1972-82. (cont.)

Lion No.	Sex	Estimated Age at Capture	Age Group*	Weight (lbs.)	Date Captured
54	M	14-15 months	K	80	2-18-78
55	F	20-24 months	SA	85	6-30-77
56	F	14-15 months	K	70	2-18-78
57	M	6 years	A	128	2-19-78
58	M	3 years	A	137	3-18-78
59	F	6 years	A	--	1-7-79
60	F	4 months	K	--	1-14-79
61	M	3 years	A	135	1-26-79
62	M	5 years	A	--	3-19-79
63	F	9-10 years	A	87	1-17-79
64	M	3 months	K	33	1-17-79
65	F	3 months	K	33	1-17-79
66	M	3 months	K	35	1-17-79
67	M	2 years	A	112	1-19-79
68	M	3 years	A	128	2-21-79
69	F	4 years	A	94	1-30-79
70	F	4 months	K	40	1-30-79
71	M	5 years	A	145	11-30-79
72	F	10+ years	A	93	1-31-79
73	F	18-20 months	SA	--	2-24-79
74	M	9 months	K	68	5-31-79
75	F	9 months	K	--	5-22-79
76	F	9 months	K	64	5-22-79
77	M	2 years	A	--	6-6-79
78	M	3 years	A	132	1-17-80
79	M	6 years	A	--	1-20-80
80	F	9-10 years	A	112	1-24-80
81	F	3 years	A	--	1-14-80
82	F	3 years	A	--	2-5-80
83	F	2 years	A	95	2-14-80
84	M	2 years	A	123	2-22-80
85	M	3 years	A	162	2-23-80
86	M	8 months	K	73	2-27-80
87	M	10+ years	A	149	5-21-80
88	M	6 years	A	121	4-29-80
89	M	18-20 months	SA	133	5-1-80
90	F	6 years	A	100	7-21-80
91	M	3 years	A	--	11-27-80
92	M	3 years	A	--	4-3-81
93	F	2 years	A	--	4-22-81
94	M	9 months	K	87	4-28-81
95	M	3 years	A	143	4-30-81
96	M	9 months	K	83	2-12-82
97	M	3 months	K	27	2-9-82

* A - Adult (24 months +)
SA - Subadult (17-23 months)
K - Kitten (0-16 months)

The location of capture for the above lions is as follows: Ruby Mountains (52), Cherry Creek-Egan (12), Monitor-Antelope (8), Schell Creek (7), Snake (4), White Pine (3), Toana (3), and one each in the Diamond-Fish Creek, Maverick, Spruce, Toiyabe, Pine Nut, Pine Grove, Wellington Hills and Independence.

TABLE 2. NUMBER OF CAPTURES AND RADIO LOCATIONS FOR 52 MOUNTAIN LIONS IN NEVADA, 1972-82.

Lion No.	Sex	No. of Captures	No. Radio-Locations	No. Months Followed
1	M	6	0	10
2	F	3	0	32
3	M	6	4	34
5	M	2	0	3
6	M	2	0	49
7	M	2	0	1
8	F	2	54	24
10	M	2	0	6
12	F	2	0	--
13	F	3	0	13
14	F	3	26	6
15	M	5	1	21
18	M	3	0	52
21	F	2	0	18
29	F	1	0	7
34	M	2	0	6
35	M	3	6	38
36	F	4	116	77
39	M	2	0	48
40	F	3	0	46
45	M	2	0	20
46	M	2	0	19
47	F	2	16	13
48	M	1	0	5
50	M	3	36	19
51	M	1	0	24
54	M	2	0	24
57	M	2	16	44
58	M	2	43	15
61	M	2	0	13
62	M	2	7	3
63	F	2	7	5
67	M	2	27	35
68	M	2	6	3
71	M	2	12	5
73	F	1	5	5
75	F	2	62	36
76	F	2	46	28
77	M	2	18	12
78	M	2	1	7
79	M	1	21	23
80	F	1	21	23
82	F	1	21	22
84	M	2	6	5
85	M	2	34	18
87	M	1	17	19
88	M	3	28	17
89	M	2	13	6
92	M	2	8	2
94	M	2	6	7
95	M	2	7	4
96	M	1	4	3
		116	695	

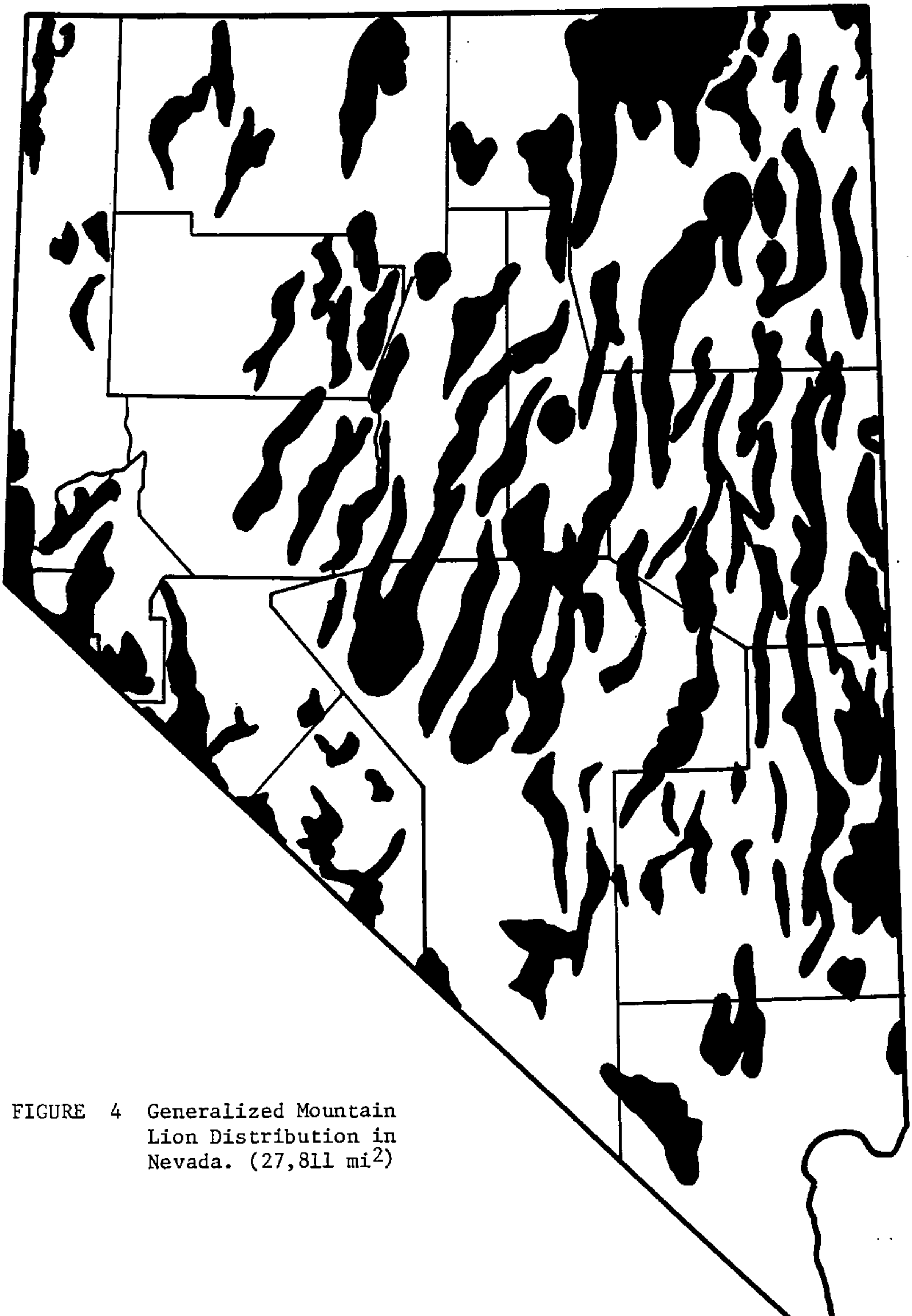


FIGURE 4 Generalized Mountain Lion Distribution in Nevada. (27,811 mi^2)

Time of Birth -- The month of birth was calculated for 135 litters by projecting forward for prenatal litters and backdating for postnatal litters. No kittens older than 12 months (estimated age) were included in the calculations (see section on aging for criteria). The majority of reproductive tracts examined were from females in the latter stages of pregnancy. Prenatal young were aged based on crown-rump measurements or by the overall size of the fetuses in the case of U.S. Fish and Wildlife Service records. The following measurements are believed to be a reasonably accurate means of determining prenatal monthly age classes:

(1) First month ------ 25 mm or less
(2) Second month ----- 26-125 mm
(3) Third month ------ 126 mm or larger

Kittens were born in every month of the year with a peak occurring during the months of June-July (Figure 5). During April-September a total of 94 litters were recorded (70%) as compared to 41 litters (30%) during the remainder of the year. Robinette et al. (1961) computed birth months for 145 litters in Nevada and Utah and found the peak months to be June-September. In central Idaho Seidensticker et al. (1973) reported most births occurred during late spring and early summer.

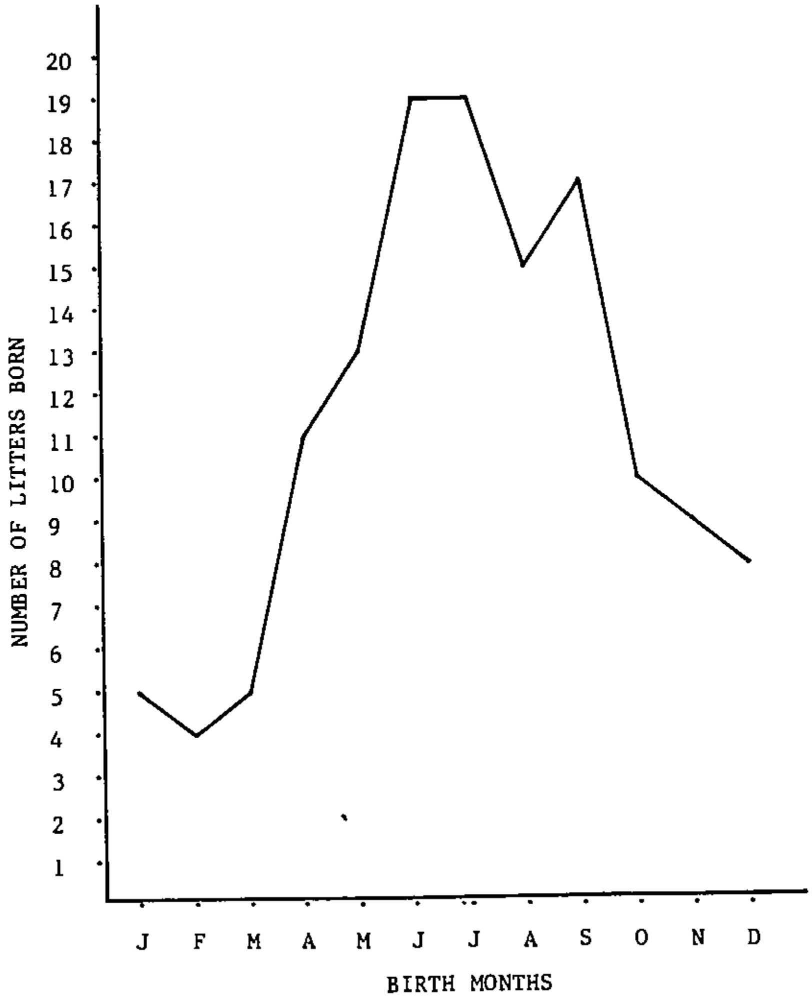


Figure 5. Birth Months for 135 Mountain Lion Litters in Nevada, 1956-82.

Frequency of Litters -- Data from 12 adult female lions indicated that the reproductive cycle (time between litters) ranged from 11.5-24 months and averaged 17.4 months.

Litter Size and Survival -- Examination of 36 prenatal litters revealed an average litter size of 3.08 kittens. The number of kittens per litter varied from 1 to 5 as shown in Table 3.

As the kittens grew there was a gradual loss and the number of kittens observed with their mothers declined to an average of 2.23 by the 12th month. Table 4 shows this loss by estimated age group. In analyzing Tables 3 and 4 it would appear that the prenatal litter size of 3.08 kittens is probably higher than the actual number of kittens born. Furthermore, the litter size for the 4-month age group (2.59) would reflect losses from birth to that time. Therefore, it is felt that the actual birth rate lies somewhere between the two and 2.8 kittens was used as the average litter size when calculations requiring this were needed.

TABLE 3. PRENATAL LITTER SIZES OF MOUNTAIN LION KITTENS.

	Number of Kittens per Litter					Total Sample	Average Litter Size
	1	2	3	4	5		
Number of Litters	1	7	18	8	2	36 litters (111) kittens	3.08

TABLE 4. MOUNTAIN LION KITTEN SURVIVAL BY AGE GROUPS.

	Number Kittens with Mother				Total Sample		
	1	2	3	4	Families Observed	Kittens Observed	Average Litter Size
Estimated Age							
4 months	3	14	21	3	41	(106)	2.59
5-11 months	6	19	15	2	42	(97)	2.31
12 months	6	25	15	1	47	(105)	2.23
TOTAL	15	58	51	6	130	(308)	2.37

Currier (1976) reported the average litter sizes for Colorado as 1.6 (13)*, California 2.0 (8)*, Arizona 2.2 (11)*, and Idaho 2.4 (33)*, while captive lions in Washington averaged 2.6 (92)*. The sample size in all of these states, except Washington, was very small.

The rate of kitten survival in Nevada is good and when coupled with the lions' high reproductive potential it can be speculated that mountain lions are capable of rapidly replacing individuals that are removed from the population.

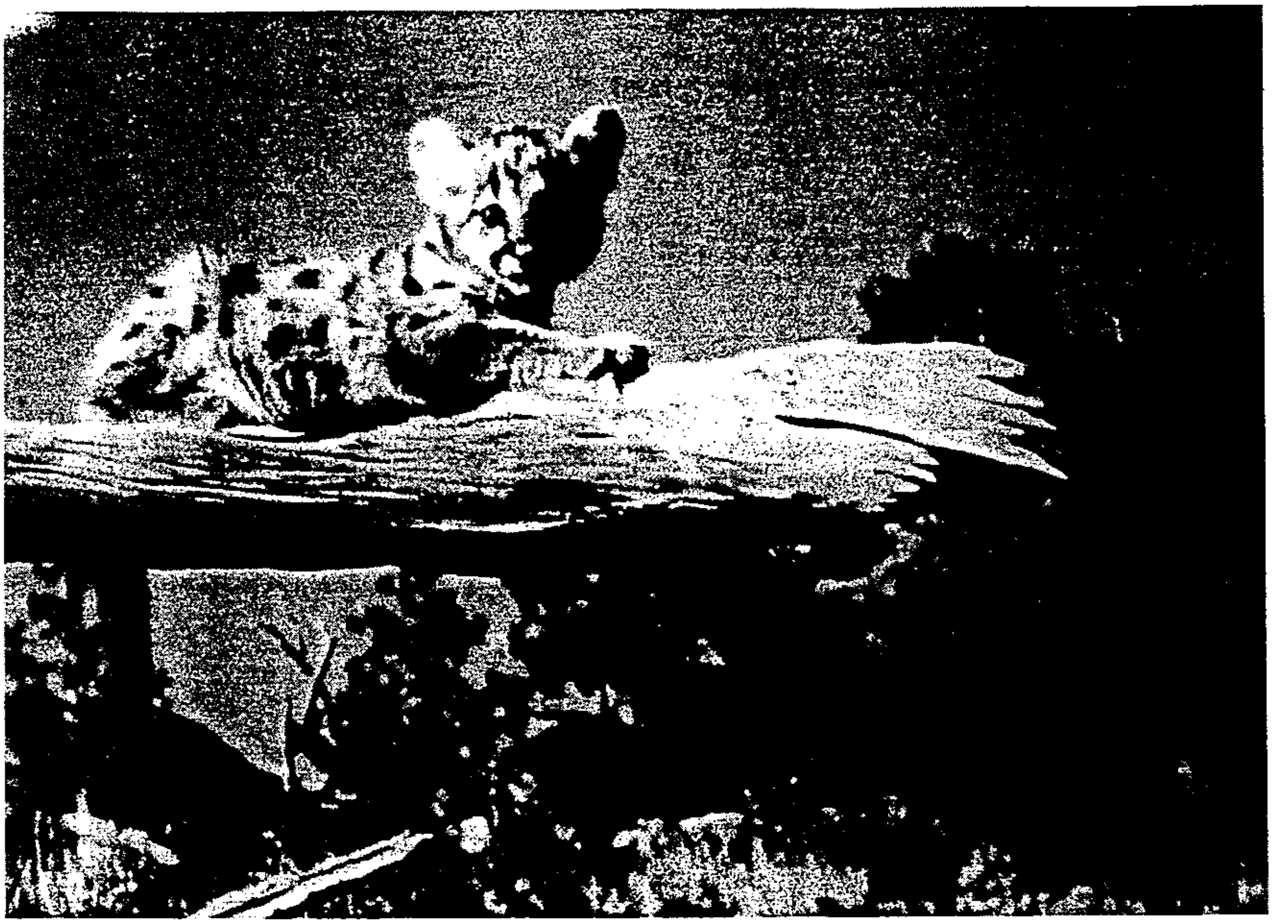
*Number of kittens in sample shown in parenthesis

Population Turnover -- Data relating to population turnover was restricted primarily to the Ruby Division, where records from track counts, captures and recaptures, and radio-telemetry locations indicated that the lion population consisted of approximately 35 animals. During the period of 1954-60 there was a sustained mortality on this population of at least 11 lions per year (30% of total). In 1974 and 1975 thirty lions were known to have been removed from the population, with sport hunting accounting for the highest percentage. Yet, three years later (1978), following the initiation of very restrictive sport hunting regulations, this population appeared to have recovered to its former level. This conforms with the findings of Robinette, et al. (1977) who felt that the annual recruitment and mortality of cougars in their Utah study area was 32%.

It appears that under moderate to heavy exploitation (30%-50% removal) Nevada lion populations have the recruitment capability of rapidly replacing annual losses.

Sex Ratios -- U.S. Fish and Wildlife Service and Nevada Department of Wildlife records for the period between 1954 and 1982 show that 83 litters containing 198 kittens had a sex composition of 89 females and 109 males (100 F; 125.5 M). The data clearly shows an unequal sex ratio, in favor of males; however, a large number of litters recorded by the U.S. Fish and Wildife Service were not sexed and the data base to date may not be representative of true conditions.

Aging -- The terminology used for classifying mountain lion age groups has been confusing to say the least. The term kitten is commonly applied to young lions and in some instances this appellation is used until the youngster finally leaves its mother (approximately 2 years old). Under this connotation the kitten can be newborn, with obvious kitten-like characteristics, or an immature lion which, on superficial examination, cannot be differentiated from an adult -- a broad category indeed. Shaw (1980) not only uses the term kitten but also classifed lions in the age group of 0-2 years as subadults. This probably can be attributed to "lion talk" between the professional hunter and the researcher, where they recognize a difference but have not defined it. Seidensticker (1973) related that "as a lion grows older, it passes through a series of relatively discrete behavioral stages: kitten, transient adult, resident adult." He also referred to small kittens and big kittens (over a year old). In this case behavioral stages and age groups could become confusing. Hornocker (1970) refers to kittens, juveniles and adults but offered no criteria for distinguishing them, other than calling a 1 year old a



A Mountain Lion Kitten at Less than 4 Months Showing Distinct Spotting.

kitten. Currier (1976) did set up a rudimentary classification for three age groups: kitten, adolescent and adult, but it is very generalized and there is some major overlap in criteria. The term yearling has also popped up in the literature and in lion discussions and could be interpreted as being interchangeable with kitten or subadult, but also has the connotation of distinguishing a large kitten from a small one. The need for some approach toward standardization of terminology and relating it to criteria has been evident for some time (Mountain Lion Workshop 1976).

When this study was initiated some broad criteria for the general classification of age groups was adopted. As the study progressed additional criteria, primarily relating to tooth eruption and growth, were incorporated into the key. Even now the distinction between the three proposed age groups (kittens, subadults and adults) often requires a subjective evaluation. However, the criteria presented in Table 5, if used, certainly will help eliminate some of the general age classification confusion.

A further refinement, for aging juveniles by months and adults by year, was explored through the use of tooth eruption sequences, growth, stain and wear. Sufficient data was not collected to be statistically sound, and initial ages had to be estimated; however, this information could be a starting point for additional research toward determining ages more accurately.

Teeth from 94 kittens and subadults were examined to develop the eruption

TABLE 5. CRITERIA FOR A GENERAL CLASSIFICATION OF MOUNTAIN LION AGE GROUPS.

KITTENS (0- 16 months)

* 1. Body weight.
2. Pelage spotting; fading by 3rd or 4th month.
3. Still with mother.
4. Deciduous teeth present or permanent teeth erupting.
   (See Table 6 for a guide to estimating kitten ages).
5. If all teeth are permanent then canines are not fully extended.
   Canine length is less than 28 mm in males and 23 mm in females.

SUBADULT (17 - 23 months) - Has passed through juvenile period but not yet attained typical adult characteristics.

* 1. Body weight.
2. Pelage spotting still present on insides of front legs.
3. Not sexually mature. Females not nursing (small teats and no areola).
4. May or may not be with mother.
5. Full extension of canines. Canines measure 28-31 mm in males and 23-25 mm in females.
6. Teeth ivory white in color, not stained.

ADULTS (24 months or over)

* 1. Body weight.
2. Independent of mother.
3. No spotting on pelage or very faint.
4. Sexually mature. Evidence of nursing in females, large teats and presence of areola (may not be evident in young females just entering this age group).
5. Tooth wear and/or stain. (See Table 8 for a guide to estimating adult ages.)

* The following standards are based on weights from Table 1.

<u>Kittens</u>
Males - up to 123 lbs.
Females - up to 81 lbs.
Weight differences between kittens and subadults are obvious up through approximately 9 months. From this age on there can be an overlap and other criteria must be used in conjunction with weight.

<u>Subadults</u>
Males - 115-140 lbs.
Females - 79-105 lbs.

<u>Adults</u>
Males - 112-162 lbs.
Females 84-115 lbs.

TABLE 6. A GUIDE FOR ESTIMATING AGES OF MOUNTAIN LION KITTENS BY TOOTH ERUPTION SEQUENCES.

Age (Months)	Sequence of Permanent Tooth Eruption
2	Complete set of deciduous teeth; permanent P^2 and M^1 erupted
3	Permanent incisors erupted
4	Upper canines and P^4 erupt
5	M_1 and lower canines erupt
6	P^3 erupts
7	P_4 erupts
8	P_3 erupts; upper canines 50-60% extended from gum lines (males: 16-18 mm, females: 12-14 mm)
9 & 10	P^4, M_1, and P^3 become fully extended
11 & 12	P_4 and P_3 fully extended; upper canines 70-80% extended (males: 20-22 mm, females: 15-17 mm)
13 & 14	Upper canines 80-90% extended (males: 24-27 mm, females: 19-21 mm)
15 & 16	Upper canines fully extended by 16th month (males: 28-31 mm, females: 23-25 mm)

TABLE 7. CRITERIA FOR ESTIMATING AGES OF ADULT MOUNTAIN LIONS.

2 YEARS OLD

1. Canines white, no staining.
2. No wear on incisors 1 and 2. Third incisor may show slight wear.
3. Tips of canines show little or no wear.

3 and 4 YEARS OLD

1. Canines lightly stained.
2. Slight wear on highest point of crown of third incisor. Area of wear 1-4 mm across.
3. Incisors 1 and 2 with little or no wear.
4. Tips of canines with little or no wear (2 mm or less).

5 and 6 YEARS OLD

1. Canines moderately stained.
2. Third incisor worn to within 1-4 mm of crest of incisors 1 and 2.
3. Incisors 1 and 2 have slight to moderate wear along crown.
4. Tips of canines with obvious wear (3-5 mm worn off).

7-9 YEARS OLD

1. Canines darkly stained.
2. Third incisor worn level with incisors 1 and 2 and to within 1-4 mm of gum line.
3. Tips of canines flattened to nearly rounded.
4. Dentine exposed on incisors.

10 + YEARS OLD

1. All incisors worn nearly to gum line, or missing.
2. Canines worn rounded to blunt, darkly stained.

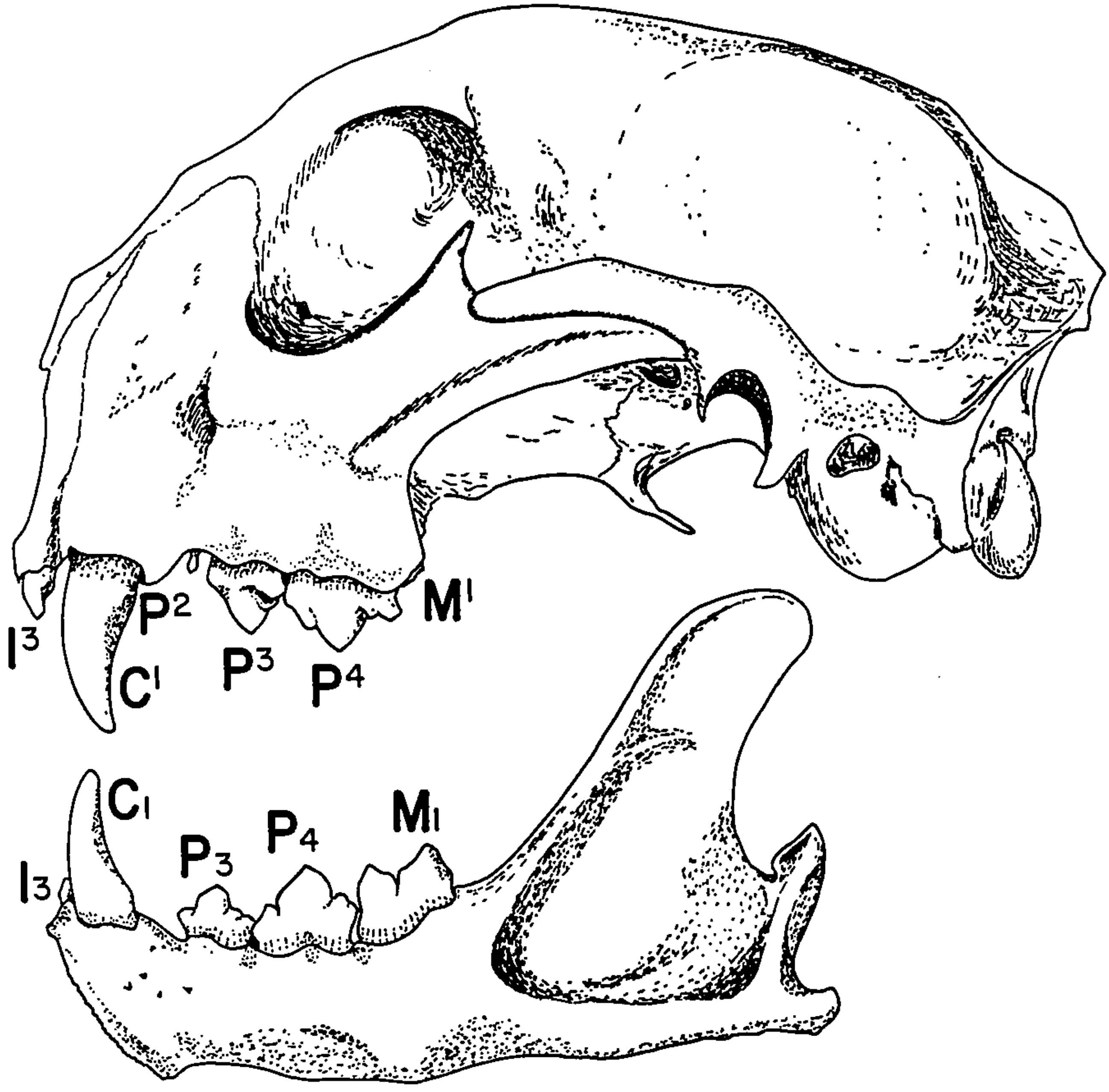


FIGURE 6 Lateral view of a mountain lion skull with letter/number designations for permanent dentition.
Drawing by M. Alderson.

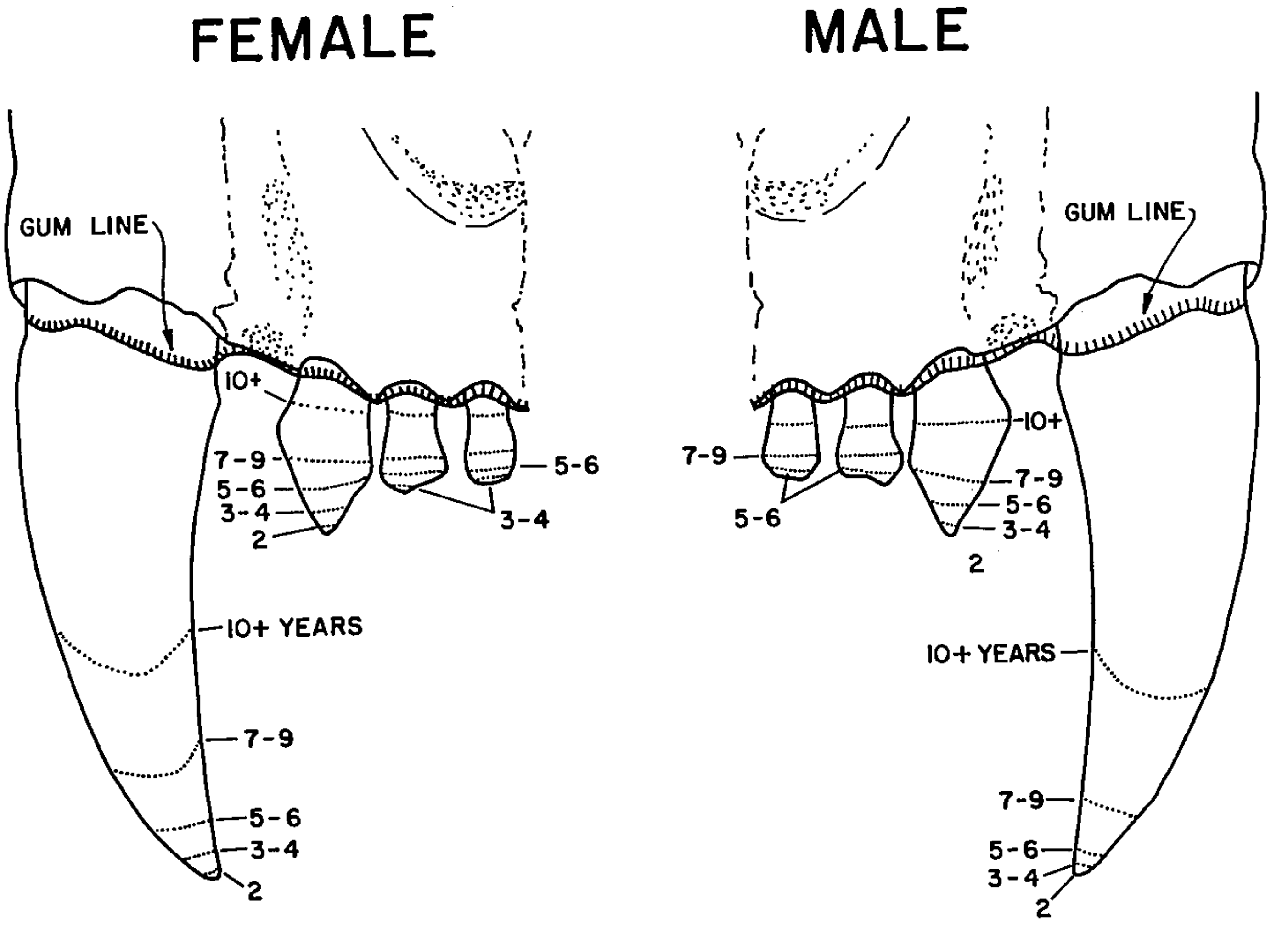


FIGURE 7 Frontal view of upper teeth of female and male mountain lions displaying relative wear by adult age classes.
Drawing by M. Alderson.

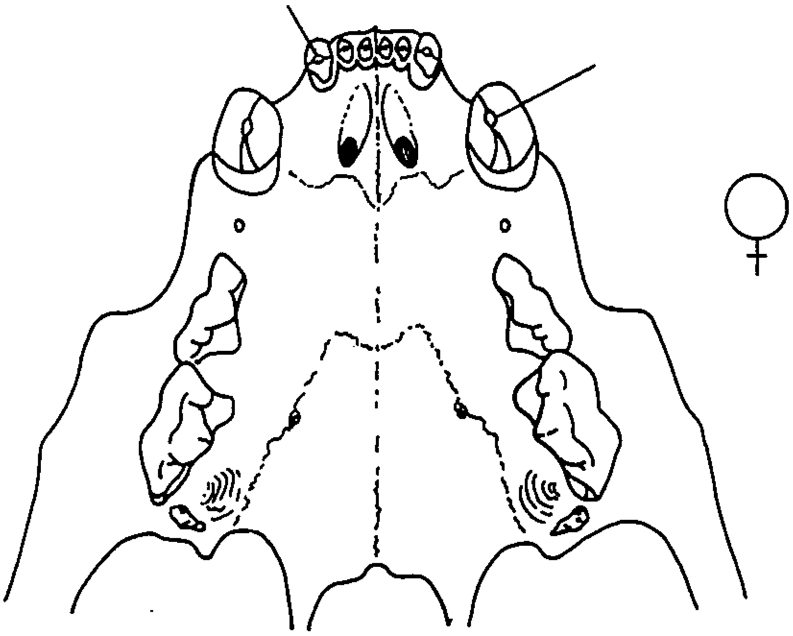


FIGURE 8 Ventral view of the upper dentition of a 3-4 year old female mountain lion showing wear points on apex of third incisor and canine teeth.
Drawing by M. Alderson

sequences and to formulate the aging guide shown in Table 6. Of this number 21 were kittens or subadults which had been captured, marked, their age estimated, and then released. When these animals moved into the adult age group they provided information concerning tooth stain and wear which was used to help develop Table 7. Figures 6, 7 and 8 illustrate permanent dentition and adult lion tooth wear patterns.

Although not shown in Table 7 there is some evidence available to show that there is differential wear on the canines and incisors of males versus females.

Weights -- Only limited data was collected on the weights of newborn kittens. Nine fetuses, judged to be in the last 2 weeks before birth, had a weight range of 0.77-1.17 pounds. Two kittens estimated to be 1-3 days of age weighed 1.06 and 1.17 pounds.

The weights of all captured lions are provided in Table 1. Based on 21 lions the adult males ranged from 112 to 162 pounds and had an average weight of 137 pounds. Thirteen adult females ranged from 84 to 115 pounds and averaged 98 pounds. The average weights recorded for lions in California was 105.8 pounds for males and 76.5 pounds for females; in Arizona, 114.5 pounds for males and 72.6 pounds for females; and in Utah, 136.9 pounds for males and 92.5 pounds for females (Sitton, 1977).

Movements

Dispersal of Juveniles -- Data was obtained from 8 family groups as to the approximate age of the kittens when they separated from their mothers. The range in ages was 10.5 months to 19 months with an average of 14 months. It was observed on several occasions that following separation from their mothers the young frequently remained in their home range for a time before finally dispersing.

To become established as part of the breeding population a newly independent mountain lion normally progresses through three phases:

(1) Independent kitten or subadult -- upon leaving its mother.
(2) Transient - when searching for a new home range.
(3) Resident - upon establishment of a new home range.

This behavioral pattern is similar to that observed by Seidensticker, et al. 1973, with the important exception that Seidensticker called all transient and resident lions adults. In contrast, the data from this study shows that when using the age classification groups in Table 5 transients can be kittens, subadults or adults and residency can be established by subadults. Behavioral patterns do not necessarily establish the age of the lion.

The transient phase can be very limited, particularly with females, as was observed with lion number 13 who stayed in the mountain range of her birth, was bred at the approximate age of 24 months, and established a home range immediately adjacent to her mother's (number 14).

Documented movements recording the dispersal of 16 young mountain lions in the Ruby Mountains and vicinity are shown in Figure 9. Eleven of these lions stayed within the mountain range where trapped (and believed to have been born) and 8 left to become established in another mountain range. Travel routes were unknown for the lions that left their home range but it is presumed they sometimes had to cross wide, barren valleys to reach their new residence. Of the 8 males tracked only 2 remained in the mountain range where first captured and presumably born. Females generally did not move as far as males (averaging 18 miles as compared to 31 miles for males) and they tended to remain in the mountain range where they appeared to have been born. Extreme movements of 36 miles for a female and 57 miles for a male lion were noted. The initial dispersal of independent kittens or subadults from their home ranges appears to be an important characteristic which contributes towards maintaining viable populations throughout their habitat. For example, in areas where mountain lions are heavily exploited (see Mortalities), such as in the Ruby Mountains, the influx of transient lions is essential in order to maintain a population.

Home Range -- Sufficient data was obtained from radio-tracking, recaptures and track sightings to at least partially construct the home range size of 13 lions. This data covered a time period which ranged from 15-77 months per lion and involved anywhere from 17-116 locations per lion (Table 8). Male lions had home ranges three times as large as females averaging 224 square miles as compared to 69.5 square miles (Figures 10-22). It is believed that smaller home ranges in the Ruby Mountains were due to higher deer densities compared with the other mountain ranges. Females occupying the South Ruby portion had considerably larger estimated home ranges than females living in higher deer density habitat in the North Rubies.

Home range overlap was documented for both adult females and adult males; however, sufficient long-term data was not collected to determine if resident lions were being recorded in all cases. In fact, the high lion turnover rate in the study area made it very difficult to distinguish between transients and residents, and in determining resident home ranges some judgements had to be made. Male home ranges either partially or completely overlapped those of neighboring adult females. Less overlap was found between members of the same sex, although on occasion there was considerable overlap during certain seasons. This occurred most frequently during the middle of winter when both deer and lions were concentrated and again during the spring and early summer (primary breeding season).

Both adult males and females tended to use the same areas month after month and year after year within their home ranges. This behavior was similar to that described by Hornocker (1969) and Seidensticker et al. (1973) in Idaho. However, there were some differences between characteristics recorded in Idaho lion populations and those observed in Nevada: (1) males were observed to fight and were not generally tolerant of each other in regard to intrusions into their home ranges, and (2) there was no obvious differences, in regard to home range size, between unexploited and exploited lion populations.

Seasonal Movements -- With the advent of winter snows in late fall the deer move to lower elevations or migrate to traditional winter ranges. The mountain lion normally follows, but may go to the wintering grounds of another herd. In doing so there may be a movement to a different mountain range and long distances can be traversed (Figures 12 and 13).

Lions usually avoided north-facing slopes in the winter when snow was deep and crossed from one drainage to another by descending to the mouth of the canyon. South-facing slopes received the most use because of less snow and the presence of greater numbers of deer. Snow, however, did not always deter the mountain lion, and they have been noted to cross over mountain passes covered with 3 to 5 feet of snow with little difficulty.

During the summer months the lions' movements were not restricted by environmental factors. North-facing slopes, which were cooler and had more vegetation than south-facing slopes, were preferred. The vegetative cover in the Ruby Mountains is sparse above 9,000 feet (subalpine zone) and lions tended to use these areas much less than the lower elevations where aspen, mountain mahogany and taller shrubs were prevalent. The highest elevation at which a lion was located was 10,400 feet and the lowest was 6,100 feet. The elevational zone of highest use by lions in eastern and central Nevada is between 6,500 and 8,500 feet where deer and other prey species are most abundant.

Movements of Deer in Relation to Lions -- On one occasion deer were observed fleeing in response to a lion's presence, while in other instances they tended to either ignore the lion or they appeared only slightly nervous, often looking in the direction of the lion. Most of these observations were made when deer were in open areas which lacked suitable stalking cover for lions. In one instance several deer were seen to wander into a dense grove of mahogany trees where a lion was present. Within a few minutes the deer walked out of the trees, seemed to be uneasy and frequently looked back in the direction of the lion but did not run. On another occasion several deer were noted to be fearful of a nearby lion and they ran approximately 300-400 yards until they reached an open hillside where they stopped and began to feed.

Food Habits -- The most comprehensive study on food habits of the mountain lions in Nevada was made by Robinette, et al. (1959). Although the emphasis in this study was not directed toward food habits, data was collected when possible. These findings showed that mountain lions ate a variety of prey species ranging in size from wood rats (Neotoma spp.) to elk (Cervus canadensis). The staple food was the mule deer. In some areas feral horses rated second in importance if deer densities were low. In the Ruby Mountains, beaver (Castor canadensis) were a favorite food source and were readily available. Another prey species not listed, but of local importance in southern Nevada, was the bighorn sheep (Ovis canadensis).

Two hundred lion scats were examined during the ten years of field effort and the following food items (listed in approximate order of importance) were found: mule deer, porcupine (Erithizon dorsatum), cottontail rabbit (Sylvilagus spp.), jackrabbit (Lepus californicus), feral horse, beaver, domestic sheep, wood rat, blue grouse (Dendragapus obscurus), coyote (Canis latrans), bobcat (Lynx rufus), unknown rodents, and elk.

In addition to scats, the contents of 14 lion stomachs were examined. This information is presented in Table 9.

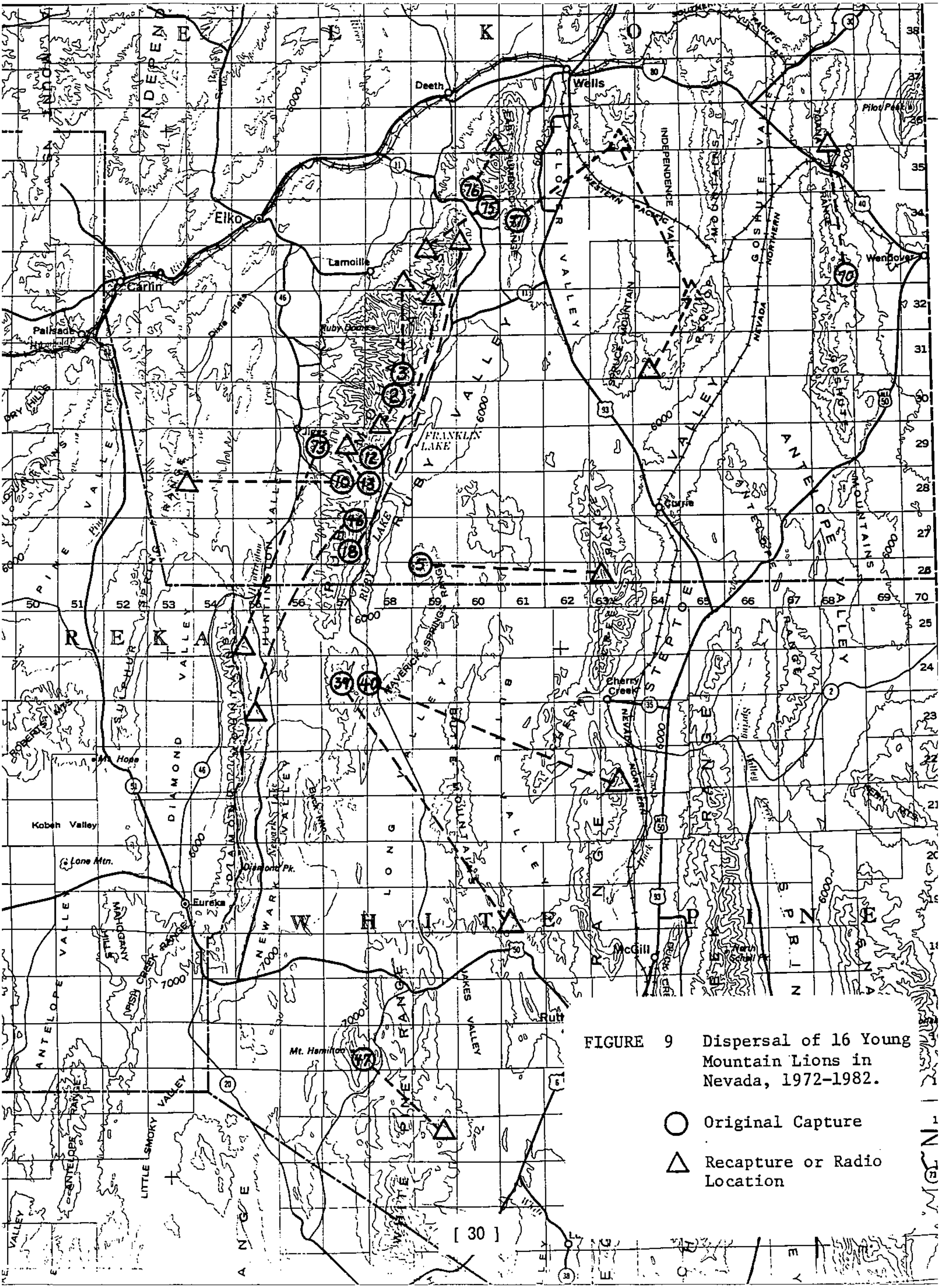


FIGURE 9 Dispersal of 16 Young Mountain Lions in Nevada, 1972-1982.

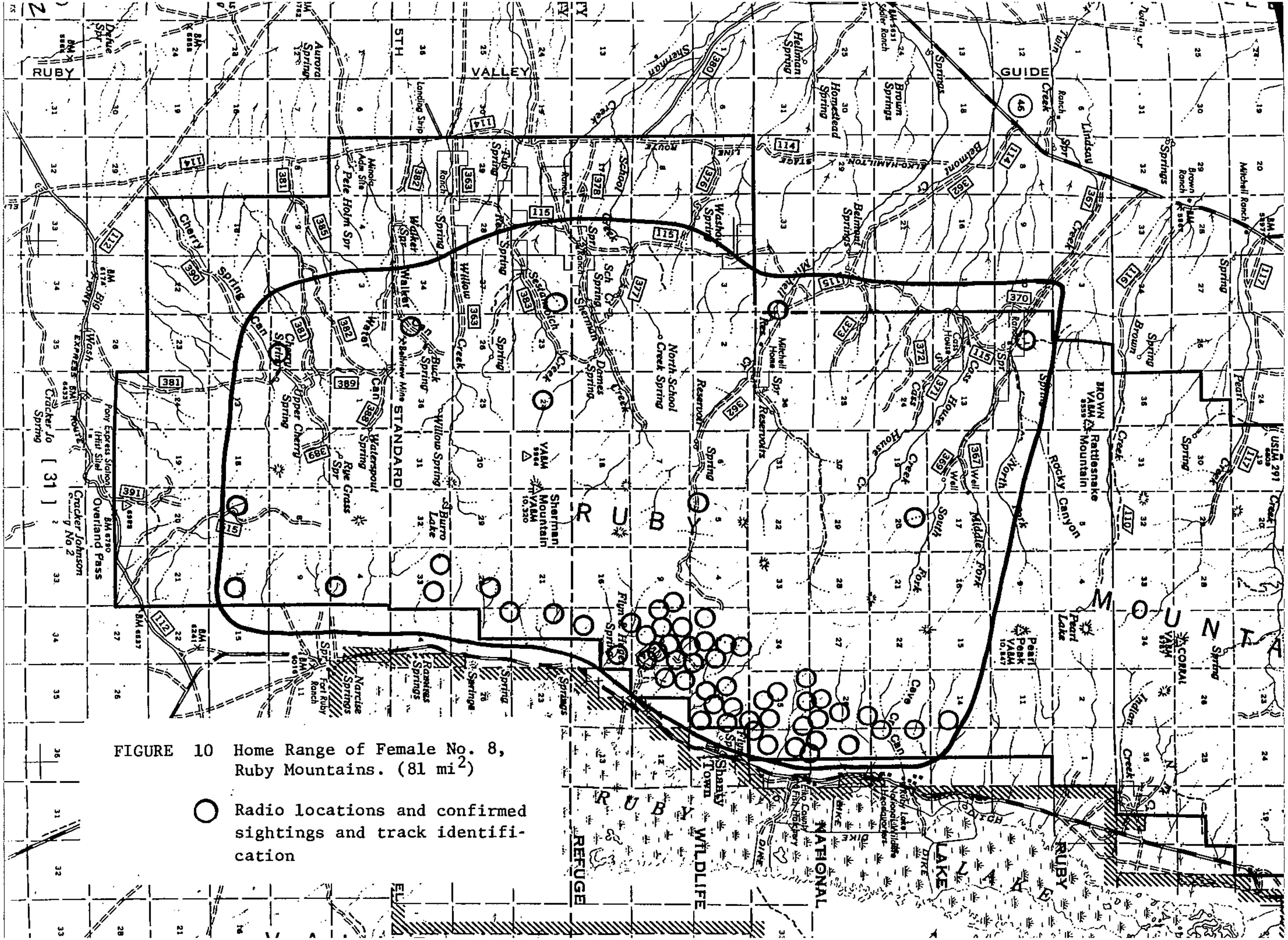


FIGURE 10 Home Range of Female No. 8, Ruby Mountains. (81 mi^2)

○ Radio locations and confirmed sightings and track identification

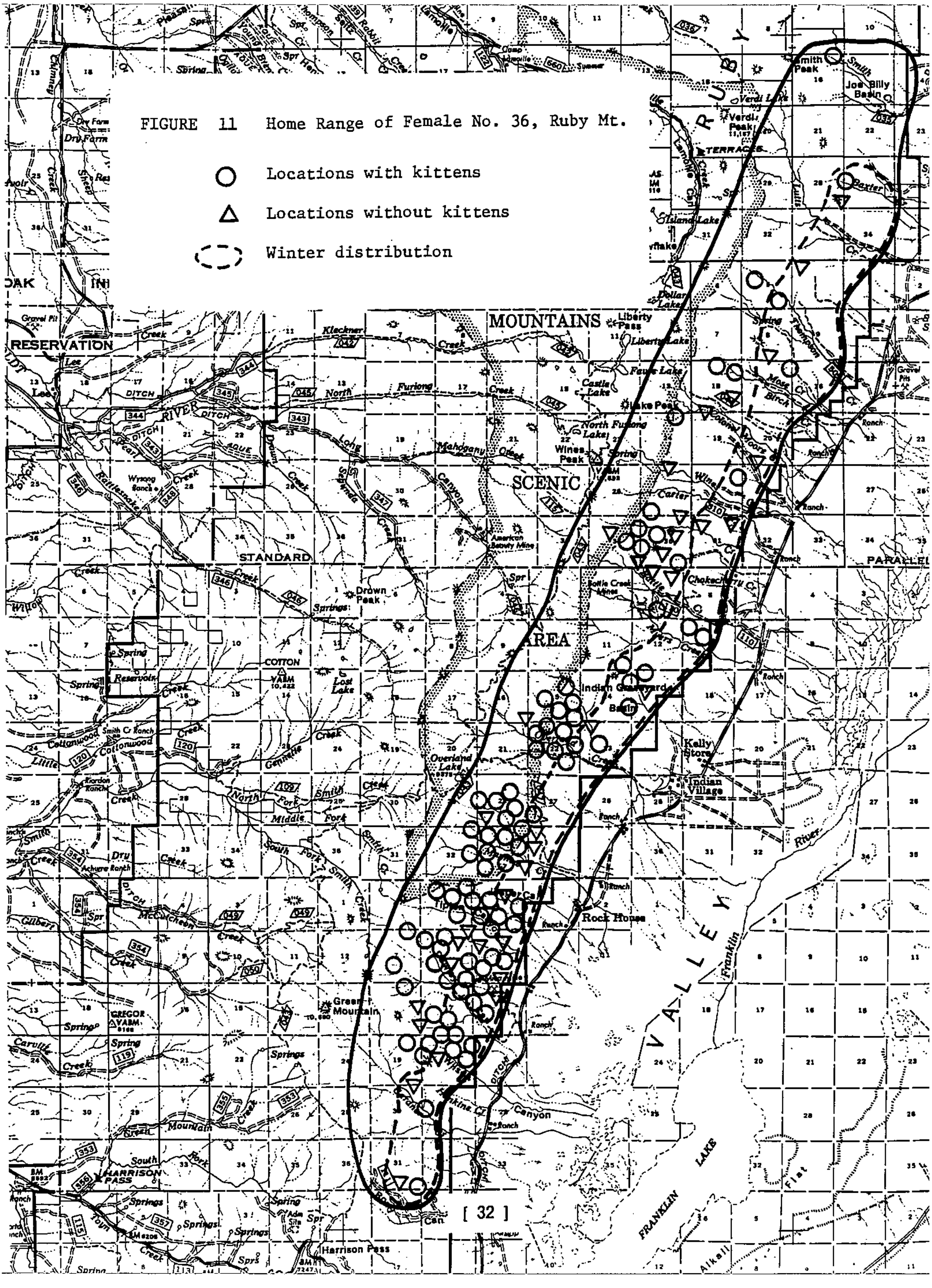


FIGURE 11 Home Range of Female No. 36, Ruby Mt.

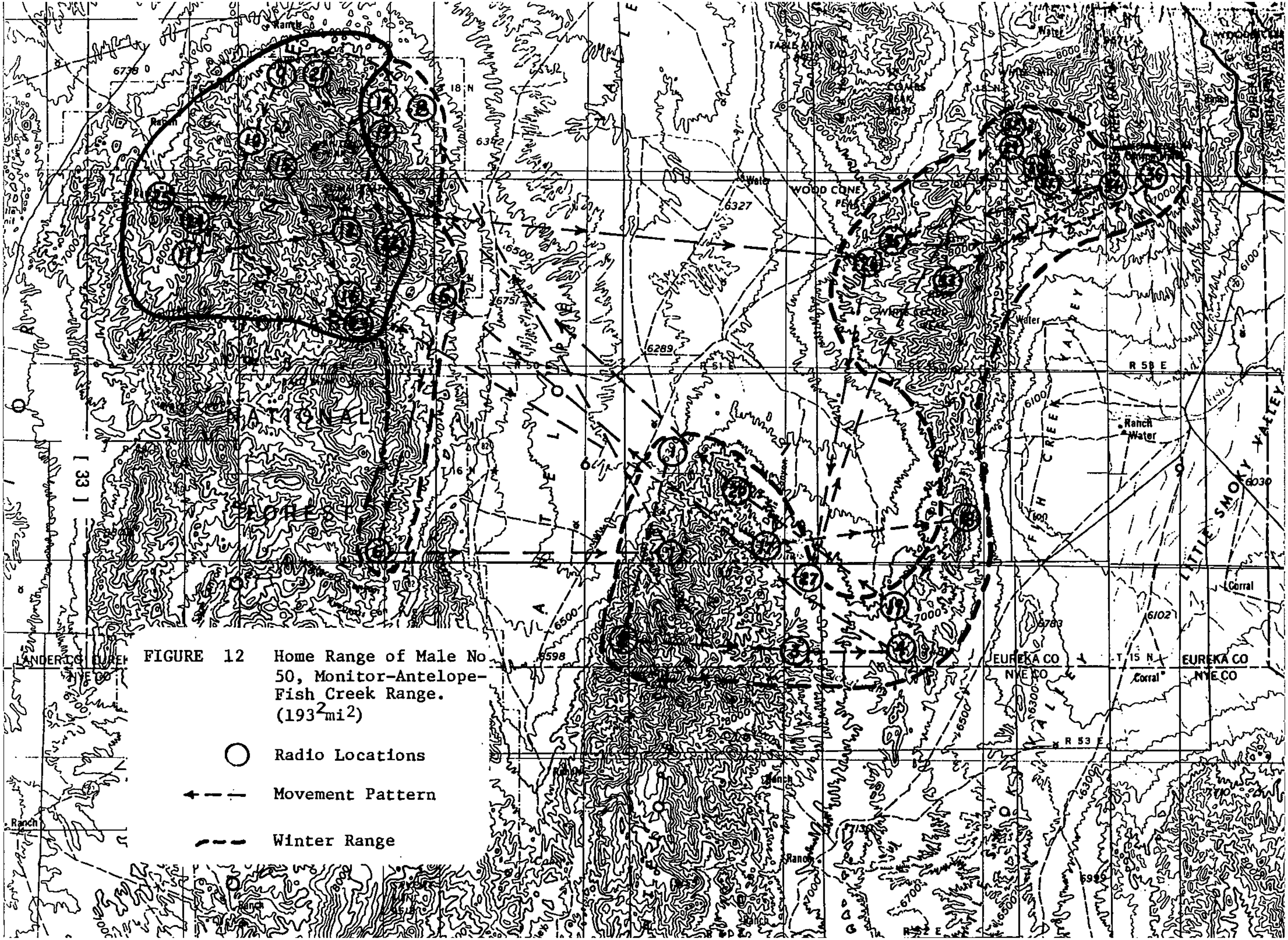


FIGURE 12 Home Range of Male No 50, Monitor-Antelope-Fish Creek Range. ($193^2 mi^2$)

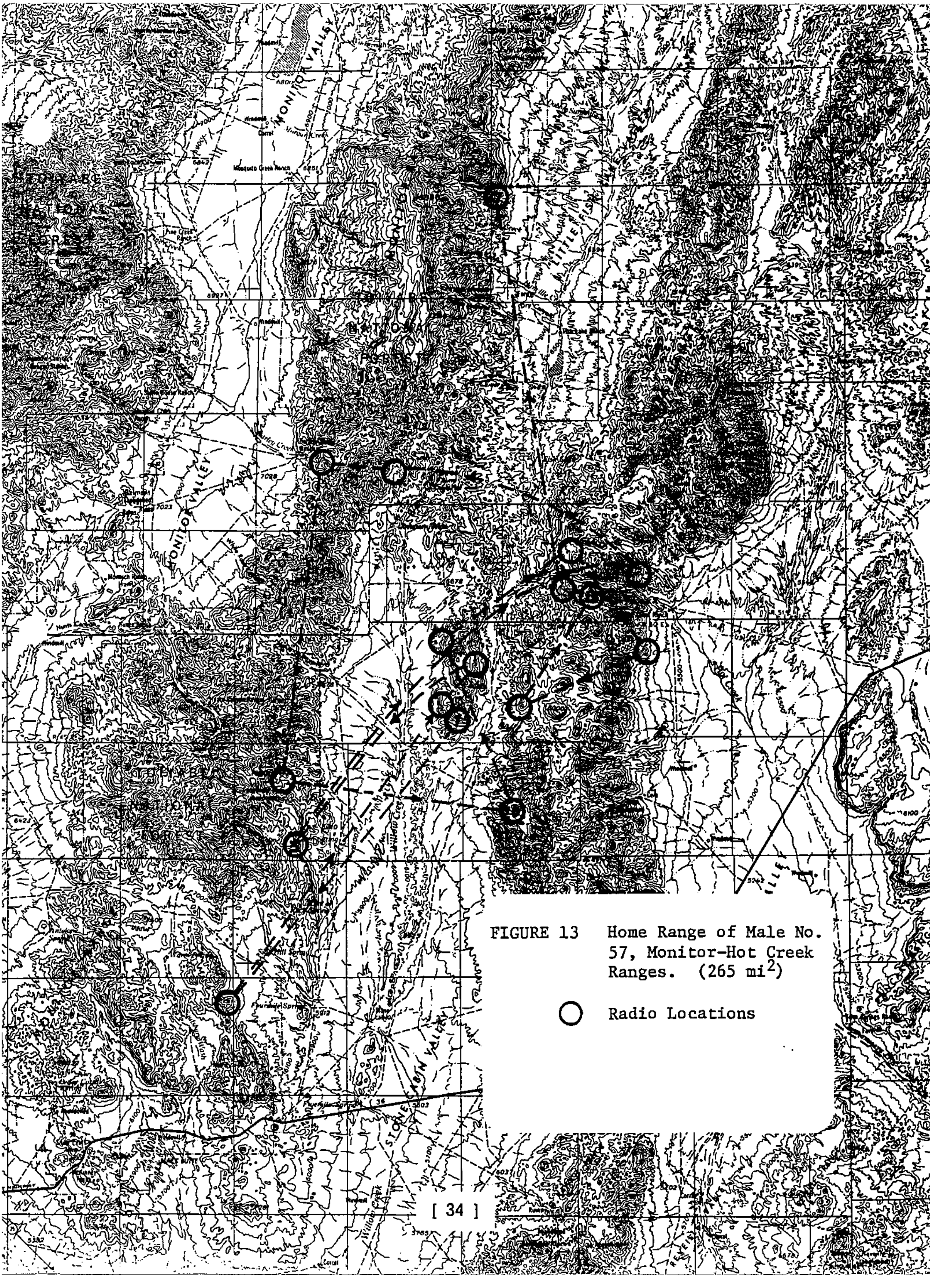


FIGURE 13 Home Range of Male No. 57, Monitor-Hot Creek Ranges. (265 mi^2)

○ Radio Locations

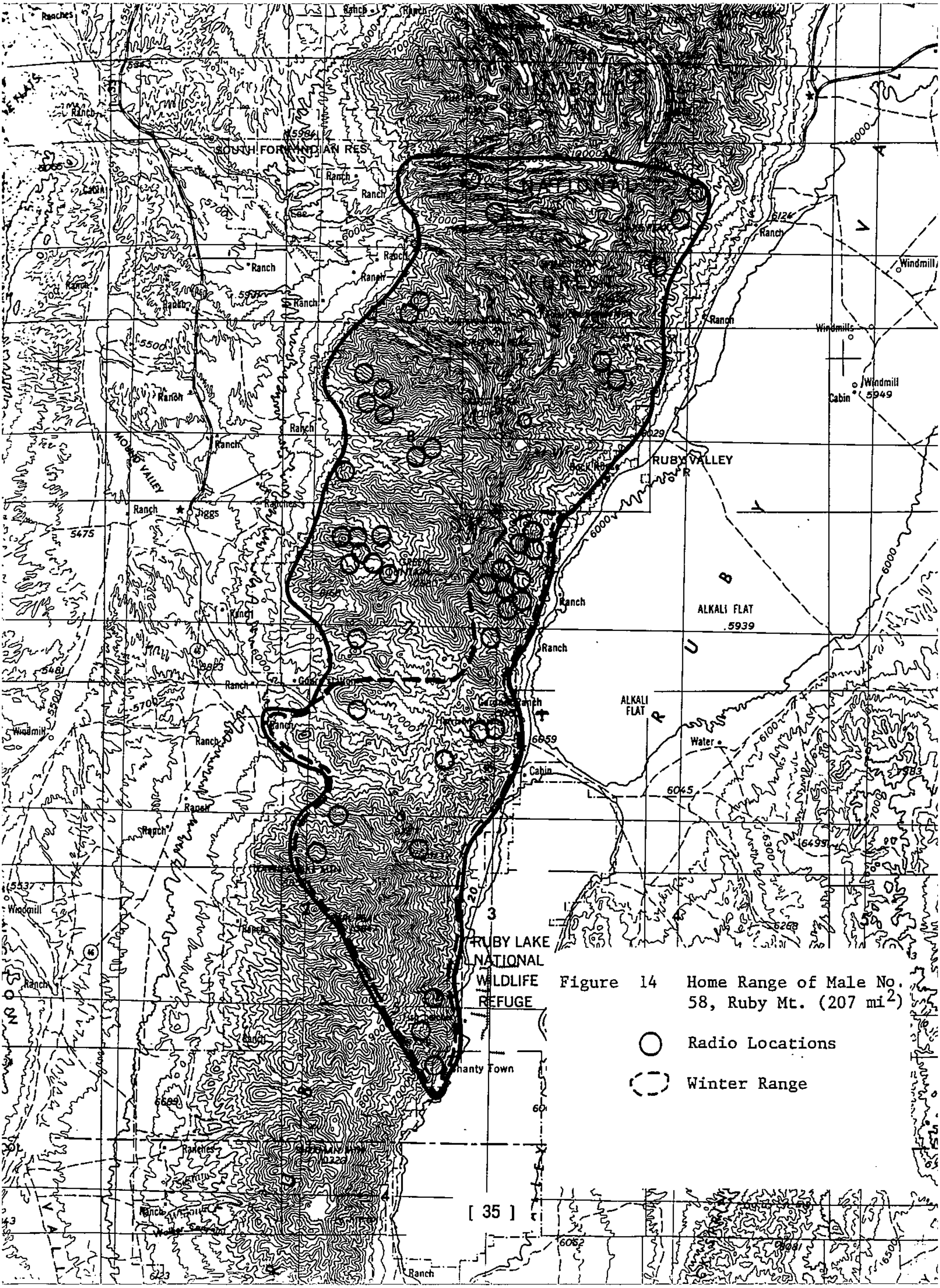


Figure 14 Home Range of Male No. 58, Ruby Mt. (207 mi²)

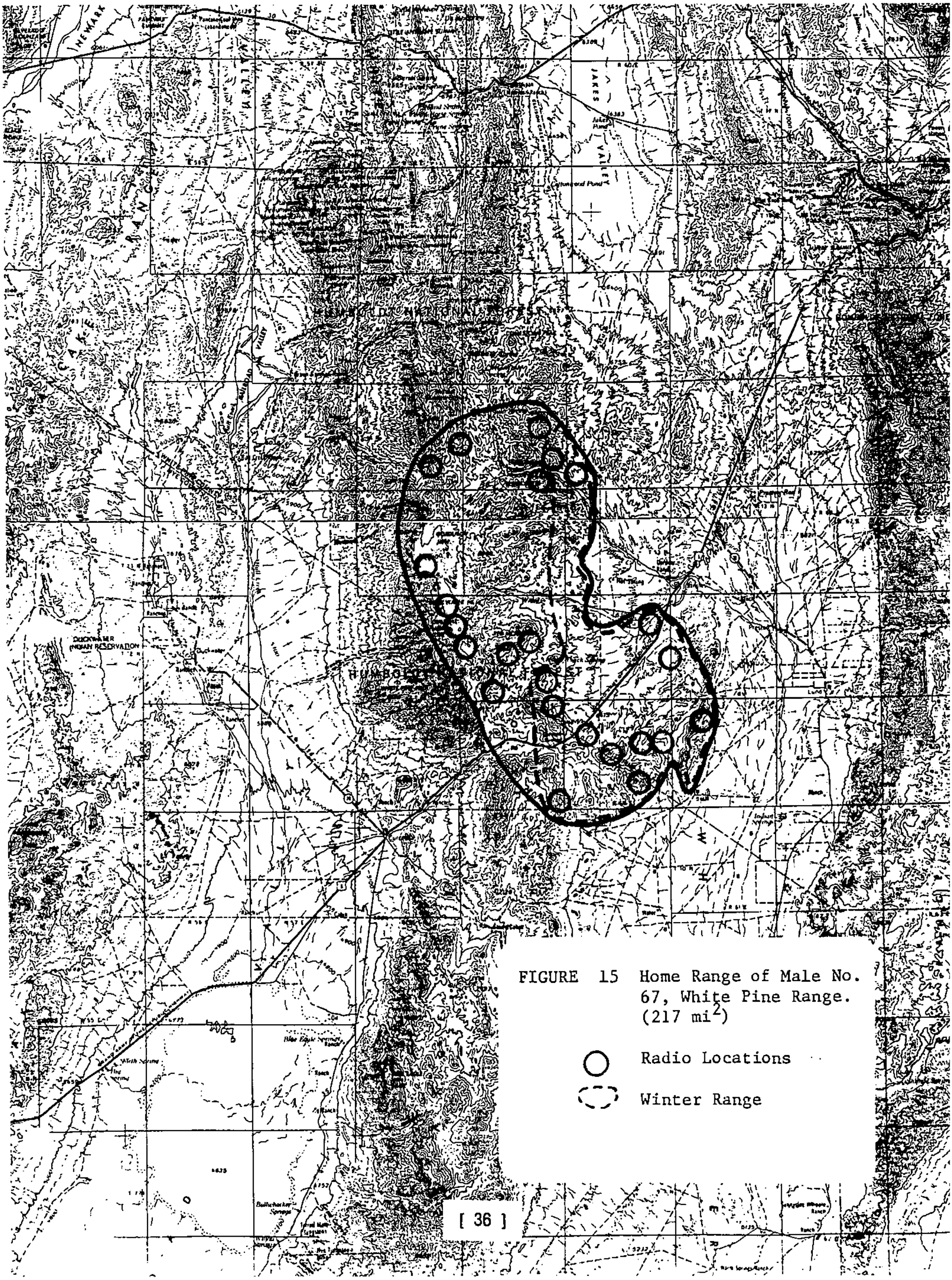


FIGURE 15 Home Range of Male No. 67, White Pine Range. (217 mi^2)

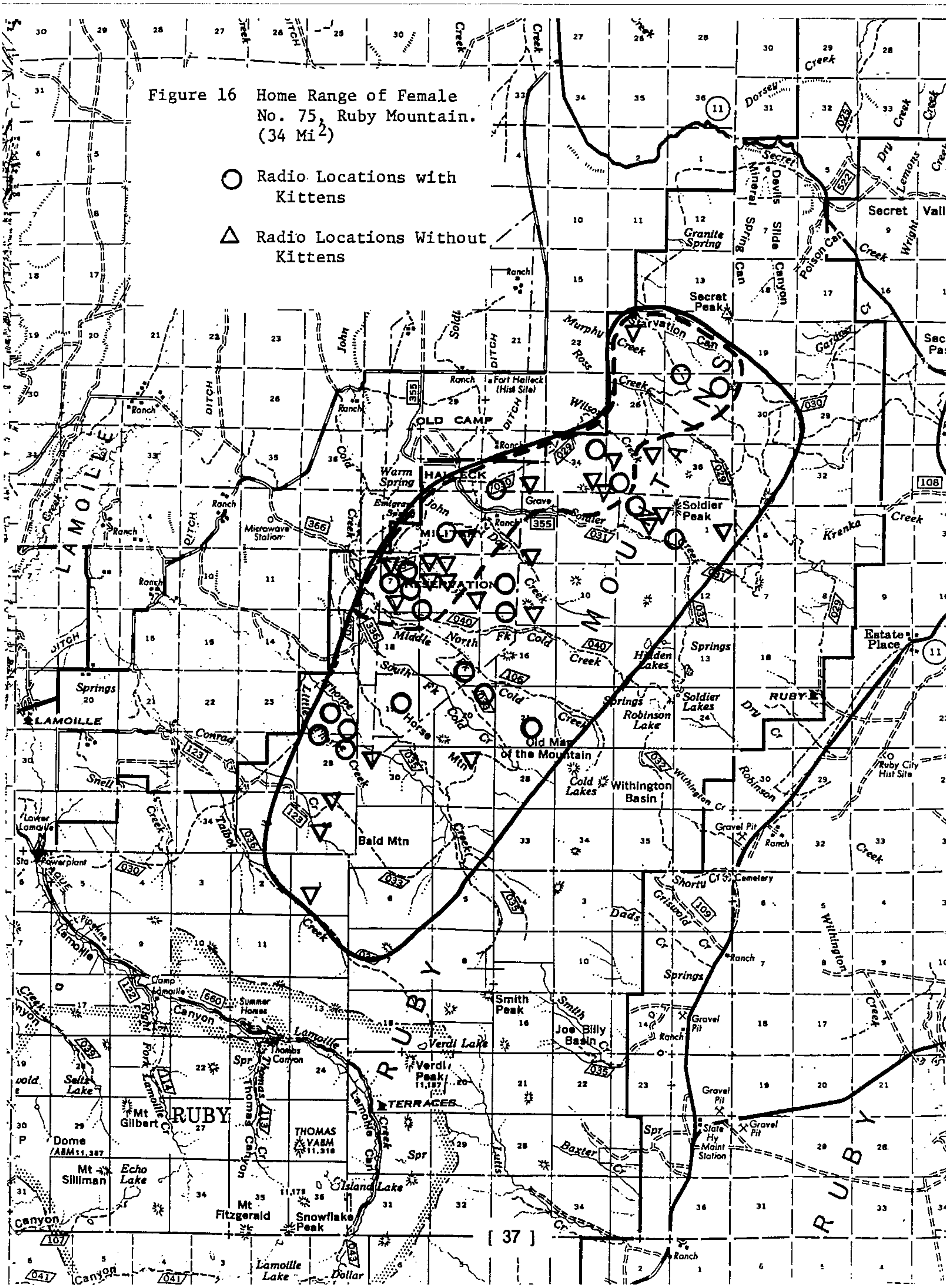
○ Radio Locations

Winter Range

Figure 16 Home Range of Female No. 75, Ruby Mountain. (34 Mi^2)

○ Radio Locations with Kittens

△ Radio Locations Without Kittens



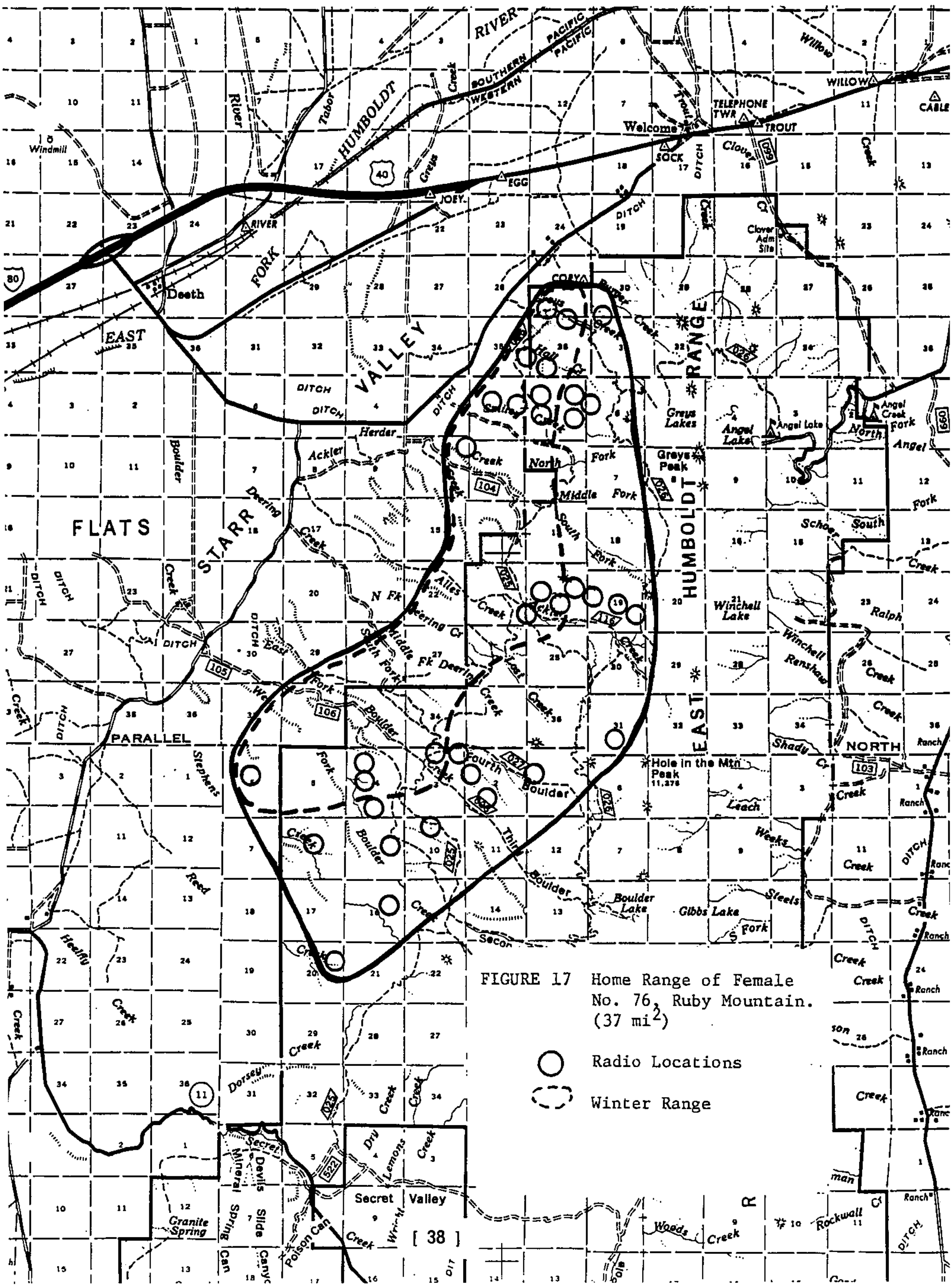


FIGURE 17 Home Range of Female No. 76, Ruby Mountain. (37 mi^2)

○ Radio Locations

Winter Range

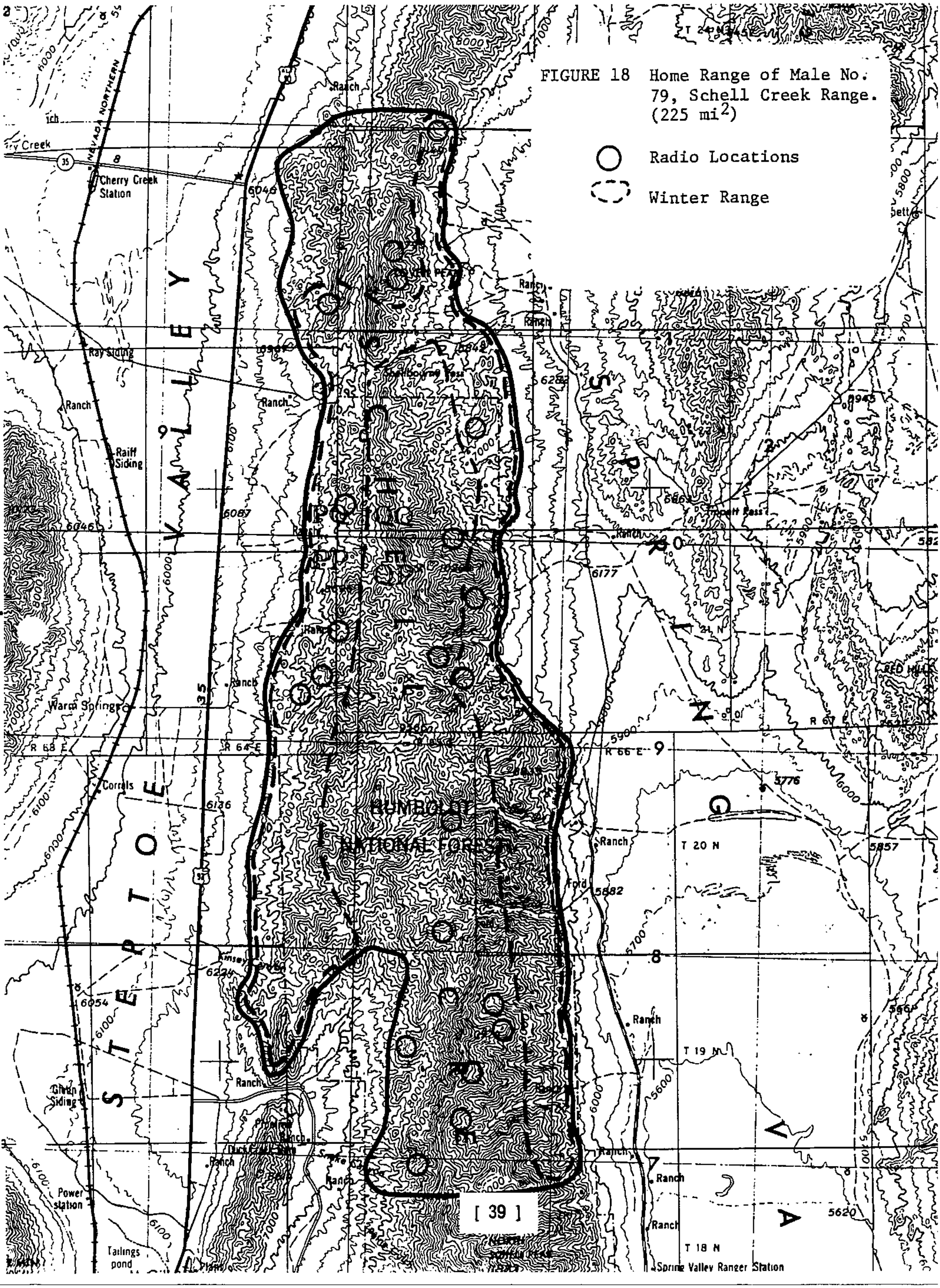


FIGURE 18 Home Range of Male No. 79, Schell Creek Range. ($225 \ mi^2$)

○ Radio Locations

Winter Range

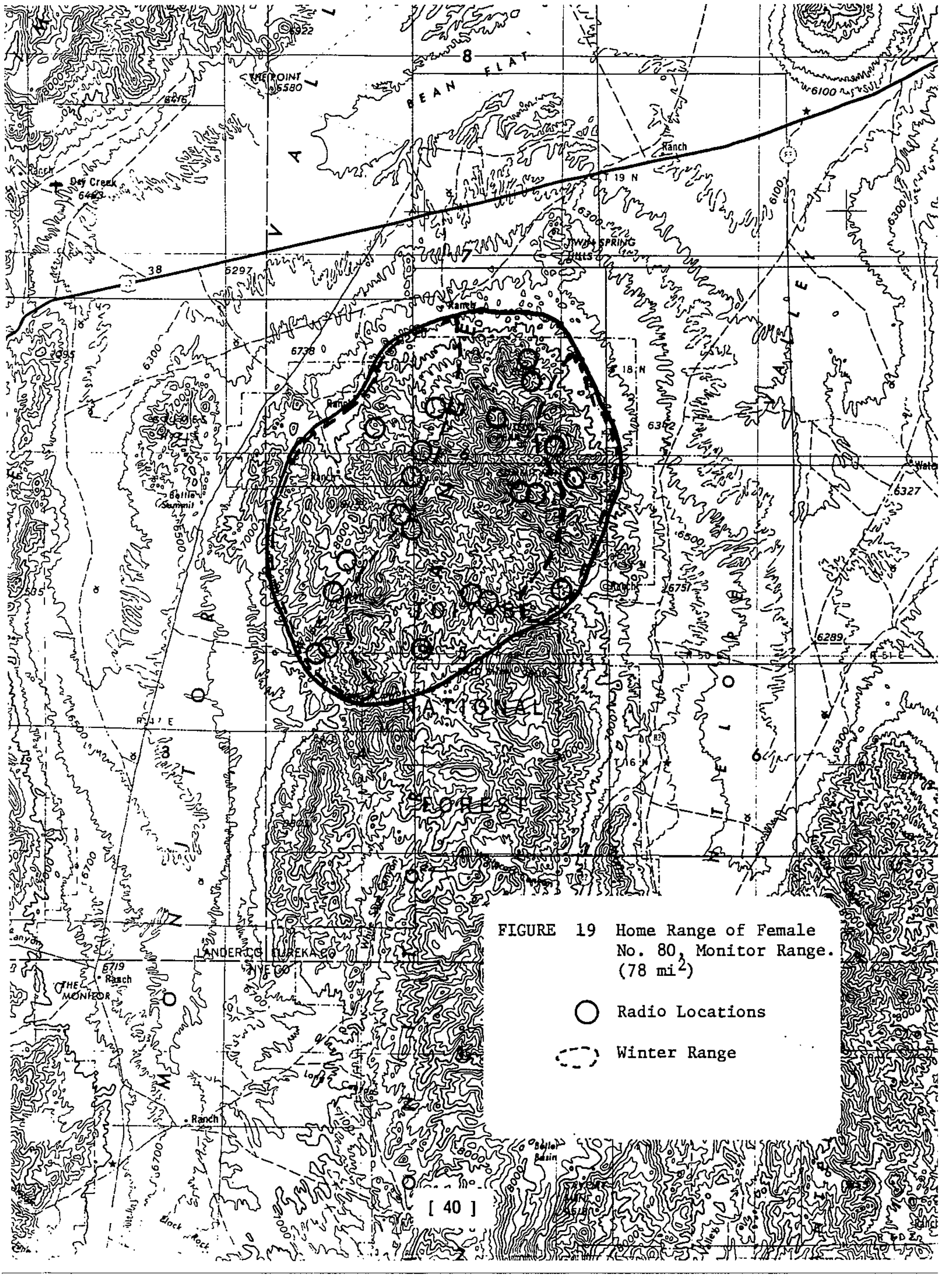


FIGURE 19 Home Range of Female No. 80, Monitor Range. (78 mi^2)

○ Radio Locations

Winter Range

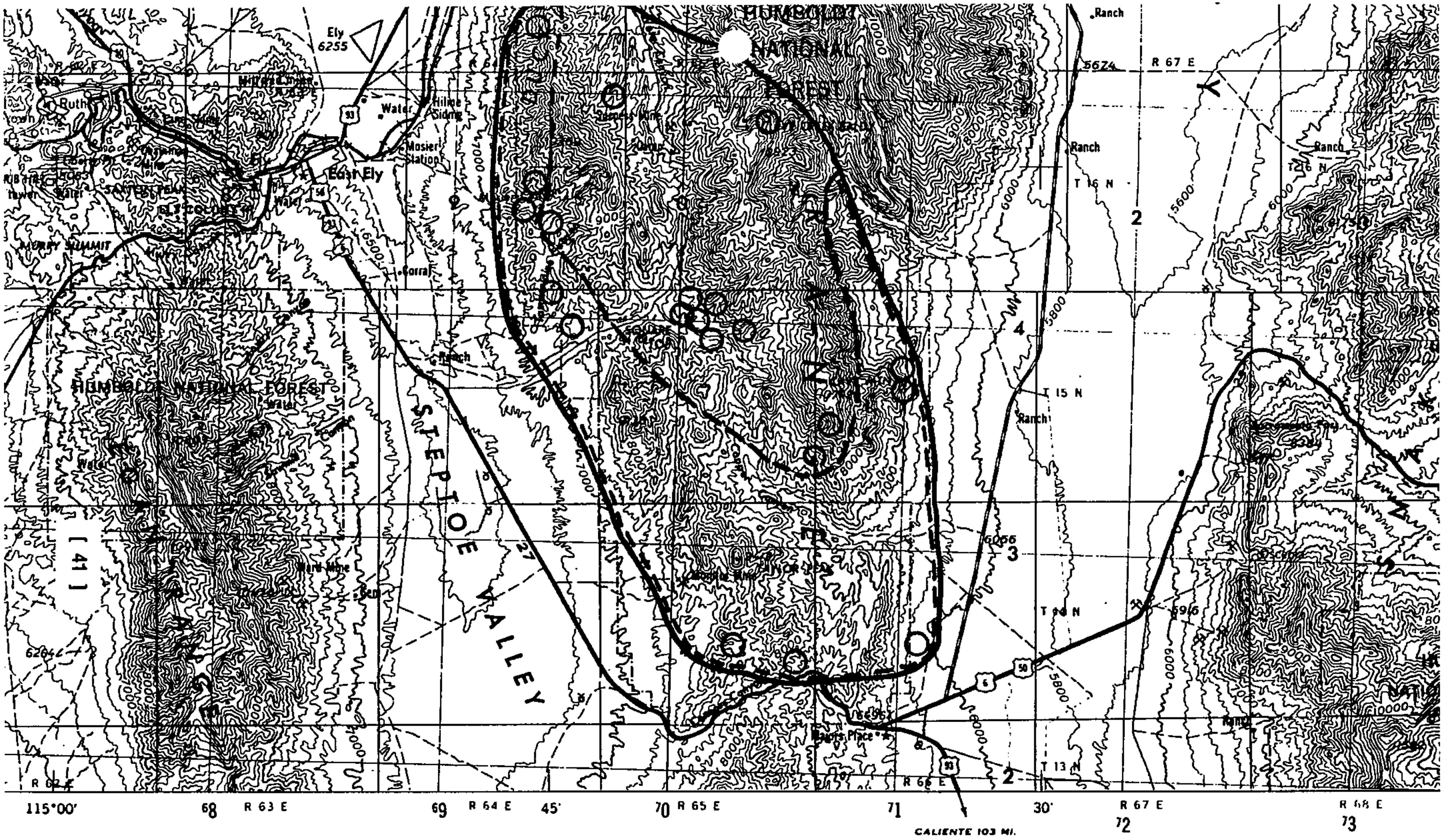


FIGURE 20 Home Range of Female No. 82, Schell Creek Range . (130 mi^2)

○ Radio Locations

◌ Winter Range

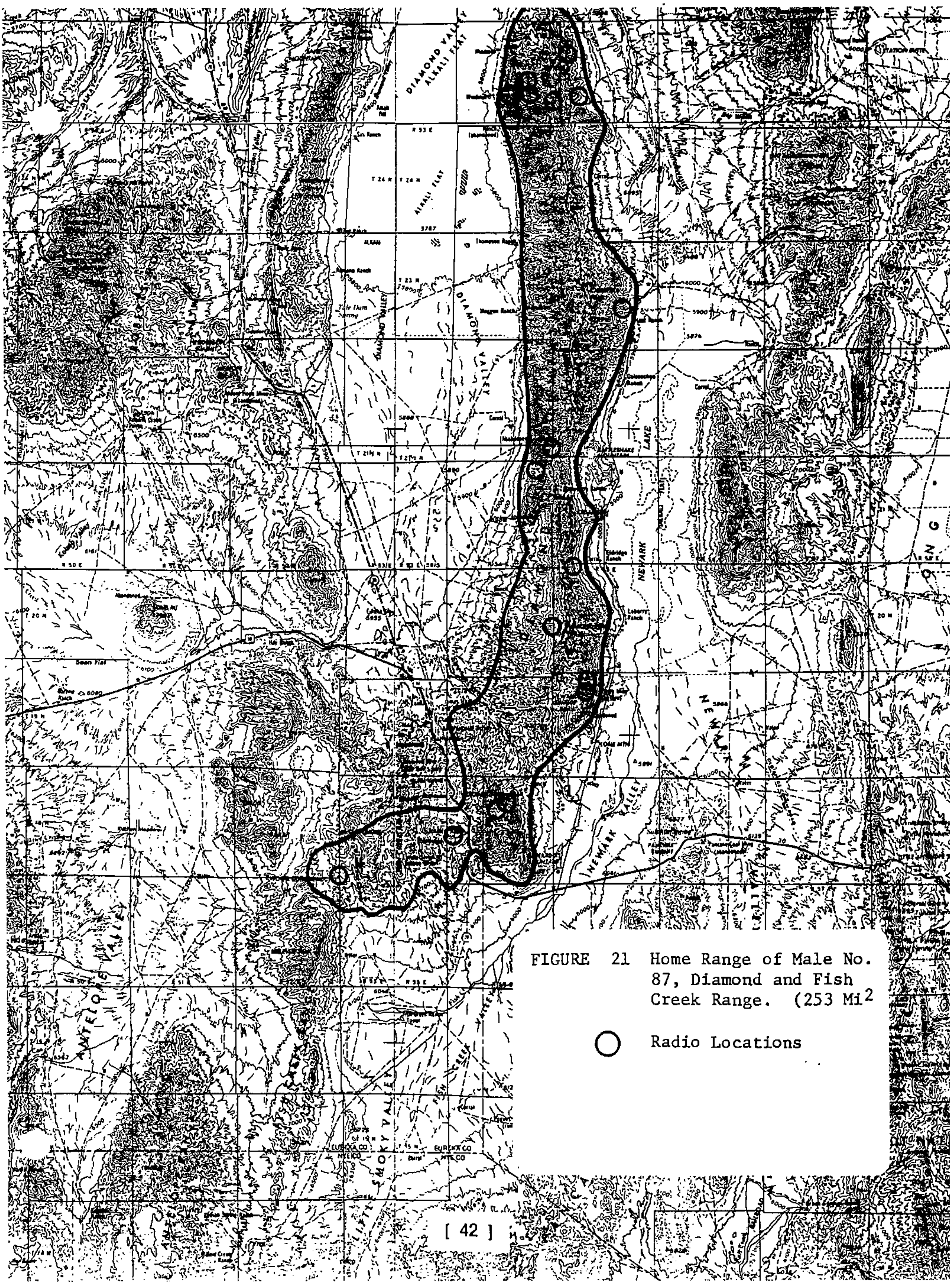


FIGURE 21 Home Range of Male No. 87, Diamond and Fish Creek Range. (253 Mi^2

○ Radio Locations

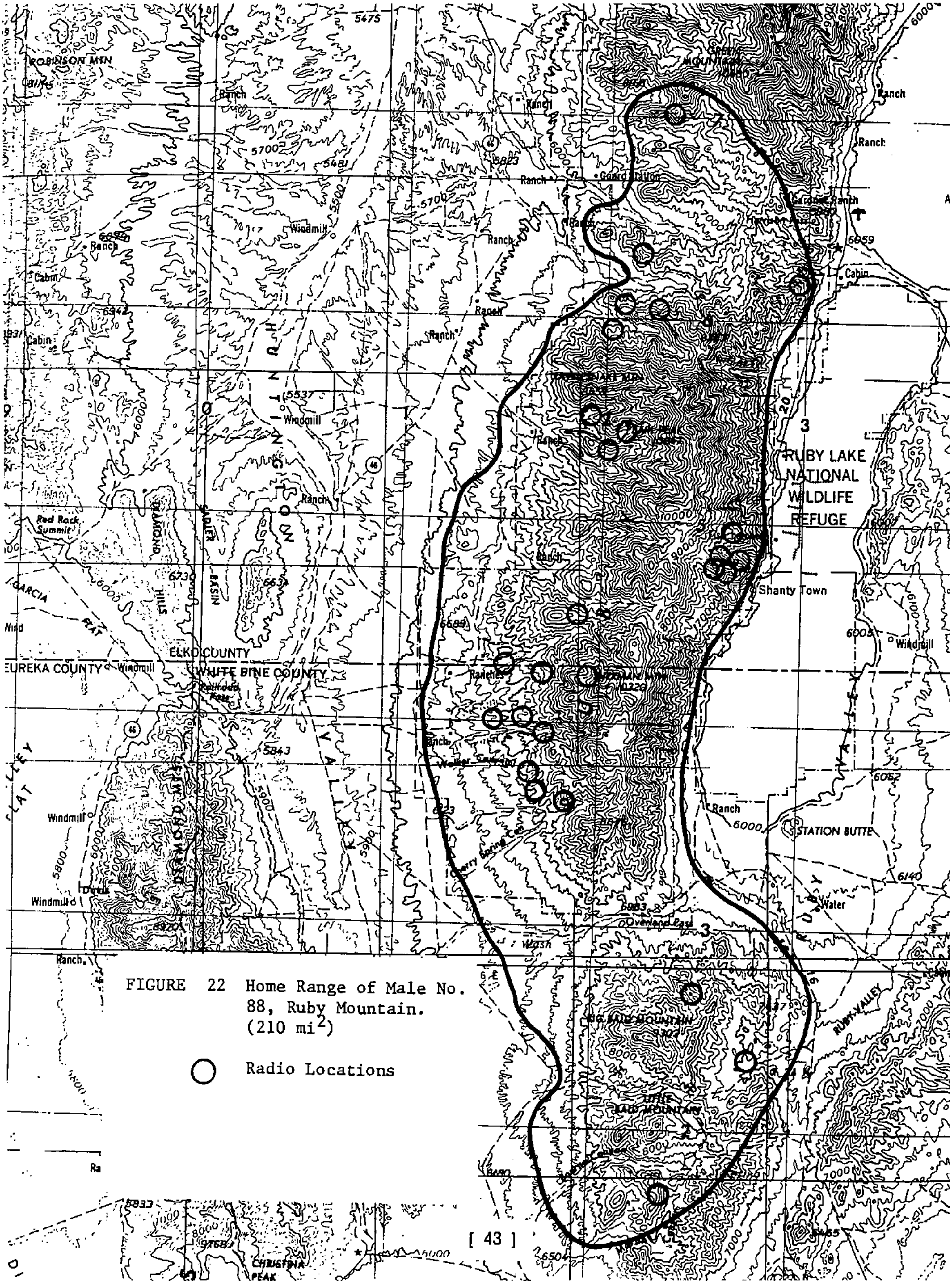


FIGURE 22 Home Range of Male No. 88, Ruby Mountain. ($210\ mi^2$)

TABLE 8. NUMBER OF RECORDED LOCATIONS AND HOME RANGE SIZE OF 13 ADULT MOUNTAIN LIONS IN NEVADA, 1972-82.

Lion No.	Sex	Initial Age	Mountain Range	No. of Radio Locations	Home Range Size (mi^2)	Period Covered
8	F	3 yr.	Ruby	54	81	1/73-1/75
36	F	13 mo.	Ruby	116	57	3/78-2/82
50	M	10 yr.	Monitor-Antelope	36	193	1/78-8/80
57	M	6 yr.	Monitor-Hot Creek	16	265	2/78-8/79
58	M	3 yr.	Ruby	43	207	3/78-7/79
67	M	2 yr.	White Pine	27	217	1/79-12/81
75	F	9 mo.	Ruby	62	34	5/79-12/81
76	F	9 mo.	Ruby	46	37	5/79-9/81
79	M	6 yr.	Schell Creek	21	225	1/80-12/81
80	F	9 yr.	Monitor	21	78	1/80-12/81
82	F	3 yr.	Schell Creek	21	130	2/80-12/81
87	M	10 yr.	Diamond-Fish Creek	17	253	5/80-6/82
88	M	6 yr.	Ruby	28	210	4/80-7/81

TABLE 9. ANALYSIS OF 14 MOUNTAIN LION STOMACHS COLLECTED IN EASTERN NEVADA.

Food Item	Number of Stomachs	Percent Occurrence	Percent Volume
Mule Deer	9	64.3	52.0
Porcupine	4	28.5	18.8
Domestic Sheep	2	14.3	15.5
Jackrabbit	1	7.1	2.3
Bobcat	1	7.1	3.8
Mountain Lion	1	7.1	3.8
Coyote	1	7.1	3.8
			100.0

Mortalities

Livestock Depredations — Since 1916 the U.S. Fish and Wildlife Service has attempted to control mountain lion populations in those states where livestock depredations were considered a problem. The Service still maintains this posture in Nevada, although they recognize that mountain lions are resident wildlife, classified as game animals, and that the State has authority for overall management of the species. However, the Service, under the terms of a cooperative agreement, has the authority for control of mountain lion depredations. This agreement states that mountain lions may be taken:

1. When they are causing or are about to cause damage to personal property. This will be coordinated with the respective State wildlife agency on a case-by-case basis; or

2. During nongrazing seasons in specific geographical areas where they have been causing damage and could not be captured during the depredation season and continuing damage is expected during the ensuing grazing season. This post-grazing season corrective control on mountain lions may be done after consultation with and concurrence of the respective State wildlife agency on a case-by-case basis; or

3. Under preventive control measures in a historically, serious, documented depredation area. Preventive control may be authorized by the Area Manager when previous steps have failed and after consultation with and concurrence of the State wildlife agency.

As a compliment to this cooperative agreement, and also as a guide for the Department, the Nevada Department of Wildlife Board of Commissioners has adopted Commission Policy No. 14 which relates to Animal Damage Control. This policy is attached in Appendix A.

SHEEP - In Nevada, mountain lion depredations upon domestic sheep has always been a controversial issue. Since domestic sheep summer use areas often coincide with occupied mountain lion habitat most depredations occur during this time. After the lambs are sold in the fall the adult and replacement ewes are usually trucked or trailed to winter ranges. Some bands of sheep in eastern Nevada are trailed as far as 400 miles (round trip) to and from winter and summer ranges. The winter sheep bands are not normally preyed upon by mountain lions to any significant degree. However, if sheep are allowed to move into tree cover or near rock outcrops, depredations are likely to occur.

The pregnant ewes are trailed or transported from the winter ranges to lambing grounds which are used during the spring months until higher elevations are free of snow and the forage has made its initial growth. These staging areas are located on public (B.L.M.) or occasionally private lands. Lion depredations on lambing grounds, although not normally as severe as on summer ranges, do occur on occasion.

Fifteen lambs killed by a mountain lion overnight.
The carcasses were gathered together to take the photo.

Although the number of sheep grazed in Nevada 20 or 30 years ago is not accurately known, it has been estimated that there were 3 to 4 times as many then as today. As recently as 1978 there was an estimated 80,000-90,000 adult sheep utilizing summer ranges in eastern Nevada. Total numbers, including lambs, were approximately 160,000-180,000 head. Since 1980 the summer ranges in eastern and central Nevada have been stocked with approximately 130,000-150,000 head of sheep (adults and lambs) per year. Table 10 lists the mountain ranges (or geographic areas) in these summer ranges and also depicts the number of domestic sheep and estimated lion populations for each area. Assuming these estimates are reasonable there is a ratio of one lion for each 1,346 sheep on these summer ranges.

The confirmed sheep losses to lions in eastern and central Nevada for the years 1978-81 are as follows:

YEAR	MINIMUM NUMBER SHEEP LOST	APPROXIMATE DOLLAR VALUE
1978	230	$16,100
1979	231	14,300
1980	380	28,700
1981	234	16,600

In some cases unconfirmed kills (those reported by herders but not verified) occurred in addition to the confirmed losses. However, these losses are believed to be less than 20% of the confirmed losses. Even if the number of sheep killed by lions was double the confirmed loss the percentage would be small compared to the total number of sheep grazed. For example, in 1982 (Table 10) an estimated 140,000 sheep were grazed in eastern and part of central Nevada. If lions killed 500 sheep the loss would amount to only 0.35% of the total number grazed. Even though total losses are not significant to the livestock industry as a whole, impacts to an individual operator are, at times, quite significant. For example, in 1978 one operator in the Ruby Mountains lost sheep valued at $6,100 during a 3-month period and another operator, in the Schell Creek Range, sustained losses of $8,000 during the same year.

CATTLE AND HORSES - For some unexplained reason cattle are not preyed upon by lions in Nevada to a significant degree. Both lions and cattle use the same areas during the summer months. Cattle are as available or even more so than are domestic sheep. The basic difference between cattle and sheep operations is the sheep are herded in large dense groups while cattle are allowed to roam individually within an allotted area. Cattle can become somewhat concentrated at times when they must congregate around a water supply or along a stream where succulent vegetation is available. The large size of cattle may preclude some attacks by lions but calves usually weigh less than 400 pounds and can easily be killed by an adult lion. Counts which are made when cattle are turned out in the spring and again when rounded up in the fall show losses from all causes are small. This indicates that lion depredations on cattle in Nevada is probably not significant in most areas.

Occasionally there are reports of lions attacking, injuring or killing domestic horses. Since most horses are kept within the confines of a corral or fenced pasture and away from lion habitat, depredations are infrequent.

TABLE 10. SUMMER USE AREAS FOR DOMESTIC SHEEP, AND MOUNTAIN LION POPULATION ESTIMATES IN EASTERN AND CENTRAL NEVADA, 1982.

Mountain Range	Number of Domestic Sheep[1]	Estimated Number of Adult Lions Present[2]
Jarbidge, Copper Basin, Tennessee Mountain	25,000	14
Independence, Bull Run	17,000	9
Stag Mountain	1,000	0
Ruby Mountains	22,000	20
Simpson Park	4,000	7
Roberts Mountain	10,000	4
Diamond Mountains	6,000	7
Butte Mountains	6,000	3
Cherry Creek	6,000	7
North Egan-Ward Mountain	12,000	10
North Schell Creek	22,000	12
Antelope	1,000	2
Kern Mountain	4,000	3
Snake (White Pine County)	4,000	6
TOTALS	140,000	104

[1] In most cases the number of sheep includes lambs, calculated at 1 lamb per each adult ewe. Some bands, e.g., Stag Mountain, are dry ewes.

[2] See population section for information on arriving at lion population estimates.

Depredation Harvest Reports

The U.S. Fish and Wildlife Service first began keeping records of the number of lions taken by government trappers and hunters in 1917 (Table 11). The sex of lions killed was recorded for the years 1917-1956 and again from 1969-1981. More males (527) were taken than females (438) with a ratio of 100 F : 120 M. During 1917-1968 many lions were removed in anticipation of future problems and the lion hunters were particularly active from 1956 through 1961. This preventative treatment resulted in lions being killed that were not responsible for depredations. In recent years (1969-1981) most of the lions which were harvested were known to be killing sheep and this was confirmed by examination of stomach contents.

Lion Mortalities in Eastern Nevada

The highest deer populations, the greatest number of lions, and the heaviest use of lion habitat by domestic sheep all center in eastern Nevada. Furthermore, eastern Nevada has historically been one of the better lion sport hunting areas and, consequently, became a favorite area of guides and their clientele. It is no wonder then that most conflicts revolving around the mountain lion occur in this portion of the state.

In analyzing data from the Ruby Mountains, the Cherry Creek-Egan area, and the Schell Creek Range, all of which have a long history of domestic sheep depredations, it was found that there were 146 documented lion mortalities during the period of 1972-81 (Table 12). Of this number 61 (41.8%) were directly associated with domestic sheep depredations.

From 1969-1982, when both sport hunting and depredation harvest have been recorded, there has been 645 lions killed for sport and 272 for depredations statewide (Table 13). The depredating lion harvest of less than 30% clearly shows that on a statewide basis the sheep depredation problem is not nearly as serious as in the study area and again demonstrates the conflict that arises from placing sheep in lion country. Over a similar period of time (1972-82) depredating lions comprised 54% of the mortality recorded from the 97 lions which were marked for this study (Table 14). So once again it becomes apparent that lions and sheep do not mix well. However, an important point to recognize is that the reverse side of the coin shows that there are many lions in the State that are not involved in depredations and that the present agreement between the Department of Wildlife and the U.S. Fish and Wildlife Service concerning livestock depredations, and restricting lion kills to the offending animal, is a great advancement in proper lion management.

Sport Harvest

The lion's classification was changed by regulation from unprotected (predator) to game animal in 1965. The initial impact of this classification was the requirement of a valid hunting license to hunt mountain lion and some restriction in the method of taking. This provision precluded the taking of lions at any time other than from sunrise to sunset and also defined legal weapons as shotgun, rifle, or bow and arrow. The season was defined as either sex, year-round and no limit was set nor was a tag required.

TABLE 11. U.S. FISH AND WILDLIFE SERVICE MOUNTAIN LION REMOVAL IN NEVADA, 1917-81.

Fiscal Year	Female	Male	Sex Unknown	Total
1917	5	3	--	8
1918	2	3	--	5
1919	3	3	--	6
1920	1	1	--	2
1921	1	2	--	3
1922	2	0	--	2
1923	0	0	--	0
1924	0	3	--	3
1925	1	3	--	4
1926	1	0	--	1
1927	1	1	--	2
1928	2	3	--	5
1929	3	0	--	3
1930	1	1	--	2
1931	2	2	--	4
1932	0	0	--	0
1933	2	0	--	2
1934	0	0	--	0
1935	0	0	--	0
1936	0	0	--	0
1937	0	0	--	0
1938	2	1	--	3
1939	6	2	--	8
1940	3	7	--	10
1941	1	4	--	5
1942	3	7	--	10
1943	3	1	--	4
1944	1	2	--	3
1945	1	0	--	1
1946	3	3	--	6
1947	0	2	--	2
1948	3	2	--	5
1949	2	3	--	5
1950	23	31	--	54
1951	33	44	--	77
1952	27	31	--	58
1953	30	36	--	66
1954	38	43	--	81
1955	52	40	--	92
1956	75	80	--	155
1957	--	--	116	116
1958	--	--	181	181
1959	--	--	108	108
1960	--	--	133	133

TABLE 11. U.S. FISH AND WILDLIFE SERVICE MOUNTAIN LION REMOVAL IN NEVADA, 1917-81. (cont.)

Fiscal Year	Female	Male	Sex Unknown	Total
1961	--	--	116	116
1962	--	--	69	69
1963	--	--	87	87
1964	--	--	97	97
1965	--	--	99	99
1966	--	--	50	50
1967	--	--	51	51
1968	--	--	70	70
1969	19	28	28	61
1970	9	11	26	46
1971	10	8	2	20
1972	5	8	1	14
1973	7	4	0	11
1974	4	8	0	12
1975	10	10	0	20
1976	5	14	0	19
1977	7	10	1	18
1978	7	17	0	24
1979	8	16	0	24
1980	11	12	0	23
1981	3	17	0	20
TOTALS	438	527	1,221	2,186

TABLE 12. LION MORTALITIES FROM 3 MOUNTAIN RANGES IN EASTERN NEVADA CONTAINING DOMESTIC SHEEP, 1972-81.

Mountain Range	No. Sheep Killed[1]	Avg. Kill/ Incident	No. Lions Removed on Depredations			No. Lions Removed by Hunters & Others		
			F	M	Total	F	M	Total
Ruby Mountains	205	10.25	8	12	20	8	16	24
Cherry Creek-Egan Range	294	9.19	10	22	32	10	11	21
Schell Creek	305	9.84	1	8	9	19	21	40
TOTALS	804	9.76	19	42	61	37	48	85

[1] Number of sheep killed includes only those sheep found and confirmed by District Field Assistants (trappers) or lion hunters.

TABLE 13. STATEWIDE SPORT AND DEPREDATION HARVEST FY 1970 THROUGH 1982.

Year	Tags	Sport Harvest	Depredation Harvest	Total Harvest
1969-70	436	42	47	89
1970-71	377	55	20	75
1971-72	259	43	20	63
1972-73	363	76	14	90
1973-74	428	91	11	102
1974-75	327	87	12	99
1975-76	261	54	20	74
1976-77	106	10	19	29
1977-78	145	22	18	40
1978-79	181	26	24	50
1979-80	272	33	24	57
1980-81	374	39	23	62
1981-82	459	67	20	89
		645 (70.4%)	272 (29.6%)	917

TABLE 14. CAUSE OF 48 MORTALITIES FROM A MARKED SAMPLE OF 97 MOUNTAIN LIONS IN NEVADA, 1972-82.

Cause of Mortality	Sex		Total	% of Total
	M	F		
Sport Hunting	10	3	13	27.1
Depredation (sheep)	22	4	26	54.2
Study Related	2	2	4	8.3
Natural	4	1	5	10.4
TOTAL	38	10	48	100.0

In 1968, a tag requirement was imposed, and although no limits were established, it became possible to record sport hunter harvest. A major change occurred in 1970 when a limit of one lion per person was set and a six month season established. During this period, the requirement that all harvested lions be validated by a representative of the Department of Wildlife within five days after the kill was also established. This regulation presented the Department the first real opportunity to collect biological data.

In 1976, twenty-six mountain lion management areas were described statewide and a harvest quota established for each to control the sport harvest. This Controlled Quota Hunt was the most restrictive season ever established for mountain lion in Nevada.

In 1979, the Controlled Quota Hunt was modified for six of the management areas, whereby a kill objective was established which allowed the hunting of lions in the area assigned until the predetermined harvest objective was reached. In 1981 this Harvest Objective hunting season concept was applied to all 26 management areas.

Sportsman participation in lion hunting has fluctuated considerably through the decade of the 1970's as a result of the many and varied season frameworks and regulations. Despite the increase in human population the sport harvest of mountain lion has not increased during the past 10 years. The sales of resident lion tags have never exceeded 500 and averaged 275 over the 1968-81 period. The resource is presently meeting the demand for sport harvest. Table 15 presents the sport harvest data from the years 1969-70 and

Sport Harvest of Mountain Lion Is Almost Exclusively Accomplished with the Aid of Trained Hounds.

TABLE 15. MOUNTAIN LION - TAG SALES, HARVEST AND HUNTER SUCCESS.

	TAG SALES			HARVEST*			HUNTER SUCCESS %		
Year	Resident	Non-Res	Total	Resident	Non-Res	Total	Resident	Non-Res	Total
1969-70	414	22	436	30	12	42	7.2	54.5	9.6
1970-71	341	36	377	37	18	55	10.9	50.0	14.6
1971-72	220	39	259	29	14	43	13.2	35.9	16.6
1972-73	289	74	363	40	36	76	13.8	48.6	20.9
1973-74	314	114	428	52	39	91	16.6	34.2	21.3
1974-75	281	46	327	57	30	87	20.3	65.2	26.6
1975-76	221	40	261	37	17	54	16.7	42.5	20.7
1976-77	98	8	106	18	2	10	8.2	25.0	9.4
1977-78	129	16	145	16	6	22	12.4	37.5	15.2
1978-79	146	36	181	18	8	26	12.3	21.0	14.1
1979-80	225	47	272	20	13	33	9.0	27.6	12.2
1980-81	313	61	374	25	14	39	7.9	22.9	10.4
1981-82	421	38	459	44	23	67	10.4	60.5	14.6

*Sport Hunter Harvest Only

1981-82. A summary of the sport hunting seasons and regulations in Nevada since the lion was classified as a game animal in 1965 is presented in Appendix B.

Population Estimates

The mountain lion is a low density predator of secretive nature whose traits make it very difficult to monitor. Several methods were used to estimate mountain lion populations and after experimenting with a number of census techniques it was determined that there were three methods which, depending on local circumstances, were best suited for use in Nevada. These were: 1) Analysis of harvest data, 2) Track counts, and 3) Home range size.

Harvest Data -- The annual harvest can reflect the population level and the analysis of historical and current harvest data provides a base which can be used in making judgements concerning population trends. Hunter success measures the ease with which the sport hunter obtains his quarry and, barring unusual circumstances which must be taken into account, will reflect availability.

In examining both sport harvest and depredation harvest records from the time that they were both recorded statewide (1969-70 through 1981-82) it is obvious that the harvest rate has never been high (Table 13). The greatest influence on the sport harvest appears to have been the initiation of the hunter quota system in 1976-77. This resulted in over a 50% decrease in harvest when comparing the 7 years prior to the quota system and the 6 years following it. However, as hunters are becoming adjusted to the system, and refinements have been made to encourage them into the quota areas, the harvest is again climbing to what appears to be normal levels. Depredations harvest, for the most part, has remained relatively constant (Statewide) with a seven year harvest average of 20 lions annually before the hunter quota system and a six year average of 21 lions annually following the quota system. On an overall basis the statewide lion population trend between 1969-82 appears to be stable.

Track Counts -- Two track count methods have been used: ground surveys and aerial surveys. The ground surveys were begun 3-6 days after a fresh snowfall and were made on foot, with snowmobiles, or by driving roads with pick-up trucks. Each track was classified, if possible, as to sex and estimated age using criteria similar to that recently described by Shaw (1979). The ground count required sampling a large area in a short time frame in order to provide a representative sample. Due to man-time commitments annual ground count surveys are not possible to implement on a statewide basis.

Aerial surveys were done with a helicopter and in a manner similar to the ground surveys except that nearly every drainage in a predetermined geographic area was flown. Each drainage was flown twice, once following the bottom and again following the south exposures where lions were most likely to be found during the winter months. Once a track was sighted the helicopter was landed or hovered over the track while one observer disembarked and the track was classified and recorded. All helicopter surveys were completed in 2 days or less so accuracy could be maintained. Snow, air and light conditions had to be optimum in order to observe tracks, land, and record data. This is the preferred method and was utilized in the major mountain lion areas during the later years of the study. Since the termination of the study this method has not been used because of the high cost.

Home Range -- It was found in eastern Nevada that adult female lions had an average home range of 69.5 square miles and males 224 square miles. However, it was also noted that the home range size for individual lions varies considerably from one mountain range to another. It was recognized that the data available on home range sizes was not as comprehensive as desired; however, it was the most accurate data available for use in computing lion densities.

Mountain Lion Population Estimates by Mountain Range -- When the Harvest Quota system was implemented in 1976 (this was a Department of Wildlife recommendation to resolve controversies over lion management between protectionists, depredation harvest proponents, and sport harvest proponents) it was necessary to define mountain lion management areas, estimate the number of lions (all age classes) in each, and set a harvest quota which would not exceed the annual recruitment to the population.

It was found that track count information was simply too limited in nature to provide a statewide approach toward determining lion populations. However, long-term harvest data did provide a general idea as to the lion population status on a statewide basis. In utilizing this information, as well as the available deer density data, Regional personnel were able to form opinions as to the general quality of the lion habitat in their areas of concern. These judgements and data were then coupled with the basic lion home range parameters from the study area and utilized to formulate lion density factors for the inhabited mountain ranges in Nevada (Table 16). Field personnel then computed the square miles of occupied habitat (based on long-term distribution records) and with this information in hand they then calculated the estimated lion populations. Population estimates have been made since 1976 and in carrying these forward to 1982 it has been computed that 792 mountain lions occupy 27,811 square miles in 104 mountain ranges in Nevada (Table 16).

Harvest Quota Calculations -- The Department of Wildlife's mountain lion harvest objective is to harvest the number of lions which can safely be removed by both depredation and sport hunting and still maintain a viable breeding population (sustained yield). The estimated annual recruitment for lion populations in Nevada is believed to be about 30% (see Population Turnover). Therefore, a harvest objective for 1982 would be 0.3 x 792 (estimated lion population) = 237 lions. However, this objective was tempered on the conservative side by using a factor of 0.25 rather than 0.3 and instead of using the population estimate of 792 lions the number 550 (which represented the estimated lion population in areas opened to hunting) was used. This resulted in a harvest quota of .25 x 550 = 138 lions. Some local adjustment was made to this quota by area biologists and the final quota for 1982 was 135 lions.

This system of arriving at a harvest quota clearly denotes the maximum number of lions which could be harvested. It then reflects a conservative attitude by slightly reducing the recruitment factor for making computations, and it makes allowances for areas of concern by individual biologists who can request further reasonable reductions or increases.

TABLE 16. MOUNTAIN LION POPULATION ESTIMATES BY MANAGEMENT AREA AND MOUNTAIN RANGE IN NEVADA, 1982.

Management Area	Mountain Range	Estimated Miles^2 Occupied Habitat	Density Ratio:[1] 1 Lion per Mi^2 of Habitat	Average No. of Lions Present[2]
1	Buffalo Hills	128	1/40	3
	Fox Mountain	104	1/40	3
	Granite	155	1/40	4
	Hays Canyon	426	1/40	10
	Subtotal	813		20
2	Virginia	-	-	0
	Fox	-	-	0
	Peavine	-	-	0
3	Sheldon Refuge	121	1/40	3
	Blackrock-Pine Forest	558	1/40	14
	Jackson	215	1/40	4
	Subtotal	894		21
4	Humboldt	369	1/40	9
	Sonoma	178	1/40	4
	Tobin	139	1/40	3
	Subtotal	686		16
5	Santa Rosa	578	1/25	23
6	Independence-Bull Run	712	1/40	18
	Tuscarora	378	1/40	9
	Subtotal	1,090		27
7	Bear Mountain - L & D	180	1/40	5
	Jarbidge	464	1/25	19
	Merritt-Mahoganies-Tennessee Mountain	378	1/40	9
	Snake	265	1/40	7
	Granites	216	1/40	5
	Pequop	441	1/40	11
	Pilot	48	1/40	1
	Toana	487	1/40	12
	Subtotal	2,479		69
8	Goose Creek-Delano	495	1/40	12

[1] High Density = 1 lion/25 mi^2, low-moderate density = 1 lion/40 mi^2 of occupied habitat.

[2] No. of lions present includes all age classes with 60% as adults and subadults and 40% as kittens still with their mothers. Estimates are for yearlong or summer ranges.

TABLE 16. MOUNTAIN LION POPULATION ESTIMATES BY MANAGEMENT AREA AND MOUNTAIN RANGE IN NEVADA, 1982. (cont.)

Management Area	Mountain Range	Estimated Miles^2 Occupied Habitat	Density Ratio: 1 Lion per Mi^2 of Habitat[1]	Average No. of Lions Present[2]
10	Buck & Bald	234	1/40	6
	Maverick-Medicine	218	1/40	5
	Ruby	850	1/25	34
	Dolly Varden	50	1/40	1
	Wood Hills	87	1/40	2
	Butte	219	1/40	5
	Subtotal	1,658		53
11	Kern	156	1/40	4
	Moriah	255	1/25	10
	Schell Creek-Antelope	672	1/40	27
	Snake	302	1/25	12
	Subtotal	1,385		53
12	Cherry Creek-Egan	594	1/25	24
13	Timpahute	305	1/40	8
	Grant-Quinn	618	1/40	15
	Seaman	106	1/40	3
	White Pine-Horse	614	1/40	15
	Worthington	27	1/40	1
	Subtotal	1,670		42
14	Cortez	234	1/40	6
	Diamond	359	1/40	9
	Roberts Mountain	210	1/25	8
	Fish Creek	207	1/40	5
	Subtotal	1,010		28
15	Shoshone	268	1/40	7
	Simpson Park	337	1/40	8
	Sulfur Springs	296	1/40	7
	Toiyabe	396	1/40	10
	Battle Mountains	77	1/40	2
	Fish Creek-Augusta	209	1/40	5
	Subtotal	1,583		39
16	Toquima	553	1/40	14
	Monitor-Hot Creek-Antelope	1,812	1/25	72
	Pancake	133	1/40	3
	Subtotal	2,498		89

[1] High Density = 1 lion/25 mi^2, low-moderate density = 1 lion/40 mi^2 of occupied habitat.

[2] No. of lions present includes all age classes with 60% as adults and subadults and 40% as kittens still with their mothers. Estimates are for yearlong or summer ranges.

TABLE 16. MOUNTAIN LION POPULATION ESTIMATES BY MANAGEMENT AREA AND MOUNTAIN RANGE IN NEVADA, 1982. (cont.)

Management Area	Mountain Range	Estimated Miles^2 Occupied Habitat	Density Ratio:[1] 1 Lion per Mi^2 of Habitat	Average No. of Lions Present[2]
17	Paradise	210	1/40	5
	Toiyabe-Shoshone	977	1/25	39
	Subtotal	1,187		44
18	Clan Alpine	392	1/40	10
	Desatoya	346	1/40	9
	Stillwater-East Range	325	1/40	8
	Subtotal	1,063		27
19	Carson-Peavine	266	1/40	7
	Virginia	161	1/40	4
	Subtotal	427		11
20	Wellington-Pine G.-Sweetwater	279	1/40	7
	Wassuk	468	1/40	12
	Excelsior-Anchorite	298	1/40	7
	Pilot Peak	91	1/40	2
	Subtotal	1,136		28
21	Monte Cristo	152	1/40	4
	Silver Peak-Montez	354	1/40	9
	Magruder-Sylvania	230	1/40	6
	White Mountains	149	1/40	4
	Subtotal	885		23
22	Egan	950	1/40	24
	Schell Creek	448	1/40	11
	Fairview-Bristol	187	1/40	5
	Highland Peak	111	1/40	3
	Subtotal	1,696		43
23	Fortification	129	1/40	3
	Wilson-White Rock	679	1/40	17
	Subtotal	808		20
24	Delamar	336	1/40	8
	Clover-Cedar	650	1/40	16
	Pahroc	97	1/40	2
	Subtotal	1,083		26

[1] High Density = 1 lion/25 mi^2, low-moderate density = 1 lion/40 mi^2 of occupied habitat.

[2] No. of lions present includes all age classes with 60% as adults and subadults and 40% as kittens still with their mothers. Estimates are for yearlong or summer ranges.

TABLE 16. MOUNTAIN LION POPULATION ESTIMATES BY MANAGEMENT AREA AND MOUNTAIN RANGE IN NEVADA, 1982. (cont.)

Management Area	Mountain Range	Estimated Miles^2 Occupied Habitat	Density Ratio:[1] 1 Lion per Mi^2 of Habitat	Average No. of Lions Present[2]
25	Armagosa	20	1/40	1
	Reveille	56	1/40	1
	Stonewall	30	1/40	1
	Sheep Range	295	1/40	7
	Groom Range	63	1/40	2
	Kawich	227	1/40	6
	Belted-Paiute Mesa	342	1/40	9
	Subtotal	1,033		27
26	Spring Range	518	1/40	13
27	Virgin	47	1/40	1
	Morman	67	1/40	2
	Subtotal	114		3
29	Pine Nut	428	1/40	11
	GRAND TOTAL	27,811		792

[1] High Density = 1 lion/25 mi^2, low-moderate density = 1 lion/40 mi^2 of occupied habitat.

[2] No. of lions present includes all age classes with 60% as adults and subadults and 40% as kittens still with their mothers. Estimates are for yearlong or summer ranges.

Goals

Goal: Maintain Nevada's mountain lion populations.

1. Problem: Changing and differing public attitudes about the mountain lion's worth and role in the ecosystem make it a difficult species to manage.

    a. Strategy: Continue to closely monitor lion populations and the affects of sport hunting, and depredation removal. Maintain comsumptive use levels consistent with the lion's ability to sustain that use.

2. Problem: Lion depredations on livestock and wildlife represents an ongoing problem.

    a. Strategy: Continue a cooperative agreement with the U.S. Fish and Wildlife Service and insure that only offending depredating lions are removed.

    b. Strategy: Where mountain lion depredations are found to be responsible for suppressing the segment of a wildlife population at or below the "threshold" level the mountain lion population involved may be reduced temporarily to allow the suppressed wildlife prey population to increase thereby ultimately resulting in a potential increase in the mountain lion population due to the larger prey base.

3. Problem: Human-lion conflicts can be anticipated in the future with continuing urban growth.

    a. Strategy: Develop a program to rapidly and safely handle lion complaints in urban areas.

RECOMMENDATIONS

There are several areas where further study could provide answers and direction for mountain lion management in Nevada. Some of these are:

1. More refined population estimates are needed, especially for low to moderate lion densities.
2. Additional investigations should be made in regard to home range overlap.
3. Lion population turnover should be determined more precisely for both exploited and unexploited populations.
4. Additional data is needed on the effects of lion predation on deer. This was an area that was not adequately investigated during this study. Do lions, in fact, exert control over low-moderate density deer populations?
5. Lion aging techniques should be pursued with an effort to obtain adequate information to supplement and validate the keys presented in this publication.
6. It is felt that lion density ratios should be modified slightly in order to provide more latitude for the field biologist when developing his lion harvest quota recommendations. The following changes are recommended:

   1/25 should be changed to 1/20-30
   1/40 should be changed to 1/31-45

7. It is apparent to the editor that there were many lost opportunities during the conduct of this study. The plan for achieving the study objectives and the monitoring system for seeing that the annual work program was accomplished, even though in place, was not adhered to. Consequently the researcher often strayed from the study plan and at times data was not collected or was recorded incorrectly. Such failings are not uncommon in Fish and Wildlife research where the dilution of manpower, because of pressing everyday needs, often results in insufficient supervision and/or monitoring. However, since Nevada is still faced with becoming even more involved with mountain lion research, past inadequacies should be recognized and every effort made to strengthen the supervision and monitoring of future studies.

LITERATURE CITED

Asdell, S.A. 1946. Patterns of mammalian reproduction. Comstock Publ. Co. Ithaca, N.Y. 437 pp.

Billings, W.D. 1951. Vegetational zonation in the great basin of Western North America. U.S.I.B. pp. 101-122.

Christensen, G.C. and R.J. Fischer 1976. Trans. of the 1st mountain lion workshop. U.S.F.W. Spec. Rept. 213 pp.

Currier, Mary Jean 1976. Characteristics of the mountain lion population near Canyon City, Colorado. M.S. thesis, Colorado State University, Fort Collins. 81 pp.

Eaton, R.L. and K.A. Velander 1977. Reproduction in the puma: biology, behavior and ontogony. The World Cats, Vol. 3:3.

Hornocker, M.G. 1969. Winter territoriality in mountain lions. J. Wildl. Mgt. 33:457-464.

__________ 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho primative area. Wildl. Monogr. No. 21. The Wildl. Soc. 39 pp.

Litton, L.W. 1977. California mountain lion investigations with recommendations for management. Calif. Dept. of Fish and Game. Spec. Rept. Proj. W-51-R. 35 pp.

Papez, N.J. 1976. The Ruby-Butte deer herd. Nev. Dept. Fish & Game Bio. Bul. No. 5. 61 pp.

Robinette, W.L., J.S. Gashwiler, and O.W. Morris 1959. Food habits of the Cougar in Utah and Nevada. J. Wildl. Mgt. 23:3, 261-273.

__________, N.V. Hancock and D.A. Jones 1977. The Oak Creek mule deer herd in Utah. Utah State Division of Wildl. Resources. Pub. No. 77-15, 148 pp.

Seidensticker, J.C., Hornocker, M.G., Wiles, W.V. and Messick, John P. 1973. Mountain lion social organization in the Idaho primative area. Wildl. Monogr. No. 35. The Wildl. Soc. 60 pp.

Shaw, H.G. 1979. A mountain lion field guide. Ariz. Game and Fish Dept. Spec. Rept. No. 9. 27 pp.

__________ 1980. Ecology of the mountain lion in Arizona. Ariz. Game and Fish Dept. Final Rept. Proj. W-78-R. 14 pp.

APPENDIX A

STATE OF NEVADA
BOARD OF WILDLIFE COMMISSIONERS

Number: 14(1)

Title: Animal Damage Control

Commission Policy No. 14

Ammendment No. 1

References: NRS 501.105, 501.110, 503.470, 503.595, 567.010 through 567.090, CGR No. 1(8) and CGR No. 4(2).

First Reading: March 13, 1981
Second Reading: April 17, 1981
Effective Date: April 17, 1981

PURPOSE

To inform the public and guide the Department of Wildlife in actions relating to animal damage contol.

In accordance with NRS 501.181, the Board of Wildlife Commissioners shall establish policies for the protection, propagation, restoration, transplanting, introduction and management of wildlife in this state. Further, the Commission shall establish policies for areas of interest including animal damage control.

POLICY

1. Major mammalian predators (coyote, mountain lion, bobcat) will be managed to minimize livestock losses from predation and minimize excessive wildlife losses from predation without endangering the existence or natural role of these predators in the ecosystem.

2. Nonpredatory wildlife will be managed to minimize their vulnerability to excessive predation. Animal damage extension efforts will be encouraged to assist private operators in husbandry practices to minimize the vulnerability of domestic livestock predation.

3. Support continued federal leadership in the Animal Damage Control program because of the national need for development and use of more efficient and humane control methods.

4. Recognize the U.S. Fish and Wildlife Service, Division of Animal Damage Control, as the authority for predator control under cooperative agreement with the Department of Wildlife, where the Department of Wildlife is an active participant in documenting the need for control programs, in planning and execution of control programs, and in enhancing public understanding of these programs.

The Department shall prepare an annual work program for predator control needed for the management of wildlife and recommend that a maximum of $20,000 annually be forwarded from the wildlife account in the state general fund to the state predatory animal and rodent committee for predatory animal control work as provided in Chapter 567 of NRS.

5. Initiate predator control efforts on the basis of the best biological information available.

6. Direct predator control efforts including sport hunting and trapping, whenever possible to prevent damage before it occurs in specific areas known to be recurring problem areas or alleviate damage as soon as possible after it occurs.

7. Direct predator control efforts at the offending animal, in so far as possible and feasible.

8. Employ predator control methods which are selected on the basis of the species involved, utilizing currently approved methods in the proper mix according to the needs. These methods may include aerial hunting, M-44, trapping, snares, denning and predacides.

    a. Predacides should only be used in certain preventative and corrective damage control operations using a delivery system which is selective, effective and efficient.

    b. Aerial hunting will be conducted only under Department of Wildlife damage control permit and limited to bobcats and coyotes. Such permits shall be issued only to the U.S. Fish and Wildlife Service or to landowners or tenants of land or property that is being damaged by wildlife.

9. The Department upon issuance of a depredation permit and with the aid and cooperation of the complainant, may take all available professional and economically feasible measures to alleviate or lesson the depredation problem.

PROCEDURE

NRS 503.595 provides that after the owner or tenant of any land or property has made a report to the Department indicating that such land or property is being damaged or destroyed, or is in danger of being damaged or destroyed, by wildlife, the Department may, after thorough investigation and pursuant to such regulations as the Commission may promulgate, cause such action to be taken as it may deem necessary, desirable and practical to prevent or alleviate such damage or threatened damage to such land or property.

The Commission has adopted regulations authorizing the Director or his designee to issue wildlife depredation permits. Specific permit programs include:

1. An annual wildlife depredation permit may be issued to the State Supervisor, U.S. Fish and Wildlife Service, Division of Animal Control, to take depredating mountain lion or bobcat in the immediate vicinity of threatened livestock.

   a. Any report of livestock depredation received by the Department of Wildlife shall be forwarded immediately to the permittee for action in accordance with subsection (b) of this section.

   b. Upon receipt of a report from a livestock owner or the Department indicating that a mountain lion or bobcat is causing or about to cause damage to livestock, the permittee shall conduct an on-site investigation. If the results of the investigation support the complaint, the permittee may take the animal. If the permittee cannot determine if the complaint is valid, he shall notify a representative of the Department, who shall conduct a joint investigation to make the final determination.

   c. During November through April, the permittee shall slavage and give the hide and skull of depredating mountain lion or bobcat to the Department within 72 hours. During May through October, the permittee shall completely destroy the animal, except the skull which shall be delivered to the Department.

2. An annual wildlife permit may be issued to State Supervisor, U.S. Fish and Wildlife Service, to take the minimum number of mountain lions, bobcats, foxes, cottontail rabbits, pigmy rabbits, white-tailed jack rabbits, bears and squirrels as necessary to control damage to persons and property.

3. Upon receipt of a valid mountain lion or bobcat complaint from an individual livestock owner, the Department may issue a limited permit to the owner to take an animal that is in the act of killing his livestock.

   a. The permittee shall notify a Department representative within 72 hours after taking a mountain lion and arrangements will be made for examining the skull and sealing the hide.

b. Mountain lion or bobcat hides, after being properly sealed, may be retained by the permittee to defray the cost of handling the depredation complaint.

4. The Department may issue permits authorizing the hunting or killing of coyotes or bobcats from an aircraft.

5. Fur-bearing animals injuring any property may be taken or killed at any time in any manner, provided a permit is first obtained from the Department. The Department is authorized to enter upon the lands of a landowner and remove beaver or otter for the relief of other landowners and the protection of the public welfare.

6. The Department may issue permits consistent with Federal law to take bald eagles or golden eagles whenever it determines that they have become seriously injurious to wildlife or agriculture or other interests that the injury can only be abated by taking some of the offending birds.

7. The State Predatory Animal and Rodent Committee shall enter into agreements with the U.S. Fish and Wildlife Service covering cooperative control of crop-destroying birds in addition to predatory animals and rodents to assure maximum protection against losses of livestock, poultry, game birds, animals and crops on a statewide basis. The State Department of Agriculture in accordance with NRS 555.010 and 555.021 responds to complaints involving vertebrate pests (excluding predators) that are injurious to agriculture or public health.

8. The Department may issue a wildlife depredation permit to a landowner if needed for the prevention or alleviation of damage to standing or stored agricultural crops.

This policy shall remain in effect until amended, repealed or superseded by the Board of Wildlife Commissioners.

BY ORDER OF THE BOARD OF WILDLIFE COMMISSIONERS IN REGULAR SESSION,
APRIL 17, 1981.

Marvin A. Einerwold, Chairman
Board of Wildlife Commissioners

APPENDIX B

MOUNTAIN LION HUNTING SEASONS 1965-1982

1965-1966

Type of Season: Either sex, statewide.
Season Length: Open year-round.
Limit or Quota: None.
License and Tag Requirement: Hunting license only.
Special Regulations: Unlawful to hunt with revolver or by use of artificial light.

1967

Type of Season: Either sex, statewide.
Season Length: Open year-round.
Limit or Quota: None.
License and Tag Requirement: Hunting license only.
Special Regulations:

1. Unlawful to use a revolver.
2. Unlawful to use artificial light.
3. Unlawful to trap lions.

1968

Type of Season: Either sex, statewide.
Season Length: Open year-round.
Limit or Quota: None.
License and Tag Requirements: Hunting license and tag.
Special Regulations:

1. Unlawful to use revolver.
2. Unlawful to use artificial light.
3. Livestock operator can take lions with proper permit.

1969

Type of Season: Either sex, statewide.
Season Length: Open year-round.
Limit or Quota: None.
License and Tag Requirement: Hunting license and tag.
Special Regulations:

1. May be hunted anytime day or night.
2. Lawful to use any weapon except crossbow.
3. Livestock operator can take depredating lions at any time.

1970

Type of Season: Either sex, statewide.
Season Length: October 10, 1970 - March 31, 1971 (171 days).
Limit or Quota: 1 per person.
License and Tag Requirement: Hunting license and tag.
Special Regulations:

1. Mandatory check-in of lion hide, skull and stomach contents within 5 days of harvest.
2. Hide must be sealed by a Department representative within 5 days of harvest.
3. Lions may be hunted anytime day or night.
4. Lawful to use any weapon except crossbow.
5. Livestock operator can take depredating lions at any time after issuance of a permit.

1971-1975

Type of Season: Either sex, statewide.
Season Length: Open year-round (1974 & 1975, 6 month season).
Limit or Quota: 1 per person.
License and Tag Requirement: Hunting license and tag.
Special Regulations:

1. Mandatory check-in of lion hide and skull within 48 hours of harvest (1973, 72 hours of harvest).
2. Hide must be sealed by a Department representative within 48 hours of harvest.
3. Lions may be hunted anytime day or night.
4. Lawful to use any weapon except crossbow.
5. Livestock operator can take depredating lions at any time after issuance of a permit.

1976-1978

Type of Season: Either sex, statewide.
Season Length: 1976 - October 1, 1976 - March 31, 1977 (6 months).
1977,1978 - October 1, 1977 - April 30, 1978 (7 months).
Limit or Quota:

1. One lion per person.
2. Resident and nonresident quotas by management area and through application only.

License and Tag Requirement: Hunting license and tag.
Special Regulations:

1. Mandatory check-in of lion hide and skull within 72 hours of harvest.
2. Hide must be sealed within 72 hours of harvest.
3. Lions may be hunted any time day or night.
4. Lawful to use any weapon except crossbow.
5. Livestock operator can take depredating lions any time after issuance of a permit.
6. Accidentally trapped lions are the property of the State of Nevada and shall be reported within 48 hours of capture.

1979-1980

Type of Season: Either sex, statewide.
Season Length: October 1, 1979 - April 30, 1980 (7 months).
Limit or Quota:

1. One lion per person.
2. Resident and nonresident "Trophy General Hunt" with quotas by management area, application only.
3. Resident and nonresident "Controlled Trophy Hunt" with quotas (allowable harvest) by management, application only.

License and Tag Requirements: Hunting license and tag.
Special Regulations:

1. Any person holding a valid tag for lion in management area 7, 8, 9, 10, 19, 20 or 21 (1980) obtain a 15-day controlled hunt permit at no cost before hunting.
2. Permit will be valid in a specified management area for 15 days. Unsuccessful hunters may reapply for the same or another management area if the harvest quota has not been filled. Hunters holding a 15-day permit will be notified by the Department when the harvest quota is filled for that area. The hunter may then reapply for another open area.
3. Mandatory 72 hour check-in and hide sealing required.
4. Accidentally trapped lions are the property of the State of Nevada and shall be reported within 48 hours of capture.

1981

Type of Season: Either sex, statewide.
Season Length: October 1, 1981 - April 30, 1982 (7 months).
Limit or Quota:

1. One lion per person.
2. Unlimited tag quota by application only.
3. Harvest quota by management area.

License and Tag Requirement:

1. Hunting license and tag.
2. 15-day permit.

Special Regulations:

1. Hunting permit reservations may be made by mail, telephone or appearing in person at the designated Department offices.
2. Hunting permits will be valid in a specified management area for a period of 15 days from the date of issue. If a hunter fails to harvest a lion in the specified period and management area, he may reapply as many times as he desires for a permit to hunt in any of the open management areas as long as the harvest quotas remain unfilled.
3. When the harvest quota is filled in any of the management areas, either by sport hunting or by depredation harvest, that area will be closed to mountain lion hunting, and no further permits will be issued for that area. Hunters holding a valid permit for a management area at the time that the harvest quota is filled will be notified by the Department that the area is closed, and that their permit is no longer valid. Hunters may then reapply for any other management area where the harvest quota has not been filled.

4. Department representatives will retain final judgement on issuance of permits and distribution of hunters in order to preclude a harvest quota or the over-loading of hunters in any one management area.
5. Unless otherwise specified by regulation of the Commission or Title 45 of NRS, any resident of Nevada, nonresident or alien is eligible to apply once for a mountain lion tag in any year.
6. A person who harvests a mountain lion shall, within 72 hours after harvesting it, present the skull and hide to a representative of the Department of Wildlife for inspection. The representative shall affix the seal of the Department permanently to the hide. It is unlawful for any person to transport such a hide from this state without a seal permanently affixed to the hide.
7. Except as provided in subsection 2, it is unlawful to possess the hide of a mountain lion without a seal permanently attached to it.
8. If a mountain lion is accidentally trapped or killed, the person trapping or killing it shall report the trapping or killing within 48 hours to a representative of the Department of Wildlife. The animal must be disposed of in accordance with the instructions of the representative.

1982

Limit: One.
Sex/Age Class: Either sex.
Hunting Hours: Any time of the day or night.
Season Dates:

October 1, 1982 through September 30, 1983, except as provided in sections 5 and 6 of this regulation.

Tag Quota: Unlimited.
Harvest Quota:

The harvest quota is the allowable harvest for each listed management area. When the harvest quota has been filled in any management area that area will be closed to hunting.

Area	Objective	Area	Objective
1	0	14	6
2	0	15	5
3	3	16	6
4	5	17	3
5	3	18	9
6	6	19	6
7	8	20	10
8	13	21	6
9	7	22	3
10	8	23	3
11	6	24	3
12	6	25	3
13	5	26	2
Total			135

Special Regulations

1. There is no quota on the number of tags that will be issued for the mountain lion management areas.

2. Tags will be available to residents and nonresidents by application only.

3. Hunters who are awarded tags for this mountain lion hunt must secure a hunting permit before they can hunt under the authority of this tag in any single management area. A valid lion hunting permit and tag must be in possession while hunting mountain lion.

4. Hunting permits will be authorized by mail, telephone, or by appearing in person only at the following department offices:

   For Management Areas 3, 4, 12, 13, 14 and 15:
   Region I Office, 380 W. "B" Street, Fallon, Nevada 89406
   (702) 423-3171

   For Management Areas 5, 6, 7, 8, 9, 10, 11, 19 and 20:
   Region II Office, 1375 Mountain City Highway, Elko, Nevada 89801
   (702) 738-5332

   For Management Areas 16, 17, 18, 21, 22, 23, 24, 25 and 26:
   Region III Office, 4747 Vegas Drive, Las Vegas, Nevada 89109
   (702) 385-0285

5. Hunting permits will be valid in the specified management area until the harvest objective for that management area is reached, or the general season closure, whichever is first. Upon attainment of the harvest objective, the management area will be closed to lion hunting.

6. Hunters holding a valid permit for a management area at the time that the harvest objective is filled will be notified by the Department that the area is closed and that their permit is no longer valid. Hunters may then reapply for any other management area where the harvest objective has not been filled.

7. Department representatives in the Fallon, Elko and Las Vegas Offices will retain final judgement on issuance of permits and distribution of hunters.

8. A hunting permit may be invalidated by the Department and reissued for another mountain lion management area.

Research to Regulation: Cougar Social Behavior as a Guide for Management

Author(s): Richard A. Beausoleil, Gary M. Koehler, Benjamin T. Maletzke, Brian N. Kertson and Robert B. Wielgus

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In My Opinion

Research to Regulation: Cougar Social Behavior as a Guide for Management

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ABSTRACT Cougar (*Puma concolor*) populations are a challenge to estimate because of low densities and the difficulty marking and monitoring individuals. As a result, their management is often based on imperfect data. Current strategies rely on a source–sink concept, which tends to result in spatially clumped harvest within management zones that are typically approximately 10,000 km^2. Agencies often implement quotas within these zones and designate management objectives to reduce or maintain cougar populations. We propose an approach for cougar management founded on their behavior and social organization, designed to maintain an older age structure that should promote population stability. To achieve these objectives, hunter harvest would be administered within zones approximately 1,000 km^2 in size to distribute harvest more evenly across the landscape. We also propose replacing the term "quota" with "harvest threshold" because quotas often connote a harvest target or goal rather than a threshold not to exceed. In Washington, USA, where the source–sink concept is implemented, research shows that high harvest rates may not accomplish the intended population reduction objectives due to immigration, resulting in an altered population age structure and social organization. We recommend a harvest strategy based on a population growth rate of 14% and a resident adult density of 1.7 cougars/100 km^2 that represent probable average values for western populations of cougars. Our proposal offers managers an opportunity to preserve behavioral and demographic attributes of cougar populations, provide recreational harvest, and accomplish a variety of management objectives. We believe this science-based approach to cougar management is easy to implement, incurs few if any added costs, satisfies agency and stakeholder interests, assures professional credibility, and may be applied throughout their range in western North America.

KEY WORDS cougar, harvest management, harvest quota, intrinsic growth rate, management zone, *Puma concolor*, regulation, social structure, source–sink, Washington.

The history of cougar (*Puma concolor*) management in Washington and for the western United States as a whole has been dominated by political and special interest agendas creating a challenge for wildlife managers (Kertson 2005, Beausoleil and Martorello 2008, Mattson and Clark 2010, Jenks 2011, Peek et al. 2012). This is magnified by the lack of reliable information on cougar population size, density, and outcomes of management strategies (Cougar Management Guidelines Working Group 2005). In recent decades, satellite and Global Positioning System telemetry and long-term field investigations in 6 different areas in Washington (Lambert et al. 2006; Robinson et al. 2008; Cooley et al. 2008, 2009*a*, *b*; Maletzke 2010; Kertson et al. 2011*a*, *b*; R. A. Beausoleil, unpublished data), and throughout the West (Logan and Sweanor 2001, Cougar Management Guidelines Working Group 2005, Stoner et al. 2006, Hornocker and Negri 2010, Robinson and DeSimone 2011) have elucidated cougar ecology, providing managers a new scientific basis to help guide management.

Behavior and social organization are important aspects of many species' biology and should be considered for management, particularly for low-density territorial carnivores occupying the apex of the trophic hierarchy (Wielgus and Bunnell 1994, Caro et al. 2009, Packer et al. 2009, Treves 2009, Estes et al. 2011). Maintaining mature cougars is important because they influence rates of immigration and emigration, spatial distribution, reproduction, and kitten survival (Cougar Management Guidelines Working Group 2005, Hornocker and Negri 2010; Cooley et al. 2009*a*, *b*).

We propose a science-based approach to regulated harvest management founded on cougar behavior and social organization, in which harvest is regulated to maintain an older age structure to promote population and social stability. This model for cougar management addresses concerns of various constituencies to 1) provide a sustainable harvest, 2) provide quality recreational experience to the hunting public, 3) maintain viable cougar populations, and 4) more explicitly

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recognize the values of the non-consumptive public by maintaining the behavioral integrity of cougar populations.

We base our recommendations on research from Washington demonstrating that a high harvest rate may not accomplish local population reductions and may result in altering the age structure and social organization of the population. This may have unplanned consequences for cougar–prey dynamics and cougar–human conflict (Knopff et al. 2010, White et al. 2011, Kertson et al. 2013). More than US$ 5 million and >13 years (1998–2011) have been invested in cougar research in Washington at 6 study sites across a diverse landscape (Fig. 1). We distill findings from these investigations and propose strategies to help managers navigate the myriad of agendas that encompass carnivore management for a more predictable management outcome, especially in the unpredictable atmosphere of politics and advocacy. Our objective for this review is to provide a data-driven management system that can be applied consistently among management units that incorporates both species behavior and human interests.

CURRENT COUGAR MANAGEMENT STRATEGIES

Management agencies throughout the west use a variety of strategies and techniques to regulate cougar harvest, including general-season hunts with no harvest limit or season restrictions, limiting the number of hunters through permits, and limiting harvest through quotas or bag limits. The use of trailing hounds to hunt cougars is permitted in the majority of states and provinces (Beausoleil et al. 2008). In this manuscript, we propose replacing the term "quota" with "harvest threshold" because quotas often connote a harvest target or goal rather than a threshold not to exceed, and we propose that harvest should not exceed the intrinsic rate of population growth.

Current management strategies rely on a source–sink concept (Laundré and Clark 2003) and are administered within cougar management zones (CMZs), that are typically about 10,000 km^2 and often have management objectives to reduce or maintain cougar populations (Logan and Sweanor 2001). However, dispersal by cougars from adjacent areas may thwart efforts to locally reduce cougar populations (Lambert et al. 2006, Robinson et al. 2008; Cooley et al. 2009*a*). Conversely, where managers want to maintain cougar populations and apply harvest thresholds to zones, harvest may still be locally excessive when CMZs are >1,000 km^2 and the majority of the harvest occurs in clusters where hunter accessibility is relatively great (Ross et al. 1996). Although local population sinks may be re-populated by immigration of subadults, disruption may occur to the intrinsic social and spatial organization of the population, which may result in a demographic composition dominated by subadults (Lambert et al. 2006; Robinson et al. 2008; Cooley et al. 2009*b*). This situation may create unanticipated consequences, including an increase in the use of residential areas by cougars and in human–cougar complaints (Maletzke 2010, Kertson et al. 2011*b*).

HISTORY OF COUGAR MANAGEMENT IN WASHINGTON

Cougar management in Washington began in 1966 when their status changed from a bounty animal to a big-game species with hunting seasons and harvest limits (Washington

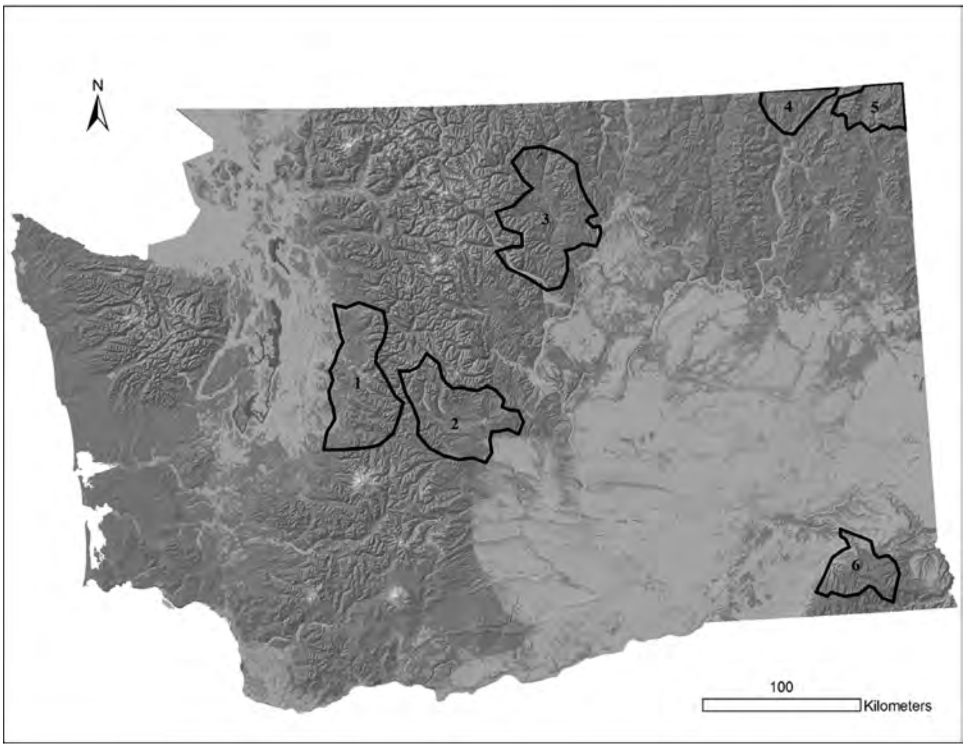

Figure 1. Six cougar research areas in Washington, USA, 2001–2012: (1) western WA; (2) central WA; (3) north-central WA; (4 and 5) northeast WA; (6) southeast WA.

Department of Fish and Wildlife [WDFW] 2008). This change came with a series of regulations, including mandatory reporting (1970), inspection and sealing of cougar pelts for demographic data (1979), and submitting a tooth from harvested animals for age analysis (mid-1980s). From 1980 to 1995, cougar harvest seasons remained static with a 6–8-week season.

Politics began to direct cougar management in 1996 when Washington voters approved Initiative 655 (I-655). Initiative 655 banned the use of dogs for hunting cougar and has been pivotal in framing the debate over cougar management in Washington since then (Kertson 2005, Beausoleil and Martorello 2008). With the use of dogs banned and anticipated decrease in cougar harvest, WDFW 1) replaced limited permit-only seasons with general seasons, 2) increased season length from 7.5 weeks to 7.5 months, 3) increased bag limits from 1 to 2 cougar/year, and 4) decreased the price of transport tags from US$ 24 to $ 5. The response to these changes resulted in increased tag sales from an annual average of 1,000 prior to I-655 to approximately 59,000/year since 1996, and this action increased harvest from an average of 121 (SD = 54, 1980–1995) to an average of 160 (SD = 44, 1996–2011)/year. Hunting opportunities and harvest were not evenly distributed, primarily increasing in areas where social tolerance for cougars was low, deer hunter density was high, and human access was high; during this time, cougar densities were unknown but assumed to be increasing (Jenks 2011, Lambert et al. 2006).

Since I-655 was approved, 16 legislative bills addressing cougar management have been introduced into the Washington legislature (http://apps.leg.wa.gov/billinfo). In 2000, Washington instituted a management concept to reduce cougar numbers in areas where complaints were high (Engrossed Substitute Senate Bill 5001-ESSB 5001). This bill and 3 others since 2003 (Substitute Senate Bill 6118-SSB 6118, Engrossed Substitute House Bill 2438-HB 2438, and Engrossed Substitute House Bill 1756-HB 1756) permitted the use of dogs in 6 counties, effectively overturning I-655 in many areas throughout Washington. In 2011, House Bill 1124 was introduced to continue hunting with hounds but failed to pass, and since the use of dogs has been prohibited statewide. However, ESSB 5001 allows the WDFW to authorize a hunt with the use of dogs when reports of conflicts with humans or their livestock exceed the previous 3-year running average.

In the midst of the political activity between 1996 and 2010, which included legislative mandates, WDFW began integrating insights from harvest monitoring (Martorello and Beausoleil 2003), and research projects (Robinson et al. 2008; Lambert et al. 2006; Cooley et al. 2009*a*, *b*; Kertson 2010; Maletzke 2010). In 2003, harvest thresholds in conjunction with a 24-hour hunter reporting hotline allowed for prompt closure of zones where the use of dogs was permitted. In 2009, the WDFW reduced the bag limit to 1 cougar/hunter/year, shortened season length to avoid some overlap with deer and elk seasons, and restricted harvest with female- and total-harvest thresholds. In 2011, WDFW managers and researchers compiled research findings and began drafting a new management strategy, an aspect of which was publicly reviewed and ultimately adopted by the Washington Fish and Wildlife Commission in spring 2012. Here, we present a synthesis of this research and develop these concepts into a management strategy.

COUGAR ABUNDANCE AND DENSITY: BEHAVIORAL CONSIDERATIONS

Estimating cougar abundance and density, as with most species, represents one of the most challenging aspects of their management. Currently, reliable estimation of cougar abundance requires expensive, field-intensive, long-term research (Hornocker and Negri 2010). Consequently, agencies use numbers of cougar complaints, cougar–human conflicts, and harvest as proxies for population size and trend (Martorello et al. 2006). However, cougar complaint reports can be unreliable (Kertson et al. 2013), and it has been shown that increasing numbers of complaints and increasing predation on mule deer (*Odocoileus hemionus*), and endangered mountain caribou (*Rangifer tarandus caribou*) in a large (10,000-km^2) heavily hunted CMZ in the Selkirk Mountains Ecosystem in northeastern Washington, northern Idaho, and southern British Columbia did not correspond to increasing densities of cougars (Katnik 2002, Robinson et al. 2002, Lambert et al. 2006). Thus, the indirect proxies of population size appeared to be plausible but were inaccurate in that heavily hunted CMZ that had approximately 38% annual removal rate of cougars.

Subsequent research in Washington was designed to examine the previous hypothesis (Lambert et al. 2006) of no direct positive correlation between harvest numbers and complaints and population densities of cougars. Working in the heavily hunted (24% of population harvested/yr), area of Kettle Falls in northern Washington, a declining female cougar population was documented as the male segment increased due to compensatory juvenile male immigration (Robinson et al. 2008). In another study area in central Washington, (Cle Elum), an opposite scenario was confirmed in that relatively low hunting mortality (11%/yr) resulted in a net emigration of younger males (Cooley et al. 2009*a*). In all cases, the population densities were remarkably similar, ranging from 1.5 to 1.7 adult (>2-yr-old), cougars/100 km^2 with total densities of about 3.5 cougars/100 km^2, including kittens and subadults. Details on estimating population densities and immigration–emigration rates have been described (Robinson et al. 2008; Cooley et al. 2009*a*, *b*; Robinson and DeSimone 2011). Additional research on 2 other study areas in western and north-central Washington showed an average resident adult density of about 1.6/100 km^2 and a total density of about 3.4/100 km^2 (R. A. Beausoleil and B. N. Kertson, unpublished data). In 3 separate study areas in Washington and Montana, increased hunting (11–38% population harvest rates) did not result in compensatory increases in cub production, cub survival, or adult survival (Robinson et al. 2008; Cooley et al. 2009*a*, *b*; Robinson and DeSimone 2011). However, variation in hunting mortality did result in compensatory immigration–emigration by primarily young males, with no net differences in total cougar numbers. Such compensatory immigration has been observed in many other highly mobile species as well (Beecham and Rohlman 1994, Merrill et al. 2006, Turgeon and Kramer 2012, Mills 2013). Therefore, increased hunting may not always result in reduced local densities of cougars, but not due to traditional density-dependent effects such as compensatory reproduction and survival; instead, increased hunting may result in compensatory immigration by mainly young males (Cooley et al. 2009*b*).

Presenting and comparing density estimates between studies is challenging because standardization is lacking (Quigley and Hornocker 2010). For example, whereas total density could temporarily fluctuate in response to immigration and emigration of subadults, density of resident breeding adults tends toward stability over time. Density estimates can also be misinterpreted from incomplete data due to differences in seasonal spatial use patterns where individuals concentrate on low-elevation ungulate winter ranges, often comprising only a portion of the population's annual distribution (Maletzke 2010). When annual boundaries of individual cougar territories are unknown, density estimates may result in inflated values and substantial overestimation of population size (Maletzke 2010). However, there is remarkable consistency in the western United States and Canada where long-term research has been conducted; resident adult densities average 1.6 cougar/100 km^2, while total densities including kittens and subadults average 2.6 cougar/100 km^2 (Quigley and Hornocker 2010). Our research in Washington corroborates these findings because adult densities averaged 1.7/100 km^2 (Cooley et al. 2009*b*; R. A. Beausoleil and B. N. Kertson, unpublished data). Therefore we encourage a more explicit, standardized approach of using estimates of adult densities for population management objectives and caution against using total densities, because they do not provide for reliable estimation of population parameters and harvest impacts (Robinson et al. 2008; Cooley et al. 2009*b*).

In Washington, where prey biomass was consistent and cougar harvest ranged from 11% to 38% of the cougar population per year, the age structure, survival, sex ratio, reproductive rate, and spatial use patterns of cougars differed (Lambert et al. 2006; Cooley et al. 2009*b*; Maletzke 2010). Where annual harvest was 24%, mean age at harvest was 27 months compared with 38 months where annual harvest was 11%. In addition, in areas of greater relative harvest, male home-range sizes were larger (753 km^2 vs. 348 km^2), and home-range overlap between males was greater (41% vs. 17%). Cougars, especially males, evolved with a social dynamic to patrol and defend a territory regardless of whether their home-range size is determined by prey density or social tolerance (Hornocker 1969, Pierce et al. 2000, Logan and Sweanor 2010). As adult mortality increases, territorial boundaries diminish. Immigrating subadults may establish home ranges readily, and their home ranges may overlap significantly, which may influence rates of predation and the distribution of prey and potentially increase probabilities for interactions with humans (K. A. Peebles, Washington State University, unpublished data).

The social system and territoriality observed for cougars is similar among many species of solitary felids, although it may manifest itself differently for males and females (Sunquist and Sunquist 2002). Although the role of social ecology for cougars will continue to be debated in the future, it is important to acknowledge that harvest intensity can affect spatial use patterns of cougars as well as their population demographics, as demonstrated for other hunted carnivore populations (Packer et al. 2009).

HARVEST MORTALITY VERSUS TOTAL MORTALITY

Although knowledge of population abundance and density is critical for sound management of cougars, it is also important that managers be aware that harvest mortality can be additive to natural mortality (Robinson et al. 2008; Cooley et al. 2009*b*; Robinson and DeSimone 2011). Failing to account for and include all mortality sources may obscure estimates of population trajectory and underestimate the impact of harvest on demographics and cougar social structure (Cooley et al. 2009*b*; Morrison 2010; Robinson and DeSimone 2011). Unfortunately, reliable knowledge of non-harvest mortality is difficult to quantify (Cougar Management Guidelines Working Group 2005), because harvest may not necessarily be representative of age structure of the population (R. A. Beausoleil, B. N. Kertson, and G. M. Koehler, unpublished data).

To illustrate the importance of considering non-harvest mortality, we documented 79 mortalities of radiomarked cougars during 4 concurrent research efforts in Washington. Of these, 49% were non-hunter harvest mortalities; 14% from agency control, 6% from intraspecific strife, 6% due to motor-vehicle collisions, 4% from disease, 4% attributed to Native American predator-control efforts, 3% due to injuries sustained during pursuit of prey, 3% from poaching or illegal harvest, and 10% from undetermined sources. In the western Washington study area, hunter harvest mortality averaged $\leq$2 animals/year from 2003 to 2008 and annual survival rate of the study population was 55% (SD $=$ 7.8, $n = 5$ yr; B. N. Kertson, unpublished data). A significant mortality factor for this population was from feline leukemia virus exposure along the wildland–urban interface, resulting in an observed average annual survival rate of 55%, less than that for a heavily hunted population in Washington with 79% annual survivorship (Cooley et al. 2009*b*). These examples demonstrate the importance that non-harvest mortality can have in cougar population dynamics.

POPULATION GROWTH AND MAXIMUM SUSTAINED YIELD

The growth rate for an unhunted population, or intrinsic rate of population growth, can be described as the rate we expect the population to grow if it did not experience additive hunting mortality. Because kitten mortality and non-harvest mortality can be additive to hunting mortality, we calculated the intrinsic growth rate by censoring all harvest mortalities. In Washington, the unhunted growth rate was 1.14 (SD $= \pm 0.023$) for 3 different populations (Selkirk Mountains, Kettle Falls, and Cle Elum; Morrison 2010). The intrinsic growth rate in northwest Montana was estimated by removing hunting that resulted in a population growth rate of 1.15–1.17 (Robinson and DeSimone 2011). Although growth rate may be considered equivalent to the maximum sustainable yield, the rate of growth for an unhunted population should not be the goal for harvest but rather a maximum not to exceed if a stable population is to be achieved. Using maximum sustainable yield as a management target has been cautioned against, because it does not incorporate the uncertainty of stochastic events on population abundance and may present a potential for over-harvest (Caughley and Sinclair 1994). Setting adult harvest limits to the intrinsic rate of growth of 14% should help to balance immigration and emigration among harvest units and result in greater stability of cougar densities and age structure.

HARVEST UNITS AND HARVEST THRESHOLDS

Cougars are often managed in administrative zones (Logan and Sweanor 2001), which represent an amalgam of smaller Game Management Units (GMUs). Commonly these CMZs are designated as population "sources" and "sinks" where management objectives are to maintain or decrease population levels, respectively (Laundré and Clark 2003). In Washington, 139 GMUs are partitioned throughout the state and are used to manage harvest and habitat for a variety of game species (Fig. 2). In 2011, these GMUs were combined into 13 CMZs, each comprised from 3 to 22 GMUs and encompassing 1,873–14,947 km^2 of forested and shrub-steppe habitat (total = 90,783 km^2; Fig. 3). Five CMZs had a harvest limit of 6–20 cougars, and 8 did not have limits. Individual GMUs with high hunter access and suitable snow conditions accounted for 25–50% of the total harvest within the CMZs, which has been repeated over multiple years (WDFW 2011). This uneven distribution of harvest, or harvest clustering, may create local population sinks in areas within CMZs designated as sources and may disrupt the social organization of cougars as previously explained. Additionally, this uneven distribution of harvest may result in some GMUs with little or no harvest, creating angst among hunters who feel harvest opportunity was inequitable.

Setting harvest thresholds can help to distribute harvest, minimize risk of overharvest (Ross et al. 1996), and help maintain recreational opportunity and quality of hunter experience. However, it is important to note that harvest thresholds may become less effective for distributing harvest as CMZ size increases, and harvest may be concentrated within areas where access is high (i.e., harvest clustering). Harvest thresholds to limit harvest may be more effective where harvest is distributed evenly among GMUs rather than applied to the larger CMZs. Where GMUs are small, habitat is limited, or a quota of ≤ 1 cougar is allocated, combining adjacent GMUs to reach a size of approximately 1,000 km^2 may be recommended.

HUNTER CONSIDERATIONS

Age and sex of harvest can be an important factor influencing population dynamics of big-game species. Unlike ungulates

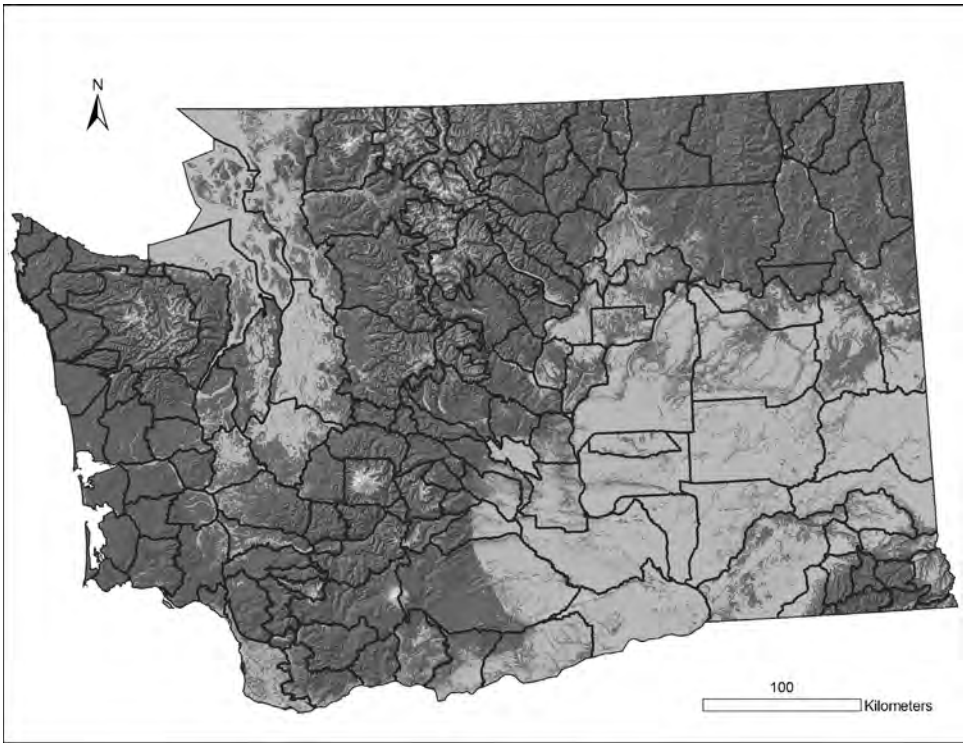

Figure 2. Distribution of cougar habitat (shaded dark) and current game-management units (outlined in black) in Washington, USA, Washington Department of Fish and Wildlife, 2012.

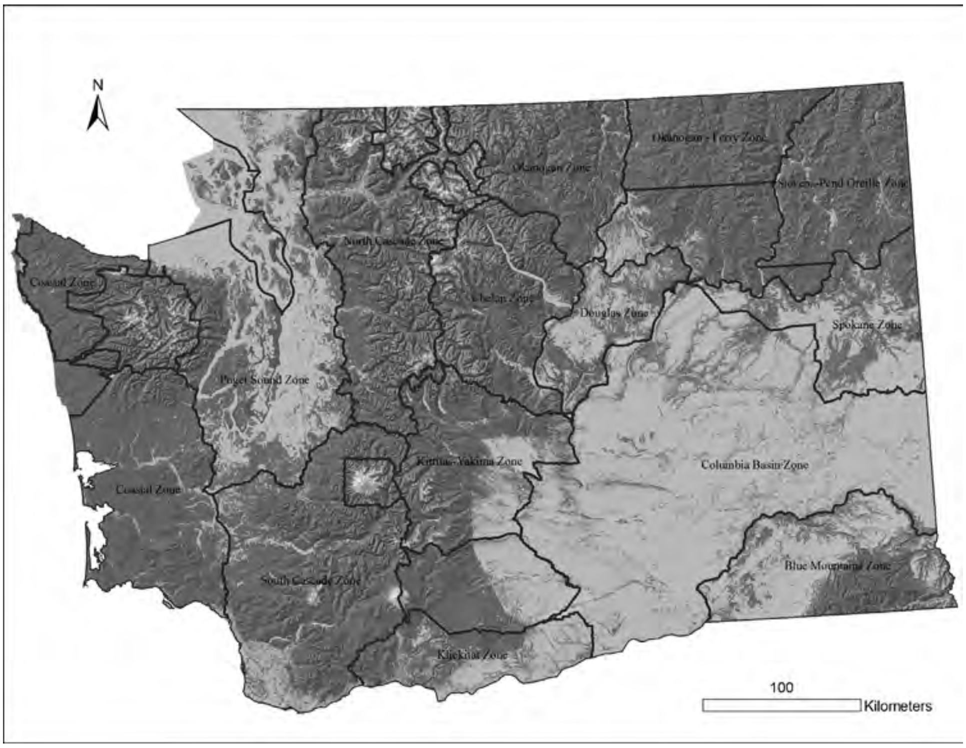

Figure 3. 2011 cougar management zones in Washington, USA, Washington Department of Fish and Wildlife, 2012.

for which juvenile status and sex are readily identifiable, most hunters are unable to distinguish female cougars from males and adults from subadults until after the animal is killed. Where the use of dogs is permitted, sex, and age determination may be more reliable but not certain due to restricted visibility of treed animals.

Many agencies employ a general open season and a permit-only season for cougar. Two concerns for hunters who participate in permit-only hunts (either limited-entry or quota hunts) are 1) when harvest threshold tallies begin during a general open season (which often overlaps with deer and elk season), and that, when filled, nullify the permit-only season; and 2) when the number of permits issued is greater than harvest threshold, thus creating a competitive atmosphere (the use it or lose it conundrum). In Washington, for example, 10–35 permits were issued for CMZs with harvest objectives for 6–20 cougars.

IMPLEMENTATION

The first step for applying our proposed management framework is to estimate the amount of cougar habitat. For Washington, we plotted 85,866 Global Positioning System and satellite telemetry locations from 117 radiocollared cougars in 5 study areas in to U.S. Fish and Wildlife Service–U.S. Geological Survey Landfire habitat coverage (LANDFIRE 2007) using ArcMap 9.3. We quantified the number of Global Positioning System locations in each habitat type, created a Geographic Information System data layer identifying habitats used by marked cougars, and extrapolated these habitats throughout the state. The result included 90,783 km^2 of the 104,000 km^2 of habitat for areas where WDFW has management authority (Fig. 1). For states and provinces lacking empirical estimation of suitable habitat for cougars, reliable and quantifiable estimates of forest cover, topographic variability, limited residential development (not to exceed exurban densities), and persistent ungulate prey may provide reasonable measure of suitable habitat for cougars (Burdett et al. 2010; Maletzke 2010; Kertson et al. 2011*b*). However, where existing Geographic Information System coverages may not reflect current landscape conditions, we advocate they be ground-truthed to avoid overestimating habitat. Including district or regional biologists and officers can also be advantageous.

We then overlaid current GMU boundaries onto this habitat coverage to calculate the available habitat within each GMU, and we applied adult densities of 1.7 cougars/100 km^2 to estimate the number of adult residents per GMU. Where GMUs were small (<750 km^2), or the habitat sparse, we combined adjacent GMUs; this resulted in 62 CMZs for Washington (Fig. 4). In jurisdictions where densities are not estimable, we suggest that the scientifically defensible average of 1.6 adults/100 km^2 be applied (Quigley and Hornocker 2010).

We applied a mean intrinsic rate of growth of 14% (Morrison 2010) to allocate harvest of adult cougar per unit of area (0.24 cougars/100 km^2 of habitat). For Washington, this resulted in a statewide annual harvest of 220 cougars, more than the average annual harvest from previous years. Although the proposed harvest would be greater, this harvest would be distributed more evenly across management units in the state, resulting in a more uniformly distributed hunter effort, less harvest clustering and population sinks, and

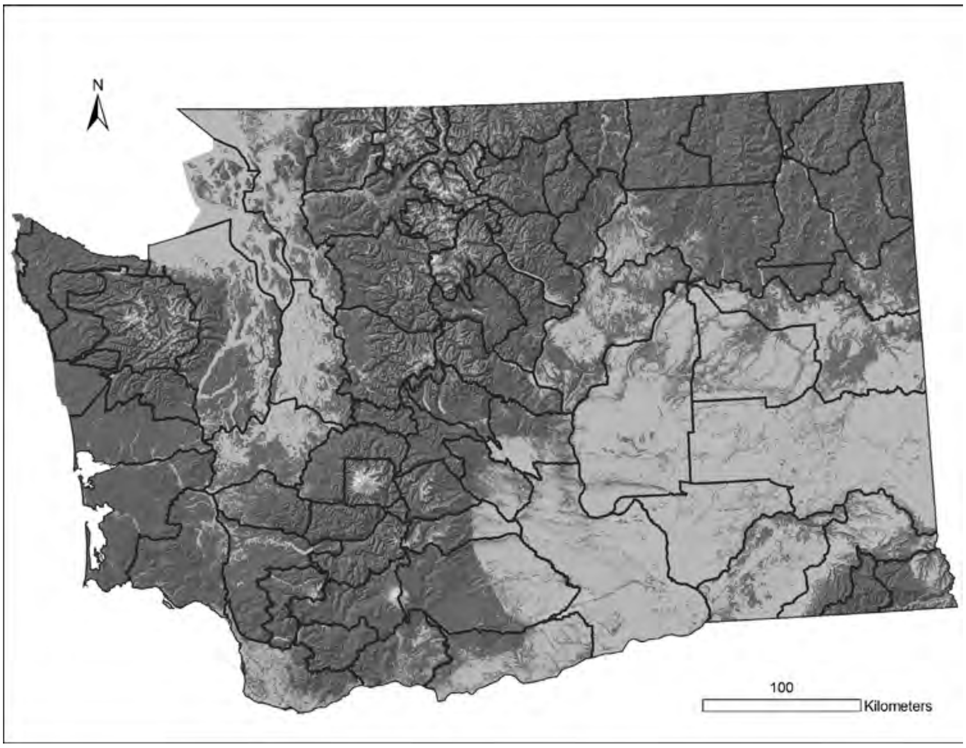

Figure 4. Proposed cougar management zones for Washington, USA, 2012.

greater stability in the cougar population. This strategy may prevent the need for harvest thresholds based on sex and could simplify harvest regulations and administration. We recommend using the harvest threshold of 14%. In addition, because subadult age classes are dynamic and difficult to estimate, and difficult to identify in the field, we recommend that harvest of this age class be counted against the allocated harvest so that recruitment is not affected in the future. Finally, we advocate administering the hunt using a 24-hour reporting and information hotline because it allows for prompt reporting of kills and CMZ closure and provides hunters the opportunity to plan hunt activity.

Administering harvest thresholds for GMUs or smaller CMZs has multiple benefits. It helps to 1) preserve the cougar's social organization by distributing harvest more evenly and avoiding creation of population sinks, 2) eliminate the need for harvest thresholds based on sex and for field identification of sex, 3) distribute hunter opportunity across the landscape, and 4) define a biological and meaningful spatial scale similar to that of their prey (ungulates), bringing management for predator and prey into alignment.

MANAGEMENT IMPLICATIONS

We acknowledge that these recommendations are based on research in Washington, but similar findings have been documented elsewhere in western North America (Quigley and Hornocker 2010). For the most part, current cougar management programs do not address the effects of harvest on social structure of cougar populations, a concept that was introduced >40 years ago (Hornocker 1969, 1970) and is supported by current research. We believe this science-based approach to cougar management is easy to implement, incurs no added costs, satisfies agency and stakeholder interests, and assures professional credibility. The current review of carnivore management has demonstrated a paradigm shift from lethal control to one of ecosystem management, and one that considers the values of multiple stakeholders and aspects of human dimensions (Treves 2009, Hornocker and Negri 2010, Van Ballenberghe 2011, Way and Bruskotter 2012, Peek et al. 2012). Our recommendations incorporating cougar behavior and social organization into a management framework addresses concerns of various constituencies, provides for quality hunter experience, and recognizes values of the non-consumptive public while maintaining viable cougar populations and the behavioral integrity of their populations.

A simple, consistent, science-based approach to cougar management can be of benefit to agencies during intervals of administrative and political uncertainty. In addition to fulfilling agency mandates for hunter opportunity, our proposal adheres to our state agency's mission to "promote development and responsible use of sound, objective science to inform decision making" (WDFW 2008). In our opinion, of equal importance is recognizing the ecological and evolutionary role of cougar in the trophic hierarchy (Estes et al. 2011); and incorporating this concept into management and education elevates the cougar's status beyond a mere predator.

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LITERATURE CITED

Beausoleil, R. A., D. Dawn, D. A. Martorello, and C. P. Morgan. 2008. Cougar management protocols: a survey of wildlife management agencies in North America. Pages 205–241 *in* D. E. Toweill, S. Nadeau, and D. Smith, editors. Proceedings of the Ninth Mountain Lion Workshop. Idaho Department of Fish and Game, Sun Valley, Idaho, USA.

Beausoleil, R. A., and D. A. Martorello. 2008. Washington mountain lion status report. Pages 18–22 *in* D. E. Toweill, S. Nadeau, and D. Smith, editors. Proceedings of the Ninth Mountain Lion workshop. Idaho Department of Fish and Game, Sun Valley, Idaho, USA.

Beecham, J. J., and J. Rohlman. 1994. A shadow in the forest: Idaho's black bear. University of Idaho Press, Moscow, USA.

Burdett, C. L., K. R. Crooks, D. M. Theobald, K. R. Wilson, E. E. Boydston, L. M. Lyren, R. N. Fisher, T. W. Vickers, S. A. Morrison, and W. M. Boyce. 2010. Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1:4.

Caro, T. M., C. R. Young, A. E. Cauldwell, and D. D. E. Brown. 2009. Animal breeding systems and big game hunting: models and application. Biological Conservation 142:909–929.

Caughley, G., and A. R. E. Sinclair. 1994. Wildlife ecology and management. Blackwell Science, Malden, Massachusetts, USA.

Cooley, H. S., H. S. Robinson, R. B. Wielgus, and C. S. Lambert. 2008. Cougar prey selection in a white-tailed deer and mule deer community. Journal of Wildlife Management 72:99–106.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, and B. T. Maletzke. 2009*a*. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Animal Conservation 12:321–328.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009*b*. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cougar Management Guidelines Working Group. 2005. Cougar management guidelines. First edition. WildFutures, Bainbridge Island, Washington, USA.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet earth. Science 333:301–306.

Hornocker, M. G. 1969. Winter territoriality in mountain lions. Journal of Wildlife Management 33:457–464.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. Wildlife Monographs 21.

Hornocker, M., and S. Negri. editors, 2010. Cougar: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Jenks, J. A. 2011. Managing cougars in North America. Jack H. Berryman Institute, Utah State University, Logan, Utah, USA.

Katnik, D. D. 2002. Predation and habitat ecology of mountain lions (*Puma concolor*) in the southern Selkirk mountains. Dissertation, Washington State University, Pullman, Washington, USA.

Kertson, B. N. 2005. Political and socio-economic influences on cougar management in Washington State: post Initiative. Pages 92–103 *in* R. A. Beausoleil, and D. A. Martorello, editors. Proceedings of the Eighth Mountain Lion workshop. Washington Department of Fish and Wildlife, Olympia, Washington, USA.

Kertson, B. N. 2010. Cougar ecology, behavior, and interactions with people in a wildland–urban environment in western Washington. Dissertation, University of Washington, Seattle, USA.

Kertson, B. N., R. D. Spencer, and C. E. Grue. 2011*a*. Cougar prey use in a wildland–urban environment in western Washington. Northwestern Naturalist 92:175–185.

Kertson, B. N., R. D. Spencer, and C. E. Grue. 2013. Demographic influences on cougar residential use and interactions with people in western Washington. Journal of Mammalogy 94:269–281.

Kertson, B. N., R. D. Spencer, J. M. Marzluff, J. Hepinstall-Cymerman, and C. E. Grue. 2011*b*. Cougar use and movements in the wildland–urban landscape of western Washington. Ecological Applications 21:2866–2881.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management 74:1435–1447.

Lambert, C. M. S., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

LANDFIRE. 2007. Existing Vegetation Type layer (EVT). U.S. Department of Interior Geological Survey. http://www.landfire.gov/index.php. Accessed 02 Dec 2011.

Laundré, J. W., and T. W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. Animal Conservation 6:159–170.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D. C., USA.

Logan, K. A., and L. L. Sweanor. 2010. Behavior and social organization of a solitary carnivore. Pages 105–117 *in* M. G. Hornocker, and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Illinois, USA.

Maletzke, B. T. 2010. Effects of anthropogenic disturbance on landscape ecology of cougars. Dissertation, Washington State University, Pullman, USA.

Martorello, D. A., and R. A. Beausoleil. 2003. Characteristics of cougar harvest with and without the use of dogs. Pages 129–135 *in* S. A. Becker, D. D. Bjornlie, F. G. Lindsay, and D. S. Moody, editors. Proceedings of the Seventh Mountain Lion workshop. Wyoming Game and Fish Department, Lander, Wyoming, USA.

Martorello, D. M., R. A. Beausoleil, and R. D. Spencer. 2006. Cougar status and trend report. Pages 170–172 *in* 2006 Game status and trend report. Washington Department of Fish and Wildlife, Wildlife Program, Olympia, Washington, USA.

Mattson, D. J., and S. G. Clark. 2010. People, politics, and cougar management. Pages 206–220 *in* M. G. Hornocker, and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Illinois, USA.

Merrill, J. A., E. G. Cooch, and P. D. Curtis. 2006. Managing an overabundant deer population by sterilization: effects of immigration, stochasticity and the capture process. Journal of Wildlife Management 70:268–277.

Mills, L. S. 2013. Conservation of wildlife populations: demography, genetics, and management. Second edition. John Wiley and Sons, Malden, Massachusetts, USA.

Morrison, D. E. 2010. Effects of trophy hunting on female cougar population growth and persistence. Thesis, Washington State University, Pullman, USA.

Packer, C., M. Kosmal, H. S. Cooley, H. Brink, L. Pintea, D. Garshelis, G. Purchase, M. Strauss, A. Swanson, G. Balme, L. Hunter, and K. Nowell. 2009. Sport hunting, predator control and conservation of large carnivores. PLoS ONE 4:1–8.

Peek, J., B. Dale, H. Hristienko, L. Kantar, K. A. Loyd, S. Mahoney, C. Miller, D. Murray, L. Olver, and C. Soulliere. 2012. Management of large mammalian carnivores in North America. Technical Review 12-1. The Wildlife Society, Bethesda, Maryland, USA.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533–1543.

Quigley, H., and M. Hornocker. 2010. Cougar population dynamics. Pages 59–75 *in* M. G. Hornocker, and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Robinson, H. S., and R. M. DeSimone. 2011. The Garnet Range mountain lion study: characteristics of a hunted population in West-central Montana. Final report, Montana Department of Fish, Wildlife, and Parks, Wildlife Bureau, Helena, Montana, USA.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. Canadian Journal of Zoology 80:556–568.

Ross, P. I., M. G. Jalkotzy, and J. R. Gunson. 1996. The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24:490–494.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation level in Utah; implications for demographic structure, population recovery and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.

Sunquist, M., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinois, USA.

Treves, A. 2009. Hunting for large carnivore conservation. Journal of Applied Ecology 46:1350–1356.

Turgeon, K., and D. L. Kramer. 2012. Compensatory immigration depends on adjacent population size and habitat quality but not on landscape connectivity. Journal of Animal Ecology 81:1161–1170.

Van Ballenberghe, V. 2011. Intensive management-or mismanagement? Exploring Alaska's predator control programs. The Wildlife Professional (Winter) 74–77.

Washington Department of Fish and Wildlife [WDFW]. 2008. 2009–2015 Game management plan. Washington Department of Fish and Wildlife, Wildlife Program, Olympia, Washington, USA.

Washington Department of Fish and Wildlife [WDFW]. 2011. 2011 Game status and trend report. Washington Department of Fish and Wildlife, Wildlife Program, Olympia, Washington, USA.

Way, J. G., and J. T. Bruskotter. 2012. Additional considerations for gray wolf management after their removal from endangered species act protections. Journal of Wildlife Management 76:457–461.

White, K. R., G. M. Koehler, B. T. Maletzke, and R. B. Wielgus. 2011. Differential prey use by male and female cougars in Washington. Journal of Wildlife Management 75:1115–1120.

Wielgus, R. B., and F. L. Bunnell. 1994. Dynamics of a small hunted brown bear population in southwestern Alberta, Canada. Biological Conservation 67:161–166.

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What can harvest data tell us about Montana's black bears?

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Abstract: Harvest data provide readily available and relatively inexpensive information about populations of game species. However, these data are not necessarily representative of standing populations and may have limited applicability in management. We applied a method of harvest data analysis based on the changing sex ratio of the harvest with age to American black bear (*Ursus americanus*) harvest data from 1985–2005 in Montana. We assessed the ability of this method to identify assumption violations and the extent of resulting bias. A change in the relative vulnerability of females at primiparity due to protection of mothers with cubs from harvest was observable as a drop in the proportion of females in the harvest at the age of maturity. A changing harvest rate produced changing harvest rate estimates, but the estimates lagged up to 10 years behind the actual rate. Other assumption violations, such as unequal non-harvest mortality between sexes and stochasticity in the harvest rate, are not apparent in the harvest data themselves. If total harvest is known and the harvest rate is estimable, it may be possible to use harvest to identify population declines. However, we found with simulations that, in many cases, 10–15 years of harvest data are needed to identify a statistically significant decline. If all assumptions are met, we estimated harvest rates in Montana as 4.6% for females and 10.4% for males; these are overestimates if males have higher non-harvest mortality than females. Montana's harvest data did not show an apparent decline in the relative vulnerability of females at maturity, despite nominal protection of mothers accompanied by cubs. Analyses of harvest data also contradicted the hypothesis, based on meta-analysis of demographic data, that black bears were declining in Montana.

Key words: American black bear, catch-at-age, harvest, Montana, population trend, relative vulnerability, sustainable harvest, *Ursus americanus*

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Wildlife managers are often charged with managing populations of game species that are rare or secretive, such as many furbearers and carnivores, using very limited resources. Many jurisdictions require hunters to bring harvested individuals through check stations where age and sex data are collected (Rupp et al. 2000), and in many cases, harvest data are the best or only source of information about the status of these populations. A variety of techniques, relying on different assumptions about population and harvest processes, can be used to estimate both harvest rates and population status or vital rates from these harvest data (Skalski et al. 2005). However, it is surprisingly common for harvest data to be collected and not used or applied to management. For instance, in eastern North America, just 13 out of 26 jurisdictions that have a legal American black bear hunt used harvest data to estimate population size in 2011 (Noyce 2011). Likewise, Rupp et al. (2000) found that while almost all surveyed jurisdictions collected white-tailed deer (*Odocoileus virginianus*) harvest data, fewer than half of them used the harvest data for population models. Four respondents stated that harvest data were collected but not actually used in decision-making, and most of the agencies used harvest data to estimate the total harvest but not harvest rate or population size and trend (Rupp et al. 2000). More generally, harvest management is often developed from a patchwork of interests and implemented piecemeal over a sometimes long time

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frame (Milner-Gulland and Rowcliffe 2007), making application of harvest data in decision-making that much more idiosyncratic. Basing decisions on harvest data may also not be a top priority when managers must consider budget priorities and constraints and incorporate public interests and input.

One reason harvest data are not used more thoroughly may be the limitations of available harvest data analysis methods. Methods with various assumptions and requirements have been used to estimate harvest rate and population status from harvest data (Roseberry and Woolf 1991). Methods such as population reconstruction and change-in-ratio use the age and sex structure of the harvest to infer information about the population. Others, such as index removal and catch per unit effort, rely on combinations of surveys and harvest data. Roseberry and Woolf (1991) reviewed 9 methods and reported that half require data in addition to information on the harvested animals, such as harvest effort or a concurrent field study. Managers often lack such auxiliary information. Of methods that do not require auxiliary data, several use the age structure of the harvest to infer information about survival rates or population trend (Skalski et al. 2005). However, the composition of the harvest may not be representative of the living population (Litvaitis and Kane 1994), and the relative numbers of different ages may reflect hunter selectivity, age- and sex-specific vulnerabilities to harvest, or the effect of harvest regulations more so than the population trend (Bunnell and Tait 1980, Noyce and Garshelis 1997). Estimates of harvest rates derived from harvest data are also more reliable when a large proportion of the population is removed each year (Harris and Metzgar 1987, Roseberry and Woolf 1991), which is thought not to be the case for many carnivores.

In this paper, we examined the robustness of a combination of the methods presented by Paloheimo and Fraser (1981) and Fraser (1984) for estimating harvest rate of black bears. The method we applied avoids some problems of other methods, such as the need for additional data, and explicitly models the differential vulnerability to harvest across groups. However, information on hunter effort is needed if it has not been constant, and the method we used relies on a number of assumptions: the initial sex ratio is even, the differential vulnerability of the sexes is constant across ages, the harvest rate is constant across time, and the natural mortality rates are equal for both sexes. Assuming these are met, if one sex is more vulnerable to harvest than the other, the ratio of males to females in sequential harvests of a cohort will change as that cohort ages. Fraser (1984) showed that the inverse of the age at which the sex ratio of the harvest is even will approximate the average harvest rate. This simple estimate works best when the harvest rate is near 0.5 or the differential vulnerability is much less than the harvest rate. Paloheimo and Fraser (1981) used the same principle, but relaxed these requirements by using generalized least squares to estimate harvest rate and relative vulnerability using a model of harvest sex ratio at each age. Harris and Metzgar (1987) explored the utility of these methods for bears in general and especially grizzly bears (*Ursus arctos*), and found that violations of the assumptions biased estimates of harvest rate more when the harvest rate, differential vulnerability, or both were low and when harvest samples are small.

In many jurisdictions, black bear harvests exceed the samples simulated by Harris and Metzgar (1987) by an order of magnitude or more, meaning the method may be more appropriate for black bears than initially suggested. We used stochastic simulations to not only explore how assumption violations bias harvest estimates, but also to assess qualitatively whether the harvest data can indicate when assumptions are violated. We then applied the method to harvest data for black bears in Montana and examined the expectation that adult female black bears experience lower harvest than immature females because it is illegal to harvest a female when she is accompanied by young. Our expectation was that the vulnerability of female black bears in Montana decreased by 50% at primiparity because adult females spend about half their time accompanied by cubs (Mace and Chilton-Radandt 2011).

When total harvest is known, it is possible to estimate the population size based on harvest rate estimates. We used simulations to determine whether we would be likely to detect population declines under constant harvest rate using total harvest and estimated population size. We then applied this concept to Montana's black bear harvest data to evaluate the hypothesis that black bears were declining in Montana, an unexpected result from a meta-analysis of demographic studies (Beston 2011). The meta-analysis indicated that, on average, black bears were declining in the western United States, at a rate of ~1–4%/year. This contradicted the general perception of managers that black bears were stable or slowly increasing throughout their range (Garshelis and Hristienko 2006). The conclusion that populations were declining could result from biases in data available for meta-analysis, but it could also mean that our impressions of growth were incorrect (Garshelis and Hristienko 2006, Lambert et al. 2006). Harvest methods and tag sales have been consistent in Montana for the past 20 years (R. Mace, unpublished data). Therefore, if the black bear population was declining we predicted that the harvest rate was increasing and the total harvest was stable, that the harvest rate was stable and the total harvest was decreasing, or some combination of increasing harvest rate and decreasing total harvest.

Black bear hunting In Montana

In Montana, black bear range is restricted to the mountainous western portion of the state, and hunting is permitted in all 5 Montana Fish, Wildlife and Parks (MFWP) regions where black bears occur. Bears were hunted in 2 seasons: in spring from April 15 through mid-May–mid-June, and in fall from September 15–late November. Black bear licenses for residents cost $15–19 and permit the take of 1 black bear/calendar year. Hunting bears using bait or dogs has been illegal in Montana since the first half of the twentieth century. It was also illegal to harvest cubs (black bears <1 year old) and mothers with young. Because family break-up occurs during the summer, a female with yearlings was illegal to harvest in the spring but legal to harvest in the fall of the same year. In addition to direct protection when accompanied by cubs, females tend to enter hibernation earlier and remain in hibernation later than males, especially when pregnant or nursing (Beecham et al. 1983). They may be in dens by mid-October and remain until late May (Jonkel and Cowan 1971, Beecham 1983), missing most of both hunting seasons. Tag sales in Montana were relatively constant for the 20 years prior to this analysis (MFWP, Helena, Montana, USA, unpublished data), and evidence from hunter surveys suggests the harvest effort, measured in hunter days, was consistent for the period for which data are available (MFWP, Helena, Montana, USA, unpublished data, 1996–2003). Therefore, we did not include hunter effort in our estimation approach. Hunters were required to bring harvested black bears through check stations, where each bear was sexed and a tooth collected for aging. Based on the call-back survey, check station compliance was believed to be nearly complete, and thus we used the numbers of bears brought through check stations as the total harvest size.

Methods

Estimation of harvest rate

Given an average harvest rate of k and a difference in vulnerability $2v$, such that the harvest rate of males is $k+v$ and the harvest rate of females is $k-v$, then the ratio of males in the harvest, H_m, to females in the harvest, H_f, at age i can be written as

$$\frac{H_{m,i}}{H_{f,i}} = \frac{M_1(1-(k+v))^{i-1}s_m^{i-1}(k+v)}{F_1(1-(k-v))^{i-1}s_f^{i-1}(k-v)},$$

where M_1 and F_1 are the numbers of males and females, respectively, in the cohort when it enters the harvestable population, and s_m and s_f are the natural survival rates of males and females. This is essentially the same equation used by Paloheimo and Fraser (1981), replacing their vulnerabilities and hunter efforts with constant harvest rates.

Two methods can be used to estimate k and v based on this equation. We took the natural logarithm of both sides and used generalized least squares estimation to find k and v, following Paloheimo and Fraser (1981). Alternatively, we used regression to estimate the age when the harvest sex ratio is 1 and coupled this with information from the youngest harvest age to create a system of 2 equations. We then solved these equations for the 2 variables, which was essentially the approach used by Fraser (1984). At the youngest age of harvest (1 year old for black bears), the sex ratio of harvest can be written:

$$\frac{H_{m,1}}{H_{f,1}} = \frac{M_1(k+v)}{F_1(k-v)},$$

and at age y, the male and female harvests are equal, yielding:

$$1 = \frac{M_1(1-(k+v))^{y-1}s_m^{y-1}(k+v)}{F_1(1-(k-v))^{y-1}s_f^{y-1}(k-v)}.$$

Note that we assumed $M_1 = F_1$ and $s_m = s_f$ in order to solve for y. We found that both methods produced similar results, so we present results from the latter method.

Analysis of assumption violations

We used simulations to assess the effects of assumption violations on the structure of the harvest data and the resulting estimates of harvest rate. For each analysis, we simulated 2,500 replicate stochastic populations for 20 years using a 60 x 60, pre-birth pulse, sex and age-based matrix model (Caswell 2000). Bears were divided into 4 stages: cubs (0 years old), yearlings (1-yr), subadults (2–5 yr), and adults (6–30 yr). Males and females had the same survival rates, except in simulations that specifically considered deviations from equal natural mortality. Adult females produced cubs in a 1:1 sex ratio. We parameterized the model with survival rates and variances from the western half of North America (Beston 2011). Harvest rates for each sex, fecundity, and their variances, as well as age at primiparity, were based on data from Montana. Each year a harvest rate for each sex was selected from beta distributions with mean equal to the initial estimates from Montana's harvest data and variance based on the variance seen in the total harvest assuming constant population size. After simulating harvest, vital rates were selected from beta distributions for survival, and a lognormal distribution for fecundity and the population was multiplied by that year's matrix model.

One assumption made when using the method described above to estimate harvest rate is that the relative vulnerability of the sexes does not change as a cohort ages. In Montana, however, we expected the relative vulnerability of female black bears to decrease at primiparity because mothers accompanied by cubs are illegal to harvest. To assess biases due to varying relative vulnerability, we simulated populations with adult females harvested at half the rate of subadult females. We assessed whether the resulting harvest data could indicate that the assumption had been violated and compared estimated rates of harvest with the actual total female harvest rate.

Application of this method of harvest rate estimation also assumes that the natural mortality is the same for both sexes. Male black bears may have higher natural mortality than female black bears, especially as subadults (Hellgren and Vaughan 1989, Koehler and Pierce 2005). However, some studies have failed to find a significant difference between the mortality rates of males and females (Kasworm and Thier 1994, Wooding and Hardisky 1994). Results are also confounded because harvest mortality is included in most mortality estimates (Hellgren and Vaughan 1989, Kasworm and Thier 1994, Wooding and Hardisky 1994, Koehler and Pierce 2005). We simulated populations as above, with male natural mortality equal to up to 130% of female natural mortality, and assessed bias in harvest estimates and changes in harvest sex- and age-structure to determine whether violations of this assumption are apparent in the harvest data themselves.

Another assumption that many harvest data sets may violate is that harvest remains constant across the years analyzed. Two types of violations, stochasticity and trends in survival and harvest rates, can affect results. If there are no temporal trends, combining several years of harvest information should ameliorate the annual variability and increase the precision of estimates. To assess how the length of harvest dataset affects the precision of estimates of harvest rate, we conducted stochastic simulations of harvested populations using the model described above. We estimated harvest rate from the harvest age and sex structure beginning in year one. For each consecutive year, we estimated harvest rate using the sums of all bears harvested to date in each age and sex class.

When harvest rates changed, Harris and Metzgar (1987) pointed out that annual harvest estimates lagged several years behind. Their analysis explored a change from a stable population harvested at 5% to a 10% harvest rate, or vice versa. To explore the effect of a more continuous trend on the data structure and the resulting bias in harvest estimates, we conducted simulations with an increasing trend in the harvest rate over a 20-year timeline. We assessed the resulting harvest age and sex structure and the length of lag in the harvest rate estimates.

Using harvest to detect declines

If the harvest rate can be estimated and the total harvest is known, this information can be used to calculate population size through time. However, due to stochasticity and variation in harvest rate estimate, the power to detect changes in population size may be low. To assess the ability of abundance estimates derived from harvest data to reflect population declines, we used the above simulation harvested at 4% for females and 8% for males to assess the power to detect a statistically significant decline in total population size as the length of the harvest dataset increased. Additionally, because managers sometimes lack information on the sex and age structure of the harvest, we also assessed the power to detect a statistically significant decline in total harvest from these simulations as an index for population size.

Initial population sizes were 10,000, 30,000, and 50,000 bears, which covers the likely range for Montana's actual black bear population size based on the estimated harvest rates (see Results) as well as the best guess of managers as of 2001 (Hristienko and McDonald 2007). For each simulation, we fit a linear regression to either the estimated total population size or the total number of bears harvested each year, starting with 3 years of harvests and adding consecutive years through the end of the dataset. Each year, we checked for a statistically significant decline by assessing whether the coefficient of year was <0 ($P = 0.05$). This is likely a conservative scenario because the spatial variation incorporated in population growth rate (via vital rate distributions from Beston [2011]) probably overestimated the temporal variation in any one population (because management and habitat varied widely among populations across western North America).

Montana black bear data

We estimated the harvest rates for male and female black bears in Montana using the method described above. We estimated y, the harvest in which the sex ratio is 1:1, using black bear harvest data collected in Montana from 1985–2005. We assumed low natural mortality over the winter (Hebblewhite et al. 2003) and combined the fall harvest with the following spring harvest to calculate the total harvest for each age class. To find y, we first summed each age class over the entire 20 year harvest dataset, and regressed y_i (proportion of females in the harvest) against i (age). We weighted the regression by total bears harvested at each age to account for smaller sample sizes at older ages. We solved the regression equation for 50% females in the harvest to estimate y and used y to estimate harvest rate.

We used qualitative comparisons of the structure of the harvest data to determine whether the assumption of constant relative vulnerability between sexes was violated. We also assessed the potential bias in differences in natural mortality by calculating male and female harvest rates using the Montana estimate of y and varying the ratio of male mortality to female mortality, $(1-s_m)/(1-s_f)$, from 1 to 1.1. We were specifically interested in the case where male mortality was higher than female mortality, the most likely situation for black bears, and quantified the bias separately for male and female harvest rates.

To assess possible trends in Montana's harvest rate, we estimated annual harvest rates using the age and sex structure of each year's harvest. We also estimated harvest rates using non-overlapping 5-year sets to increase precision of estimates. We used the estimated harvest rates through time to estimate population size. Finally, we examined the total population size estimates and the total harvest to determine whether the population appeared to be decreasing.

Results

Analysis of assumption violations

Simulations in which adult females were harvested at half the rate of subadult females produced a noticeable break in both the proportion of females harvested and in the number of females harvested at each age (Fig. 1). If the relative vulnerability of females decreased at age of primiparity, the proportion of females in the harvest at that age dropped, and if total vulnerability decreased, the total number harvested dropped. In this scenario, the average estimated female harvest rate (2.72%) underestimated the actual simulated harvest rate of adult females (3.05%) by about 10%. Other simulations were explored with varying violations of this assumption, with the same general result.

The sex and age structure of the harvest when male natural mortality was greater than female natural mortality was not distinguishable from a scenario with a greater harvest rate and equal adult survival for both sexes. Increased male mortality resulted in an overestimation of both male and female harvest rates (Fig. 2).

An increase in the number of years incorporated in the estimation yielded more precise estimates of the harvest rate. Given the levels of variance seen in black bear vital rates across the western half of their range, much improvement was gained in the first 5 years of data gathering (Fig. 3). The

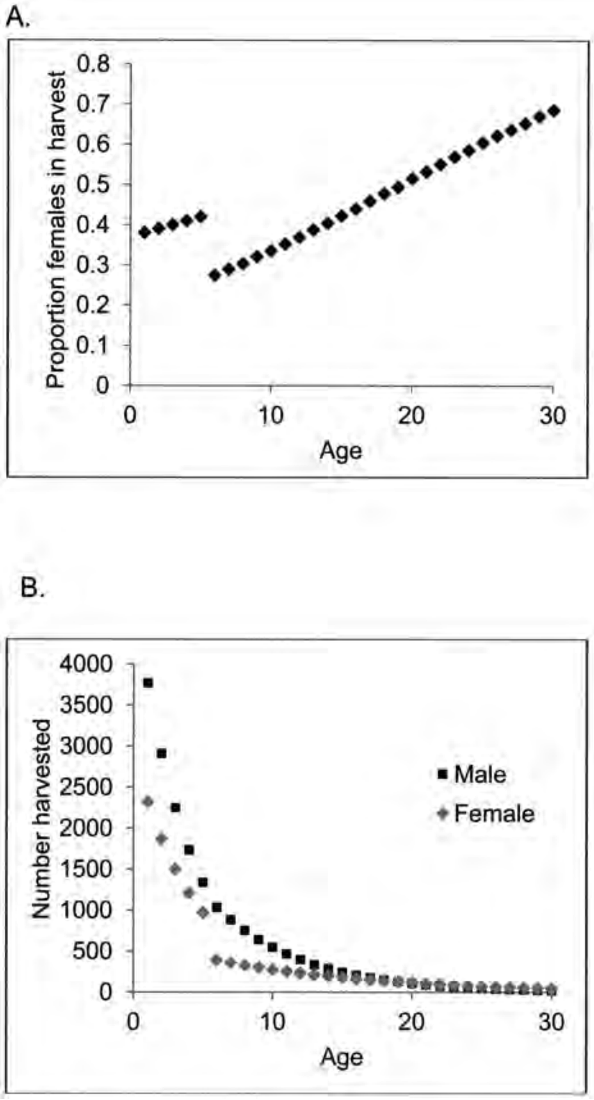

Fig. 1. Proportion of females in the harvest by age (A) and total harvest by age (B) in a simulated western American black bear population in which adult female vulnerability to harvest decreases by 50% at the age of primiparity.

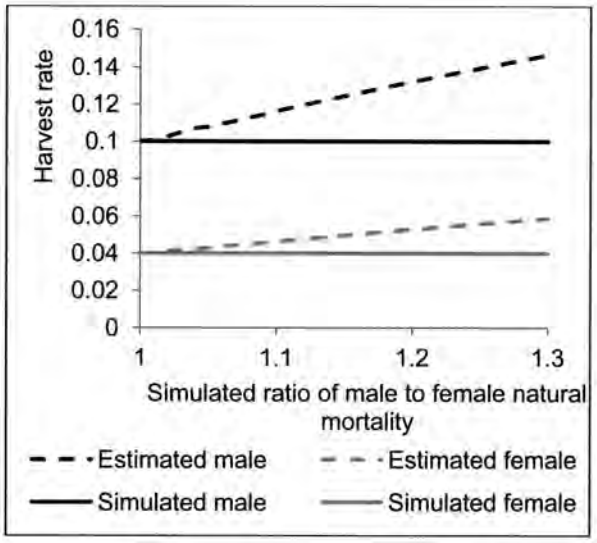

Fig. 2. Average estimates of male and female American black bear harvest rates and the actual simulated rates as the simulated ratio of male to female natural mortality increases for a western American black bear population.

inter-percentile ranges in the estimate of harvest rate leveled out after about 15 years. Populations experiencing lower levels of variance would require fewer years to gain similar precision in harvest rate estimates.

Simulations indicated that estimates of harvest rate lagged as much as 10 years behind actual changes in rates (Fig. 4). The age structure of the harvest data, however, did not change over time as harvest rate changed, and was therefore not helpful in indicating a violation of this assumption. The sex ratio of the harvest at young ages (1–4 yrs) did not change over the 20-year timeline, but the proportion of females in the harvest at older ages, especially 10–20 years, changed by about 1%/year. This change was much smaller than the variation among the

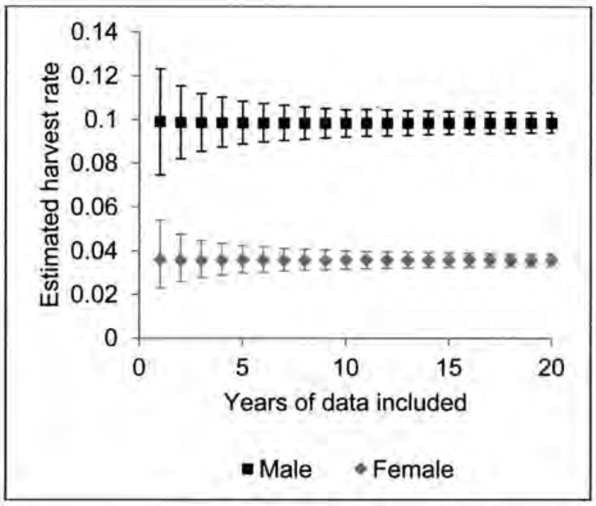

Fig. 3. Average estimates of male and female American black bear harvest rates and associated inter-percentile range from 2.5–97.5% in 2,500 simulated western populations as an increasing number of years of simulated data were combined in the harvest rate estimations.

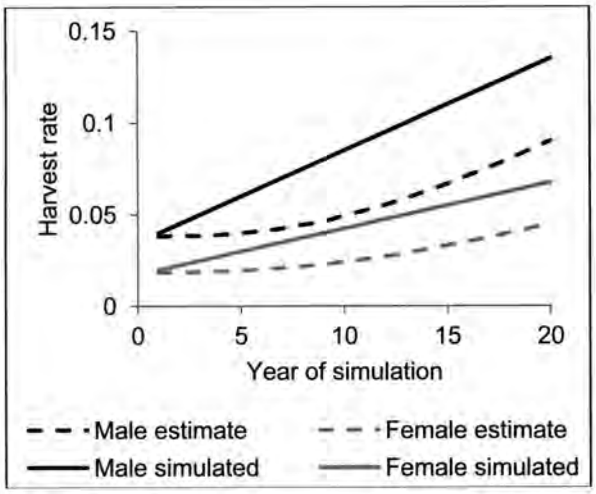

Fig. 4. Estimates of annual American black bear harvest rates in 2,500 simulated western populations as the harvest rates increased linearly from 4–14% for males and from 2–7% for females over a 20-year time horizon.

simulated populations and was therefore also not helpful in indicating a violation of this assumption.

Using harvest to detect declines

Given the estimated harvest rate and variation in Montana (described below) and the population growth rate and variance for western North America, a decline in the population was observed in the harvest in 80–86% of simulations after 15 years of harvest data collection (Fig. 5). Only 44–80% of the population estimate series showed statistically significant declines after 15 years of harvest data collection (Fig. 5). Larger population sizes produced larger harvests, better estimates of total population size, and greater power to detect declines.

As the population growth rate approached 1, the number of years required to reach 90% power in detecting declines using only the harvest numbers increased dramatically (Fig. 5B). Populations decreasing at 1–5% a year were reliably identified with 10–20 years of harvest data; annual decreases of less than 1% a year took considerably longer to detect. After 5 years, only 20% of the most rapidly declining populations, λ = 0.95, displayed statistically significant declines in the harvest numbers.

Montana black bear data

The R^2 of the regression of proportion females in Montana's harvest from 1985–2005 against age was 0.94, and the estimated value of y, the age at which males and females are equally represented in the harvest, was 14.2 years (Fig. 6). The high R^2 value implies either that the basic tenets of this model were borne out by Montana's data, or that biases created by assumption violations were in opposite directions and canceled each other out. The estimated annual harvest rates for male and female black bears in Montana were 10.6% and 4.3%, respectively, given

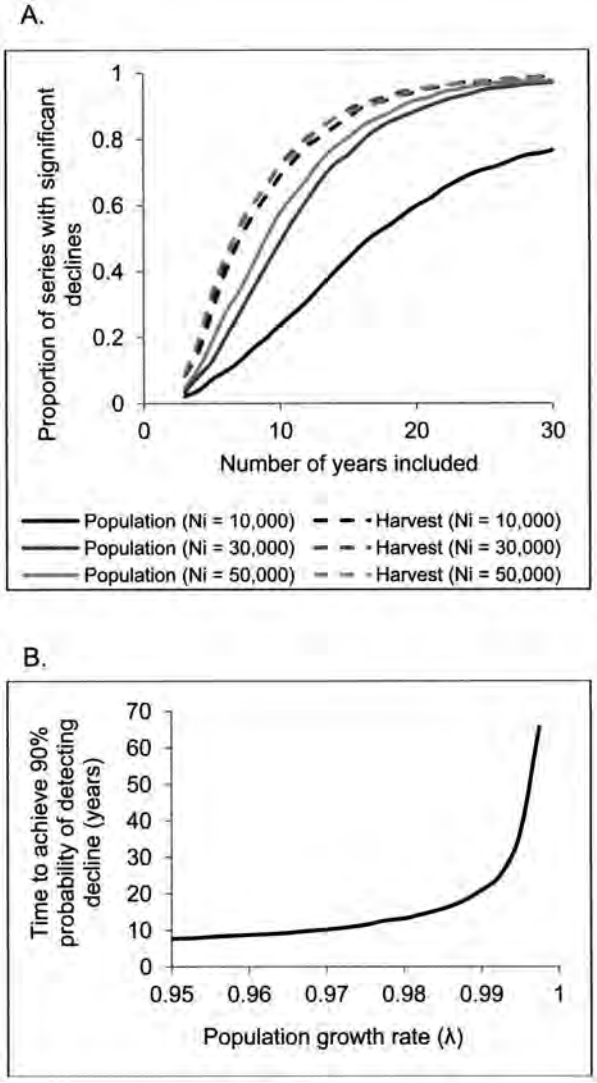

Fig. 5. Estimate of the proportion of simulated American black bear populations in which a statistically significant negative trend was identified in the estimated population size or the total number of bears harvested through time (A) and the time it took to achieve 90% power to detect decline using total harvest numbers of simulated unstructured populations (B).

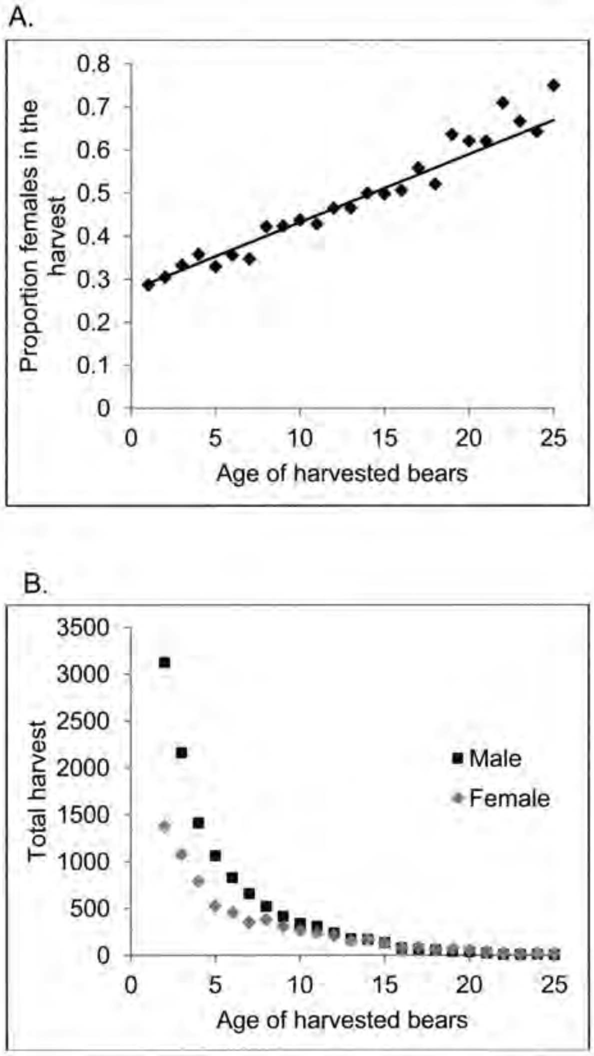

Fig. 6. The proportion of female American black bears by age (A) and total harvest of female black bears by age in Montana's harvests (B), 1985–2005.

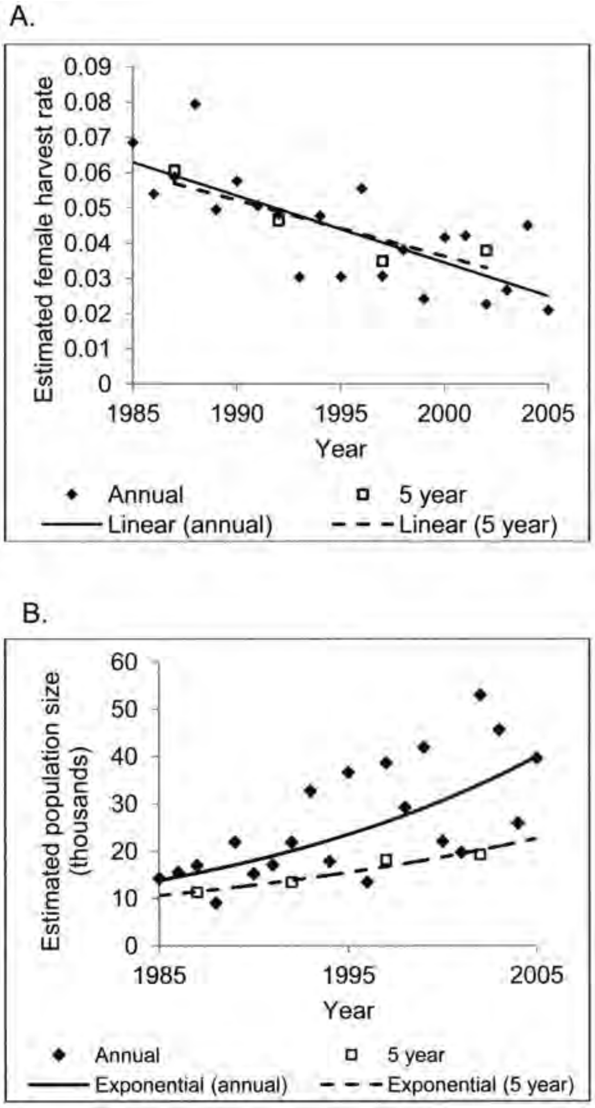

Fig. 7. Annual and 5-year pooled estimates of female American black bear harvest rate (A) and black bear population size (calculated as total male harvest/estimated male harvest rate + total female harvest/estimated female harvest rate) in Montana (B), 1985–2005.

an initial sex ratio of 1, constant relative vulnerability of the sexes, equal natural mortality rates for males and females, and constant harvest rate through time. These estimated rates are an average across the state and most representative of the harvest rates in western Montana, where the largest harvests occur, rather than the harvest rates in the sparser populations in central Montana.

Montana's proportion of females in the harvest was not consistent with expectations based on reduced relative vulnerability at primiparity (Fig. 6). At the age when vulnerability changed in the simulations, a break was noticeable in both the proportion of females harvested and in the number of females harvested at each age (Fig. 1).

Annual estimates of harvest rate and estimates using 5-year periods suggested a declining trend in Montana's harvest rate, with some autocorrelation evident in the annual estimates (Fig. 7). Estimates of population size calculated from annual harvest rates and pooled 5-year harvest rates and the reported total number of bears harvested each year depicted a population that had risen from approximately 12,000 bears in 1985 to between 20,000 and 40,000 bears in 2005 (Fig. 7B), for an average annual population growth rate of approximately $\lambda = 1.05$.

Discussion

Though estimation of harvest rate from the sex and age of harvested individuals has several limitations, the method we applied can produce usable harvest rate estimates and information on population status or trend that can be applied in decision making. The confidence in these estimates is higher given more years of harvest data and lower temporal stochasticity. Our results supported the hypothesis that at least some assumption violations of Fraser's (1984) and Paloheimo and Fraser's (1981) methods can be identified by the harvest data themselves. Additionally, biases due to violations of assumptions in our simulations were generally less dramatic than those found by Harris and Metzgar (1987), likely due to much larger harvest samples. Furthermore, the expectations that Montana's black bear population was declining and that the relative vulnerability of females compared to males changed as bears reach adulthood due to the protection of mothers with cubs were not borne out by the data.

Examination of harvest data can reveal whether some of the assumptions needed for this method are violated. If the relative vulnerability of the sexes changes with age, a discontinuity will be present in the proportion of females in the harvest at the transition ages. If the absolute vulnerability of either sex changes with age, a discontinuity will be present in the total harvest of that sex at the transition ages. It is important that this violation is identified because it can lead to non-conservative underestimation of harvest rate if the relative vulnerability of females decreases at primiparity (our results, also Harris and Metzgar 1987).

We were unable to identify whether the assumption of equal natural mortality for both sexes was violated using harvest data. However, harvest rate estimates based on this assumption will be conservative when male mortality is higher than female mortality, which is likely true in a variety of mammalian and avian species (Promislow 1992, Promislow et al. 1992), because they will overestimate harvest rate. If these harvest rates are used to estimate population size, they will underestimate population size.

Changing harvest rates will be apparent if annual sex and age structures are used to estimate yearly harvest rates, although the estimates will lag behind the actual value of harvest rate until it stabilizes. This generally agrees with the results of Harris and Metzgar (1987), which were based on scenarios where harvest rates changed between 2 seasons then remained constant rather than changing across all seasons in the time horizon. It is important to note that the age structure of the harvest data did not show an obvious trend, and the sex structure changed slowly in the adult age classes and not at all in the young age classes. It has been shown that age and sex composition of the harvest reflected relative vulnerability rather than population size or structure (Harris and Metzgar 1987, Garshelis 1990). Likewise, monitoring harvest via mean age or sex ratio alone is inappropriate. Despite this, Miller et al. (2011) point out that these sex and age ratios are still used inappropriately by managers to monitor populations.

It appeared unlikely that the vulnerability of female black bears to harvest in Montana changed dramatically at the presumed age of primiparity, and this contradicted our expectation that protection of females accompanied by cubs reduces the vulnerability of adult females (McLoughlin et al. 2005). Estimates based on reproductive tracts suggest adult females spend half their time accompanied by cubs (Mace and Chilton-Radandt 2011), which implies that vulnerability of adult females should be half that of subadults because females with young are illegal to take. Females are more likely to be accompanied by young in the spring than in the fall because family break-up occurs over the summer; thus, it is possible that the vulnerability to the spring harvest changes but the unchanged vulnerability and larger total harvest during the fall obscure that change. Alternatively, a greater proportion of young female bears could be producing their own cubs or accompanying their mothers or siblings than we expect, giving them as much protection as adults, or hunters could be taking females with cubs more often than previously assumed. If cubs are in trees or hiding as a hunter approaches, it may not be obvious to the hunter that the mother has young. Because bears are not baited or hunted with dogs, hunters may have less opportunity to observe young nearby than in jurisdictions where these methods are allowed. Hristienko et al. (2004) estimated only a 2% orphaning rate for black bear cubs during spring hunts in Manitoba, but Montana's may be near 4% if protection of mothers with young is completely ineffective.

In Montana, harvest data show annual negative autocorrelation in harvest rate as well as a declining trend in the harvest rate, and this trend remained when 5-year periods were pooled to increase precision. Autocorrelation can be induced even by weak responses by managers to change quotas each year and can make populations more variable and susceptible to decline (Fryxell et al. 2010). Unless new information is available about the population status, it may be unwise to tinker with harvest quotas based solely on the number of individuals harvested the previous year. Because Montana's estimated harvest rate leveled out from 1997 onward, more recent estimates are probably more accurate.

The total number of individuals harvested may reflect changes in population size more accurately than estimates of total population produced by dividing the total harvest by the estimated harvest rate. This is likely due to the amplification of error that occurs when going from an estimated rate to an estimated population size. In either case, identification of declines lagged well behind changes in simulated population size, even when the population was declining relatively rapidly. Annual changes in environmental conditions, such as natural food availability, can affect the vulnerability of individuals to hunters (Fieberg et al. 2010), and the ability to detect changes in population size will depend on how variable that vulnerability is and how consistent harvest effort and methods are. Hristienko and McDonald (2007) suggested that occasional overharvest of black bears will not be a problem because managers will respond rapidly to reduce harvest in subsequent years. The time lags apparent in both the decline of harvest numbers and the estimates of harvest rate indicate that managers may not be able to respond rapidly because they cannot discover the problem quickly enough.

It is encouraging that with more than 20 years of harvest data for Montana, we do not have evidence of a negative trend, let alone a statistically significant one. Indeed, annual estimates of harvest show that harvest rates have declined while the total harvest has been fairly stable. Because the same number of bears harvested represents a smaller proportion of the population (the harvest rate), these results suggest the population has increased. This is consistent with the fact that our estimated rates (4.3% for females and 10.6% for males) are well below reported estimates of sustainable harvest rates for black bears (14.2% [Miller 1990], 15% [McLaughlin 1998], 21% [Klenzendorf 2002], 12.6% [Dobey et al. 2005]).

On its face, this contradicts our hypothesis, based on the meta-analysis of demography (Beston 2011), that black bears have been decreasing in western North America. The average population growth rate based on the demographic work was less than 1, but our present harvest analyses indicate that, if anything, the population was increasing. The actual growth rate may be in the right tail of the distribution (at or above 1), the demographic work could be biased, or there may be other processes occurring for which we have not accounted. Although demographic studies are often considered the gold standard, they are more limited in space and time and therefore may not be representative of the true population status across large geographic areas. Demographic studies included in the meta-analysis had a median sample size of about 30 bear-years (Beston 2011), and because adult female survival rates are close to 1 (0.88 in the west; Beston 2011), researchers might only observe 3 or 4 deaths over the course of such a study. The small sample sizes typical of bear demographic work reduce precision of resulting estimates and make added information from harvests even more valuable. Harvest data can provide another means of estimating population trends at large scales to check against intensive demographic studies at smaller scales. If the demographic work is concurrent with harvest data collection, it can be used as auxiliary information in a statistical catch-at-age analysis that uses the age structure of harvest and prior knowledge about demography to estimate harvest rate and population size (Gove et al. 2002).

Another possibility is that spatial structuring and source–sink dynamics allow growing populations to support those that would otherwise decline. Some regions rely on wildlife refuges and sanctuaries to boost populations subjected to harvest in surrounding habitats (Powell et al. 1996). The meta-analysis suggested about 34% of western populations were growing (Beston 2011), and these could serve as sources that allow bears to persist despite low population growth rates elsewhere. In Montana, Glacier National Park provides protection from harvest, and black bears living deep in the Bob Marshall and other wilderness areas may be essentially inaccessible to most hunters. Further work needs to be done to determine the effect of these and other potential source habitats on surrounding populations.

In theory, the harvest rate estimation method we used can be applied to any game species with differential selectivity in the harvest for which we can collect sex and age data. Male-biased harvesting occurs in mammals with multi-annual parental care, such as bears and elephants (*Loxodonta africana*), when females with young are protected and when adult males are targeted as trophies (McLoughlin et al. 2005). It is also intentionally applied in some ungulate systems because females are considered the limiting component of the population (Ginsberg and Milner-Gulland 1994). In reality, harvests need to be large enough to overwhelm demographic stochasticity, and the nature and degree of assumption violations need to be explored. The largest biases and sensitivities to assumption violations for the method we used occur when harvests are small (Harris and Metzgar 1987). This method could also be extended to incorporate differing harvest rates and relative vulnerabilities for spring and fall harvest seasons and geographic structuring to analyze different regions or management units. Because we analyzed the state as a whole, our estimated harvest rates are probably most representative of the western part of Montana, where most black bears live and are harvested. Extensions would require harvest sample sizes in each season or geographic area to be large. Although this method can be applied in principle to many game species, other methods may be more appropriate in some situations. For example, if it is possible to couple field studies with harvest data in approaches such as statistical catch-at-age analysis, researchers can obtain more accurate information in fewer years (Gove et al. 2002). When management is consistent across years, the target species has a short life-span and simple age structure, or the harvests are relatively large (in the hundreds), the method we employed could be a valuable way to garner information about the target population.

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Literature cited

BEECHAM, J.J. 1983. Population characteristics of black bears in west central Idaho. Journal of Wildlife Management 47:405–412.

BESTON, J.A. 2011. Variation in life history and demography of the American black bear. Journal of Wildlife Management 75:1588–1596.

BUNNELL, F.L., AND D.E.N. TAIT. 1980. Bears in models and in reality: Implications to management. International Conference Bear Research and Management 4:15–23.

CASWELL, H. 2000. Matrix population models: Construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.

DOBEY, S., D.V. MASTERS, B.K. SCHEICK, J.D. CLARK, M.R. PELTON, AND M.E. SUNQUIST. 2005. Ecology of Florida black bears in the Okefenokee–Osceola ecosystem. Wildlife Monographs 158.

FIEBERG, J.R., K.W. SHERTZER, P.B. CONN, K.V. NOYCE, AND D.L. GARSHELIS. 2010. Integrated population modeling of black bears in Minnesota: Implications for monitoring and management. PLoS ONE 5(8):e12114. doi: 10.1371/journal.pone.0012114.

FRASER, D. 1984. A simple relationship between removal rate and age–sex composition of removals for certain animal populations. Journal of Applied Ecology 21:97–101.

FRYXELL, J.M., C. PACKER, K. MCCANN, E.J. SOLBERG, AND B.-E. SAETHER. 2010. Resource management cycles and the sustainability of harvested wildlife populations. Science 328:903–906.

GARSHELIS, D.L. 1990. Monitoring effects of harvest on black bear populations in North America: A review and evaluation of techniques. Proceedings of the Eastern Black Bear Workshop 10:120–144.

———, AND H. HRISTIENKO. 2006. State and provincial estimates of American black bear numbers versus assessments of population trend. Ursus 17:1–7.

GINSBERG, J.R., AND E.J. MILNER-GULLAND. 1994. Sex-biased harvesting and population dynamics in ungulates: Implications for conservation and sustainable use. Conservation Biology 8:157–166.

GOVE, N.E., J.R. SKALSKI, P. ZAGER, AND R.L. TOWNSEND. 2002. Statistical models for population reconstruction using age-at-harvest data. Journal of Wildlife Management 66:310–320.

HARRIS, R.B., AND L.H. METZGAR. 1987. Estimating harvest rates of bears from sex ratio changes. Journal of Wildlife Management 51:802–811.

HEBBLEWHITE, M., M. PERCY, AND R. SERROUYA. 2003. Black bear (*Ursus americanus*) survival and demography in the Bow Valley of Banff National Park, Alberta. Biological Conservation 112:415–425.

HELLGREN, E.C., AND M.R. VAUGHAN. 1989. Demographic analysis of a black bear population in the Great Dismal Swamp. Journal of Wildlife Management 53:969–977.

HRISTIENKO, H., D. PASTUCK, K.J. REBIZANT, B. KNUDSEN, AND M.L. CONNOR. 2004. Using reproductive data to model American black bear cub orphaning in Manitoba due to spring harvest of females. Ursus 15:23–34.

———, AND J.E. MCDONALD, JR. 2007. Going into the 21st century: A perspective on trends and controversies in the management of the American black bear. Ursus 18:72–88.

JONKEL, C.J., AND I.M. COWAN. 1971. The black bear in the spruce–fir forest. Wildlife Monographs 27.

KASWORM, W.F., AND T.J. THIER. 1994. Adult black bear reproduction, survival, and mortality sources in Northwest Montana. International Conference Bear Research and Management 9(1):223–230.

KLENZENDORF, S.A. 2002. Population dynamics of Virginia's hunter black bear population. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

KOEHLER, G.M., AND D.J. PIERCE. 2005. Survival, cause-specific mortality, sex, and ages of American black bears in Washington state, USA. Ursus 16:157–166.

LAMBERT, C.M.S., R.B. WIELGUS, H.S. ROBINSON, D.D. KATNIK, H.S. CRUICKSHANK, R. CLARKE, AND J. ALMACK. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

LITVAITIS, J.A., AND D.M. KANE. 1994. Relationship of hunting technique and hunter selectivity to composition of black bear harvest. Wildlife Society Bulletin 22:604–606.

MACE, R.D., AND T. CHILTON-RADANDT. 2011. Black bear harvest research and management in Montana: Final report. Montana Department of Fish, Wildlife & Parks, Wildlife Division, Helena, Montana, USA.

MCLAUGHLIN, C.R. 1998. Modeling effects of food and harvests on female black bear populations. Dissertation, University of Maine, Orono, Maine, USA.

MCLOUGHLIN, P.D., M.K. TAYLOR, AND F. MESSIER. 2005. Conservation risks of male-selective harvest for mammals with low reproductive potential. Journal of Wildlife Management 69:1592–1600.

MILLER, S.D. 1990. Population management of bears in North America. International Conference Bear Research and Management 8:357–373.

———, J.W. SCHOEN, J. FARO, AND D.R. KLEIN. 2011. Trends in intensive management of Alaska's grizzly bears, 1980–2010. Journal of Wildlife Management 75:1243–1252.

MILNER-GULLAND, E.J., AND J.M. ROWCLIFFE. 2007. Conservation and sustainable use. Oxford University Press, Oxford, UK.

NOYCE, K.V., AND D.L. GARSHELIS. 1997. Influence of natural food abundance on black bear harvests in Minnesota. Journal of Wildlife Management 61:1067–1074.

———. 2011. 2011 Bear management survey of jurisdictions in the eastern United States and Canada. http://www.ebbwnc.org/State%20Province%20Status%20Reports_Noyce.pdf, accessed 26 January 2012.

PALOHEIMO, J.E., AND D. FRASER. 1981. Estimation of harvest rate and vulnerability from age and sex data. Journal of Wildlife Management 45:948–958.

POWELL, R.A., J.W. ZIMMERMAN, D.E. SEAMAN, AND J.F. GILLIAM. 1996. Demographic analyses of a hunted black bear population with access to a refuge. Conservation Biology 10:224–134.

PROMISLOW, D.E.L. 1992. Costs of sexual selection in natural populations of mammals. Proceedings of the Royal Academy of Science B 247:203–210.

———, R. MONTGOMERIE, AND T.E. MARTIN. 1992. Mortality costs of sexual dimorphism in birds. Proceedings of the Royal Academy of Science B 250:143–150.

ROSEBERRY, J.L., AND A. WOOLF. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildlife Monographs 117.

RUPP, S.P., W.B. BALLARD, AND M.C. WALLACE. 2000. A nationwide evaluation of deer hunter harvest survey techniques. Wildlife Society Bulletin 28:570–578.

SKALSKI, J.R., K.E. RYDING, AND J.J. MILLSPAUGH. 2005. Wildlife demography: Analysis of sex, age, and count data. Elsevier Academic Press, Burlington, Massachusetts, USA.

WOODING, J.B., AND T.S. HARDISKY. 1994. Home range, habitat use, and mortality of black bears in north-central Florida. International Conference Bear Research and Management 9(1):349–356.

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Does Hunting Regulate Cougar Populations? A Test of the Compensatory Mortality Hypothesis

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Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis

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Abstract. Many wildlife species are managed based on the compensatory mortality hypothesis, which predicts that harvest mortality (especially adult male mortality) will trigger density-dependent responses in reproduction, survival, and population growth caused via reduced competition for resources. We tested the compensatory mortality hypothesis on two cougar (*Puma concolor*) populations in Washington, USA (one heavily hunted and one lightly hunted). We estimated population growth, density, survival, and reproduction to determine the effects of hunting on cougar population demography based on data collected from 2002 to 2007. In the heavily hunted population, the total hunting mortality rate (mean ± SD) was 0.24 ± 0.05 (0.35 ± 0.08 for males, 0.16 ± 0.05 for females). In the lightly hunted population, the total hunting mortality rate was 0.11 ± 0.04 (0.16 ± 0.06 for males, 0.07 ± 0.05 for females). The compensatory mortality hypothesis predicts that higher mortality will result in higher maternity, kitten survival, reproductive success, and lower natural mortality. We found no differences in rates of maternity or natural mortality between study areas, and kitten survival was lower in the heavily hunted population. We rejected the compensatory mortality hypothesis because vital rates did not compensate for hunting mortality. Heavy harvest corresponded with increased immigration, reduced kitten survival, reduced female population growth, and a younger overall age structure. Light harvest corresponded with increased emigration, higher kitten survival, increased female population growth, and an older overall age structure. Managers should not assume the existence of compensatory mortality when developing harvest prescriptions for cougars.

Key words: carnivore; compensatory mortality hypothesis; cougar; density; emigration; hunting; immigration; mortality; population growth; Puma concolor; *source–sink; survival.*

INTRODUCTION

Density-dependent population regulation has been experimentally demonstrated for a variety of animals and forms the theoretical basis for sustainable hunting of polygynous mammals (Caughley 1977, Caughley and Sinclair 1994, Ginsberg and Milner-Gulland 1994, Strickland et al. 1994). The compensatory mortality hypothesis predicts that harvest mortality, especially of adult males, triggers density-dependent responses in reproduction, offspring survival, and female population growth by reducing competition for resources (Connell 1978). In unhunted or lightly harvested populations, higher densities generate increased competition for resources, resulting in decreased reproduction, offspring survival, and female population growth. Therefore, removal of adult males in polygynous mating systems is generally considered to have benign or beneficial effects on population growth (Errington 1945, Frank and Woodroffe 2001, Johnson et al. 2001).

The compensatory mortality model has been demonstrated for a variety of ungulates (Staines 1978, Burnham and Anderson 1984, Peek 1986, Bartmann et al. 1992, White and Bartmann 1998), but little evidence suggests that the model fits carnivore populations (Franke and Woodroffe 2001, Milner et al. 2007). Because life histories of carnivores and ungulates differ, we would also expect that density dependence might operate differently. Ungulates typically have restrictive or limited dispersal movements compared to carnivores (Chepko-Sade and Halpin 1987, Howe et al. 1991, Franke and Woodroffe 2001, Zimmerman et al. 2005, Whitman et al. 2007). Therefore hunting males is likely to reduce local herbivore densities but may not have the same effect on carnivores, which display long-distance, density-independent dispersal by males. Such intrinsic emigration can depress population density, and intrinsic immigration can increase population density regardless of birth and death rates (Franke and Woodroffe 2001, Festa-Bianchet 2003). This exchange of animals via immigration and emigration may offset expected chang-

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es in density and associated effects on vital rates of resident female animals. As a result, harvest levels that are considered beneficial or benign to an ungulate population may impose additive mortality on carnivores (Franke and Woodroffe 2001, Festa-Bianchet 2003, Swenson 2003).

Cougars (*Puma concolor*) are managed for sport harvest and population control based on compensatory mortality throughout the western United States (Strickland et al. 1994, Cougar Management Guidelines Working Group 2005:71–82). Managers seeking to provide trophy-hunting opportunities often adopt strategies that seek to reduce male densities and keep female numbers high (Hemker et al. 1984, Ross and Jalkotzy 1992, Lindzey et al. 1994, Spreadbury et al. 1996, Logan and Sweanor 2001, Martorello and Beausoleil 2003). However, young male cougars often disperse long distances. Harvesting of adult males can create vacancies that attract these young dispersers to vacated territories (Hemker et al. 1984, Logan et al. 1986, Ross and Jalkotzy 1992, Logan and Sweanor 2001, Stoner et al. 2006, Robinson et al. 2008). Robinson et al. (2008) showed that heavy hunting pressure on cougars did not reduce the population in a small-scale management area because of compensatory immigration. Their results suggest that density dependence in cougar populations may act through dispersal and that models of cougar management based on the compensatory mortality hypothesis may be inappropriate.

We tested whether hunting supported the compensatory mortality hypothesis by comparing demographic parameters from two Washington State cougar populations, one heavily hunted and one lightly hunted, from 2002 to 2007. The compensatory mortality hypothesis predicts that heavy hunting of cougars will result in (1) decreased male densities, (2) increased maternity rates, (3) increased survival of young, (4) decreased natural mortality, and (5) increased female population growth; and that low levels of harvest will result in (1) increased male densities, (2) decreased maternity rates, (3) decreased survival of young, (4) higher natural mortality rates, and (5) decreased female population growth.

STUDY AREAS

We monitored cougar population in two study areas >250 km apart and managed under different hunting strategies. Heavy hunting with the aid of hounds (hunting mortality rate = 0.24) was permitted in the Northeast Washington study area and light hunting without the use of hounds (hunting mortality rate = 0.11) was permitted in the Central Washington study area.

Heavily hunted area (HH)

The 735-km^2 study area lies north of the town of Kettle Falls, and includes a patchwork of federal, state, and privately owned lands. The study area is bounded on the southeast and southwest by the Columbia and Kettle Rivers. The Canadian–United States border forms the northern boundary. The area is part of a glacially subdued mountainous region (400–2130 m elevation) known as the Okanogan Highlands, and occupies the transition between the East-slope Cascades and Northern Rocky Mountain physiographic province (Bailey et al. 1994). Tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Most of the 46-cm annual precipitation falls as snow, with an average of 136 cm falling from mid-November to mid-April annually. Mean annual temperatures range from −6°C in January to 21°C in July. White-tailed deer (*Odocoileus virginianus*) are the most abundant ungulate, but mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) are also present. Common predator species besides cougar include coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*).

Lightly hunted area (LH)

The study area is located along the East-slope foothills of the North Cascades Mountains near the town of Cle Elum. The area covers 594 km^2 and includes a portion of the upper Yakima River watershed. The study area is bounded by the Cascade Mountains on the west, the Enchantment Wilderness on the north, and unforested agricultural lands of the Kittitas Valley on the south and east. Sagebrush steppe foothills (below 550 m elevation) transition upward to slopes covered with ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Psuedotsuga menziesii*). Subalpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), silver fir (*Abies amabilis*), and western hemlock (*Tsuga heterophylla*) dominate ridges at elevations >1550 m. Precipitation averages 56.4 cm/yr, with 160 cm of snowfall during winter. Mean annual temperature ranges from −7°C in January to 27°C in July. Elk and mule deer occur throughout the study area, and mountain goats (*Oreamnos americanus*) are present at higher elevations. Common predator species besides cougar include coyotes, black bears, and bobcats.

METHODS

Captures and monitoring

We attempted to capture and mark all cougars each year, from January 2002 through December 2007, by conducting thorough and systematic searches of each study area during winter when tracks can be detected in snow. We used hounds to track and tree cougars (Hornocker 1970). We immobilized treed cougars with a mixture of ketamine hydrochloride (200 mg/mL) and xylazine hydrochloride (20 mg/mL) at a dosage of 0.4 mL/10 kg of body mass, or with Telazol at a dosage of 6 mg/kg, using a projectile dart in the hindquarter (Ross and Jalkotzy 1992, Spreadbury et al. 1996). We determined sex and classified animals as kittens (0–12 months), juveniles (13–24 months), or adults (25+ months) based on physical measurements and gum regression measurements of the canine teeth (Laundre et al. 2000).

We fitted each animal with a mortality-sensing Very High Frequency collar (VHF; Advanced Telemetry Systems, Isanti, Minnesota, USA) or Global Positioning System (GPS; Lotek Wireless, Newmarket, Ontario, Canada and Televilt, Lindesberg, Sweden). Beginning in January 2005, we investigated den sites of collared females and captured kittens by hand. We implanted kittens <6 weeks old with PIT (Passive Integrated Transponder) tags (AVID, Norco, California, USA), and collared kittens that were >6 weeks old with expandable VHF (Telonics, Mesa, Arizona, USA; T. Ruth, *personal communication*) radio collars to accommodate growth. We handled all animals in accordance with Washington State University Animal Care (IACUC Permit #3133) and Animal Welfare Assurance Committee (AWAC Permit #A3485-01). GPS collars were programmed to collect locations at 4-hour intervals (six times/day). The data were retrieved using a remote communication unit. We recorded location coordinates of VHF-collared animals at one-week intervals from ground or aerial telemetry.

Despite attempts to systematically search and mark animals, we were not able to mark the entire population. Therefore, to establish a minimum population estimate for each study area we included demographic data from collared and uncollared cougars that were harvested by hunters, killed during depredation hunts, and killed by vehicle collisions (Stoner et al. 2006, Robinson et al. 2008). Washington Department of Fish and Wildlife recorded sex and age (determined by cementum annuli) for uncollared cougars killed by hunters or killed by special harvest permits or other causes. Because measurements of gum regression and cementum annuli yield comparable ages (Robinson et al. 2008), we included all collared and uncollared animals in a linear regression analysis to examine trends in age structure over the study period.

Survival

We used radiotelemetry to monitor survival of all radio-collared cougars and assigned cause of mortality as hunting, vehicle, or natural. Natural mortalities were confirmed with necropsies. We inferred cause of kitten mortalities by examining the carcass and proximity to other collared cougars.

We used the modified Mayfield method (Heisey and Fuller 1985) to estimate survival of animals because it provides increased precision when mortality rates are high, performs well in the case of small sample size typical of large carnivore species, and can identify cause-specific mortality rates (Winterstein et al. 2001, Murray 2006). We calculated annual survival rates for male and female kittens, juveniles, and adults from January 2002 to December 2007.

To determine intervals when survival probabilities were constant, we analyzed the statistical distribution of deaths over a 365-day period (Lambert et al. 2006). This yielded two mortality seasons: a high-mortality season (LH: 1 August to 31 December, HH: 1 October to 31 January) and a low-mortality season (LH: 1 January to 31 July, HH: 2 February to September 31). Annual survival was the product of seasonal survival rates (Heisey and Fuller 1985). We chose intervals for each period based on the median date of the deaths for each period. We used the Taylor series approximation method to compute variances of class-specific survival rates, and a one-tailed z test to determine whether survival rates in LH were higher than in HH (Micromort version 1.3; Heisey and Fuller 1985).

Maternity and fecundity

We calculated maternity as the mean number of kittens observed during inspection of maternal dens and from snow tracking, divided by the number of adult females observed that year (Case 2000:183). We calculated fecundity rates, $F = S_F \times M_{x+1}$, from the female survival rate in year x multiplied by their mean maternity rate in the following year (Ebert 1999). We used two-tailed t tests assuming unequal variance to compare maternity and fecundity rates from each area (Zar 1999).

Deterministic and stochastic growth rates

We constructed a survival/fecundity dual-sex Leslie matrix (Leslie 1945) to model closed-population growth for each area using RAMAS GIS (Akçakaya 2002). We assigned female age at first reproduction as 24 months, assumed an equal sex ratio at birth, and maximum age or age at senescence of 13 years (Robinson et al. 2008).

We calculated the deterministic growth rate (λ_D) as the dominant eigenvalue of the matrix under a stable age distribution. We calculated the stochastic growth rate (λ_S) by incorporating annual environmental variability (standard deviation of annual survival and fecundity rates) and demographic stochasticity. To estimate demographic stochasticity, we sampled the number of survivors in each sex and age class from a binomial distribution, and the number of kittens born each year from a Poisson distribution using the random number generator in RAMAS GIS (Akçakaya 2002). We sampled vital rates from a lognormal distribution to avoid truncations, which can occur if standard deviations are large due to sampling and measurement error. We projected each population for six years (five transitions), and calculated λ_S as the average geometric mean growth rate from 200 simulations, the point at which rates converged (Robinson et al. 2008).

Observed growth, immigration, and emigration

We determined observed growth rates (λ_O) from annual counts of collared and unmarked cougars. Each year we tallied the number of cougars (adults, juveniles,

Table 1. Sources of mortality of radio-collared cougars in northeast (HH, heavily hunted) and central (LH, lightly hunted) Washington State, 2002–2007.

		HH area		
Sex and age	n	Hunting	Depredation	Natural
Female				
Kitten (0–12 months)	10		0.14 ± 0.13 (1)	0.54 ± 0.18 (4)
Juv. (13–24 months)	6			
Adult (24+ months)	19	0.22 ± 0.07 (7)		0.12 ± 0.06 (4)
Total	35	0.16 ± 0.05 (7)	0.02 ± 0.02 (1)	0.18 ± 0.06 (8)
Male				
Kitten (0–12 months)	13			0.69 ± 0.14 (6)
Juv. (13–24 months)	12	0.46 ± 0.17 (4)		
Adult (24+ months)	12	0.46 ± 0.12 (8)	0.06 ± 0.24 (1)	
Total	37	0.35 ± 0.08 (12)	0.03 ± 0.03 (1)	0.17 ± 0.06 (6)
Population totals	72	0.24 ± 0.05 (19)	0.03 ± 0.02 (2)	0.18 ± 0.04 (14)

Note: Sample sizes (n = total number of animals at risk), mortality rates (mean ± SD), and number of mortalities (in parentheses) are shown.

and kittens) in each study area and calculated λ_O as $\lambda_x = (n_t/n_0)^{1/t}$, where λ_x is the annual finite growth rate, n_0 is the starting population, n_t is the final population, and t is the number of transitions between the start and end of the population projection (Case 2000). We used a one-tailed, one-sample t test to determine whether deterministic (λ_D) and stochastic (λ_S) growth rates were higher than the average six-year observed (λ_O) growth rate for LH, and whether λ_D and λ_S were lower than λ_O for HH (Zar 1999). We estimated net immigration/emigration rate (i/e) using the equations $i/e = \lambda_D - \lambda_O$ and $e = \lambda_S - \lambda_O$ (Peery et al. 2006). We also used observations of radio-collared cougars to document net emigration and immigration in each area from 2005 through 2007, the period during which we radio-monitored kittens (radio collars enabled us to document emigrants).

Population density

We estimated mean annual densities of cougars (number of cougars/100 km^2) for each study area as the number of animals multiplied by the mean proportion of male and female locations that fell inside a mean annual 95% composite kernel home range of collared females (McLellan 1989). For unmarked cougars, we used the mean proportion of marked animals. We back-calculated the life span of each marked and unmarked cougar to the beginning of the study, its birth date (females), or immigration date (males) as described by Logan and Sweanor (2001:66), Stoner et al. (2006), and Robinson et al. (2008). We used a general linear model (GLM) to test for independent effects of study area and time on cougar density. We included study area, time, time^2, time × study area, and time^2 × study area as independent variables and then selected variables stepwise in a backward fashion, removing those that failed to be significant at the 0.10 probability level (Zar 1999).

Age structure

We calculated sex ratios (F:M) from collared cougars only to prevent bias that may result from hunters selecting for male cougars (trophies). We determined whether ratios were different from equality with a chi-square goodness-of-fit test (Zar 1999). We compared mean age of cougars in each area with a two-sample t test and examined the trend over time in age structure with simple linear regression (Zar 1999).

Confounding factors

To account for possible differences in per capita resources affecting maternity, kitten survival, and female population growth, we compared cougar densities and female predation rates in the two study areas. We compared densities with a general linear model and tested for differences in predation rates with a two-tailed t test (Zar 1999).

RESULTS

Captures and monitoring

We captured and marked 103 cougars in the two study sites (57 in HH, 46 in LH) between January 2002 and December 2007. Hunters killed 50 unmarked cougars (nine females, 13 males in HH; 14 females, 13 males, one of unknown sex in LH), and one uncollared female in LH was killed by a vehicle collision. We observed 26 unmarked kittens (six females, two males, nine of unknown sex in HH; three females, four males, two of unknown sex in LH) traveling with collared females.

Survival and mortality

Fifty-three (35 in HH, 18 in LH) radio-collared cougars died during the study (Table 1). Hunters killed 26 cougars, 22 died from natural causes, three died in vehicle collisions, and two were killed from depredation hunts. Eight juveniles (two in HH, six in LH) emigrated and were censored at the last known date of their location. An additional nine (four in HH, five in LH) animals were censored due to shed collars or lost VHF signals. Of 42 radio-collared kittens, 18 survived to one

Table 1. Extended.

	LH area		
n	Hunting	Vehicle	Natural
6			0.28 ± 0.24 (1)
5	0.24 ± 0.21 (1)		
12	0.04 ± 0,04 (1)		0.09 ± 0.06 (2)
23	0.07 ± 0.05 (2)		0.10 ± 0.05 (3)
13			0.47 ± 0.17 (4)
8	0.25 ± 0.22 (1)	0.25 ± 0.22 (1)	
12	0.20 ± 0.09 (4)	0.10 ± 0.07 (2)	0.05 ± 0.05 (1)
33	0.16 ± 0.06 (5)	0.09 ± 0.05 (3)	0.16 ± 0.06 (5)
56	0.11 ± 0.04 (7)	0.05 ± 0.03 (3)	0.13 ± 0.04 (8)

year of age, 16 died from natural causes, and four were censored. Six of the "natural" kitten mortalities in HH (three females, two males, one unknown sex) were presumed to have been killed by male cougars, as confirmed by canine tooth punctures in the skull and close proximity of a collared male at estimated time of death.

Average annual survival rates, including all sources of mortality, for all radio-collared cougars in HH were 0.56 ± 0.05 (mean ± SD) and 0.71 ± 0.06 in LH, but survival varied with age and sex classes (Table 2). Overall survival and survival of adults was higher in LH than in HH (overall: $Z = 1.98$, $P = 0.02$; adults: $Z = 1.75$, $P = 0.04$). Survival of adult females and survival of kittens was also higher in LH (adult females: $Z = 1.88$, $P = 0.03$; kittens: $Z = 1.49$, $P = 0.07$). We did not detect differences among other sex or age comparisons. Overall mortality rate from hunting was higher ($Z = 2.02$, $P = 0.04$) in HH (0.24 ± 0.05) than in LH (0.11 ± 0.04). We found no differences in natural mortality rates (HH = 0.18 ± 0.04, LH = 0.13 ± 0.04; $Z = 0.77$, $P = 0.44$). The standard deviation of annual survival rates, including all sources of mortality for all cougars, was 0.09 in HH and 0.06 in LH. These values were used in the standard deviation matrix of RAMAS. We removed the six kittens from the analysis that were killed by male cougars in HH, recalculated survival rates, and found that kitten survival was not different ($Z = 0.96$, $P = 0.96$) in HH (0.59 ± 0.02) and LH (0.58 ± 0.02).

Maternity and fecundity

Mean litter size was 2.63 ± 0.80 ($n = 18$ litters) in HH and 2.47 ± 0.83 ($n = 15$ litters) in LH, and did not differ between study areas ($t = 2.04$, df = 30, $P = 0.94$). Proportions of females producing newborns (0.44 in HH and 0.51 in LH) were not different ($Z = -0.41$, $P = 0.68$), and proportions of females with dependent kittens (0.58 in HH and 0.75 in LH) were also not different ($Z = 1.15$, $P = 0.25$). Mean maternity in HH did not differ from that in LH (HH: 1.15 kittens/female/year vs. LH: 1.12 kittens/female/year; $t = 2.26$, df = 9, $P = 0.94$). Fecundity rates in HH and LH also did not differ (HH, 0.76 ± 0.63; LH, 0.97 ± 0.38; $t = 2.31$, df = 8, $P = 0.49$). The standard deviation of annual fecundity rates was 0.25 in HH and 0.27 in LH. These values were used in the standard deviation matrix of RAMAS.

Population growth

The deterministic annual female growth rate (λ_D) based on survival and fecundity models was 0.80 in HH and 1.13 in LH. The stochastic growth rate (mean λ_S ± SD) for HH (0.78 ± 0.19) was lower than in LH (1.10 ± 0.12; $t = 21.09$, $P < 0.01$). The observed growth rates (λ_O) based on the actual number of cougars in the study area were 0.91 (female $\lambda_O = 0.86$, male $\lambda_O = 1.02$) for HH and 0.98 (female $\lambda_O = 0.97$, male $\lambda_O = 0.96$) for LH, and were not different ($t = 0.86$, $P = 0.42$). Modeled growth rates were significantly higher than λ_O in LH (for λ_D, $t = 2.09$, $P = 0.05$; for λ_S, $t = 1.68$, $P = 0.09$) and lower than λ_O in HH (for λ_D, $t = 2.10$, $P = 0.07$; for λ_S, $t = 2.46$, $P = 0.05$. The HH population had net immigration rates of 0.11 ($\lambda_O - \lambda_D$) and 0.13 ($\lambda_O - \lambda_S$), and the LH population had net emigration rates of 0.12 ($\lambda_O - \lambda_S$)

Table 2. Radio-days and survival rates (mean ± SD) by sex and age class for radio-collared cougars in northeast (HH, heavily hunted) and central (LH, lightly hunted) Washington State, 2002–2007.

	HH area			LH area		
Sex and age	Radio-days	*n*	Survival rate	Radio-days	*n*	Survival rate
Female						
Kitten (0–12 months)	1611	5 (10)	0.32 ± 0.16	1094	1 (6)	0.72 ± 0.24
Juvenile (13–24 months)	1871	0 (6)	1.00 ± 0.00	1310	1 (5)	0.76 ± 0.21
Adult (24+ months)	9645	11 (19)	0.66 ± 0.08	7601	3 (12)	0.87 ± 0.07
Total	13 126	16 (35)	0.64 ± 0.07	10,005	5 (23)	0.83 ± 0.07
Male						
Kitten (0–12 months)	1885	6 (13)	0.31 ± 0.15	2295	4 (13)	0.53 ± 0.17
Juvenile (13–24 months)	2392	4 (12)	0.54 ± 0.52	1084	2 (8)	0.51 ± 0.24
Adult (24+ months)	4470	9 (12)	0.48 ± 0.12	5851	7 (12)	0.65 ± 0.11
Total	8746	19 (37)	0.45 ± 0.08	9230	13 (33)	0.60 ± 0.08
Population totals	21 872	35 (72)	0.56 ± 0.05	19,235	18 (56)	0.71 ± 0.06

Note: Sample size *n* is the number of mortalities, with the total number of monitored animals in parentheses.

TABLE 3. Densities and ages (mean ± SD) for monitored cougars in northeast (HH, heavily hunted) and central (LH, lightly hunted) Washington State, 2002–2007.

Age and sex	HH area Density (cougars/100 km^2)	HH area Age (months)	LH area Density (cougars/100 km^2)	LH area Age (months)
Adults (>24 months)				
Female	1.35 ± 0.12	51 ± 7	1.07 ± 0.38	68 ± 13
Male	0.23 ± 0.10	42 ± 5	0.80 ± 0.05	59 ± 5
Total	1.58 ± 0.17	48 ± 5	1.87 ± 0.42	61 ± 3
All ages				
Female	2.83 ± 0.76	33 ± 7	2.32 ± 0.44	40 ± 6
Male	0.63 ± 0.12	24 ± 5	1.30 ± 0.15	41 ± 5
Total	3.46 ± 0.69	27 ± 4	3.62 ± 0.58	39 ± 4

and 0.15 ($\lambda_O - \lambda_D$). Observations of radio-collared cougars supported these trends; we documented five emigrants and three immigrants in LH, and four immigrants and zero emigrants in HH from 2005 through 2007.

Population density

The mean 95% composite range of females was 772 km^2 (95% CI = 316–1228) for HH and 655 km^2 (95% CI = 425–885) for LH. The annual proportion (mean ± SD) of male GPS points within the composite range of females was 0.32 ± 0.08 in HH and 0.43 ± 0.16 in LH.

Time and time × area explained significant variation in cougar density ($P < 0.10$). The final model included: area, time, and time × area. Mean annual densities of all cougars were 3.46 ± 0.69/100 km^2 in HH and 3.62 ± 0.58/100 km^2 in LH, and were not different ($P = 0.26$) (Tables 3 and 4). Compared to LH, mean densities of males were lower in HH (0.63 ± 0.12 vs. 1.30 ± 0.15/100 km^2; $P < 0.01$) and mean densities of females were higher (2.83 ± 0.76 vs. 2.32 ± 0.44; $P = 0.02$). Within HH, densities of all cougars and females declined over the study period, whereas we detected no change in male densities. In LH, we did not detect a change in density for any sex and age class (all $P > 0.05$; Table 4).

Sex and age structure

Mean age of the cougar population was 27 months (2.3 years) in HH and 38 months (3.2 years) in LH (Table 3). Most mean ages of cougars were higher in the LH than in HH for all age and sex classes (all $P < 0.05$), with one exception being mean age of females, which was actually higher in the HH ($P = 0.10$) (Table 3). Mean age of female cougars in HH increased ($P = 0.03$) over time and mean age of males decreased ($P = 0.07$). We detected no changes in age for LH ($P > 0.10$) across the study period.

Confounding factors

We detected no differences in mean maternity rates ($t = 2.26$, df = 9, $P = 0.94$), predation rates ($t = 0.79$, df = 34, $P = 0.44$), or population density ($t = 1.47$, df = 1, $P = 0.26$) between areas. The female predation rate in HH was 6.68 days/kill (Cooley et al. 2008) and 7.04 days/kill in LH (K. White, *unpublished data*).

DISCUSSION

Data comparing demographics of two Washington cougar populations suggest that hunting does not act in a compensatory manner in cougar populations. The compensatory mortality hypothesis predicts that increased harvest mortality of males will reduce population density, resulting in lower competition for resources, reduced natural mortality, and increased reproduction and survival of young. The compensatory mortality hypothesis predicted that low levels of harvest will result in increased densities and rates of natural mortality, and decreased reproduction and survival.

In the heavily hunted area, female densities declined and male densities remained unchanged, whereas we

TABLE 4. Effects of study area (hunting level) and time (2002–2007) on density estimates of cougars (cougars/100 km^2) using a general linear model.

Parameter	Estimate	SE	*t*	*P*
Total cougars				
Intercept	4.05	0.38	10.71	<0.01
HH area	0.65	0.54	1.21	0.26
LH area	0.00			
Time	−0.15	0.10	−1.53	0.17
Time × area HH	−0.27	0.14	−1.94	0.09
Time × area LH	0.00			
Male cougars				
Intercept	1.41	0.14	10.17	<0.01
HH area	−0.78	0.20	−3.97	<0.01
LH area	0.00			
Time	−0.04	0.04	−1.04	0.33
Time × area HH	0.02	0.05	0.47	0.65
Time × area LH	0.00			
Female cougars				
Intercept	2.64	0.33	7.92	<0.01
HH area	1.43	0.47	3.02	0.02
LH area	0.00			
Time	−0.11	0.09	−1.30	0.23
Time × area HH	−0.29	0.12	−2.38	0.04
Time × area LH	0.00			

observed no change in male or female densities in the lightly hunted area. We found no differences in rates of natural mortality (0.18 in the heavily hunted area and 0.13 in lightly hunted area) or maternity rates (1.15 in the heavily hunted area vs. 1.12 in lightly hunted area). Kitten survival was lower in the heavily hunted area (0.32 in the heavily hunted area and 0.58 in the lightly hunted area), with none of the kitten mortalities resulting from hunting or death of the mother. Our findings reject the compensatory mortality hypothesis because vital rates did not compensate for hunting mortality.

Resource availability could have influenced vital rates; however, both populations were at similar densities (3.46 cougars/100 km^2 in the heavily hunted area and 3.62 cougars/100 km^2 in the lightly hunted area) and female predation rates were not different, suggesting that resources were similar between areas. Densities were maintained via a net immigration into the heavily hunted area and a net emigration out of the lightly hunted area. The net emigration could indicate poorer resources; however, kitten survival and female population growth were higher there, suggesting that this is not the case. The net immigration rate in the heavily hunted area could suggest better resources, but kitten survival and female population growth were lower there, also contrary to the compensatory mortality hypothesis.

Instead of hunting influencing survival and reproduction, hunting was compensated by immigration and emigration in both cougar populations. The stochastic population model, based on the compensatory mortality hypothesis, predicted a 27% population decline, whereas we observed a 9% decline in overall numbers and no decline in the male population. The difference in growth rates resulted from immigration. The stochastic model assumed a closed population structure and did not account for immigration, whereas the observed growth rate accounted for the open nature of cougar populations by including immigration. Many of the mortalities resulting from hunting were replaced by animals immigrating from surrounding areas.

In the lightly hunted population, the stochastic model predicted a 10% increase in population growth, yet cougar numbers remained stable. The projected population increase was compensated by emigration rather than by decreased vital rates. Therefore, neither total population density nor competition among cougars appeared to be influenced by hunting, with immigration and emigration counteracting the effects predicted by the compensatory mortality hypothesis

Long-distance dispersal is common in cougars (Sweanor et al. 2000, Logan and Sweanor 2001, Stoner et al. 2006) and can help to maintain overall numbers by replacing harvest mortalities with animals dispersing from neighboring areas (Hanski 2001). Rebound from heavy hunter harvest by immigration has been documented in cougar populations elsewhere (Ross and Jalkotzy 1992, Logan et al. 1986, Logan and Sweanor 2001, Anderson and Lindzey 2005, Stoner et al. 2006, Robinson et al. 2008). As a consequence, harvest models based on compensatory mortality hypothesis are unable to accurately predict the responses of cougar populations to hunting.

The heavily hunted population compensated for heavy harvest in overall numbers of cougars through male immigration. However, the female population declined ($\lambda_O' = 0.86$). Although male cougars commonly disperse long distances, females are usually philopatric (Sweanor et al. 2000). As a result, fewer female immigrants are available to immigrate and replace those that are harvested, resulting in decreased numbers of females. Adult female survival is therefore vital for population growth and recovery from harvest (Martorello and Beausoleil 2003).

Harvesting adult males may increase incidences of infanticide by allowing immigration of new, unrelated males (Ross and Jalkotzy 1992, Whitman and Packer 1997, Murphy et al. 1999, Logan and Sweanor 2001). Lower kitten survival in the heavily hunted area may be a result of high male turnover from hunting. Male carnivores are known to kill unrelated young in order to induce estrous and gain breeding opportunities (Packer and Pusey 1983, Smith and McDougal 1991, Wielgus and Bunell 1995, Swenson et al. 1997, Logan and Sweanor 2001). Our observations suggest that six kittens of three litters in the heavily hunted area may have been killed by unrelated male cougars. When we removed those six kittens from the survival analysis, we found no difference in survival rates of kittens between areas, suggesting that infanticide may have been responsible for lower kitten survival in the heavily hunted area. High rates of immigration following heavy male harvest were also documented for brown bears *Ursus arctos* (Wielgus and Bunnell 1994) and black bears *Ursus americanus* (Sargeant and Ruff 2001). Female population growth declined because of sexually selected infanticide in brown bears (Wielgus and Bunnell 1994, Swenson et al. 1997). This may indicate that the compensatory mortality hypothesis may not be appropriate for many solitary, territorial, or quasi-territorial carnivores.

It is unlikely that age structure ever stabilizes in long-lived species such as cougars, which may bias our estimates of deterministic growth. Because this lack of variability assumes a stable age distribution, we have little confidence that differences between deterministic growth rates and observed growth rates act as predictors of actual population growth and believe that differences between stochastic growth rates and observed growth rates more accurately project growth rates. Additionally, despite intense trapping efforts conducted each winter, we may have missed some cougars that were present on the landscape during the study, resulting in biased estimates of observed growth and subsequent net immigration and emigration rates. The addition of the same number of cougars each year would increase density estimates, but would not change the observed growth and emigration rates. A temporal bias, such as missing cougars only early in the study (most likely error), would yield an even lower true observed growth rate, whereas missing cougars only later in the study (least likely error) would yield a higher true observed growth rate. For example, a count of 10 cougars in 2002 and 11 cougars in 2003 would yield an observed growth rate of 1.10. If we missed three cougars in 2002, the true growth rate would have been 11/13, or 0.85. We have neither reason nor evidence to suspect that we missed more cougars as the study progressed, therefore any bias in our observed population growth rates is conservative.

Conservation Implications

Harvest models that are based on the compensatory mortality hypothesis rely on the assumption that density reductions result in reduced competition for resources, thereby increasing survival and reproduction of remaining animals. However, our results suggest that dispersal movements may mitigate for mortalities resulting from hunting and negate compensation by other vital rates. These findings have two management implications. (1) Recovery from harvest relies on nearby source populations; therefore, cougar harvest should be managed at the metapopulation scale (Cougar Management Guidelines Working Group 2005:73–74). (2) Even when healthy source populations exist, prolonged harvest will cause female population declines via direct harvest of adult males and increased kitten mortality caused by immigration of potentially infanticidal males (Ross and Jalkotzy 1992, Logan and Sweanor 2001), and kitten abandonment from harvest of mothers (R. Beausoleil, *personal communication*). The compensatory mortality hypothesis may not be appropriate for modeling hunter harvest for cougars and other large carnivores that exhibit long-distance dispersal. Assumptions of closed populations are not appropriate for solitary carnivore species.

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Literature Cited

Akçakaya, H. R. 2002. RAMAS Metapopulations: viability analysis for stage-structured metapopulations. Version 4.0. Applied Biomathematics, Setauket, New York, USA.

Anderson, C. R., Jr., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildlife Society Bulletin 33: 179–188.

Bailey, R. G., P. E. Avers, T. King, and W. H. McNab, editors. 1994. Ecoregions and subregions of the United States (1:7,500,000 map). USDA Forest Service, Washington, D.C., USA.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121:1–39.

Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory vs. additive hypothesis of mortality in mallards. Ecology 65:105–112.

Case, T. J. 2000. An illustrated guide to theoretical ecology. Oxford University Press, New York, New York, USA.

Caughley, G. 1977. Analysis of vertebrate population. John Wiley, New York, New York, USA.

Caughley, G., and J. Sinclair. 1994. Wildlife ecology and management. Blackwell Science, Malden, Massachusetts, USA.

Chepko-Sade, B. D., and Z. T. Halpin. 1987. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, Illinois, USA.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Cooley, H. S., R. B. Wielgus, H. S. Robinson, and C. S. Lambert. 2008. Cougar prey selection in a white-tailed deer and mule deer community. Journal of Wildlife Management 72:99–106.

Cougar Management Guidelines Working Group. 2005. Cougar management guidelines. First edition. Wildfutures, Bainbridge Island, Washington, USA.

Ebert, T. A. 1999. Plant and animal methods in demography. Academic Press, San Diego, California, USA.

Errington, P. L. 1945. Some contributions of a fifteen-year study of the northern bobwhite to a knowledge of population phenomena. Ecological Monographs 15:1–34.

Festa-Bianchet, M. 2003. Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. Pages 191–207 *in* M. Festa-Bianchet and M. Apollonio, editors. Animal behavior and wildlife conservation. Island Press, Washington, D.C., USA.

Franke, L. G., and R. Woodroffe. 2001. Behaviour of carnivores in exploited and controlled populations. Pages 419–442 *in* J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, UK.

Ginsberg, J. R., and E. J. Milner-Gulland. 1994. Sex-biased harvesting and population dynamics: implications for conservation and sustainable use. Conservation Biology 8:157–166.

Hanski, I. 2001. Population dynamic consequences of dispersal in local populations and in metapopulations. Pages 283–298 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, New York, New York, USA.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. Journal of Wildlife Management 48:1275–1284.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:1–39.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of sink populations. Biological Conservation 57:239–255.

Johnson, W. E., E. Eizirik, and G. Lento. 2001. The control, exploitation, and conservation of carnivores. Pages 196–220 *in* J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, UK.

Lambert, C. M., R. B. Wielgus, H. R. Robinson, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

Laundre, J. W., L. Hernandez, D. Strenbel, K. Altendorf, and C. Lopez Gonzalez. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.

Lindzey, F. G., W. D. Vansickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics in southern Utah. Journal of Wildlife Management 58:619–623.

Logan, K. A., L. L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648–654.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Martorello, D. A., and R. A. Beausoleil. 2003. Characteristics of cougar populations with and without the use of dogs. Pages 129–135 *in* S. A. Beacker, D. D. Bjornlie, F. G. Lindzey, and D. S. Moody, editors. Proceedings of the Seventh Mountain Lion Workshop, May 15–17, 2003. Wyoming Game and Fish Department, Lander, Wyoming, USA.

McLellan, B. N. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age–sex composition. Canadian Journal of Zoology 67: 1856–1860.

Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:36–47.

Murphy, K. M., R. I. Ross, and M. G. Hornocker. 1999. The ecology of anthropogenic influences on cougars. Pages 77–101 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

Murray, D. L. 2006. On improving telemetry-based survival estimation. Journal of Wildlife Management 70:1530–1543.

Packer, C., and A. E. Pusey. 1983. Adaptations of female lions to infanticide by incoming males. American Naturalist 121: 716–728.

Peek, J. M. 1986. A review of wildlife management. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Peery, M. Z., B. H. Becker, and S. R. Beissinger. 2006. Combining demographic and count-based approaches to identify source–sink dynamics of a threatened seabird. Ecological Applications 16:1516–1528.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417–426.

Sargeant, G. A., and R. L. Ruff. 2001. Demographic response of black bears at Cold Lake, Alberta, to the removal of adult males. Ursus 12:59–68.

Smith, J. L. D., and C. McDougal. 1991. The contribution of variance in lifetime reproduction to effective population size in tigers. Conservation Biology 5:484–490.

Spreadbury, B. R., K. Musil, J. Musil, C. Kaisner, and J. Kovak. 1996. Cougar population characteristics in southeastern British Columbia. Journal of Wildlife Management 64:962–969.

Staines, B. W. 1978. The dynamics and performance of a declining population of red deer (*Cervus elaphus*). Journal of Zoology 184:403–419.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.

Strickland, M. D., H. J. Harju, K. R. Mccaggery, H. W. Miller, L. M. Smith, and R. J. Stoll. 1994. Harvest management. Pages 445–473 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. The Wildlife Society, Bethseda, Maryland, USA.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.

Swenson, J. E. 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171–189 *in* M. Festa-Bianchet and M. Apollonio, editors. Animal Behavior and Wildlife Conservation. Island Press, Washington, D.C., USA.

Swenson, J. E., F. Sandegren, A. Soderberg, A. Bjarvall, R. Franzen, and P. Wabakken. 1997. The infanticide caused by hunting of male bears. Nature 386:450–451.

White, G. C., and R. M. Bartmann. 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. Journal of Wildlife Management 62:214–225.

Whitman, K., and C. Packer. 1997. The effect of sport hunting on the social organization of the African lion (*Panthera leo*). Pages 177–183 *in* Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals. Ondestepoort, South Africa.

Whitman, K. L., A. M. Starfield, H. Quadling, and C. Packer. 2007. Modeling the effects of trophy selection and environmental disturbance on a simulated population of African lions. Conservation Biology 21:591–601.

Wielgus, R. B., and F. L. Bunnell. 1994. Dynamics of a small, hunted brown bear (*Ursus arctos*) population in southwestern Alberta, Canada. Biological Conservation 67:161–166.

Wielgus, R. B., and F. L. Bunnell. 1995. Tests of hypotheses for sexual segregation in grizzly bears. Journal of Wildlife Management 59:552–560.

Winterstein, S. R., K. H. Pollock, and C. M. Bunk. 2001. Analysis of survival data from radiotelemetry studies. Pages 352–380 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, New York, New York, USA.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Zimmerman, F., C. Breitenmoser-Wursten, and U. Breitenmoser. 2005. Natal dispersal of Eurasion lynx (*Lynx lynx*) in Switzerland. Journal of Zoology 267:381–395.

APPENDIX

Comparison of seasonal survival by year for radio-collared cougars in central (LH, lightly hunted) and northeast (HH, heavily hunted) Washington State, USA, 2002–2007 (*Ecological Archives* E090-207-A1).

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Research Article

Density of American Black Bears in New Mexico

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ABSTRACT Considering advances in noninvasive genetic sampling and spatially explicit capture–recapture (SECR) models, the New Mexico Department of Game and Fish sought to update their density estimates for American black bear (*Ursus americanus*) populations in New Mexico, USA, to aide in setting sustainable harvest limits. We estimated black bear density in the Sangre de Cristo, Sandia, and Sacramento Mountains, New Mexico, 2012–2014. We collected hair samples from black bears using hair traps and bear rubs and used a sex marker and a suite of microsatellite loci to individually genotype hair samples. We then estimated density in a SECR framework using sex, elevation, land cover type, and time to model heterogeneity in detection probability and the spatial scale over which detection probability declines. We sampled the populations using 554 hair traps and 117 bear rubs and collected 4,083 hair samples. We identified 725 (367 male, 358 female) individuals. Our density estimates varied from 16.5 bears/100 km^2 (95% CI = 11.6–23.5) in the southern Sacramento Mountains to 25.7 bears/100 km^2 (95% CI = 13.2–50.1) in the Sandia Mountains. Overall, detection probability at the activity center (g0) was low across all study areas and ranged from 0.00001 to 0.02. The low values of g0 were primarily a result of half of all hair samples for which genotypes were attempted failing to produce a complete genotype. We speculate that the low success we had genotyping hair samples was due to exceedingly high levels of ultraviolet (UV) radiation that degraded the DNA in the hair. Despite sampling difficulties, we were able to produce density estimates with levels of precision comparable to those estimated for black bears elsewhere in the United States. © 2018 The Wildlife Society.

KEY WORDS American black bear, capture–recapture, density estimation, DNA degradation, New Mexico, *Ursus americanus*.

State agencies spend a large portion of their annual budget estimating abundance and population trends of game animals, in part, so they can set sustainable harvest levels. Survey methods for large ungulates are well-developed and can provide relatively robust estimates of abundance for common game species such as deer (*Odocoileus* spp.) and elk (*Cervus canadensis*; Bleich et al. 2001, Zabransky et al. 2016). In contrast, estimating the abundance or density of large carnivores such as American black bears (*Ursus americanus*; hereafter, black bears) is more difficult because their cryptic behavior and low population densities make common survey methods used for large ungulates (e.g., aerial counts) ineffective because of low detection rates (Miller 1990, Obbard et al. 2010). Historically, many state agencies set harvest limits for carnivores based on harvest data, including sex ratio and age structure of the harvested animals, which can be used to infer harvest effects on a population (Garshelis 1990, Hristienko and McDonald 2007). Yet, hunter selectivity and sex-specific vulnerability may influence harvest composition (Miller 1990, Beston and Mace 2012).

In New Mexico, USA, as in other parts of the American Southwest, black bears inhabit forested mountain ranges separated by desert and grassland valleys resulting in fragmented populations with varying degrees of connectivity (Atwood et al. 2011). Prior to their designation as a game species in 1927, the statewide black bear population was reduced to 660 owing to unlimited hunting and government sponsored anti-predator programs (New Mexico Department of Game and Fish [NMGFD] 1926). With legislative

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protection in place, the statewide population increased to 3,000 animals by the mid-1960s (Lee 1967). For nearly 20 years, this population estimate, paired with hunter harvest data, was the basis for setting harvest limits by the NMDGF. However, uncertainty in trends in black bear abundance during the late 1980s resulted in NMDGF initiating a decade-long study of black bear ecology in the 1990s (Costello et al. 2001).

New Mexico's most recent density estimates for black bear were derived from Costello et al. (2001) by dividing the minimum population size that was calculated using population reconstruction, which counts the number of individuals known to be alive during the study based on known age, by the effective trapping area (Dice 1938, Wilson and Anderson 1985, Eberhardt and Knight 1996). Their minimum density estimates were 17.0 bears/100 km^2 for the more mesic Sangre de Cristo Mountains in northern New Mexico and 9.4 bears/100 km^2 for the more xeric Mogollon Mountains of west-central New Mexico with intermediate habitat conditions being assigned a density equal to the mean of these 2 density estimates (i.e., 13.2 bears/100 km^2). Using a habitat suitability model, the NMDGF extrapolated these density estimates to similar land cover types throughout New Mexico. This extrapolation served as the basis for statewide estimates of abundance for black bears that were then incorporated into a population projection model to monitor abundance and its trend in each Bear Management Zone (BMZ).

Innovations in non-invasive genetic sampling techniques (NGS; Woods et al. 1999), coupled with robust statistical analyses such as spatially explicit capture–recapture (SECR; Efford 2004), have provided researchers with improved tools to estimate the abundance and density of carnivore populations from which harvest limits can be established. These tools have facilitated monitoring efforts and produced density estimates for black bear populations across much of their range (Stetz et al. 2014, Hooker et al. 2015, Sun et al. 2017).

Considering advances in NGS and SECR models, the NMDGF sought to update their density estimates for New Mexico black bear populations. Our objectives were to estimate the density of black bears in primary bear habitat within 7 of the 14 BMZs in New Mexico.

STUDY AREA

The 7 BMZs were encompassed by 5 study areas located in the northern (NSC; 6,400 km^2) and southern (SSC; 3,525 km^2) Sangre de Cristo, Sandia (300 km^2), and northern (NSacs; 925 km^2) and southern (SSacs; 2,775 km^2) Sacramento Mountains, New Mexico (Fig. 1). We sampled the Sandia Mountains in their entirety because of their smaller size. The 2 BMZs located in the NSC and the 2 in the SSacs are managed by NMDGF using the same estimate of density. Thus, we only report density for 5 study areas instead of 7 BMZs. Sampling within each study area was limited to primary bear habitat, which is defined as closed-canopy forest and woodland cover types (Fig. 1; Thompson et al. 1996, Costello et al. 2001). All 5 study areas were managed as multiple-use forests by federal and state agencies and private landowners encompassing portions of 4 National Forests, 6 wilderness areas, and 25 parcels of private land. The topography was diverse for each mountain range and maximum elevation was 4,011 m, 3,254 m, and 3,649 m for the Sangre de Cristo, Sandia, and Sacramento Mountains and minimum elevation was approximately 1,900 m, 1,700 m, and 1,500 m, respectively. The Southern Rocky Mountains floristic district characterized the Sangre de Cristo Mountains, whereas the Mogollon floristic district characterized the Sandia and Sacramento Mountains. Dominant vegetation types in the study areas included oak-mountain mahogany (*Quercus* spp.-*Cercocarpus* spp.) scrublands, piñon pine-juniper (*Pinus edulis-Juniperus* spp.) woodlands, ponderosa pine (*P. ponderosa*), white pine (*P. monticola*), Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), Engleman spruce-subalpine fir (*Picea engelmannii-Abies lasiocarpa*) mixed-forest, and bristlecone (*P. aristata*) and limber (*P. flexilis*) pine forests (Costello et al. 2001). Important mast-producing species included oak, piñon pine, juniper, red barberry (*Mahonia haematocarpa*), chokecherry (*Prunus virginiana*), gooseberry (*Ribes* spp.), alpine cancer-root (*Conopholis alpina*), cactus (*Opuntia* spp.), and sumac (*Rhus* spp.; Kaufmann et al. 1998, Costello et al. 2001). The average monthly temperature was highest in July across the Sangres (24–29°C), Sacramentos (22–29°C) and Sandias (33°C), and lowest in January across the Sangres

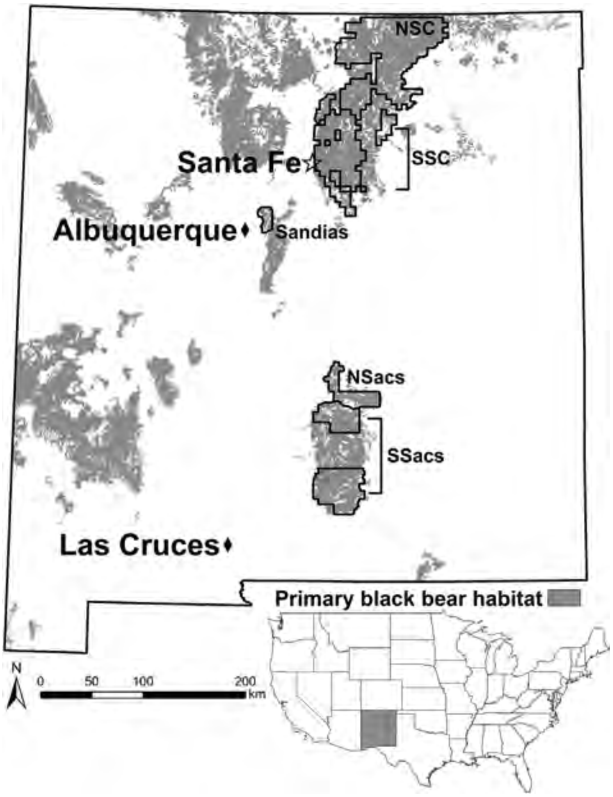

Figure 1. Primary American black bear habitat in New Mexico, USA highlighting the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains study areas.

(−15°C to −8°C), Sacramentos (−7°C to −5°C), and Sandias (−5°C; Western Regional Climate Center 2017). The average monthly precipitation was highest during the monsoon season (Jul–Oct) with rainfall peaking in August across the Sangres (7.10–8.15 cm), Sacramentos (7.62–12.70 cm), and Sandias (5.3 cm; Western Regional Climate Center 2017). Other common predators in the study areas included mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and common ungulates included elk, mule-deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), Rocky Mountain bighorn sheep (*Ovis canadensis*), and exotic barbary sheep (*Ammotragus lervia*).

METHODS

Field Sampling and Genetic Analysis

We used hair traps (Woods et al. 1999) and bear rubs (Kendall et al. 2008) concurrently to sample each black bear population. We set hair traps and bear rubs across 4 sampling occasions in the NSC (22 Apr–5 Sep 2012) and SSC (29 Apr–9 Sep 2013) and across 6 sampling occasions in the Sandias, NSacs, and SSacs (5 May–6 Aug 2014). Because of logistical constraints, sampling occasions in the NSC and SSC lasted 4 weeks, whereas sampling occasions for the Sandias, NSacs, and SSacs were 2 weeks. We distributed a grid of 5-km × 5-km cells across the landscape with a randomly determined origin. Within each cell, we set a single hair trap. We located trap sites based on suspected travel routes, occurrence of seasonal forage (e.g., newly emergent green grass and ripe soft and hard mast), and presence of bear sign (Fig. 2; Figs. S1 and S2, available online in Supporting Information). A hair trap consisted of a single strand of barbed wire wrapped around ≥ 3 trees at a height of 45 cm, with a lure pile constructed from woody debris at the center (Woods et al. 1999). During each sampling occasion in the NSC and SSC, we randomly selected and applied 1 of 4 non-consumable lures (cow blood and fish emulsion mixture, anise oil, fatty acid scent tablet, or skunk tincture and lanolin mixture) to the lure pile to attract bears. A chi-square test of independence showed that the 4 lures were not collecting similar proportions of hair samples ($\chi^2_3 = 616.29$, $P \leq 0.001$); thus, we discontinued the use of anise oil and fatty acid scent tablets in the Sandia and Sacramento Mountains. A sample consisted of all hair caught in one barb. Bears will also roll around in the lure pile depositing hair. We used our best judgement to define hair samples in the lure pile that we believed originated from a single individual. We deposited each hair sample in a separate paper coin envelope and incinerated any remaining hair with a propane torch to prevent false recaptures. We moved hair traps (100 m to 2.5 km) each occasion to increase novelty and recapture rates (Boulanger and McLellan 2001, Boulanger et al. 2004).

Bears rub on a myriad of objects including trees and power poles (Burst and Pelton 1983, Kendall et al. 2008). We opportunistically identified and collected hair from bear rubs along trails used en route to hair traps. We identified bear rubs using evidence of rubbing behavior such as a smoothed surface with snagged hair. We attached 3 to 4 short, vertical strands of barbed wire to the rub object covering the area of rubbing to collect discrete hair samples (Kendall et al. 2008, 2009; Stetz et al. 2014). We identified rubs at varying time intervals across sampling occasions, but once established we monitored them concurrently with nearby hair traps. We collected hair samples only from the barbed wire to ensure that the samples collected were from individuals that visited the rub during the sampling occasion. Hair collection protocols for bear rubs were identical to hair traps, and we stored all hair samples in an airtight container on silica desiccant at room temperature.

We genotyped each hair sample using 8 polymorphic microsatellite loci (G1D, G10B, G10L, G10M, G10H, G10J, G10U, MU59; Paetkau et al. 1995, 1998; Taberlet et al. 1997). We also used the ZFX-ZFY marker to identify sex (Durnin et al. 2007). We selected specific markers for individual identification by ensuring that the mean expected heterozygosity for each marker was between 0.70 and 0.80 (Paetkau 2003, 2004). These markers were determined from an initial subsample from the NSC population in 2012. All hair samples were genotyped by Wildlife Genetics International in Nelson, British Columbia, Canada (WGI; Paetkau 2003, Kendall et al. 2009).

Technicians screened samples for suitability before analysis. First, they eliminated samples that contained insufficient genetic material for analysis (no root, <1 guard hair, or <5 underfur hairs) or appeared to be from heterospecifics. Next, they used the ZFX-ZFY marker as a prescreen to remove low-quality hair samples that were likely to fail during the multilocus genotyping phase. After the prescreen, technicians amplified the 9-candidate markers for each sample. They eliminated samples that amplified ≥ 3 alleles at 1 marker (indication of a mixed sample) or failed to amplify ≥ 3 loci. They reamplified the samples that failed at <3 loci, resulting in either a full 9-locus genotype or a discarded sample. They examined pairs of samples that were mismatched at 1 or 2 markers for evidence of amplification or human error. Technicians reamplified any mismatched pair under the assumption that genotyping error may have created the similarity between the 2 samples (Paetkau 2003). If 1 or 2 mismatched pairs remained between samples, we concluded the 2 samples were from separate individuals. We assigned an individual identification number to each sample with a unique multilocus genotype based upon the unique catalogue code from the first sample to identify the individual's genotype. Given each study area is not an isolated population, we calculated the expected and observed heterozygosity for each mountain range using program GENEPOP (Raymond and Rousset 1995, Rousset 2008; www.genepop.curtin.edu.au, accessed 15 Mar 2016).

Density Estimation

We used SECR models (Efford 2004, Borchers and Efford 2008) implemented in the R software package secr (v. 2.9.5 and 2.10.4; Efford 2015, 2016) to estimate 3 parameters in separate analyses for each study area: density (D), detection probability of an individual at its activity center (g0), and the

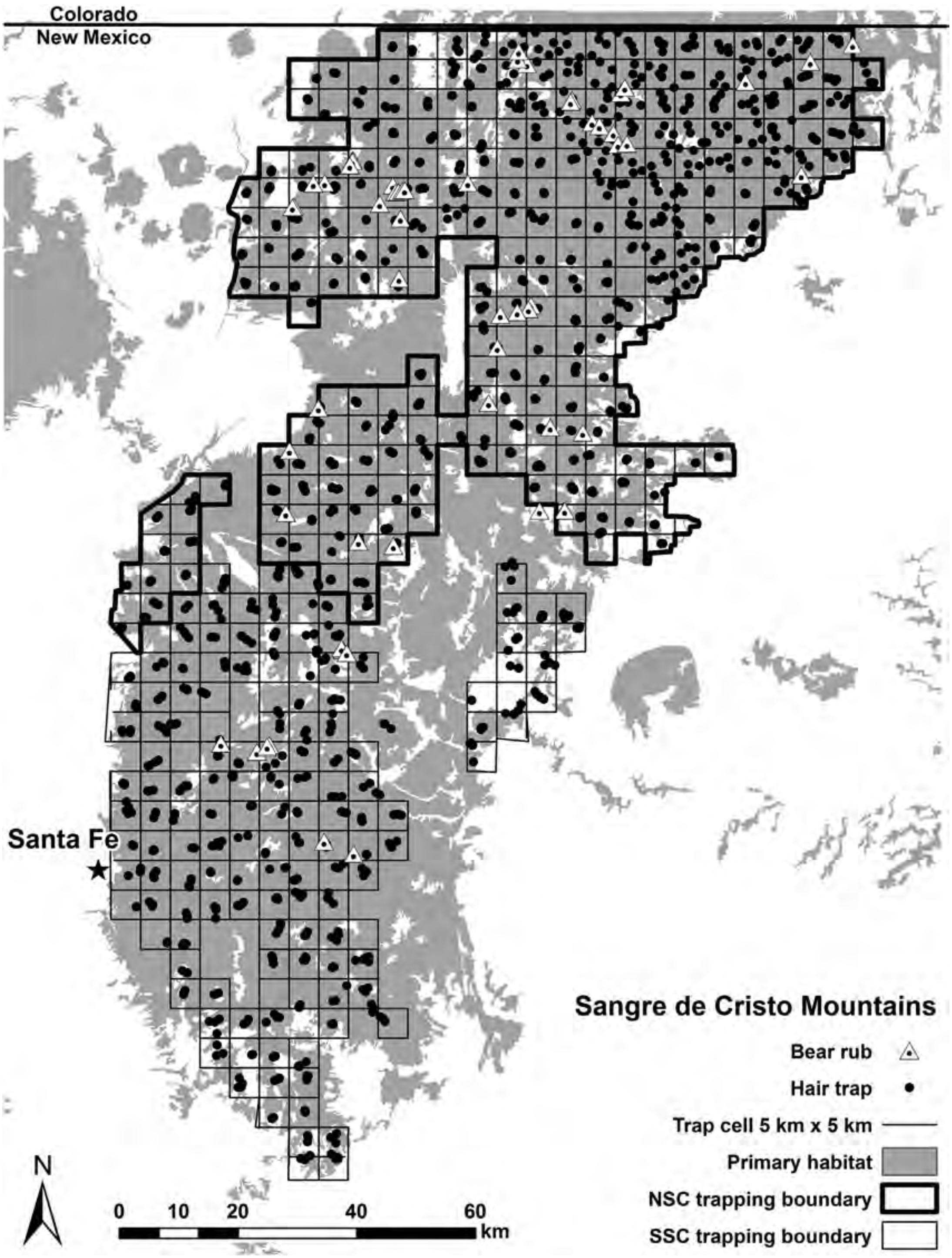

Figure 2. Primary American black bear habitat identified by Costello et al. (2001) overlaid with hair traps and bear rubs set for the northern (NSC) and southern (SSC) Sangre de Cristo Mountains, New Mexico, USA, 2012–2013.

spatial scale over which detection probability declines as the distance between an individual's activity center to the detection device increases (σ). We used a half-normal detection function for our observation model and a homogeneous Poisson distribution as our state model, which assumes latent activity centers are distributed evenly across the landscape (Efford et al. 2009). Spatially explicit capture–recapture also requires a habitat mask. The habitat mask is the area of integration (i.e., area of interest that contains all possible latent activity center locations) and includes all animals with a non-zero probability of detection (Ivan et al. 2013). Individuals may reside beyond the habitat mask, but they have a negligible probability of detection (Borchers and Efford 2008, Royle et al. 2014). We generated the habitat mask by buffering the sampling detectors in the NSC, SSC, Sandias, NSacs, and SSacs by 18.75 km, 25.40 km, 13.23 km, 14.84 km, and 11.03 km, respectively, which we derived from the capture data using the suggest. buffer function (Efford 2016). Within our habitat mask, we limited our density estimates to primary habitat as identified by Costello et al. (2001) for black bears in New Mexico. Variability in sampling effort may negatively bias density estimates and reduce the ability to explain variation in detection probability, so we accounted for variable sampling effort by using the number of days each sampling detector was active (Efford et al. 2013).

Predictors of g0 and σ included time (t; 4 or 6 sampling occasions depending on the study area), sex, elevation (elev), detector type (type; hair trap vs. bear rub), and 5 land cover categories (cover). We chose time and sex as covariates because detection probability and movement patterns may fluctuate over the sampling period and differ between males and females (Sawaya et al. 2012, Stetz et al. 2014). We selected elevation and land cover to represent the spatial heterogeneity of black bear food resources because this heterogeneity could influence g0 and σ depending on food availability and distribution (Rovang et al. 2015). We did not include land cover type and elevation in the same model because a box plot of elevation by land cover type revealed that these variables were not independent. We then conducted a 1-way analysis of variance that indicated within each study area elevation significantly differed among land cover types (NSC: $F_4 = 618.02$, $P \leq 0.001$; SSC: $F_4 = 367.14$, $P \leq 0.001$; Sandias: $F_1 = 7.39$, $P = 0.008$; NSacs: $F_2 = 278.06$, $P \leq 0.001$; SSacs: $F_2 = 582.95$, $P \leq 0.001$). Within each study area, *post hoc* pairwise comparisons of elevation across land cover types were also significant (Tukey-Kramer test, $P \leq 0.01$ for all comparisons). We extracted elevation for each detector using the National Elevation Dataset 30-m resolution digital elevation model (www.nationalmap.gov, accessed 10 May 2015). We standardized elevation by subtracting the mean from each observation and dividing by 1 standard deviation (Gelman and Hill 2007).

We extracted land cover using the Interagency Landfire Project (Rollins 2009; www.landfire.gov, accessed 10 May 2015) land cover classification at 30-m spatial resolution. We combined 6 land cover classifications into 5 categories: aspen-conifer, mixed conifer (combination of Douglas fir and white pine), piñon pine-juniper, ponderosa pine, and spruce-fir. Variation in the abundance and distribution of each land cover class across the study areas resulted in a different number of categories and, consequently, a different number of parameters modeled for each study area. Aspen-conifer and spruce-fir were included only in the NSC and SSC. Mixed-conifer was included in all study areas except the Sandia Mountains. Piñon pine-juniper and ponderosa pine were included in all study areas. We visually assessed and assigned the dominant land cover classification surrounding the location of each detector using ArcGIS 10.2.1 (Environmental Systems Research Institute [ESRI], Redlands, CA, USA).

We modeled g0 and σ concurrently by fitting a model where both parameters varied by elevation, land cover, or time. We also included models that varied by time for g0 and land cover for σ (g0 ~ t, σ ~ cover), time for g0 and elevation for σ (g0 ~ t, σ ~ elev), land cover for g0 and time for σ (g0 ~ cover, σ ~ t), and elevation for g0 and time for σ (g0 ~ elev, σ ~ t). We also constructed models for g0 and σ with time in an additive relationship with each covariate (g0 ~ t + covariate, σ ~ t + covariate). We included additive effects because g0 and σ are likely to vary because the black bear mating season occurs during the late-spring and early summer, when male bears might be expected to move more than females; because hyperphagic foraging behavior occurs during early fall, when all bears move more to find food; and because the distribution of food varies across the period when bears are active (e.g., grasses green-up in the spring and mast ripens in the late summer and fall). We also ran each model with the addition of an animal by site learned response (bk) for g0 (g0 ~ covariate(s) + bk) because density estimates can be severely biased when a behavioral response occurs in the presence of missing data (e.g., hair samples that failed to amplify a complete genotype; Augustine et al. 2014). However, we believe we mitigated a behavioral response by moving hair traps and randomly applying lures between sampling occasions, and Murphy et al. (2016) reported negligible bias to SECR-based density estimates in such a scenario. Thus, our inclusion of the bk parameter was a precautionary measure.

We modeled density as a function of sex to investigate for an uneven sex ratio (Tredick and Vaughan 2009, Sun et al. 2017). We did so by selecting the top ranked model from each study area and comparing that model to another with the same detection submodel but with density as a function of sex. We did not use land cover type or elevation as predictors of density because black bears track the spatiotemporal variability of food resources resulting in a fluid use of the landscape (Costello and Sage 1994, Sun et al. 2017). Also, because the New Mexico black bear hunting season occurs from mid-August to November, the seasonal distribution of black bears may change from summer to fall. Consequently, fall harvest regulations based on the variation in density of black bears across land cover types during the summer would be inappropriate. This enabled us to estimate density in a way that would be most conducive to the current management system employed by the NMDGF, which was a single density estimate for each study area given the large extent and heterogeneous landscape encompassed by the BMZs.

We could not fit 4 models for the NSC because the computer we used for analysis was unable to allocate enough memory to initialize all models. The 4 models were when g0 and σ were modeled concurrently with elevation (i.e., g0 ~ elev, σ ~ elev), concurrently with time and elevation (i.e., g0 ~ t + elev, σ ~ t + elev), and with time and elevation for different parameters (i.e., either g0 ~ t, σ ~ elev or g0 ~ elev, σ ~ t). We also excluded detector type in our model set for the NSacs because only 1 bear rub was set in the study area. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank our model sets (Akaike 1973, Hurvich and Tsai 1989). When the top model received

<0.90 of the model weight we model averaged the estimates of the model parameters across all models to account for model selection uncertainty (Burnham and Anderson 2002). We assessed the strength of evidence (SOE) for variables in the top model by calculating the likelihood that the beta coefficient was not 0 (i.e., evidence ratios for the beta coefficients):

$$\frac{£(\beta\widehat{\{l\}})}{£(0)} = \exp\left(\left\{\frac{\widehat{\beta(1)}}{SE(\widehat{\beta(1)})}\right\}^2\right),$$

where $\widehat{\beta(1)}$ is the beta coefficient for variable *i* and $SE(\widehat{\beta(1)})$ is the standard error of the beta coefficient for variable *i* (Burnham 2015).

We obtained permits under the Convention on International Trade in Endangered Species (Export Permits 12US86417A/9, 13US19950B/9, and 14US43944B/9) to export samples to Canada for analysis. Our research was authorized by the NMDGF (Taking Protected Wildlife for Scientific and or Education Purposes Permit 3504) and approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocol number 2011-027).

RESULTS

Field Sampling and Genetic Analysis

We set 557 hair traps that were open for 57,010 trap days and we collected 3,825 hair samples. In addition, we identified and sampled 112 bear rubs, which yielded 258 hair samples over 7,007 trap days (Fig. 2; Figs. S1 and S2; Table S1). Sampling effort varied across study areas and was dependent on the number of detectors set, the length of a sampling occasion (4 weeks vs. 2 weeks), and accessibility due to weather and wildfire. The number of hair samples collected during an occasion increased over the course of the summer and decreased toward the conclusion of sampling with peak collection during June and July.

The mean observed heterozygosity was 0.73, 0.73, and 0.68 for the Sangre de Cristo, Sandia, and Sacramento Mountains, respectively. Of the 4,083 total hair samples collected, we eliminated 26.08% because of insufficient genetic material, 1.49% because of heterospecific contamination, and 0.17% because the samples contained DNA from >1 individual. We generated a full 9-locus genotype from 49.56% of the 2,950 remaining hair samples from which we identified 726 (368 males: 358 females) individuals (Table S1). The number of individuals that were mismatched at 1 or 2 markers was low with only 3 observed 1-mismatched pairs and 8 observed 2-mismatched pairs across all samples. Genotyping success varied across study areas (44–61%), but overall, success rates were lower than the 75% success rate observed in similar studies (D. Paetkau, Wildlife Genetics International, personal communication). When we shortened the length of the sampling occasion from 4 weeks (NSC and SSC) to 2 weeks (Sandias, NSacs, and SSacs), the percentage of successful genotypes increased by only 4%.

Density Estimation

We detected the majority (61–85%) of individuals in each study area only once with a similar number of repeat detections for males and females (Table 1). The number of unique individuals detected during each occasion for the NSC, NSacs, and SSacs increased over the course of sampling, peaking mid-summer, and subsequently decreasing toward the end of summer; this pattern was similar to the number of hair samples collected per sampling occasion. The number of unique individuals detected increased each occasion for the Sandias and SSC. Mean maximum recapture distance for males in a single year of sampling ranged from 4.23 km to 12.46 km with a maximum distance of 52 km by 1 individual in the NSC. Mean maximum recapture distance for females in a single year of sampling ranged from 0.38 km to 4.59 km with a maximum distance of 47 km by 1 individual, also in the NSC (Table 1). Three individuals were detected in 2 study areas in successive years. We detected 2 males in the NSC in 2012 and then again in the SSC in 2013; we detected 1 female in the SSC in 2013 and 90 km away in the Sandia Mountains in 2014.

Table 1. A summary of the capture history data for American black bears identified by hair samples collected across the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains, New Mexico, USA, 2012–2014.

	Males								Females							
	N[a]	Det[b]	Avg[c]	SD[d]	Max[e]	R[f]	MMR (km)[g]	MaxD (km)[h]	*N*[a]	Det[b]	Avg[c]	SD[d]	Max[e]	R[f]	MMR (km)[g]	MaxD (km)[h]
NSC	190	239	1.26	0.43	3	33	7.57	52.03	189	216	1.14	0.35	3	23	3.98	47.41
SSC	67	80	1.19	0.38	3	8	12.46	29.33	64	77	1.20	0.39	2	12	2.53	20.33
Sandias	9	15	1.67	0.46	2	3	8.27	9.84	9	14	1.56	0.73	3	4	0.38	0.69
NSacs	49	74	1.51	0.74	5	14	9.22	36.18	39	58	1.49	0.72	3	12	2.47	7.05
SSacs	53	69	1.30	0.41	3	10	4.23	8.02	57	73	1.28	0.54	3	11	4.59	14.88
Total	368	477	1.39	0.48	5	68	8.35	27.08	358	438	1.33	0.55	3	62	2.79	18.07

[a] Number of animals detected.
[b] Number of detections across all sampling occasions.
[c] Average number of detections per individual detected across all sampling occasions.
[d] Standard deviation for the average number of detections.
[e] Maximum number of detections of a single individual across all sampling occasions.
[f] Number of recaptured individuals across all sampling occasions.
[g] Mean maximum recapture distance.
[h] Maximum distance moved by an individual.

Table 2. The top *a priori* spatially explicit capture–recapture models that accounted for the total model weight (w_i) for American black bears in the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains, New Mexico, USA, 2012–2014, derived using Akaike's Information Criterion corrected for small sample size (AIC_c). Models were ranked by the difference in AIC_c score (ΔAIC_c) between the top-ranked model and competing models were evaluated using changes in model deviance.

Study area	g0[a]	σ[a]	*K*[b]	AIC_c	ΔAIC_c	w_i	Deviance[c]
NSC	t + cover	t + cover	17	3,149.15	0.00	1.00	3,113.5
SSC	t + elev	t + elev	11	1,169.98	0.00	0.87	1,145.8
	t + cover	t + cover	17	1,173.85	3.87	0.13	1,134.4
Sandias	sex	sex	5	209.23	0.00	0.96	194.23
	constant	constant	3	216.23	6.99	0.03	208.51
	elev	elev	5	219.20	9.97	0.01	204.20
NSacs	t + cover	t + cover	17	868.31	0.00	0.96	825.57
	cover	t + cover	10	874.86	6.55	0.04	852.01
SSacs	cover	cover	7	1,168.68	0.00	0.50	1,153.58
	t + cover	t + cover	17	1,169.62	0.94	0.31	1,128.97
	t + elev	t + elev	15	1,170.58	1.90	0.19	1,135.47

[a] Detection probability at the activity center (g0) and the spatial scale over which g0 declines (σ) a function of elevation (elev), sex, time variation (t), or land cover type (cover); + = additive effect; constant = no variation. Density was held constant for all models listed.

[b] Number of model parameters.

[c] Model deviance = −2(log-likelihood).

None of the top models included an animal by site learned response; however, the parameter structure of the top model with the addition of bk was the second ranked model in each study area except for the SSacs, where the behavioral model was third (Tables S2–S6). Although models that included bk reduced the deviance and appeared competitive in the model set, the deviances were nearly identical to the top model, so the extra parameter failed to substantially improve model fit. As a result, the support for bk models was likely a result of an identical model structure to the well-supported top models (Arnold 2010). Therefore, we removed all models that included bk from our model sets, and we report only on the reduced model sets hereafter.

There was little model selection uncertainty in each study area except in the SSacs with the top model garnering 50% of the total model weight (Table 2; Tables S7–S11). Detection probability (g0) was highest for the Sandias (g0 = 0.029 and 0.0017 for females and males, respectively), but overall, g0 was low across all study areas (Table 3). The land cover type or elevation at which the detector was deployed were helpful covariates in explaining heterogeneity in both g0 and σ for all study areas except for the Sandias, which included sex as the only important explanatory variable (Table 2; Tables S7–S11). Models allowing g0 to vary over time were supported because g0 was low in early summer, increased as the summer progressed, and then decreased in late summer except in the SSC where g0 increased in each occasion. Detection probability increased as elevation increased in the SSC with σ exhibiting an inverse relationship. The SOE that the effect of elevation was not 0 was high for both g0 and σ (Table A1). In the Sandias, males showed a lower detection probability (g0) and higher movement rate (σ) than female black bears, and the SOE that the effect of sex on both parameters was not 0 was high (Table A1). The influence of land cover on g0 and σ across the NSC, NSacs, and SSacs was variable. The most consistent relationship was that g0 was lower and σ was higher within the piñon pine-juniper land cover type with aspen-conifer (NSC) and mixed conifer (NSacs and SSacs) land cover types as reference categories, respectively (Table A1). The SOE that the effect of land cover type was not 0 was high for all parameter-study area combinations except for σ in the NSacs. The effect of the

Table 3. Estimated abundance ($\widehat{N}$) and density ($\widehat{D}$; bears/100 km^2), coefficient of variation of the density estimate (CV[$\widehat{D}$]), detection probability at the activity center (g0), spatial scale over which detection probability declines (σ; km), and their 95% confidence intervals for American black bears in the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains, New Mexico, USA, 2012–2014. We model averaged $\widehat{N}$ and $\widehat{D}$ for the SSC and SSacs using models with model weights > 0.00 and for the NSacs using the top-ranked model with density held constant and varying by sex.

Study area[a]	$\widehat{N}$ (95% CI)	$\widehat{D}$ (95% CI)	CV($\widehat{D}$)	$\widehat{g0}$ (95% CI)	$\widehat{\sigma}$ (95% CI)
NSC	1,249.5 (1,019–1,532.1)	21.9 (17.8–26.8)	0.10	0.00060 (0.00023–0.0015)	3.31 (2.09–5.25)
SSC	646.8 (444.3–941.6)	19.7 (13.8–28.3)	0.19	0.000018 (0.0000061–0.000052)	18.12 (12.38–26.53)
Sandias	43.3 (22.2–84.2)	25.7 (13.2–50.1)	0.35	0.029[b](0.015–0.078)	0.76[b](0.49–1.15)
				0.0016[c](0.00048–0.0055)	4.99[c](2.47–10.10)
NSacs	77.5[b](56.2–107.1)	10.0[b](7.2–13.9)	0.17	0.0027 (0.00058–0.012)	5.42 (2.03–14.44)
	85.8[c](62.8–117.3)	11.0[c](7.8–15.5)	0.18		
SSacs	412.3 (293.2–579.8)	16.5 (11.6–23.5)	0.18	0.0032 (0.0011–0.0093)	2.67 (1.69–4.21)

[a] Primary bear habitat: NSC = 5,716 km^2; SSC = 2,944 km^2; Sandias = 168 km^2; NSacs = 776 km^2; SSacs = 2,488 km^2.

[b] Parameter estimate for female black bears.

[c] Parameter estimate for male black bears.

ponderosa pine cover type on both g0 and σ was negligible relative to aspen-confer and mixed conifer (Table A1). In the NSC, spruce-fir and mixed conifer showed a negative relationship with g0 and a positive relationship with σ relative to aspen-conifer (Table A1).

There was marginal support that density varied by sex in the NSacs ($\Delta AIC_c = 0.87$; $w_i = 0.61$ for the top model) and no support in all other study areas ($w_i \geq 0.75$ for the top models holding density constant; Table S12). Mean density estimates varied within and between mountain ranges (range = 16.6–25.3 bears/100 km^2; Table 3) as did estimates of abundance given the different sizes of the study areas (range = 43.3–1,249.5 bears; Table 3).

DISCUSSION

By employing NGS with SECR models, we provided density estimates that will aid in setting harvest limits and serve as a benchmark for comparison with future research for multiple black bear populations in New Mexico. Our density estimates were similar to (SSacs) or higher (NSC, SSC, Sandias, and NSacs) than the previous estimates used by NMDGF to manage these populations (Costello et al. 2001). The differences in our estimates of density from those of Costello et al. (2001) are most likely due to differences in analytical techniques (the previous method did not account for imperfect detection) and we speculate due to potential changes in black bear population dynamics over the past decade. It should be noted, however, that the 95% confidence intervals surrounding our estimates typically encompassed those of Costello et al. (2001).

There is strong evidence that piñon pine-juniper land cover is associated with lower detection rates and increased movement rates, whereas an increase in elevation has the opposite association (Table A1). Like other ursid NGS studies, estimates of detection probability and movement rate varied over time and by sex in our study (Kendall et al. 2009, Sawaya et al. 2012, Stetz et al. 2014). For example, detection probabilities were lower and movement rates were higher during early and late summer, and males, in general, had higher movement rates than females. Detection probabilities also differed between the sexes in the Sandias (Table 3).

The importance of a temporal effect on g0 and σ in the NSC, SSC, NSacs, and SSacs is likely a result of seasonal mating and foraging behaviors (Alt et al. 1980, Garshelis and Pelton 1981, Costello et al. 2003). During the breeding season, males increase movement rates as they traverse their home range searching for receptive females (Young and Ruff 1982, Costello 2008, Lewis and Rachlow 2011). In fall, bear home range size and distance between sequentially recorded movements increases as bears travel outside their core area to exploit the spatially and temporally variable oak mast (Ostfeld et al. 1996, Costello 2008), which is an important food source that was previously shown to be correlated with black bear reproductive output in New Mexico (Costello et al. 2003). These behavioral differences during mating season and hyperphagia would increase movement rates and enlarge home range size, thereby reducing g0 while increasing σ because of the compensatory relationship between the 2 parameters (Efford and Mowat 2014).

The influence of land cover and elevation on g0 and σ is also likely a function of black bears responding to spatiotemporal changes in food abundance (Costello and Sage 1994, Mazur et al. 2013, McCall et al. 2013). During spring, or the pre-mast season, grasses, forbs, and ants dominate bear diets (den emergence to mid-Jul; Costello et al. 2001). Diets then shift toward soft mast species such as berries in the late summer and early fall (56% of scat volume, mid-Jul to mid-Sep), with fall (mid-Sep through Oct, den immergence) diets dominated by acorns (87% of scat volume) and supplemented with juniper berries (Costello et al. 2001, Guntley 2016). Mid-elevation land cover types (i.e., mixed conifer) are more likely to contain a higher abundance of grasses and forbs because of earlier snowmelt compared to higher elevations and higher levels of precipitation compared to lower elevations (Zlotin and Parmenter 2008). As snow melts, the availability of grasses and forbs increases with soft mast ripening with the arrival of summer rains. Once hard mast species begin to ripen in late August (Zlotin and Parmenter 2008), black bears shift their attention toward land cover types containing those species (Costello and Sage 1994, Onorato et al. 2003). Thus, the availability of grasses and soft mast at mid- to high- elevations and the scarcity of food in the low elevation piñon pine-juniper cover type during summer (Zlotin and Parmenter 2008) may explain the negative relationship with g0 and the positive relationship with σ for piñon pine-juniper and low elevations for all study areas except the Sandias (Table A1). Black bears are also predators of elk calves in portions of New Mexico and they may move toward calving grounds in spring, which are commonly found at higher elevations (Quintana 2016).

Half of our samples that met our quality threshold failed to produce a reliable genotype, which reduced the number of unique individuals identified and the number of recaptures. The lack of data also likely contributed to the low detection probabilities and affected our ability to estimate σ precisely (Efford et al. 2004, Sollmann et al. 2012, Sun et al. 2014). However, simulation has shown that SECR models provide relatively robust estimates of density under data dilution scenarios (Mollet et al. 2015). The relatively more precise NSC density estimate, despite a low g0, may be a result of a greater number of unique individuals and recaptures, which provided sufficient data for the model to predict unobserved movement distances (Table 1; Sollmann et al. 2012, Sun et al. 2014). Whereas g0 was the highest for the Sandias, the density estimate was the least precise. This relatively low level of precision was most likely caused by the few individuals detected ($n = 18$) and a low number of spatial recaptures, which may have contributed to poor estimates of σ and an inability to predict unobserved movement distances (Sollmann et al. 2012). The low sample size and few recaptures is further evident in the simple structure of the top models and the high coefficient of variation for the estimate of density (Tables 2 and 3).

We suspect that for all study areas, intense ultraviolet (UV) radiation coupled with extended sampling intervals were the

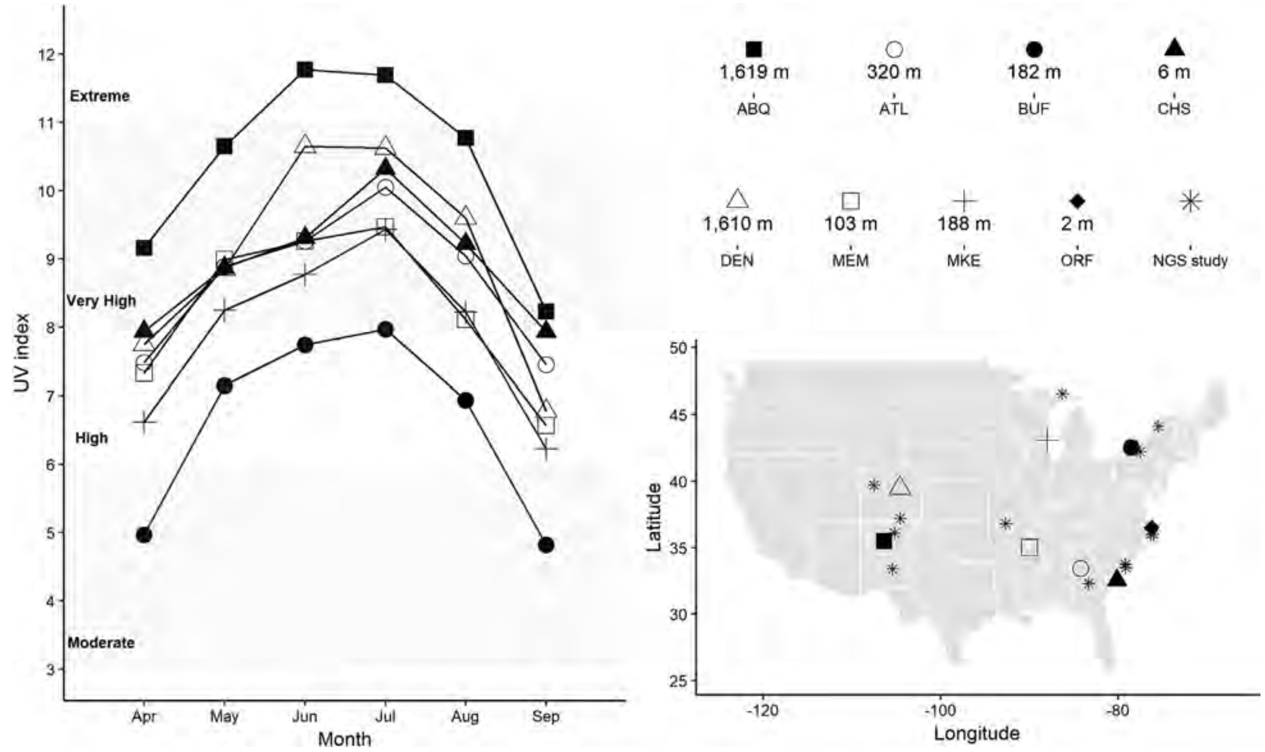

Figure 3. Mean monthly ultraviolet radiation (UV) index generated by the National Oceanic and Atmospheric Administration showing estimated noontime intensity of UV radiation coupled with the World Health Organization human health hazard UV index classification for Albuquerque, New Mexico (ABQ); Atlanta, Georgia (ATL); Buffalo, New York (BUF); Charleston, South Carolina (CHS); Denver, Colorado (DEN); Memphis, Tennessee (MEM); Milwaukee, Wisconsin (MKE); and Norfolk, Virginia (ORF), USA, 2012 (left) along with a map showing the aforementioned cities and the non-invasive genetic sampling studies conducted on American black bears in the United States that used a spatially explicit capture–recapture framework (bottom right) and their elevations (top right).

Table 4. Mean density estimates ($\widehat{D}$) for American black bears (bears/100 km^2), 95% confidence intervals, and the proportion of hair samples successfully genotyped for noninvasive genetic sampling studies conducted in the United States that used a spatially explicit capture–recapture framework.

Study area	State	$\widehat{D}$	95% CI	Genotyping success	Reference
Ozark Highlands	MO	1.70	1.10–2.40	0.70	Wilton et al. 2014[a]
Carver Bay	SC	4.60	2.40–6.70	0.90[b]	Drewry et al. 2013
Picture Rocks National Lakeshore	MI	10.56	8.59–12.79	0.91	Sollmann et al. 2012[cd]
Glacier National Park	MT	12.00	10.00–14.40	0.72	Stetz et al. 2014[de]
Southern Black Bear Range	NY	11.20[f]	1.50–77.80[g]	0.89	Sun et al. 2017[a]
Southern Sacramento Mountains	NM	16.55	11.64–23.53	0.44	This study
Southern Sangre de Cristo Mountains	NM	19.74	13.77–28.30	0.48	This study
Fort Drum Military Installation	NY	20.00	15.00–26.00	0.89	Gardner et al. 2010[c]
Northern Sacramento Mountains	NM	20.17	15.35–26.52	0.61	This study
Durango	CO	21.00–38.00	16.00–55.00	0.75[b]	Apker et al. 2016
Spanish Peaks	CO	21.00–44.00	16.00–57.00	0.73[b]	Apker et al. 2016
Northern Sangre de Cristo Mountains	NM	21.86	17.83–26.80	0.49	This study
Central Georgia Population	GA	23.20–24.00	15.95–30.45	0.87[b]	Hooker et al. 2015[d]
Sandia Mountains	NM	25.75	13.22–50.14	0.53	This study
Kentucky-Virginia Border	KY, VA	26.00	18.00–37.00	0.45[b]	Murphy et al. 2016
Greenhorn Mountain	CO	26.00–33.00	19.00–43.00	0.74[b]	Apker et al. 2016
Piedra	CO	32.00–60.00	25.00–82.00	0.72[b]	Apker et al. 2016
Lewis Ocean Bay	SC	33.90	22.90–44.80	0.88[b]	Drewry et al. 2013
Alligator River NWR	NC	37.00–46.00	30.70–66.00	0.82[b]	Tredick and Vaughan 2009
Great Dismal Swamp NWR	NC, VA	46.00	34.60–57.30	0.84	Tredick and Vaughan 2009
Pocosin Lakes NWR	NC	58.00–77.00	49.10–88.50	0.85[b]	Tredick and Vaughan 2009

[a] Genetic analysis not conducted by Wildlife Genetics International.
[b] Value averaged over multiple sampling years.
[c] Bayesian-based analysis.
[d] Analyzed hair samples were a subset of the total hair samples collected.
[e] Black bear population sympatric with grizzly bears (*Ursus arctos*).
[f] Baseline density estimate averaged across all top models.
[g] 85% confidence interval.

main factors explaining the poor genotyping success we observed (Stetz et al. 2015). Ultraviolet radiation causes DNA degradation by forming dimers between adjacent pyrimidine bases, instead of those bases binding with their cross-strand partners, which prevents the DNA polymerase from progressing past the dimer and results in an incomplete genotype (Jagger 1985). Factors influencing UV levels include cloud cover, elevation, latitude, shade, length of exposure, season, ozone depletion, and atmospheric turbidity (Piazena 1996, Stetz et al. 2015). For example, UV radiation increases with decreasing cloud cover, increases with elevation (9–11% per 1,000 m), and increases with decreasing latitude (Blumthaler et al. 1997). The UV radiation levels across much of New Mexico are higher than across most of the United States and are higher than other regions where NGS methods have been used to estimate bear abundance and density (Fig. 3; National Oceanic and Atmospheric Administration [NOAA] 2012). Further, we would expect UV radiation levels to be 1–26% higher in our study areas compared to those for Albuquerque, New Mexico, where the NOAA (2012) UV measurement was taken, because our study areas were at equal or higher elevations. Reducing the sampling interval should have increased genotyping success; however, when we reduced our sampling interval from 4 to 2 weeks (which is a common period used by similar NGS studies in the western United States), we observed only marginal improvement in genotyping success (4%).

In the SSC, we also lost hair samples because of 2 forest fires, the Tres Lagunas (4,135 ha) and the Jaroso (4,511 ha). These fires affected 450 km^2 (12.7%) of the trapping grid and prevented us from accessing and checking hair traps located near the fire, primarily during the second and third sampling occasions (3–13% of total hair traps; Fig. S3). Moreover, many of the fire-affected traps were in an area where we expected higher bear abundance. Anecdotally, these hair traps consistently yielded more hair samples post-fire than hair traps located in some areas that were unaffected by the fires. The limited access also prevented us from identifying more bear rubs across the SSC, restricting our use of multiple sampling methods and hindering our ability to minimize the impacts of capture heterogeneity present with any one survey method (Boulanger et al. 2008).

Despite UV radiation and sampling difficulties, our density estimates had levels of precision comparable to those obtained in other black bear studies conducted across the United States that used NGS and a SECR estimator (Table 4). The level of precision we achieved may have been a consequence of the large extent of our study areas, which may have allowed us to detect a large proportion of the population within each mountain range even though we failed to amplify approximately half of our samples. Our density estimates fell within the middle range of NGS and SECR-based black bear density studies (Table 4). Black bear density was highest on the east coast in pocosin, which is characterized by high food production and cover, low human disturbance, and agricultural food resources mixed throughout (Tredick and Vaughan 2009, Drewry et al. 2013). Eastern populations inhabiting pine plantations were at densities comparable to New Mexico populations likely because pine plantations had limited food, insufficient cover, and fewer agricultural food resources as compared to pocosin (Tredick and Vaughan 2009, Drewry et al. 2013, Hooker et al. 2015). Locally, our estimates are similar to or lower than those in southern Colorado, USA, and similar to or higher than those in northern Colorado (Table 4); however, estimates for southern Colorado fluctuated substantially within each study area and over multiple years. Populations with densities lower than ours were expanding their range (Sun et al. 2017), recolonizing (Wilton et al. 2014), residing in habitat with low food resources (Drewry et al. 2013), or were sympatric with grizzly bears (*Ursus arctos*; Stetz et al. 2014).

We provided updated density estimates for an important game species in New Mexico. Our estimates add to a growing number of studies that have used NGS coupled with SECR models to estimate the density of black bear populations across the United States. Our data suggest that the detection probability of black bears is likely influenced by the abundance and distribution of food resources on the landscape, which in turn, may be influenced by land cover type and elevation. Furthermore, UV radiation levels in New Mexico appear to be higher than elsewhere in the contiguous United States and are also most likely responsible for our low rate of genotyping success, a rate comparable to those in the high Arctic of North America (Dumond et al. 2015).

MANAGEMENT IMPLICATIONS

Our estimates of density will assist the New Mexico Department of Game and Fish in setting sustainable harvest limits for multiple populations of black bears in New Mexico. We suggest that researchers using hair samples to monitor wildlife populations incorporate a pilot study to evaluate the effects of UV degradation, among other factors, on genotyping success. To help reduce UV exposure, researchers could set detectors in more shaded areas (e.g., north facing slopes), set fewer detectors so that they can be checked more frequently, or increase the number of personnel used to check detectors. We believe more personnel is preferable to fewer detectors because it allows for a larger study area, a denser trapping array, or alternative trapping configurations to be sampled. A larger study area will help mitigate the effects that seasonal movement patterns can have on parameter estimates, particularly in areas with highly variable food resources, and provide density estimates at the spatial scale at which many agencies make management decisions.

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LITERATURE CITED

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.

Alt, G. L., G. J. Matula Jr., F. W. Alt, and J. S. Lindzey. 1980. Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. Bears: Their Biology and Management 4:131–136.

Apker, J. A., J. Runge, H. Johnson, J. Mao, A. Vitt, M. Vieira, J. Yost, and K. Oldham. 2016. Non-invasive genetic-based black bear investigations in Colorado—2009–2015. Colorado Division of Wildlife, Monte Vista, USA.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Atwood, T. C., J. K. Young, J. P. Beckman, S. W. Breck, J. Fike, O. E. Rhodes, and K. D. Bristow. 2011. Modeling connectivity of black bears in a desert sky island archipelago. Biological Conservation 144:2851–2862.

Augustine, B. C., C. A. Tredick, and S. J. Bonner. 2014. Accounting for behavioral response to capture when estimating population size from hair snare studies with missing data. Methods in Ecology and Evolution 5:1154–1161.

Beston, J. A., and R. D. Mace. 2012. What can harvest data tell us about Montana's black bears? Ursus 23:30–41.

Bleich, V. C., C. S. Y. Chun, R. W. Anthes, T. E. Evans, and J. K. Fischer. 2001. Visibility bias and development of a sightability model for tule elk. Alces 37:315–327.

Blumthaler, M., W. Ambach, and R. Ellinger. 1997. Increase in solar UV radiation with altitude. Journal of Photochemistry and Photobiology 39:130–134.

Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385.

Boulanger, J., K. C. Kendall, J. B. Stetz, D. A. Roon, L. P. Waits, and D. Paetkau. 2008. Multiple data sources improve DNA based mark-recapture population estimates of grizzly bears. Ecological Applications 18:577–589.

Boulanger, J., and B. McLellan. 2001. Closure violation in NDA-based mark-recapture estimation of grizzly bear populations. Canadian Journal of Zoology 79:642–651.

Boulanger, J., B. N. McLellan, J. G. Woods, M. F. Proctor, and C. Strobeck. 2004. Sampling design and bias in DNA-based capture-mark-recapture population and density estimates of grizzly bears. Journal of Wildlife Management 68:457–469.

Burnham, K. P. 2015. Multimodel inference: understanding AIC relative variable importance values. https://sites.warnercnr.colostate.edu/kenburnham/model-selection-issues/. Accessed 13 Oct 2016.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Burst, T. L., and M. R. Pelton. 1983. Black bear mark trees in the Smoky Mountains. International Conference on Bear Research and Management 5:45–53.

Costello, C. M. 2008. The spatial ecology and mating system of black bears (*Ursus americanus*) in New Mexico. Dissertation, Montana State University, Bozeman, Montana, USA.

Costello, C. M., D. E. Jones, K. A. Green-Hammond, R. M. Inman, K. H. Inman, B. C. Thompson, R. A. Deitner, and H. B. Quigley. 2001. A study of black bear ecology in New Mexico with models for population dynamics and habitat suitability. Final Report, Federal Aid in Wildlife Restoration Project W-131-R, New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA.

Costello, C. M., D. E. Jones, R. M. Inman, K. H. Inman, B. C. Thompson, and H. B. Quigley. 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. Ursus 14:1–16.

Costello, C. M., and R. W. Sage Jr. 1994. Predicting black bear habitat selection from food abundance under 3 forest management systems. Ursus 9:375–387.

Dice, L. R. 1938. Some census methods for mammals. Journal of Wildlife Management 2:119–130.

Drewry, J. M., F. T. Van Manen, and D. M. Ruth. 2013. Density of and genetic structure of black bears in coastal South Carolina. Journal of Wildlife Management 77:153–164.

Dumond, M., J. Boulanger, and D. Paetkau. 2015. The estimation of grizzly bear density through hair-snagging techniques above the tree line. Journal of Wildlife Management 39:390–402.

Durnin, M. E., P. J. Palsboll, O. A. Ryder, D. R. McCullough. 2007. A reliable genetic technique for sex determination of giant panda (*Aliuropoda melanoleuca*) from non-invasively collected hair samples. Conservation Genetics 8:715–720.

Eberhardt, L. L., and R. R. Knight. 1996. How many grizzlies in Yellowstone? Journal of Wildlife Management 60:416–421.

Efford, M. G. 2004. Density estimation in live-trapping studies. Oikos 106:598–610.

Efford, M. G. 2015. secr: spatially explicit capture-recapture models. R package version 2.9.5. http://CRAN.R-project.org/package=secr. Accessed 15 Jun 2015.

Efford, M. G. 2016. secr: spatially explicit capture-recapture models. R package version 2.10.4. http://CRAN.R-project.org/package=secr. Accessed 3 Dec 2016.

Efford, M. G., D. L. Borchers, and A. E. Byrom. 2009. Density estimation by spatially explicit capture-recapture: likelihood-based methods. Pages 255–269 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York, New York, USA.

Efford, M. G., D. L. Borchers, and G. Mowat. 2013. Varying effort in capture-recapture studies. Methods in Ecology and Evolution 4:629–636.

Efford, M. G., D. K. Dawson, and C. S. Robbins. 2004. DENSITY: software for analyzing capture-recapture data from passive detector arrays. Animal Biodiversity and Conservation 27:217–228.

Efford, M. G., and G. Mowat. 2014. Compensatory heterogeneity in spatially explicit capture-recapture data. Ecology 95:1341–1348.

Gardner, B., J. A. Royle, M. T. Wegan, R. E. Rainbold, and P. D. Curtis. 2010. Estimating black bear density using DNA from hair snares. Journal of Wildlife Management 74:318–325.

Garshelis, D. L. 1990. Monitoring effects of harvest on black bear populations in North America: a review and evaluation of techniques. Eastern Workshop on Black Bear research and Management 10:120–144.

Garshelis, D. L., and M. R. Pelton. 1981. Movements of black bears in the Great Smoky National Park. Journal of Wildlife Management 45:912–925.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, United Kingdom.

Guntley, K. M. 2016. Black bear (*Ursus americanus*) movements, diet, and impacts on ungulate neonate survival on the National Rifle Association Whittington Center, New Mexico. Thesis, Texas Tech University, Lubbock, USA.

Hooker, M. J., J. S. Laufenberg, A. K. Ashley, J. T. Sylvest, and M. J. Chamerlain. 2015. Abundance and density estimation of the American black bear population in central Georgia. Ursus 26:107–115.

Hristienko, H., and J. E. McDonald Jr. 2007. Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. Ursus 18:72–88.

Hurvich, C. M., and C. L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Ivan, J. S., G. C. White, and T. M. Shenk. 2013. Using simulation to compare methods for estimating density from capture-recapture data. Ecology 94:817–826.

Jagger, J. 1985. Solar-UV actions on living cells. Praeger Publishers, New York, New York, USA.

Kaufmann, M. R., L. S. Huckaby, C. M. Regan, and J. Popp. 1998. Forest reference conditions for ecosystem management in the Sacramento Mountains, New Mexico. U.S Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. Macleod, D. Paetkau, and G. C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. Journal of Wildlife Management 73:3–17.

Kendall, K. C., J. B. Stetz, D. A. Roon, L. P. Waits, J. B. Boulanger, and D. Paetkau. 2008. Grizzly bear density in Glacier National Park, Montana. Journal of Wildlife Management 72:1693–1705.

Lee, L. 1967. Bears in New Mexico wildlife management. New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA.

Lewis, J. S., and J. L. Rachlow. 2011. Activity patterns of black bears in relation to sex, season, and daily movement rates. Western North American Naturalist 71:388–395.

Mazur, R., A. P. Klimley, and K. Folger. 2013. Implications of the variable availability of seasonal foods on the home ranges of black bears, *Ursus americanus*, in the Sierra Nevada of California. Animal Biotelemetry 1:1–9.

McCall, B. S., M. S. Mitchell, M. K. Schwartz, J. Hayden, S. A. Cushman, P. Zager, and W. F. Kasworm. 2013. Combined use of mark-recapture and genetic analyses reveals response of a black bear population to changes in food productivity. Journal of Wildlife Management 77:1572–1582.

Miller, S. D. 1990. Population management of bears in North American. International Conference on Bear Research and Management 8:350–373.

Mollet, P., M. Kery, B. Gardner, G. Pasinelli, and J. A. Royle. 2015. Estimating population size for capercaillie (*Tetrao urogallus* L.) with spatial capture-recapture models based on genotypes from one field sample. PLoS ONE 10(6):e0129020.

Murphy, S. M., J. J. Cox, B. C. Augustine, J. T. Hast, J. M. Guthrie, J. Wright, J. McDermott, S. C. Maehr, and J. H. Plaxico. 2016. Characterizing recolonization by a reintroduced bear population using genetic spatial capture-recapture. Journal of Wildlife Management 80:1390–1407.

National Oceanic and Atmospheric Administration [NOAA]. 2012. UV Index: annual time series http://www.cpc.ncep.noaa.gov/products/stratosphere/uv_index/uv_annual.shtml. Accessed 11 Nov 2015.

New Mexico Department of Game and Fish. 1926. Report of the fiscal years 1925–1926. New Mexico Department of Game and Fish, Santa Fe, USA.

Obbard, M., E. J. Howe, and C. J. Kyle. 2010. Empirical comparison of density estimators for large carnivores. Journal of Applied Ecology 47:76–84.

Onorato, D. P., E. C. Hellgren, F. S. Mitchell, and J. R. Skiles Jr. 2003. Home range and habitat use of American black bear on a desert montane island in Texas. Ursus 14:120–129.

Ostfeld, R. S., C. G. Jones, and J. O. Wolff. 1996. Of mice and mast. BioScience 46:323–330.

Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. Molecular Ecology 12:1375–1387.

Paetkau, D. 2004. The optimal number of markers in genetic capture-recapture studies. Journal of Wildlife Management 68:449–452.

Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347–354.

Paetkau, D., G. F. Shields, and C. Strobeck. 1998. Gene flow between insular, coastal, and interior populations of brown bears in Alaska. Molecular Ecology 7:1283–1292.

Piazena, H. 1996. The effect of altitude upon the solar UV-B and UV-A irradiance in the tropical Chilean Andes. Solar Energy 57:133–140.

Quintana, N. T. 2016. Predator-prey relationships between rocky mountain elk and black bears in Northern, NM. Dissertation, Texas Tech University, Lubbock, USA.

Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. International Journal of Wildland Fire 18:235–249.

Rousset, F. 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. Molecular Ecology Resources 8:103–106.

Rovang, S., S. E. Nielsen, and G. Stenhouse. 2015. In the trap: detectability of fixed hair trap DNA methods in grizzly bear population monitoring. Wildlife Society Bulletin 21:68–79.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture-recapture. Academic Press, Waltham, Massachusetts, USA.

Sawaya, M. A., J. B. Stetz, A. P. Clevenger, M. L. Gibeau, and S. T. Kainowski. 2012. Estimating grizzly and black bear population abundance and trend in Banff National Park using noninvasive genetic sampling. PLoS ONE 7(5):e34777.

Sollmann, R., B. Gardner, and J. L. Belant. 2012. How does spatial study design influence density estimates from spatial capture recapture models? PLoS ONE 7(4):e34574.

Stetz, J. B., K. C. Kendall, and A. C. Macleod. 2014. Black bear density in Glacier National Park, Montana. Wildlife Society Bulletin 38:60–70.

Stetz, J. B., T. Seitz, and M. A. Sawaya. 2015. Effects of exposure on genotyping success rates of hair samples from brown and American black bears. Journal of Fish and Wildlife Management 6:191–198.

Sun, C., A. K. Fuller, M. P. Hare, and J. E. Hurst. 2017. Evaluating population expansion of black bears using spatial capture-recapture. Journal of Wildlife Management 81:814–823.

Sun, C., A. K. Fuller, and J. A. Royle. 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. PLoS ONE 9(2):e88025.

Taberlet, P., J. J. Camarra, S. Griffin, O. Hanotte, L. P. Waits, C. Dubois-Paganon, T. Burke, and T. Bouvet. 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. Molecular Ecology 6:869–876.

Thompson, B. C., P. J. Crist, J. S. Prior-Magee, R. A. Deitner, D. L. Garber, and M. A. Hughes. 1996. Gap analysis of biological diversity conservation in New Mexico using geographic information systems. Research completion report, New Mexico Cooperative Fish and Wildlife Research Unit, Las Cruces, USA.

Tredick, C. A., and M. R. Vaughan. 2009. DNA-based population demographics of black bears in coastal North Carolina and Virginia. Journal of Wildlife Management 73:1031–1039.

Western Regional Climate Center. 2017. Cooperative climatological data summaries: period of record general climate summaries for Capitan, Cimmaron, Cloudcroft, Pecos, Placitas, Red River, and Ruidoso, New Mexico. https://www.wrcc.dri.edu/summary/Climsmnm.html. Accessed 26 Dec 2017.

Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66:13–21.

Wilton, C. M., E. E. Puckett, J. Beringer, B. Gardner, L. S. Eggert, and J. L. Belant. 2014. Trap array configuration influences estimates and precision of black bear density and abundance. PLoS ONE 9(10):e111257.

Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

Young, B. F., and R. L. Ruff. 1982. Population dynamics and movements of black bears in east central Alberta. Journal of Wildlife Management 46:845–86.

Zabransky, C. J., D. G. Hewitt, R. W. DeYoung, S. S. Gray, C. Richardson, A. R. Litt, and C. A. DeYoung. 2016. A detection probability model for aerial surveys of mule deer. Journal of Wildlife Management 80:1379–1389.

Zlotin, R. I., and R. R. Parmenter. 2008. Patterns of mast production in pinyon and juniper woodlands along a precipitation gradient in central New Mexico (Sevilleta National Wildlife Refuge. Journal of Arid Environments 72:1562–1572.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

APPENDIX A. Relationship and effect of covariates on spatially explicit capture–recapture model parameters.

Table A1. The beta coefficient (Beta), standard error (SE), and lower (LCL) and upper (UCL) 95% confidence intervals for covariate variables from the top ranked spatially explicit capture–recapture model for American black bears in the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains, New Mexico, USA, 2012–2014. Included is the strength of evidence (SOE) of the likelihood that the beta coefficient is not 0 where larger values indicate a greater SOE that the effect of the variable is not 0. The reference categories for land cover type were aspen-conifer (NSC) and mixed-conifer (NSacs and SSacs), and the reference category for sex (Sandias) was female. Model parameters include detection probability at the activity center (g0) and the spatial scale over which g0 declines (σ).

Variable	Parameter	Study area	Beta	SE	LCL	UCL	SOE
Elevation	g0	SSC	1.57	0.25	1.08	2.07	273,870,708.14
Elevation	σ	SSC	−0.62	0.12	−0.84	−0.39	1,570,914.27
Sex	g0	Sandias	−2.92	0.80	−4.49	−1.36	824.02
Sex	σ	Sandias	1.89	0.42	1.07	2.71	26,688.19
Piñon pine-juniper	g0	NSC	−3.07	0.48	−4.02	−2.12	564,259,121.57
Piñon pine-juniper	g0	NSacs	−2.55	0.71	−3.93	−1.16	669.32
Piñon pine-juniper	g0	SSacs	−2.38	0.52	−3.40	−1.36	33,281.84
Piñon pine-juniper	σ	NSC	1.33	0.24	0.87	1.79	8,592,700.16
Piñon pine-juniper	σ	NSacs	−0.04	0.38	−0.80	0.71	1.01
Piñon pine-juniper	σ	SSacs	0.72	0.25	0.23	1.21	63.55
Ponderosa	g0	NSC	−0.59	0.49	−1.56	0.37	2.06
Ponderosa	g0	NSacs	0.15	0.33	−0.50	0.79	1.11
Ponderosa	g0	SSacs	0.39	0.52	−0.63	1.41	1.32
Ponderosa	σ	NSC	0.05	0.23	−0.40	0.50	1.03
Ponderosa	σ	NSacs	−0.24	0.19	−0.62	0.14	2.19
Ponderosa	σ	SSacs	−0.39	0.24	−0.86	0.09	3.54
Mixed-conifer	g0	NSC	−1.84	0.44	−2.71	−0.97	5,363.23
Mixed-conifer	σ	NSC	0.94	0.21	0.52	1.35	16,038.76
Spruce-fir	g0	NSC	−2.09	0.53	−3.13	−1.04	2,140.41
Spruce-fir	σ	NSC	1.21	0.26	0.70	1.71	56,102.60

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Compounding effects of human development and a natural food shortage on a black bear population along a human development-wildland interface

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ABSTRACT

Human development and climate change are two stressors that threaten numerous wildlife populations, and their combined effects are likely to be most pronounced along the human development-wildland interface where changes in both natural and anthropogenic conditions interact to affect wildlife. To better understand the compounding influence of these stressors, we investigated the effects of a climate-induced natural food shortage on the dynamics of a black bear population in the vicinity of Durango, Colorado. We integrated 4 years of DNA-based capture-mark-recapture data with GPS-based telemetry data to evaluate the combined effects of human development and the food shortage on the abundance, population growth rate, and spatial distribution of female black bears. We documented a 57% decline in female bear abundance immediately following the natural food shortage coinciding with an increase in human-caused bear mortality (e.g., vehicle collisions, harvest and lethal removals) primarily in developed areas. We also detected a change in the spatial distribution of female bears with fewer bears occurring near human development in years immediately following the food shortage, likely as a consequence of high mortality near human infrastructure during the food shortage. Given expected future increases in human development and climate-induced food shortages, we expect that bear dynamics may be increasingly influenced by human-caused mortality, which will be difficult to detect with current management practices. To ensure long-term sustainability of bear populations, we recommend that wildlife agencies invest in monitoring programs that can accurately track bear populations, incorporate non-harvest human-caused mortality into management models, and work to reduce human-caused mortality, particularly in years with natural food shortages.

1. Introduction

Human development and climate change are two important stressors threatening global biodiversity (Bellard et al., 2012; Newbold et al., 2015). Expanding human development and infrastructure affect wildlife by eliminating habitat (Theobald, 2010), fragmenting and degrading existing habitat (Riitters et al., 2009), and increasing human disturbance (Trombulak and Frissell, 2000; Hansen et al., 2005), impacts which have been shown to displace wildlife (Vogel, 1989; Sawyer et al., 2006), affect movement behavior (Hurst and Porter, 2008; Cushman and Lewis, 2010), reduce demographic rates (Hansen et al., 2005), and contribute to population declines (Sorensen et al., 2008). Climate change affects wildlife by shifting long-term averages of climatic variables (e.g., warmer overall temperatures, earlier growing season) and increasing the frequency and intensity of extreme climatic events (e.g., droughts, floods; Stocker et al., 2013), which all can have substantial effects on animal behavior (Wong and Candolin, 2015), physiology (Vázquez et al., 2015), distributions (Chen et al., 2011), and population dynamics (Koenig and Liebhold, 2016).

Recent research efforts have increasingly focused on understanding the cumulative and interactive effects of multiple stressors on wildlife populations as investigators have recognized the diverse pressures influencing animals and the potential for detrimental additive or synergistic effects (Brook et al., 2008; Mantyka-Pringle et al., 2012; Côté et al., 2016). Such interactions are likely to be particularly pronounced along the human development-wildland interface where multiple stressors can converge and have compounding impacts on wildlife populations. Animals living along the development-wildland interface

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must contend with climate change-induced stressors in the natural environment such as shifts in vegetative phenology (Post and Forchhammer, 2008; Monteith et al., 2011), altered weather patterns (Rodenhouse et al., 2009; Skagen and Adams, 2012), and increased frequency of extreme climatic events (Altwegg et al., 2006; Boersma and Rebstock, 2014), while also coping with development-induced habitat loss and fragmentation, and increased exposure to disease, pollution, and human-caused mortality (McCleery et al., 2014). For example, climate-induced declines in sea-ice have reduced foraging opportunities for some polar bears (*Ursus maritimus*), and have forced them to reside on land during summer months. While this shift to land has been associated with reduced body condition of bears, it has also been accompanied by increases in conflicts with people (Stirling and Derocher, 2012), which can result in higher rates of human-caused mortality.

The compounding effects of multiple stressors along the human development-wildland interface are particularly concerning for the American black bear (*Ursus americanus*). Black bear behavior and demography are strongly tied to climate-induced variation in natural vegetative foods (Reynolds-Hogland et al., 2007; Baruch-Mordo et al., 2014; Johnson et al., 2015), and extreme weather events can cause seasonal food shortages which have been associated with reduced reproduction (Rogers, 1987a; Elowe and Dodge, 1989) and cub survival (Rogers, 1987a; Obbard and Howe, 2008). However, such events can also elevate levels of human-bear conflicts and human-caused mortalities (Zack et al., 2003; Baruch-Mordo et al., 2014) as bears increase their use of areas of human development in search of alternative food resources (Johnson et al., 2015). Because bear populations occurring along the human development-wildland interface are subject to the combined effects of climate-induced food shortages and increased human-caused mortality (e.g., vehicle collisions, lethal management removals, and illegal kills), their populations may be particularly susceptible to decline (Lewis et al., 2014). Improving our understanding of how multiple stressors drive black bear population dynamics is critical for developing future management policies that will ensure the sustainability of bear populations as changes in climate and land use continue.

We investigated the combined effects of human development and a climate-induced natural food failure on a black bear population located near the city of Durango in southwestern Colorado. In 2012, our study area experienced a late-spring hard freeze (Peterson, 2013; Rice et al., 2014) which caused a widespread natural food shortage for black bears in the region. Johnson et al. (2015) found that, under those conditions, black bears increased their use of human development to obtain anthropogenic resources for subsidy, a behavioral shift that had unknown consequences on the bear population. Our objective was to evaluate the effects of human development and the food shortage on the population of bears in our study area based on the hypothesis that combination of those stressors would result in a substantial population decline. We integrated spatial capture-recapture data and GPS collar data to quantify the abundance, density, and population growth rate of bears before and after the food shortage along the development-wildland interface. In addition, we used our integrated spatial capture-recapture models to investigate the influence of human development on the distribution of bears on the landscape (2nd order selection; Johnson, 1980) before and after the food failure. Our analysis provides important insight about the combined effects of multiple stressors facing black bear populations along the development-wildland interface, with key implications for bear management and conservation.

2. Study area

Our study area (Fig. 1) was located in southwestern Colorado and contained the city of Durango, Colorado (37.2753°N, 107.8801°W). Durango (~18,000 residents; https://www.census.gov/quickfacts/) is surrounded by mountainous terrain ranging in elevation from 1930 to 3600 m, and is generally characterized as having mild winters and warm summers that experience monsoon rains. Vegetation in the region is dominated by ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), pinyon pine (*Pinus edulis*), juniper (*Juniperus* ssp.), mountain shrubs (*Prunus virginiana*, *Amelanchier alnifolia*, etc.) and agriculture. Agriculture in the region is primarily irrigated pasture for grazing livestock, which provides negligible food resources or cover habitat for black bears. Durango is largely surrounded by public land managed by the San Juan National Forest, Bureau of Land Management (BLM), Colorado Parks and Wildlife (CPW), La Plata County and the City of Durango.

3. Methods

3.1. General approach

To estimate population parameters for bears before and after the food shortage, we combined DNA-based spatial capture-recapture (SCR) data with GPS-telemetry based resource selection data into a single integrated spatial capture-recapture (ISCR) analysis. We limited our analysis to female black bears because we had reliable DNA and telemetry data for this segment of the population and because female demography is the key to understanding changes in the population dynamics of bears (Freedman et al., 2003; Beston, 2011). We assumed our estimates of demographic parameters applied only to the population of bears ≥1 year old because bears < 1 year old are unlikely to be detected by the sampling methods we used (Drewry et al., 2013; Laufenberg et al., 2016). Our approach was organized into a 2-stage analysis. In the first stage, we used GPS data and resource selection function (RSF) models to identify important 3rd-order resource selection covariates (within the home-range; Johnson, 1980) that were then used in the second stage. In the second stage, we integrated GPS and SCR data into a single model that allowed us to estimate abundance, density, detection probabilities, 3rd-order resource selection coefficients for habitat covariates identified in the first analysis, coefficients relating habitat covariates to the distribution of bears across the landscape (2nd-order selection; Johnson, 1980), and relative variable importance measures for 2nd-order habitat covariates. We obtained productivity data on important black bear foods collected during our study to characterize the natural food shortage caused by the late-spring freeze in 2012. We also obtained records of observed bear mortalities collected by CPW within our study area to use as an index of annual human-caused mortality during before and after the food shortage.

3.2. Data sources

3.2.1. Non-invasive DNA data

We used non-invasive hair sampling methods to obtain unique, multilocus genotypes for individual bears, determine individual identities, and record capture histories for capture-mark-recapture analysis (Woods et al., 1999). Each year from 2011 to 2014 we constructed an array of baited, barbed-wire enclosures (hereafter referred to as hair snares) from which we collected hair samples over multiple survey occasions. Hair snare locations were based on a regular 6 × 6 grid pattern with the grid-cell size set at 4 × 4 km. Each cell contained 1 hair snare consisting of a single strand of 4-point barbed wire stretched around and attached to ≥3 trees at 50 cm above ground and enclosing an area 6–10 m in diameter. We baited each hair snare with liquid scent applied to burlap hung in a tree approximately 3 m above ground and to an imitation "cache" of woody debris constructed at the center of the wire enclosure. Scent bait consisted of decomposing fish liquids, various commercial bear scents, and decomposing road-killed deer liquids. Following construction, hair snares were baited and subsequently checked every 7 days for 6 consecutive weeks each year from approximately the second week of June through the last week of July. Prior to initial baiting and after subsequent sample collections, we heat-

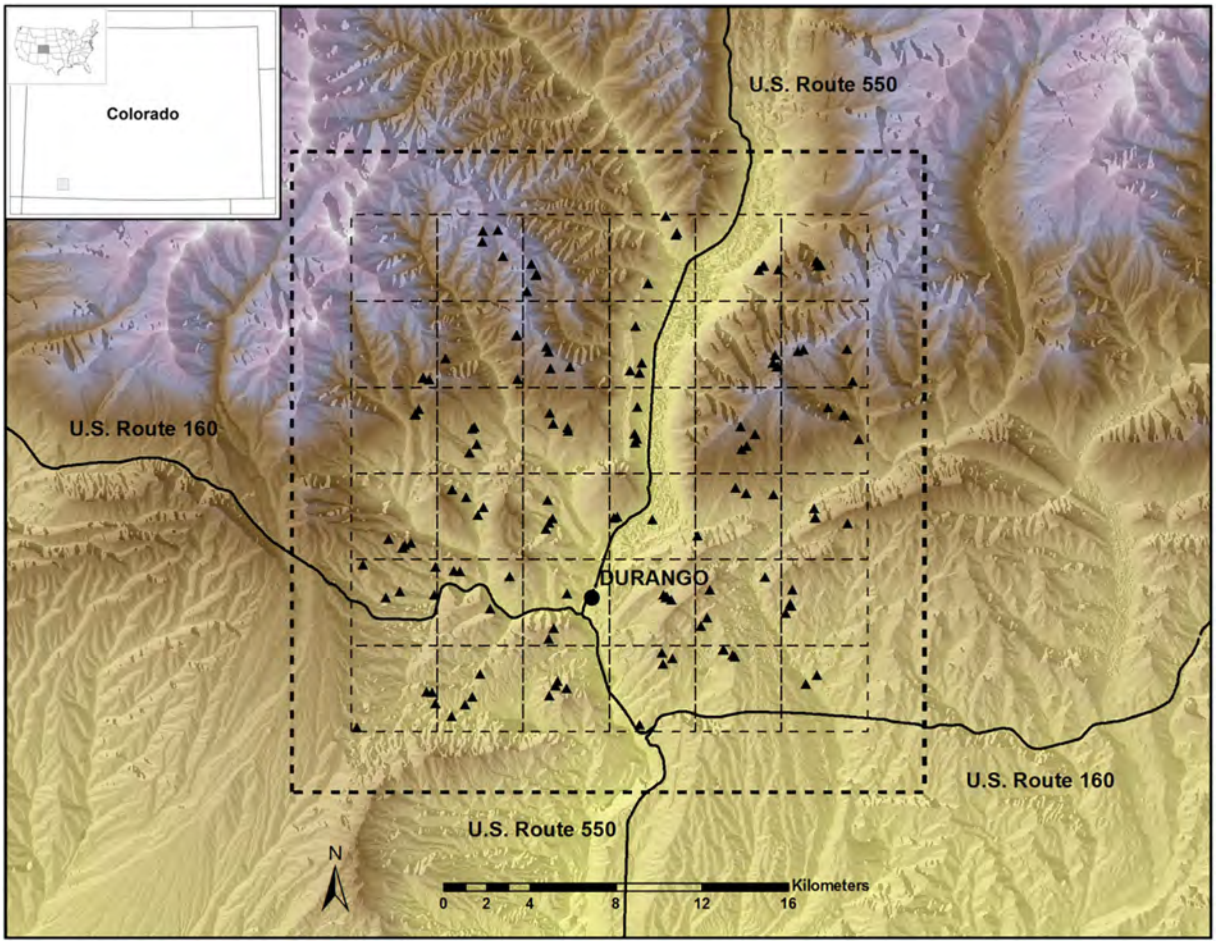

Fig. 1. Map of the study area showing the noninvasive sampling grid (thin dashed lines), hair snare locations (filled triangles) from 2011 to 2014, and state-space extent (thick dashed lines) in southwestern Colorado, USA near the city of Durango (filled circle). Major highways represented by solid lines. A single hair snare was operated per cell each year and the location of most snares changed across years resulting in multiple symbols per cell.

sterilized the barbed wire with a handheld lighter to prevent sample contamination between collection periods.

We submitted all samples to Wildlife Genetics International, Inc. (WGI; Nelson, BC, Canada) for DNA extraction and microsatellite genotyping following standard protocols (Woods et al., 1999; Paetkau, 2003; Roon et al., 2005). We selected 8 microsatellite markers (G10J, G10L, G10B, G1D, G10H, G10M, G10U, and MU59) that, when combined with a sex marker, provided sufficient power to reliably differentiate unique genotypes and identify individual black bears (Paetkau, 2003).

3.2.2. GPS-collar data

We captured black bears between May and September 2011–2014 within approximately 10 km of Durango using cage traps and Aldrich foot snares (Jonkel, 1993) following protocols described in Colorado Parks and Wildlife Animal Care and Use Protocol #01-2011. Adult female bears estimated to be ≥3 years old were immobilized and fitted with Vectronics Globstar collars (Vectronic Aerospace GmbH, Berlin). The collars were programmed to collect hourly GPS locations and were maintained during annual winter den visits so that individuals were continuously monitored until death or the collar malfunctioned. We only used GPS locations collected during the same period that hair-snare operations occurred to ensure that our SCR and GPS data sets were temporally matched for our joint analysis.

3.2.3. Mortality data

We used reports of bear mortalities opportunistically collected by CPW from 2007 to 2014 to calculate annual counts of cause-specific mortalities that occurred within our study area. We classified mortalities into 3 cause-specific categories (vehicle, harvest, and lethal management removal) and 1 "other" category (e.g., electrocution, natural, unknown). We lacked the data to correct counts for imperfect detection and, thus, consider them a relative index of different sources of mortality rather than measures of true mortality rates.

3.2.4. Natural food data

We used productivity indices of 5 hard and soft mast-producing species (Gambel oak [*Quercus gambeii*], chokecherry [*Prunus virginiana*], crabapple [*Malus* spp.], serviceberry [*Amelanchier alnifolia*], and pinyon pine [*Pinus edulis*]) important to black bears in our study area to characterize annual natural food conditions. Indices were derived from bi-weekly surveys conducted along 15 transects each year during the months of August and September (for details see Johnson et al., 2017). For each transect, the possible range of values for each species was 0 to 100 with 0 indicating no mast detected, and 100 indicating that all plants observed had abundant mast. Based on the maximum score for each mast species on each transect across the sampling period, we calculated the annual median value of mast available for each species.

3.3. Data analysis

3.3.1. RSF variable selection

We developed an RSF model of space use that was later embedded into our ISCR model to effectively scale detection probability as a

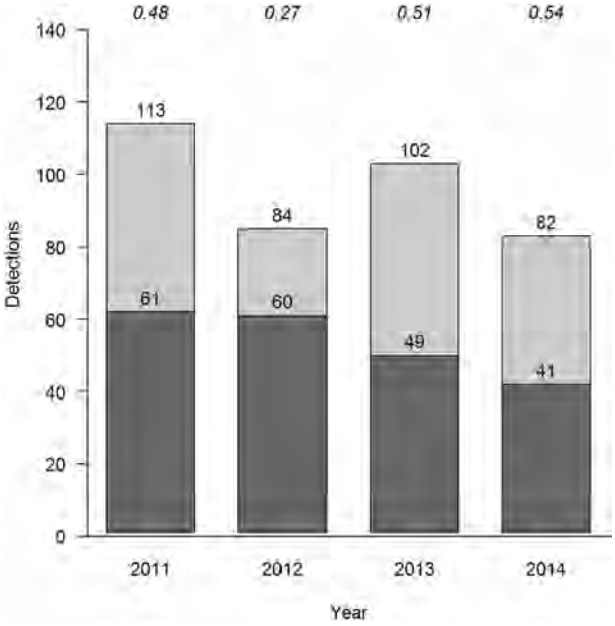

Fig. 2. Summary of DNA-based capture-mark-recapture data for female American black bears collected in southwestern Colorado, USA from 2011 to 2014. Annual number of unique bears identified are represented by dark gray columns and total number of annual detections are represented by light gray columns. Italicized values are annual proportions of unique females detected more than once.

function of distance between a hair snare and animal activity centers *and* as a function of 3rd-order resource selection. We used a standard RSF model based on a multinomial formulation of a spatial point process model for discretized space (i.e., raster data) and extended to account for resource availability as a function of distance from animal activity centers (Johnson et al., 2008; Forester et al., 2009; Royle et al., 2013). This formulation conditions on the total number of telemetry locations for each bear which is a fixed component of study design based on a known frequency for collecting locations. We assumed that missing GPS locations were randomly distributed and chose not to explicitly model them given our average fix success rate across collared female bears was high ($\bar{x} = 0.92$). Formally, our model of space use for an individual was defined as:

$$\pi(\boldsymbol{x} \mid \boldsymbol{s}) = \frac{exp(-\alpha_1 d(\boldsymbol{x},\boldsymbol{s})^2 + \boldsymbol{\alpha z}(\boldsymbol{x}))}{\sum_x exp(-\alpha_1 d(\boldsymbol{x},\boldsymbol{s})^2 + \boldsymbol{\alpha z}(\boldsymbol{x}))},$$

where $\pi(\boldsymbol{x}|\boldsymbol{s})$ is the probability of an animal using a raster pixel located at center coordinates $\boldsymbol{x}$ given that animal's activity center located at coordinates $\boldsymbol{s}$, $\alpha_1 = 1/(2\sigma^2)$ describes the rate of decrease in probability of use as a function of distance in terms of a scale parameter σ, $d(\boldsymbol{x},\boldsymbol{s})^2$ is the squared distance between a raster pixel and activity center, and $\boldsymbol{\alpha}$ is a vector of regression coefficients that describes the effects that covariate values $\mathbf{z}(\boldsymbol{x})$ have on the probability of use.

We fit all possible additive combinations of 14 candidate RSF covariates (i.e., percent agriculture, aspen, conifer, meadow, oak shrub, pinyon-juniper association, riparian, shrub, and subalpine, elevation, slope, terrain ruggedness, and distance to drainage; for more detailed descriptions of resource selection covariates see Supplementary material 'Spatial Covariate Descriptions') to year-specific GPS data sets. We included a quadratic term for elevation in any model that contained elevation as a main effect, as bears are known to select for intermediate elevations within the study area (Johnson et al., 2015). The final model set contained 16,383 covariate models and was balanced with respect to each covariate occurring in an equal number of models. We used a maximum likelihood approach in R (v3.2.1, R Core Team, 2015) based on code adapted from Royle et al. (2013) to fit RSF models and obtain estimates of model coefficients and variable importance. We ranked models using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2002) and calculated model weights to estimate variable importance. For each covariate, we summed AICc model weights for all models in which the covariate of interest occurred and retained only those covariates that had cumulative weights ≥0.5 for subsequent analyses (Barbieri and Berger, 2004).

3.3.2. *Integrated spatial capture-recapture analysis*

We used SCR models extended by Royle et al. (2013) to account for the effects that heterogeneous space use has on the detection process (i.e., allowing non-circular home ranges) by explicitly modeling 3rd-order resource selection. A common approach to modeling the spatial distribution of animals in SCR models is to use a homogeneous Poisson point process model that assumes constant population density across the landscape. However, we were interested in how the distribution of female black bears across the landscape was related to habitat covariates, particularly human development, and whether those relationships changed in response to the food shortage. Therefore, we used an inhomogeneous Poisson (IP) point process model to relate habitat characteristics to black bear density (2nd-order selection). Because our habitat covariates for density were derived in discretized space (i.e., raster format), we formulated our IP model using a multinomial distribution conditional on total population size (N) for the entire state space to describe pixel-specific abundance (N_m) as a function of covariates (Royle et al., 2013). Pixel-specific abundance was linearly related to habitat covariates through the use of a log-link function and estimated regression coefficients ($\boldsymbol{\beta}$). We modeled bear density as a function of human development (DEVELOPMENT), elevation (ELEVATION), forest cover (FOREST), and stream density (STREAMS), which are similar to covariates important to predicting black bear densities in other studies (Evans et al., 2017, Sun et al., 2017; for more detailed descriptions of density covariates see Supplementary material 'Spatial Covariate Descriptions'). We fit all possible additive combinations of the 4 candidate density covariates and a constant density model (CONSTANT) to each year of data. We included a quadratic term for ELEVATION in any model that contained that covariate as a main effect. The final model set contained 16 density models and was balanced with respect to each covariate occurring in an equal number of models.

The detection model governs the observation process that produces SCR data, and includes a spatial component that scales detection probabilities as a function of space use conditional on the location of an animal's activity center. Under this formulation, space use and, thus, detection probability is modeled as a function of distance between a hair snare and an animal activity center controlled by a spatial scale parameter (σ) and as a function of resource selection coefficients ($\boldsymbol{\alpha}$). Following Royle et al. (2013), we assumed our SCR data was a random subset of use locations (e.g., GPS) "thinned" by the sampling effectiveness of the hair snare. We calculated year-specific detection probabilities, but assumed that the detection probability did not vary across occasions within a year (e.g., time effects) or was influenced by a behavioral response to bait because we used liquid lures designed to stimulate interest yet offer no food reward that would increase the likelihood of a bear revisiting a specific site. We also did not consider modeling additional sources of individual heterogeneity in detection probability because individual-level covariates were not available for bears only detected by hair snares and relatively small sample sizes precluded the use of latent heterogeneity models (e.g., finite mixtures, logit-normal).

To integrate our GPS data into our SCR analysis, we combined the likelihoods for the SCR model and the RSF model into a single analysis. Formally, we specified our ISCR model as a joint likelihood for the 2 data sets (i.e., SCR and GPS) assuming complete independence between data sets (Royle et al., 2013). Because both likelihoods contain the same model parameters governing space use (i.e., σ, $\boldsymbol{\alpha}$), information on resource selection and home range scale is shared between the two data

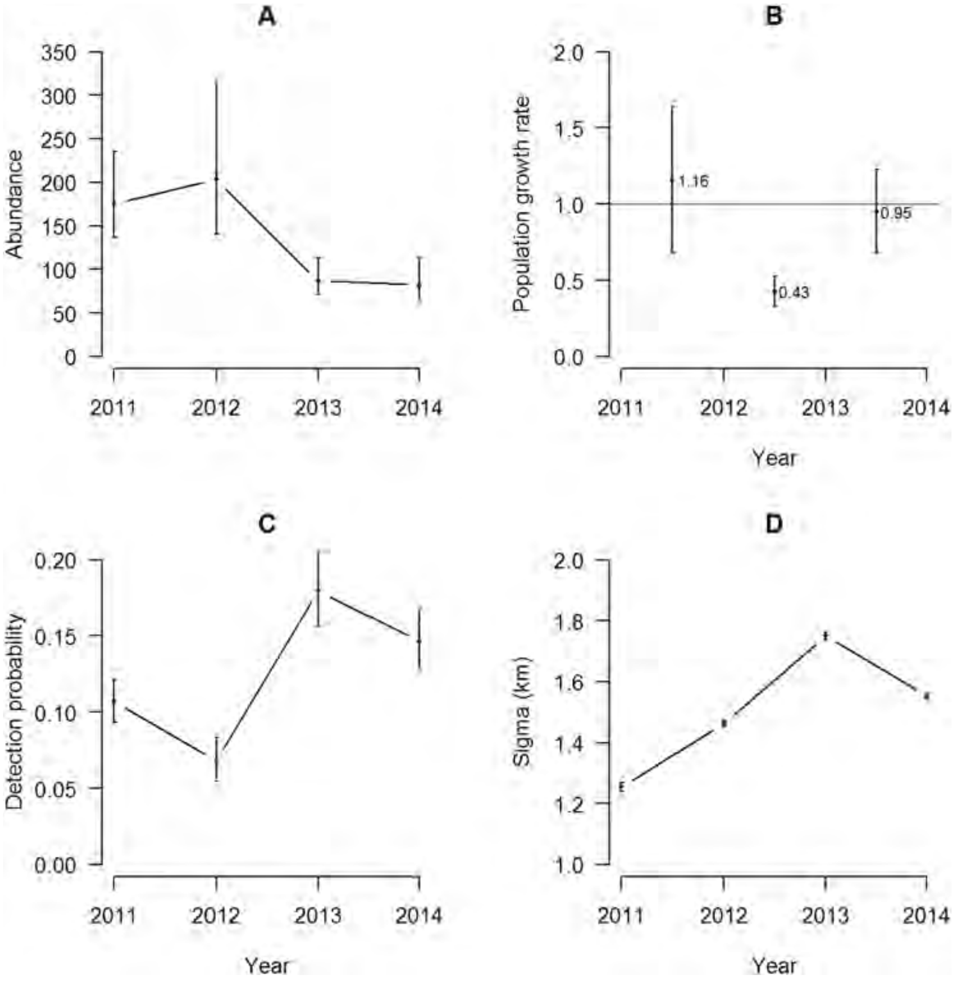

Fig. 3. Annual model-averaged parameter estimates from integrated spatial capture-recapture analyses using capture-recapture and GPS-telemetry data for female American black bears in southwestern Colorado from 2011 to 2014. Annual parameter estimates are abundance (panel A), realized population growth rate (panel B), population-level detection probability (panel C), and spatial scale of movement (panel D).

sets, allowing them to jointly estimate model parameters with improved precision. Understanding spatial patterns of resource selection, in turn, improved inferences about spatial heterogeneity in detection probabilities which then improved inferences for the point process governing estimates of abundance and spatial variation in density. Furthermore, integrating telemetry can greatly improve estimation of σ, a key detection model parameter in SCR models. As Royle et al. (2013) found, telemetry data is particularly useful for estimating σ when SCR data is sparse, which we anticipated was the case for our SCR data set.

We used a maximum likelihood approach in R based on code from Royle et al. (2013) to fit our ISCR models to each year of SCR-GPS data. We defined our state space by buffering our array of hair snares by 3 km which corresponded to a distance equivalent to $2 \times \sigma$; a distance that ensured the extent of our state space included the activity centers of all bears with access to the hair snare array (Fig. 1). The final state space had an area of 841 km^2 which we also used to define the extent of our habitat covariate rasters for modeling space use and density. We ranked models using AICc and calculated model weights for model averaging. By fitting our model set to each year of data independently, we were able to obtain year-specific model-averaged estimates of abundance and density. We derived realized population growth rates (λ) from our estimates of abundance and calculated associated sampling variances using the delta method (Powell, 2007). We derived year-specific model-averaged estimates of population-level detection probability (p) which we defined as the probability of a bear being detected at ≥ 1 hair snare in a given week. We used parametric bootstrapping to calculate sampling variances for p. Additionally, we obtained year-specific estimates of relative importance for habitat covariates in our density analysis and produced model-averaged expected-density surfaces that provided inference on how bear distribution changed within the study area over time.

4. Results

We collected 2556 hair samples between 2011 and 2014. A total of 873 were excluded due to insufficient material ($n = 840$) or being hair from other species ($n = 33$). Of the remaining 1683 samples, 423 failed to produce reliable genotypes and 2 were classified as samples containing hair from ≥ 1 bear. The final data set contained 1258 successfully genotyped samples corresponding to a genotyping success rate of 74.7%. We identified a total of 138 unique female bears across all years with year-specific counts of unique females ranging from 41 to 61 (Fig. 2). We considered all genotyped samples for an individual collected at a given trap during a given sampling occasion to represent a single detection event. Pooling samples in this fashion resulted in year-specific SCR data sets containing counts of weekly detection events (y_{ij}) indexed by individual (i) and trap (j). The total number of detections for all years was 381 with annual totals of detections ranging from 84 to 113 and annual proportion of females detected more than once ranging from 0.27 in 2012 to 0.54 in 2014 (Fig. 2). The annual average number of sampling occasions during which females were detected ranged from 1.4 (SD = 0.7) in 2012 to 2.0 (SD = 1.3) in 2013 (Supplementary

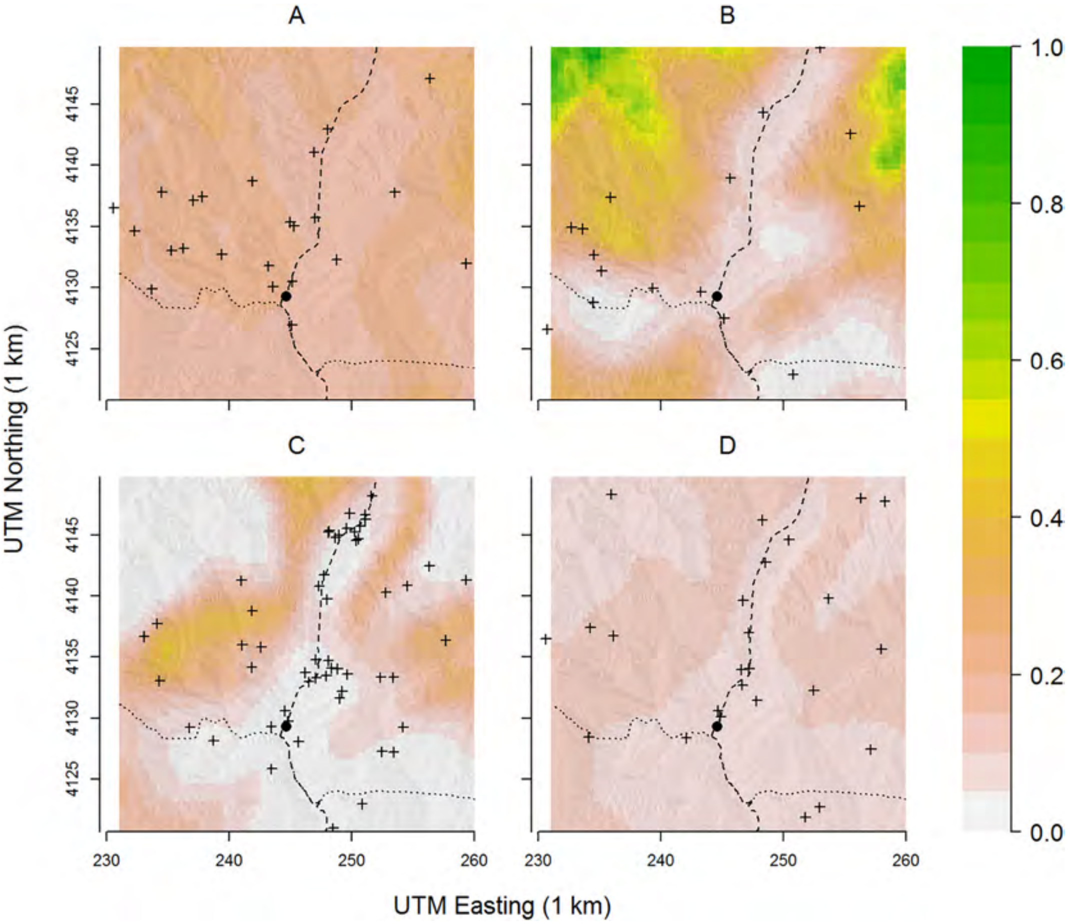

Fig. 4. Annual model-averaged predicted density (female bears/km^2) surfaces for integrated spatial capture-recapture analyses using DNA-based capture-recapture and GPS-telemetry data for female American black bears in southwestern Colorado from 2011 to 2014. Panels A–D correspond to years 2011–2014 and the city of Durango, Colorado is represented by the filled circle. Locations of reported mortalities that occurred during the 12 months prior to each year of hair sample collection (e.g., 9 June 2012 to 9 June 2013 for panel C) represented by + symbols. U.S. Route 550 and U.S. Route 160 represented by dashed and dotted lines, respectively.

material Table S1) and the annual average number of hair snares at which females were detected was 1.10 (SD = 0.3–0.4) in 2011, 2012, and 2014 and was 1.22 (SD = 0.55) in 2013 (Supplementary material Table S1).

We collected a total of 80,081 successful GPS locations from 45 unique female bears during annual hair-snare periods conducted from 2011 to 2014: 7451 locations in 2011 (10 bears), 23,476 in 2012 (27 bears), 22,423 in 2013 (23 bears), and 26,734 in 2014 (27 bears). The annual mean number of locations per female bear ranged from 745.1 (SD = 202.3) in 2011 to 990.1 (SD = 166.4) in 2014.

The number of RSF covariates identified as important (i.e., cumulative AICc weights > 0.50) in our first analysis stage and retained for the ISCR analysis varied across years from 13 to 15. Of the 15 possible covariates tested, distance-to-drainage was dropped in 2011, shrub and subalpine variables were dropped in 2012, and oak shrub and subalpine were dropped in 2013.

We estimated female abundance to be 175.6 (SE = 24.7) in 2011, 203.2 (SE = 43.0) in 2012, 86.7 (SE = 10.4) in 2013, and 82.4 (SE = 12.1) in 2014 (Fig. 3A, Supplementary material Table S2), exhibiting a marked population decline between 2012 and 2013 when the natural food shortage occurred. This corresponded to a rate of population change (λ) of 0.43 (SE = 0.05; Fig. 3B), which was significantly different (i.e., non-overlapping CIs) than λ estimates before and after the food shortage. Density estimates for the 841-km^2 state space followed the same temporal patterns as abundance and ranged from a high of 0.24 (SE = 0.05) female bears/km^2 in 2012 to a low of 0.10 (SE = 0.01) female bears/km^2 in 2014 (Supplementary material Table S2). Year-specific model-averaged estimates of detection probability (p) ranged from 0.07 (SE = 0.01) in 2012 to 0.18 (SE = 0.01) in 2013 (Fig. 3C, Supplementary material Table S2). Annual model-averaged estimates of the spatial scale of movement parameter (σ) ranged from 1.25 km (SE = 0.01) in 2011 to 1.75 km (SE = 0.01) in 2014 (Fig. 3D, Supplementary material Table S2).

Model selection uncertainty was high with no single model attaining an AICc weight > 0.50 in any year (Supplementary material Tables S3–S6). Constant density models were most supported in 2011 and 2014, whereas more complex models with multiple covariates were most supported in 2012 and 2013 suggesting greater heterogeneity in the spatial distribution of female bears in those years (Fig. 4). Using a cumulative weight threshold of 0.5 to classify a covariate as an important predictor of density, DEVELOPMENT and STREAMS were important in 2012 (Fig. 5) when bear density was lower in areas of denser human development and higher in areas with greater stream densities (Fig. 4), and DEVELOPMENT and ELEVATION were important in 2013 (Fig. 5) when density was also lower in developed areas and higher in mid-elevation areas (Fig. 4). In general, during all years, bear density was lower in developed areas than undeveloped areas; however, this pattern was particularly notable in 2013 when developed areas were nearly devoid of female bears (Fig. 5).

Between 2007 and 2014, we obtained 206 bear mortality records opportunistically collected within our study area. Annual total counts ranged from 11 in 2009 to 54 in 2012, the latter being a 3-fold increase over the 5-year average prior to the food shortage in 2012 ($\bar{x}$ = 20.0 [SD = 7.2]; Fig. 6). In 2012, mortalities caused by vehicle collisions

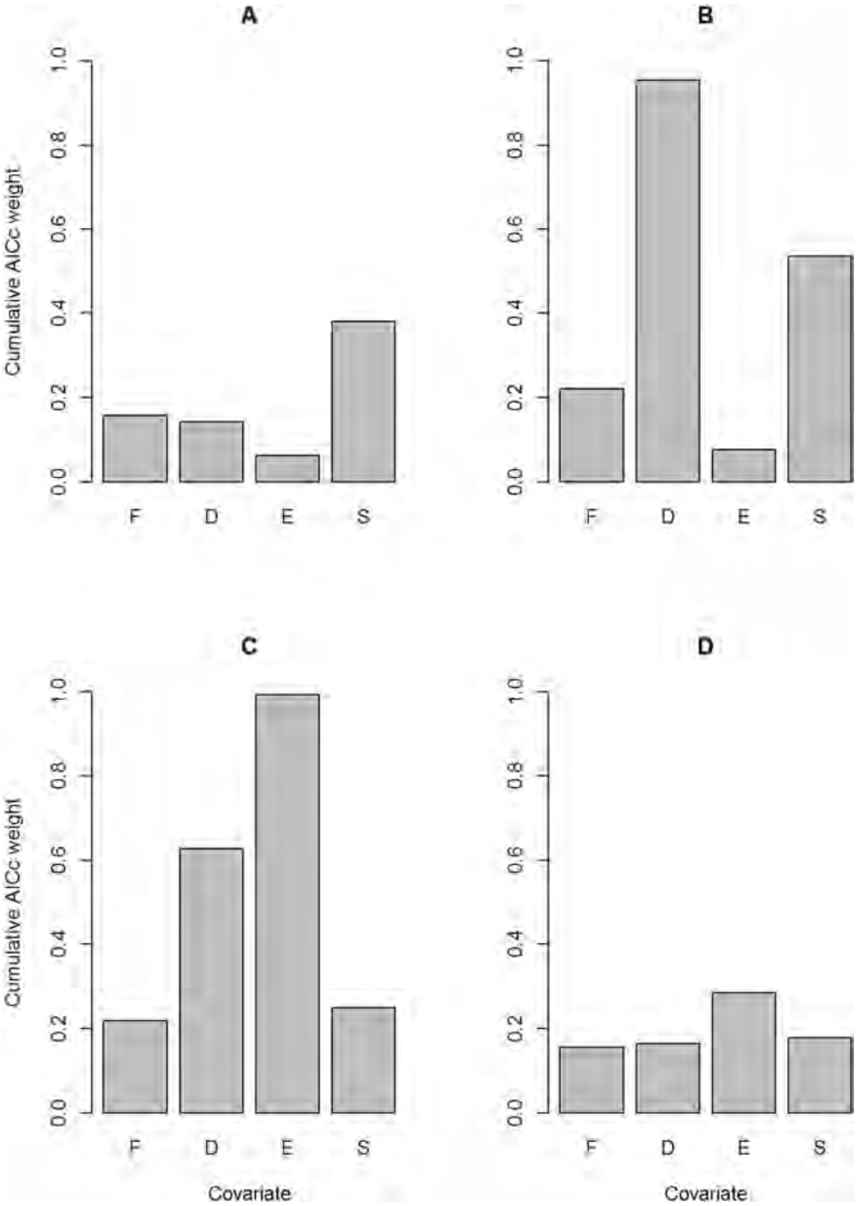

Fig. 5. Importance measures of covariates based on cumulative AICc model weights for integrated spatial capture-recapture analyses using capture-recapture and GPS-telemetry data for female American black bears in southwestern Colorado from 2011 to 2014. Panels A–D correspond to years 2011–2014 and letters F, D, E, and S correspond to FOREST, DEVELOPMENT, ELEVATION, and STREAMS covariates.

increased over 4-fold from the 5-year average of 3.4 (SD = 3.4) to 16 and 2 other human-caused sources, hunter harvest and lethal conflict removals, approximately doubled (Fig. 6).

Indices of natural foods available to bears were highly variable among years within species with species-specific CV values ranging from 0.8 to 1.4 (Fig. 7). Of the 5 mast species included in the natural food index surveys, 4 completely failed (i.e., index value = 0) to produce mast in 2012 (Fig. 7). Although no species completely failed in 2013 after the primary food shortage, productivity for 4 species remained below the mean value observed during the study indicating a possible residual climatic effect on bear foods from the previous year (Fig. 7).

5. Discussion

Our results provide evidence that human development can compound the effects of a climate-induced food shortage to significantly reduce a black bear population. Previous studies have found that food shortages are often associated with reduced recruitment in black bears (Rogers, 1987a; Elowe and Dodge, 1989; Obbard and Howe, 2008), but to our knowledge, this is the first time that such a shortage has been associated with a major decline in a contiguous black bear population; notably the most severe decline that has been documented over a 1-year period. Hellgren et al. (2005) documented a similar decline, but their study focused on a small bear population ($N = 23$) existing in marginal habitat. In the absence of human development, natural food shortages have been found to have limited effects on bear populations. Under such conditions, recruitment is suppressed, which has little relative influence on bear population growth, whereas adult survival is unaffected (Beck, 1991; Kasbohm et al., 1996; Clark et al., 2005), the vital rate most important in driving bear population dynamics (Freedman et al., 2003; Beston, 2011). However, bears living near human development become much more susceptible to human-caused mortality (Hostetler et al., 2009; Baruch-Mordo et al., 2014; Obbard et al., 2014) as they shift their behaviors to forage on anthropogenic foods during natural food shortages. Indeed, the ultimate cause of the increase in

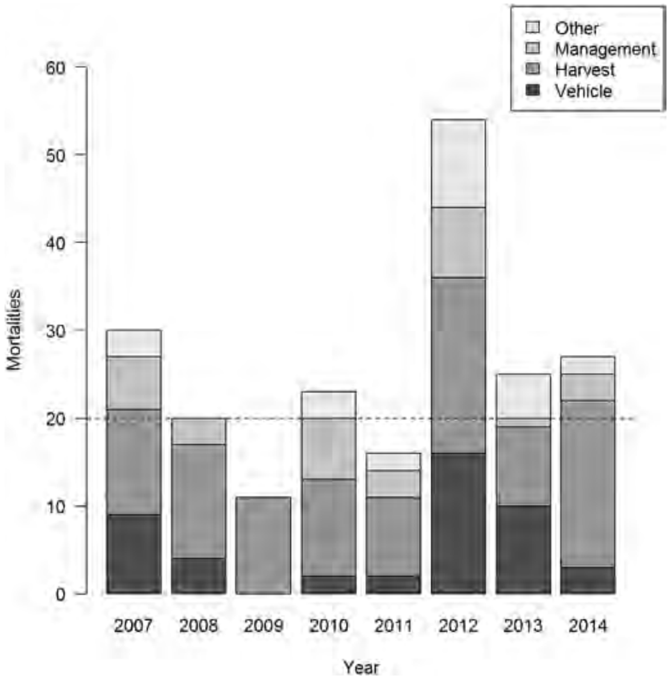

Fig. 6. Annual reported counts of 3 primary sources of human-caused mortality and all other sources combined (e.g., electrocution, natural, unknown) for male and female American black bears within the 841-km^2 study area in southwestern Colorado from 2007 to 2014. Horizontal dashed line represents the 5-year average of total counts preceding a natural food shortage in 2012.

mortalities and population decline was the food shortage of 2012, which intensified proximate factors (e.g., human-bear interactions) that led to a much greater level of human-caused mortality within our study area compared with the previous 5 years. In particular, mortalities caused by vehicle collisions considerably increased. A similar pattern was recently observed in the vicinity of Aspen, Colorado, where subadult and adult survival declined (≥26%) during poor natural forage years, largely as a consequence of bear-use of development and human-induced mortality (Baruch-Mordo et al., 2014).

The food shortage during the summer–fall period of 2012 primarily was the result of a late-spring frost event that severely reduced berry and nut production (Peterson, 2013; Rice et al., 2014). Late-spring frosts are known to cause mast crop failures (Neilson and Wullstein, 1980; Sharp and Sprague, 1967) and have been implicated in summer and fall food shortages in other bear populations (Beck, 1991; Obbard and Howe, 2008; Honda, 2013) indicating this phenomenon is not unique to our study system. Climate models predict, however, that these kinds of extreme weather events will likely become more common in the future (Karl et al., 2009), which may be problematic for bears; particularly as human development continues to expand across western landscapes. Lewis et al. (2014) used stochastic population simulation to evaluate the effects of increasing frequency of poor natural food years and various management-related removal scenarios on black bear populations. They found that a bear population could be sustained in scenarios with greater frequency of food failures if management removals were minimal, but would decline rapidly under scenarios where removals were high. However, the simulated demographic rates used by Lewis et al. (2014) to reflect poor food years corresponded to an asymptotic population growth rate of 0.77, a value far above the growth rate we estimated immediately following the food shortage in our study system ($\lambda = 0.43$). Although future food shortages may not be as severe as that which we observed in southwestern Colorado, we suggest that the effects of rare catastrophic events (e.g., population decline by ≥50%) be incorporated into long-term population assessments. This is especially important in the management of bears and other k-selected large carnivores, which are demographically constrained in their ability to recover from population declines induced by episodes of high human-caused mortality.

Given our modeling approach, we could not explicitly separate individual contributions of in situ mortality and emigration to the observed population decline, but suspect that the decline was primarily caused by increased mortality. Emigration for female bears is rare, as they exhibit high natal site fidelity (Beeman and Pelton, 1976; Rogers, 1987b; Jones et al., 2015), a pattern supported by our telemetry data, as only 2 of 22 GPS-collared females emigrated from the study area in response to the food shortage of 2012. Alternatively, bears may temporarily shift or expand their home ranges or undertake long-range movements in response to food shortages (Pelton, 1989; Kasbohm et al., 1998; Hellgren et al., 2005; Baruch-Mordo et al., 2014). Such changes in space-use patterns may increase use of developed areas by bears, thereby increasing exposure to human-related sources of mortality (Noyce and Garshelis, 1997; Ryan et al., 2004; Ryan et al., 2007; Obbard et al., 2014). The high concentration of mortalities we observed in developed areas in 2012 indicates such a shift in space use likely occurred in response to the food shortage. Taken collectively, the relatively low number of collared females that emigrated, the increased level of human-caused mortalities reported during the food shortage (Fig. 6), and the concentration of those mortalities in developed areas (Fig. 4) further supports our conclusion that the population decline was primarily driven by human-caused mortality rather than emigration.

We also could not disentangle in situ reproduction and immigration processes with our SCR data set. However, we believe the effects of the food shortage on reproduction can be deduced from our estimates of population growth rate between 2013 and 2014 by making a similar assumption about immigration as for emigration in that high natal site fidelity of female bears also limits immigration. Reproductive failures commonly occur in bear populations immediately following mass food shortages due to poor body condition of parous females (Eiler et al., 1989; Bridges et al., 2011). Because black bear cubs (< 1 year old) typically were too small to be detected by our hair sampling methods (Laufenberg et al., 2016), evidence of contributions from in situ recruitment processes would lag (Clark et al., 2005) and not be detected until the following year. Based on the expectation of a 1-year lag in observing a recruitment failure in our data, the net effect would be a population growth rate slightly below 1.0 for the second year following a food shortage (assuming adult survival returned to pre-food shortage levels). Our growth rate estimate from 2013 to 2014 was 0.95 (SE = 0.14) which supports the conclusion that in situ reproduction was also affected by the food shortage.

In addition to detecting a major overall population decline following the food shortage, we detected temporal changes in spatial distribution of female bears across the study area. In particular, we found that fewer female bears occurred in or near developed areas relative to undeveloped areas after the food shortage compared with density patterns prior to the food shortage (Fig. 4). We surmise that the observed changes were primarily driven by the spatial distribution and intensity of human-caused mortalities associated with roads and urban areas in those years (Fig. 4). Our inference was supported by greater estimated importance of the DEVELOPMENT covariate, a variable with a strong negative relationship with density, in 2013 following the failure. We also found that densities of female bears declined in areas of marginal habitat (e.g., high-elevation alpine) far from human development, which we presume was due to some bears leaving those areas to access food in or near areas of human development. Despite some benefits for bears of anthropogenic foods in developed environments (e.g., increased reproduction, larger body size, reduced home range; Beckmann and Berger, 2003, Beckmann and Lackey, 2008) the costs of elevated human-caused mortality can result in human development-wildland interfaces that operate as ecological traps (Nielsen et al., 2004; Beckmann and Lackey, 2008; Hostetler et al., 2009; Baruch-Mordo et al., 2014). Given the sharp decline in bear abundance estimated for

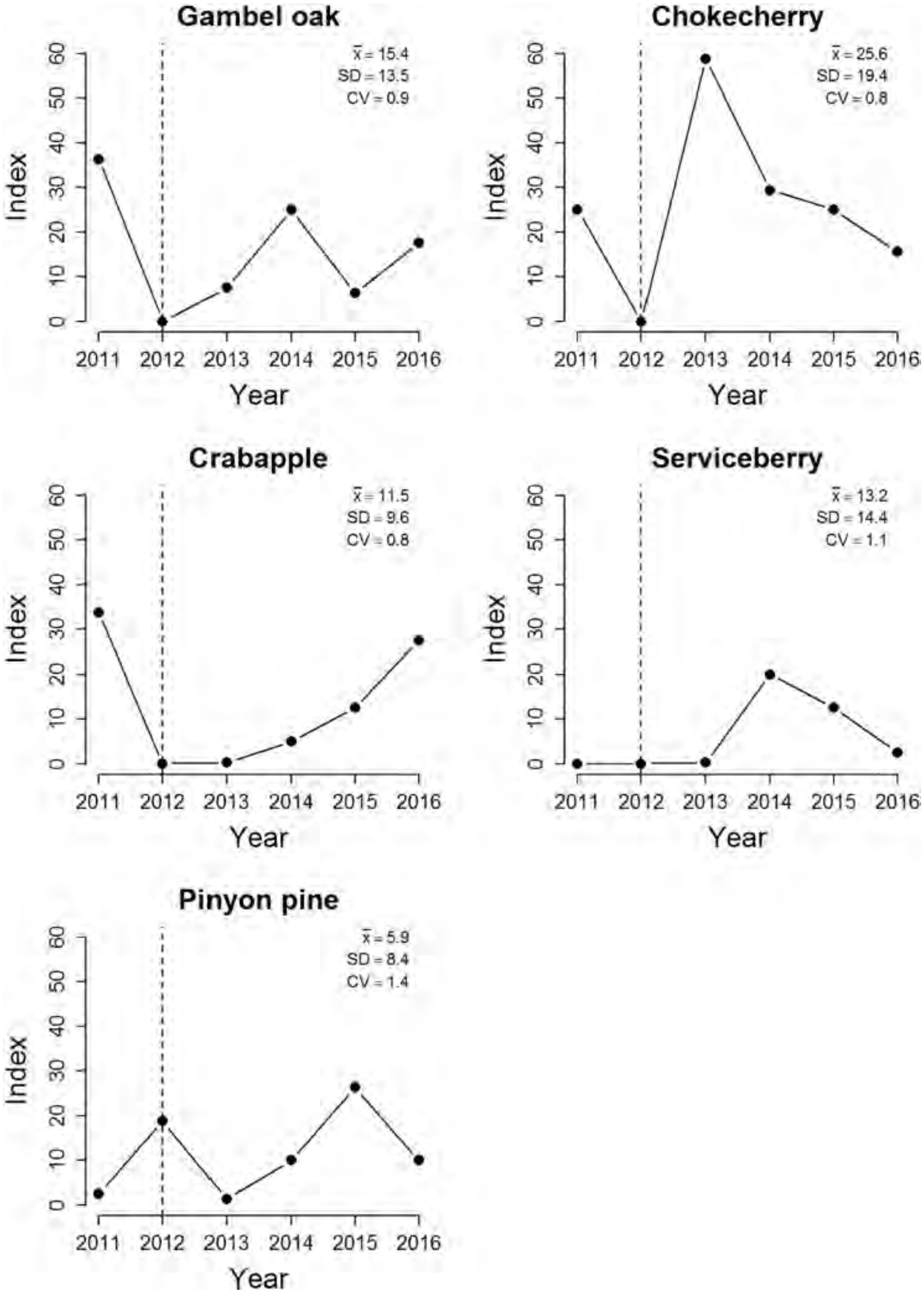

Fig. 7. Median abundance indices of 5 plants that provide hard and soft mast foods for American black bears in southwestern Colorado, USA from 2011 to 2016. The vertical dashed line indicates 2012, when there was a shortage of naturally occurring foods for black bears.

areas surrounding Durango, the overall increase in human-caused mortality following the food shortage, and the high density of those mortalities that occurred in and around development, our data would certainly support the notion that human development can serve as a population sink (Knight et al., 1988; Mattson et al., 1992; Ryan et al., 2007). This particularly is the case in poor natural food years when bears move greater distances in search for food, are attracted to town for access to anthropogenic foods, and suffer high mortality rates as a consequence (Baruch-Mordo et al., 2014). Furthermore, warmer temperatures and use of anthropogenic foods by bears have been linked to increased length of the active season which may result in even greater increases in human-caused mortality associated with developed areas thereby further exacerbating the compounding effects of predicted changes in human development and climate (Johnson et al., 2017).

Given expected increases in human development across the western U.S. (Leu et al., 2008), black bear population dynamics are likely to be increasingly influenced by non-harvest human-caused sources of mortality (e.g., vehicle collisions, lethal removals). Indeed, the annual number of non-harvest mortalities have been steadily increasing in Colorado over the past couple decades (Colorado Parks and Wildlife, 2015) as the state has seen corresponding increases in residential development, particularly in exurban and rural areas. If the frequency and severity of climate-related extreme weather events across the U.S. increases as predicted (Karl et al., 2009), the compounding effects of increasing human development and climate-induced natural food shortages may become an important determinant of long-term viability for a greater number of bear populations (Lewis et al., 2014). This shift has important implications for management agencies that typically rely on harvest data to manage bear populations with limited information about bear population size or trend (Garshelis and Hristienko, 2006). The severe population decline detected in our study would have gone unnoticed from harvest data that are commonly collected and used to manage bears in Colorado, and was only detected due to monitoring efforts associated with an intense research project. Our results indicate management agencies may need to invest more resources into monitoring bear population trends, while accounting for non-harvest morality rates in population models. For example, the novel integrated spatial capture-recapture approach we used could be optimized in terms of relative sampling effort for the both data types (i.e., capture-recapture and telemetry) to develop a cost-effective long-term monitoring solution.

Our results raise important questions about how management agencies can mitigate the compounding impacts of human development and natural food failures on bear populations in the future. In our system, vehicle collisions were a primary source of mortality, but effective mitigation strategies for this mortality source are unclear. In the southeastern United States, researchers have recommended the construction of highway underpasses (McCown et al., 2008; van Manen et al., 2012) but those systems differ in that bears are more continuously exposed to areas of high human density. In our system, bears are primarily drawn to development during periods of poor natural food availability. Therefore, a better strategy may be to reduce anthropogenic attractants and, thus, reduce the incentives for bears to forage within development (Baruch-Mordo et al., 2013; Johnson et al., 2018). As non-harvest human-caused mortality increases, management agencies may also need to reduce harvest and other lethal management actions to increase survival and ensure the long-term sustainability of bear populations.

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Appendix A. Supplementary materials

Supplementary materials to this article can be found online at https://doi.org/10.1016/j.biocon.2018.05.004.

References

Altwegg, R., Roulin, A., Kestenholz, M., Jenni, L., 2006. Demographic effects of extreme winter weather in the barn owl. Oecologia 149, 44–51.

Barbieri, M.M., Berger, J.O., 2004. Optimal predictive model selection. Ann. Stat. 32, 870–897.

Baruch-Mordo, S., Webb, C.T., Breck, S.W., Wilson, K.R., 2013. Use of patch selection models as a decision support tool to evaluate mitigation strategies of human-wildlife conflict. Biol. Conserv. 160, 263–271.

Baruch-Mordo, S., Wilson, K.R., Lewis, D.L., Broderick, J., Mao, J.S., Breck, S.W., 2014. Stochasticity in natural forage production affects use of urban areas by black bears: implications to management of human-bear conflicts. PLoS One 9, e85122.

Beck, T.D.I., 1991. Black Bears of West-Central Colorado. Technical Publication No. 39 Fort Collins. Colorado Division of Wildlife, Colorado, USA.

Beckmann, J.P., Berger, J., 2003. Using black bears to test ideal-free distribution models experimentally. Journal of Mammology 84, 594–606.

Beckmann, J.P., Lackey, C.W., 2008. Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. Human-Wildlife Conflicts 2, 168–174.

Beeman, L.E., Pelton, M.R., 1976. Homing of black bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 3, 87–95.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377.

Beston, J.A., 2011. Variation in life history and demography of the American black bear. J. Wildl. Manag. 75, 1588–1596.

Boersma, P.D., Rebstock, G.A., 2014. Climate change increases reproductive failure in Magellanic penguins. PLoS One 9, e85602.

Bridges, A.S., Vaughan, M.R., Fox, J.A., 2011. Reproductive ecology of American black bears in the Alleghany Mountains of Virginia, USA. J. Wildl. Manag. 75, 1137–1144.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 23, 453–460.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, New York, USA.

Chen, I.C., Hill, J.K., Ohlemuller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026.

Clark, J.D., van Manen, F.T., Pelton, M.R., 2005. Bait stations, hard mast, and black bear population growth in Great Smoky Mountains National Park. J. Wildl. Manag. 69, 1633–1640.

Colorado Parks and Wildlife, 2015. Human-Bear Conflicts. Report to the legislature, Denver Colorado, USA.

Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. Royal Proceedings of the Royal Society B. http://dx.doi.org/10.1098/rspb.2015.2592.

Cushman, S.A., Lewis, J.S., 2010. Movement behavior explains genetic differentiation in American black bears. Landsc. Ecol. 25, 1613–1625.

Drewry, M.J., van Manen, F.T., Ruth, D.M., 2013. Density and genetic structure of black bears in coastal South Carolina. J. Wildl. Manag. 77, 153–164.

Eiler, J.H., Wathen, W.G., Pelton, M.R., 1989. Reproduction in black bears in the southern Appalachian Mountains. J. Wildl. Manag. 53, 353–360.

Elowe, K.D., Dodge, W.E., 1989. Factors affecting black bear reproductive success and cub survival. J. Wildl. Manag. 53, 962–968.

Evans, M.J., Rittenhouse, T.A.G., Hawley, J.E., Rego, P.W., 2017. Black bear recolonization patterns in a human-dominated landscape vary based on housing: new insights from spatially explicit density models. Landsc. Urban Plan. 162, 13–24.

Forester, J.D., Im, H.K., Rathouz, P.J., 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90, 3554–3565.

Freedman, A.H., Portier, K.M., Sunquist, M.E., 2003. Life history analysis for black bears (*Ursus americanus*) in a changing demographic landscape. Ecol. Model. 167, 47–64.

Garshelis, D.L., Hristienko, H., 2006. State and provincial estimates of American black bear numbers versus assessments of population trend. Ursus 17, 1–7.

Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H., Jones, K., 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecol. Appl. 15, 1893–1905.

Hellgren, E.C., Onorato, D.P., Skiles, J.R., 2005. Dynamics of a black bear population within a desert metapopulation. Biol. Conserv. 122, 131–140.

Honda, T., 2013. Late spring frosts induce human-Asiatic black bear conflicts. Mammal Study 38, 287–292.

Hostetler, J.A., McCown, J.W., Garrison, E.P., Neils, A.M., Barrett, M.A., Sunquist, M.E., Simek, S.L., Oli, M.K., 2009. Demographic consequences of anthropogenic influences: Florida black bears in north-central Florida. Biol. Conserv. 142, 2456–2463.

Hurst, J.E., Porter, W.F., 2008. Evaluation of shifts in white-tailed deer winter yards in the Adirondack region of New York. J. Wildl. Manag. 72, 367–375.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Johnson, H.E., Breck, S.W., Baruch-Mordo, S., LOewis, D.L., Lackey, C.W., Wilson, K.R., Broderick, J., Mao, J.S., Beckmann, J.P., 2015. Shifting perceptions of risk and reward: dynamic selection for human development by black bears in the western United States. Biol. Conserv. 187, 164–172.

Johnson, H.E., Lewis, D.L., Lischka, S.A., Breck, S.W., 2018. Bear-resistant containers reduce human-black bear conflicts and improve public perceptions. J. Wildl. Manag. http://dx.doi.org/10.1002/jwmg.21472.

Johnson, H.E., Lewis, D.L., Verzuh, T.L., Wallace, C.F., Much, R.M., Willmarth, L.K., Breck, S.W., 2017. Human development and climate affect hibernation in a large carnivore with implication for human-carnivore conflicts. J. Appl. Ecol. 55, 663–672.

Johnson, D.S., Thomas, D.L., Ver Hoef, J.M., Christ, A., 2008. A general framework for the analysis of animal resource selection from telemetry data. Biometrics 64, 968–976.

Jones, M.D., Tri, A.N., Edwards, J.W., Spiker, H., 2015. Home-range dynamics of female *Ursus americanus* (Pallas) (American black bear) in a recovering population in western Maryland. Northeast. Nat. 22, 830–841.

Jonkel, J.J., 1993. A Manual for Handling Bears for Managers and Researchers. Office of Grizzly Bear Recovery, US Fish and Wildlife Service. University of Montana, Missoula, Montana, USA.

Karl, T.R., Melillo, J.M., Peterson, T.C., 2009. Global Climate Change Impacts in the United States. Cambridge University Press, New York, New York, USA.

Kasbohm, J.W., Vaughan, M.R., Kraus, J.G., 1996. Effects of gypsy moth infestation on black bear reproduction and survival. J. Wildl. Manag. 60, 408–416.

Kasbohm, J.W., Vaughan, M.R., Kraus, J.G., 1998. Black bear home range dynamics and movement patterns during a gypsy moth infestation. Ursus 10, 259–267.

Knight, R.R., Blanchard, B.M., Eberhardt, L.L., 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. Wildl. Soc. Bull. 16, 121–125.

Koenig, W.D., Liebhold, A.M., 2016. Temporally increasing spatial synchrony of North American temperature and bird populations. Nat. Clim. Chang. 6, 614–617.

Laufenberg, J.L., Clark, J.D., Hooker, M.J., Lowe, C.L., O'Connell-Goode, K.C., Troxler, J.C., Davidson, M.M., Chamberlain, M.J., Chandler, R.B., 2016. Demographic rates and population viability of black bears in Louisiana. Wildl. Monogr. 194, 1–37.

Leu, M., Hanser, S.E., Knick, S.T., 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. Ecol. Appl. 18, 1119–1139.

Lewis, D.L., Breck, S.W., Wilson, K.R., Webb, C.T., 2014. Modeling black bear population dynamics in a human-dominated stochastic environment. Ecol. Model. 294, 51–58.

van Manen, F.T., McCollister, M.F., Nicholson, J.M., Thompson, L.M., Kindall, J.L., Jones, M.D., 2012. Short-term impacts of a 4-lane highway on American black bears in eastern North Carolina. Wildl. Monogr. 181, 1–15.

Mantyka-Pringle, C.S., Martin, T.G., Rhodes, J.R., 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Glob. Chang. Biol. 18, 1239–1252.

Mattson, D.J., Blanchard, B.M., Knight, R.R., 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. J. Wildl. Manag. 56, 432–442.

McCleery, R.A., Moorman, C.E., Peterson, M.N. (Eds.), 2014. Urban Wildlife Conservation: Theory and Practice. Springer, New York, New York, USA.

McCown, J.W., Kubilis, P., Eason, T.H., Scheick, B.K., 2008. The effect of traffic volume on American black bears in central Florida, USA. Ursus 20, 39–46.

Monteith, K.L., Bleich, V.C., Stephenson, T.R., Pierce, B.M., Conner, M.M., Klaver, R.W., Bowyer, R.T., 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere. http://dx.doi.org/10.1890/ES10-00096.1.

Neilson, R.P., Wullstein, L.H., 1980. Catkin freezing and acorn production in Gambel oak in Utah, 1978. Am. J. Bot. 67, 426–428.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennet, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echevaerria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Marin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50.

Nielsen, S.E., Herrero, S., Boyce, M.S., Mace, R.D., Benn, B., Gibeau, M., Jevons, S., 2004. Modeling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biol. Conserv. 120, 101–113.

Noyce, K.V., Garshelis, D.L., 1997. Influence of natural food abundance on black bear harvests in Minnesota. J. Wildl. Manag. 61, 1067–1074.

Obbard, M.E., Howe, E.J., 2008. Demography of black bears in hunted and unhunted areas of the boreal forest of Ontario. J. Wildl. Manag. 72, 869–880.

Obbard, M.E., Howe, E.J., Wall, L.L., Allison, B., Black, R., Davis, P., Dix-Gibson, L., Gatt, M., Hall, M.N., 2014. Relationships among food availability, harvest, and human-bear conflict at landscape scales in Ontario, Canada. Ursus 25, 98–110.

Paetkau, D., 2003. An empirical exploration of data quality in DNA-based population inventories. Mol. Ecol. 12, 1375–1387.

Pelton, M.R., 1989. The Impacts of Oak Mast on Black Bears in the Southern Appalachians. In: McGee, C.E. (Ed.), Proceedings of the Workshop: Southern Appalachian Mast Management. University of Tennessee, Knoxville, Tennessee, USA, pp. 7–11.

Peterson, B., 2013. Why Are some Bear Seasons Easier? Durango Herald. (13 August 2013).

Post, E., Forchhammer, M.C., 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philos. Trans. R. Soc. B 363, 2369–2375.

Powell, L.A., 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor 109, 949–954.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reynolds-Hogland, M.J., Pacifici, L.B., Mitchell, M.S., 2007. Linking resources with demography to understand resource limitation for bears. J. Appl. Ecol. 44, 1166–1175.

Rice, W., Parmenter, D., Felsen, G., 2014. Fruit-gleaning Program Connects Trees, Harvesters. Durango Herald (3 September 2014).

Riitters, K., Wickham, J., Wade, T., 2009. Evaluating anthropogenic risk of grassland and forest habitat degradation using land-cover data. Lanscape Online 13, 1–14.

Rodenhouse, N.L., Christenson, L.M., Parry, D., Green, L.E., 2009. Climate change effects on native fauna of northeastern forests. Canadian Journal of Forest Resources 39, 249–263.

Rogers, L.L., 1987a. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl. Monogr. 97, 1–72.

Rogers, L.L., 1987b. Factors Influencing Dispersal in Black Bear. In: Chepko-Sade, B.D., Haplin, Z.T. (Eds.), Mammalian Dispersal Patterns, the Effects of Social Structure on Population Genetics. University of Chicago, Chicago, Illinois, USA, pp. 75–84.

Roon, D.A., Waits, L.P., Kendall, K.C., 2005. A simulation test of the effectiveness of several methods for error-checking non-invasive genetic data. Anim. Conserv. 8, 203–215.

Royle, J.A., Chandler, R.B., Sun, C.C., Fuller, A.K., 2013. Integrating resource selection information with spatial capture–recapture. Methods Ecol. Evol. 4, 520–530.

Ryan, C.W., Pack, J.C., Igo, W.K., Billings, A., 2007. Influence of mast production on black bear non-hunting mortalities in West Virginia. Ursus 18, 46–53.

Ryan, C.W., Pack, J.C., Igo, W.K., Rieffenberger, J.C., Billings, A.B., 2004. Relationship of mast production to big-game harvests in West Virginia. Wildl. Soc. Bull. 32, 786–794.

Sawyer, H.R., Nielson, M., Lindzey, F., McDonald, L.L., 2006. Winter habitat selection of mule deer before and during development of a natural gas field. J. Wildl. Manag. 70, 396–403.

Sharp, W.M., Sprague, V.G., 1967. Flowering and fruiting in the white oaks: pistillate flowering, acorn development, weather, and yields. Ecology 48, 243–251.

Skagen, S., Adams, A.A.Y., 2012. Weather effects on avian breeding performance and implications of climate change. Ecol. Appl. 22, 1131–1145.

Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., Boutin, S., 2008. Determining sustainable levels of cumulative effects for boreal caribou. J. Wildl. Manag. 72, 900–905.

Stirling, I., Derocher, A.E., 2012. Effects of climate warming on polar bears: a review of the evidence. Glob. Chang. Biol. 18, 2694–2706.

Stocker, T.F., Qin, D., Plattner, G.-K., Alexander, L.V., Allen, S.K., Bindoff, N.L., Bréon, F.-M., Church, J.A., Cubasch, U., Emori, S., Forster, P., Friedlingstein, P., Gillett, N., Gregory, J.M., Hartmann, D.L., Jansen, E., Kirtman, B., Knutti, R., Krishna Kumar, K., Lemke, P., Marotzke, J., Masson-Delmotte, V., Meehl, G.A., Mokhov, I.I., Piao, S., Ramaswamy, V., Randall, D., Rhein, M., Rojas, M., Sabine, C., Shindell, D., Talley, L.D., Vaughan, D.G., Xie, S.-P., 2013. Technical Summary. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 33–115.

Sun, C.C., Fuller, A.K., Hare, M.P., Hurst, J.E., 2017. Evaluating population expansion of black bears using spatial capture-recapture. J. Wildl. Manag. http://dx.doi.org/10.1002/jwmg.21248.

Theobald, D.M., 2010. Estimating natural landscape changes from 1992 to 2030 in the conterminous US. Landsc. Ecol. 25, 999–1011.

Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14, 18–30.

Vázquez, D.P., Gianoli, E., Morris, W.F., Bozinovic, F., 2015. Ecological and evolutionary impacts of changing climatic variability. Biol. Rev. http://dx.doi.org/10.1111/brv.12216.

Vogel, W.O., 1989. Response of deer to density and distribution of housing in Montana. Wildl. Soc. Bull. 17, 406–413.

Wong, B.B.M., Candolin, U., 2015. Behavioral responses to changing environments. Behav. Ecol. 26, 665–673.

Woods, J.G., Paetkau, D., Lewis, D., McLellan, B.N., Proctor, M., Strobeck, C., 1999. Genetic tagging of free-ranging black and brown bears. Wildl. Soc. Bull. 27, 616–627.

Zack, C.S., Milne, B.T., Dunn, W.C., 2003. Southern oscillation index as an indicator of encounters between humans and black bears in New Mexico. Wildl. Soc. Bull. 31, 517–520.

POPULATION MANAGEMENT OF BEARS IN NORTH AMERICA[1]

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Abstract: Population management for black bears (*Ursus americanus*), brown-grizzly bears (*U. arctos*) and polar bears (*U. maritimus*) in North America is reviewed. In different areas bear populations are managed to achieve goals of population control, conservation, or sustained yield. Most North American bears are managed for sustained yields and this topic is emphasized. The consequence of error in population management is high as bears reproduce slowly and reduced populations will require many years to recover. Simulation results where reproductive rates were generous, natural mortality rates were low, and harvests were 75% of maximum sustainable rates indicated that populations reduced by half will require >40 years to recover for brown (grizzly) bears and >17 years for black bears. Under optimal conditions for reproduction, natural mortality, and with males twice as vulnerable as females, maximal sustainable hunting mortality was estimated as 5.7% of total population for grizzly bears and 14.2% for black bears. In recent decades, all 3 species have obtained the status of game animals in most jurisdictions and management for control objectives is increasingly uncommon. Management for conservation requires primary emphasis on habitat protection and on minimizing mortalities from any source. Managers of hunted bear populations use information from hunters, from sex and age composition of killed bears, from research programs, and from computer simulation studies. Non-critical uses of data from any of these sources may lead to management error. Data on age-at-harvest is especially prone to misinterpretation. Techniques used to limit harvests by managers of hunted bear populations are reviewed. The primary constraints facing bear population management derive from inadequate habitat protection, political pressures, technological limitations of available population management techniques, and inadequate financial support for management.

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Population management efforts designed to enhance or stabilize bear numbers are recent in the United States and Canada. In the last century and early portion of the present century, black and grizzly bears were widely regarded as impediments to desired development and human safety. Bounties for killing bears were offered in many jurisdictions. This attitude, combined with habitat destruction, led to the elimination of grizzly bears throughout most of the United States except Alaska and the reduction of black bears especially in the southern and southeastern United States (Cowan 1972, Jonkel 1987). By the mid-19th century, polar bear populations were also greatly reduced by market hunting for their hides (Anon. 1965, Stirling 1986).

Attitudes towards bears began to change in the 20th century. Instead of being classified as "predators" or "vermin" that could be killed indiscriminately, bears were classified as fur animals subject to regulated commercial harvests. By the 1920's, bears were elevated to the status of "game" animals in most areas (Table 1). Typically, limitations on sale of hides, meat or other bear products came along with game animal status as well as significant limitations on hunting opportunities (seasons, bag limits, techniques, etc.). In some areas further limitations resulted when bear populations were greatly depleted. At this point populations were classified as "threatened", the status of the grizzly in the lower 48 states, or "endangered", such as the black bears in Texas since 1987 (Wallace 1987). There is nothing inevitable about a downward trend in bear numbers to a threatened or endangered status. For black bears, at least, populations currently are stable in much of the United States and Canada. Also, in some regions, with formerly depleted populations of all 3 species, bears have recovered to a secure status.

The techniques used in modern bear management are the subject of this paper. These techniques are applied to 3 general goals for population management listed by Caughley (1977:168): *control* (treatment of a population that is too dense to stabilize or reduce its density), *conservation* (treatment of a small or declining population in such a way as to raise its density), and *sustained yield* (exploitation to take from a population a long-term sustained yield of surplus animals without causing a population decline). Although all 3 of these goals are discussed, primary emphasis in this paper is on sustained yield management.

This paper was prepared in response to an invitation from F. Bunnell to prepare a plenary paper for this conference. Numerous persons very kindly responded to my request for management plans and other information that described how bears are managed in their jurisdictions including: S. Amstrup (AK), R. Archibald (BC), J. Beecham (ID), L. Berchielli (NY), J. Brown (MT), J. Collins (NC), A. Dood (MT), K. Elowe (MA), D. Garshelis (MN), J. Gunson (AB), R. Johnson (WA), D. Koch (CA), G. Kolenosky (ON), O. Oedekoven (WY), A. LeCount (AZ), D. Martin (VA), R. Masters (OK), C. McLaughlin (MA), E. Orff (NH), J. Pederson (UT), A. Polenz (OR), J. Rieffenberger (WV), S. Schliebe (AK), L. Schaaf (KY), C. Servheen (MT), B. Smith (YK), J. Stuht (MI), D. Taylor (AK), M. Taylor (NWT), C. Winkler (TX), and J. Wooding (FL). K. Schneider, C. Schwartz, S. Stringham, and 3 anonymous referees offered many valuable suggestions on an earlier draft of this manu-

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[1] Invited paper.

Table 1. Year in which bears were declared to be game animals in different portions of North America. Dates refer to black bears except where indicated by "G" for grizzly bear or "P" for polar bear.

Location	Year classified as game animal	Source
Alaska	1902(G)[a]	57th Cong. Sess. I Chap. 1037
New York	1903	Clark (1978)
Pennsylvania	1905[a]	Alt and Lindsey (1980)
British Columbia	1909[a]	Anon. 1980
Montana	1923	Dood et al. (1986)
Montana	1923(G)	Dood et al. (1986)
Oregon	1925, 1970[b]	Anon. (1987*a*)
Texas	1925	Winkler (1975)
Michigan	1925	Harger (1980)
Quebec	1926[c]	Caron (1980)
Yukon Territory	1928[a]	MacHutchon and Smith (1988)
Alberta	1929(G)	Nagy and Gunson (1988)
Arkansas	1927[d]	Conley (1977)
Arizona	1927[a]	LeCount (1977)
South Carolina	1927	Stokes (1977)
Arizona	1929(G)	Brown (1985:154)
Wisconsin	1930	Kohn (1982)
Maine	1931[e]	McLaughlin (1986)
Washington	1933, 1969[f]	Poelker and Hartwell (1973)
Alaska	1939	Code Fed. Reg. Title 50(91.1)
Vermont	1941	Wiley (1978)
Colorado	1941	Beck (1979)
Manitoba	1942	Shoesmith (1977)
Idaho	1943	Beecham (1986)
California	1948[g]	Anon. (1987*b*)
Alaska	1948(P)[a]	Anon. (1965:51)
Northwest Territories	1949(P)	Urquhart and Schweinsburg (1984)
Maryland	1949	Taylor (1984)
Yukon	1950(P)[h]	Stirling and Calvert (1985)
Oklahoma	1951	Vohs (1977)
Massachusetts	1953[a]	Cardoza (1978)
Newfoundland	1961	Russell and Forsey (1978)
Ontario	1961[i]	Clarke (1961)
New Brunswick	1961	Cartwright (1978)
Newfoundland	1962	Mahoney (1984)
Saskatchewan	1963	R. Seguin (Sask. Parks, Recreation and Culture, Meadow Lake, pers. commun.)
Nova Scotia	1966	Patton (1978)
Utah	1967	Burruss (1979)
West Virginia	1969	Rieffenberger and Allen (1978)
Quebec	1969(P)[h]	Stirling and Calvert (1985)
Ontario	1970(P)[h]	Stirling and Calvert (1985)
Manitoba	1970(P)[h]	Stirling and Calvert (1985)
Newfoundland	1971(P)	Stirling and Calvert (1985)
Minnesota	1971	Hugie et al. (1978)
New Hampshire	1983[j]	Orff (1987)

[a] Date of first bag limit or season restriction.

[b] First declared game in 1928, replaced, then redeclared in 1970.

[c] Vallee (1977) gives 1970 as date game status was assigned in Quebec.

[d] Date of total season closure.

[e] Hermes and Hugie (1977) note black bears were bountied until 1957 and game status was being recommended in 1977.

[f] Date of first season, game animal status repealed in 1951 in some areas, reinstituted in 1969.

[g] Burton (1977) gives 1957 as date game status was assigned in California.

[h] Date of legal basis for current management.

[i] Polar bears in Ontario have been treated, for management purposes, as a furbearer since 1971 (G. Kolenosky, Ont. Ministry of Nat. Resour., Maple, pers. commun.).

[j] $20 bounty removed from bears in 1955, first season in 1961.

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CONSEQUENCE OF ERROR

For all 3 management objectives the consequence of error in managing bear populations is high. Bear populations that are inadvertently reduced to lower levels than desired will require many years to recover. This is because all 3 species of North American bears have long lifespans (>20 years), low reproductive rates (an average of 2 cubs produced by adult females every 2-6 years), delayed reproductive maturity (first breeding at 3-7 years), high survivorship of adults, variable survivorship of young, which is frequently dependent on environmental conditions (Rogers 1983), and typically little fluctuation in number of adults from year to year (Jonkel 1987, Kolenosky and Strathern 1987, Kolenosky 1987).

The period required for recovery of reduced populations of black and grizzly bears was simulated using a simple deterministic model (Miller and Miller 1988) in a scenario involving overharvests by hunters. In these simulations, maximally productive populations of black and grizzly bears that were stabilized by hunting were suddenly overharvested by doubling the exploitation rate. When the population declined to half its original size, hunting was restricted and the time required for the population to recover to its initial size was noted. When no hunting occurred during the recovery period, the black bear population recovered in 6 years compared to 10 years for grizzly bears (Table 2). When hunting during the recovery period occurred at 75% of the maximum sustainable hunting rate, it took almost 3 times longer for black bears to recover and 4 times longer for grizzly bears (Table 2). These results are minimal values as the reproductive and natural mortality rates used were set at the most optimistic values that have been reported (Miller 1989).

Table 2. Simulation results for estimating period required to recover from overhunting that caused a 50% reduction in maximally productive grizzly bear and black bear populations. During recovery period population was subject to hunting rates of 0, 50, and 75% of the initial rates at which populations were stable.

	Grizzly bear	Black bear
Years required to recover from reduction when hunting is held at following fractions of initial hunting rate:		
(No hunting)	10	6
50%	19	9
75%	40	17

MANAGEMENT FOR CONTROL OF BEAR NUMBERS

Until the current century, reduction of bear numbers was the most common objective for bear population management. In some parts of North America, bears are still sufficiently abundant or troublesome to humans that management efforts involve reducing bear densities (e.g., Poelker and Hartwell 1973, Jorgensen et al. 1978, Ambrose and Sanders 1978, Poelker and Parsons 1980, Will 1980, Miller 1990*a*, Gasaway in press). Such areas have become increasingly rare and geographically restricted in recent decades. They will likely become even rarer.

However, where human and bear populations coexist, managers will have to deal with some problems. These problems can result in bear mortalities that are large enough to be significant from a population management standpoint. For Yellowstone grizzlies, control killings of only a few additional females may mean the difference between continued population decline and recovery (Knight and Eberhardt 1984, 1985). In such cases, human populations, not bear populations, must make the needed accommodations for coexistence.

Many states and provinces compile data on the number of human-bear conflicts reported. It is sometimes implied that an increase in the number of nuisance bear complaints reflects an increase in bear numbers. More often, however, increased complaints reflect a change in human use of bear habitat. Increased human-bear conflicts more commonly correspond to a decline in bear populations, not an increase.

Research in Alaska and other northern regions has demonstrated that predation from bears and wolves (*Canis lupus*) can inhibit recovery of depleted moose (*Alces alces*) and caribou (*Rangifer tarandus*) populations (Ballard et al. 1980, Franzmann et al. 1980, Gasaway et al. 1983, Ballard and Larsen 1987, Ballard and Miller 1987, Boertje et al. 1988). These findings have resulted in pressure from sportsmen and subsistence hunters to reduce numbers of predators to permit faster growth and higher harvests of prey populations. In response to such pressures, grizzly bear seasons have been liberalized and harvests have increased in many portions of interior Alaska (Miller 1989). These changes represent a geographically widespread shift from conservative grizzly bear management strategies to more aggressive ones in which the likelihood of management error in these areas is increased. In at least 2 areas, increased harvests have resulted in declines in grizzly bear populations (Reynolds and Hechtel 1988, Miller 1990*a*). Elsewhere, results are inconclusive (Gasaway 1988) or no field studies designed to evaluate trends in bear numbers are ongoing.

Responsible management of bear populations under circumstances such as these is especially challenging because the techniques available to document changes in bear populations are imprecise. This makes it difficult to establish realistic criteria by which to judge when bear population reduction goals have been met. Also, there sometimes is inadequate recognition that management prescriptions for predator reduction programs that involve bears (e.g., Gasaway in press) need to be different than for predators like wolves that have much higher reproductive rates.

MANAGEMENT FOR CONSERVATION

Conservation is the general objective for grizzly bear management efforts in the lower 48 states, for black bear management in southern and southeastern states, and for management of all species in national parks. In some large Alaskan parks where grizzly bears are abundant, population management is less important than people management and habitat protection. Most national parks in the U.S. and Canada are not so fortunate and require active bear management to assure perpetuation of bear populations (Knight and Eberhardt 1987, Knight et al. 1988, Horejsi 1989).

Even in parks and other protected areas, baseline data on population density and composition may be critically important in evaluating impacts of environmental accidents or changing patterns of human use of areas occupied by bears. The absence of a systematically obtained baseline estimate of bear density in Katmai National Park made it difficult to evaluate whether the bear population had declined as a result of the 1989 oil spill from the *Exxon Valdez*. Similarly, in Glacier National Park, the lack of a systematically collected historical record of bear numbers made it difficult to isolate human use patterns, which may have caused a reduction in bear numbers (Hayward 1989, Keating 1989).

In parts of North America small bear populations survive only in small pockets of habitat isolated from each other. This fragmentation exposes these populations to higher probabilities of extinction because of chance events and environmental variation. Managers of these populations must determine how large these populations and reserves should be to insure persistence in the face of natural catastrophes, and random environmental, demographic, and genetic events (Schaffer and Sampson 1985). For Yellowstone grizzlies the minimum viable population that gave a 95% probability of surviving for 100 years was estimated at 50-90 bears (Schaffer and Sampson 1985). Using the same general approach but with different data on mortality rates, the estimated minimum viable population was estimated at 125 bears (Suchy et al. 1985).

The Interagency Grizzly Bear Committee formed in 1983 is an example of the kind of coordination that is essential if remnant populations of grizzly bears are to survive in the lower 48 states (Salwasser et al. 1987). This committee includes representatives of 5 U.S. agencies that manage portions of grizzly habitat plus 6 state or provincial wildlife agencies, and 2 Indian tribes. Working together, these agencies have developed a coordinated set of objectives and strategies to direct conservation efforts. The International Agreement on the Conservation of Polar Bears and their Habitat is another example of the kind of cooperation needed to perpetuate healthy bear populations (Stirling 1986, 1988*a*).

Techniques for estimating population size and trend, discussed below, are especially needed in management of reduced populations for conservation objectives. Unfortunately, some of the techniques that provide the most accurate population estimates may frequently be inappropriate for very small remnant populations of bears because these techniques are usually imprecise when applied to small populations. In addition, subjecting such populations to the additional stress and mortality associated with marking studies may be unwise. In managing greatly reduced remnant populations of bears, managers may find it more productive to concentrate on habitat protection issues rather than on efforts to document bear numbers or mortality rates with marking studies that may produce only uncertain results.

SUSTAINED YIELD

Sustained yield management of bear populations is the management goal in most areas of North America inhabited by bears. Most commonly the yields are taken by hunters. Perhaps because sustained yield management is not usually conducted in a crisis atmosphere where bear populations are threatened or where bears are seen as damaging to humans' economic interests, sustained yield management has not received as much attention as it deserves. More concern is merited because correct management of populations that have sustained yield goals may prevent crisis situations from developing. Also, population management techniques are especially important in managing for sustained yields. For these reasons this topic is given primary emphasis in this review.

The principle behind sustained yield management is that populations produce a surplus of animals that can be removed or harvested without causing population declines. Under sustained yield management, harvesting takes the place of mortalities that would occur from old age and other causes. In very dense populations, reproductive rates of bears are suppressed by density-dependent mechanisms that act to prevent the population from overshooting carrying capacity. Because population growth is suppressed by these mechanisms, populations at carrying capacity can support little harvest. If such dense populations are harvested and bear density declines, reproductive rates should increase and natural mortality rates should decline,which produces a surplus that can be taken annually without causing declines in bear numbers. Maximum sustainable yield (MSY) is the point where population size and productivity balance to produce the maximum size of harvest without causing a population decline. At populations lower than MSY, productivity and sustainable harvest rates remain high but fewer total bears can be harvested without causing a population decline.

For bear managers the MSY population size is more useful theoretically than practically since the "optimum" population size will be unknown. This is because reproductive and mortality rates can vary from year to year in a density independent fashion based on fluctuations in food supply (Jonkel and Cowan 1971; Rogers 1976, 1983, 1987). Managers striving for sustained yields from exploited bear populations try to maintain populations that have good average reproductive rates and small average natural mortality rates in the expectation that such populations will be producing harvestable surpluses at high levels.

The challenge facing managers managing bear populations for sustained high harvests is to identify correctly what harvest levels are sustainable and when sustainable levels are exceeded. To assist in making these determinations the population manager may have information available from hunters, from the animals that are harvested, from field investigations, and from simulation studies.

Information Provided by Hunters

Hunters can provide valuable information to managers of exploited bear populations. Information from hunters is most useful as a flag that alerts managers to potential problems or helps to form hypotheses about population status. These hypotheses can then be evaluated using other lines of evidence.

Number Killed.—Perhaps the single most basic and useful piece of information that can be provided by hunters is the number of bears killed. Increasing numbers of bears killed should alert managers that populations could be declining. Of course, population trend is not necessarily correlated with number killed; increasing harvests could occur without population decline as long as sustainable harvest levels were not exceeded.

Probably the best way to use data on harvest number requires calculation of sustainable harvest rate. With information on reproductive and mortality rates derived from research, this rate can be estimated using simulation models, discussed below. The calculated sustainable rate can be compared with actual harvest rate obtained by dividing number killed by estimated population size. This approach resulted in a recommendation against an increase in polar bear hunting quotas in the Northwest Territories (Stirling et al. 1985).

In a few instances, efforts have been made to use kill numbers to derive population size by assuming the kill represents some percentage of the total population, usually the calculated sustainable harvest rate, and back-calculating from this rate to derive a total population estimate. This is a reasonable procedure only if managers have independent evidence that the population is stable.

Unreported sport or nuisance kills and wounding losses can represent significant sources of mortality that managers should consider. In rural northwestern Alaska, less than half the grizzly bear sport and subsistence harvest is reported as required (W. Ballard, Alas. Dep. of Fish and Game, Nome, pers. commun.). On the heavily hunted Kenai Peninsula in Alaska, where reporting is thought to be fairly complete, wounding loss of black bears was estimated to be 13-16% of reported kill based on mortalities of radio-marked bears (Schwartz and Franzmann in prep.). "Control kills" of nuisance black bears accounted for 36% of known human-caused mortalities and unreported control kills were estimated to equal or exceed reported ones in the Yukon (MacHutchon and Smith 1988). Poaching accounted for 9% of deaths of marked black bears in Maine (Hughie 1982). A third of the known grizzly bear mortality was illegal harvest in Alberta (Peek et al. 1987). The mortality rate of marked grizzlies in Montana was estimated at 0.47, all from illegal, unreported kills (Knick and Kasworm 1989). In 6 studies of marked grizzly bears, 26% of mortalities were caused by illegal harvests compared to 42% by legal hunting (McLellan 1990). Managers need to incorporate estimates of all significant mortality sources into their bear management efforts.

Hunter Effort.—Number of bears killed is best interpreted along with information on level of hunting effort. Increases in number of bears killed under conditions where effort is constant may lead managers to suspect an increasing bear population. The same increase in harvest number where effort is also increasing may suggest an increased exploitation rate and a declining bear population. This indicator was used in Alberta, where managers noted that harvests of grizzly bears increased 100% during a period when effort increased 350% (Nagy and Gunson 1988). In a heavily hunted area in south-central Alaska where grizzly bear density was reduced by about half as a consequence of liberalized hunting regulations, successful hunters reported spending more time before shooting a bear than before the density was reduced (Miller 1990*a*). Typically, hunter effort data are highly variable and statistical tests seldom reveal significant differences. This does not, however, invalidate the cautious use of such effort data to assist managers in forming hypotheses about population trends.

Hunter Success.—Hunter success rates are influenced by improved access or hunter technology, motivation, and number of bears. This means that effort indices should be used with caution. Variability in effort unrelated to population status is apparent in Alaska where non-resident grizzly bear hunters are required to hunt with guides and pay high fees. Resident hunters have no such restriction and need only buy a $25 tag. These differences in cost of hunt affects motivation and is reflected in success rates. The statewide success rate for non-residents is much higher (52% in 1987) than for residents (8.4%) (Alaska Dep. of Fish and Game [ADF&G] unpublished file data). However, in the Game Management Unit that includes Kodiak Island, where highly prized brown bear hunting permits are allocated by lottery, both types of hunters had higher success rates: 19% for residents and 74% for non-residents (ADF&G unpublished file data for 1986). In contrast, average harvest success rate for grizzly bear hunters in Alberta was 3% for residents and 12% for non-residents during 1971-1987 (Nagy and Gunson 1988). Even where hunting is limited by permits, hunter success can be low; Arkansas black bear permittees had 0.4-2.2% success in different years (Pharris and Clark 1987). This variability underscores the need to look for trends in success rates within groups that are as homogeneous as possible with respect to residency, transportation type, motive, and area hunted.

Kill density.—The geographic location of hunter kills is also important. Harvest number with geographic location permits managers to estimate kill per unit area or kill density. Excluding effects of immigration, sustainable kill density can either be calculated (like sustainable harvest numbers) or estimated based on areas where both population trend and kill density are known. Kill density divided by population density was used to approximate grizzly bear harvest rate in a heavily hunted portion of Alaska (Miller 1988, 1990*a*). Kill density estimates were used to illustrate that dangers of overkill of a grizzly bear population was higher in the Canadian portion of the Northern Continental Divide Ecosystem where a legal hunting season was in place than on the U.S. side (Horejsi 1989). Kill density also can be used to establish quantifiable management objectives in management plans.

Integrated Approaches.—In Minnesota, black bear population managers use a hunter survey to collect data on hunting success and bears killed per hunter-day. Data are adjusted to correct for annual variation in food abundance and are used to select the most conservative growth curve that fits this trend from a series of model-generated curves of population growth. Managers then use the selected curve and some subjective criteria to develop estimates of population size and to set harvest quotas (D. Garshelis, Minn. Dep. of Nat. Resour., Grand Rapids, pers. commun.). This approach appears to be a worthwhile effort toward integrating information obtained from hunters with that from other sources into a standardized management framework useful in making objective management decisions.

Information Provided by Harvest Composition

Detection of bear population trend from the sex and/or age structure of harvested bears is more often attempted than achieved (Caughley 1974; Wiley 1980; Gilbert et al. 1978; Bunnell and Tait 1980, 1981; Miller and Miller 1988). Procedures that are appropriate for more productive ungulate populations (e.g., Fraser 1976, Fryxell et al. 1988) are difficult to apply to bears because they are a long-lived and low density species that can sustain only low harvest rates (Harris and Metzgar 1987*a*). Low harvest rates provide a small sample of harvested animals from which to make inferences about the population and a delay in the time required for harvest to perturb the population's sex and age structure. Sex ratio of harvest is more sensitive as an indicator of population status than age structure (Harris 1984), perhaps because all the harvest is distributed between only 2 sexes compared to 20 or more age classes. It is popular to try to use data on age composition of harvest because hunters can be required to submit teeth from their kills. These can be sectioned and age estimated by counting cementum annuli (Stoneberg and Jonkel 1966). The age of harvest results in tables of supposedly "hard" data, the utility of which is more frequently assumed than demonstrated.

Differences in the sex and age composition of bear populations subjected to different levels of hunting have been documented (Jonkel and Cowan 1971; Beecham 1980; Kolenosky 1986; Reynolds and Hechtel 1988;

Miller 1988, 1990*a*). As yet, these differences have not been clearly related to differences in the age composition of bears harvested from these populations. Increases in number of black bear females harvested has been correlated with increased harvest rate in Ontario (Kolenosky 1986).

The sample of bears shot by hunters will seldom directly reflect the population composition. Hunters are selective and bears have differential vulnerability based on sex, age, or reproductive status (Bunnell and Tait 1980). A further problem is that most interpretations of harvest composition data assume a stable age distribution, which is usually inappropriate. Relaxation of stable age distribution assumptions may be possible if independent information on rate of change in population is available (Eberhardt 1985, 1988).

Commonly, age data on sex or age composition of bear harvests are used to infer that populations are stable because mean (or median) age or sex ratio of harvested animals is constant. Similarly, some managers look for decreasing mean (or median) age of harvest (especially of males) or increasing proportions of females in the kill as indicators of overharvest. Such interpretations can lead managers into unwarranted complacency about population status. When birth and death rates are constant, the sex and age composition of the population will stabilize regardless of population trend. This has been recognized since the 1907 paper by Lotka (Caughley 1977) but remains a source of confusion. When birth and death rates are not constant or vulnerability by sex or age class is changing, harvest composition may change in response. This change, however, is not necessarily related to a change in population status.

Managers should be cautious in setting planning objectives based on age or sex ratio in harvest statistics. Benchmarks such as "no fewer than 60% males in the total harvest" may be inadequate to prevent overexploitation. The sex ratio of harvest at sustainable harvest levels is not a constant. Instead, this value is a function of a number of factors including the relative vulnerability of each sex to human-caused mortality, sex and age-specific natural mortality rates, proportion of total mortality that is represented by harvest, and sex ratio at age of first vulnerability to hunters. Failure to meet an objective of at least 60% males could, for example, be "remedied" by adding an early spring season when males have high vulnerability (O'Pezio et al. 1983, Miller 1990*b*, Van Daele et al. 1990) rather than by decreasing kill of females. It is preferable to set exploitation guidelines in terms of the total adult female harvest as has been done for polar bears (Taylor et al. 1987*b*).

A promising approach to interpretation of sex and age composition of black bear harvest data was suggested by Fraser et al. (1982). This approach exploits the higher harvest vulnerability of males compared to females (Bunnell and Tait 1980), which results in a progressive decline in the proportion of males in older age classes. At some age, the higher vulnerability of males will be offset by the larger number of surviving females and the harvest at that age and older will favor females. In lightly exploited populations the age at which females predominate in the harvest will be older than in heavily exploited populations. A regression of percent males in harvest on age class will have a steeper negative slope in heavily hunted populations (Fraser et al. 1982).

Simulation studies have indicated that for bears this model is sensitive to a number of likely violations of underlying assumptions (Harris and Metzgar 1987*a*). Even if it lacks robustness, however, this approach may be useful as a tool to examine conflicting interpretations of available data. In a portion of south-central Alaska, the Fraser et al. (1982) approach was successfully used to document that current grizzly bear exploitation rate was higher than formerly (Miller 1988). Even though harvest rate could not be directly estimated because of violations of the model's assumptions, this analysis was useful in discrediting the hypothesis that the bear population was unaffected by increased harvests. Also, the most likely bias in the use of the Fraser et al. (1982) approach in Alaska would have resulted in an underestimation of harvest rate. This was because vulnerability of females declined in the adult age classes when females were periodically protected by being accompanied by offspring (it is illegal to shoot grizzly bears accompanied by cubs or yearling offspring). Because the estimated harvest rate was an overestimate but was still higher than the calculated sustainable rate, it was useful in demonstrating a clear need for reduced harvests.

A more complex approach for interpreting sex and age composition of harvest data was developed by Tait (1983). Using sex and age composition of harvest data, Tait's approach uses non-linear optimization procedures to develop maximum likelihood estimates for historic population size, hunting rate, recruitment rate, and other parameters. Unfortunately, Tait's model has yet to be adequately tested with real harvest data or evaluated to see how robust it is when underlying assumptions are violated. Alaska is currently making an effort to conduct such tests.

The limitations of sex and age composition of harvest data should not discourage managers from collecting these data and continuing to investigate meaningful ways of using them. Compared to field studies as a way of evaluating population status, harvest data are much less expensive to collect. In using these data, managers must be aware of the limitations, however, as common misinterpretations could lead managers into misclassifying declining populations as stable. With existing technology, it is clear that the limitations on use of composition of bear harvest data are such that hunting remnant populations of bears cannot be justified on the basis that such data would be helpful in evaluating population status.

Information Obtained from Research

Research is an important component of sustained yield management for bears. Research is necessary because bear population management has few generally accepted techniques that can be widely applied to evaluate population size or trend (Harris 1986). Research is not needed for each exploited population. Frequently, adequate results can be obtained by cautious extrapolation from research done elsewhere. However, it should be recognized that responsible sustained yield management of a bear population will be expensive and may require field studies to estimate population size, population density, movements, or critical reproductive and mortality rates.

Population Size and Trend.—Research programs most commonly address estimation of population size. Frequently, population size is estimated using some variation of capture-mark-recapture procedures such as the Seber-Jolly technique (DeMaster et al. 1980, Beecham 1983, Amstrup et al. 1986, Kolenosky 1986). This technique requires an estimate of survival rate in addition to the other standard assumptions of capture-recapture procedures (Seber 1982). Where survival estimates are not available, black bear population estimates have been obtained using more traditional Lincoln Index procedures (Jonkel and Cowan 1971, LeCount 1982, Young and Ruff 1982, Miller and Ballard 1982, Beecham 1983, Aune and Brannon 1987). Frequently it is difficult to convert population estimates obtained using such techniques to density estimates because of uncertainty about size of the area occupied by the estimated population.

In Alaska, intensive capture-recapture techniques using radio-telemetry to correct for lack of population closure have been used to derive black and grizzly bear density estimates in small (<2,000 km^2) areas (Miller et al. 1987). With this approach the area occupied by the estimated population does not have to be estimated. In 1 area this technique was used to document statistically significant declines in bear numbers caused by hunting (Miller 1990*a*). Elsewhere, these estimates serve as baselines for documenting potential changes in density caused by hunting, development, or habitat deterioration (Schoen and Beier 1989, Miller and Sellers 1989, Ballard et al. 1990). Such density estimates were made for 9 grizzly bear and 3 black bear populations in Alaska in a variety of habitats and over a range of bear densities from 6.7-380 bears/1,000 km^2 (Miller et al. 1987, Barnes et al. 1988, Schoen and Beier 1989, Miller and Sellers 1989, Miller 1990*a*, Ballard et al. 1990, Schwartz and Franzmann in prep.). Not all of the problems associated with using these techniques have been resolved. The best methods for dealing with capture bias, small sample sizes, and extrapolation of results to larger areas need additional study. A correction factor for small sample bias in such estimates was developed by Eberhardt (in press).

Other approaches to estimating bear density are based on movements of radio-marked bears (Rogers 1977, Hughie 1982, Reynolds et al. 1987, Schwartz and Franzmann in prep.). Typically, these techniques involve plotting home ranges of individual bears over a study area and calculating the proportions of each home range overlapping the study area. These proportions are summed to derive a population estimate and divided by the size of the study area to obtain a density estimate. Such estimates are usually identified as minimum values because of the possibility that not all bears in the study area were radio-marked. These estimates usually do not include a variance estimate and may contain subjective elements that make them difficult to replicate by different observers. However, they may provide more accurate density estimates than capture-recapture procedures used when the size of the area occupied by the estimated population is uncertain (Hughie 1982).

In the small but politically significant populations of grizzly bears in Glacier and Yellowstone National Parks, grizzly bear population size and trend were estimated from direct observations of bears (Martinka 1971, 1974; Craighead et al. 1974; Knight and Eberhardt 1984, 1985; Keating 1986; McDonald et al. 1988; Hayward 1989). In a Montana study area, number of grizzlies was estimated by adding marked bears known present with unmarked bears seen (Aune and Brannon 1987). Systematic application of direct observation techniques may be preferable for deriving such estimates for critically small populations of grizzly bears such as in the Yellowstone area (Harris 1986). However, these approaches are too labor-intensive to be useful to managers of exploited bear populations. They also lack variance estimates, which makes it difficult to evaluate the significance of reported changes in population numbers.

Another promising approach towards estimating bear density without marking animals was described by Dean (1987). This method employs intensive aerial surveys and a sightability correction factor to estimate number of animals missed during aerial searches.

Research aimed at developing indicators of population trend have not yet produced consistently reliable procedures. Different techniques have been used to detect changes in bear numbers (see review in Harris 1986 and discussions in Pelton et al. 1978, Phelps 1979, LeFranc et al. 1987). There are ongoing efforts to develop trend indices based on use of bait stations (D. Garshelis, Minn. Dep. of Nat. Resour., Grand Rapids, pers. commun.), scent stations (Lindzey et al. 1977, J. Beecham, Id. Dep. of Fish and Game, Boise, pers. commun.), and on track counts in Florida (J. Wooding, Fla. Game and Fresh Water Fish Comm., Wildl. Res. Lab., Gainesville, pers. commun.). In some parts of Alaska, annual aerial counts of bears are conducted at food concentration sites such as along salmon streams. Correct interpretation of such data from any 1 year requires many replicate counts (Erickson and Siniff 1963). Also, the utility of counts at food concentration areas to detect population trend is questionable. Numerous bears would likely be observed in such areas long after the number of bears in less preferred habitats had declined significantly. Away from food concentration areas, high direct annual counts from aircraft may provide a useful index of trend where bear populations are dense and visibility is high. Such counts in alpine habitats are conducted in southeastern Alaska (Schoen and Beier 1989) and on Kodiak Island (R. Smith, Alas. Dep. of Fish and Game, Kodiak, pers. commun.).

Vital Rates.—Rates of birth, death, and recruitment for bear populations can only be established by research programs or by extrapolation from research. For long-lived species with low reproductive and adult mortality rates like bears, estimation of these parameters requires many years of study of >10 radio-marked females (Miller 1989). Estimates of survivorship rates based on regular locations of radio-marked animals can be calculated using procedures developed by Heisley and Fuller (1985) and Pollock et al. (1989). These procedures have been applied on populations of grizzly and black bears (Knick and Kasworm 1989, Schwartz and Franzmann in prep.). Other approaches using kill rates of tagged black bears were described by LeCount (1982), Kolenosky (1986), and Miller (1987). For polar bears and grizzly bears, mortality rate of adult females was shown to be the most critical factor in correctly estimating population growth rate or sustainable mortality rates (Knight and Eberhardt 1985, Taylor et al. 1987*b*).

In cases where research objectives require capture or handling of bears, the studies themselves will result in some mortalities or other stresses on bear populations. These stresses may not be significant to healthy bear populations (Ramsay and Stirling 1987), but they may make such studies inappropriate for depleted populations. Whether conducted on depleted populations or not, all proposed studies requiring handling of bears should receive adequate peer review to assure that poorly designed or implemented projects are not authorized.

Information Obtained from Simulation Studies

Information obtained from hunters, from harvested bears, and from field studies needs to be integrated into a conceptual framework or model where it can be used to make management decisions. Managers are increasingly finding mathematical models of populations to be useful tools for organizing and making decisions from such information. Computers are useful tools for examining such models as they permit managers to quickly make the lengthy and repetitive calculations needed to estimate parameters like sustainable harvest levels.

Deterministic models used to estimate sustainable harvest levels have only 1 result per set of inputs. These models are relatively simple to make. Useful deterministic models can be made by persons without programming talents using conventional spreadsheet software. Such models may introduce systematic error in species, like bears, with multi-year periods of maternal care (Taylor et al. 1987*c*).

Stochastic models, where life history events are assigned probabilities instead of fixed rates, are useful in examining the range of possible outcomes per set of inputs. Software useful in constructing stochastic models for species with any kind of life history has been developed by Harris et al. (1986). This software was used to evaluate sensitivity of harvest data (Harris and Metzgar 1987*b*) and is useful in predicting, for example, probability of survival of small populations of bears.

Deterministic models based on ANURSUS (Taylor et al. 1987*a*) with optional stochastic features have been developed specifically for each of the 3 North American bear species. ANURSUS attempts to mimic the dynamics of bear populations and, as a result, requires a daunting number of input parameters. The 3 species models based on ANURSUS are currently being linked and documented (M. Taylor, Northwest Territ. Dep. of Renewable Resour., Yellowknife, pers. commun.). When this is accomplished, ANURSUS can be more widely tested and used to establish management objectives based on sustainable yield.

ANURSUS was used to estimate sustainable harvest levels for adult female polar bears. Less than 1.6% of the total population of all bears could be harvested as adult females (Taylor et al. 1987*b*). Based on this finding sustainable harvest number can be approximated (M. Taylor, Northwest Territ. Dep. of Renewable Resour., Yellowknife, pers. commun.) as:

$$H = (N)(0.015/F),$$

where H is number of bears that can be harvested, N is total population number, F is the proportion of adult females in the harvest, and the 0.015 constant is derived from the simulation result that <1.6% population can be harvested as adult females (Taylor et al. 1987*b*). It follows that if the whole harvest is adult females, then harvests of 1.5% of the population can be sustained. If a proportion of the harvest is male then a larger percent harvest can be sustained. The maximum sustainable harvest rate for polar bears was estimated at 4.5%; this occurred when 33% of the harvest is female (Stirling 1988*b*). In the Yukon Territory, ANURSUS was used to make preliminary estimates of maximum sustainable harvest levels for male (6%) and female (2.5%) segments of regional grizzly bear populations (B. Smith, Yukon Dep. of Renewable Resour., Fish and Wildl. Branch, Whitehorse, pers. commun.).

Deterministic models were used by Bunnell and Tait (1980) to estimate sustainable mortality from all causes. When natural mortalities are subtracted separately, such models estimate sustainable harvest levels. The consequence of error simulation discussed earlier illustrates this application. With the generous estimates of reproductive rates and survivorship from natural mortality used to estimate population recovery period (Table 1), maximum sustainable harvests were estimated at 7.8% for grizzly bears older than 2.0 and at 15.9% for black bears >1.0 (Table 3). These were converted to estimates of sustainable harvest of the whole population using typical values for mortality of cub and yearling grizzly bears and cub black bears (Bunnell and Tait 1985). Under these conditions and assumptions, maximal sustainable annual hunting mortality was 5.7% for grizzly bears and 14.2% for black bears (Table 3). Elsewhere this approach was used to estimate that sustainable harvests for Yukon grizzlies was 2-3% of the population (Sidorowicz and Gilbert 1981). McCullough (1981, 1986) estimated higher sustainable harvest levels than other models by incorporating density-dependent effects on recruitment. There is both direct and indirect evidence for such relationships (Rogers 1983; Kemp 1972; Stringham 1980, 1983; Young and Ruff 1982; Schwartz and Franzmann in prep.). In my view, however, these relationships are as yet too poorly understood to be safely incorporated into estimates of sustainable harvest levels for hunted populations.

Estimates of sustainable harvest rates derived from models may be compared with calculated harvest rates derived from kill numbers and population estimates. In cases where different sexes have different vulnerability to hunters, population harvest rate can be estimated directly from information on the sex and age composition of the population (Bunnell and Tait 1985) or harvest (Fraser et al. 1982). Such comparisons should be viewed skeptically especially when age distributions are not stable (Caughley 1974, 1977; Harris 1984).

Harvest Controls

Managers have numerous regulatory tools for influencing the number or composition of bears harvested (Phelps 1979, Harger 1978). The effectiveness of any particular tool will vary among areas depending on hunting conditions and the type and motives of the hunter.

Seasons and Bag Limits.—Number of bears taken by hunters can usually be reduced by shortening seasons and increased by lengthening seasons. However, season length works to reduce kill only to a point; in Pennsylvania, 736 black bears were taken in a 1979 open hunting season only 1 day long (Lindzey et al. 1983). A similar number are currently being taken with a 3-day season (G. Alt, Pa. Game Comm., Moscow, pers. commun.). Seasons can be held periodically instead of shortened. On the Alaska Peninsula in southwestern Alaska, grizzly bear hunting has been allowed only on alternate years in an effort to reduce harvest and maintain open hunting (Sellers and McNay 1984).

Shorter seasons may give managers just as many bears killed by hunters in a shorter time, hunting under more crowded conditions. When this occurs, managers may choose to limit the number of hunters by issuing permits. Hunting by limited permit can augment the quality of the

Table 3. Estimated sustainable yield from maximally productive populations of grizzly and black bears (input parameters reported in Miller [1989]).

Annual hunting rate for initial stabilized population of grizzly bears (>2.0-years-old) and black bears (>1.0-years-old)	7.8%	15.9%
Equivalent hunting rate for total population (all ages)	5.7[a]	14.2%[b]

[a] Total population estimated from number of 2-year-olds by assuming yearling and cub mortality rates of 0.20 and 0.35, respectively, for each sex.

[b] Total population estimated from number of yearlings by assuming cub mortality rates of 0.22 for each sex.

hunting experience and, depending on number issued, may serve to maintain trophy bears in the population.

In some parts of Alaska, special permits and seasons are also used to minimize damage by and danger from grizzly bears that enter rural villages. By providing for these bears to be taken legally, managers achieve more accurate records on kill rates and allow the public to effect control actions that would otherwise have to be accomplished at public expense.

Seasons can also be adjusted to influence the sex of bears taken. This is particularly true during spring seasons because male bears tend to leave dens earlier than females, move greater distances, are not accompanied by cubs, and spring hunters may be more selective for large (male) bears (O'Pezio et al. 1983, Schoen et al. 1987, Miller 1990*b*, Van Daele et al. 1990). During spring grizzly bear seasons in Alaska (1984-1988), 74% of grizzly bears taken (*n* = 2,563) were male compared to 55% of bears taken in fall seasons (*n* = 2,963) (ADF&G unpublished data). A similar pattern was evident for black bear where 75% of spring bears harvested during 1984-1988 were male (*n* = 4,691 bears killed) compared to 64% in fall harvests (*n* = 2,887). In some areas, polar bears killed in seasons open during the den entrance and emergence period are more likely to be females because dens are typically on land, which may be near villages of native hunters, and only pregnant females use dens (Stirling 1986, Kolenosky 1987). In parts of Canada pregnant females are protected from hunting by delaying opening of hunting until 1 December, after the den entrance period (Stirling and Calvert 1985). Black bear tracking studies in Maine revealed that black bears are likely to be distant from their breeding ranges during early fall seasons. The geographic distribution of kill at such times would not, as a result, accurately depict the origins of harvested bears (Hughie 1982).

A chronology of sex ratio in kill of grizzly bears harvested in a portion of southcentral Alaska was given by Miller (1990*b*). There was little change in sex ratio of kill over time during fall seasons, but there was an increase in the proportion of females killed as the spring season progressed. This suggested that the last part of spring seasons should be eliminated if hunter kills need to be reduced. However, 2-4 times as many females are killed during each of the first 2 weeks of September than during any week of the spring seasons. Also, the percentage of females in the kill is higher in the early fall than at any other time of the year (Miller 1990*b*). In this area, more females would be protected from hunters if the first 2 weeks of the fall season were closed than could be accomplished by closing the whole spring season.

Bag limits can also be adjusted to influence the number of bears taken. In most of Alaska, grizzly bear bag limits are 1 per 4 years. The multi-year bag limit serves to make hunters more selective as by taking a bear they forego the opportunity to take a better bear in subsequent years. In Alaska's Game Management Unit 13, grizzly bear bag limits were changed from 1 per 4 years to 1 per year during fall seasons in 1982-1986 and harvests averaged 81 bears per season (range 59-96). When bag limits were 1 per 4 years, fall harvests were lower averaging 60 bears (range 40-73) in the 5 years before the change and 53 (range 48-58) bears per season in the 2 years after the change (ADF&G unpublished data).

Increase in reported kill for certain areas may result from misreporting by hunters. This may occur when areas with multiple-year and annual-year bag limits are mixed. Differences in bag limits and seasons give hunters incentives to report location of their kills incorrectly. In Alaska, an investigation by Fish and Wildlife Protection Officers resulted in the prosecution of a guide who had misreported the location of at least 25 grizzly bears killed by himself, his relatives, and his clients during 1 season. Half of these were wrongly reported as having been taken in areas with a 1 per year bag limit when they had, in fact, been taken in an area with a 1 per 4 year bag. Such misreporting can result in serious management error in circumstances where managers rely on accuracy in these statistics.

Another way to affect bear harvests is to time bear seasons to occur at the same time as hunts for other species. In some areas harvests will be increased if hunters can take bears incidental to hunts designed primarily to take ungulates. This approach has been used in a number of different areas to influence taking black bears (Burk 1977) as well as grizzly bears in Alaska.

Closed Areas.—Areas closed to hunting are also a potentially useful tool for managers. Closed or lightly hunted reservoir areas can be sources of surplus animals that immigrate to open or more accessible areas where they can be hunted (Beecham 1986). To be effective such areas must be large.

Methods, Means, and Legal Bear Definitions.—Besides season adjustments and limited entry systems, managers use restrictions on methods and means of hunting to influence harvest. These include restrictions on weapon type, transportation methods, use of attractants like bait, and use of dogs. In Michigan, the age of black bears taken by hunters using dogs was older than for hunters not using dogs (Harger 1978). However, regulations that permit baiting or hunting with dogs could result in adverse population impacts if hunters select for females, which are more likely to "tree" when chased by dogs.

One of the most effective ways to maximize sustainable harvest of bears with minimal influence on the reproductive capability of the population is to direct hunter harvest away from adult females by prohibiting shooting females accompanied by offspring. Where female bears produce new litters every 2 or 3 years, adult females are vulnerable only 1/2 to 1/3 as frequently as males. Experiments are ongoing in the Yukon Territory to direct the harvests of outfitters away from female grizzly bears by giving them incentives to harvest males (Smith 1990). Clearly, it is difficult to differentiate between sexes of bears but it will be done more often if hunters have incentives to do so. In Ontario it was shown that not all females contribute equally to reproduction (Kolenosky 1990). Protection of maternal black bear females, which are producing the bulk of recruits, is especially important when this is the case (Kolenosky 1990).

Commercialization and Restrictions by Class of Hunter.—Limitations on commercial use of bear parts is a useful tool in preventing excessive harvests. Commercial exploitation of wildlife has the potential to reduce and eliminate wildlife populations and species quickly (Geist 1988). The Lacy Act of 1900 in the United States was a largely successful effort to stop the trend of commercial overexploitation of many wildlife species and populations (Trefethen 1961). In many areas the sale of black or grizzly bear hides or parts, such as gall bladders, is illegal as is the sale of polar bear hides. These restrictions reduce harvests over what would occur if commercial sales of bear parts were allowed (Geist 1988). Commercial sales of bear parts could be allowed in some states without creating local management problems, but this may exacerbate problems elsewhere by giving lawbreakers the ability to claim the parts came from somewhere sales were legal.

Regulations designed to benefit or restrict special groups of hunters such as resident, non-resident, native, sport, trophy, or subsistence hunters can be used to constrain harvests. As an alternative to using limited entry permits, such regulations allow only certain classes of hunters to participate. This is the system in effect for polar bear in both Canada and the United States where only indigenous people have hunting rights.

DISCUSSION

In most areas, bear population management has evolved from efforts to reduce bear numbers to objectives based on maintenance or augmentation of population numbers. The ability of managers to maintain or increase bear population numbers successfully is limited by 4 major constraints.

The first constraint is adequate protection of bear habitat. This topic is treated elsewhere (McLellan and Shackleton 1988, McLellan 1990, Mattson 1990, Schoen 1990).

The second constraint on bear population management is political. Bear population managers are pressured by many special interest groups, frequently with diametrically opposed objectives. In Alaska, for example, subsistence and sport hunters frequently pressure managers to reduce populations of bears and other predators. On the other extreme are groups that agitate to reduce or eliminate hunting. One such group managed to eliminate the black bear hunting season in California in 1989 (D. Koch, Calif. Dep. of Fish and Game, Sacramento, pers. commun.). Wildlife managers must spend an increasing amount of their personnel and financial resources dealing with the demands and proposals of special interest groups. These expenditures represent resources that are diverted from habitat and population management programs. Some groups, commonly those opposed to hunting, even target resource management agencies as the problem. These activities reduce public confidence and support for management efforts. An important challenge facing wildlife managers is to direct the activities of these groups into activities that increase support for soundly based management. This is easier to say than to do. Clearly, however, in the North American political system, the concerns of such groups cannot be ignored without ultimate counter-productive consequences. Although it may be frustrating at the time, it will help if these special-interest groups are involved in the development of management plans. This provides a forum where their concerns can be heard by managers and managers' concerns can be heard by them.

There appears to be more political will to protect remnant populations of bears than there is to reestablish bears in areas where they have been eliminated. Although grizzlies have been eliminated from 99% of their former range south of Canada (Servheen 1987 cited by Jonkel 1987), there is little interest in reestablishing them in places like California, Colorado, or Arizona (Brown 1985). In Texas much of the public is opposed to management actions that would result in a significant increase in black bear population numbers or distribution (C. Winkler, Tex. Parks and Wildl. Dep., Austin, pers. commun.). Reintroduction of bears into an area where they have been eliminated is a positive action that will provoke some opposition. In North American political systems, it appears to be more difficult to take action than to do nothing. Thus, it is important to assure that the *status quo* includes bears.

The third constraint is the technological tool kit available for use by managers. Many of the tools used by managers to assess the success or failure of bear management strategies lack precision, estimates of variability, or produce potentially biased results. It is easier to detect potential sources of bias and imprecision in analyses of bear populations than it is to develop approaches without these flaws. Unfortunately, the decisions managers have to make do not disappear just because the information available has uncertain accuracy or precision. In making these decisions, however, managers should incorporate the limitations of the data into their management strategies. Usually this will mean setting management objectives and guidelines on the conservative side of what might be estimated to be optimal. The costs associated with unintended population declines and the difficulties of detecting such declines until they are far advanced mandate a conservative approach to bear population management.

The fourth major constraint to population management is financial. Some of the technological constraints of existing bear population management techniques can be overcome if adequate funds were available. Where the commitment to spend the necessary money is lacking, bear population managers have little choice but to implement conservative management strategies.

LITERATURE CITED

ALT, G.L., AND J.S. LINDSEY. 1980. Management of Pennsylvania's black bear: past, present and future. Pages 58-70 *in* Trans. Northeast Fish and Wildl. Conf. (mimeo).

AMBROSE, J.T., AND O.T. SANDERS. 1978. Magnitude of black bear depredations on apiaries in North Carolina. Pages 167-179 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

AMSTRUP, S.C., I. STIRLING, AND J.W. LENTFER. 1986. Past and present status of polar bears in Alaska. Wildl. Soc. Bull. 14(3):241-254.

ANON. 1965. Proceedings of the first international scientific meeting on the polar bear. Univ. of Alaska, Fairbanks, 1965. U.S. Dep. Inter. Resour. Publ. 16 and Univ. of Alas. Int. Conf. Proc. Series, No. 1. 72pp.

_____. 1980. Preliminary black bear management plan for British Columbia. Fish and Wildl. Branch, Ministry of Environ., Victoria, B.C. 32pp. (mimeo).

_____. 1987*a*. Oregon black bear management plan 1987. Oreg. Dep. of Fish and Wildl. 26pp.

_____. 1987*b*. A plan for black bear in California. Calif. Dep. of Fish and Game, The Resources Agency. 8pp.

AUNE, K., AND B. BRANNON. 1987. East Front grizzly studies. Mont. Dep. of Fish, Wildl. and Parks. 195pp.

BALLARD, W.B., AND D. LARSEN. 1987. Implications of predator-prey relationships to moose management. Second Int. Moose Symp., Swedish Wildl. Res. Viltrevy Suppl. 1, Part 2:581-602.

_____, AND S.D. MILLER. 1987. Brown and black bear predation on moose in southcentral Alaska. Proc. Int. Congr. Game Biol. 18: In press.

_____, _____, AND T.H. SPRAKER. 1980. Moose calf mortality studies. Alas. Dep. of Fish and Game. Fed. Aid in Wildl. Restoration Proj. W-17-9, W-17-10, W-17-11 and W-21-1. 123pp.

_____, K.E. RONEY, L.A. AYRES, AND D.N. LARSEN. 1990. Estimating grizzly bear density in relation to development and exploitation in northwest Alaska. Int. Conf. Bear Res. and Manage. 8:405-413.

BARNES, V.G., R.B. SMITH, AND L.G. VAN DAELE. 1988. Density estimates and estimated population of brown bears on Kodiak and adjacent islands, 1987. Draft report to the Kodiak Brown Bear Res. and Hab. Maintenance Trust 15 April 1988. 34pp (mimeo).

BEECHAM, J. 1980. Some population characteristics of two black bear populations in Idaho. Int. Conf. Bear Res. and Manage. 4:201-204.

_____. 1983. Population characteristics of black bears in west central Idaho. J. Wildl. Manage. 47(2):405-412.

_____. 1986. Black bear management plan 1986-1990. Id. Dep. of Fish and Game, Boise. 16pp.

BECK, T. 1979. Colorado black bear status report. Pages 45-52 *in* A. LeCount, ed. First western black bear workshop. Tempe, Ariz. 339pp.

BOERTJE, R.D., W.C. GASAWAY, D.V. GRANGAARD, AND D.G. KELLEYHOUSE. 1988. Predation on moose and caribou by radio-collared grizzly bears in east central Alaska. Can. J. Zool. 66:2492-2499.

BROWN, D.E. 1985. The grizzly in the southwest. Univ. Okla. Press, Norman. 274pp.

BUNNELL, F.E., AND D.E.N. TAIT. 1980. Bears in models and reality—implications to management. Int. Conf. Bear Res. and Manage. 4:15-23.

_____, AND _____. 1981. Population dynamics of bears—implications. Pages 75-98 *in* C.W. Fowler and T.D. Smith, eds. Dynamics of large mammal populations. J. Wiley and Sons, Inc., New York. 477pp.

_____, AND _____. 1985. Mortality rates of North American bears. Arctic 38(4):316-323.

BURK, D., ED. 1977. The black bear in modern North America. Proc. of the workshop on the management biology of North American black bear. Kalispell, Mont. Boone and Crockett Club and Camp Fire Club of America. 299pp.

BURRUSS, J.S. 1979. Pages 83-89 *in* A. LeCount, ed. First western black bear workshop. Tempe, Ariz. 339pp.

BURTON, T.S. 1977. Report from California. Pages 24-29 *in* D. Burk, ed. The black bear in modern North America. Proc. of the workshop on the management biology of North American black bear. Kalispell, Mont. Boone and Crockett Club and Camp Fire Club of America. 299pp.

CARDOZA, J.E. 1978. Status report for Massachusetts. Pages 18-19 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

CARON, F. 1980. Status of the black bear in Quebec. Pages 32-37 *in* J.M. Collins and A.E. Ammons, chm. Fifth eastern black bear workshop on black bear management and research. Wrightsville Beach, N.C. 292pp.

Cartwright, D.J. 1978. Status report for New Brunswick. Pages 25-26 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

Caughley, G. 1974. Interpretation of age ratios. J. Wildl. Manage. 38:557-562.

_____. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York. 234pp.

Clark, S.H. 1978. Status report for New Brunswick. Pages 35-42 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

Clarke, C.H.D. 1961. The black bear is a game animal. Ont. Fish and Wildl. Rev. 1:2-3.

Conley, B.W. 1977. Report from Arkansas. Pages 21-24 *in* D. Burk, ed. The black bear in modern North America. Proc. of the workshop on the management biology of North American black bear. Kalispell, Mont. Boone and Crockett Club and Camp Fire Club of America. 299pp.

Cowan, I.M. 1972. The status and conservation of bears (Ursidae) of the world-1970. Int. Conf. Bear Res. and Manage. 2:343-371.

Craighead, J.J., J.R. Varney, and F.C. Craighead, Jr. 1974. A population analysis of the Yellowstone grizzly bear. Mont. For. and Conserv. Exp. Stn., Univ. of Mont. School of For., Missoula. Bull. 40. 20pp.

Dean, F.C. 1987. Brown bear density, Denali National Park, Alaska, and sighting efficiency adjustment. Int. Conf. Bear Res. and Manage. 7:37-43.

DeMaster, D., M.C.S. Kingsley, and I. Stirling. 1980. A multiple mark and recapture estimate applied to polar bears. Can. J. Zool. 5:633-638.

Dood, A.E., R.D. Brannon, and R.D. Mace. 1986. Final programmatic environmental impact statement: the grizzly bear in northwestern Montana. Mont. Dep. of Fish, Wildl., and Parks, Helena. 287pp.

Eberhardt, L.L. 1985. Assessing the dynamics of wild populations. J. Wildl. Manage. 49(4):997-1012.

_____. 1988. Using age structure data from changing populations. J. Appl. Ecol. 25:373-378.

_____. in press. Using radio-telemetry for mark-recapture studies with edge effects. J. Appl. Ecol. (19), 27.

Erickson, A.W., and D.B. Siniff. 1963. A statistical evaluation of factors influencing aerial survey results on brown bears. Trans. North Am. Wildl. and Nat. Resour. Conf. 28:391-409.

Franzmann, A.W., C.C. Schwartz, and R.O. Peterson. 1980. Causes of summer moose calf mortality on the Kenai Peninsula. J. Wildl. Manage. 44:764-768.

Fraser, D.J. 1976. An estimate of hunting mortality based on the age and sex structure of the harvest. North Am. Moose Conf. Workshop 12:236-273.

_____, F. Gardner, G.B. Kolenosky, and S. Strathern. 1982. Estimation of harvest rate of black bears from age and sex data. Wildl. Soc. Bull. 10(1):53-57.

Fryxell, J.M., W.E. Mercer, and R.B. Gellately. 1988. Population dynamics of Newfoundland moose using cohort analysis. J. Wildl. Manage. 52(1):14-21.

Gasaway, W.C., R.O. Stephenson, J.L.Davis, P.E.K. Shepherd, and O.E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. 84. 50pp.

_____, R.D. Boertje, D.V. Grangaard, D.G. Kelleyhouse, and R.O. Stephenson. 1988. Factors limiting moose population growth in subunit 20E. Alas. Dep. of Fish and Game, Fed. Aid in Wildl. Restoration Proj. W-22-3. 53pp.

_____. in press. Management of complex predator-prey systems in Alaska. Symposium on wolf-prey dynamics and management, Vancouver B.C. May 1988.

Gilbert, J.R., W.S. Kordek, J. Collins, and R. Conley. 1978. Interpreting sex and age data from legal kills of bears. Pages 253-262 *in* R. Hughie, ed. Fourth eastern black bear workshop. Greenville, Me. 409pp.

Geist, V. 1988. How markets in wildlife meat and parts, and the sale of hunting privileges, jeopardize wildlife conservation. Conserv. Biol. 2(1):15-26.

Harger, E.M. 1978. Hunting methods and their effect on the black bear population. Pages 200-206 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

_____. 1980. Status of the black bear in Michigan. Pages 11-13 *in* J.M. Collins and A.E. Ammons, chm. Fifth eastern workshop on black bear management and research. Wrightsville Beach, N.C. 292pp.

Harris, R.B. 1984. Harvest age-structure as an indicator of grizzly bear population status. M.S. Thesis. Univ. of Mont., Missoula. 204pp.

_____. 1986. Grizzly bear population monitoring: current options and considerations. Mont. For. and Conserv. Exp. Stn., Univ. of Mont., Missoula Misc. Publ. 45. 80pp.

_____, and L.H. Metzgar. 1987*a*. Estimating harvest rates of bears from sex ratio changes. J. Wildl. Manage. 51(4):802-811.

_____, and _____. 1987*b*. Harvest age structures as indicators of decline in small populations of grizzly bears. Int. Conf. Bear Res. and Manage. 7:109-116.

_____, _____, and C.D. Bevins. 1986. GAPPS, Generalized animal population projection system, user's manual. Mont. Cooperative Wildl. Res. Unit, Univ. Mont., Missoula. 123pp.

Hayward, G.D. 1989. Historical grizzly bear trends in Glacier National Park: a critique. Wildl. Soc. Bull. 17(2):195-197.

Heisley, D.M., and T.K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. 49:668-674.

Hermes, J., and R.D. Hugie. 1977. Report from Maine. Pages 43-45 *in* D. Burk, ed. The black bear in modern North America. Proc. of the workshop on the management biology of North American black bear. Kalispell, Mont. Boone and Crockett Club and Camp Fire Club of America. 299pp.

Horejsi, B.J.. 1989. Uncontrolled land-use threatens an international grizzly bear population. Conserv. Biol. 3(3):220-223.

Hugie, R.D. 1982. Black bear ecology and management in the northern conifer-deciduous forests of Maine. Ph.D. Thesis. Univ. of Mont., Missoula. 203pp.

_____, S. Svirsky, and L. Rutske. 1978. Status report for Minnesota. Pages 22-24 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

JONKEL, C.J. 1987. Brown bear. Pages 457-473 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch eds. Wild furbearer management and conservation in North America. Ont. Trappers Assoc. 1150pp.

_____, AND I.M. COWAN. 1971. The black bear in the spruce-fir forest. Wildl. Monog. 27. 57pp.

JORGENSEN, C.J., R.H. CONLEY, R.J. HAMILTON, AND O.T. SANDERS. 1978. Management of black bear depredation problems. Pages 297-319 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

KEATING, K.A. 1986. Historical grizzly bear trends in Glacier National Park, Montana. Wildl. Soc. Bull. 14:83-87.

_____. 1989. Historical grizzly bear trends in Glacier National Park, Montana: a response. Wildl. Soc. Bull. 17(2):198-201.

KEMP. G.A. 1972. Black bear population dynamics at Cold Lake, Alberta, 1968-1970. Int. Conf. Bear Res. and Manage. 2:26-31.

KNICK, S.T., AND W. KASWORM. 1989. Shooting mortality in small populations of grizzly bears. Wildl. Soc. Bull. 17:11-15.

KNIGHT, R.R., AND L.L. EBERHARDT. 1984. Projected future abundance of the Yellowstone grizzly bear. J. Wildl. Manage. 48(4):1434-1438.

_____, AND _____. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:323-334.

_____, AND _____. 1987. Prospects for Yellowstone grizzly bears. Int. Conf. Bear Res. and Manage. 7:45-50.

_____, B.M. BLANCHARD, AND L.L. EBERHARDT. 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973-1985. Wildl. Soc. Bull. 16(2):121-125.

KOHN, B.E. 1982. Status and management of black bears in Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. 129. 31pp.

KOLENOSKY, G.B. 1986. Effects of hunting on an Ontario black bear population. Int. Conf. Bear Res. and Manage. 6:45-55.

_____. 1987. Polar bear. Pages 474-485 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, eds. Wild furbearer management and conservation in North America. Ont. Trappers Assoc. 1150pp.

_____. 1990. Reproductive biology of black bears in east-central Ontario. Int. Conf. Bear Res. and Manage. 8:385-392.

_____, AND S.M. STRATHERN. 1987. Black bear. Pages 457-473 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, eds. Wild furbearer management and conservation in North America. Ont. Trappers Assoc. 1150pp.

LECOUNT, A.L. 1977. Report from Arizona. Pages 18-21 *in* D. Burk, ed. The black bear in modern North America. Proc. of the workshop on the management biology of North American black bear. Kalispell, Mont. Boone and Crockett Club and Camp Fire Club of America. 299pp.

_____. 1982. Characteristics of a central Arizona black bear population. J. Wildl. Manage. 46(4):861-868.

LEFRANC, M.N., JR., M.B. MOSS, K.A. PATNODE, AND W.C. SUGG, III, EDS. 1987. Grizzly bear compendium. Interagency Grizzly Bear Comm., Bozeman, Mont. 540pp.

LINDZEY, F.G., S.K. THOMPSON, AND J.I. HODGES. 1977. Scent station index of black bear abundance. J. Wildl. Manage. 41(1):151-153.

LINDZEY, J.B., G.L. ALT, C.R. MCLAUGHLIN, AND W.S. KORDEK. 1983. Population response of Pennsylvania black bears to hunting. Int. Conf. Bear Res. and Manage. 5:34-39.

MACHUTCHON, A. G., AND B.L. SMITH. 1988. A review of the status and management of the black bear (*Ursus americanus*) in the Yukon. Draft report, Yukon Renewable Resour. Fish and Wildl. Branch, Whitehorse. 109pp.

MAHONEY, S. 1984. Newfoundland status report. Proc. East. Workshop Black Bear Manage. Res. 7:17-20.

MARTINKA, C.J. 1971. Status and management of grizzly bears in Glacier National Park, Montana. Trans. North Am. Wildl. and Nat. Resour. Conf. 36:312-322.

_____. 1974. Population characteristics of grizzly bears in Glacier National Park, Montana. J. Mammal. 55:21-29.

MATTSON, D.J. 1990. Human impacts on bear habitat use. Int. Conf. Bear Res. and Manage. 8:33-56.

MCCULLOUGH, D.R. 1981. Population dynamics of the Yellowstone grizzly bear. Pages 173-196 *in* C.W. Fowler and T.D. Smith, eds. Dynamics of large mammal populations. J. Wiley and Sons, Inc., New York. 477pp.

_____. 1986. The Craigheads' data on Yellowstone grizzly bear populations: relevance to current research and management. Int. Conf. Bear Res. and Manage. 6:21-32.

MCDONALD, L.L., R.L. SCHMEHL, AND A.H. WHEELER. 1988. Sightings of grizzly bears in the greater Yellowstone ecosystem; results of a mail survey covering 1983-1987, a progress report. U.S. Natl. Park Serv., mimeo.

MCLAUGHLIN, C.R. 1986. Black bear assessment—1985. Pages 360-405 *in* Planning for Maine's inland fish and wildlife. Part 1.4, species assessments and strategic plans, fur and game mammals. Me. Dep. Inland Fish. and Wildl., Bangor.

MCLELLAN, B.N. 1990. Relationships between human industrial activity and grizzly bears. Int. Conf. Bear Res. and Manage. 8:57-64.

_____, AND D.M. SHACKLETON. 1988. Grizzly bears and resource extraction industries: effects of roads on behavior, habitat use and demography. J. Appl. Ecol. 25:451-460.

MILLER, S.D. 1987. Vol. VI, Black bear and brown bears. Susitna Hydroelectric Project. Final Rep., big game studies. Alas. Dep. of Fish and Game and Alas. Power Authority. 276pp. (mimeo).

_____. 1988. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13. Prog. Rep., Alas. Dep. of Fish and Game, Fed. Aid in Wildl. Restoration Project W-22-6, Job 4.21. 151pp.

_____. 1989. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13. Prog. Rep., Alas. Dep. of Fish and Game, Fed. Aid in Wildl. Restoration Project W-22-6, Job 4.21. in press.

_____. 1990*a*. Detection of differences in brown bear density and population composition caused by hunting. Int. Conf. Bear Res. and Manage. 8:393-404.

_____. 1990*b*. Denning ecology of brown bears in southcentral Alaska and comparisons with a sympatric black bear population. Int. Conf. Bear Res. and Manage. 8:279-287.

_____, AND W.B. BALLARD. 1982. Density and biomass estimates for an interior Alaskan brown bear, *Ursus arctos*, population. Can. Field. Nat. 96(4):448-454.

_____, AND S.M. MILLER. 1988. Interpretation of bear harvest data. Alas. Dep. of Fish and Game, Fed. Aid in Wildl. Restoration Project W-22-6, Job 4.18R. 65pp.

_____, AND R.D. SELLERS. 1989. Brown bear density on the Alaska Peninsula at Black Lake, Alaska, preliminary report. Alas. Dep. of Fish and Game. 38pp. (mimeo).

_____, E.F. BECKER, AND W.B. BALLARD. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. Int. Conf. Bear Res. and Manage. 7:23-35.

NAGY, J.A., AND J.R. GUNSON. 1988. Draft management plan for grizzly bears in Alberta. Alberta For., Lands and Wildl., Fish and Wildl. Div. 168pp.

ORFF, E. 1987. New Hampshire bear management plan. N.H. Fish and Game Dep. 4pp.

O'PEZIO J., S.H. CLARKE, AND C. HACKFORD. 1983. Chronology of denning by black bears in the Catskill region of New York. N.Y. Fish and Game 30(1):1-11.

PATTON, A. 1978. Status report for Nova Scotia. Pages 46-48 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

PEEK, J.M., M.P. PELTON, H.D. PICTON, J.W. SCHOEN, AND P. ZAGER. 1987. Grizzly bear conservation and management: a review. Wildl. Soc. Bull. 15:160-169.

PELTON, M., J. CARDOZA, B. CONLEY, C. DUBROCK, AND J. LINDZEY. 1978. Census techniques and population indices. Pages 242-252 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 409pp.

PHARRIS, L.D., AND J.D. CLARK. 1987. Arkansas black bear hunter survey. Int. Conf. Bear Res. and Manage. 7:373-375.

PHELPS, J., CHM. 1979. Black bear management techniques. Pages 183-200 *in* A. LeCount, ed. First western black bear workshop. Tempe, Ariz. 339pp.

POELKER, R.J., AND H.D. HARTWELL. 1973. Black bear of Washington. Wash. State Game Dep., Biol. Bull. 14. 180pp.

_____, AND L.D. PARSONS. 1980. Black bear hunting to reduce forest damage. Int. Conf. Bear Res. and Manage. 4:191-193.

POLLOCK, K.H., S.R. WINTERSTEIN, C.M. BUNCK, AND P.D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wildl. Manage. 53(1):7-15.

RAMSAY, M.A., AND I. STIRLING. 1987. Long-term effects of drugging and handling free-ranging polar bears. J. Wildl. Manage. 50(4):619-626.

REYNOLDS, H.V., AND J.L. HECHTEL. 1988. Population dynamics of a hunted grizzly bear population in the northcentral Alaska Range. Prog. Rep., Alas. Dep. of Fish and Game, Fed. Aid in Wildl. Restoration. Project W-22-6 Job 4.19. 52pp.

_____, _____, AND D.J. REED. 1987. Population dynamics of a hunted grizzly bear population in the northcentral Alaska Range. Prog. Rep., Alas. Dep. of Fish and Game, Fed. Aid in Wildl. Restoration. Project W-22-6 Job 4.19. 59pp.

RIEFFENBERGER, J.C., AND T.J. ALLEN. 1978. Status report for West Virginia. Pages 81-91 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

ROGERS, L.L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Trans. North Am. Wildl. and Nat. Resour. Conf. 41:431-438.

_____. 1977. Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. Ph.D. Thesis, Univ. of Minn., Minneapolis. 194pp.

_____. 1983. Effects of food supply, predation, cannibalism, parasites, and other health problems on black bear populations. Pages 194-211 *in* F.L. Bunnell, D.S. Eastman, and J.M. Peek, eds. Proc. symp. on natural regulation of wildlife populations. For., Wildl. and Range Exp. Stn., Univ. of Id., Moscow. 225pp.

_____. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bear in northeastern Minnesota. Wildl. Monogr. 97. 72pp.

RUSSELL, L.L., AND O. FORSEY. 1978. Status report for New Brunswick. Pages 27-31 *in* R.D. Hugie, ed. Fourth eastern black bear workshop. Greenville, Me. 408pp.

SALWASSER, H., C. SCHONEWALD-COX, AND R. BAKER. 1987. The role of interagency cooperation in managing for viable populations. Pages 159-173 *in* M. Soulé, ed. Viable populations for conservation. Cambridge Univ. Press. 189pp.

SCHAFFER, M.L., AND F.B. SAMPSON. 1985. Population size and extinction: a note on determining critical population sizes. Am. Nat. 125(1):144-152.

SCHOEN, J.W. 1990. Bear habitat management: a review and future perspective. Int. Conf. Bear Res. and Manage. 8:143-154.

_____, AND L.R. BEIER. 1989. Brown bear habitat preferences and brown bear logging and mining relationships in southeast Alaska. Prog. Rep., Fed. Aid in Wildl. Restoration Project W-22-5, Job 4.17R. 32pp.

_____, _____, AND J.W. LENTFER. 1987. Denning ecology of coastal brown bears on Admiralty and Chichagof Islands, southeast Alaska. Int. Conf. Bear Res. and Manage. 7:293-304.

SCHWARTZ, C.C., AND A.W. FRANZMANN. In prep. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildl. Monogr.

SEBER, G.A.F. 1982. The estimation of animal abundance and related parameters. Second ed. Charles Griffin and Co. Ltd., London. 654pp.

SELLERS, R., AND M. MCNAY. 1984. Population status and management considerations of brown bear, caribou, moose and wolves on the Alaska Peninsula. Rep. to the Alas. Board of Game, Alas. Dep. of Fish and Game. 53pp.

SHOESMITH, M. 1977. Report from Manitoba. Pages 154-161 *in* D. Burk, ed. The black bear in modern North America. Proc. of the workshop on the management biology of North American black bear. Kalispell, Mont. Boone and Crockett Club and Camp Fire Club of America. 299pp.

SIDOROWICZ, G.A., AND F.F. GILBERT. 1981. The management of grizzly bears in the Yukon, Canada. Wildl. Soc. Bull. 9(2):125-135.

SMITH, B.L. 1990. Sex weighted point system regulates grizzly bear harvest. Int. Conf. Bear Res. and Manage. 8:375-383.

STIRLING, I. 1986. Research and management of polar bears *Ursus maritimus*. Polar Record 23(143):167-176.

_____. 1988*a*. Polar bears. Univ. of Mich. Press, Ann Arbor. 220pp.

_____. 1988*b*. Comments summarizing preliminary conclusions of Feb. 1988 Yellowknife population modeling meeting reported in the draft minutes of NSB-IGC Polar Bear Technical Committee Meeting, Anchorage, 17 Oct 1988.

_____, AND W. CALVERT. 1985. Polar bear management changes in Canada 1978-80. Pages 99-118 *in* Polars bears: Proc. of the 8th working meeting of the IUCN/SSC Polar Bears Specialists Group, Jan 1981. 151pp.

_____, R.E. SCHWEINSBURG, G.B. KOLENOSKY, I. JUNIPER, R.J. ROBERTSON, S. LUTTICH, AND W. CALVERT. 1985. Research on polar bears in Canada 1978-1980. Pages 71-98 *in* Polars bears: Proc. of the 8th working meeting of the IUCN/SSC Polar Bears Specialists Group, Jan. 1981. 151pp.

STOKES, S.M. 1977. Report from South Carolina. Pages 95-97 *in* D. Burk, ed. The black bear in modern North America. Proc. of the workshop on the management biology of North American black bear. Kalispell, Mont. Boone and Crockett Club and Camp Fire Club of America. 299pp.

STONEBERG, R.P., AND C.J. JONKEL. 1966. Age determination of black bear by cementum layers. J. Wildl. Manage. 30(2):411-414.

STRINGHAM, S.F. 1980. Possible impacts of hunting on the grizzly/brown bear, a threatened species. Int. Conf. Bear Res. and Manage. 4:337-349.

_____. 1983. Roles of adult males in grizzly bear population biology. Int. Conf. Bear Res. and Manage. 5:140-151.

SUCHY, W.J., L.L. MCDONALD, M.D. STRICKLAND, AND S.H. ANDERSON. 1985. New estimates of minimum viable population size for grizzly bears of the Yellowstone ecosystem. Wildl. Soc. Bull. 13(3):223-228.

TAIT, D.E.N. 1983. An analysis of hunter kill data. Ph.D. Thesis, Univ. of B.C., Vancouver. 129pp.

TAYLOR, G.J. 1984. Maryland status report. Pages 10-11 *in* D.S. Maehr and J.R. Brady, eds. Proc. seventh eastern workshop black bear res. and manage. 85pp.

TAYLOR, M.K., F. BUNNELL, D. DEMASTER, R. SCHWEINSBURG, AND J. SMITH. 1987*a*. ANURSUS: a population analysis system for polar bears. Int. Conf. Bear Res. and Manage. 7:117-125.

_____, D. DEMASTER, F. BUNNELL, and R. SCHWEINSBURG. 1987*b*. Modeling the sustainable harvest of female polar bears. J. Wildl. Manage. 51(4):811-820.

_____, J. CARLEY, AND F. BUNNELL. 1987*c*. Correct and incorrect use of recruitment rates for marine mammals. Marine Mammal Sci. 3(2):171-187.

TREFETHEN, J.B. 1961. Crusade for wildlife. Boone and Crockett Club, Stackpole Co. 377pp.

URQUHART, D.R., AND R.E. SCHWEINSBURG. 1984. Life history and known distribution of polar bear in the Northwest Territories up to 1981. Northwest Territ. Renewable Resour. 70pp.

VALLEE, J. 1977. Report from Quebec. Pages 167-171 *in* D. Burk, ed. The black bear in modern North America. Proc. of the workshop on the management biology of North American black bear. Kalispell, Mont. Boone and Crockett Club and Camp Fire Club of America. 299pp.

VAN DAELE, L.J., V.G. BARNES, AND R.B. SMITH. 1990. Denning characteristics of brown bears on Kodiak Island, Alaska. Int. Conf. Bear Res. and Manage. 8:257-267.

VOHS, P.A., JR. 1977. Report from Oklahoma. Pages 87-88 *in* D. Burk, ed. The black bear in modern North America. Proc. of the workshop on the management biology of North American black bear. Kalispell, Mont. Boone and Crockett Club and Camp Fire Club of America. 299pp.

WALLACE, J. 1987. Status of black bear. Federal Aid in Wildl. Restoration Performance Rep., Tex. Parks and Wildl. Dep. 16pp.

WILLEY, C.H. 1978. The Vermont black bear. Vt. Fish and Game Dep. Fed. Aid in Wildl. Restoration Proj. W-38-R, viii + 73pp.

_____. 1980. Interpretation of black bear age data. Pages 167-186 *in* J.M. Collins and A.E. Ammons, chm. Fifth eastern workshop on black bear management and research. Wrightsville Beach, N.C. 292 pp.

WILL, G.B. 1980. Black bear-human conflicts and management considerations to minimize and correct these problems. Pages 75-88 *in* J.M. Collins and A.E. Ammons, chm. Fifth eastern workshop on black bear management and research. Wrightsville Beach, N.C. 292pp.

WINKLER, C.K. 1975. Black bear status report-Texas. Page 81 *in* A. LeCount, ed. First western black bear workshop. Tempe, Ariz. 339pp.

YOUNG, B.F., AND R.L. RUFF. 1982. Population dynamics and movements of black bears in east central Alberta. J. Wildl. Manage. 46(4):845-860.

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Improving estimation of puma (*Puma concolor*) population density: clustered camera-trapping, telemetry data, and generalized spatial mark-resight models

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Obtaining reliable population density estimates for pumas (*Puma concolor*) and other cryptic, wide-ranging large carnivores is challenging. Recent advancements in spatially explicit capture-recapture models have facilitated development of novel survey approaches, such as clustered sampling designs, which can provide reliable density estimation for expansive areas with reduced effort. We applied clustered sampling to camera-traps to detect marked (collared) and unmarked pumas, and used generalized spatial mark-resight (SMR) models to estimate puma population density across 15,314 km^2 in the southwestern USA. Generalized SMR models outperformed conventional SMR models. Integrating telemetry data from collars on marked pumas with detection data from camera-traps substantially improved density estimates by informing cryptic activity (home range) center transiency and improving estimation of the SMR home range parameter. Modeling sex of unmarked pumas as a partially identifying categorical covariate further improved estimates. Our density estimates (0.84–1.65 puma/100 km^2) were generally more precise (CV = 0.24–0.31) than spatially explicit estimates produced from other puma sampling methods, including biopsy darting, scat detection dogs, and regular camera-trapping. This study provides an illustrative example of the effectiveness and flexibility of our combined sampling and analytical approach for reliably estimating density of pumas and other wildlife across geographically expansive areas.

Pumas (cougars or mountain lions; *Puma concolor*) are the most widely distributed large carnivore in the western hemisphere[1]. Similar to other large carnivores, pumas have considerable resource requirements and provide important ecological benefits over expansive areas[1–3]. Their presence sometimes results in conflicts with humans, however, and predation by pumas can influence vital rates of terrestrial ungulate populations[4,5]. Although some puma populations have recently expanded range and present novel management challenges[6,7], other populations are small, isolated, or otherwise imperiled and might necessitate conservation intervention[8,9]. Conservation and management of pumas are often contentious issues that are influenced by multiple political, social, and economic interest groups, and resolving disputes has increasingly hinged on managing authorities possessing reliable and contemporary estimates of puma population density and abundance[10–12]. However, pumas are wide-ranging, cryptic, and notoriously difficult to detect; consequently, few jurisdictions within the species' occupied range have reliable estimates of those demographic parameters. Most puma populations are instead managed based on population indices, such as hunter effort, mortality trends, or expert opinion, extrapolation of densities from

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small study areas and other jurisdictions, or a combination thereof[10,13–15], all of which may be unreliable and could result in flawed conservation and management[16,17].

Spatially explicit capture-recapture models integrate a detection process model with an ecological process model that describes the spatial distribution of animal activity centers, or home range centers, across a study area, and can produce unbiased estimates of population density[18,19]. Recent studies have applied spatially explicit models to multiple types of detection data to estimate puma population density; for example, tissue samples collected by biopsy darting pumas that were treed using hounds[20–22], puma scat collected via area searches by scat detection dogs[23], and photographs of pumas collected from regular or contiguous arrays of remote camera-traps[24–27]. However, biopsy darting and scat detection dog sampling necessitate often expensive laboratory genetic analyses to produce individual identities from detection data[28]. Additionally, treeing pumas with hounds for biopsy darting is likely most efficient during winter and in locales with sufficient snow cover that improves tracking[20,22], and because of high DNA degradation rates in scat that can reduce sample sizes, optimal effectiveness of scat detection dog sampling is generally limited to locales with cool and dry climates[29,30]. In contrast, remote camera-trapping can be a cost-efficient and logistically feasible approach for effectively detecting pumas and other large carnivores across habitats, ecosystems, and climatic conditions[31,32].

A critical assumption of most capture-recapture models is that all detected animals are individually identifiable[19]. This can be difficult to achieve if camera-traps are used to detect pumas or other wildlife that lack visible, individually unique natural markings, such as the rosettes on jaguars (*Panthera onca*)[24,33]. To overcome this issue, mark-resight models and their spatially explicit analogues, spatial mark-resight (SMR) models, were developed to estimate the density of populations in which only a portion of animals are individually identifiable[26,34–37]. Attempting to assign individual identities to pumas *ad hoc* based on perceived natural marks, such as scars, ear nicks, body shapes, or carriages[25,27], can result in biased and unreliable density estimates, however, because multiple individuals may have similar physical features, causing observers to agree on incorrect identity assignments or disagree on correct identity assignments[24]. Furthermore, given the ambiguity, it is not always possible to identify a sufficient number of individually unique pumas based solely on natural marks to estimate population density[24,38].

For pumas and other species that lack unambiguous natural markings, physically capturing and applying artificial marks, such as radiocollars or ear tags, to a portion of animals in a population is likely necessary for accurate density estimation when using camera-traps for detection[26,32,34–37]. Such mark-resight methods can be viable, cost-effective alternatives to capture-recapture methods, because only a single marking event of a portion of a population is required and camera-trapping to collect resighting data is efficient. Using Global Positioning Systems (GPS) collars as marks can permit unambiguous individual identification for nearly all camera-trap detections of marked individuals, assist with determining whether an animal is marked or unmarked, and also provide telemetry location data that can be integrated in spatially explicit models to improve estimation of individual activity centers, the detection function spatial scale (home range) parameter (σ), and ultimately, population density[26,36,37,39].

One challenge associated with using researcher-applied artificial marks is that in SMR models, the spatial distributions of marked and unmarked individuals across the landscape are informed by the capture and marking process; therefore, correctly specifying those distributions in the process model is critical for accurately estimating population density[35,37]. Conventional spatial mark-resight (conSMR) models assume that marked and unmarked individuals have the same spatial distribution, typically uniformity or that the two distributions can be specified correctly with parametric distributions[26,34,36]. Although the assumption of spatial uniformity may be valid for jaguars and other species that are identifiable by their individually unique natural markings, it is likely inappropriate if animals are physically captured and artificially marked, because of the juxtaposition between marking and resighting locations[35,37]. If the marking and resighting detector arrays overlap, animals that are captured for marking are located on average closer to the resighting array than unmarked individuals and, therefore, likely will have higher detection rates than unmarked individuals. Consequently, if researcher-applied artificial marks are used for individual identification, conSMR models, which do not account for the capture and marking process, may underestimate the numbers of both unmarked and undetected individuals and thus, population density[35,37].

A generalized spatial mark-resight model (genSMR) was recently developed that resolves this problem by including sub-models for both the marking and resighting processes[37]. This allows the differing spatial distributions of marked and unmarked individuals to be determined by the marking process, and simulations have demonstrated that the genSMR model produces unbiased estimates of population density when marking is not random across a study area[37]. The parameters of the genSMR model developed by Whittington *et al.*[37] are estimated via Bayesian methods using Markov chain Monte Carlo (MCMC) algorithms. In contrast, Efford and Hunter[35] developed a pseudolikelihood-based model and estimation procedure that is analogous to genSMR, which they refer to as spatial capture-mark-resight. A primary limitation of this pseudolikelihood estimation procedure is that it ignores information contained in the spatial distribution of detections of unmarked individuals. Efford and Hunter[35] argued that the information lost by discarding these data is minimal; however, the magnitude of information in the spatial locations of detections of unmarked animals can be increased through the use of partial identity covariates[34,39].

A key source of uncertainty in SMR models stems from the need to probabilistically resolve the individual identities for detections of unmarked animals, as well as detections of marked but unidentifiable animals and animals with unknown mark status, if available[34,39]. Reducing uncertainty in the individual identity assignments can reduce the uncertainty in population density estimates, which can be accomplished with partial identity covariates[39,40]. The use of categorical partial identity covariates in the form of microsatellite loci genotypes has been demonstrated[39,40], but the utility of partially identifying information in camera-trap studies, where animal sex and other potential covariates are fewer in number and less reliably determined from photographs, has not been explored. Such covariates are typically either not recorded or are discarded from camera-trap detection data, so evaluating their effectiveness for improving the precision of parameter estimates from spatially explicit models could result in improved density estimation in camera-trapping studies.

Because of the logistical and financial constraints associated with currently available puma sampling methods and survey designs, researchers are often forced to estimate puma population density for areas that are smaller than the geographical extent of populations or the scale at which conservation and management occur[10,15]. Population density estimates are then extrapolated to larger areas, typically with considerable uncertainty and unverified assumptions[10,13–15]. By incorporating spatial information about when and where individual animals are detected, spatially explicit models are robust to irregular sampling designs, such as clusters of detectors with gaps between clusters, which can permit efficient surveying of large geographical areas[18,41–45]. Recent studies evaluated clustered sampling designs of noninvasive genetic hair-traps in the spatially explicit framework for estimating American black bear (*Ursus americanus*) population density, which demonstrated that density estimates were improved, largely because more individuals were exposed to detectors and spatial recaptures were obtained over expansive areas[41,43–45]. Remote camera-trapping is arguably the most widely used and practical noninvasive method for surveying wildlife populations globally[31,32]; therefore, considerable potential exists for using clustered sampling designs in camera-trap studies to estimate population density over spatially extensive areas, which could have widespread practical utility across terrestrial wildlife species and geographical locales.

Herein, we apply clustered sampling to camera-traps in the spatially explicit framework to demonstrate the potential for this approach to survey pumas over expansive areas with reduced effort. We then apply recently developed genSMR models to the obtained camera-trap detection data to estimate puma population density and abundance. In addition, we evaluate the influence on parameter estimates of integrating telemetry data from GPS collars on marked pumas, incorporating sex as a categorical identity covariate for unmarked pumas, and accommodating activity center transiency. Our results demonstrate the flexibility of genSMR models and provide an illustrative example of the effectiveness of this combined sampling and analytical approach to produce precise and reliable population density estimates over large geographical areas.

Materials and Methods

Study area. Our study occurred during 2017 in the Southern Rocky Mountains ecoregion in north-central New Mexico, USA (Fig. 1). The area was rugged, with steep mountains, deep canyons, and expansive mesas, and elevations ranging from 1,540 to 3,524 m a.s.l. The climate was semi-arid, with average annual rainfall ranging from 22.58 to 57.63 cm and average annual snowfall ranging from 18.03 to 305.31 cm, depending on elevation; average annual high temperatures ranged from 13.72 to 22.05 °C and average annual low temperatures ranged from −4.17 to 3.00 °C, depending on elevation[46]. The majority of lands (63%) were under federal management by the U.S. Forest Service, National Park Service, or Bureau of Land Management; tribal lands (29%) and a combination of state government, local government, and privately owned lands (8%) accounted for the remainder of land area.

Live-capture and marking. To apply artificial marks to a portion of individuals, we live-captured pumas throughout our study area using Aldrich spring-activated foothold cable restraints, foothold traps, and to a lesser extent, treeing with a team of trained hounds[47,48]. We chemically immobilized captured pumas using one of the following drug combinations[49]: (1) tiletamine and zolazepam (Telazol®; Zoetis Services LLC, Parsippany, USA) at a dosage of 5.0 mg/kg combined with 1.0 mg/kg of xylazine (AnaSed®, LLOYD Inc., Shenandoah, USA), the latter of which was antagonized using 0.12 mg/kg of yohimbine (ZooPharm, Windsor, USA); or (2) 2.0 mg/kg of ketamine combined with 0.07 mg/kg of medetomidine, the latter of which was antagonized using 0.30 mg/kg of atipamezole (ZooPharm). During immobilization, we monitored the respiratory rate, heart rate, and body temperature of each puma at five-minute intervals to ensure maintenance of bodily function. We outfitted captured pumas that were field-aged based on gum recession measurements[50] as being ≥ two years-old (i.e., subadults and adults)[48] with a uniquely numbered ear tag and an Iridium GPS collar (Advanced Telemetry Systems [Isanti, USA] or Vectronic Aerospace [Berlin, Germany]). We programmed collars to acquire location fixes every one to three hours (i.e., 8–24 fixes per calendar day) and we remotely downloaded location data every three to seven days. All pumas were released at the location where captured.

Clustered camera-trap resighting. We created a survey design comprised of nine total clusters of 3 × 3 sampling cells in each cluster (Fig. 1). Cell spacing within a cluster was 3.5 × 3.5 km, or 12.25-km^2 coverage per cell and 110.25-km^2 coverage per cluster; this spacing corresponded to the recommended ≥two detectors within the smallest female home range size[43,45] reported for pumas in New Mexico (30.10 km^2)[51]. Clusters were staggered with 28-km longitudinal spacing and 36–45-km latitudinal spacing between the centers of clusters, or 4.5–7× the diameter of said smallest female home range size, assuming a bivariate normal distribution (i.e., circular home range)[19]. Prior to deploying camera-traps, we used simulation to evaluate the performance of this clustered survey design for estimating population density, given pessimistic parameter estimates and various numbers of sampling occasions[19,41,45]. For a simulated hypothetical population with low density (1.0 puma/100 km^2), low baseline detection rate ($\lambda_0 = 0.05$), and large spatial scale of the detection function ($\sigma = 5.0$ km)[20,25], results from a fitted null spatial capture-recapture model indicated that surveying this design for 17 consecutive occasions would likely estimate population density with high precision and accuracy (CV = 0.18; RMSE = 0.19), negligible bias (+0.05, 95% CI = 0.00–0.09), and nominal coverage (0.97, 95% CI = 0.94–1.00; see Supplementary Table S1). These simulations assumed that all individuals had unambiguous identities, which deviates from the mark-resight framework, but the effectiveness of survey designs for spatial capture-recapture and SMR models are similar[19].

We attempted to establish a single camera-trap within each sampling cell along canyon rims, ridges, saddles, drainages, trails, and other terrain features that could be likely travel routes for pumas; we did not place camera-traps on roads. Because of restricted property access, we were unable to establish camera-traps in some cells; thus, our final array was comprised of 68 total camera-traps (range: 3–9 camera-traps/cluster). Each camera-trap consisted of two cameras with passive infrared motion-activated sensors (Reconyx® HyperFire PC800; Holmen, USA), which we placed four to six m apart, facing each other, and mounted to trees

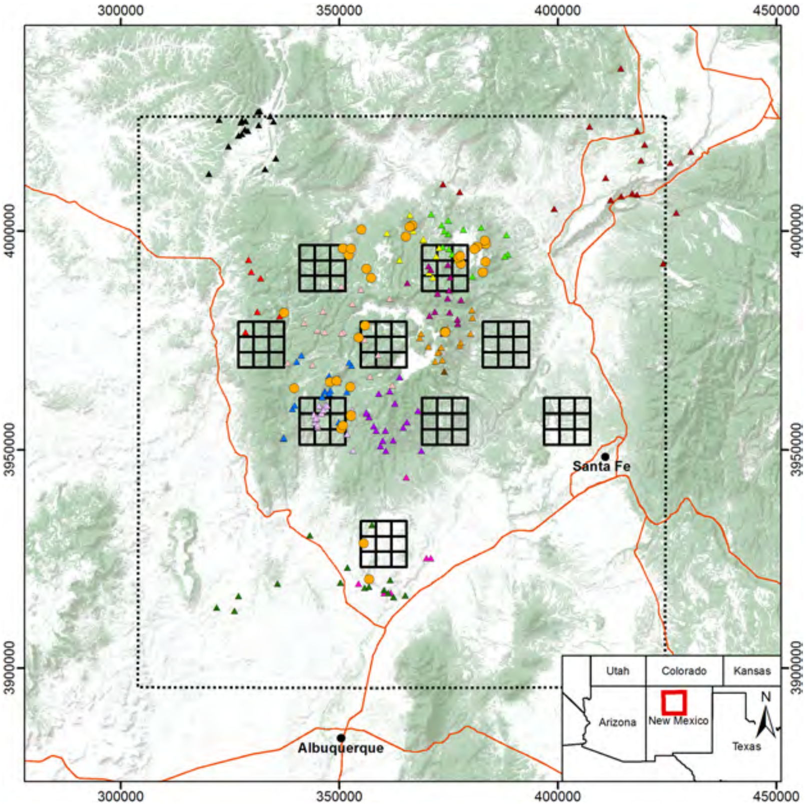

Figure 1. Study area in New Mexico, USA, where pumas were live-captured and marked with GPS collars, and camera-traps were deployed in a systematic cluster design for resighting of marked and unmarked pumas to estimate population density with generalized spatial mark-resight models. The spatial locations of live-traps (orange circles), camera-trap sampling cells (solid black outline squares), thinned telemetry locations collected during the resighting period (triangles with discrete colors corresponding to individual), and parameter estimation area (state space; dashed black line) are presented. Image created by S.M.M. with ESRI® ArcMap™ 10.4.1 software (http://desktop.arcgis.com/en/) under license (https://technology.ky.gov/gis/Pages/PostSecondarySiteLicense.aspx), with forest-shrub land cover data (green shaded areas) from the U.S. Government (https://www.mrlc.gov/data/nlcd-2011-land-cover-conus)[79]; topography data (background) from ESRI, U.S. Geological Survey, and National Oceanic and Atmospheric Administration (https://server.arcgisonline.com/ArcGIS/rest/services/World_Terrain_Base/MapServer); and major highways data (red lines) from New Mexico Department of Transportation (http://services.arcgis.com/hOpd7wfnKm16p9D9/arcgis/rest/services/NMDOT_Functional_Class/FeatureServer).

or shrubs ~one m above the ground[52]. We set cameras to medium sensitivity with bursts of five photos per detection and 30-s delays between bursts. We placed ~1.0 mL of bobcat (*Lynx rufus*) gland-based or rub-eliciting scent lure on the ground in the center of each camera-trap. These lures provided no caloric reward, and felids do not have the extraordinary olfactory capabilities that canids and ursids do[53]; neither pumas, jaguars, nor leopards (*Panthera pardus*) have exhibited a behavioral response (i.e., trap-happy or trap-shy) to detection when bobcat lure was applied[54–56]. If a camera-trap is visited, however, bobcat lure can entice pumas to linger for a slightly extended period of time, thereby affording researchers the opportunity to identify the sex and marked status of an individual from photographs[24,57,58].

We operated camera-traps for 17 consecutive seven-day occasions from July to November 2017, and we visited each camera-trap every 21–28 days to retrieve photographs, check battery levels, and reapply lure. We considered individual photographs of pumas that were acquired ≥one hr apart as unique detections[24,25]. We excluded dependent kittens, which are not reproductively mature, from the detection history to prevent inflation of density estimates[13,20]; therefore, our results represent subadult and adult pumas only. We first classified photographs by the mark status of each puma based on the presence or absence of a GPS-collar: (1) marked and identifiable, (2) marked but unidentifiable, (3) unmarked, or (4) unknown. We then identified marked pumas to the individual level based on a combination of ear tag, collar type, sex, and telemetry locations from GPS collars[26,37]. We did not attempt to assign individual identities to any non-collared pumas based on perceived natural marks, because of the inherent uncertainty that could bias density estimates[24]. We reclassified all pumas that we initially assigned unknown mark status as unmarked if photograph date and time did not align with telemetry location data for GPS-collared individuals. Similarly, we resolved all cases of marked but unidentifiable individuals by comparing telemetry locations with photograph date and time. We identified the sex of unmarked pumas when possible; for photographs from which puma sex was inconclusive, we assigned individuals unknown sex.

Spatial mark-resight analysis. We estimated puma population density using the live-capture history (marking), the camera-trap detection history (resighting), and the telemetry locations from GPS-collared pumas. Because only two pumas were captured and marked via treeing with hounds, we did not explicitly model a separate hound capture process; however, we retained hound-captured pumas in our data as marked individuals that were exposed to both the marking and resighting processes, and they also provided telemetry data that informed their activity center locations and contributed to estimation of the detection function spatial scale parameter. To jointly use all of those sources of information and account for dependency among data types, we used a Bayesian genSMR model[37] that specified a spatial capture-recapture density and activity center process model that was observed in three ways: (1) through the marking process in which all individual identities were known; (2) through the resighting process in which only the individual identities of marked pumas were known and unmarked identities could be partially known if sex was observed; and (3) through the telemetry process for the marked individuals with known identity. To reduce the uncertainty in probabilistically resolving the latent identities of unmarked individuals[34], we used sex as a categorical identity covariate to exclude particular combinations of detections[39,40]; for example, an unmarked male detection could not be from the same individual as an unmarked female detection. This assumed that the sex of individual i, $sex_i \sim$ Bernoulli(p^{sex}), where p^{sex} is the probability that an individual is female, which must be estimated. Using this assumption, sex can be probabilistically resolved for detections of individuals whose sex was not identified from photographs[22], and the individual identities of unmarked pumas can be probabilistically resolved using the algorithms developed by Chandler and Royle[34], excluding identity matches between detections of different sexes. We also fit conSMR models, which ignore the marking process[26,34,36], to permit comparisons with genSMR models. We accommodated all of the aforementioned features using MCMC algorithms that are maintained in the R statistical software package SPIM[59,60].

We considered the following two process models for activity centers ($\boldsymbol{s}$). First, we used a typical spatial capture-recapture point process model in which individual i had a single $\boldsymbol{s}_i$ for the entirety of the study (marking and resighting combined), and all $\boldsymbol{s}_i$ were uniformly distributed across space ($\boldsymbol{s}_i \sim$ Uniform($\boldsymbol{S}$) for $i = 1, \ldots, N$, where $\boldsymbol{S}$ denotes the two-dimensional state space [parameter estimation area])[19]. To define the state space for genSMR models, we buffered the minimum and maximum longitude and latitude extents of the combined live-trap and camera-trap locations by 25 km, or ~3× the maximum estimated spatial scale of the detection function parameter that was pooled between marking and resighting processes (σ^d)[19], resulting in $\boldsymbol{S}^G = 15{,}314\,\text{km}^2$. In contrast, because conSMR models do not incorporate the marking process, the 25-km buffer was applied only to the camera-trap locations to define a state space for conSMR models of $\boldsymbol{S}^C = 14{,}707\,\text{km}^2$. Second, GPS-collar telemetry data indicated that the activity centers for four marked pumas may have spatially shifted large distances between the marking and resighting processes, and one marked puma died prior to the onset of resighting (see Results). Therefore, we also specified a spatial point process model for activity center transiency, which estimated the locations of individuals' activity centers separately for each the marking and resighting processes[61,62]. This process model accommodated activity center relocations between marking and resighting, including if individuals relocated to fill the territorial vacancy that resulted from the death of one marked puma[63,64]. An individual's activity centers were connected by a spatially constrained relocation event (described in detail below), which entailed that resighting activity centers must be spatially linked to the location where each marked puma was live-captured, thereby constituting an activity center model that was intermediate between conSMR and genSMR models[61,62].

We defined data for the marking and resighting processes using the M and R superscripts, respectively. The previously mentioned two-step process model for genSMR models required us to specify two sets of activity centers, s_i^M and s_i^R, for $i = 1, \ldots, N$. We assumed spatial uniformity of activity centers for the marking process, $s_i^M \sim$ Uniform($\boldsymbol{S}^G$). For the resighting process, we assumed $s_i^R \sim$ Bivariate Normal(s_i^M, Σ)[($x_{\min}$, $y_{\min}$), ($x_{\max}$, $y_{\max}$)], where $\Sigma = \sigma^t \boldsymbol{I}$, and σ^t is the spatial scale parameter for activity center transiency; the bivariate normal redistribution kernel was truncated by the extent of $\boldsymbol{S}^G$ to prevent σ^t underestimation[62]. This model for redistribution (i.e., spatial shift) has been used in both open and closed population spatial capture-recapture models[62,65], the latter of which allowed fully transient activity centers and was recently applied to conSMR models[61]. In contrast to those implementations, we only allowed one spatial redistribution of activity centers, because that was all that was necessary to accommodate the spatial dynamics that we observed, and fewer activity center shifts should maintain greater precision and better MCMC mixing, which is typically poor for spatially explicit models that accommodate transient activity centers[61,62].

Conditional on the aforementioned process models, the population was observed via three processes. For the marking and resighting processes, observations were made at the $J^M \times 2$ live-trap locations X^M and the $J^R \times 2$ camera-trap locations X^R, where J^M and J^R are the number of live-trap and camera-trap locations, respectively. We assumed a hazard half-normal detection function with binomial detections for the marking process, producing individual by live-trap detections summed across occasions, $Y_{ij}^M \sim$ Binomial(p_{ij}^M, K^M), where K^M is the number of marking occasions. For the resighting process, we assumed a Poisson detection function, producing individual by camera-trap counts that were summed across occasions; specifically, $Y_{ij}^R \sim$ Poisson($K^R \times p_{ij}^R$), where K^R is the number of resighting occasions. These observation models had σ^d and baseline detection rate parameters that varied by process (λ_0^M and λ_0^R). Telemetry locations from GPS collars could be recorded anywhere within the extent of $\boldsymbol{S}$. We used only the telemetry locations that were collected during the resighting period, which we thinned to one randomly selected location per survey occasion for each marked puma (i.e., one location/week). We applied this thinning to decrease temporal dependence among telemetry locations for each puma, because temporal dependence could cause underestimation of the variance of σ^d and σ^t, activity centers, and population density[26,36,37]. Telemetry locations informed the estimation of σ^d and $\boldsymbol{s}_i$, or σ^d, s_i^R, and σ^t for models that included activity center transiency.

We accounted for unequal live-trap and camera-trap operation (effort) across time, and also a puma that died prior to initiation of resighting, using individual by trap exposure matrices. These matrices are similar to a trap operation file[19], except that the exposure of each puma to each trap and trap type could differ; this allowed for known entries and exits into and out of the population, but did not account for unknown violations of the population closure assumption[37,39]. For the marking process, the $A \times J^M$ exposure matrix E^M contained the number of occasions that individual i was exposed to detection at a live-trap j, where A indicates the level of data augmentation[66]. For the resighting process, the $A \times J^R$ exposure matrix E^R contained the number of occasions that individual i was exposed to detection at camera-trap j. These exposure matrices were substituted into the binomial and Poisson observation models for K^M and K^R, respectively. To correctly allocate latent identity samples for two pumas that were live-captured and marked during the resighting period and one marked puma that died prior to resighting, we used an $n^M \times K^M$ matrix m, where n^M is the number of marked pumas, to denote the marked status of each GPS-collared puma during each resighting occasion ($0 = $ unmarked, $1 = $ marked, and $2 = $ dead)[37]. Thus, if a puma was unmarked on occasion k, it could be allocated latent identity unmarked detections. If a puma was marked on occasion k, it could be allocated latent identity marked detections. If a puma was dead on occasion k, it could not be allocated any latent identity detections.

Several process and observation models were described, so we detail below exactly which combinations we fit. Our model specifications were designed to test the relative importance of four items: (1) telemetry data from marked pumas, (2) sex as a categorical identity covariate for unmarked pumas, (3) activity center transiency for marked pumas between the marking and resighting processes, and (4) conSMR versus genSMR models. The influence of telemetry data was of particular interest, because the activity centers for four marked pumas likely relocated between marking and resighting, and we also had limited prior home range size data to inform camera-trap and cluster spacing. Therefore, we fit two genSMR models that included sex identity constraints for the resighting process, but differed as to whether telemetry data were incorporated or not (models 1 and 2). We extended models 1 and 2 to accommodate activity center transiency between the marking and resighting processes for marked pumas (models 3 and 4). Because models 3 and 4 best described the observed spatial dynamics of pumas during our study, we tested the importance of sex identity constraints by fitting these models without sex identity constraints (models 5 and 6). To test the importance of using genSMR over conSMR models, we fit models 1 and 2 excluding the marking process (models 7 and 8). Finally, to investigate if sex-specific detection function parameters were necessary to estimate puma density and the sex ratio, we fit a version of model 1 that included sex-specific detection function parameters (model 9).

We ran each genSMR model for 5×10^5 iterations, thinned by 75 iterations, and we discarded the first 5×10^3 iterations as burn-in. The large number of iterations was more than required for the models that excluded activity center transiency, but for models that included activity center transiency, σ^t mixed poorly and required many iterations to accurately characterize this posterior distribution. In contrast, we ran each conSMR model for 4×10^4 iterations and discarded the first 5×10^3 iterations as burn-in. We used data augmentation to augment the sample of marked pumas with up to $A = 250$, 325–375, and 600 hypothetical individuals that had all-zero detection histories for conSMR models, genSMR models that included telemetry data, and genSMR models that excluded telemetry data, respectively[26,36,37,66]. We used the posterior modes for parameter point estimates, and we used the 95% highest posterior density intervals (HPDI) for interval estimates. We assessed precision of density estimates using the widths of 95% HPDIs and the posterior coefficients of variation (CV), or the posterior standard deviation divided by the posterior mode.

Ethics statement. Experimental protocols were approved by New Mexico Department of Game & Fish (per NMAC 19.35.6), Pueblo of Santa Ana Tribal Council, and a U.S. National Park Service Institutional Animal Care and Use Committee (IMR-VALL-Cain-LargeMammals-2015.A2). Data collection methods were carried out in accordance with standardized guidelines for humane wild mammal handling and welfare[67], scientific research permits (VALL-2017-SCI-0002 and VALL-2017-SCI-0049), and with explicit permission from relevant authorities.

Results

Marking and resighting. We deployed 30 live-traps, each for an average of 22 days (range: 2–64 days). We live-captured and marked 15 pumas (12 males:3 females); one marked female died of starvation prior to initiation of camera-trapping. We used a total of 190 telemetry locations ($n_{\text{males}} = 156$; $n_{\text{females}} = 34$) collected from GPS collars during the resighting period (mean = 14 locations/puma; range = 3–17). We acquired 68 unique detections of subadult and adult pumas at 31 camera-traps (46% of traps); the average number of detections per occasion was four (range: 1–7). Twenty (29%) camera-trap detections were of eight marked pumas (6 males:2 females); 17 spatial recaptures of marked pumas were obtained during the marking and resighting processes combined ($n_{\text{males}} = 15$; $n_{\text{females}} = 2$). Among the 48 detections of unmarked pumas, sex was definitively identified for 25 detections (52%; 10 male:15 female).

Population density and abundance. Puma population density point estimates ranged from 0.66 to 1.65 pumas/100 km², with the lowest estimates produced by conSMR models and the highest estimates produced by genSMR models that excluded telemetry data (Table 1). Integrating telemetry data approximately doubled σ^d estimates and decreased estimates of puma density in the genSMR models, whereas estimated puma density from conSMR models were similar regardless of whether telemetry data were used or not (0.66 versus 0.70 puma/100 km², respectively). The estimated number of unmarked pumas that were detected during resighting (n^{UM}) was between 18 and 26 individuals, with the smallest estimates from conSMR models (18–20 pumas) and the genSMR models that excluded telemetry data (20–22 pumas). The genSMR model that included telemetry data, activity center transiency, and sex as a partially identifying categorical covariate (model 3), which best explained the observed spatial dynamics of pumas during our study, estimated population density to be 0.84 puma/100 km² (95% HPDI: 0.50–1.28) with a CV of 0.24. This corresponded to an estimated population size

Model	Type	Specifications	λ_0^M	λ_0^R	σ^d	σ^t	n^{UM}	*D* (95% HPDI)	Width	CV	*N* (95% HPDI)
1	Gen	Sex + Tel	0.004	0.016	7.54	—	25	0.94 (0.59–1.48)	0.89	0.25	144 (91–227)
2	Gen	Sex	0.016	0.061	2.85	—	22	1.54 (0.96–2.75)	1.79	0.31	236 (147–421)
3	Gen	Sex + Tel + Trans	0.007	0.019	6.51	17.40	26	0.84 (0.50–1.28)	0.78	0.24	129 (74–193)
4	Gen	Sex + Trans	0.018	0.064	2.89	0.35	22	1.57 (0.93–2.65)	1.72	0.29	240 (142–406)
5	Gen	Tel + Trans	0.008	0.020	6.54	17.02	26	0.84 (0.54–1.34)	0.81	0.26	129 (82–206)
6	Gen	Trans	0.021	0.068	2.63	2.71	20	1.65 (0.95–2.72)	1.77	0.29	252 (145–417)
7	Con	Sex + Tel	—	0.025	6.64	—	20	0.66 (0.37–1.03)	0.66	0.26	97 (55–151)
8	Con	Sex	—	0.082	3.62	—	18	0.70 (0.33–1.27)	0.94	0.37	102 (49–187)
9	Gen-SS	Males + Tel	0.005	0.015	8.10	—	24	0.95 (0.59–1.43)	0.84	0.24	145 (90–219)
		Females + Tel	0.005	0.042	4.22	—					

Table 1. Parameter estimates from generalized (Gen) and conventional (Con) spatial mark-resight models. Models with and without a categorical identity constraint for puma sex (Sex), telemetry data from GPS collars (Tel), activity center transiency between marking and resighting processes (Trans), and sex-specific detection functions (SS) were considered. Baseline detection rates for the marking (λ_0^M) and resighting (λ_0^R) processes, spatial scale of the detection function (σ^d; km), spatial scale of activity center transiency (σ^t; km), the number of unmarked pumas detected during resighting (n^{UM}), population density ($D = \text{puma}/100\,\text{km}^2$), and population size (*N*) were estimated. The 95% highest posterior density intervals (HPDI) are presented for *D* and *N*, as well as 95% HPDI width and coefficient of variation (CV = SD/*D*) for *D*. See Supplementary Table S2 for further details, including 95% HPDIs for all parameter estimates.

of 129 pumas (95% HPDI: 74–193) across the 15,314 km^2 estimation area, of which an estimated 26 unmarked pumas (95% HPDI: 18–32) were detected by camera-traps. Given those point estimates, 11.63% of pumas were marked and 22.81% of unmarked pumas were detected by camera-traps, indicating that we acquired spatial detection information for a combined 34.44% of pumas within $\boldsymbol{S}^G$.

Density estimate precision. Modeling sex as a partially identifying categorical covariate for the detections of unmarked pumas improved precision of estimated density by 8%, reducing CV from 0.26 to 0.24 (model 5 versus model 3). Allowing activity center transiency for marked pumas between the marking and resighting processes improved precision of estimated puma density by 4% (based on CV), despite introducing more uncertainty into the process model via more complex model structure. Integrating telemetry data from GPS collars on marked pumas improved precision of estimated density by 17%, reducing CV from 0.29 to 0.24 (model 4 versus model 3); although, determining how much of the CV reduction resulted from a lower point estimate instead of a decrease in variance is difficult to disentangle.

Spatial scale of detection and activity center transiency. Estimates of σ^d from models that incorporated telemetry data ranged from 6.51 to 7.54 km, whereas estimates from models that excluded telemetry data ranged from 2.63 to 3.62 km. The smallest estimated σ^d was from the genSMR model that only included activity center transiency (model 6), whereas the largest σ^d was from the genSMR model that excluded activity center transiency but incorporated sex identity constraints and telemetry data (model 1). Estimated σ^t was 17.40 and 17.02 km from genSMR models that included both activity center transiency and telemetry data (models 3 and 5, respectively), but was just 0.35 and 2.71 km from genSMR models that excluded telemetry data (models 4 and 6, respectively). In models 4 and 6, σ^t was either not identifiable or was barely identifiable, so these considerably lower estimates are likely unreliable. Importantly, telemetry data from the GPS-collared pumas were critical to estimating σ^t, because the four individuals whose activity centers relocated between the marking and resighting processes were never detected by the camera-traps (Fig. 2).

Sex ratio. The genSMR model that included sex-specific detection functions (model 9) produced a similar population density estimate as the comparable genSMR model that had a pooled detection function (model 1). The estimated female and male σ^d from model 9 was 4.22 km (95% HPDI: 3.65–5.10) and 8.10 km (95% HPDI: 7.57–8.61), respectively, compared to the pooled estimate from model 1 of 7.54 km (95% HPDI: 7.06–8.12). The probability that a puma was female was 0.33 (95% HPDI: 0.16–0.49) and 0.34 (95% HPDI: 0.19–0.52) from models 3 and 9, respectively, which supports that sex-specificity of detection function parameters was unnecessary for accurately estimating the population sex ratio. The fact that the density and sex ratio estimates were nearly identical between models with and without sex-specificity suggests close to perfect compensation between λ_0^R and σ^d on the total exposure to detection[68]. We note that with just two spatial recaptures for marked females, our female density and sex ratio estimates are largely dependent on how representative the telemetry data (i.e., movements) for the two marked females were of the entire female cohort within $\boldsymbol{S}^G$.

Discussion

Previous puma mark-resight studies in the spatially explicit framework used conSMR models to estimate population density[25–27]. If individual animals are live-captured to apply artificial marks, and this process occurs across the same area in which resighting will occur, marked individuals will on average likely reside closer to the resighting array than unmarked individuals[37]. Modeling the marking process via genSMR models accounts for

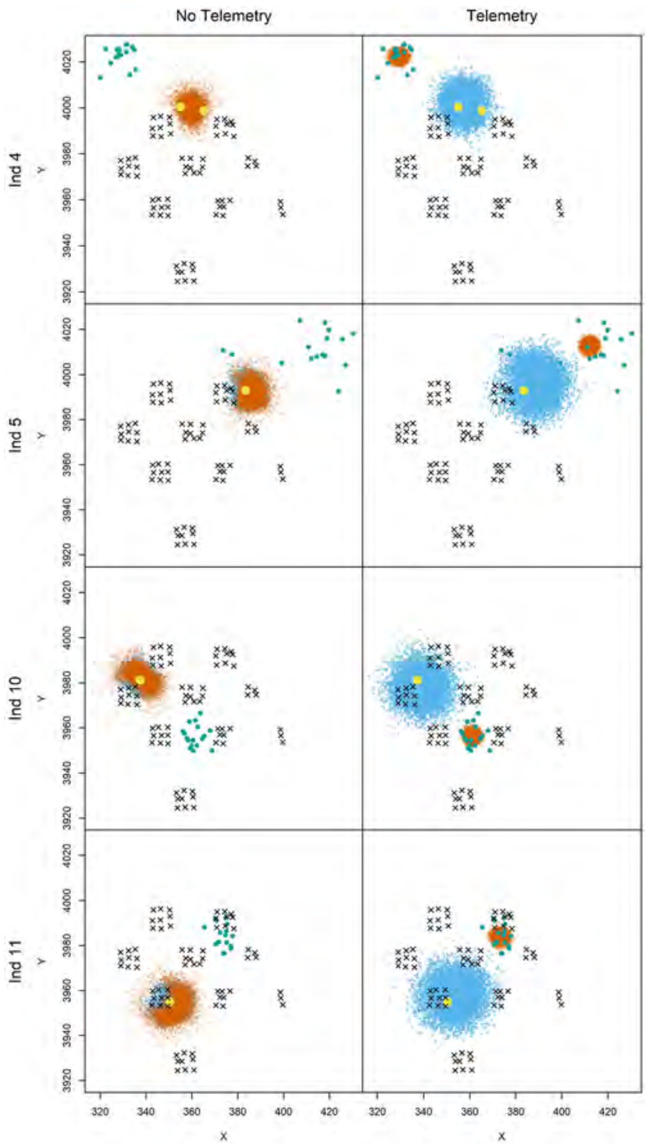

Figure 2. Estimated activity center locations for four marked pumas from generalized spatial mark-resight models that accommodated activity center transiency between marking and resighting processes, and excluded or included telemetry location data from GPS collars. The estimated posterior densities of individual activity centers for the marking and resighting processes are denoted by blue and orange, respectively. The spatial locations where each puma was live-captured, the locations of camera-traps, and thinned telemetry locations from the resighting period are denoted by yellow circles, black × , and green circles, respectively. Image created by B.C.A. with the R statistical software[60].

these spatial patterns in activity centers, but conSMR models exclude the marking process and consequently may produce negatively biased density estimates[37,39]. Indeed, our puma density estimates from conSMR models were ~17% lower than density estimated by our best genSMR model (model 3), chosen because of its most accurate characterization of the observed puma spatial dynamics (e.g., activity center transiency [through telemetry data] and spatial information about sex of unmarked pumas). Thus, our results support that genSMR models are preferable to conSMR models when the marking process involves live-capture and the marking and resighting arrays spatially overlap; particularly if researchers cannot assume that marked animals are uniformly distributed across the landscape, or the spatial distribution of marked animals is unknown and cannot be correctly specified.

Integrating telemetry data from GPS collars on marked pumas substantially improved parameter estimate precision and was critical for accurately estimating population density. First, the telemetry data allowed us to definitively determine individual identities from photograph detections. This was arguably more reliable than attempting to assign identities *ad hoc* based on researcher-perceived natural marks for a species that generally does not have unambiguous, individually unique physical features[24–27]. Although researchers may be tempted to treat all pumas detected by camera-traps as unmarked and apply the 'unmarked' spatial capture-recapture model[34] to estimate population density, the large home ranges and generally low detection rates of pumas, regardless of sampling method, will likely result in biased, imprecise, and unreliable density estimates from this model[39,40]. Applying artificial marks to even a small portion of a population and using SMR models can greatly improve estimation of detection function parameters and population density[26,34,36,37,39].

Telemetry data also facilitated accurate estimation of σ^d, which our results suggest was substantially underestimated by the models that relied solely on camera-trap detection data (models 2, 4, and 6). To establish our clustered camera-trap design, we based simulations on parameter estimates from previously published spatially explicit puma density studies. Based on the σ that we used in simulations (5.0 km), we presumed that our camera-trap and cluster spacing were 0.70σ and $5.60–7.20\sigma$, respectively; however, based on the σ^d estimated by our best model (model 3), camera-trap and cluster spacing turned out to be 30% smaller ($0.54\sigma^d$ and $4.30–5.53\sigma^d$, respectively). If home ranges are large and detection rates are low ($\lambda_0 < 0.10$), detector spacing as small as 0.5σ may be too close to accurately characterize the true scale of animal movement within a single cluster[43,45]. Estimated λ_0^R was <0.10 among all of our considered models, and each of the nine clusters of camera-traps was considerably smaller than the average puma home range size derived from estimated σ^d, assuming a bivariate normal distribution[19] (110.25-km^2 cluster size versus 799.23-km^2 home range size, based on model 3). Consequently, the full extent of individual puma space use likely could not be captured within a single cluster[45], which resulted in underestimation of σ^d and overestimation of puma density by the models that excluded telemetry data. Employing a wider camera-trap spacing of $1–2\sigma^d$ (6.51–13.02 km) within each cluster likely would have resulted in detections via the camera-traps alone that more accurately reflected the larger than expected puma space use[45]. Although our spacing between clusters was well within the movement capabilities of pumas in the study area (based on estimated σ^d), a wider camera-trap spacing within clusters would also decrease the distance between clusters, which might have the added benefit of increasing the number of spatial recaptures[43,45].

An alternative but unlikely explanation for the smaller σ^d and higher puma density estimates from models that excluded telemetry data could be that the marked pumas were not a random sample of the population, but were instead representative of a cohort of pumas that had larger than average home ranges[36]. Subadult male pumas are generally transient and typically have the largest home ranges among all sex-specific cohorts of puma populations[69]. We live-captured and marked both subadults and adults and both males and females, however, and although just 20% of our marked pumas were females, genSMR model results suggested that only 33–34% of the population was female. Furthermore, the point and interval estimates of puma density from the genSMR model with sex-specific detection function parameters (model 9) were nearly identical to the analogous model with detection function parameters pooled between sexes (model 1). This strongly supports that a sex imbalance among marked individuals was not a source of incongruous σ^d estimates between models that included and excluded telemetry data, thereby indicating that density estimates from the genSMR models that integrated telemetry data more accurately reflected puma space use during our study.

A third reason supporting the importance of telemetry data, and a primary reason why the transient activity center model improved density estimation, was to accurately estimate activity center locations for the pumas who relocated considerable distances between the marking and resighting processes. Efford and Hunter[35] raised concerns about the potential for such activity center transiency between observation processes to influence SMR model parameter estimates, but those authors had no independent data to test for this. In contrast, the telemetry data that we had from marked pumas allowed us to document and model large activity center relocations between processes. Because the four marked pumas who relocated were not detected by camera-traps, the resighting data provided little information about whether or not those individuals' activity center locations moved, and if so, how far. Although two pumas (individuals 10 and 11) moved to areas of the camera-trap array where they likely had similar detectability as the locations at which they were live-captured and marked, two other pumas (individuals 4 and 5) moved to areas where they were effectively undetectable by all camera-traps (Fig. 2). In model 1, which did not accommodate activity center transiency, the distances between live-capture locations and the estimated activity center locations, which were primarily informed by the telemetry data, were larger than reality. This inflated the σ^d estimate (7.54 versus 6.51 km from models 1 and 3, respectively), which in turn decreased the λ_0^R and λ_0^M estimates. These differences in detection function parameters corresponded to a ~12% difference in puma density point estimates (0.94 versus 0.84 puma/100 km^2), suggesting that accommodating activity center transiency may be important for reliably estimating population density in SMR studies. Additionally, σ^t was substantially underestimated without the telemetry data, because all four major movements were not discernable from the camera-trap data; this caused poor estimation of those pumas' activity center locations and introduced bias into detection function and density parameter estimates. Thus, having considerable telemetry data likely will lead to a more robust application of SMR models, informing if activity center transiency needs to be accommodated in the model structure to improve parameter estimation.

Fully transient activity centers have been considered in conSMR models[61], but our study is the first application of a single activity center transition that was used to explain observed animal movement dynamics. The base genSMR model provides an adequate description of the distribution of marked and unmarked individuals if they do not relocate between the marking and resighting processes; if individuals randomly relocate between processes, which is unlikely, the spatial uniformity activity center model may be appropriate. Accommodating activity center transiency as we did results in an intermediate activity center model in which individuals are not at exactly the same spatial location between processes and the similarity of locations is determined by the σ^t parameter. However, if individual animals exhibit multiple substantial movements during observation processes, an activity center model that accommodates fully transient activity centers might be more appropriate[61,62]. Nevertheless, distinguishing between a process model with stationary activity centers and a large σ^d value and a model with transient activity centers and a small σ^d value will be difficult without considerable telemetry data, given the sparsity of typical capture-recapture and mark-resight detection data.

Despite the relatively small improvement in density estimate precision from using sex as a categorical identity covariate compared to the substantial improvement from incorporating telemetry data, using categorical identity covariate data that is available from camera-trap detections has considerable promise. The 8% precision improvement that we observed by using sex of unmarked pumas comes from data that has not been used in SMR models to date, but ecologists and managers should be interested in extracting as much precision out of detection data as possible. Additionally, sex was a single categorical identity covariate that we confirmed for only approximately half of the detections of unmarked pumas. Other populations of pumas or other wildlife species may provide more categorical identity covariate information from photographs; for example, the natural marks used by previous studies to attempt to assign individual identities for estimating population density[24,25,27,61,70] could instead be treated as categorical identity covariates, allowing for the possibility that more than one individual in a population has a similar physical feature. This would obviate the requirement that potentially erroneous individual identities are assigned, but it may also reduce the precision of density estimates, perhaps appropriately, depending on the accuracy of categorical identities assigned by observers.

We acknowledge that using GPS collars as the primary mark can be expensive, but our results indicate that the realized and potential benefits of marking a portion of a population with GPS collars outweigh the costs. Clearly, integrating telemetry data in spatially explicit analyses can substantially improve estimation of the spatial scale parameter, activity center locations, and population density, as also noted by previous studies[26,36,37,39]. Furthermore, by marking a portion of animals with GPS collars, which are typically functional for multiple years, additional demographic and ecological information that are important to conservation and management can be obtained, effectively constituting SMR as a population ecology research approach. This includes data on survival and cause-specific mortality, home range size, and resource selection[71,72], as well as seasonal and annual variation in population density if camera-traps are active across seasons and years, respectively. Additionally, if population genetics are of interest, genetic samples can be collected when animals are captured for marking. If study budgets are limited, a cheaper alternative may be to mark some animals with GPS collars and others with only ear tags or non-GPS collars that have visually unique numbers or patterns that can be identified from photographs. For example, Whittington *et al.*[37] GPS-collared some individuals, only ear-tagged others, and used camera-traps and genSMR models to precisely estimate brown bear (*Ursus arctos*) population density.

Pumas occupy tens to hundreds of thousands of square kilometers within most jurisdictions across their extant range[1,69,73]. In general, precision and accuracy of spatially explicit population density estimates for wide-ranging large carnivores improve with increasing study area size[44,45,74]. By deploying camera-traps in a systematic cluster design with gaps between clusters where no cameras existed, we were able to use a small number of camera-traps to estimate puma density for a 15,317-km^2 area. This area was five-fold larger than the average spatial extent among all previous puma density studies that also used spatially explicit models (mean = 2,849 km^2; range: 215–8,800 km^2), and our density estimates were among the most precise estimates that have been produced for pumas to date ($CV_{[genSMR]} = 0.24–0.31$; Table 2). Therefore, clustered camera-trapping in an SMR framework can facilitate efficient and reliable estimation of puma population density at the broad regional scales that conservation and management typically occur. For example, endangered Florida panthers (*P. c. coryi*) reside within a ~16,000-km^2 area that encompasses multiple patches of suitable habitat[75], and a portion of panthers are annually captured and collared[26,76]. Applying clustered camera-trapping across that entire area and using genSMR models to analyze detection data could result in the first range-wide spatially explicit estimates of Florida panther population density and abundance, with little additional effort compared to other available puma sampling approaches in the spatially explicit framework. Our sampling and analytical combination is likely also applicable to other terrestrial mammals that similarly lack individually unique natural markings. For instance, obtaining reliable population density and abundance estimates for imperiled Mexican gray wolves (*Canis lupus baileyi*) and red wolves (*C. rufus*) is important to their recovery, and individual wolves in those populations are routinely monitored via radiocollars that could serve as effective marks. Nevertheless, we agree with other studies that suggested researchers should use simulation to develop study area- and species-specific survey designs prior to deploying camera-traps[43,45,74]. Having home range size data beforehand to inform camera-trap and cluster spacing would be ideal[45], but if such data are unavailable, our results support that marking a portion of animals with GPS collars and integrating their telemetry location data in spatially explicit models can serve as insurance if detector spacing turns out to be insufficient[36].

Our study provides the first spatially explicit population density estimates for pumas in the semi-arid to arid southwestern United States, where hot summer temperatures, high ultraviolet radiation, and generally limited winter snow cover may impede effectiveness of, or preclude, scat detection dog and biopsy dart sampling of pumas. Regardless of model specification, all of our puma density estimates were within the range of reported spatially explicit estimates for the species, but density estimated by our best model (0.84 puma/100 km^2) was towards the lower bound of that range (Table 2). Estimates acquired using the biopsy dart and scat detection dog methods may not be directly comparable to our estimates, however, because estimates from those techniques might be inflated as a result of including dependent juveniles in the detection histories[20,23], whereas our estimates pertain solely to independent pumas. Nonetheless, the majority of our study area was characterized as high quality puma habitat relative to elsewhere in the Southwest[73]; thus, our estimates suggest that the Southwest might commonly support pumas at lower densities than ecosystems in the Northwest and Northern Rockies regions[20–24,51]. Additional research is needed to evaluate the influence that legal harvest of pumas and prey availability and distribution may have on seasonal and annual variation of puma population density in our study area and across the Southwest in general.

Study	Location	Methods	Models	Area	Densities	Widths	CVs
This study	New Mexico, USA	CC + TL	genSMR	15,314	0.84–1.65	0.8–1.8	0.24–0.31
Sollmann *et al.*[26]	Florida, USA	RC + TL	conSMR	1,719	1.46–1.51	1.9–2.2	0.33–0.38
Rich *et al.*[25]	Belize, Bolivia, Argentina	RC	conSMR	4,329*	0.30–6.50	0.5–8.1	0.26–0.38
Zanón-Martinez *et al.*[27]	Argentina	RC	conSMR	1,179*	1.38–4.90	3.3–5.9	0.31–0.66
Quiroga *et al.*[77]	Argentina	RC	SCR	1,882*	0.08–1.26	0.2–1.0	—
Noss *et al.*[78]	Bolivia	RC	SCR	215*	0.36–7.99	0.7–9.9	0.20–0.85
Alexander and Gese[24]	Wyoming, USA	RC	SCR	1,287	0.39–4.04†	0.6–9.9	—
Proffitt *et al.*[21]	Montana, USA	BD + SB + DR	SCR	5,912	3.20–5.60	2.9–14.0	—
Russell *et al.*[22]	Montana, USA	BD + SB	SCR	8,800	3.70–6.70	1.5–7.9	0.24–0.46
Beausoleil *et al.*[20]	Washington, USA	BD	SCR	7,939	1.90–2.40	3.2–3.9	—
Davidson *et al.*[23]	Oregon, USA	SD	SCR	1,225	2.31–5.50	1.2–5.8	—

Table 2. Study locations, sampling methods, model types, and parameter estimation areas (km^2) for studies that used spatial capture-recapture (SCR), conventional spatial mark-resight (conSMR), or generalized spatial mark-resight (genSMR) models to estimate puma population density (puma/100 km^2), ordered by sampling methods and model types. Methods included biopsy darting (BD), snow-backtracking (SB), scat detection dogs (SD), regular camera-trapping (RC), clustered camera-trapping (CC), dead recoveries (DR), and telemetry locations from GPS collars (TL). Coefficient of variation (CV), standard errors, or standard deviations were not reported by multiple studies (—), so we also present 95% interval widths for comparing precision of density estimates. Densities are presented as the ranges of point estimates. *Average among multiple study areas; †excludes one density estimate for which variance of the corresponding spatial scale parameter (σ) was inestimable.

Data Availability

All data generated for analysis and all R code of MCMC algorithms for reproducing the analysis are available from the PANGAEA® digital repository, https://doi.org/10.1594/PANGAEA.897113. Data were made available under provisions of the State of New Mexico Inspection of Public Records Act (1978 NMSA 14.2).

References

1. Ripple, W. J. *et al.* Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484, https://doi.org/10.1126/science.1241484 (2014).
2. Ripple, W. J. & Beschta, R. L. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biol. Conserv.* **133**, 397–408, https://doi.org/10.1016/j.biocon.2006.07.002 (2006).
3. Ripple, W. J. & Beschta, R. L. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biol. Conserv.* **141**, 1249–1256, https://doi.org/10.1016/j.biocon.2008.02.028 (2008).
4. Morehouse, A. T. & Boyce, M. S. Troublemaking carnivores: conflicts with humans in a diverse assemblage of large carnivores. *Ecol. Soc.* **22**, 4, https://doi.org/10.5751/ES-09415-220304 (2017).
5. Rominger, E. M. The Gordian knot of mountain lion predation and bighorn sheep. *J. Wildlife Manage.* **82**, 19–31, https://doi.org/10.1002/jwmg.21396 (2018).
6. LaRue, M. A. *et al.* Cougars are recolonizing the midwest: analysis of cougar confirmations during 1990–2008. *J. Wildlife Manage.* **76**, 1364–1369, https://doi.org/10.1002/jwmg.396 (2012).
7. Thompson, D. J. & Jenks, J. A. Dispersal movements of subadult cougars from the Black Hills: the notions of range expansion and recolonization. *Ecosphere* **1**, 1–11, https://doi.org/10.1890/ES10-00028.1 (2010).
8. Benson, J. F. *et al.* Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. *P. Roy. Soc. B.-Biol. Sci.* **283**, https://doi.org/10.1098/rspb.2016.0957 (2016).
9. Johnson, W. E. *et al.* Genetic restoration of the Florida panther. *Science* **329**, 1641–1645, https://doi.org/10.1126/science.1192891 (2010).
10. Beausoleil, R. A., Dawn, D., Martorello, D. A. & Morgan, C. P. Cougar management protocols: a survey of wildlife agencies in North America. [Toweill, D. E., Nadeau, S. & Smith, D. (eds)] *Proceedings of the 9th Mountain Lion Workshop*, 205–241. (Idaho Department of Fish and Game, Sun Valley, 2008).
11. Beausoleil, R. A., Koehler, G. M., Maletzke, B. T., Kertson, B. N. & Wielgus, R. B. Research to regulation: cougar social behavior as a guide for management. *Wildlife Soc. B.* **37**, 680–688, https://doi.org/10.1002/wsb.299 (2013).
12. Darimont, C. T., Paquet, P. C., Treves, A., Artelle, K. A. & Chapron, G. Political populations of large carnivores. *Conserv. Biol.* **32**, 747–749, https://doi.org/10.1111/cobi.13065 (2018).
13. Beausoleil, R. A. Standardization of cougar population metrics. [McLaughlin, C. R. & Vieira, M. (eds)] *Proceedings of the 12th Mountain Lion Workshop, 35*, (Colorado Parks & Wildlife, Estes Park, 2017).
14. Apker, J. Jurisdictional mountain lion management survey: synthesis of research and management. [McLaughlin, C. R. & Vieira, M. (eds)] *Proceedings of the 12th Mountain Lion Workshop*, 37–173, (Colorado Parks & Wildlife, Estes Park, 2017).
15. Whittaker, D. & Wolfe, M. L. Assessing and monitoring cougar populations. [Jenks, J. A. (ed)] *Managing Cougars in North America*, 74–94, (Berryman Institute Press, Utah State University, Logan, 2011).
16. Choate, D. M., Wolfe, M. L. & Stoner, D. C. Evaluation of cougar population estimators in Utah. *Wildlife Soc. B.* **34**, 782–799, https://doi.org/10.2193/0091-7648(2006)34[782:EOCPEI]2.0.CO;2 (2010).
17. Sollmann, R., Mohamed, A., Samejima, H. & Wilting, A. Risky business or simple solution - relative abundance indices from camera-trapping. *Biol. Conserv.* **159**, 405–412, https://doi.org/10.1016/j.biocon.2012.12.025 (2013).
18. Efford, M. G. & Fewster, R. M. Estimating population size by spatially explicit capture-recapture. *Oikos* **122**, 918–928, https://doi.org/10.1111/j.1600-0706.2012.20440.x (2013).
19. Royle, J. A., Chandler, R. B., Sollmann, R. & Gardner, B. *Spatial Capture-Recapture*. (Academic Press, Waltham, 2014).
20. Beausoleil, R. A., Clark, J. D. & Maletzke, B. T. A long-term evaluation of biopsy darts and DNA to estimate cougar density: an agency-citizen science collaboration. *Wildlife Soc. B.* **40**, 583–592, https://doi.org/10.1002/wsb.675 (2016).
21. Proffitt, K. M. *et al.* Integrating resource selection into spatial capture-recapture models for large carnivores. *Ecosphere* **6**, 1–15, https://doi.org/10.1890/ES15-00001.1 (2015).

22. Russell, R. E. *et al.* Estimating abundance of mountain lions from unstructured spatial sampling. *J. Wildlife Manage.* **76**, 1551–1561, https://doi.org/10.1002/jwmg.412 (2012).
23. Davidson, G. A., Clark, D. A., Johnson, B. K., Waits, L. P. & Adams, J. R. Estimating cougar densities in northeast Oregon using conservation detection dogs. *J. Wildlife Manage.* **78**, 1104–1114, https://doi.org/10.1002/jwmg.758 (2014).
24. Alexander, P. D. & Gese, E. M. Identifying individual cougars (*Puma concolor*) in remote camera images - implications for population estimates. *Wildlife Res.* **45**, 274–281, https://doi.org/10.1071/WR17044 (2018).
25. Rich, L. N. *et al.* Comparing capture-recapture, mark-resight, and spatial mark-resight models for estimating puma densities via camera traps. *J.Mammal.* **95**, 382–391, https://doi.org/10.1644/13-MAMM-A-126 (2014).
26. Sollmann, R. *et al.* Using multiple data sources provides density estimates for endangered Florida panther. *J. Appl. Ecol.* **50**, 961–968, https://doi.org/10.1111/1365-2664.12098 (2013).
27. Zanón-Martinez, J. I. *et al.* Density and activity patterns of pumas in hunted and non-hunted areas in central Argentina. *Wildlife Res.* **43**, 449–460, https://doi.org/10.1071/WR16056 (2016).
28. Puckett, E. E. Variability in total project and per sample genotyping costs under varying study designs including with microsatellites or SNPs to answer conservation genetic questions. *Conserv. Genet. Resour.* **9**, 289–304, https://doi.org/10.1007/s12686-016-0643-7 (2017).
29. Long, R. A., Donovan, T. M., Mackay, P., Zielinski, W. J. & Buzas, J. S. Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. *J. Wildlife Manage.* **71**, 2018–2025, https://doi.org/10.2193/2006-292 (2007).
30. Murphy, M. A., Kendall, K. C., Robinson, A. & Waits, L. P. The impact of time and field conditions on brown bear (*Ursus arctos*) faecal DNA amplification. *Conserv. Genet.* **8**, 1219–1224, https://doi.org/10.1007/s10592-006-9264-0 (2007).
31. Burton, A. C. *et al.* Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* **52**, 675–685, https://doi.org/10.1111/1365-2664.12432 (2015).
32. Foster, R. J. & Harmsen, B. J. A critique of density estimation from camera-trap data. *J. Wildlife Manage.* **76**, 224–236, https://doi.org/10.1002/jwmg.275 (2012).
33. Jędrzejewski, W. *et al.* Density and population structure of the jaguar (*Panthera onca*) in a protected area of Los Llanos, Venezuela, from 1 year of camera trap monitoring. *Mammal Res.* **62**, 9–19, https://doi.org/10.1007/s13364-016-0300-2 (2017).
34. Chandler, R. B. & Royle, J. A. Spatially explicit models for inference about density in unmarked or partially marked populations. *Ann. Appl. Stat.* **7**, 936–954, https://doi.org/10.1214/12-AOAS610 (2013).
35. Efford, M. G. & Hunter, C. M. Spatial capture-mark-resight estimation of animal population density. *Biometrics* **74**, 411–420, https://doi.org/10.1111/biom.12766 (2018).
36. Sollmann, R. *et al.* A spatial mark-resight model augmented with telemetry data. *Ecology* **94**, 553–559, https://doi.org/10.1890/12-1256.1 (2013).
37. Whittington, J., Hebblewhite, M. & Chandler, R. B. Generalized spatial mark-resight models with an application to grizzly bears. *J. Appl. Ecol.* **55**, 157–168, https://doi.org/10.1111/1365-2664.12954 (2018).
38. Rowe, C. B., Augustine, B. C. & Kelly, M. J. Estimating puma densities from camera trap data using generalized spatial partial identity models. [McLaughlin, C. R. & Vieira, M. (eds)] *Proceedings of the 12th Mountain Lion Workshop*, 32, (Colorado Parks & Wildlife, Estes Park, 2017).
39. Augustine, B. C., Stewart, F., Royle, J. A., Fisher, J. & Kelly, M. J. Spatial mark-resight for categorically marked populations with an application to genetic capture-recapture. *bioRxiv*, https://doi.org/10.1101/299982 (2018).
40. Augustine, B. C. *et al.* Spatial capture-recapture for categorically marked populations with an application to genetic capture-recapture. *Ecosphere* **10**, e02627, https://doi.org/10.1002/ecs2.2627 (2019).
41. Humm, J. M., McCown, J. W., Scheick, B. K. & Clark, J. D. Spatially explicit population estimates for black bears based on cluster sampling. *J. Wildlife Manage.* **81**, 1187–1201, https://doi.org/10.1002/jwmg.21294 (2017).
42. Sollmann, R., Gardner, B. & Belant, J. L. How does spatial study design influence density estimates from spatial capture-recapture models? *PLoS One* **7**, e34575, https://doi.org/10.1371/journal.pone.0034575 (2012).
43. Sun, C. C., Fuller, A. K. & Royle, J. A. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. *PLoS One* **9**, e88025, https://doi.org/10.1371/journal.pone.0088025 (2014).
44. Wilton, C. M. *et al.* Trap array configuration influences estimates and precision of black bear density and abundance. *PLoS One* **9**, e111257, https://doi.org/10.1371/journal.pone.0111257 (2014).
45. Clark, J. D. Comparing clustered sampling designs for spatially explicit estimation of population density. *Popul. Ecol.* **16**, 93–101, https://doi.org/10.1002/1438-390X.1011 (2019).
46. Western Regional Climate Center. Cooperative climatological data summaries: monthly climate summaries for Bernalillo and Wolf Canyon, New Mexico. http://www.wrcc.dri.edu/ (2018).
47. Logan, K. A., Sweanor, L. L., Smith, J. F. & Hornocker, M. G. Capturing pumas with foot-hold snares. *Wildlife Soc. B.* **27**, 201–208 (1999).
48. Wilckens, D. T., Smith, J. B., Tucker, S. A., Thompson, D. J. & Jenks, J. A. Mountain lion (*Puma concolor*) feeding behavior in the Little Missouri Badlands of North Dakota. *J. Mammal.* **97**, 373–385, https://doi.org/10.1093/jmammal/gyv183 (2016).
49. Kreeger, T. J. & Arnemo, J. M. *Handbook of Wildlife Chemical Immobilization*, fourth edition (Authors, 2012).
50. Laundré, J. W., Hernández, L., Streubel, D., Altendorf, K. & López González, C. Aging mountain lions using gum-line recession. *Wildlife Soc. B.* **28**, 963–966 (2000).
51. Logan, K. A., Sweanor, L. L., Ruth, T. K. & Hornocker, M. G. *Cougars of the San Andreas Mountains, New Mexico*. Final Report to New Mexico Department of Game & Fish for Project W-128-R (Hornocker Wildlife Institute, University of Idaho, Moscow, 1996).
52. Pease, B. S., Nielsen, C. K. & Holzmueller, E. J. Single-camera trap survey designs miss detections: impacts on estimates of occupancy and community metrics. *PLoS One* **11**, e0166689, https://doi.org/10.1371/journal.pone.0166689 (2016).
53. Sunquist, M. & Sunquist, F. *Wild Cats of the World* (University of Chicago Press, Chicago, 2002).
54. Braczkowski, A. R. *et al.* Scent lure effect on camera-trap based leopard density estimates. *PLoS One* **11**, e0151033, https://doi.org/10.1371/journal.pone.0151033 (2016).
55. Long, E. S. *et al.* Efficacy of photographic scent stations to detect mountain lions. *West. N. Am. Naturalist* **63**, 529–532 (2003).
56. Portella, T. P., Bilski, D. R., Passos, F. C. & Pie, M. R. Assessing the efficacy of hair snares as a method for noninvasive sampling of Neotropical felids. *Zoologia-Curitiba* **30**, 49–54, https://doi.org/10.1590/S1984-46702013000100006 (2013).
57. McBride, R. & McBride, C. Florida panther flehmen response recorded at baited trail camera site. *Southeast. Nat.* **9**, 629–631, https://doi.org/10.1656/058.009.0319 (2010).
58. McBride, R. & Sensor, R. Efficacy of trail cameras to identify individual Florida panthers. *Southeast. Nat.* **14**, 351–360, https://doi.org/10.1656/058.014.0215 (2015).
59. Augustine, B. C. *SPIM: spatial partial identity models*. R package version 0.1, https://www.github.com/benaug/SPIM/ (2018).
60. R Core Team. R: a language and environment for statistical computing, v. 3.5.0. R Foundation for Statistical Computing, Vienna, https://www.r-project.org/ (2018).
61. Jiménez, J., Higuero, R., Charre-Medellin, J. F. & Acevedo, P. Spatial mark-resight models to estimate feral pig population density. *Hystrix* **28**, 208–213, https://doi.org/10.4404/hystrix-28.2-12141 (2017).
62. Royle, J. A., Fuller, A. K. & Sutherland, C. Spatial capture-recapture models allowing Markovian transience or dispersal. *Popul. Ecol.* **58**, 53–62, https://doi.org/10.1007/s10144-015-0524-z (2016).
63. Gonzalez-Borrajo, N., López-Bao, J. V. & Palomares, F. Spatial ecology of jaguars, pumas, and ocelots: a review of the state of knowledge. *Mammal Rev.* **47**, 62–75, https://doi.org/10.1111/mam.12081 (2016).

64. Maletzke, B. T. *et al.* Effects of hunting on cougar spatial organization. *Ecol. Evol.* **4**, 2178–2185, https://doi.org/10.1002/ece3.1089 (2014).
65. Schaub, M. & Royle, J. A. Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. *Methods Ecol. Evol.* **5**, 1316–1326, https://doi.org/10.1111/2041-210X.12134 (2014).
66. Royle, J. A., Karanth, K. U., Gopalaswamy, A. M. & Kumar, N. S. Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology* **90**, 3233–3244, https://doi.org/10.1890/08-1481.1 (2009).
67. Sikes, R. S. *et al.* Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J. Mammal.* **97**, 663–688, https://doi.org/10.1093/jmammal/gyw078 (2016).
68. Efford, M. G. & Mowat, G. Compensatory heterogeneity in spatially explicit capture-recapture data. *Ecology* **95**, 1341–1348, https://doi.org/10.1890/13-1497.1 (2014).
69. Fecske, D. M., Thompson, D. J. & Jenks, J. A. Cougar ecology and natural history. [Jenks, J. A. (ed)] *Managing Cougars in North America*, 6–38, (Berryman Institute Press, Utah State University, Logan, 2011).
70. Kane, M. D., Morin, D. J. & Kelly, M. J. Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodivers. Conserv.* **24**, 3527–3541, https://doi.org/10.1007/s10531-015-1012-7 (2015).
71. Cagnacci, F., Boitani, L., Powell, R. A. & Boyce, M. S. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos. T. R. Soc. B.* **365**, 2157–2162, https://doi.org/10.1098/rstb.2010.0107 (2010).
72. Hebblewhite, M. & Haydon, D. T. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philos. T. R. Soc. B.* **365**, 2303–2312, https://doi.org/10.1098/rstb.2010.0087 (2010).
73. Dickson, B. G., Roemer, G. W., McRae, B. H. & Rundall, J. M. Models of regional habitat quality and connectivity for pumas (*Puma concolor*) in the southwestern United States. *PLoS One* **8**, e81898, https://doi.org/10.1371/journal.pone.0081898 (2013).
74. Tobler, M. W. & Powell, G. V. N. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. *Biol. Conserv.* **159**, 109–118, https://doi.org/10.1016/j.biocon.2012.12.009 (2013).
75. Frakes, R. A., Belden, R. C., Wood, B. E. & James, F. E. Landscape analysis of adult Florida panther habitat. *PLoS One* **10**, e0133044, https://doi.org/10.1371/journal.pone.0133044 (2015).
76. McClintock, B. T., Onorato, D. P. & Martin, J. Endangered Florida panther population size determined from public reports of motor vehicle collision mortalities. *J. Appl. Ecol.* **52**, 893–901, https://doi.org/10.1111/1365-2664.12438 (2015).
77. Quiroga, V. A., Noss, A. J., Paviolo, A., Boaglio, G. I. & Di Bitetti, M. S. Puma density, habitat use and conflict with humans in the Argentine Chaco. *J. Nat. Conserv.* **31**, 9–15, https://doi.org/10.1016/j.jnc.2016.02.004 (2016).
78. Noss, A. J. *et al.* Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del Gran Chaco landscape. *Anim. Conserv.* **15**, 527–535, https://doi.org/10.1111/j.1469-1795.2012.00545.x (2012).
79. Homer, C. *et al.* Completion of the 2011 National Land Cover Database for the conterminous United States – representing a decade of land cover change information. *Photogramm. Eng. Rem. S.* **81**, 345–354, https://doi.org/10.14358/PERS.81.5.345 (2015).

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Author Contributions

S.M.M. conceived the idea and led manuscript writing; S.M.M. and D.T.W. designed the study; S.M.M., D.T.W., M.A.P. and G.C.H. collected the data; S.M.M. and B.C.A. analyzed the data. All authors contributed to writing, reviewed drafts, and gave final approval for publication.

Additional Information

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A Test of the Compensatory Mortality Hypothesis in Mountain Lions: A Management Experiment in West-Central Montana
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Research Article

A Test of the Compensatory Mortality Hypothesis in Mountain Lions: A Management Experiment in West-Central Montana

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ABSTRACT Mountain lions (*Puma concolor*) are widely hunted for recreation, population control, and to reduce conflict with humans, but much is still unknown regarding the effects of harvest on mountain lion population dynamics. Whether human hunting mortality on mountain lions is additive or compensatory is debated. Our primary objective was to investigate population effects of harvest on mountain lions. We addressed this objective with a management experiment of 3 years of intensive harvest followed by a 6-year recovery period. In December 2000, after 3 years of hunting, approximately 66% of a single game management unit within the Blackfoot River watershed in Montana was closed to lion hunting, effectively creating a refuge representing approximately 12% (915 km^2) of the total study area (7,908 km^2). Hunting continued in the remainder of the study area, but harvest levels declined from approximately 9/1,000 km^2 in 2001 to 2/1,000 km^2 in 2006 as a result of the protected area and reduced quotas outside. We radiocollared 117 mountain lions from 1998 to 2006. We recorded known fates for 63 animals, and right-censored the remainder. Although hunting directly reduced survival, parameters such as litter size, birth interval, maternity, age at dispersal, and age of first reproduction were not significantly affected. Sensitivity analysis showed that female survival and maternity were most influential on population growth. Life-stage simulation analysis (LSA) demonstrated the effect of hunting on the population dynamics of mountain lions. In our non-hunted population, reproduction (kitten survival and maternity) accounted for approximately 62% of the variation in growth rate, whereas adult female survival accounted for 30%. Hunting reversed this, increasing the reliance of population growth on adult female survival (45% of the variation in population growth), and away from reproduction (12%). Our research showed that harvest at the levels implemented in this study did not affect population productivity (i.e., maternity), but had an additive effect on mountain lion mortality, and therefore population growth. Through harvest, wildlife managers have the ability to control mountain lion populations. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS additive mortality, carnivore, compensatory mortality, cougar, hunting, life-stage simulation analysis, Montana, population dynamics, *Puma concolor*, survival.

Errington (1956) coined the term "doomed surplus" to describe animals that would die by other natural causes if not killed by predators. Many hunting programs assume a similar relationship to human harvest, namely, density-dependent compensatory mortality. Modern wildlife management and hunting programs are premised on the idea of sustainable yield, and the concept of a harvestable surplus due to compensatory mortality (Larkin 1977). Under the compensatory mortality hypothesis, harvest mortalities are compensated by reductions in non-harvest mortality (compensatory mortality), increases in reproduction (compensatory natality), or immigration (Boyce et al. 1999, Williams et al. 2002, Turgeon and Kramer 2012). Evidence of compensation has been shown in a variety of species including game birds (Burnham and Anderson 1984, Sandercock et al. 2011), ungulates (Bartmann et al. 1992, Simard et al. 2013), and carnivores (Sterling et al. 1983, Sparkman et al. 2011). All mortality is not compensatory, however, as evidenced by the numerous populations that

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have been threatened or driven to extinction by overharvest (e.g., Baker and Clapham 2004, McGlone 2012). Managers would benefit from a better understanding of the life-history traits and harvest levels where mortality moves from compensatory to additive in many exploited populations (Sandercock et al. 2011, Peron 2013).

Carnivores are hunted for both sport, where population stability is desired, and population control, where mortality must be additive to achieve reduced population levels. In North America, perhaps because of their conflict with humans, a great deal of early research into the effect of harvest on a carnivore species focused on coyotes (*Canis latrans*). This work suggested that harvest mortality was largely compensatory through immigration and density-dependent or compensatory natality (Knowlton 1972, Todd and Keith 1983, Knowlton et al. 1999). These early findings, combined with a reluctance to study other disturbed or hunted populations of large carnivores, shaped management perceptions through the 1970s and 1980s (Frank and Woodroffe 2001). Recent research has suggested that hunting mortality in other carnivores may be almost perfectly additive (Creel and Rotella 2010, Murray et al. 2010).

Evidence of the additive nature of hunting to mountain lion mortality and population growth has been shown in past studies where populations were reduced through hunting, and/or increased once harvest level was reduced (Lindzey et al. 1992, Ross and Jalkotzy 1992, Lambert et al. 2006). Conversely, non-hunted populations often show high levels of intraspecific strife and mortality, leading some to speculate that hunting may be compensatory (Quigley and Hornocker 2010). The effect of harvest on a population is dependent on total harvest rate, age, and sex classes being harvested, and compensation for harvest by increases in survival or other vital rates such as maternity and immigration (Mills 2007).

The combined effects of harvest and dispersal include changes to age and social structure that may cascade through a hunted population, magnifying or reducing the effects of harvest. Mountain lions display high levels of juvenile dispersal (Chepko-Sade et al. 1987, Sweanor et al. 2000, Zimmermann et al. 2005). Males disperse to avoid inbreeding regardless of population density (intrinsic dispersal), whereas females disperse, albeit at much lower levels than males, to avoid intraspecific competition (Greenwood 1980, Logan and Sweanor 2001). Hunting can therefore skew the sex and age ratio of a population towards younger males as harvested males are quickly replaced through juvenile immigration (Robinson et al. 2008). Vertebrate species have adapted to specific age and sex population structures. Males, in general, reach sexual maturity more quickly than females because of reduced life spans (Jones et al. 2008, Ricklefs 2008). Deviations from "natural" population age and demographic structure could reduce productivity (Nussey et al. 2009). Reproductive senescence is common in mammalian females as they age (Packer et al. 1998, Berube et al. 1999). Hostetler et al. (2012) found reduced litter production in female mountain lions (Florida panthers) >9 years. Maternity of mountain lions may be reduced in hunted populations if younger males do not breed successfully, or if female recruitment is restricted and kitten production is reduced as females senesce (Berube et al. 1999), both additive effects. Conversely, harvest may reduce direct resource competition among females, resulting in increased litter sizes or maternity rates (Ordiz et al. 2008), a compensatory effect.

Logan et al. (1986) and Logan and Sweanor (2001) suggested that removal of male mountain lions from a population may decrease survival of remaining resident males by disrupting social organization and increasing direct or exploitative competition for mates and territory. Also, the loss of dominant, territorial males may increase instances of infanticide, an unexpected additive form of mortality (Logan and Sweanor 2001). Male mountain lions may kill kittens to induce their mothers into estrous, thus increasing breeding opportunities (Packer et al. 2009). However, the role played by infanticide in shaping kitten survival remains unclear. Harvest programs can induce immigration of new males, thereby increasing infanticide rates and limiting population growth (Swenson et al. 1997). A high level of male turnover resulted in increased levels of infanticide in African felids (Whitman et al. 2004, Balme et al. 2010).

Unlike ungulate species that give birth in a single "birth pulse" in early spring, mountain lions give birth year-round. In the United States, mountain lions are most heavily hunted from September to March (Cooley et al. 2011), which exposes dependent kittens to the risk of starvation due to abandonment following harvest of their mothers, perhaps increasing their naturally high mortality (Logan and Sweanor 2001). Similar to the effects of hunting on adult mortality, however, how this source of mortality is compensated for by decreases in other natural mortality is not well understood.

Ultimately, the compensatory or additive effects of harvest are best measured at the population level in terms of population growth. Matrix population models are a widely used tool for exploring the relationship of various population parameters, or vital rates, on population growth (Getz and Haight 1989, Caswell 2001). Ecologists have used matrix models and the quantifiable properties of sensitivity and elasticity to mathematically describe the consequences of varying vital rates of several species with differing life strategies. Evolutionary theory suggests that natural selection will favor low levels of variation in population parameters that contribute most to population growth (Pfister 1998). In long-lived vertebrates, and other K-selected species, adult female survival normally has the highest demographic elasticity (Gaillard et al. 1998, 2000); that is, small changes in female survival will result in the largest proportional changes in population growth rate.

Although sensitivity analysis will reveal which vital rates have the greatest effect on population growth, those same vital rates may have such low natural variability that they functionally account for little variation in population growth between years. If K-selected species have adapted life strategies where the most important vital rates have the lowest degree of variability, hunting may disrupt this adaptive

Table 1. Predictions of how mountain lion population vital rates should respond to harvest under the compensatory and additive mortality hypothesis.

Vital rate	Compensatory mortality hypothesis	Additive mortality hypothesis
Reproduction		
Litter size	Increase	No effect or reduce
Maternity	Increase	No effect or reduce
Survival	No effect	Reduce
Dispersal		
Male emigration	Reduce	No effect
Female emigration	Reduce	No effect
Male immigration	Increase	No effect
Female immigration	Increase	No effect
Population growth	No effect	Reduce

strategy by increasing their variance. Wisdom et al. (2000) developed an extension of elasticity analysis called life-stage simulation analysis (LSA), which measures the direct effects of annual variance in vital rates on population growth.

We used temporal and spatial variation in harvest structure to test the compensatory mortality hypothesis by directly comparing population parameters (i.e., survival, maternity, etc.), population structure (i.e., mean age of independent males), and population growth between hunted and non-hunted segments of a mountain lion population. Specifically, if harvest mortality was compensatory, we expected population growth to tend toward stability regardless of harvest level because of compensatory reductions in other mortality sources, or through increases in reproduction and recruitment (Table 1). If harvest mortality was additive, we expected population growth to decline with increased harvest because of reduced survival accompanied by no change in reproduction or recruitment (Table 1). We also used matrix population modeling, sensitivity analysis, and LSA to quantify how harvest affects the natural variability of vital rates, and how those changes are reflected in annual population growth.

STUDY AREA

We conducted the study in the Blackfoot River watershed (7,908 km^2) in Powell, Granite, Lewis and Clark, and Missoula counties in West-Central Montana. Hunting district 292 served as our refuge area, hereafter referred to as the Garnet study area (915 km^2). This area was protected from hunting for 6 years of the 9-year study (Fig. 1). The entire watershed is characterized by relatively moderate rolling topography, with gentle to moderate slopes dissected by steep limestone canyon areas along drainages (Brainerd 1985). This area is representative of much of western Montana, a mountainous mix of private (i.e., Plum Creek Timber Company and private land owners) and public lands (i.e., Bureau of Land Management, Helena and Lolo National Forests) with elevations ranging from 1,160 m to 2,156 m (Montana Department of Fish, Wildlife and Parks 2004). Daily mean temperatures range from −8.7°C in January to 16.5°C in July with annual precipitation ranging from 19 cm to 33 cm, occurring primarily from December to June (Western Regional Climate Center, Ovando, MT).

Dominant land cover varies from high-elevation mixed lodgepole pine (*Pinus contorta*)-subalpine fir (*Abies lasiocarpa*)

Figure 1. The Garnet study area (915 km^2), and greater Blackfoot River watershed (7,908 km^2) in western Montana. Numbers (i.e., 292) represent Montana Fish, Wildlife and Parks regional mountain lion management unit designations.

stands, to more mesic Douglas-fir (*Pseudotsuga menziesii*)-western larch (*Larix occidentalis*) stands at mid-elevations, and Douglas fir, ponderosa pine (*P. ponderosa*), and aspen (*Populus tremuloides*) at low elevations. Valley bottoms consist of a mixture of irrigated and dry land agriculture, cattle rangelands, and native bunchgrass-sagebrush (*Artemisia* spp.)-juniper (*Juniperus scopulorum*) communities (Lehmkuhl 1981). The majority of the low to mid-elevation forests have been logged in the past 50 years (Raithel 2005).

Ungulate prey species present in the area included elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*). Elk populations were stable over the course of the study (Montana Department of Fish, Wildlife and Parks 2004), whereas deer populations may have been recovering from the El Nino-induced severe winter of 1996–1997 (Montana Department of Fish, Wildlife and Parks 2006). Cattle grazing occurred on private and public lands, however, cattle and other livestock depredations by mountain lions were rare. Carnivores besides mountain lions included black bear (*Ursus americanus*) and grizzly bear (*Ursus arctos*). Smaller predators included bobcat (*Lynx rufus*), Canada lynx (*Lynx canadensis*), coyote (*C. latrans*), wolverine (*Gulo gulo*), pine marten (*Martes americana*), and long-tailed weasel (*Mustela frenata*). Wolf (*Canis lupus*) had not recovered during the study period; the first confirmed pack established in 2006, the last year of our study (Montana Department of Fish, Wildlife and Parks 2006).

METHODS

In December 2000, following 3 years of heavy harvest, approximately 66% of a single hunting district was closed to mountain lion hunting, effectively creating a refuge representing approximately 12% (915 km^2) of the greater Blackfoot watershed (7,908 km^2) in West-Central Montana (Fig. 1). Hunting continued in the remainder of the watershed, but harvest levels declined between 2001 and 2006 as quotas were reduced (Table 2).

Capture and Monitoring

From 1997 to 2000, we applied capture efforts approximately equally across the entire watershed (Fig. 1). Following protection of the Garnet study area, we focused most capture efforts there, towards the goal of capturing all resident individuals (i.e., census). In the remainder of the Blackfoot, we continued to monitor radioed lions marked during the first 3 years of the study including re-instrumenting individuals when their radiocollar's battery life was spent. In addition, we monitored animals that either dispersed from the Garnet or had home ranges overlapping the boundary between the 2 areas.

We used trained hounds to tree mountain lions when we located fresh tracks in the snow. We darted treed animals and drugged them with a 0.06 ml/kg estimated weight mixture of ketamine hydrochloride and xylazine hydrochloride (1.45 ml xylazine to 10 ml ketamine) delivered using a Pneu-Dart Model 193SS cartridge fired rifle with disposable darts (Pneu-Dart, Inc., Williamsport, PA). We gave animals the antagonist yohimbine hydrochloride to counteract the xylazine before release.

We estimated age of captured mountain lions by tooth replacement, wear, gum recession, and cementum age analysis (Ashman et al. 1983, Laundre et al. 2000). We fitted radiocollars (Telonics, Mesa, AZ) depending on the size and age of the individual: an expandable (20–34 cm) kitten collar equipped with either a Mod-073 or Mod-305 transmitter, or an adult collar equipped with a Mod-500 transmitter. We located collared animals from fixed-wing aircraft approximately twice per week. Beginning in 2001, we fitted Telonics global positioning system (GPS) collars programmed to acquire a location every 5 hours to newly collared animals and replaced very high frequency (VHF) collars on already marked animals as opportunity allowed.

We collared both newborn kittens at the den, and those traveling with newly collared adult females. We collared newborn kittens without chemical immobilization approximately 1 month from the time the mother localized at a den site. When we located kittens outside the den (from 3 to 12 months) we treed and immobilized them as with adults. Expandable Mod-073 collars remained on kittens up to 7 months of age; mod-305 collars remained on kittens up to 10 months of age; and a mod-500 adult collar was worn by the animal through adulthood. Capture and handling protocols were approved by Montana Fish, Wildlife and Parks and conducted by their staff (Montana Department of Fish, Wildlife and Parks 2007).

Population Characteristics

Sex and age structure.—We calculated a minimum population for the Garnet study area each year by back-

Table 2. Mountain lion harvest, quotas (harvest/quota), and harvest density (animals/1,000 km^2) for the Blackfoot River watershed in West-Central Montana, 1998–2006. Beginning in December 2000, the Garnet was managed separately from the remainder of the Blackfoot watershed.

Area	Sex	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet	Female	8[a]	8[a]	8[a]	0	0	0	0/1[b]	0	0
	Harvest density	8.74	8.74	8.74						
	Male	5[a]	6[a]	6[a]	0	0	0	1/1[b]	1/1	1/1
	Harvest density	5.46	6.55	6.55				1.09	1.09	1.09
Black-foot	Female	35/30	42/41	30/30	15/15	10/9	4/3	4/3	0/0	1/0
	Harvest density	4.42	5.31	3.79	1.89	1.26	0.5	0.5	0	0.12
	Male	41/40	30/33	27/29	19/21	12/9	8/7	7/7	6/7	8/7
	Harvest density	9.61	9.10	7.20	4.29	2.78	1.51	1.39	0.75	1.13

[a] Garnet managed as part of the Blackfoot watershed.

[b] One either-sex permit issued in 2004.

calculating the lifespan of all mountain lions known to have been present in the study area including collared and harvested animals (Logan and Sweanor 2001, Stoner et al. 2006, Robinson et al. 2008). This technique assumes that animals collared or harvested without being collared at time t were present within the watershed but undetected at time $t-1$ (specific to each animal's age and sex); as such, this method may underestimate population levels towards the end of the study period because of fewer sampling occasions. We assumed that all males were immigrants, whereas all females were recruited from within the population. Therefore, we backdated males to 24 months of age, immigrating into the population after their second birthday. We assumed females were philopatric and were likely born inside the Blackfoot watershed; however, we could not be sure if they were born inside or outside the protected Garnet study area. Therefore, we backdated females to 12 months, accounting for our philopatric assumption without biasing further any total population estimate of the Garnet study area. We used a Z-test to compare mean ages and proportion of the population consisting of adults of each sex between the hunted and non-hunted populations (Zar 1999). We hypothesized that harvest would reduce the mean age of males while increasing their proportion in the population because of a compensatory immigration response to harvest, whereas harvest would increase the mean age of adult females in the population while reducing their proportion in the population because of reduced recruitment (i.e., high juvenile mortality and/or low immigration) as resident animals aged.

Reproduction.—We estimated maternity, the mean number of young born per reproductive female per year (Caswell 2001), and its component, litter size, based on females of reproductive age within the Garnet study area only. We felt monitoring effort was sufficient within the Garnet that no litters born to, or traveling with, collared females would be missed, but logistical constraints prevented this level of monitoring in the larger watershed. We estimated average litter size based on kittens observed at den sites (i.e., <7 weeks), which assumes no kitten mortality had occurred prior to observation. The compensatory mortality hypothesis predicts that litter size will increase in a hunted population because of increased available resources (Table 1). The additive mortality hypothesis predicts that litter size will be unaffected or decline with harvest because of the age structure of females (Table 1). We tested the effect of harvest on litter size (as observed at den sites when kittens were <7 weeks) using a repeated-measures analysis of variance (ANOVA) comparing litter size within the Garnet study area during hunting and non-hunting periods. We used a repeated-measures ANOVA as the sample consisted of females with multiple litters (Zar 1999).

We observed age at dispersal and, for animals that did not leave the study area, first reproduction by radiocollaring dependent kittens and juveniles. As some hunted populations have a population skewed towards older females, we also tested how or if female age affected litter size. Using a repeated-measures ANOVA, we tested for an age effect on litter size in the females that we monitored (Zar 1999). Reduced fertility in older females could be an additive effect of harvest (Table 1).

Some researchers have used litter size, mean birth interval, and proportion of females traveling with young as surrogate measures of maternity (e.g., Lambert et al. 2006); however, these measures may introduce a bias by excluding females that fail to reproduce. We estimated maternity rate based on the total number of kittens born to all radiocollared females of reproductive age (>24 months) monitored, thus including the proportion of non-reproductive females in the population. As with litter size, the compensatory mortality hypothesis predicts that maternity rate will increase in the hunted population because of reduced competition and increased resource availability, whereas the additive mortality hypothesis predicts that maternity will be reduced or unchanged between hunted and non-hunted periods (Table 1). We tested for a hunting effect on maternity rate using a Z-test to compare the mean annual maternity rate within the Garnet study area during hunting and following protection (Zar 1999).

Dispersal.—We defined dispersal as a juvenile establishing a home range with <5% overlap of its natal home range, whereas we considered juveniles establishing home ranges with >5% overlap to be philopatric (Logan and Sweanor 2001). Dispersal rate was based on the number of independent juveniles in each year that moved outside their natal home range compared to the number monitored. We modeled juvenile dispersal as a binomial function of the estimated total population size for males and females separately (i.e., we used a generalized linear model specifying a logit link and binomial family; Hardin and Hilbe 2007). The additive mortality hypothesis predicts density-independent dispersal, whereas the compensatory mortality hypothesis suggests reduced dispersal of both sexes in the hunted population (Table 1).

Survival and Mortality

We examined mountain lion mortality in 3 ways: survival modeling, survival rate analysis, and cause-specific mortality analysis. We used survival modeling to examine the effect of independent variables (i.e., sex, age, geographic location, and hunting pressure as dictated by quota levels) on mountain lion survival and to objectively determine the best method of breaking the population into segments or cohorts with similar survival experiences. We used survival analysis to calculate and compare the survival probabilities of animals within those cohorts. Finally, we calculated and compared cause-specific mortality rates.

We derived a spatially explicit encounter history from telemetry data for each individual mountain lion to estimate survival rates and test hypotheses about factors influencing survival. We removed duplicate same-day locations from GPS collar data and combined them with VHF data to create a continuous record based on calendar time for each animal (Fieberg and DelGiudice 2009). We censored (interval truncated) animals not located for >61 days until relocated (Winterstein et al. 2001). During the first 4 years of the study, before we began to deploy GPS collars, we scheduled telemetry flights twice a week. During some periods, most notably the winter and spring of 2001, we could conduct flights only once a month because of weather, financial, and logistical constraints. We began deploying GPS collars in October 2001 and aerial telemetry flights were again limited during short periods for the remainder of the study. The 61-day period allowed some animals to be missed on 2 consecutive flights during these times of infrequent aerial telemetry. If not located after 61 days, we right-censored animals at the date of their last location in the study area.

We modeled factors influencing mountain lion survival using a combination of manual backward stepwise and best-subsets model selection (Hosmer et al. 2008). First, we conducted a univariate analysis using Cox regression (Cox 1972) to test the significance of sex, age, and hunting quota on mountain lion survival. We coded sex as an indicator variable with females coded as 1 and males coded as 0. We coded age and quota level as continuous variables, with age estimated in months and quota based on the annual-, sex-, and location-specific quotas as set by Montana Fish, Wildlife and Parks (Table 2).

We modeled mountain lion survival on the landscape by constructing 12 spatiotemporal a priori models, each suggesting a different hypothesized response in survival of the population to our experimental harvest design. We discuss 4 of these models in detail here (see online Supplementary Material for graphical depiction and explanation of all 12). For instance, the single-population (1-segment) model tested the hypothesis of total compensatory mortality by modeling survival as constant across the landscape and study period; equivalent to a null model relative to management (Fig. S1). The other 3 models represented different ways in which hunting mortality might be manifest. The management model tested the hypothesis that survival responded to small incremental changes in management or quota level, thus dividing the population into 6 segments, equivalent to a global model relative to management (Fig. S2, see also Table 2). The 3-segment population model grouped animals across the drainage between 1998 and 2000 (segment 1), then divided the population into 2 segments (segments 2 and 3) based on the protection of the Garnet study area following 2000, while hunting continued in the remainder of the Blackfoot drainage (Fig. S3). Under the compensatory mortality hypothesis, hunting replaces other forms of mortality, causing survival to remain relatively constant. Therefore, this model would not be supported if the compensatory hypothesis were true because survival between segments 2 and 3 would not differ. The 4-segment model (Fig. S4) tested the hypothesis that survival before protection of the Garnet study area differed between the watershed and the Garnet although management was the same for both areas, and that survival increased significantly outside the protected area once female quotas were set to 0. We used Akaike's Information Criterion for small sample sizes (AIC$_c$) to select among competing models to evaluate the strength of evidence for each hypothesis regarding the relationship of survival to temporal and geographical quota levels, as well as age and sex (Burnham and Anderson 1998, Hosmer et al. 2008).

We modeled survival time using a parametric Weibull distribution (Hosmer et al. 2008):

$$\ln(T) = \beta_0 + \beta_1 x + \sigma \times \varepsilon \tag{1}$$

where T is survival time, β_0 the model intercept, β_1 the covariate, σ a parameter estimating the shape of the hazard function based on the data, and ε the error term. We checked model specification using a link test (Cleves et al. 2004).

We calculated annual survival rates for 3 age classes of mountain lions: kitten (1–12 months), juvenile (13–24 months), and adult (>25 months) for each population model segment (as delineated by our a priori model selection, see above) using the Nelson–Aalen estimator (Nelson 1972, Aalen 1978). Because kittens were first collared at a range of ages (1–12 months) rather than only at the den (i.e., within the first 7 weeks), our estimate of kitten survival is biased high. We based survival rates on a biological year (1 Dec–30 Nov) reflecting the start of the hound-hunting season on 1 December. We raised the cumulative hazard estimate for each segment to the power of $1/t$, where t represents the length of that period in years, to calculate a mean annual survival rate across that period. To test for differences in survival between the various segments of the population, we used a Peto–Prentice test (Peto and Peto 1972, Prentice 1978, Hosmer et al. 2008). The compensatory mortality hypothesis predicts no difference in survival between hunted and non-hunted segments of the population. Conversely, reduced survival in the hunted population would indicate additive mortality.

We calculated cause-specific mortality rates using cumulative incidence functions (CIFs; Kalbfleisch and Prentice 1980, Heisey and Patterson 2006). These functions allow the estimation of mortality rates in the presence of competing risks, which are defined as >1 mutually exclusive, cause of death (Pintilie 2006). Unlike the modified Mayfield or Heisey–Fuller (Mayfield 1961, Heisey and Fuller 1985) methods of mortality estimation, which assume a normal or constant distribution of mortality risk, CIFs are non-parametric and make no assumption regarding the underlying hazard distribution.

We grouped mortalities by 6 causes. We classified animals that were harvested as part of a legal hunt, or kittens that were orphaned and starved after their mothers were shot as hunting mortality. Illegal mortality included animals killed in snares or otherwise killed out of season. We classified animals that died naturally because of starvation, disease, or intraspecific strife (including cases of infanticide) as natural mortalities. The category depredation included animals shot because of conflict with humans (i.e., livestock depredation permits, and self-defense). The final 2 categories were vehicle collisions and unknown, where a clear cause of death could not be determined.

We used cause-specific mortality rates to test the compensatory mortality hypothesis in 2 ways. First, we regressed survival of juvenile and adult mountain lions against hunting mortality. We omitted kittens because of their non-independence from adult females. We included juveniles because they spend approximately half of their juvenile year independent of their mothers and, unlike kittens, no juveniles starved after being orphaned by hunting. If hunting were compensatory, we would expect survival to remain constant as hunting mortality increased (Table 1). Conversely if hunting mortality were additive, we would expect a monotonic decrease in survival with an increase in hunting mortality (Williams et al. 2002). This regression used survival and hunting mortality probabilities based on the management model population structure (i.e., 6 population segments based on varying hunting quota levels, see Fig. S2). A similar analysis could have been conducted on annual survival and mortality values (e.g., Murray et al. 2010). However, because the management goal during the first 3 years of the study was to reduce the population, almost ensuring additive mortality, using annual rates may have biased our analysis towards inferring additivity of hunting mortality. We assumed this structure was less biased than an annual model towards an additive finding because the first 3 years of mortality are captured in a single data point and the model contains both hunting and natural mortality based on the protected and hunted portions of the Blackfoot watershed following December 2000.

We also tested the compensatory mortality hypothesis in adult and kitten survival by comparing the CIF for hunting and all other mortality sources between the hunted and non-hunted periods. Pepe and Mori (1993) provided a method for comparing the CIF of a main mortality source and competing risks simultaneously between 2 groups. This method tests the hypothesis of equality in the CIF of a main event (i.e., hunting mortality) while also testing for equality in the remaining competing risks (Pintilie 2006). If hunting mortality were additive, we would expect an increase in the hunting mortality rate, whereas the CIF for competing risks would be constant (i.e., no compensatory decrease in other mortality sources in the presence of hunting). Conversely, if hunting mortality were compensatory, we would expect an increase in the hunting CIF, with a concurrent reduction in the CIF for competing risks in the hunted population.

Population Modeling and Growth

Methods described thus far examined how harvest affected individual population parameters (i.e., survival, maternity, etc.). Ultimately, we were interested in how changes in these parameters combined to affect population growth. To quantify the population effects of harvest, we constructed a stage-based, 2-site, dual-sex Leslie matrix model (Leslie 1945) in MATLAB ® (The MathWorks, Natick, MA). The model consisted of 2 transition matrices joined by juvenile dispersal terms and was based on the 2 top survival models using the estimated survival and fecundity parameters described below. We calculated stochastic growth rates and associated standard deviations by running 10,000 2- to 6-year iterations (dependent on population segment, see Supplementary Material).

Vital rates.—We used age- and sex-specific survival rates previously discussed, estimated using the Nelson–Aalen estimator. We estimated variance of the Nelson–Aalen survival estimator following Anderson et al. (1997):

$$\mathrm{Var}(\hat{S}(t)) = (\hat{S}(t))^2 V^2(t) \tag{2}$$

and

$$V^2(t) = \sum_{(i:t_i<t)} \frac{d_i(r_i - d_i)}{r_i^3} \tag{3}$$

where $\hat{S}(t)$ is the survival estimate to time t, d_i is the number of deaths at time t_i, and r is the number at risk at time t_i. We then used White's method to remove sampling variance from annual estimations of survival variance, and included this value of process variance in a beta-distributed variance vector in each matrix model (White 2000).

We assumed that females did not breed until becoming adults (>24 months; Root 2004, Robinson et al. 2008, Treves 2009). We also assumed an equal ratio of male and female kittens (total fecundity divided equally between sexes; Logan and Sweanor 2001). We modeled variance in maternity using a stretched beta distribution with a maximum value of 2.5 annually, or maximum litter size of 5 every 2 years (Morris and Doak 2002). We modeled fecundity as a birth-pulse post-breeding process. Kittens entered the matrix as newborns and fecundity was the product of adult female survival (S_a) and average annual maternity (M_a; Morris and Doak 2002):

$$F = S_a \times M_a \tag{4}$$

We calculated a dispersal rate based on the number of independent juveniles in each year that moved between the Garnet study area and the remainder of the Blackfoot drainage compared to the number monitored. In this sense, our modeling definition of dispersal does not match the more traditional definition (reported above), where juveniles that establish home ranges with >5% overlap of their maternal home range are considered to be philopatric rather than dispersers (Logan and Sweanor 2001). Our model assumed a closed system consisting only of 2 populations, the Garnet study area and the remainder of the Blackfoot watershed. Therefore, for parameterization of our population models, an animal could have established a home range adjacent or overlapping with its mother's (philopatry) but still be classified as a disperser if its new home range was primarily (>50%) outside its maternal area (the Garnet area or the remainder of the drainage). We did not consider juveniles that dispersed out of the Blackfoot watershed completely to be dispersers because they were effectively lost to this system and population model and we therefore censored them.

Initial abundance and density dependence.—We set initial 1998 abundances at 37 total animals (i.e., kittens, juveniles, and adults) for the Garnet study area based on a minimum population back-calculated using known-aged animals, and 283 total individuals in the remainder of the Blackfoot drainage, extrapolating a similar total density (4.0 mountain lions/100 km^2) to the remainder of the watershed. We started all models in 1998 at a stable age distribution, then the mean modeled age distribution for further projections.

For instance, we started the 3-segment population model in 1998 with a stable age distribution and projected for 3 years, when survival rates changed or diverged between the Garnet and remainder of the Blackfoot. We projected a second period from 2001 to 2007 based on the age distribution outputs from the 1998 to 2000 model.

We applied a ceiling density dependence to stochastic models that affected survival of adults only (>24 months; Root 2004). We set a ceiling density of 27 adults for the Garnet study area and 210 adults for the remainder of the Blackfoot drainage based on an average density of 3 adults per 100 km^2. This liberal estimate of maximum adult density was commensurate with observed levels of 2.92 mountain lions/100 km^2 in Wyoming (Anderson and Lindzey 2005) and 2.58 mountain lions/100 km^2 in northeastern Washington (Robinson et al. 2008) both hunted populations.

Sensitivity and life-stage simulation analysis.—If harvest is additive, its effect on total population growth should vary based on which population parameter is affected in an additive manner and how reliant population growth is on that parameter. We tested the effect of each population parameter on population growth rate through perturbation. The sensitivity of lambda to each vital rate (i.e., survival, maternity, and dispersal) was calculated by individually reducing each rate by 0.10 and recalculating lambda for each population as well as the total population combined (Caswell 2001). The inclusion of lower-level parameters (maternity and female survival combined to calculate fecundity) in our matrix model negated the use of elasticities (Caswell 2001). We conducted an LSA to quantify the effects of variance on population growth within the Garnet study area separately during the hunted period (1998–2000), and the non-hunted period (2001–2006), comparing the r^2 values for each vital rate, for each period (Wisdom et al. 2000). We conducted sensitivity analysis using the 3-segment population model. Because we were only interested in the effect of harvest on vital rate variability and population growth, we conducted LSA on only the Garnet portion of the 3-segment population model pre- and post-harvest (i.e., segment 1 vs. segment 2, see Fig. S3).

Finally, given the results of our sensitivity and LSA analysis, we constructed a deterministic population model to quantify how varying levels of maternity, female kitten survival, and adult female survival combine to affect population growth. In this model, we fixed all male survival rates as well as juvenile female survival at the average levels observed for the entire study population, but ran successive simulations in which we incrementally increased kitten and adult female survival from 0.01 to 1.0, at 3 levels of maternity (1.08, 1.29, and 1.40; maternity during the hunting period, mean maternity across the study period, and maternity during the non-hunting period, respectively). We used standard matrix analysis techniques (Caswell 2001) to calculate the projected long-term population growth rate (λ) for each possible parameter combination. The probability of a kitten surviving to become a juvenile was the combined function of kitten and adult survival (i.e., kitten survival × adult survival) to mimic the effect of kitten abandonment following an adult's death. We modeled fecundity levels as in the other population models.

RESULTS

Harvest, Capture, and Monitoring

From 1998 to 2006, 299 mountain lions (158 M and 141 F) were harvested from the Blackfoot watershed, with 41 (18 M, 23 F) harvested from the Garnet study area. Mean age of harvested animals was 2.88 years (M $\bar{x} = 2.64$ yr and F $\bar{x} = 3.16$ yr). A female quota existed in all but the last 2 years of the study in the Blackfoot watershed. This quota was filled or exceeded in each year (i.e., 100–133% quota), and females composed 37% of the animals harvested (Table 2).

We captured 121 individual mountain lions 152 times between January 1998 and December 2006, including 82 kittens, 8 juveniles, and 31 adults. Of these, we collared 117 individuals and monitored them for habitat use and survival. We monitored animals for an average of 502 days (range: 7–3,231 days) with males remaining on the air for shorter periods ($\bar{x} = 284$ days) than females ($\bar{x} = 658$ days). We recorded known fates for 63 animals, and right-censored the remainder. We used right-censored animals in analysis until loss due to collar failure ($n = 16$), dispersal from the Blackfoot River drainage ($n = 7$), or survival to the end of the study ($n = 31$).

Population Characteristics

Sex and age structure.—The minimum total population count for the Garnet study area ranged from 37 mountain lions (4.0/100 km^2) in 1997 to a low of 20 (2.2/100 km^2) in 1999, before recovering to 33 (3.6/100 km^2) in 2006 (Table 3). The average age of adult females increased from 3.53 years during the hunted period to 4.83 in the non-hunted population, although this difference was not significant ($Z = -1.47$, $P = 0.14$). Similarly, the average age of adult males increased from 2.73 to 3.53, also a non-significant increase ($Z = -1.46$, $P = 0.14$). The oldest radiocollared female monitored during the study was 10 years old and the oldest male was 6 years old.

From 1997 to 2006, the Garnet population averaged 37% adult females, 15% adult males, 17% juveniles, and 30% kittens. Although the proportion of adult females in the population remained relatively constant between the hunted and non-hunted phases ($Z = 1.20$, $P = 0.22$), the proportion of adult males in the hunted population was higher (21%) than in the non-hunted (10%; $Z = 2.87$, $P < 0.01$; Table 3.).

Reproduction.—Mean total litter size of litters visited early in the den (<7 weeks) was 2.92 ($n = 24$, 95% CI: 2.70–3.13). Litter size was not affected by hunting ($F_{1,11} = 0.27$, $P = 0.61$). Of 32 litters where birth month could be confirmed, mountain lions gave birth in all months but December, February, and March. Most litters were produced from July to October. The mean age of sires in our population was 35 months (Onorato et al. 2011). Fourteen known-aged females gave birth to their first litter at a mean age of 31.4 months (range: 23–37 months). We found no effect of female age on litter size ($F_{6,6} = 1.39$, $P = 0.35$). Average birth interval was 602.6 days (95% CI: 503–702

Table 3. Minimum total mountain lion population (including kittens, juveniles, and adults), mean adult age, and proportion of total population consisting of adult male and female mountain lions censused on 1 December, 1997–2006, Garnet study area, western Montana.

		Mean adult age (yr)		Adult proportion of total population	
Year	Minimum total population	Male	Female	Male	Female
1997	37	2.29	3.79	0.189	0.378
1998	27	2.83	3.91	0.222	0.407
1999	20	2.8	3.7	0.25	0.5
2000	21	3	2.75	0.19	0.381
Hunted mean		2.73	3.53	0.21	0.42
2001	25	3.67	3.75	0.12	0.32
2002	24	3	4.44	0.125	0.375
2003	30	4	4.82	0.1	0.367
2004	32	3	4.91	0.094	0.344
2005	33	3.5	5.27	0.121	0.333
2006	33	4	5.8	0.061	0.303
Non-hunted mean		3.53	4.83	0.10	0.34

days) or 19.8 months. Approximately 58% of females $\geq$24 months gave birth each year, and 89% of females were traveling with dependent young.

The mean maternity rate across the study period was 1.29 ($n=9$, 95% CI: 0.84–1.76) kittens per female per year. Although maternity was lower during the hunting period ($\bar{x}=1.08$, $n=3$, 95% CI: 0–3.59) compared to the protected population ($\bar{x}=1.40$, $n=6$, 95% CI: 1.02–1.78), this difference was not significant ($Z=-0.53$, $P=0.59$). In 1999, we documented no litters born to collared females; however, because of heavy harvest pressure, we monitored only 2 adult females.

Dispersal.—We monitored 66 mountain lions (39 F and 27 M) during their juvenile year (13–24 months of age) during 1998–2006. Of these 66 individuals, 47 survived to independence. Mean age of dispersal was 15 months ($n=33$, range: 11–23 months). Dispersal was severely constrained in the hunted population before 2001. During the first 3 years of study when harvest level was high, only 2 of 12 juvenile females survived to independence. One dispersed out of the Blackfoot drainage, and 1 established a philopatric home range inside the Garnet study area. Between 2001 and 2006, during protection of the Garnet from hunting, we monitored 54 juvenile mountain lions, 45 of which survived to independence. In total, female juveniles showed essentially equal levels of dispersal ($n=12$) and philopatric behavior ($n=14$). We found no relationship between population level and dispersal rate of juvenile females ($Z_5=0.60$, $P=0.55$). We did not document any philopatric behavior in radiocollared juvenile males ($n=19$; 100% dispersal).

Survival and Mortality

We recorded mortalities in every month but October, with the majority coinciding with the start of the hound-hunting season in December (Fig. 2). Sex was the best predictor of mountain lion survival followed by quota and age. Females were 73% less likely than males to die (hazard ratio [HR] $=0.27$, $Z=-4.79$, $P<0.01$), with risk of mortality increasing 10% with each numerical increase in quotas (HR $=1.10$, $Z=2.77$, $P<0.01$). Risk of mortality was highest for kittens, declining by 1% for each month survived (HR $=0.99$, $Z=-1.52$, $P=0.11$). Although age was not a significant model covariate at the 0.05 level, Hosmer and Lemeshow (2000) recommend retaining variables with a probability of significance of 20% ($P=0.2$) for inclusion in further modeling following univariate analysis. This recommendation, coupled with our desire to create age-based population models as the next phase of our research, led to inclusion of all 3 variables in our subset models, with age broken into 3 categories.

Two models, 3-segment and 4-segment, including 3 age classes and sex, were the top models (Table 4; Figs. S3 and S4). The management model, which we thought best fit the actual quota levels, was the seventh ranked model (Table 4). A linktest showed that both the 3-segment ($Z=-0.51$, $P=0.61$) and the 4-segment ($Z=-0.58$, $P=0.56$) models were properly parameterized.

Mean annual survival, pooling all individuals across all years, was 0.651 (SD $=0.03$). Survival of kittens ($\bar{x}=0.785$, SD $=0.05$) and juveniles ($\bar{x}=0.592$, SD $=0.09$) did not vary by sex (kitten: $\chi^2_1=0.14$, $P=0.70$; juvenile: $\chi^2_1=0.18$, $P=0.66$). Among adults, female survival ($\bar{x}=0.786$,

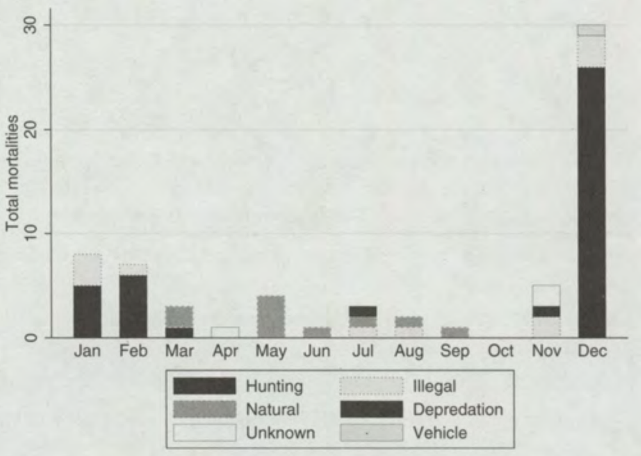

Figure 2. Timing and cause of 63 radiocollared mountain lion mortalities, 1998–2006, in the Blackfoot River watershed, Montana.

Table 4. Top models in best-fit analysis of mountain lion survival patterns in Blackfoot watershed Montana, 1998–2006. Null model log likelihood (LL) was −54.2168 (8 remaining models in Table S1).

Rank	Model	LL	df	AIC$_c$	ΔAIC$_c$
1	3-Segment	−36.1078	7	87.1115	0
2	4-Segment	−35.5328	8	88.2269	1.1154
–					
7	Management	−35.4528	10	92.7088	5.5973
–					
10	1-Segment	−44.1786	5	98.8296	11.7181

SD = 0.05) was higher than males ($\bar{x} = 0.515$, SD = 0.12; $\chi^2_1 = 5.04$, $P = 0.02$).

Adult survival (F: $n = 13$, M: $n = 3$) was similar between the Garnet study area and the remainder of the Blackfoot drainage before December 2000 ($\chi^2_1 = 0.45$, $P = 0.50$), but differed once hunting was halted in the Garnet ($\chi^2_1 = 17.62$, $P < 0.01$; F: $n = 38$, M: $n = 17$; Table 5), consistent with the additive mortality hypothesis. Once adult female quotas were reduced to 0 outside the Garnet study area (segment 4 of the 4-segment population model, see Fig. S4), adult survival increased from 0.60 to 0.87 ($\chi^2_1 = 3.08$, $P = 0.08$) compared to survival before quota reduction (population segment 2). The marginal significance in total adult survival is explained by an increase in adult female survival while adult male survival remained relatively constant (Table 5).

Hunting was the main cause of mortality for all age and sex classes across the study period, accounting for 36 of 63 mortalities documented. Additional factors were illegal mortalities, natural, unknown, depredation, and vehicle collision (Table 6). Across the study period, mountain lions in the Blackfoot watershed had a 22% annual probability of mortality due to hunting. Regression analysis of hunting-caused mortality and survival of juveniles and adults showed a significant negative slope of −0.97 ($F_{1,4} = 21.97$, $P = 0.01$), consistent with the additive-hunting mortality hypothesis and suggesting hunting mortality is completely additive (Fig. 3). For adults and juveniles, PepeMori tests of equality in cause-specific mortality rates were significant (hunting mortality $\chi^2 = 31.18$, $P < 0.01$; all other mortality $\chi^2 = 3.58$, $P = 0.06$). The difference in other mortality sources between hunted and non-hunted populations was due to higher mortality in the hunted populations, supporting the additive-hunting mortality hypothesis.

During the heavy hunting period before closure of the Garnet study area, 6 kittens died of starvation following the harvest of their mothers, leading to a kitten cause-specific mortality rate of 0.41 (SE = 0.14). During the same period, no kittens died of natural mortality; however, following closure of the Garnet study area, 6 kittens died of natural causes including cannibalism or infanticide, a cause-specific mortality rate of 0.16 (SE = 0.06). Kitten mortality

Table 5. Mean annual survival rates of radiocollared mountain lions broken into population segments according to our 3- and 4-segment model structures 1998–2006, western Montana. Sample sizes (*n*) include animals that were counted in the risk pool of more than 1 model segment. The 3-segment model assumes that survival was similar across the watershed prior to protection of the Garnet (combined hunted), but differed after December 2000 when hunting ceased in the Garnet (Garnet protected and Blackfoot hunted). The 4-segment model assumes survival differed among 4 groups: 1) Garnet study area before December 2000 (Garnet hunted), 2) Garnet study area after hunting ceased in the area (Garnet protected), 3) Blackfoot watershed before 2005 (Blackfoot hunted), and 4) Blackfoot watershed during the last 2 years of the study when female quotas were reduced to 0 (Blackfoot hunted reduced). Survival of kittens and juveniles did not vary by sex; therefore, we present pooled estimates.

Model and segment	Area (yr)	Age and sex	*n*	Mean survival	SD
3-segment 1	Combined hunted (1998–2000)	Kitten	24	0.6566	0.09
		Juvenile	12	0.3117	0.12
		Female adult	13	0.6737	0.09
		Male adult	3	0.7167	0.21
3-Segment 2	Garnet protected (2001–2006)	Kitten	60	0.8505	0.06
		Juvenile	43	1.0	
		Female adult	25	0.9654	0.03
		Male adult	10	0.7788	0.15
3-Segment 3	Blackfoot hunted (2001–2006)	Kitten	29	0.9672	0.05
		Juvenile	44	0.6920	0.08
		Female adult	31	0.7130	0.08
		Male adult	16	0.4699	0.13
4-Segment 1	Garnet hunted (1998–2000)	Kitten	16	0.7281	0.11
		Juvenile	10	0.2326	0.13
		Female adult	9	0.5740	0.13
		Male adult	3	1.0	
4-Segment 2	Blackfoot hunted (1998–2004)	Kitten	34	0.5352	0.15
		Juvenile	32	0.2735	0.13
		Female adult	29	0.5985	0.11
		Male adult	7	0.5387	0.13
4-Segment 3	Garnet protected (2001–2006)	Kitten	60	0.6151	0.12
		Juvenile	43	1.0	
		Female adult	25	0.9654	0.03
		Male adult	10	0.7788	0.15
4-Segment 4	Blackfoot hunted reduced (2005–2006)	Kitten	9	0.9048	0.12
		Juvenile	21	0.6218	0.14
		Female adult	17	0.8746	0.09
		Male adult	10	0.5488	0.21

Table 6. Number of cause-specific mortalities and associated mortality rates (cumulative incidence function, CIF) of radiocollared mountain lions in 1998–2006 in western Montana.

Age class	Sex	Hunting	Illegal	Natural	Depredation	Unknown	Vehicle
Kitten	Male	2		5	1		1
	Female	4		2			
Juvenile	Male	9	2		1		
	Female	4	1			1	
Adult	Male	8	2				
	Female	9	6	3		2	
Total		36	11	10	2	3	1
CIFs		0.221	0.055	0.038	0.007	0.011	0.006
SE		0.03	0.01	0.01	0.006	0.006	0.006

attributed to hunting was higher during the 3-year period of heavy hunting than in the 6 years following protection of the Garnet study area ($\chi^2 = 7.58$, $P = 0.01$). However, we found no change in all other sources of mortality between the 2 periods ($\chi^2 = 0.49$, $P = 0.48$), supporting the additive mortality hypothesis.

Population Modeling and Growth

We monitored 47 kittens until independence from their mothers. One female and 6 males dispersed out of the watershed completely and were censored from dispersal rate calculations. Dispersal rates of juveniles from the Garnet study area to the Blackfoot was 0 prior to the cessation of hunting, but increased to 0.82 ± 0.19 per year for females and 0.71 ± 0.39 per year for males once the Garnet was closed to hunting. No radiocollared juveniles immigrated into the Garnet study area from the remainder of the Blackfoot watershed, where hunting was allowed, although low juvenile survival reduced the number of independent juveniles in our Blackfoot sample to 4 (3 F and 1 M), all of which remained in the hunted area.

Our population models indicted that the mountain lion population in the Blackfoot watershed declined by approximately 11–12% per year between 1998 and 2000 (Table 7). With cessation of hunting in the Garnet study area in 2001, the 3-segment model predicted recovery beginning immediately, with the watershed population growing at approximately 3% annually (Table 7). The 4-segment model indicated that mountain lion numbers in the watershed were still slightly declining between 2001 and 2004, before climbing rapidly following reductions in quotas outside the Garnet in 2005 (Table 7). Both models predicted a watershed-wide population level in January 2007 slightly below 1998 levels (Fig. 4). Both models also predicted final abundances in the Garnet study area of approximately 28 individuals, 9 fewer than at the start of the study. The trend in watershed-wide estimates from both modeled populations matches the minimum count for the Garnet based on backdating (Fig. 4); however, both models predicted a slower recovery within the Garnet study area than the minimum count for the number of animals based on backdating (Fig. 4).

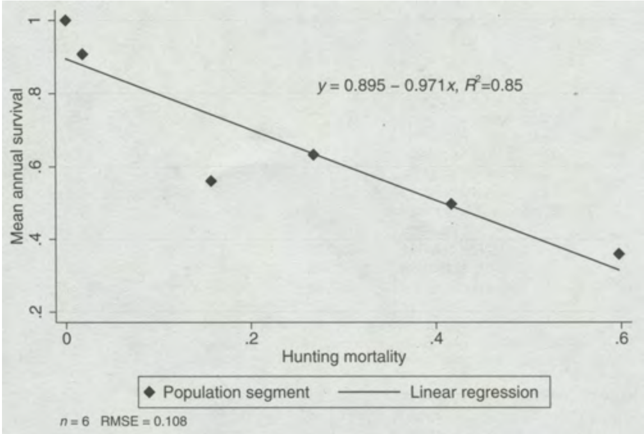

Figure 3. Regression of the relationship of hunting mortality and survival of independent mountain lions, 1998–2006, in the Blackfoot River watershed, Montana based on the management model population breakdown (see also Fig. S2).

The growth rate of the watershed-wide, mountain lion population was most sensitive to changes in adult female survival followed by juvenile and kitten female survival and maternity (Fig. 5). Negative sensitivities of dispersal from the Garnet to the hunted area of the watershed following 2001 attest to the lower survival probability of adults in the hunted area compared to the protected Garnet. LSA showed that hunting increased the importance of adult female survival to population growth by 50%, while reducing the significance of kitten survival and maternity (Fig. 6). The sum of adult female survival, female kitten survival, and maternity accounted for 92% and 57% of the variability in annual population growth of non-hunted and hunted populations, respectively. In general, adult female survival levels below 0.80 should lead to declining population levels (Fig. 7).

DISCUSSION

Population Characteristics

Hunting directly reduced population size from 37 to 20 animals between 1997 and 2000, but population parameters such as litter size, birth interval, maternity, age at dispersal, and age at first breeding were not significantly affected. Increased harvest increased the proportion of adult males in the population, while reducing the average age of both adult males and females, likely because of a compensatory immigration response into vacated home ranges (Cooley et al. 2009). We had hypothesized that female recruitment would be reduced by harvest, perhaps more greatly than

Table 7. Modeled population growth rate (λ; ±SD) based on the 3- and 4-segment population models in western Montana, 1998–2006.

Study area	Model	1998–2000 (λ)	2001–2004 (λ)	2005–2006 (λ)
Garnet	3-Segment	0.8686 (0.08)	1.024 (0.06)	1.024 (0.06)
	4-Segment	0.9352 (0.11)	0.9855 (0.05)	1.016 (0.09)
Blackfoot	3-Segment	0.8797 (0.08)	1.033 (0.06)	1.033 (0.06)
	4-Segment	0.8829 (0.12)	0.9375 (0.11)	1.176 (0.10)
Combined	3-Segment	0.8795 (0.08)	1.034 (0.05)	1.034 (0.05)
	4-Segment	0.8928 (0.11)	0.9475 (0.09)	1.155 (0.09)

males because of shorter female dispersal distance and reduced juvenile survival, resulting in an increased adult female age structure. Both female and male immigration were likely occurring during the heavy harvest period despite very low juvenile survival in the study area. The change in age structure of the population to a greater proportion of males did not affect productivity.

We estimated a mean litter size of 2.92 (measured at the den <7 weeks); however, this did not differ between hunted and unhunted periods. Estimates of litter size have ranged from a low of 1.9 in Florida (Maehr and Caddick 1995) to a high of 3.1 in southeastern British Columbia (Spreadbury et al. 1996), with most averaging around 2.5 (Logan and Sweanor 2001). Logan and Sweanor (2001), Cooley et al. (2009), and most recently Hostetler et al. (2012) have likely produced the least biased estimates of litter size by visiting den sites within the first month of birth, producing means of 3.0 ($n = 53$), 2.55 ($n = 33$), and 2.6 ($n = 94$), respectively. Similarly, our estimated birth interval of 19.8 months closely matched others in the literature, including 17.4 in New Mexico (Logan and Sweanor 2001), 19.7 in Alberta (Ross and Jalkotzy 1992), and 24.3 in Utah (Lindzey et al. 1994).

We found no effect of hunting on maternity rates, and the mean maternity rate of 1.29 was also similar to other published rates (e.g., New Mexico ranged from 1.3 to 1.6 kittens/F/yr [Logan and Sweanor 2001], whereas Robinson et al. [2008] and Cooley et al. [2009] reported maternity rates in hunted populations of 1.2 and 1.1 kittens/F/yr). Onorato et al. (2011) found the mean age of sires in our population, 35 months (range: 15–57 months), was younger than reported elsewhere. For instance, Logan and Sweanor (2001) found that 71% of litters in their non-hunted population were sired by males 35–88 months of age. However, as indicated above, the younger age structure of the male population during the hunted period did not affect kitten production.

Mean age at dispersal in our study population was similar to other mountain lion studies, where dispersal occurred between 10 and 33 months (Sweanor et al. 2000). Levels of philopatry were also similar to non-hunted populations. Sweanor et al. (2000) found that 68% of female recruits came from the local population, compared to a 50% philopatry rate in juvenile females in our work. We documented 100% male juvenile dispersal following protection from hunting.

Perhaps our most striking finding of the effects of hunting on the characteristics of this mountain lion population was the elimination of emigration during the heavy harvest period. Although this result may suggest a compensatory response (i.e., increased philopatry) of juveniles to reduced conspecific densities, juvenile survival was reduced to a level such that only 2 females and no males survived to dispersal

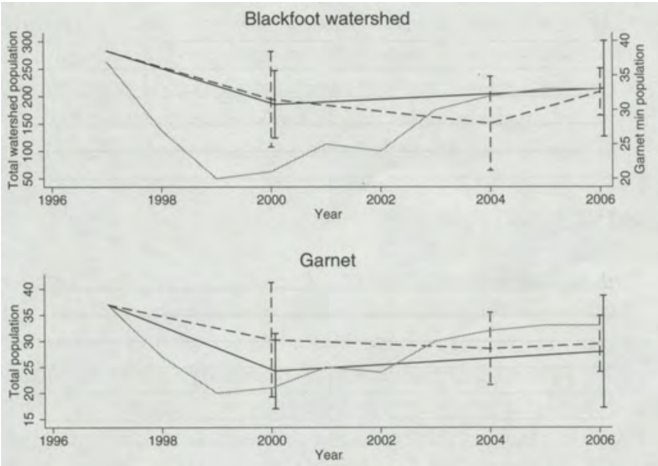

Figure 4. Projected population levels (±1 SD) for the entire Blackfoot watershed and Garnet study area based on the top population models: 3-segment model (solid black line) and 4-segment model (dashed line). The minimum population for the Garnet study area, based on backdating known-aged animals, is included for comparison (solid gray line).

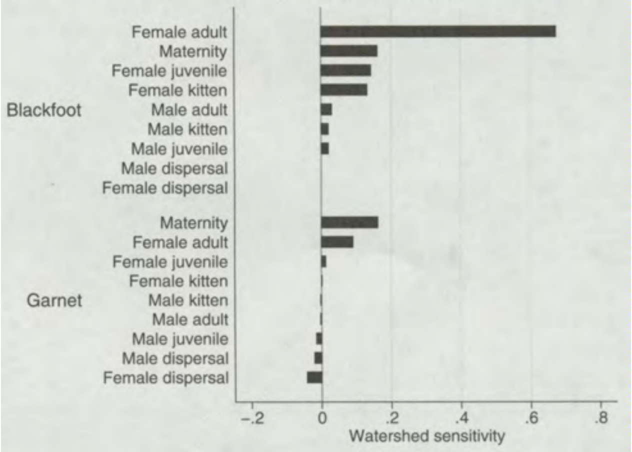

Figure 5. Sensitivities of mountain lion population growth to matrix vital rates of the 3-segment population model, 2001–2006. Maternity sensitivity is for both the Garnet and Blackfoot hunted area subpopulations in western Montana. For ease of interpretation, we present only sensitivities of the entire watershed population based on the 3-segment model 2001–2006; the sensitivities for all population segments from other population models were similar.

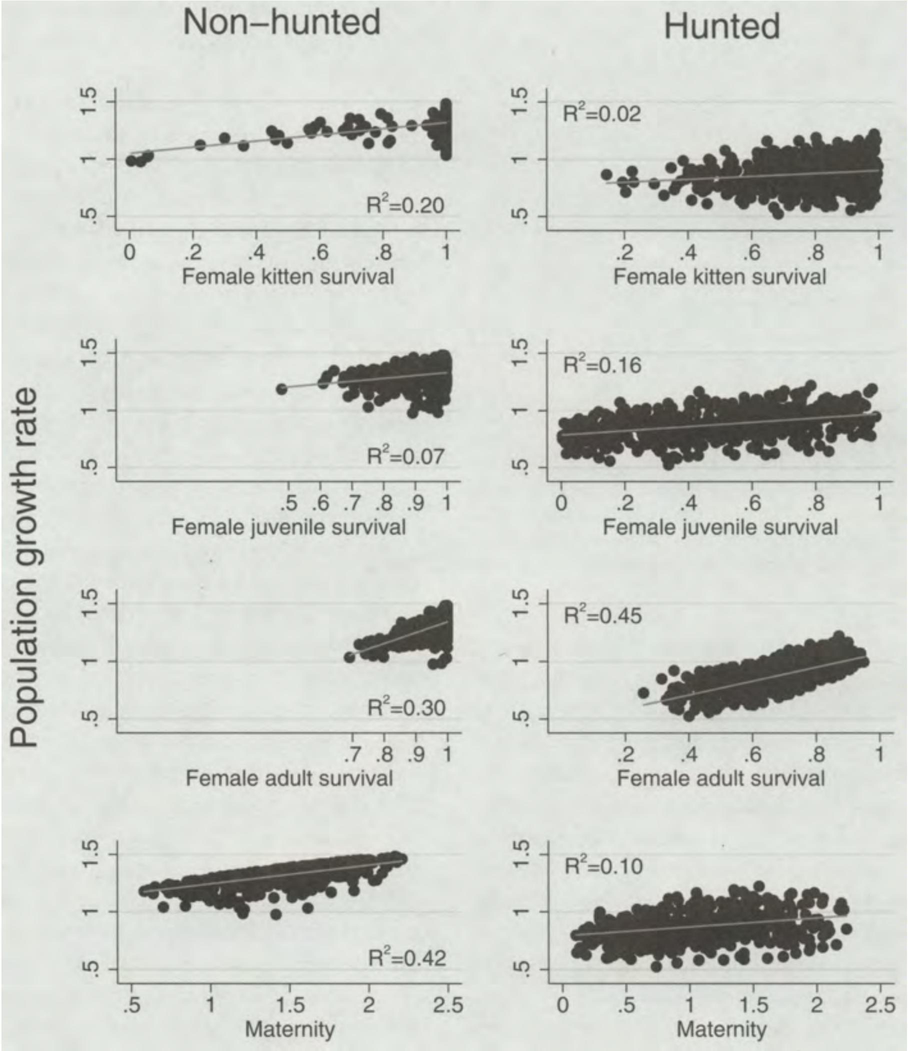

Figure 6. Life-stage simulation analysis (LSA) for mountain lions in the Garnet study area in West-Central Montana during the hunted and protected periods from 1998–2006. The R^2 value describes the proportion of the variation in population growth explained by variation in the vital rate. We omitted values for males because their survival rates and associated variances had little effect on population growth.

age (Table 5). Metapopulation dynamics are an increasingly important focus of mountain lion management and immigration, and emigration can play a major role in balancing hunted and non-hunted mountain lion populations (Beier 1993, Robinson et al. 2008, Cooley et al. 2009). Harvest levels equivalent to those recorded during the first 3 years of our study may severely reduce a population's ability to act as a source of immigration to other areas, affecting not only the focal population level, but also those populations surrounding it (Liu et al. 2011).

Survival and Mortality

Human-caused mortality shaped the survival of mountain lions in our study area, with hunting being the leading cause of mortality. The compensatory mortality hypothesis posits that harvest reduces the probability of animals experiencing other sources of mortality, thus allowing survival rates to remain relatively constant. We found an almost perfectly linear decrease in total survival of adults and juveniles with increased hunting mortality. We also found that mortality due to all other causes (i.e., illegal, natural, depredation, vehicle, and unknown) was actually lower in the non-hunted population when compared to the hunted population. Both of these findings support the additive mortality hypothesis. The 3-segment model demonstrated the distinct difference between harvest pressures and resultant survival within the Garnet study area and remainder of the Blackfoot following the restriction of hunting in 2001. We interpret the relatively poor performance of the management model as evidence that the small incremental reductions in quotas following 2000 (Table 1) did not result in significant differences in population-level survival rates.

We believe an important mechanism rendering the effects of harvest as additive is kitten mortality due to starvation following harvest of adult females. We found an essentially equal number of kitten mortalities due to the direct effects of hunting through abandonment and natural mortality following closure of the Garnet to hunting. However, because of the timing of hunting mortalities (early in the biological yr), and the longer period of monitoring and

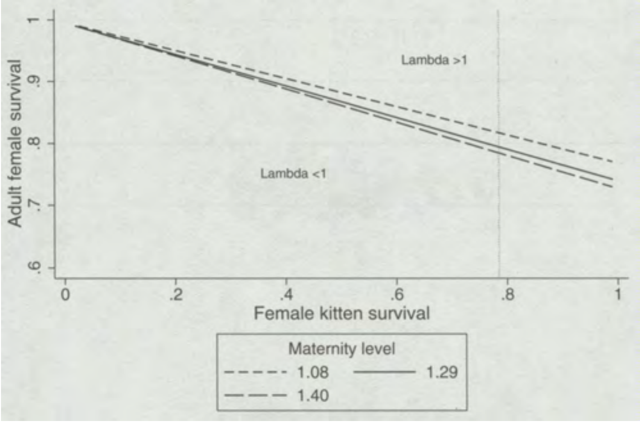

Figure 7. The relationship between mountain lion female kitten survival, adult female survival, and population growth at maternity rates of 1.08, 1.29, and 1.4. Areas above the lines represent possible lambda values greater than 1.0 and areas below represent survival levels that may lead to a decline in population. The dotted reference line represents our kitten survival estimate of 0.785 from 1998 to 2006 in the Blackfoot River watershed, Montana.

sample size following closure of the Garnet to hunting, estimated mortality rates due to hunting were significantly higher. The main influence of hunting on kitten survival may be starvation due to abandonment, not infanticide, and reductions in natural mortality do not compensate for hunting losses of kittens. Our results regarding the additive nature of hunting mortality in mountain lion populations build on Cooley et al. (2009). The additive effects of harvest, not only on adults but also through the orphaning of kittens, suggests that hunting, especially of adult females, shapes survival in hunted populations and has the potential to quickly reduce population levels.

Logan and Sweanor (2001) described the "sledgehammer approach," where hunting quotas are set mainly by the previous season's hunter success rate. As success rates decline, quotas may be reduced. However, because of a lack of inexpensive and reliable methods for tracking populations, even reduced quotas may not match existing population levels leading to further declines (Fryxell et al. 2010). Our survival modeling suggested that incremental reductions in quotas outside the protected Garnet study area did not result in significant increases in adult survival until female quotas were reduced to 0, possibly because of a mismatch between quota levels and existing population levels.

Population Modeling and Growth

Matrix population models based on the structure of our 2 top survival models resulted in similar predicted population-level outcomes. They suggested that the mountain lion population in the greater Blackfoot watershed was declining annually between 11% and 12% before protection of the Garnet study area in 2001, but recovered to levels slightly below 1998 by the end of the study in 2007. This was due to protection of the Garnet area, dispersal out of the protected Garnet, and reduced quotas in the remainder of the watershed beginning in 2004. Differences in the predicted level of decline, and the speed and level of the recovery is the result of slightly different estimated survival rates for the various survival model segments. Our estimates of kitten survival were biased high because of inclusion of kittens first marked as late as 12 months. However, even with this optimistic estimate of kitten survival, both population models predict declining populations in response to the heaviest harvest levels. If our kitten sample was based purely on animals marked at the den, our estimate of survival would most certainly be lower as would our estimate of population growth, thus strengthening our conclusion of harvest being additive.

Our sensitivity analyses showed that maternity was second in importance to female survival rates in influencing population growth rates. Sensitivity analysis does not account for annual variability, as the LSA does. Although maternity rate was held constant for all models at 1.29 kittens per female per year, fecundity is a function of maternity and adult female survival. Differences in fecundity also partially explain the different performance of each model segment.

Sensitivity analysis also showed that dispersal of both juvenile males and females from the protected Garnet into the hunted Blackfoot watershed had a strong negative effect on Garnet population growth and a weak negative effect on growth in the watershed as a whole. The population demonstrated a negative sensitivity of dispersal from the Garnet to the Blackfoot (Fig. 5), which is due to the lower survival rates in the unprotected portion of the Watershed. The matrix model suggested that juveniles would be better off remaining where their probability of survival and reproduction were higher (i.e., inside the Garnet).

Our LSA clearly demonstrated the effect of hunting on the normal population dynamics of mountain lions. In the non-hunted population, adult female survival accounted for approximately 30% of the variation in population growth between years, whereas reproduction (kitten survival and maternity) accounted for approximately 62%. Hunting reversed this balance, shifting the reliance of population growth towards adult survival (45% of the variation in growth), and away from reproduction (12%). In general, we found little effect of male survival on population growth. In the non-hunted segment of our population, male survival accounted for less than 1% of the variability in annual population growth; this level increased to 5% in the hunted population.

By varying 3 important vital rates to population growth (adult female survival, female kitten survival, and maternity) in a deterministic matrix model, we showed that adult female survival rates >0.80 (depending on kitten survival) are required for population growth (Fig. 7). However, kitten survival estimated with minimal bias due to delayed marking (e.g., Cooley et al. 2009, Hostetler et al. 2010) suggests that rates may rarely be >0.50 (see also Logan and Sweanor 2001). At that level, adult female survival <0.85 will likely result in population reduction (Fig. 7). Consistent with these results, Lambert et al. (2006) modeled broad mountain lion population declines in British Columbia, Washington, and Idaho with adult female survival rates of 0.77. Our estimates of mean kitten survival may have been biased high as the average age of a kitten when first marked was 4.7 months. As a result, our population models may slightly overestimate true growth. However, the predictions of our deterministic model regarding the relationship of kitten survival, adult female survival, maternity, and population growth (Fig. 7) are not affected by our measure of kitten survival.

Immigration and emigration have dramatic effects on real population growth rates when compared to modeled rates that do not account for dispersal. Our population models assumed a closed system consisting of only 2 populations, the Garnet and the remainder of the Blackfoot drainage. We found no juvenile dispersal from the Blackfoot back into the Garnet and therefore could not model the effect of immigration into the Garnet. We found a difference of approximately 8 animals between our modeled population estimates, and our minimum count for the Garnet. This small difference over a 9-year period could be explained by as few as 3 litters that were born inside the Garnet and were not accounted by our estimate of mean maternity rates. However, immigration into the Garnet was likely occurring, but from outside the Blackfoot watershed. Accounting for immigration and emigration, Cooley et al. (2009) showed real population decline ($\lambda = 0.91$) in a heavily hunted area with adult female survival estimated at 0.66. Without immigration, population growth would have been significantly lower, that is, $\lambda = 0.78$. That same study found an essentially stable real population growth rate ($\lambda = 0.98$) in a lightly hunted population with adult female survival of 0.87, with emigration reducing modeled growth from 1.10.

MANAGEMENT IMPLICATIONS

Our research indicates that mountain lion populations are affected by human harvest through additive effects on survival of all age classes and a resultant disruption of juvenile dispersal. We found no effect of harvest on reproductive parameters (i.e., litter size, birth interval, maternity, age at dispersal, and age at first breeding). The consistency in litter size and associated birth interval and maternity rate observed by several studies with varying levels of protection suggests that mountain lions do not possess the ability to respond to harvest through increased reproduction. This lack of elasticity in reproduction and therefore recruitment increases the need for connectivity to facilitate immigration into hunted populations. The high reliance on adult female survival for population growth should dictate very conservative female harvest unless population reduction is the stated management goal. Our results show the strong effect of harvest on targeted populations through shaping survival, and perhaps on neighboring untargeted populations by affecting dispersal patterns. Given the limitations of techniques of abundance estimation currently available and the effect of harvest on mountain lion populations, we recommend lion population objectives and harvest strategies that account for this lack of precision. A source-sink or zone management strategy, as proposed by Logan and Sweanor (2001) would protect the biological integrity of mountain lion populations, while providing public harvest opportunity and flexibility to managers in addressing management concerns.

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LITERATURE CITED

Aalen, O. 1978. Nonparametric inference for a family of counting processes. Annals of Statistics 6:701–726.

Anderson, C. R., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildlife Society Bulletin 33:179–188.

Anderson, P. K., O. Borgan, R. D. Gill, and N. Keiding. 1997. Statistical models based on counting processes. Springer, New York, New York, USA.

Ashman, D. L., G. C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wickersham. 1983. The mountain lion in Nevada. Federal Aid in Wildlife Restoration Final, Report W-48-15, Reno, Nevada, USA.

Baker, C. S., and P. J. Clapham. 2004. Modelling the past and future of whales and whaling. Trends in Ecology & Evolution 19:365–371.

Balme, R. A., L. T. B. Hunter, P. Goodman, H. Ferguson, J. Craige, and R. Slotow. 2010. An adaptive management approach to trophy hunting of leopards (*Panthera pardus*): a case study from KwaZulu-Natal, South Africa. Pages 341–352 *in* D. Macdonald and A. J. Loveridge, editors. The biology and conservation of wild felids. Oxford University Press, New York, New York, USA.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121:1–39.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:94–108.

Berube, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. Ecology 80:2555–2565.

Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation and harvesting. Oikos 87:419–426.

Brainerd, S. M. 1985. Reproductive ecology of bobcats and lynx in western Montana. Thesis, University of Montana, Missoula, USA.

Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. Ecology 65:105–112.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.

Chepko-Sade, B. D., Z. T. Halpin, and American Society of Zoologists. 1987. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, Illinois, USA.

Cleves, M. A., W. W. Gould, and R. G. Gutierrez. 2004. An introduction to survival analysis using Stata. Stata Press, College Station, Texas, USA.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cooley, H. S., K. D. Bunnell, D. C. Stoner, and M. L. Wolfe. 2011. Population management: cougar hunting. Pages 111–133 *in* J. A. Jenks, H. S. Cooley, and M. R. Conover, editors. Managing cougars in North America. Jack H. Berryman Institute, Utah State University, Logan, Utah, USA.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society Series B—Statistical Methodology 34:187–220.

Creel, S., and J. J. Rotella. 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (*Canis lupus*). PLoS ONE 5:1–7.

Errington, P. L. 1956. Factors limiting higher vertebrate populations. Science 124:304–307.

Fieberg, J., and G. D. DelGiudice. 2009. What time is it? Choice of time origin and scale in extended proportional hazards models. Ecology 90:1687–1697.

Frank, L. G., and R. Woodroffe. 2001. Behaviour of carnivores in exploited and controlled populations. Pages 419–442 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, United Kingdom.

Fryxell, J. M., C. Packer, K. McCann, E. J. Solberg, and B. E. Sæther. 2010. Resource management cycles and the sustainability of harvested wildlife populations. Science 328:903–906.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Getz, W. M., and R. G. Haight. 1989. Population harvesting: demographic models of fish, forest, and animal resources. Princeton University Press, Princeton, New Jersey, USA.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Hardin, J. W., and J. Hilbe. 2007. Generalized linear models and extensions. Second edition. Stata Press, College Station, Texas, USA.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. Journal of Wildlife Management 70:1544–1555.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. Wiley, New York, New York, USA.

Hosmer, D. W., S. Lemeshow, and S. May. 2008. Applied survival analysis: regression modeling of time-to-event data. Second edition. Wiley-Interscience, Hoboken, New Jersey, USA.

Hostetler, J. A., D. P. Onorato, J. D. Nichols, W. E. Johnson, M. E. Roelke, S. J. O'Brien, D. Jansen, and M. K. Oli. 2010. Genetic introgression and the survival of Florida panther kittens. Biological Conservation 143:2789–2796.

Hostetler, J. A., D. P. Onorato, B. M. Bolker, W. E. Johnson, S. J. O'Brien, D. Jansen, and M. K. Oli. 2012. Does genetic introgression improve female reproductive performance? A test on the endangered Florida panther. Oecologia 168:289–300.

Jones, O. R., J. M. Gaillard, S. Tuljapurkar, J. S. Alho, K. B. Armitage, P. H. Becker, P. Bize, J. Brommer, A. Charmantier, M. Charpentier, T. Clutton-Brock, F. S. Dobson, M. Festa-Bianchet, L. Gustafsson, H. Jensen, C. G. Jones, B. G. Lillandt, R. McCleery, J. Merila, P. Neuhaus, M. A. C. Nicoll, K. Norris, M. K. Oli, J. Pemberton, H. Pietiainen, T. H. Ringsby, A. Roulin, B. E. Sæther, J. M. Setchell, B. C. Sheldon, P. M. Thompson, H. Weimerskirch, E. J. Wickings, and T. Coulson. 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. Ecology Letters 11:664–673.

Kalbfleisch, J. D., and R. L. Prentice. 1980. The statistical analysis of failure time data. Wiley, New York, New York, USA.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369–382.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52:398–412.

Lambert, C. M. S., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

Larkin, P. A. 1977. Epitaph for concept of maximum sustained yield. Transactions of the American Fisheries Society 106:1–11.

Laundre, J. W., L. Hernandez, D. Streubel, K. Altendorf, and C. L. Gonzalez. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

Lehmkuhl, J. F. 1981. Distribution and habitat selection of elk in the northern Garnet Mountains of western Montana. Thesis, University of Montana, Missoula, USA.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–222.

Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Cougar population response to manipulation in southern Utah. Wildlife Society Bulletin 20:224–227.

Lindzey, F. G., W. D. Van Sickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics in southern Utah. Journal of Wildlife Management 58:619–624.

Liu J., V. Hull, A. T. Morzillo, and J. A. Wiens, editors. 2011. Sources, sinks and sustainability. Cambridge University Press, Cambridge, United Kingdom.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Logan, K. A., L. L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648–654.

Maehr, D. S., and G. B. Caddick. 1995. Demographics and genetic introgression in the Florida panther. Conservation Biology 9:1295–1298.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

McGlone, M. 2012. The hunters did it. Science 335:1452–1453.

Mills, L. S. 2007. Conservation of wildlife populations: demography, genetics, and management. Blackwell, Malden, Massachusetts, USA.

Montana Department of Fish, Wildlife and Parks. 2004. Montana statewide elk management plan. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.

Montana Department of Fish, Wildlife and Parks. 2006. White-tailed deer studies in the Salish Mountains of northwest Montana. Federal Aid in Wildlife Restoration Project W-120-R. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.

Montana Department of Fish, Wildlife and Parks. 2007. Biomedical protocol for free-ranging mountain lions (*Felis concolor*), bobcat (*Lynx rufus*), and lynx (*Lynx canadensis*) in Montana: capture, anaesthesia, tagging, sampling and necropsy procedures. Wildlife Research Laboratory, Bozeman, Montana, USA.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

Nelson, W. 1972. Theory and applications of hazard plotting for censored failure data. Technometrics 14:945–965.

Nussey, D. H., L. E. B. Kruuk, A. Morris, M. N. Clements, J. M. Pemberton, and T. H. Clutton-Brock. 2009. Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. American Naturalist 174:342–357.

Onorato, D., R. Desimone, C. White, and L. P. Waits. 2011. Genetic assessment of paternity and relatedness in a managed population of cougars. Journal of Wildlife Management 75:378–384.

Ordiz, A., O. G. Stoen, J. E. Swenson, I. Kojola, and R. Bischof. 2008. Distance-dependent effect of the nearest neighbor: spatiotemporal patterns in brown bear reproduction. Ecology 89:3327–3335.

Packer, C., M. Tatar, and A. Collins. 1998. Reproductive cessation in female mammals. Nature 392:807–811.

Packer, C., M. Kosmala, H. S. Cooley, H. Brink, L. Pintea, D. Garshelis, G. Purchase, M. Strauss, A. Swanson, G. Balme, L. Hunter, and K. Nowell. 2009. Sport hunting, predator control and conservation of large carnivores. PLoS ONE 4:1–8.

Pepe, M. S., and M. Mori. 1993. Kaplan–Meier, marginal or conditional probability curves in summarizing competing risks failure time data. Statistics in Medicine 12:737–751.

Peron, G. 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. Journal of Animal Ecology 82:408–417.

Peto, R., and J. Peto. 1972. Asymptotically efficient rank invariant test procedures. Journal of the Royal Statistical Society Series A—General 135:185–206.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences of the United States of America 95: 213–218.

Pintilie, M. 2006. Competing risks: a practical perspective. John Wiley & Sons, Chichester, England.

Prentice, R. L. 1978. Linear rank-tests with right censored data. Biometrika 65:167–179.

Quigley, H., and M. G. Hornocker. 2010. Cougar population dynamics. Pages 59–75 *in* M. G. Hornocker, and S. Negri, editors. Cougar: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Raithel, J. D. 2005. Impact of calf survival on elk population dynamics in West-Central Montana. Thesis, University of Montana, Missoula, USA.

Ricklefs, R. E. 2008. The evolution of senescence from a comparative perspective. Functional Ecology 22:379–392.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Root, K. V. 2004. Florida panther: using models to guide recovery efforts. Pages 491–504 *in* H. R. Akcakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjogren-Gulve, and J. S. Hatfield, editors. Species conservation and management: case studies. Oxford University Press, New York, New York, USA.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417–426.

Sandercock, B. K., E. B. Nilsen, H. Broseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology 80:244–258.

Simard, M. A., C. Dussault, J. Huot, and S. D. Côté. 2013. Is hunting an effective tool to control overabundant deer? A test using an experimental approach. Journal of Wildlife Management 77:254–269.

Sparkman, A. M., L. P. Waits, and D. L. Murray. 2011. Social and demographic effects of anthropogenic mortality: a test of the compensatory mortality hypothesis in the red wolf. PLoS ONE 6:1–9.

Spreadbury, B. R., K. Musil, J. Musil, C. Kaisner, and J. Kovak. 1996. Cougar population characteristics in southeastern British Columbia. Journal of Wildlife Management 60:962–969.

Sterling, B., W. Conley, and M. R. Conley. 1983. Simulations of demographic compensation in coyote populations. Journal of Wildlife Management 47:1177–1181.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.

Swenson, J. E., F. Sandegren, A. Soderberg, A. Bjarvall, R. Franzen, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. Nature 386:450–451.

Todd, A. W., and L. B. Keith. 1983. Coyote demography during a snowshoe hare decline in Alberta. Journal of Wildlife Management 47:394–404.

Treves, A. 2009. Hunting for large carnivore conservation. Journal of Applied Ecology 46:1350–1356.

Turgeon, K., and D. L. Kramer. 2012. Compensatory immigration depends on adjacent population size and habitat quality but not on landscape connectivity. Journal of Animal Ecology 81:1161–1170.

White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288–331 *in* L. Boitani, and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Whitman, K., A. M. Starfield, H. S. Quadling, and C. Packer. 2004. Sustainable trophy hunting of African lions. Nature 428:175–178.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California, USA.

Winterstein, S. R., K. H. Pollock, and C. M. Bunck. 2001. Analysis of survival data from radiotelemetry studies. Pages. 351–380 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81:628–641.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zimmermann, F., C. Breitenmoser-Wursten, and U. Breitenmoser. 2005. Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. Journal of Zoology 267:381–395.

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Special Section on Mountain Sheep Management

The Gordian Knot of Mountain Lion Predation and Bighorn Sheep

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ABSTRACT The objective of this review is to generate a synthesis of research conducted on predation of bighorn sheep (*Ovis canadensis*) and to suggest directions for future research relative to current knowledge gaps and a novel hypothesis. This review is primarily based on literature from the last 60 years on desert bighorn sheep (*O. c. nelsoni*), Rocky Mountain bighorn sheep (*O. c. canadensis*), and mountain lion (*Puma concolor*) predation. Although, many predators kill bighorn sheep, only mountain lions are currently considered to be the primary proximate cause of mortality for many bighorn sheep populations. The ultimate cause of this phenomenon has vexed wildlife managers for >40 years. There are 3 primary reasons for increased predation on bighorn sheep by mountain lions. First, there is an increased presence of mountain lions in habitats where they were historically absent or rare because of the expansion of mule deer (*Odocoileus hemionus*) following the extensive conversion of fire-maintained grasslands to shrublands in the late-1800s. Second, is the extirpation of the 2 dominant apex carnivores (wolves [*Canis lupus*] and grizzly bears [*Ursus arctos*]) during this same time period and a hypothesized numerical response of mountain lions to those extirpations. Finally, the response of mountain lions to the cessation of >70 years of intensive predator control has often resulted in unsustainable mountain lion-bighorn sheep ratios, especially for desert bighorn sheep. Additionally, the effect of mountain lion predation is exacerbated by declines in bighorn sheep that do not result in declines in mountain lions because of their ability to prey switch to mule deer, elk (*Cervus canadensis*), or domestic cattle; kleptoparasitism of mountain lions kills, by ursids and canids, resulting in higher kill rates for mountain lions; and a possible ecological trap where adaptations derived over evolutionary time are no longer adaptive because of human-induced changes in the sympatric apex predator guild. Control of mountain lions, when mountain lion-ungulate ratios are high, might be required to protect small or endangered bighorn sheep populations, and to produce bighorn sheep for restoration efforts. © 2017 The Wildlife Society.

KEY WORDS apparent competition, bighorn sheep, ecological trap, kleptoparasitism, mountain lion, Native American fire, predation, predator control, predator-prey ratio.

Predation on bighorn sheep (*Ovis canadensis*), specifically mountain lion (*Puma concolor*) predation on isolated populations of bighorn sheep, has hindered restoration efforts for bighorn sheep in western North America. This review paper synthesizes our current knowledge and includes a novel hypothesis for the ultimate cause of high mountain lion predation that has confounded wildlife managers for >4 decades. This review is derived primarily from historical literature published in the last 60 years on desert bighorn sheep (*O. c. nelsoni*), Rocky Mountain bighorn sheep (*O. c. canadensis*), and mountain lion predation.

Predation has a profound influence on prey population dynamics in many ecosystems. Laboratory, mesocosm, or natural experiments have assessed the role of predation on non-ungulate prey including relationships between starfish (*Pisaster* spp.) and tidal pool prey (Paine 1969), mites (*Typhlodromus occidentalis*) and mite prey (*Tarsonemus pallidus* and *Eotetranychus sexmaculatus*; Huffaker 1958), mesocarnivores and waterfowl (Garrettson and Rohwer 2001), weasels (*Mustela nivalis*) and voles (*Microtis agrestis*; Graham and Lambin 2002), mountain lions and porcupines (*Erethizon dorsatum*; Sweitzer et al. 1997), lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*; Krebs et al. 1995), and numerous other species. Hairston et al. (1960:424) noted "herbivores are seldom food-limited and appear most often to be predator-limited." Excluding anthropogenic associated mortality, only disease has the potential for greater population-level consequences on prey populations (Pedersen et al. 2007).

The scientific literature on predation and ungulates is replete with evidence of the depressive effects that carnivores can have on ungulate populations (Gasaway et al. 1992, Harrington et al. 1999, Hayes et al. 2003, Wittmer et al. 2005, Bergerud et al. 2007). For example, some species of African ungulates increased ≥7 times following the removal

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of apex carnivores and all prey species <150 kg declined to near pre-removal densities after those predators were reestablished (Sinclair et al. 2003).

Asymptotic densities of ungulate populations, including bighorn sheep, on predator-free islands and in predator-free enclosures are examples of the profound influence the absence of predation can have on prey density. In North America, maximum ungulate densities in those settings are remarkably similar across an array of ecosystems and study area sizes ranging from 2.5–8,000 km^2 (McCullough 1979, Bowyer et al. 1999, Bergerud et al. 2007, Simard et al. 2010, Rominger 2015). In predator-free environments the median maximum density of deer-size ungulates is approximately 35 individuals/km^2 and compared to adjacent mainland areas with predators, ungulate densities are generally an order of magnitude, or more, greater (Rominger 2015).

High ungulate densities in the absence of predation have been documented in many cases for decades (Matthews 1973, New Mexico Department of Game and Fish [NMDGF], unpublished data) and for 80–130 years in the case of the Slate Islands, Ontario, Canada, Anticosti Island, Quebec, Canada, and Antelope Island, Utah, USA (Wolfe and Kimball 1989, Potvin et al. 2003, Bergerud et al. 2007) despite dramatic changes in vegetation composition. In other northern hemisphere predator-free islands, the non-irruptive mean ungulate density is like that reported on North American islands (Kaji et al. 2004). Density of tropical fauna is also 10 to 100 times greater on tropical predator-free islands compared with adjacent mainland densities, which mirrors the ratio of ungulate densities on temperate islands to adjacent mainlands (Terborgh et al. 2001).

The predator evasion strategy of bighorn sheep relies on the combination of keen eyesight to detect predators at distance and the ability to navigate steep terrain and outmaneuver predators following visual detection (Geist 1999). Sexual segregation of female and juvenile bighorn sheep, from male bighorn sheep, is hypothesized to be related to anti-predator behavior that includes proximity to steep escape terrain (Bleich et al. 1997). Both strategies are more effective, and therefore likely to have evolved, in response to coursing predators (e.g., wolves [*Canis lupus*]; Festa-Bianchet 1991). These strategies are less effective against a stalking predator (e.g., mountain lions).

Bighorn sheep-predator relationships are associated with potential proximate and ultimate causes. High mountain lion predation on bighorn sheep, particularly desert bighorn sheep and Sierra Nevada bighorn sheep (*O. c. sierrae*) has been the proximate factor hindering restoration in many historical ranges (Wehausen 1996, Hayes et al. 2000, Kamler et al. 2002, Rominger et al. 2004). High mountain lion predation on bighorn sheep, seen since the 1970s, appears to be related to the cessation of intensive predator control used during much of the twentieth century. This release of mountain lions from predator control has resulted in increased mountain lion-bighorn ratios that can be unsustainable based on native ungulate density, especially for desert bighorn sheep (Rominger 2013).

The ultimate cause of high mountain lion predation on bighorn sheep appears to be related to a restructuring of the apex predator guild following the extirpation of wolves and grizzly bears (*Ursus arctos*; Young and Goldman 1944, Brown 1985), major shifts in biotic communities (Berger and Wehausen 1991, McPherson 1995), and the associated restructuring of the ungulate guild across much of western North America. This restructuring has been primarily influenced by the cessation of widespread Native American burning and hunting (Turner 1991, Kay 1995, Stewart 2002), the introduction of livestock and feral equids (Berger and Wehausen 1991, Brown 1994), and the resulting expansion of mule deer (*Odocoileus hemionus*) and mule deer habitats.

Other ecological factors affecting predation and bighorn sheep include apparent competition (Rominger et al. 2004, Johnson et al. 2013), specialist predators (Ross et al. 1997, Logan and Sweanor 2001, Knopff and Boyce 2007, Knopff et al. 2010), kleptoparasitism (Elbroch et al. 2015), vulnerability of small populations (Berger 1990), subsidized predators (Rominger et al. 2004), indirect effects of predation (Bourbeau-Lemieux et al. 2011), and declining native prey (Unsworth et al. 1999). The extirpation of wolves and grizzly bears from the predator guild associated with bighorn sheep resulted in mountain lions becoming the primary bighorn sheep predator. This human-induced change might have resulted in an ecological trap (Dwernychuk and Boag 1972, Schlaepfer et al. 2002). Continued restoration of wolf and grizzly bear populations throughout Rocky Mountain and desert bighorn sheep habitat will add complexity associated with multi-predator, multi-prey systems (Knopff and Boyce 2007, Kortello et al. 2007, Knopff et al. 2010, Ruth et al. 2011) compared to many systems that only have had mountain lions as a resident apex carnivore for most of the last century.

Virtually all predators, sympatric with bighorn sheep, ranging in size from gray fox (*Urocyon cinereoargenteus*) to grizzly bear, have been documented to prey upon bighorn sheep (Sawyer and Lindzey 2002) and except for foxes, have been documented to prey on adults and juveniles. Although smaller predators (e.g., coyotes [*Canis latrans*], bobcats [*Lynx rufus*], and golden eagles [(*Aquila chrysaetos*)), and less cursorial predators (e.g., black bear [*U. americanus*] and grizzly bear) are likely more effective predators of neonates, mountain lions have been documented as the primary predator of lambs (Parsons 2007, Smith et al. 2014, Karsch et al. 2016).

The consensus in the earliest review of the effects of predation on desert bighorn sheep was that no predators had population-level consequences (Desert Bighorn Council [DBC] 1957). At the inaugural DBC meeting, a special session on predation concluded that bobcats and golden eagles were the primary predators of desert bighorn sheep but that neither species limited population demographics (DBC 1957). Most biologists working on desert bighorn sheep thought that mountain lion numbers were so low, and the predator-control programs so strict (private and government year-round trapping and hunting, bounties, poisons), that mountain lions simply could not induce population declines. The first monograph and 2 of the earliest books on Rocky Mountain and desert bighorn sheep ecology (Buechner 1960, Geist 1971, Monson and Sumner 1980) were written during a period when mountain lions were unprotected, or just recently protected by law, and wolves had been extirpated from all bighorn sheep habitats in the conterminous United States (Young and Goldman 1944). Mountain lion predation was not considered to be an important influence on bighorn sheep population dynamics.

In contrast, 5–6 decades later, a different predator-management paradigm, with mountain lions protected throughout the United States (except TX) and Canadian provinces, has shifted our interpretation of the consequences of predation. The demographic recovery of mountain lions in virtually all bighorn sheep ranges, and the advent and use of radio-telemetry to assess mortality causes, has resulted in multiple examples of population-level effects of mountain lion predation on bighorn sheep (Harrison and Hebert 1988, Wehausen 1996, Hayes et al. 2000, Rominger et al. 2004, Festa-Bianchet et al. 2006). In a recent review, Sawyer and Lindzey (2002) determined that mountain lions were capable of depressing bighorn sheep populations and numerous publications have corroborated that conclusion (Kamler et al. 2002, McKinney et al. 2006, Foster and Whittaker 2010, Brewer et al. 2013, Johnson et al. 2013).

CHANGES IN THE PREDATOR-PREY COMMUNITY

Predation on bighorn sheep hypothetically has been influenced by a change in the apex predator guild following the extirpation of wolves and grizzly bears and a change in the ungulate guild following the conversion of much of western North America from a grassland ecosystem maintained with fire by Native Americans to a shrub-dominated ecosystem. Changes in the ungulate guild are primarily related to the extensive range expansion of mule deer throughout large portions of bighorn sheep range (Berger and Wehausen 1991, Turner 1991, McPherson 1995, Kay 1995, Stewart 2002).

Changes in Predator Guild

Grizzly bear and wolf distribution overlapped nearly all Rocky Mountain bighorn sheep range and some desert bighorn ranges (Young and Goldman 1944, Lamb et al. 2017). These 2 predators were absent only from the most xeric parts of Mexico, western Arizona, California, and Nevada (Young and Goldman 1944, Lamb et al. 2017). The extirpation of wolves (Young and Goldman 1944) and near extirpation of grizzly bears (Brown 1985, Lamb et al. 2017) is well documented. Mountain lions are subordinate to wolves and bears (Boyd and Neale 1992, Kortello et al. 2007, Ruth et al. 2011, Elbroch et al. 2015) and much like the well documented response of subordinate coyotes to the absence of wolves (Berger and Gese 2007, Merkle et al. 2009), mountain lions almost certainly have responded numerically to competitive release from these 2 dominate carnivores. Evidence of this subordination is the observation that when pursued by hounds, mountain lions in North America will climb trees. In South America, where mountain lions did not evolve with a large canid predator, they do not climb trees when pursued by hounds (B. M. Jansen, Arizona Game and Fish Department [AZGFD], personal communication.). Although the total cost to mountain lions of sympatry with wolves has not been assessed, it is hypothesized that interactions could affect reproduction, survival rates, habitat selection, and home range size (Kortello et al. 2007, Ruth et al. 2011). Mountain lion survival was negatively affected by increasing annual wolf use, wolves were responsible for 15% of adult mountain lion deaths, and wolf predation decreased annual kitten production 10–39% (Ruth et al. 2011).

Anecdotal evidence suggests that mountain lions and coyotes were rare or absent where grizzly bears and wolves occurred in New Mexico (Barker 1953, Stevens 2002). Stevens (2002) hunted grizzly bears, black bears, and mountain lions with dogs throughout the late 1800s, in the portion of New Mexico that is now the Gila Wilderness, but only mentioned 2 mountain lions in his book. In 1882, a Professor Dyche from the University of Kansas came to New Mexico to collect grizzly bears in what is now the Pecos Wilderness. Using a tree blind and a deer for bait, Dyche reported bobcats and foxes but not a single coyote in his diary, although they became common after the turn of the century following the extirpation of wolves (Barker 1953).

Extirpation of wolves and grizzly bears was facilitated by intensive predator control. Private predator control efforts began in the western United States soon after livestock was introduced following the end of warfare with Native Americans. In 1914, following a Congressional appropriation, federal agencies employed 300 predator control agents to protect livestock and remnant wild ungulate populations (Brown 1992). Control efforts included year-round trapping, poisoning, hunting with hounds, denning, and bounties paid from private and government sources (Buechner 1960, Brown 1992).

Xeric ecoregions with sufficient numbers of deer to maintain resident mountain lions, but without wolves or grizzly bears, presumably functioned much like systems where high mountain lion predation on bighorn occurs today. Historical accounts suggest that native ungulate densities may have been low in multi-prey ecosystems with sympatric mountain lions as the primary apex predator. As Charles Sheldon embarked on a bighorn sheep hunt into Mexico in 1915, his guide remarked that he had recently been to the Sierra Pintas in Arizona and "lions are numerous there but sheep are scarce" (Sheldon 1979:66). During the 1907 William Hornaday expedition from Tucson, Arizona to the Pinacate Mountains in Sonora, Mexico, a single adult deer was seen in a trip that lasted more than 30 days (Hornaday 1908).

Mountain lions may have been less common historically because of interspecific competitors (Stevens 2002, Riley et al. 2004, Wittmer et al. 2005) and a much more limited distribution of mule deer (Berger and Wehausen 1991, Potter 1995, Heffelfinger and Messmer 2003). Although mountain lion abundance might have been briefly released following the extirpation of wolves, >70 years of intensive predator control kept numbers low. Quantifying abundance of mountain lions is difficult (Logan and Sweanor 2001) and there are no reliable estimates from periods of intensive predator control. Bounty records from 1902–1906 in Montana indicate that bounties paid for wolves outnumbered those paid for mountain lions by >30:1. By region, there was an inverse relationship between the number of wolves and mountain lions for which a bounty was paid suggesting that in areas where wolves were prevalent, mountain lions were rare (Riley et al. 2004).

Changes in Prey Guild

Grasslands were maintained across western North America with fire by Native Americans for millennia (Turner 1991, Kay 1995, McPherson 1995, Stewart 2002). Shrubs, which are the primary forage of mule deer, were an inconspicuous component of desert grasslands prior to 1880 (McPherson 1995). Reports of mule deer were rare in the diaries of early travelers and were reported to be a minor component of Native American diets (Berger and Wehausen 1991, Potter 1995, Heffelfinger and Messmer 2003, Kay 2007). The landscape conversion, of historical grasslands to shrub or chaparral, was influenced by grazing of excessive numbers of livestock and feral equids (Berger and Wehausen 1991). This conversion resulted in range expansion of mule deer and concomitantly the presence of mountain lions (Berger and Wehausen 1991). This conversion of grasslands to chaparral and shrublands occurred throughout bighorn sheep ranges in western North America. Range expansion of mountain lions following invasion by white-tailed deer (*Odocoileus virginianus*) into areas of clear-cut old-growth forests converted to shrub-dominated habitats also has been documented (Compton et al. 1995, Wittmer et al. 2005).

The 500,000-km^2 Great Basin ecoregion is hypothesized to have been void of deer and mountain lions because grass-dominated basin and range habitats, maintained by burning by Native Americans, did not support deer (Berger and Wehausen 1991). The Great Basin contains extensive bighorn sheep habitat and pronghorn (*Antilocapra americana*) and bighorn sheep were likely the primary ungulates present in this vast landscape. Therefore, bighorn sheep in the Great Basin may have encountered little predation by mountain lions just 125 years ago. Niche separation between pronghorn and bighorn sheep would have resulted in this ecosystem functioning much like a single-prey system. Analysis of Native American diets at 2 pueblo sites in New Mexico reported the ratio of pronghorn specimens to deer specimens was 25:1 and 79:1, respectively (Potter 1995).

Mountain lions are most effective at limiting bighorn sheep populations when they are able to prey switch onto deer, elk, or cattle and there is little evidence that mountain lions can limit bighorn sheep populations without alternative prey (Berger and Wehausen 1991, Wehausen 1996). Resident mountain lions were undocumented in bighorn sheep habitat of the Providence and New York Mountains, California, United States, until the introduction of mule deer (R. A. Weaver, California Department of Fish and Wildlife, personal communication). Mountain lion predation is rare in the most xeric mountain ranges without sympatric deer or livestock (Berger and Wehausen 1991, Cronin and Bleich 1995).

THE PARADOX OF MOUNTAIN LION DENSITY

Regardless of the mechanisms that have resulted in the predator-prey guilds present today, it is the current ratio of mountain lions to native ungulate populations that appears to influence the primary proximate cause of mortality for bighorn sheep. Following decades of intensive predator control, mountain lions have increased numerically and in distribution (Fecske et al. 2011, Knopff et al. 2014). Predator control across North America was initially directed primarily toward wolves; however, the emphasis switched to mountain lions, black bears, and coyotes following the near-extirpation of wolves. Some states paid higher bounties for female mountain lions to incentivize population reduction (Buechner 1960). Until the cessation of large-scale predator control, mountain lion predation on bighorn sheep populations was insignificant (DBC 1957).

In a review of 12 studies assessing the effects of sport hunting on mountain lions, the range of densities was 1.1–7.1 mountain lions/100 km^2, although the low density does not include subadults or kittens (Cooley et al. 2011). A density of 1–3 mountain lions/100 km^2 when coupled with a standard ungulate kill rate (Wilckins et al. 2016) may have a profound influence on ungulate population dynamics (Table 1).

Global positioning system (GPS) collaring of mountain lions has allowed for a refinement of kill rates by visiting waypoint clusters associated with kills and most studies have confirmed that mountain lions kill about 1 ungulate/week (Anderson and Lindzey 2003, Knopff et al. 2009, Wilckins et al. 2016). This value is used as the mean for calculating the number of ungulate kills/100 km^2 with the 95% confidence interval for a high and low kill rate (Table 1; Wilckins et al. 2016). At a high density of 3 mountain lions/100 km^2 and a high kill rate of 1.1 ungulate/week, there would be a predicted 172 kills/100 km^2 annually (Table 1). Most small desert bighorn sheep populations in New Mexico were predicted to go extinct with 5% additive mountain lion mortality (Fisher et al. 1999). For 172 kills to be 5% of a wild ungulate population, the density required would be 3,440 ungulates/100 km^2. At a low density of 1 mountain lion/100 km^2 and a low kill rate of 0.9 ungulate/week there would be 47 kills annually (Table 1). For 47 kills to be 5% of a wild ungulate population, the density required would be 940 ungulates/100 km^2. Both numbers are essentially 1–2 orders of magnitude greater than currently estimated ungulate densities in desert bighorn sheep ranges in New Mexico (Bender et al. 2012, Rominger 2013). This is the paradox that influences high mountain lion predation in desert bighorn sheep ranges. Cunningham et al. (1999) estimated that 44% of mountain lion dietary biomass was comprised of livestock at an Arizona study area. The fact that mountain lions are a subsidized predator (Soule et al. 1988) is a partial explanation for their ability to persist despite low native

Table 1. Kills as a percentage of 3 hypothetical deer-size ungulate-prey population densities using 3 values of mountain lion density and 3 values of kill rates (e.g., low lion density [1.0] × low kill rate [0.9] × 52 weeks = 47 kills/annually). The final column is number of deer-size ungulates/100 km^2 required for the number of kills to be a 5% mortality rate (e.g., 47 kills/5 × 100) = 940.

Mountain lion density/100 km^2[a]	Mountain lion weekly kill rates[b] (no. prey)	No. annual kills	Annual % mortality[c] at 50 prey/100 km^2	Annual % mortality[c] at 100 prey/100 km^2	Annual % mortality at 200 prey/100 km^2	No./100 km^2 if % mortality = 5%
1	0.9	47	94	47	24	940
1	1.0	52	>100	52	25	1,040
1	1.1	57	>100	57	28	1,140
2	0.9	94	>100	94	47	1,880
2	1.0	104	>100	>100	52	2,080
2	1.1	114	>100	>100	57	2,280
3	0.9	140	>100	>100	70	2,800
3	1.0	156	>100	>100	78	3,120
3	1.1	172	>100	>100	86	3,440

[a] These values lower than most values in Cooley et al. (2011).

[b] Mean kill rate ±95% confidence intervals from Wilckins et al. (2016).

[c] >100 indicates the estimated annual kill exceeds population size.

ungulate densities (Cunningham et al. 1999, Rominger et al. 2004).

In the Fra Cristobal Mountains, New Mexico, mountain lion control conducted from 1999 until 2013 resulted in the highest estimated ungulate density of any desert mountain range in the state (New Mexico Department of Game and Fish [NMDGF], unpublished data). The combined bighorn sheep and mule deer density is approximately 400/100 km^2 (NMDGF, unpublished data). From 2003 to 2013, an average of 3.3 mountain lions were killed annually on the 107-km^2 mountain range (NMDGF, unpublished data). However, even at this high ungulate density, 2 resident mountain lions could potentially kill nearly 25% of the resident ungulates annually.

A long-term mountain lion study on the San Andres Mountains, New Mexico documented 1.72–4.25 mountain lions/100 km^2 including adults, subadults, and cubs. This study was completed in 1995 just as high mountain lion predation adversely affected mule deer density and was also the predominant mortality cause associated with the biological extinction of desert bighorn sheep (Logan and Sweanor 2001, Rominger and Weisenberger 2000). Following this study, mule deer density declined to one of the lowest ungulate densities reported in North America with an estimated 10–12 deer/100 km^2 (Bender et al. 2012, Rominger 2013). Although mountain lion density in the San Andres Mountains is currently unknown, they persist in this habitat despite a very low deer density. There has been no discernable recovery of mule deer in >20 years.

DIRECT PREDATION

Although predation by mountain lions had been anecdotally noted by several authors (Leopold 1933, DBC 1957, Blaisdell 1961), it was not until the earliest stages of the restoration of desert bighorn sheep in Texas that high mountain lion predation was documented to cause population declines (Kilpatric 1976). In rapid succession, other western states and provinces began documenting instances of high mountain lion predation (Table 2). Most early data are reported as a percentage of radio-collared bighorn sheep killed annually (Muñoz 1982, Harrison and Hebert 1988, Creeden and Graham 1997, Ross et al. 1997).

Table 2. Examples of high mountain lion predation on bighorn sheep (bhs) in western North America.

Location	Year	Citation	Specifics
TX	1975	Kilpatric (1976, 1982)	21 bhs killed inside captive breeding facility by mountain lions at Black Gap State Wildlife Area; the wild population estimated to have declined from 20 to <10
NM	1979	Muñoz (1982)	9 of 25 (36%) bhs killed by mountain lions in 14 months
NM	1980–1989	Hoban (1990)	22 of 43 bhs mortalities attributed to mountain lion predation
NM	1996–1997	Rominger and Weisenberger (2000)	Bhs decline from ~25 to 1 resulting in biological extinction. Mountain lion predation the primary cause of death
BC	1986–1988	Harrison and Hebert (1988)	2 female mountain lions kill a minimum of 21 bhs in 14 months
CO	1995	Creeden and Graham (1997)	5 of 14 (36%) radio-collared bhs killed by mountain lions within 12 months
AB	1985–1994	Ross et al. (1997)	13% of winter bhs population killed; 1 female mountain lion killed 9% of total population and 26% of lambs in 1 winter
OR	1995–2002	Foster and Whittaker (2010)	Hart Mountain bhs herd declined from 600 to 125 with mountain lion predation the primary cause of mortality
CA	1997–1999	Schaefer et al. (2000)	Mountain lion predation cause of 75% of bhs mortality
CA	1976–1988	Wehausen (1996)	49 bhs documented killed by mountain lions without telemetry
AZ	1979–1997	Kamler et al. (2002)	In meta-analysis of 365 translocated bhs, 66% of mortality was mountain predation

Table 3. Cause-specific mortality rates (CSMR) on bighorn sheep (bhs) attributed to mountain lion predation in western North America.

Location	Year	Citation	Mortality rates
CA	1988–1995	Wehausen (1996)	CSMR due to mountain lions was 0.38
AZ	1979–1997	Kamler et al. (2002)	In meta-analysis of 365 translocated bhs, the highest CSMR due to mountain lions was 0.29
AZ	1993–1996	Bristow and Olding (1998)	CSMR due to mountain lions was 0.12 for females and 0.15 for males
NM	1992–2000	Rominger et al. (2004)	CSMR due to mountain lions was 0.13 for males and 0.09 for females in desert habitat
OR	2004	Foster and Whittaker (2010)	CSMR due to mountain lions for 44 radio-collared bhs was 0.17 for males and 0.10 for females
AB/MT	1983–2003	Festa-Bianchet et al. (2006)	During years of high mountain lion predation, the CSMR due to mountain lions was 0.26 for males and 0.32 for females
CA	1992–1998	Hayes et al. (2000)	CSMR due to mountain lions for 113 radio-collared bhs ranged between 0.08 and 0.26

The development of survival models (Heisey and Fuller 1985, White and Burnham 1999) that incorporate data from telemetrically monitored bighorn sheep, allow researchers to calculate cause-specific mortality rates (CSMR; Table 3). Mountain lion-specific mortality rates of adult bighorn sheep have been as high as 0.26 (Hayes et al. 2000), 0.29 (Kamler et al. 2002), and 0.31 (Goldstein and Rominger 2012) in some ranges. Statewide lion-specific mortality rates for desert bighorn sheep in New Mexico between 1992 and 2002 were 0.16 (Goldstein and Rominger 2012) and 88% of New Mexico desert bighorn sheep populations went extinct or declined to <10 females during this period.

The high mortality rates on state-endangered desert bighorn, attributed to mountain lion predation, in New Mexico during the 1990s were unsustainable and caused populations to decline rapidly (Goldstein and Rominger 2012). However, substantially lower mountain lion mortality rates are projected to be detrimental to the persistence of small populations of bighorn sheep. A Vortex model for state-endangered desert bighorn sheep in New Mexico predicted that all extant populations had a 100% probability of extinction with just 10% mountain lion predation added to baseline non-predation demographic parameters (Fisher et al. 1999). Initial population sizes of these small herds ranged from 10–120 and just a 5% mountain lion predation rate induced an extinction probability of 0.82–1.0 for 6 extant herds (Fisher et al. 1999).

Following the initiation of mountain lion control in desert bighorn sheep ranges in New Mexico, numbers increased from <170 in 2001 to >1,100 in 2016 (Fig. 1; Ruhl and Rominger 2015). After 31 years on the New Mexico threatened and endangered species list, desert bighorn sheep were delisted in 2012 and returned to a state-protected game species (Rominger et al. 2009, Goldstein and Rominger 2013).

Predation is the dominant cause of mortality for ungulate neonates (Smith et al. 1986, Scotton 1998, Gustine et al. 2006, Quintana et al. 2016). Predation caused 82% and 86% of mortality of desert bighorn sheep lambs in 2 studies in New Mexico (Parsons 2007, Karsch et al. 2016). In both studies, mountain lions were the apex predator.

Although wolves are currently considered to be a predator of minor consequence, as mountain lions were in 1957, wolves are still recolonizing many Rocky Mountain bighorn sheep ranges and have just begun to re-occupy historical desert bighorn sheep ranges in Arizona and New Mexico. The ecological relationship between wolves and mountain lions is not well understood (Husseman et al. 2003, Kortello et al. 2007, Ruth et al. 2011, Krawchuck 2014) and research has been primarily conducted in ecosystems recently recolonized by one or both predators, or where both carnivores have responded to less intensive predator control (Knopff and Boyce 2007, Kortello et al. 2007, Ruth et al. 2011). Most of these studies have reported mountain lions to be subordinate to wolves resulting in usurpation of kills, direct mortality of adult and juveniles, and constriction of home ranges (Boyd and Neale 1992, Kortello et al. 2007, Ruth et al. 2011).

In North American ecosystems occupied by Dall's sheep (*O. dalli dalli*), the primary predator is the wolf and there is little evidence of consistent population-level consequences of predation (Barichello and Carey 1988, Hayes et al. 2003), although Bergerud and Elliot (1998) reported improved recruitment of Stone's sheep (*O. d. stonei*) following the reduction of wolf numbers in British Columbia. Barichello and Carey (1988) reported no evidence that a substantial reduction in wolf density influenced demographics of Dall's sheep. However, Arthur and Prugh (2010) reported high

Figure 1. Desert bighorn sheep population estimates, New Mexico, 1980–2016. From 1979–1999, there were 253 desert bighorn sheep released into wild populations. From 2000–2016, there were 274 desert bighorn sheep released into wild populations. Mountain lion control began in 1999 in all endangered desert bighorn sheep herds when statewide population estimates declined to <170 in 6 herds.

levels of Dall's sheep lamb mortality by coyotes, which are hypothesized to have increased because of wolf control.

Coyotes are reported to kill adult and juvenile ungulates (Hass 1989, Kelley 1980) and were the second-most important predator of juvenile desert bighorn sheep after mountain lions in the Peloncillo Mountains, New Mexico (Karsch et al. 2016). Coyotes may be more effective predators than wolves on wild sheep neonates (Arthur and Prugh 2010) and the extirpation of wolves has resulted in a competitive release of coyotes (Berger and Gese 2007). Hebert and Harrison (1988) reported coyote predation as a major source of lamb mortality in British Columbia, Canada, and that predator control targeting coyotes was responsible for a 2–2.5-fold increase in lamb:female ratios. Bobcats are reported to kill adult and juvenile ungulates (Kelley 1980, DeForge 2002); however, there is little evidence that they have population-level effects on bighorn sheep populations. Bobcats were not confirmed to have killed desert bighorn sheep lambs in the 2 New Mexico studies (Parsons 2007, Karsch et al. 2016).

Most bighorn sheep herds are comprised of <100 individuals (Berger 1990) and therefore may be more vulnerable to extinction (Berger 1990, Fisher et al. 1999), although Wehausen (1999) found less support for a strong population size effect on extinction probability. High levels of predation can cause the extirpation of small isolated populations of bighorn sheep (Rominger and Weisenberger 2000), woodland caribou (*Rangifer tarandus*; Kinley and Apps 2001), and other species (Williams et al. 2004). However, bighorn sheep populations >100 also have been documented to decline substantially, with mountain lion predation the primary cause of mortality (Wehausen 1996, Hayes et al. 2000, Foster and Whittaker 2010).

Bighorn sheep populations with sympatric deer have been documented to decline to low density, with mountain lion predation the primary mortality factor (Wehausen 1996, Foster and Whittaker 2010, Rominger 2013). This apparent competition in multiple-prey systems was first described by Holt (1977) and has been documented in bighorn sheep populations (Rominger et al. 2004, Johnson et al. 2013) and other ungulates (Bergerud and Elliot 1986, Harrington et al. 1999, McLellan et al. 2010, Wittmer et al. 2014). For Sierra Nevada bighorn sheep, the more common prey species is mule deer (Johnson et al. 2013); however, in most desert bighorn sheep habitats in Arizona and New Mexico, domestic cattle, usually juveniles, are also alternative prey (Cunningham et al. 1999, Rominger et al. 2004).

The usurpation of mountain lion kills by interspecific competitors, primarily bears or wolves, can influence predation dynamics. In Colorado and California, mountain lion kill rates increased 48% in the presence of sympatric black bears because of kleptoparasitism, with bears detected at 48–77% of mountain lion kills (Elbroch et al. 2015). Although mountain lions may occasionally kill small black bears at cache sites, it appears that mountain lions generally depart permanently following the arrival of larger black bears (Elbroch et al. 2015). Wolves were documented to usurp 12% and scavenge 28% of mountain lion kills during a 4-year period (Kortello et al. 2007). In southern British Columbia, where wolves and grizzly bears were extirpated, or greatly reduced, mountain lions are the dominant predator of woodland caribou (Compton et al. 1995, Kinley and Apps 2001, Wittmer et al. 2005). However, in north-central British Columbia, where wolves and grizzly bears persist, mountain lions are not the dominant predator (Wittmer et al. 2005).

After work by Ross et al. (1997) that documented high mortality on a wintering bighorn sheep herd by an individual mountain lion, it has been debated whether most predation on bighorn sheep is a function of specialist mountain lions. Although, specialist predators exist (Ross et al. 1997, Logan and Sweanor 2001, Knopff and Boyce 2007), other data suggest that most sympatric mountain lions will kill bighorn sheep. In the Peninsular Ranges of California, 18 of 23 individually identified mountain lions were associated with bighorn sheep kills (Ernest et al. 2002) and in the Fra Cristobal Mountains, New Mexico 16 of 18 radio-collared mountain lions either killed or attempted to kill desert bighorn sheep (NMDGF, unpublished data).

The predator-evasion strategy of bighorn sheep is far more effective against a coursing predator than a stalking predator (Festa-Bianchet 1991) and the abrupt removal of wolves and widespread replacement by mountain lions may have resulted in an evolutionary trap where past selection pressures shaped cue-response systems that were adaptive but no longer are in the face of human-induced changes. Additionally, the sexual segregation behavior of bighorn sheep might be associated with the potential for an ecological trap. Mortality rates for female bighorn sheep, attributed to mountain lion predation can be as high or higher than those for males, suggesting the benefit of this sexual segregation strategy is not particularly effective against mountain lion predation (Krausman et al. 1989, Hayes et al. 2000, Kamler et al. 2002, Festa-Bianchet et al. 2006).

DISCUSSION

Recent studies throughout western North America provide evidence that direct predation by mountain lions is a primary proximate mortality factor of bighorn sheep. The increase in mountain lion predation on bighorn sheep has followed the demographic recovery of mountain lion populations following the cessation of intensive predator control efforts. The recovery of mountain lions was preceded by expansion of their primary prey, mule deer, following the vast conversion of grasslands that had been maintained with fire by Native Americans. This shift in the mountain lion prey guild allowed for range expansion of mountain lions into habitats where wolves and grizzly bears have been extirpated. The combination of restructured predator-prey guilds and elimination of Native American fire and hunting has resulted in bighorn sheep with sympatric mountain lion densities unlikely to have occurred previously.

Additionally, livestock and feral equids responsible for conversion of grasslands contribute to the alternative prey-base for mountain lions. In ecosystems with low densities of native prey, cattle subsidize mountain lion populations and may comprise >40% of the biomass in mountain lion diets, precluding a decline in mountain lion numbers despite declining native ungulate populations (Cunningham et al. 1999, Rominger et al. 2004). Feral equids are also reported to subsidize mountain lion populations, although they are much less numerous than cattle (Berger 1986, Turner et al. 1992, Knopff and Boyce 2007). Low densities of native ungulates are correlated with increased depredation of livestock by felids and canids (Brown 1992, Khorozyan et al. 2015).

The intensity of mountain lion predation has been reported to be nearly continuous in some ecosystems and more pulse-like in other ecosystems (Ross et al. 1997, Rominger et al. 2004). Because bighorn sheep density is rarely but a fraction of that observed on predator-free islands and predator-free enclosures, most predation is considered additive mortality, especially at low bighorn sheep densities. The stalking hunting style of mountain lions is hypothesized to result in more prime-age bighorn sheep kills compared to the effect of a coursing hunting style (e.g., wolves), which exposes compromised individuals. Additionally, the encroachment of woody vegetation due to the exclusion of fire for more than a century has enhanced stalking cover for mountain lions (Wakelyn 1987).

Increased mountain lion predation and related declines in New Mexico desert bighorn sheep populations have been correlated with declines in sympatric mule deer. These populations declined sharply in the mid-1990s and there has been no discernable recovery in the last 20 years (Rominger and Weisenberger 2000, Bender et al. 2012, NMDGF, unpublished data). Observations of deer during helicopter surveys in the San Andres Mountains were as high as 150 deer/hour and have declined to <5.5 deer/hour for all bighorn sheep surveys flown since 1996 (NMDGF, unpublished data). The estimated deer density in the San Andres has declined to 0.08–0.11 mule deer/km^2, making this one of the lowest densities of North American ungulates ever reported (Bender et al. 2012, Rominger 2013). Because of this low density, there has been no deer hunting on the entire 8,300-km^2 White Sands Missile Range, New Mexico since 1999. Similarly, low mule deer observation rates have been recorded in all other desert bighorn sheep surveys in New Mexico for the last 20 years (NMDGF, unpublished data). However, it was the ratio of mountain lions to these very low-density ungulates that precluded recovery and has required mountain lion control to increase desert bighorn sheep numbers.

Declines in bighorn sheep populations, due to mountain lion predation, have been reported for nearly every state and province where this species occurs. There is little evidence that these populations recover in the absence of predator control. One exception appears to be the federally endangered Peninsular bighorn sheep population. Although this herd is still listed as endangered, it has increased from approximately 275 (Rubin et al. 1998) to approximately 980 (Botta 2011) without mountain lion control. Peninsular bighorn sheep have an elevational niche separation from mule deer that use habitat at higher elevations in the Peninsular Ranges (Hayes et al. 2000), much like the niche separation of pronghorn and bighorn sheep in the Great Basin (Berger and Wehausen 1991). Thus, mountain lions hunting in low-elevation desert bighorn habitat have virtually no opportunity to prey switch onto deer without vacating bighorn sheep habitat.

Management of predation deemed excessive relative to bighorn sheep population objectives generally involves lethal predator control. Controlling apex carnivores is much more controversial than culling mesocarnivores (Reiter et al. 1999, Rominger 2007) despite documented success in the protection and recovery of endangered species (Hecht and Nickerson 1999, Rominger et al. 2009, Johnson et al. 2013, Hervieux et al. 2014).

Predator control is used by most western state and provincial wildlife agencies to protect endangered ungulate species (Hervieux et al. 2014) and big game populations (Rominger 2007). Predator control to protect translocated desert bighorn was first advocated by Wilson et al. (1973) and has been used to aid the restoration of bighorn sheep in New Mexico, California, Texas, Arizona, Utah, and elsewhere (Rominger 2007). High levels of mountain lion predation associated with desert bighorn sheep translocations and some Rocky Mountain bighorn sheep translocations (Krausman et al. 1999, Rominger et al. 2004, McKinney et al. 2006) can be reduced by removing resident mountain lions prior to translocation. After multiple failed translocations due to mountain lion predation, NMDGF no longer translocates desert bighorn sheep without a pre-treatment mountain lion control program to reduce the density of resident mountain lions, usually beginning 3–4 months prior to translocation.

Following the extirpation of desert bighorn sheep in the Catalina Mountains, Arizona in the 1980s, desert bighorn sheep were released into historical habitat in 2013 (Krausman 2017). The initial translocation, done without a pre-treatment removal of resident mountain lions, had high mortality with mountain lions killing 15 of 30 radio-marked bighorn sheep within 4 months. Post-release control of offending mountain lions resulted in the lethal removal of 7 mountain lions. To date, mountain lions have killed a minimum of 27 of 86 radio-marked bighorn sheep from 3 releases. In the absence of mountain lion control, this attempted restoration of a native faunal component would have almost certainly failed.

Ernest et al. (2002) modeled predator control management options to mitigate mountain lion predation and determined that for populations or subpopulations with <15 females, range-wide control (habitat control) of mountain lions was the most effective paradigm. At higher female numbers, less strict take of mountain lions was recommended (e.g., only remove offending mountain lions [kill-site removal]). However, this model assumes that a documented offending mountain lion will be removed prior to making additional kills. A large data set from NMDGF suggests this is unlikely and offending mountain lions were taken at <20% of bighorn sheep kills (Rominger et al. 2011). During a period of range-wide mountain lion control, 68 mountain lion-killed bighorn sheep with very high frequency (VHF) radio-collars were documented. However, only 13 (19%) offending mountain lions were culled.

The 2 primary reasons mountain lions were not culled were the bighorn sheep kill was not detected and located prior to the mountain lion departing (59% of all kills) and the mountain lion was present but missed at the kill site (54% of attempted removals were unsuccessful because the mountain lion did not step into snare, substrate was not conducive to snare placement, hounds were unable to tree or bay mountain lion). Although sample sizes were substantially reduced, the data set was partitioned between attempts to snare offending mountain lions and attempts to hound-hunt offending mountain lions. Use of hounds was successful in 5 of 14 attempts, whereas use of snares was successful in 8 of 14 attempts (Rominger et al. 2011). Culling offending mountain lions in the Catalina Mountains, Arizona restoration project has been successful in 6 of 15 attempts and this higher success rate is attributed to the use of GPS collars that alerted managers to mountain lion kills more quickly than VHF radio-collars (B. D. Brochu, AZGFD, personal communication).

Trapping and translocation is the primary management tool used to reestablish bighorn sheep populations into unoccupied habitats (Foster 2004). Currently, most bighorn sheep used for translocation come from mountain lion-free islands (e.g., Tiburon Island, Sonora, Carmen Island, Baja California Sur, MX; Wild Horse Island, MT, USA, Antelope Island) or predator-free enclosures (e.g., Red Rock, NM, USA and Pilares, Coahuila, MX). Very few desert bighorn sheep populations with uncontrolled sympatric mountain lions produce surplus bighorn sheep for translocations.

Restoration of natural grasslands, maintained by frequent fires, at scales that would substantially reduce deer numbers is unlikely to be a near-term management option. However, most state and provincial agencies have developed habitat management plans to reduce woody vegetation to increase bighorn habitat, and potentially reduce stalking habitat for mountain lions. Although, mountain lion predation seems to be lowest in single-prey systems in the most xeric habitats, most bighorn sheep currently occur in habitats with multiple sympatric ungulates. It is hypothesized that high levels of alternative buffer prey are preferable to low-density buffer prey when habitats have high mountain lion density.

Kill rates may increase substantially in ecosystems with high levels of kleptoparasitism and if deemed excessive, population reduction of kleptoparasites, specifically bears, would be a novel management action. The cumulative effects of predation on all sex and age classes of a bighorn sheep population must be recognized. Total predation in ecosystems with a diverse predator guild may have a much more profound influence on bighorn sheep demography; therefore, wildlife managers must decide on the appropriate response relative to management needs (Griffin et al. 2011). Small, isolated bighorn sheep herds, reduced to very low numbers by predation, will require human-mediated translocations to mitigate genetic loss and demographic declines.

Factors that influence rates of mountain lion predation should be examined experimentally to enable managers to better understand this complex system that appears to be substantially altered by anthropogenic causes. Experiments should be designed and conducted in bighorn sheep herds that are large enough to sustain high levels of predation without the need to manipulate mountain lion numbers during the experiment. Understanding the role of alternative prey, including livestock, will be a potential research direction. Understanding the influence of wolf restoration on bighorn sheep and mountain lions, particularly the effect on recruitment of adult female mountains lions, will be important. Because mountain lions are relatively long-lived, this research should be conducted over long periods following the reestablishment of wolves.

MANAGEMENT IMPLICATIONS

Productive bighorn sheep populations are required for restoration via translocation, sport hunting, and endangered species recovery. Management practices to decrease mountain lion densities that adversely affect bighorn sheep populations can be ideally addressed via sport harvest levels regulated by state wildlife agencies. In habitats or states (e.g., CA) where sport harvest does not meet management objectives, facilitated mountain lion control may be required to prevent population declines of bighorn sheep. Removal of resident mountain lions, prior to translocation of desert bighorn sheep, has increased the probability of successful restoration (Rominger et al. 2009).

There is still the potential that bighorn sheep can remain a viable faunal component in the North American west. If the public and wildlife managers are interested in keeping and restoring bighorn to their native ranges for viewing, hunting, and as source populations for recovery in landscapes that have been anthropogenically altered, difficult decisions will have to be made. Continued research on predation and other ecological factors will aid in the conservation of this species.

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LITERATURE CITED

Anderson, C. R. Jr., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management 67:307–316.

Arthur, S. M., and L. R. Prugh. 2010. Predator-mediated indirect effects of snowshoe hares on Dall's sheep in Alaska. Journal of Wildlife Management 74:1709–1721.

Barichello, N., and J. Carey. 1988. The effect of wolf reduction on Dall sheep demography in the southwest Yukon. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 6:307.

Barker, E. S. 1953. Beatty's cabin. University of New Mexico Press, Albuquerque, USA.

Bender, L. C., B. D. Hoenes, and C. L. Rodden. 2012. Factors influencing survival of desert mule deer in the greater San Andres Mountains, New Mexico. Human–Wildlife Interactions 6:245–260.

Berger, J. 1986. Wild horses of the Great Basin: social competition and population size. University of Chicago Press, Chicago, Illinois, USA.

Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. Conservation Biology 4:91–98.

Berger, J., and J. D. Wehausen. 1991. Consequences of a mammalian predator-prey disequilibrium in the Great Basin Desert. Conservation Biology 5:244–248.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution of coyotes? Journal of Animal Ecology 76:0175–1085.

Bergerud, A. T., W. J. Dalton, H. Butler, L. Camps, and R. Ferguson. 2007. Woodland caribou persistence and extirpation in relic populations on Lake Superior. Rangifer Special Issue 17:57–78.

Bergerud, A. T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Canadian Journal of Zoology 64:1515–1529.

Bergerud, A. T., and J. P. Elliot. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. Canadian Journal of Zoology 76:1551–1569.

Blaisdell, J. A. 1961. Bighorn-cougar relationships. Desert Bighorn Council Transactions 5:42–46.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:1–50.

Botta, R., compiler. 2011. Results of the 2010 bighorn sheep helicopter survey in the Peninsular Ranges of southern California. California Department of Fish and Wildlife, Sacramento, USA.

Bourbeau-Lemieux, A. L., M. Festa-Bianchet, J. M. Gaillard, and F. Pelletier. 2011. Predator-driven component Allee effects in a wild ungulate. Ecology Letters 14:358–363.

Bowyer, R. T., M. C. Nicholson, E. M. Molvar, and J. B. Faro. 1999. Moose on Kalgin Island: are density-dependent processes related to harvest? Alces 35:73–89.

Boyd, D. K., and G. K. Neale. 1992. An adult cougar (*Felis concolor*) killed by gray wolves (*Canis lupus*) in Glacier National Park, Montana. Canadian Field-Naturalist 106:524–525.

Brewer, C., R. S. Henry, E. J. Goldstein, J. D. Wehausen, and E. M. Rominger. 2013. Strategies for managing mountain lion and desert bighorn interactions. Desert Bighorn Council Transactions 52:1–15.

Bristow, K. D., and R. J. Olding. 1998. Status and future of a native desert bighorn sheep population in southeastern Arizona. Desert Bighorn Council Transactions 42:27–42.

Brown, D. E. 1985. The grizzly in the southwest. University of Oklahoma Press, Norman, USA.

Brown, D. E. 1992. The wolf in the southwest: the making of an endangered species. University of Arizona Press, Tucson, USA.

Brown, D. E. 1994. Biotic communities: southwestern United States and northwestern Mexico. University of Utah Press, Salt Lake City, USA.

Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. Wildlife Monographs 4:3–174.

Compton, B. B., P. Zager, and G. Servheen. 1995. Survival and mortality of translocated woodland caribou. Wildlife Society Bulletin 23:490–496.

Cooley, H. S., K. D. Bunnell, D. C. Stoner, and M. L. Wolfe. 2011. Population management: cougar hunting. Pages 111–134 *in* J. A. Jenks, editor. Managing cougars in North America. Jack H. Berryman Institute, Utah State University, Logan, USA.

Creeden, P. J., and V. K. Graham. 1997. Reproduction, survival, and lion predation in the Black Ridge/Colorado National Monument desert bighorn herds. Desert Bighorn Council Transactions 41:37–43.

Cronin, M. A., and V. C. Bleich. 1995. Mitochondrial DNA variation among populations and subspecies of mule deer in California. California Fish and Game 81:45–54.

Cunningham, S. C., C. R. Gustavson, and W. B. Ballard. 1999. Diet selection of mountain lions in southeastern Arizona. Journal of Range Management 52:202–207.

DeForge, J. R. 2002. A four year study of cause-specific mortality of desert bighorn sheep lambs near an urban interface and a community response. Desert Bighorn Council Transactions 46:3.

Desert Bighorn Council. 1957. Predation. Desert Bighorn Council Transactions 1:43–50.

Dwernychuk, L. W., and D. A. Boag. 1972. Ducks nesting in association with gulls: an ecological trap? Canadian Journal of Zoology 50:559–563.

Elbroch, L. M, P. E. Lendrum, M. L. Allen, and H. U. Wittmer. 2015. Nowhere to hide: pumas, black bears, and competition refuges. Behavioral Ecology 26:247–254.

Ernest, H. B., E. S. Rubin, and W. M. Boyce. 2002. Fecal DNA analysis and risk assessment of mountain lion predation of bighorn sheep. Journal of Wildlife Management 66:75–85.

Fecske, D. M, D. J. Thompson, and J. A. Jenks. 2011. Cougar ecology and natural history. Pages 15–40 *in* J. A. Jenks, editor. Managing cougars in North America. Jack H. Berryman Institute, Utah State University, Logan, USA.

Festa-Bianchet, M. 1991. The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. Animal Behaviour 42:71–82.

Festa-Bianchet, M., T. Coulson, J. M. Gaillard, J. T. Hogg, and F. Pelletier. 2006. Stochastic predation events and population persistence in bighorn sheep. Proceedings of the Royal Society B 273:1537–1543.

Fisher, A., E. Rominger, P. Miller, and O. Byers. 1999. Population and habitat viability assessment workshop for the desert bighorn sheep of New Mexico (*Ovis canadensis*): final report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota, USA.

Foster, C. L. 2004. Wild sheep capture guidelines. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 14:211–282.

Foster, C. L., and D. G. Whittaker. 2010. Poor population performance of California bighorn sheep on Hart Mountain National Antelope Refuge. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 17:129–137.

Garrettson, P. R., and F. C. Rohwer. 2001. Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. Journal of Wildlife Management 65:398–405.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kellyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120:3–59.

Geist, V. 1971. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago, Illinois, USA.

Geist, V. 1999. Adaptive strategies in American mountain sheep: effects of climate, latitude and altitude, Ice Age evolution, and neonatal security. Pages 192–208 *in* R. Valdez and P. R. Krausman, editors. Mountain sheep of North America. University of Arizona Press, Tucson, USA.

Goldstein, E. J., and E. M. Rominger. 2012. A comparison of mortality rates for desert and Rocky Mountain bighorn sheep under two cougar control regimes. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 18:137–145.

Goldstein, E. J., and E. M. Rominger. 2013. Status of desert bighorn sheep in New Mexico, 2011–2012. Desert Bighorn Council Transactions 52:32–34.

Graham, I. M., and X. Lambin. 2002. The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. Journal of Animal Ecology 71:946–956.

Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, D. H. Jackson, B. K. Johnson, W. L. Meyers, J. D. Raithel, M. Schlegel, B. L. Smith, C. White, and P. J. White. 2011. Neonatal mortality of elk driven by climate, predator phenology, and predator community composition. Journal of Animal Ecology 80:1246–1257.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. Wildlife Monographs 165:1–32.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control and, competition. American Naturalist 94:421–425.

Harrington, R., N. Owen-Smith, P. C. Viljoen, H. C. Biggs, D. R. Mason, and P. C. Funston. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. Biological Conservation 90:69–78.

Harrison, S., and D. Hebert. 1988. Selective predation by cougar within the Junction Wildlife Management Area. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 6:292–306.

Hass, C. C. 1989. Bighorn lamb mortality: predation, inbreeding, and population effects. Canadian Journal of Zoology 67:699–705.

Hayes, C. L., E. S. Rubin, M. C. Jorgensen, R. A. Botta, and W. M. Boyce. 2000. Mountain lion predation of bighorn sheep in the Peninsular Ranges, California. Journal of Wildlife Management 64:954–959.

Hayes, R. D., R. Farnell, R. M. P. Ward, J. Carey, M. Dehn, G. W. Kuzyk, A. M. Baer, C. L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. Wildlife Monographs 152:1–35.

Hebert, D., and S. Harrison. 1988. The impact of coyote predation on lamb mortality patterns at the Junction Wildlife Management Area. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 6:283–291.

Hecht, A., and P. R. Nickerson. 1999. The need for predator management in conservation of some vulnerable species. Endangered Species UPDATE 16:114–118.

Heffelfinger, J. R., and T. A. Messmer. 2003. Introduction. Pages 1–11 *in* J. C. deVos Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Berryman Institute Press, Utah State University, Logan, USA.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Hervieux, D., M. Hebblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. Canadian Journal of Zoology 92:1029–1037.

Hoban, P. A. 1990. A review of desert bighorn sheep in the San Andres Mountains, New Mexico. Desert Bighorn Council Transactions 34:14–22.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Hornaday, W. T. 1908. Camp-fires on desert and lava. Charles Scribner's Sons, New York, New York, USA.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27:343–383.

Husseman, J. S., D. L. Murray, G. Power, C. Mack, C. R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. Oikos 101:591–601.

Johnson, H. E., M. Hebblewhite, T. R. Stephenson, D. W. German, B. M. Pierce, and V. C. Bleich. 2013. Evaluating apparent competition in limiting the recovery of an endangered ungulate. Oecologia 171:295–307.

Kaji, K., H. Okada, M. Yamanaka, H. Matsuda, and T. Yabe. 2004. Irruption of a colonizing sika deer population. Journal of Wildlife Management 68:889–899.

Kamler, J. F., R. M. Lee, J. C. deVos Jr., W. B. Ballard, and H. A. Whitlaw. 2002. Survival and cougar predation of translocated bighorn sheep in Arizona. Journal of Wildlife Management 66:1267–1272.

Karsch, R., J. W. Cain III, E. M. Rominger, and E. J. Goldstein. 2016. Desert bighorn sheep lambing habitat: parturition, nursery, and predation sites. Journal of Wildlife Management 80:1069–1080.

Kay, C. E. 1995. Aboriginal overkill and native burning: implications for modern ecosystem management. Western Journal of Applied Forestry 10:121–126.

Kay, C. E. 2007. Were native people keystone predators? A continuous-time analysis of wildlife observations made by Lewis and Clark in 1804–1806. Canadian Field-Naturalist 121:1–16.

Kelley, W. E. 1980. Predator relationships. Pages 186–196 *in* G. Monson and L. Sumner editors. Desert bighorn sheep: its life history, ecology, and management. University of Arizona Press, Tucson, USA.

Khorozyan, I., A. Ghoddousi, M. Soofi, and M. Waltert. 2015. Big cats kill more livestock when wild prey reaches a minimum threshold. Biological Conservation 192:268–275.

Kilpatric, J. 1976. Texas bighorn sheep reintroduction status report. Desert Bighorn Council Transactions 20:4.

Kilpatric, J. 1982. Status of bighorn sheep in Texas—1982. Desert Bighorn Council Transactions 26:102–103.

Kinley, T. A., and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin 29:158–164.

Knopff, K. H., and M. S. Boyce. 2007. Prey specialization by individual cougars in multiprey systems. Transactions of the 72nd North American Wildlife and Natural Resources Conference 72:194–210.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management 74:1435–1447.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586–597.

Knopff, K. H., N. F. Webb, and M. S. Boyce. 2014. Cougar population status and range expansion in Alberta during 1991–2010. Wildlife Society Bulletin 38:116–121.

Kortello, A. D., T. E. Hurd, and D. L. Murray. 2007. Interactions between cougars and gray wolves in Banff National Park. Écoscience 14:214–222.

Krausman, P. R. 2017. And then there were none: the demise of desert bighorn sheep in the Pusch Ridge Wilderness. University of New Mexico Press, Albuquerque, USA.

Krausman, P. R., B. D. Leopold, R. F. Seegmiller, and S. G. Torres. 1989. Relationships between desert bighorn sheep and habitat in western Arizona. Wildlife Monographs 102:3–66.

Krausman, P. R., A. V. Sandoval, and R. C. Etchberger. 1999. Natural history of desert bighorn sheep. Pages 139–191 *in* R. Valdez and P. R. Krausman, editors. Mountain sheep of North America. University of Arizona Press, Tucson, USA.

Krawchuck, K. E. 2014. Is niche separation between wolves and cougars realized in the Rocky Mountains? Thesis, University of Alberta, Edmonton, Canada.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science 269:1112–1115.

Lamb, C. T., G. Mowat, B. N. McLellan, S. E. Nielson, and S. Boutin. 2017. Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. Journal of Animal Ecology 86:55–65.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York, New York, USA.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Matthews, J. W. 1973. Ecology of bighorn sheep of Wild Horse Island, Flathead Lake, Montana. Thesis, University of Montana, Missoula, USA.

McCullough, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor, USA.

McLellan, B. N., R. Serrouya, H. U. Wittmer, and S. Boutin. 2010. Predator-mediated Allee effects in multi-prey systems. Ecology 91:286–292.

McKinney, T., J. C. DeVos Jr., W. B. Ballard, and S. R. Boe. 2006. Mountain lion predation of translocated desert bighorn sheep in Arizona. Wildlife Society Bulletin 34:1255–1263.

McPherson, G. R. 1995. Role of fire in desert grasslands. Pages 130–151 *in* M. P. McClaran and T. R. Van Devender, editors. The desert grassland. University of Arizona Press, Tucson, USA.

Merkle, J. A., D. R. Stahler, and D. W. Smith. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology 87:56–63.

Monson, G., and L. Sumner. 1980. Desert bighorn sheep: its life history, ecology, and management. University of Arizona Press, Tucson, USA.

Muñoz, R. 1982. Movements and mortalities of desert bighorn of the San Andres Mountains, New Mexico. Desert Bighorn Council Transactions 26:107–108.

Paine, R. T. 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference and intertidal community structure. Ecology 50:950–961.

Parsons, Z. D. 2007. Cause specific mortality of desert bighorn sheep lambs in the Fra Cristobal Mountains, New Mexico, USA. Thesis, University of Montana, Missoula, USA.

Pedersen, A. B., K. E. Jones, C. L. Nunn, and S. Altizer. 2007. Infectious diseases and extinction risk in wild mammals. Conservation Biology 21:1269–1279.

Potter, J. M. 1995. The effects of sedentism on the processing of hunted carcasses in the southwest: a comparison of two Pueblo IV sites in central New Mexico. Kiva 60:411–428.

Potvin, F., P. Beaupre, and G. Laprise. 2003. The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Quebec: a 150 year process. Écoscience 10:487–495.

Quintana, N. T., W. B. Ballard, M. C. Wallace, P. R. Krausman, J. deVos Jr., O. Alcumbrac, C. A. Cariappa, and C. O'Brien. 2016. Survival of mule deer fawns in central Arizona. Southwestern Naturalist 61:93–100.

Reiter, D. K., M. W. Brunson, and R. H. Schmidt. 1999. Public attitudes toward wildlife damage management and policy. Wildlife Society Bulletin 27:746–758.

Riley, S. J., G. M. Nesslage, and B. A. Maurer. 2004. Dynamics of early wolf and cougar eradication efforts in Montana: implications for conservation. Biological Conservation 119:575–579.

Rominger, E. M. 2007. Culling mountain lions to protect ungulate populations—some lives are more sacred than others. Transactions of the 72nd North American Wildlife and Natural Resources Conference 72:186–193.

Rominger, E. M. 2013. Puma:ungulate ratios in the sky-islands of the Chihuahuan desert. Desert Bighorn Council Transactions 52:52–53.

Rominger, E. M. 2015. The paradox of North American ungulate density in predator-free enclosures and on predator-free islands. Desert Bighorn Council Transactions 53:63.

Rominger, E. M., E. J. Goldstein, and D. L. Weybright. 2009. Recovery of an endangered ungulate using predator control and captive breeding, 1979–2007. Desert Bighorn Council Transactions 50:74–75.

Rominger, E. M., E. J. Goldstein, and D. L. Weybright. 2011. Culling offending lions to protect endangered desert bighorn sheep: is it practical or effective? Desert Bighorn Council Transactions 51:91.

Rominger, E. M., and M. E. Weisenberger. 2000. Biological extinction and a test of the "conspicuous individual hypothesis" in the San Andres Mountains, New Mexico. Transactions of the North American Wild Sheep Conference 2:293–307.

Rominger, E. M., H. A. Whitlaw, D. L. Weybright, W. C. Dunn, and W. B. Ballard. 2004. The influence of mountain lion predation on bighorn sheep translocations. Journal of Wildlife Management 68:993–999.

Ross, P. I., M. G. Jalkotzy, and M. Festa-Bianchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. Canadian Journal of Zoology 74:771–775.

Rubin, E. S., W. M. Boyce, M. C. Jorgensen, S. G. Torres, C. L. Hayes, C. S. O'Brien, and D. A. Jessup. 1998. Distribution and abundance of bighorn sheep in the Peninsular Ranges, California. Wildlife Society Bulletin 26:539–551.

Ruhl, C. Q., and E. M. Rominger. 2015. Status of desert bighorn sheep in New Mexico 2013–2014. Desert Bighorn Council Transactions 53:45–48.

Ruth, T. K., M. A. Haroldson, K. M. Murphy, P. C. Buotte, M. G. Hornocker, and H. B. Quigley. 2011. Cougar survival and source-sink structure in the Greater Yellowstone's northern range. Journal of Wildlife Management 75:1381–1398.

Sawyer, H., and F. Lindzey. 2002. A review of predation on bighorn sheep (*Ovis canadensis*). Wyoming Fish and Wildlife Cooperative Research Unit, Laramie, USA.

Schaefer, R. J., S. G. Torres, and V. C. Bleich. 2000. Survivorship and cause-specific mortality in sympatric populations of mountain sheep and mule deer. California Department of Fish and Game 86:127–135.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17:474–480.

Scotton, B. D. 1998. Timing and causes of neonatal Dall sheep mortality in the central Alaska Range. Thesis, University of Montana, Missoula, USA.

Sheldon, C. 1979. The wilderness of desert bighorns and Seri Indians. Reprinted by Arizona Desert Bighorn Sheep Society, Phoenix, USA.

Simard, M. A., T. Coulson, A. Gingras, and S. D. Côté. 2010. Influence of density and climate on population dynamics of a large herbivore under harsh environmental conditions. Journal of Wildlife Management 74:1671–1685.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288–290.

Smith, J. B., J. A. Jenks, T. W. Grovenberg, and R. W. Klaver. 2014. Disease and predation: sorting out causes of a bighorn sheep (*Ovis canadensis*) decline. PLoS ONE 9(2):e88271.

Smith, R. H., D. J. Neff, and N. G. Woolsey. 1986. Pronghorn response to coyote control: a benefit: cost analysis. Wildlife Society Bulletin 14:226–231.

Soule, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75–92.

Stevens, M. 2002. Meet Mr. Grizzly. High Lonesome Press, Silver City, New Mexico, USA.

Stewart, O. C. 2002. Forgotten fires: Native Americans and the transient wilderness. University of Oklahoma Press, Norman, USA.

Sweitzer, R. A., S. H. Jenkins, and J. Berger. 1997. Near-extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin Desert. Conservation Biology 11:1407–1417.

Terborgh, J., L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Alder, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Turner, J. W., M. L. Wolfe, and J. F. Kirkpatrick. 1992. Seasonal mountain lion predation on a feral horse population. Canadian Journal of Zoology 70:929–934.

Turner, N. J. 1991. Burning mountainsides for better crops: aboriginal landscape burning in British Columbia. Archeology in Montana 32:57–73.

Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315–326.

Wakelyn, L. A. 1987. Changing habitat conditions on bighorn sheep ranges in Colorado. Journal of Wildlife Management 51:904–912.

Wehausen, J. D. 1996. Effect of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24:471–479.

Wehausen, J. D. 1999. Rapid extinction of mountain sheep populations revisited. Conservation Biology 13:378–384.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement:120–139.

Wilckins, D. T., J. B. Smith, S. A. Tucker, D. J. Thompson, and J. A. Jenks. 2016. Mountain lion (*Puma concolor*) feeding behavior in the Little Missouri Badlands of North Dakota. Journal of Mammalogy 92:373–385.

Williams, T. M., J. A. Estes, D. F. Doak, and A. M. Springer. 2004. Killer appetites: assessing the role of predators in ecological communities. Ecology 85:3373–3384.

Wilson, L. O., J. Day, J. Helvie, G. Gates, T. L. Hailey, G. K. Tsukamoto. 1973. Guidelines for capturing and re-establishing desert bighorns. Desert Bighorn Council Transactions 17:137–154.

Wittmer, H. U., M. Hasenbank, L. M. Elbroch, and A. J. Marshall. 2014. Incorporating preferential prey selection and stochastic predation into population viability analysis for rare prey species. Biological Conservation 172:8–14.

Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144:257–267.

Wolfe, M. L., and J. F. Kimball. 1989. Comparison of bison population estimates with a total count. Journal of Wildlife Management 53:593–596.

Young, S. P., and E. A. Goldman. 1944. The wolves of North America. American Wildlife Institute, Washington, D.C., USA.

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Using multiple data sources provides density estimates for endangered Florida panther

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Summary

1. To assess recovery of endangered species, reliable information on the size and density of the target population is required. In practice, however, this information has proved hard to acquire, especially for large carnivores that exist at low densities, are cryptic and range widely. Many large carnivore species such as the endangered Florida panther *Puma concolor coryi* lack clear visual features for individual identification; thus, using standard approaches for estimating population size, such as camera-trapping and capture–recapture modelling, has so far not been possible.

2. We developed a spatial capture–recapture model that requires only a portion of the individuals in the population to be identifiable, using data from two 9-month camera-trapping surveys conducted within the core range of panthers in southwestern Florida. Identity of three radio-collared individuals was known, and we incorporated their telemetry location data into the model to improve parameter estimates.

3. The resulting density estimates of 1·51 (±0·81) and 1·46 (±0·76) Florida panthers per 100 km^2 for each year are the first estimates for this endangered subspecies and are consistent with estimates for other puma subspecies.

4. A simulation study showed that estimates of density may exhibit some positive bias but coverage of the true values by 95% credible intervals was nominal.

5. *Synthesis and applications.* This approach provides a framework for monitoring the Florida panther – and other species without conspicuous markings – while fully accounting for imperfect detection and varying sampling effort, issues of fundamental importance in the monitoring of wildlife populations.

Key-words: camera-trapping, mark–resight, population estimation, *Puma concolor coryi*, spatial capture–recapture, telemetry, unmarked populations

Introduction

An accurate understanding of population status is fundamental for the management and recovery of endangered species (Campbell *et al.* 2002; Hoekstra *et al.* 2002). However, estimates of population size and density are lacking for many of the world's most endangered species. As a result, it has been difficult to quantify extinction risk and monitor the effects of conservation actions.

The Florida panther *Puma concolor coryi* is the last remaining puma subspecies in eastern North America. Originally occurring from Arkansas and Louisiana to South Carolina and Florida (Young & Goldman 1946), the current distribution is restricted to about 10 000 km^2 in southern Florida (Kautz *et al.* 2006). Due to unregulated hunting in the 19th century and large-scale loss of habitat during the 20th century (Onorato *et al.* 2010), Florida panthers were listed as endangered in 1967 (US Federal Register 1967) and subsequently protected under the Endangered Species Act of 1973 (Public Law 93-205).

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Nevertheless, by the early 1990s, their population had dwindled to 20–30 individuals (McBride *et al.* 2008). Intensive population management, including introduction of wild-caught pumas from Texas to alleviate effects of inbreeding (Seal 1994; USFWS 1994), legal protection (O'Brien & Mayr 1991; Janis & Clark 2002), efforts to reduce road mortality (Foster & Humphrey 1995), and habitat and prey conservation (Janis & Clark 2002) have led to an increase in panther abundance (McBride *et al.* 2008) and genetic diversity (Johnson *et al.* 2010). Still, the Florida panther remains one of the most endangered felids world-wide (Onorato *et al.* 2010).

The Florida Fish and Wildlife Conservation Commission (FWC), with assistance from the federal government (e.g. National Park Service – NPS, U.S. Fish and Wildlife Service – USFWS), commenced research on the Florida panther in 1981, resulting in publications covering a variety of topics including: estimates of demographic parameters, habitat selection, assessment of genetic restoration and documentation of biomedical issues (Beier *et al.* 2003; Onorato *et al.* 2010). Despite the intensive research effort, producing rigorous estimates of population size for the Florida panther has eluded scientists for decades (Beier *et al.* 2003), yet abundance remains a central tenet of the USFWS recovery plan objectives (USFWS 2008).

Large, elusive carnivores such as pumas are typically difficult to sample, and accurate estimates of population-related parameters are often challenging to obtain. Obstacles include low sample sizes due to rarity, wide-ranging behaviour and concerns about invasive sampling methods. Mark–recapture techniques are generally considered the gold standard for generating robust estimates of population parameters. For many felid species, camera-trapping is increasingly used for abundance estimates because the technique is non-invasive and efficient. The resulting data, in combination with traditional capture–recapture (CR) models (e.g. Otis *et al.* 1978) or spatial capture–recapture (SCR) models (e.g. Efford 2004; Royle & Young 2008), have largely facilitated the estimation of demographic parameters of many felid species with unique pelage patterns (e.g. Karanth & Nichols 1998; Karanth *et al.* 2006; Royle *et al.* 2009). Although some puma studies use this combination of methods (Kelly *et al.* 2008; Negrões *et al.* 2010), the species generally lacks clear features for individual identification from photographs, seemingly rendering camera-trapping an unfeasible option for capture–recapture modelling of Florida panthers.

Alternatively, scat sampling in combination with genetic analyses can provide capture–recapture data (Royle, Kéry & Guélat 2011). Although this sampling technique has been applied in the study of felid populations (e.g. Ruell *et al.* 2009; Gopalaswamy *et al.* 2012), it would be difficult to implement for the Florida panther due to the subspecies' low genetic diversity (Roelke, Martenson & O'Brien 1993) and the fast decay of DNA in Florida's warm and moist climate (Farrell, Roman & Sunquist 2000; Lucchini *et al.* 2002).

Given the obstacle of individual identification, collecting capture–recapture data would require that animals be physically marked and recaptured. The high cost and safety issues to both animal and handler make such approaches impractical for elusive and potentially dangerous animals like large carnivores. This risk is compounded when dealing with the small populations of endangered species. Thus, non-invasive sampling techniques are preferable whenever possible (Long *et al.* 2008).

Florida panthers have been extensively studied using traditional very high frequency (VHF) and Global Positioning System (GPS) telemetry (e.g. Land *et al.* 2008; Onorato *et al.* 2011). Potentially, telemetry collars permit individual identification based on collar characteristics (e.g. different brands on different individuals or modifying collars with unique marks) observable in photographs. Under these circumstances, camera-trap surveys concurrent with existing telemetry studies can provide data suitable for population estimation in the framework of mark–resight models (e.g. Rice & Harder 1977; McClintock *et al.* 2009; McClintock & White 2010), which do not require that individuals be physically captured multiple times. Rather, a sample of individuals is captured and marked during a single marking event that occurs prior to resighting surveys, and a non-invasive technique such as camera-trapping or visual resighting can be used to collect 'recapture' data on these individuals. While mark–resight models provide robust estimates of abundance, they suffer from the same shortcomings as traditional capture–recapture models when it comes to estimating population density. To estimate density, we need to define the area sampled. This generally relies on ad-hoc approaches, which renders density estimates somewhat arbitrary.

Our objective was to provide a rigorous and statistically sound density estimate for Florida panthers in the Picayune Strand Restoration Project area (PSRP). We used data collected during a 21-month camera-trapping study (Shindle & Kelly 2007) and telemetry data simultaneously collected by the FWC in a new modelling framework that, analogous to traditional mark–resight, allows for only a portion of the population to be identified (Chandler & Royle In Press; Sollmann *et al.* 2013). Further, analogous to SCR models, this new framework explicitly links abundance to a clearly defined area, thus providing unambiguous density estimates. To improve the estimation of model parameters associated with individual location and movement, and to produce more precise estimates of density, we extend the model by also incorporating telemetry location data. We confirm the reliability of model results using a simulation study. Providing a rigorous estimate of Florida panther density, this modelling approach has wide application for animal conservation and endangered species management.

Materials and methods

STUDY AREA

The study was conducted in PSRP, an area that encompasses the former Southern Golden Gate Estates subdivision development, covering approximately 241 km^2 in Collier County, Florida. Originally slated for housing development, the area is currently undergoing vegetative and hydrological restoration (U.S. Army Corps of Engineers 2004). Together with two neighbouring reserves, the PSRP forms a large block of panther habitat in the core of the subspecies' range. The climate of the study area is that of a tropical savannah with distinct wet (May–October) and dry (November–April) seasons (Duever *et al.* 1985).

CAMERA-TRAPPING AND RADIOTELEMETRY

From 2005 to 2007, 98 camera traps (Digital CamTrakkerTM, CamTrak South Inc., Watkinsville, GA, USA) with passive infrared heat-in-motion detectors were deployed in PSRP for 21 consecutive months as part of a pre-restoration baseline survey for panther and white-tailed deer *Odocoileus virginianus* (Shindle & Kelly 2007). A grid with 2-km^2 cells was overlaid on the study area, and one camera was placed within each grid cell (Fig. 1). Most cameras were deployed along roads or trails and secured to trees approximately 45 cm above ground. Cameras operated 24 h per day with a minimum 20-s delay between sequential photographs. Camera traps were checked every 21–28 days to retrieve images and ensure units were functioning.

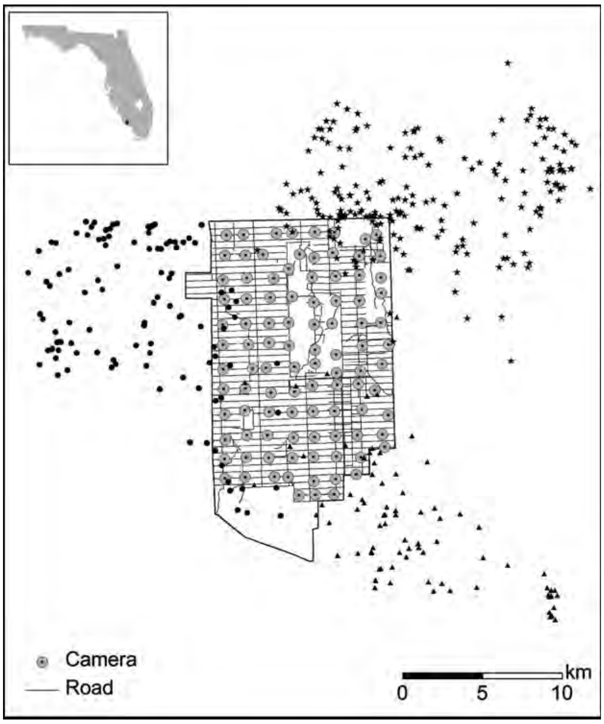

Fig. 1. Picayune Strand Restoration Project area, Southern Florida, with camera-trapping grid used to survey Florida panthers between 2005 and 2007, and radiotelemetry locations for three collared panthers (stars, circles and triangles) used in the spatial mark–resight model as the marked portion of the population.

The FWC monitors Florida panthers in the PSRP and neighbouring areas using radiotelemetry. Locations were collected via aerial telemetry three times per week (see Land *et al.* (2008) for methods). Manufacturers of radiocollars included Telonics (Mesa, Arizona, USA), Advanced Telemetry Systems (Isanti, MN, USA) and Followit (Lindesberg, Sweden). Collars from different manufacturers have distinct physical features and therefore provided a visual means of individual identification of collared panthers from camera-trap pictures.

Mark–resight models require that all marking takes place before resighting. Here, we regard those panthers as the marked part of our population that wore radiocollars throughout one or both primary camera-trapping occasions (see below) and used the PSRP as part of their home range. Panthers that were collared during the course of a primary occasion were regarded as 'unmarked'. Although some photographs of uncollared panthers could be attributed to individuals based on natural marks, many photographs of uncollared panthers were ambiguous. Since mark–resight models require that individuals can always correctly be identified as marked or unmarked, we treated all photographs of uncollared individuals as unmarked. For photographic records of uncollared individuals, we treated subsequent pictures at a given camera trap as independent if they were separated by at least an hour. Photographs that showed two (three, etc.) individuals were treated as two (three, etc.) independent records. We discarded pictures that we were unable to verify whether the individual was collared or not. We further excluded dependent kittens and juveniles from our analysis.

DATA ANALYSIS

Spatial capture–recapture models

We analysed concurrent photographic and telemetry data, building on the SCR model for partially marked populations described by Chandler & Royle (In press). Generally, SCR combines a model for individual location and movement with a model describing detection by traps, using individual and site specific detection data (Borchers & Efford 2008; Royle & Young 2008; Gardner, Royle & Wegan 2009; Borchers 2012). In SCR models, we assume that each individual i has an activity centre, $\mathbf{s}_i$, and that all $\mathbf{s}_i$ are distributed uniformly across the state space S, an area including the trapping grid, chosen large enough to include all animals potentially exposed to sampling. We assume that the number of records of individual i at trap j and occasion k, y_{ijk}, is a Poisson random variable with mean encounter rate λ_{ij}, which is a decreasing function of the distance, d_{ij}, from trap j to the individual's activity centre $\mathbf{s}_i$. Under a half-normal encounter rate model,

$$\lambda_{ij} = \lambda_0 * \exp(-d_{ij}^2/2\sigma^2),$$

λ_0 is the baseline trap encounter rate at $d_{ij} = 0$ and σ is the scale parameter of the half-normal function.

To estimate N, the number of activity centres in S, we employ data augmentation (Royle, Dorazio & Link 2007). Let n be the number of observed individuals. Then this approach is equivalent to augmenting the observed data set with $M - n$ 'all-zero' encounter histories or 'hypothetical individuals' that were never observed. N is estimated as the sum of an individual auxiliary variable, z_i,

$$z_i \sim \text{Bernoulli}(\Psi)$$

where i = 1,2,3…M and z_i = 1 if the animal is part of the population and 0 otherwise. The prior probability of Ψ is uniform (0,1), which corresponds to a discrete uniform (0,M) prior probability for N. M is an arbitrary value set sufficiently large as to not truncate estimates of N. Density, D, can be derived by dividing N by the area of S.

Extension of the SCR model to a mark–resight situation

Chandler & Royle (In press) extended this model to a mark–resight situation, where only part of the population can be individually identified. Under these circumstances, the individual encounter histories y_{ijk} are partially latent – only y_{ijk} for the m marked animals are observed. For the unmarked individuals, we observe only the accumulated counts $n_{jk} = \sum \mathbf{y}_{\text{ujk}},$ where $\mathbf{u} = \{m + 1, \ldots, N\}$ is an index vector of the $N - m = U$ unmarked individuals. Unobserved encounter histories are essentially missing data. Adopting a Bayesian framework and using Metropolis-within-Gibbs (MwG) Markov chain Monte Carlo (MCMC) sampling, we can update missing data using their full conditional distribution (Gelman *et al.* 2004, Ch. 11). For the y_{ijk} from unmarked animals, the full conditional is multinomial with sample size n_{jk}:

$$\mathbf{y}_{ujk} \sim \text{Multinomial}(n_{jk}, \boldsymbol{\lambda}_{uj}/\sum \boldsymbol{\lambda}_{uj})$$

The remaining model parameters are then updated conditional on the full set of encounter histories.

When the number of marked individuals, m, is known, estimating N reduces to estimating the number of unmarked individuals U. In this situation, $M - m$ = size of the hypothetical unmarked population in S. By updating the latent encounter histories (see above), we assign records of unmarked individuals to some of these hypothetical individuals, so that their encounter histories are no longer 'all-zero'.

In non-spatial mark–resight models, an important model assumption is that marked individuals represent a random subset of the population. This assumption is still required in spatial mark–resight, but additionally, the marked individuals must represent a random sample of individuals in the state space S. Here, we have only a small set of marked individuals (see results), and the telemetry information for these individuals indicates that they are distributed throughout most of S (Fig. 1).

Incorporating telemetry location data

We can relate the parameters of the half-normal encounter rate model to those of a bivariate normal movement model (Calhoun & Casby 1958), with mean = $\mathbf{s}_\text{i}$, and variance–covariance matrix $\sum$, where the variance in both dimensions is σ^2 and covariance is 0. Under this model, σ can be related to a measure of how far individuals move (Reppucci, Gardner & Lucherini 2011). Ordinarily, these parameters are estimated only from the trapping data. Telemetry data, however, provide more detailed information on individual location and movement. By assuming that the R_i locations of individual i, $\mathbf{l}_\text{i}$, are a bivariate normal (Normal$_2$) random variable:

$$\mathbf{l}_i \sim \text{Normal}_2(\mathbf{s}_i, \sum)$$

we can estimate σ, as well as $\mathbf{s}_\text{i}$ for the collared individuals, directly from telemetry location data using their full conditional distributions within the MwG sampler. Under this formulation, σ and $\mathbf{s}_\text{i}$ for the collared individuals are no longer conditional on the resighting data $\mathbf{y}$, but only on $\mathbf{l}$. For the unmarked individuals, $\mathbf{s}_\text{i}$ are estimated as in conventional SCR, conditional on the encounter histories. The full MwG MCMC sampler can be found in Appendix S1 (Supporting Information).

Model application to Florida panther data

To account for the lack of demographic population closure over 21 months of camera-trapping, we defined two primary occasions, from 1 July 2005 to 31 March 2006 and from 1 July 2006 to 31 March 2007. Within primary occasions, we grouped data by month and accounted for the number of days each camera trap was functional each month, t_{jk}, using $\lambda_{ij} * t_{jk}/30$. We limited telemetry data used in our model to the same time periods. To define S, we used a 15-km buffer from the outermost coordinates of the trapping grid and removed parts of the resulting rectangle that comprised ocean or islands. This resulted in an area for S of 1719·13 km^2.

We ran three chains of the MwG sampler with 200 000 iterations each, discarding 10 000 iterations as burn-in using the software R 2.13.0 (R Development Core Team 2011). To check for chain convergence, we calculated the Gelman-Rubin statistic R-hat (Gelman *et al.* 2004) using the R package coda (Plummer *et al.* 2006). Values below 1·1 indicate convergence; in our results, all model parameters had R-hat <1·1. We report the posterior mean (± standard deviation), mode, and 95% Bayesian credible intervals (95BCI) for all parameters.

Results

During the two primary occasions, we accumulated 43 890 trap days and obtained 445 photographs of Florida panthers. We discarded 137 pictures that we were unable to determine whether they belonged to a radio-collared individual or not and one picture of a collared panther that traversed the study area but was not resident (see Discussion for further treatment of this topic). Of the remaining photographs, 17 were records of identifiable radio-collared individuals and 290 pictures showed uncollared panthers (Table 1).

Three individuals met our requirements of being collared throughout one or both primary sampling occasions, with two collared individuals being present in one primary occasion only, while one was present in both occasions. For each collared individual, we accumulated an average

Table 1. Collared Florida panthers present in the Picayune Strand Restoration Project area and used as marked individuals in the spatial mark–resight model, total number of photographs and number of photographic records of these collared individuals in the two 9-month primary camera-trapping occasions

Occasion	No. collared individuals	Total number of pictures	No. pictures of collared individuals
1	2	131	2
2	2	176	15
Total*	3	307	17

*One individual from year 1 was present again in year 2.

of 99·5 (SD 10·6) telemetry locations per primary occasion (Fig. 1).

The posterior mean for the movement parameter σ was 4·45 (±0·11) km. The baseline trap encounter rate λ_0 had a posterior mean of 0·09 (±0·02) expected photographs per 30 days. The posterior mean for population density D was 1·63 (±0·50) individuals per 100 km^2 in year 1 and 1·66 (± 0·56) individuals per 100 km^2 in year 2; for both years, the posterior mode was slightly lower, at 1·51 and 1·46 individuals per 100 km^2, respectively. Posterior summaries of parameter estimates are given in Table 2.

SIMULATION STUDY

To investigate potential bias and precision of our estimators, we generated 100 data sets consisting of both camera detection and telemetry location data under the same conditions observed for the surveyed panthers (i.e. with parameters equal to the posterior means obtained in our analyses, and the trapping grid, sampling effort, number of known individuals and telemetry locations equivalent to values in the actual field study). Across 100 data sets, parameters were estimated with low accuracy (relative root mean squared error (RMSE) 26–39%); only the RMSE of σ was low, at 3%. For N, the posterior mode presented a less biased estimator (relative bias 11–13%) than the mean (27–29%). For λ_0 and σ, relative bias of the mean was 4 and 0·3%, respectively. Coverage of the true values by 95% BCI was between 92% and 99% for all parameters (see Appendix S2, Supporting Information).

Discussion

Large felids such as the Florida panther are notoriously difficult to monitor. Low population densities and elusive behaviour often result in sparse data, requiring intensive sampling over several years. Camera traps are an ideal tool for the study of large and wide-ranging species, but inference from camera-trap data for populations that cannot be individually identified is limited. Mark–resight methods have long been used as an alternative to traditional mark–recapture studies (e.g. Rice & Harder 1977; Minta & Mangel 1989), but only recently has the concept of mark–resight modelling been extended to SCR models (Chandler & Royle In press). This development has made it possible to address a major problem facing wildlife managers who are in need of reliable density estimates for rare and elusive species without conspicuous natural marks.

Table 2. Posterior summaries of parameter estimates from a spatial mark–resight model applied to Florida panther camera-trapping and telemetry data from the Picayune Strand Restoration Project area, Florida. Density is estimated for two 9-month primary occasions (t)

Parameter	Unit	Mean (SE)	Mode	2·5%	97·5%
σ	km	4·45 (0·11)	4·46	4·24	4·68
λ_0	Pictures per 30 days	0·09 (0·02)	0·09	0·06	0·14
N (t = 1)	individuals in S	27·98 (8·54)	25	14	47
N (t = 2)	individuals in S	28·59 (9·67)	25	13	51
D (t = 1)	individuals per 100 km^2	1·63 (0·50)	1·51	0·81	2·73
D (t = 2)	individuals per 100 km^2	1·66 (0·56)	1·46	0·76	2·97

FLORIDA PANTHER DENSITY

The density estimates of approximately 1·5 individuals per 100 km^2 summarize the current state of knowledge on Florida panthers in PSRP. Historically, there have been no reliable estimates of abundance or density for the Florida panther (Beier *et al.* 2003). Although the density estimate by Maehr, Land & Roof (1991) of one individual in 110 km^2 was considered reasonable, it lacked confidence intervals and could not be applied elsewhere (Beier *et al.* 2003). Similarly, counts based on physical evidence (e.g. tracks, scats; McBride *et al.* 2008) do not account for varying sampling effort, possible double-counting of or failure to detect individuals, and they lack the potential for repeatability due to a reliance on expert observers for accurate interpretation of panther signs.

Our density estimates fall within reported densities of pumas in other parts of their geographical range. Generally, the lowest puma densities of ≤ 1 individual per 100 km^2 are found in the northern part of the species' range (e.g. Hemker, Lindzey & Ackerman 1984; Laundré & Clark 2003). Except for areas heavily impacted by poaching and logging, Central and South America generally harbour higher puma densities, ranging from just over 1 to almost 7 individuals per 100 km^2 (Kelly *et al.* 2008; Paviolo *et al.* 2009; Negrões *et al.* 2010; Soria-Diaz *et al.* 2010). Given the tropical climate and habitat of Florida, and the fact that PSRP is still recovering from heavy anthropogenic impacts, our density estimates of approximately 1·5 panthers per 100 km^2 are consistent with previous findings.

The panther population of PSRP most likely declined because of the severe habitat degradation caused by water management practices and direct human disturbance. However, PSRP has two neighbouring reserves, the Florida Panther National Wildlife Refuge (FPNWR) and the Fakahatchee Strand Preserve State Park, both of which have been protected for several decades. Compared with these reserves, PSRP probably has less suitable habitat. Indeed, until recently, the PSRP area was mainly used by dispersing male Florida panthers, and reproductive events in the area were rare (Shindle & Kelly 2007). Applying the bivariate normal model to telemetry data from VHF and GPS collared individuals in the neighbouring FPNWR showed that individuals at this site have smaller home ranges (average σ

was 3·44 km based on seven individuals), which in carnivore populations is often linked to a higher population density (e.g. Dahle & Swenson 2003; Benson, Chamberlain & Leopold 2006). Most likely, individuals from neighbouring reserves are immigrating into the PSRP area as it recovers from the severe anthropogenic impacts and as panther populations in the neighbouring areas expand.

RELIABILITY OF ESTIMATES

The precision of density estimates from spatial mark–resight models depends on the number of marked individuals (Chandler & Royle In press). In the present study, photographic data on the small number of radio-collared individuals were particularly sparse (17 pictures total), but incorporating telemetry information about individual locations and movements increased the precision of our density estimate. According to our simulation study, although we can expect some positive small-sample bias in estimates of N, we also expect the true value to fall within the 95BCI. As a result, our modelling framework represents a promising tool for population monitoring of far-ranging, elusive species. For species that are studied extensively using radiotelemetry (Land *et al.* 2008; Onorato *et al.* 2011), the combination of traditional sampling techniques such as radiotelemetry with the increasingly popular methods of camera traps and SCR modelling (Royle *et al.* 2009) is likely to replace more traditional inference methods (Nichols, O'Connell & Karanth 2011). This approach is not limited to Florida panthers, but applies to other species that are not 'naturally marked' but can be tagged or otherwise recognized, and can also be applied to other types of spatial resighting data, such as point counts for birds or amphibians. With adequate sample size, telemetry locations are not necessary to estimate population size, so tags can be anything that permits identification.

Current spatial mark–resight models assume that marked individuals are a random sample from the total population of S. This means, ideally, defining S should be part of the study design and marking efforts should be spread evenly within S. In practice, that may often not be realistic. When marked individuals are not a random sample of S, but were taken from a smaller area, density estimates are likely negatively biased. Relaxing this assumption is the focus of current SMR model development.

IMPLICATIONS FOR FUTURE FLORIDA PANTHER RESEARCH

Despite the progress made towards recovery in over 30 years of research, the Florida panther population continues to require close monitoring. Our method is an improvement over monitoring methods historically implemented for three main reasons:

1. Our model enables researchers to use camera traps, which allow for non-invasive monitoring of Florida panthers in regions where they are also monitored by telemetry.

2. The spatial mark–resight model provides a standardized analytical framework that accounts for imperfect individual detection and varying sampling effort, so that estimates of density across time and space are comparable.

3. Our modelling approach provides estimates of uncertainty about density estimates. As such, we can fully assess whether a sampling design is yielding appropriate data to monitor the Florida panther population or whether sampling has to be modified (in terms of sampling technique, design and effort).

Still, there is room for improvement. A basic assumption of any mark–resight approach is that the marked individuals are a representative sample of the population (McClintock & White 2010). This is generally accomplished by applying a technique that is different from the resighting method to mark a random sample of individuals (Bowden & Kufeld 1995). While the methods for marking and resighting were distinct in the present study, the extremely low number of collared individuals may not be representative of the entire population. Considering the difficulties, risks and costs associated with capturing large felids, tagging a larger sample of panthers may be challenging. But even adequate coordination of marking and resighting would be an improvement. In the present study, marking and resighting occurred concurrently and individuals tagged within the primary camera-trapping occasions had to be treated as 'uncollared'. By tagging animals ahead of the resight surveys, this loss of valuable data could be avoided.

Owing to the low number of collared individuals, we were unable to incorporate sex- or year-specific differences in movement and detection into our model. Differences in these parameters between males and females are known to be pronounced for large carnivores (e.g. Gardner *et al.* 2010; Sollmann *et al.* 2011). For Florida panthers, males are known to have larger home ranges than females (Onorato *et al.* 2010). Further, collared individuals were photographed more frequently during the second primary occasion, which could indicate higher trap encounter rates. Ideally, future studies should aim at collecting enough data to allow for the modelling of these effects.

The sparseness of the data also precluded any formal treatment of transiency. Transiency is a common issue in open population capture–recapture studies (e.g. Pradel *et al.* 1997). In closed population studies, formally, the presence of transient individuals violates the fundamental assumption of population closure and is therefore generally not explicitly addressed but 'assumed away'. Only because we had radiotelemetry locations, we were able to identify one of the collared panthers in our study as a transient and we decided to remove that individual from the data set. We cannot apply such a correction to the uncollared individuals. By removing transients from the collared individuals but not the uncollared, the former are arguably no longer a representative sample of the latter, which may introduce some positive bias into the estimates of density. We found, however, that retaining the transient individual resulted in unreasonable estimates of the movement parameter σ (data not shown). Given the transient's large movements this is not surprising: when applying the bivariate normal movement model to individual sets of telemetry locations, σ for the transient was 3·5 times larger than for the remaining individuals. Within the spatial mark–resight model, the estimate of σ almost doubled when retaining the transient. While it is disconcerting that a single individual impacted estimates to such a degree, this is a consequence of the small data set, where one outlier has disproportionate effects on model outcomes. With an adequate sample size (i.e. larger number of marked individuals), presence of a single outlier would have a much smaller impact. Further, the problem could be avoided or diminished by shortening the sampling time frame to better approximate a closed population. Even if a transient is present, over a short time interval, its movements are unlikely to be so pronouncedly different from resident individuals, thus diminishing its effect on parameter estimates. Alternatively, with adequate sample size, or as information on the proportion of transients in the population accumulates over time, transiency could be addressed explicitly within the model, for example, using an individual covariate describing transiency state. Regardless of the approach, future study design for Florida panther population monitoring has to both strive for larger sample sizes and consider the assumption of population closure.

Finally, identifiability of individuals on pictures could be improved, for example, by increasing camera trigger speed to allow more centred subjects and by taking multiple pictures per camera-trapping event. We discarded 137 pictures from analysis because we were unable to tell whether an animal was wearing a collar or not. If individuals can at least be identified as 'marked' (but not to individual level), their data can still be included in mark–resight models (e.g. McClintock *et al.* 2009; Sollmann *et al.* 2013).

In spite of these caveats, spatial mark–resight models allow for the development of a standardized protocol that can be applied by different investigators and at different study sites without compromising the comparability of results. As such, these models provide a valuable population monitoring tool for wildlife species that are not consistently identifiable to the individual level. For Florida panthers, spatial mark–resight models could be the cornerstone of a distribution-wide survey protocol to estimate the density or size of the Florida panther population. This is a current research priority and will be indispensable in helping quantify the level of success conservation, and management measures are having at achieving recovery objectives outlined by the USFWS.

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References

Beier, P., Vaughan, M.R., Conroy, M.J. & Quigley, H. (2003) *An Analysis of Scientific Literature Related to the Florida Panther. Final Report*. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL.

Benson, J.F., Chamberlain, M.J. & Leopold, B.D. (2006) Regulation of space use in a solitary felid: population density or prey availability? *Animal Behaviour*, **71**, 685–693.

Borchers, D. (2012) A non-technical overview of spatially explicit capture–recapture models. *Journal of Ornithology*, **152**, 435–444.

Borchers, D.L. & Efford, M.G. (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, **64**, 377–385.

Bowden, D.C. & Kufeld, R.C. (1995) Generalized mark-sight population size estimation applied to Colorado moose. *Journal of Wildlife Management*, **59**, 840–851.

Calhoun, J.B. & Casby, J.U. (1958) Calculating home range and density of small mammals. *Public Health Reports*, **73**, 1143–1145.

Campbell, S.P., Clark, J.A., Crampton, L.H., Guerry, A.D., Hatch, L.T., Hosseini, P.R., Lawler, J.J. & O'Connor, R.J. (2002) An assessment of monitoring efforts in endangered species recovery plans. *Ecological Applications*, **12**, 674–681.

Chandler, R.B. & Royle, A.J. (In press) Spatially-explicit models for inference about density in unmarked populations. *Annals of Applied Statistics*, (In press).

Dahle, B. & Swenson, J.E. (2003) Home ranges in adult Scandinavian Brown Bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology*, **260**, 329–335.

Duever, J.M., Carlson, J.E., Meeder, J.F., Duever, L.C., Gunderson, L.H., Riopelle, L.A., Alexander, T.R., Myers, R.L. & Spangler, D.P. (1985) *The Big Cypress National Preserve. Research Report No. 8*. National Audubon Society, New York, NY.

Efford, M. (2004) Density estimation in live-trapping studies. *Oikos*, **106**, 598–610.

Farrell, L.E., Roman, J. & Sunquist, M.E. (2000) Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology*, **9**, 1583–1590.

Foster, M.L. & Humphrey, S.R. (1995) Use of highway underpasses by Florida panthers and other wildlife. *Wildlife Society Bulletin*, **23**, 95–100.

Gardner, B., Royle, J.A. & Wegan, M.T. (2009) Hierarchical models for estimating density from DNA mark-recapture studies. *Ecology*, **90**, 1106–1115.

Gardner, B., Royle, J.A., Wegan, M.T., Rainbolt, R.E. & Curtis, P.D. (2010) Estimating black bear density using DNA data from hair snares. *Journal of Wildlife Management*, **74**, 318–325.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2004) *Bayesian Data Analysis*, 2nd edn. CRC/Chapman & Hall, Bocan Raton, FL.

Gopalaswamy, A.M., Royle, J.A., Delampady, M., Nichols, J.D., Karanth, K.U. & Macdonald, D.W. (2012) Density estimation in tiger populations: combining information for strong inference. *Ecology*, **93**, 1741–1751.

Hemker, T.P., Lindzey, F.G. & Ackerman, B.B. (1984) Population characteristics and movement patterns of cougars in southern Utah. *Journal of Wildlife Management*, **48**, 1275–1284.

Hoekstra, J.M., Clark, J.A., Fagan, W.F. & Boersma, P.D. (2002) A comprehensive review of Endangered Species Act recovery plans. *Ecological Applications*, **12**, 630–640.

Janis, M.W. & Clark, J.D. (2002) Responses of Florida panthers to recreational deer and hog hunting. *Journal of Wildlife Management*, **66**, 839–848.

Johnson, W.E., Onorato, D.P., Roelke, M.E., Land, E.D., Cunningham, M., Belden, R.C., McBride, R., Jansen, D., Lotz, M., Shindle, D. & others. , (2010) Genetic restoration of the Florida panther. *Science*, **329**, 1641–1645.

Karanth, K.U. & Nichols, J.D. (1998) Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, **79**, 2852–2862.

Karanth, K.U., Nichols, J.D., Kumar, N.S. & Hines, J.E. (2006) Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology*, **87**, 2925–2937.

Kautz, R., Kawula, R., Hoctor, T., Comiskey, J., Jansen, D., Jennings, D., Kasbohm, J., Mazzotti, F., Mcbride, R. & Richardson, L. (2006) How much is enough? Landscape-scale conservation for the Florida panther. *Biological Conservation*, **130**, 118–133.

Kelly, M.J., Noss, A.J., Di Bitetti, M.S., Maffei, L., Arispe, R.L., Paviolo, A., De Angelo, C.D. & Di Blanco, Y.E. (2008) Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *Journal of Mammalogy*, **89**, 408–418.

Land, E.D., Shindle, D.B., Kawula, R.J., Benson, J.F., Lotz, M.A. & Onorato, D.P. (2008) Florida panther habitat selection analysis of concurrent GPS and VHF telemetry data. *Journal of Wildlife Management*, **72**, 633–639.

Laundré, J. & Clark, T.W. (2003) Managing puma hunting in the western United States: through a metapopulation approach. *Animal Conservation*, **6**, 159–170.

Long, R.A., MacKay, P., Zielinski, W.J. & Ray, J. (2008) *Noninvasive Survey Methods for Carnivores*. Island Press, Washington DC, USA.

Lucchini, V., Fabbri, E., Marucco, F., Ricci, S., Boitani, L. & Randi, E. (2002) Noninvasive molecular tracking of colonizing wolf (Canis lupus) packs in the western Italian Alps. *Molecular Ecology*, **11**, 857–868.

Maehr, D.S., Land, E.D. & Roof, J.C. (1991) Social ecology of Florida panthers. *National Geographic Research and Exploration*, **7**, 414–431.

McBride, R.T., McBride, R.T., McBride, R.M. & McBride, C.E. (2008) Counting pumas by categorizing physical evidence. *Southeastern Naturalist*, **7**, 381–400.

McClintock, B.T. & White, G.C. (2010) From NOREMARK to MARK: software for estimating demographic parameters using mark–resight methodology. *Journal of Ornithology*, **152**, 1–10.

McClintock, B.T., White, G.C., Antolin, M.F. & Tripp, D.W. (2009) Estimating abundance using mark–resight when sampling is with replacement or the number of marked individuals is unknown. *Biometrics*, **65**, 237–246.

Minta, S. & Mangel, M. (1989) A simple population estimate based on simulation for capture-recapture and capture-resight data. *Ecology*, **70**, 1738–1751.

Negrões, N., Sarmento, P., Cruz, J., Eira, C., Revilla, E., Fonseca, C., Sollmann, R., Torres, N.M., Furtado, M.M., Jácomo, A.T.A. & Silveira, L. (2010) Use of camera-trapping to estimate puma density and influencing factors in Central Brazil RID B-5100-2008. *Journal of Wildlife Management*, **74**, 1195–1203.

Nichols, J.D., O'Connell, A.F. & Karanth, K.U. (2011) Camera Traps in Animal Ecology and Conservation: What's Next? *Camera Traps in Animal Ecology: Methods and Analyses* (eds A.F. O'Connell, J.D. Nichols & K.U. Karanth), pp. 253–263. Springer Publishing, Tokyo, Japan.

O'Brien, S.J. & Mayr, E. (1991) Bureaucratic mischief: recognizing endangered species and subspecies. *Science*, **251**, 1187–1188.

Onorato, D.P., Belden, C., Cunningham, M., Land, D., McBride, R. & Roelke, M. (2010) Long-term research on the Florida panther (Puma concolor coryi): historical findings and future obstacles to population persistence. *The Biology and Conservation of wild Felids* (eds D.W. Macdonald & A. Loveridge), pp. 453–468. Oxford University Press, Oxford, UK.

Onorato, D., Criffield, M., Lotz, M., Cunningham, M., McBride, R., Leone, E., Bass, O. Jr & Hellgren, E. (2011) Habitat selection by critically endangered Florida panthers across the diel period: implications for land management and conservation. *Animal Conservation*, **14**, 196–205.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, **62**, 1–135.

Paviolo, A., Di Blanco, Y.E., De Angelo, C.D. & Di Bitetti, M.S. (2009) Protection affects the abundance and activity pattern of pumas in the Atlantic Forest. *Journal of Mammalogy*, **90**, 926–934.

Plummer, M., Best, N., Cowles, K. & Vines, K. (2006) CODA: Convergence diagnosis and output analysis for MCMC. *R News*, **6**, 7–11.

Pradel, R., Hines, J.E., Lebreton, J.-D. & Nichols, J.D. (1997) Capture-recapture survival models taking account of transients. *Biometrics*, **53**, 60–72.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reppucci, J., Gardner, B. & Lucherini, M. (2011) Estimating detection and density of the Andean cat in the high Andes. *Journal of Mammalogy*, **92**, 140–147.

Rice, W.R. & Harder, J.D. (1977) Application of multiple aerial sampling to a mark-recapture census of white-tailed deer. *Journal of Wildlife Management*, **41**, 197–206.

Roelke, M.E., Martenson, J.S. & O'Brien, S.J. (1993) The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Current Biology*, **3**, 340–350.

Royle, J.A., Dorazio, R.M. & Link, W.A. (2007) Analysis of multinomial models with unknown index using data augmentation. *Journal of Computational and Graphical Statistics*, **16**, 67–85.

Royle, J.A., Kéry, M. & Guélat, J. (2011) Spatial capture-recapture models for search-encounter data. *Methods in Ecology and Evolution*, **2**, 602–611.

Royle, J.A. & Young, K.V. (2008) A hierarchical model for spatial capture-recapture data. *Ecology*, **89**, 2281–2289.

Royle, J.A., Nichols, J.D., Karanth, K.U. & Gopalaswamy, A.M. (2009) A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology*, **46**, 118–127.

Ruell, E.W., Riley, S.P.D., Douglas, M.R., Pollinger, J.P. & Crooks, K.R. (2009) Estimating Bobcat population sizes and densities in a fragmented urban landscape using noninvasive capture–recapture sampling. *Journal of Mammalogy*, **90**, 129–135.

Seal, U. (1994) *A Plan for Genetic Restoration and Management of the Florida Panther (Felis Concolor Coryi). Report to the Florida Game and Freshwater Fish Commission*. Conservation Breeding Specialist Group, Apple Valley, MN.

Shindle, D. & Kelly, B. (2007) *Short Term Analysis Service (STAS) on Scientific and Technical Support for Completion of a Two Year Pre-construction Panther Prey Baseline Monitoring Survey in the Picayune Strand Restoration Project (PSRP) Area*. Conservancy of Southwest Florida, Naples, FL.

Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T.A., Tôrres, N.M. & Silveira, L. (2011) Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. *Biological Conservation*, **144**, 1017–1024.

Sollmann, R., Gardner, B., Parsons, A.W., Stocking, J.J., McClintock, B., Simons, T.R., Pollock, K.H. & O'Connell, A.F. (In press) A spatial mark-resight model augmented with telemetry data. *Ecology*, **94**, 553–559.

Soria-Diaz, L., Monroy-Vilchis, O., Rodriguez-Soto, C., Zarco-Gonzalez, M.M. & Urios, V. (2010) Variation of abundance and density of Puma concolor in zones of high and low concentration of camera traps in Central Mexico. *Animal Biology*, **60**, 361–371.

U.S. Army Corps of Engineers. (2004) *Biological Assessment or the Picayune Strand Restoration Project Prepared for the U*. S. Fish and Wildlife Service. U.S, Army Corps of Engineers, Jacksonville, FL.

US Federal Register (1967) *Native Fish and Wildlife: Endangered Species*. Federal Register – Department of the Interior – Fish and Wildlife Service, Washington, DC.

USFWS (1994) *Final Environmental Assessment: Genetic Restoration of the Florida Panther*. United States Fish and Wildlife Service, Atlanta, GA.

USFWS (2008) *Florida Panther Recovery Plan (Puma Concolor Coryi)*. Third Revision. United States Fish and Wildlife Service, Atlanta, GA.

Young, S.P. & Goldman, E.A. (1946) *The Puma, Mysterious American Cat. Part I. History, Life Habits, Economic Status, and Control*. The American Wildlife Institute, Washington, DC.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Description of the Metropolis-within-Gibbs MCMC sampler.

Appendix S2. Simulation results.

Cougar Exploitation Levels in Utah: Implications for Demographic Structure, Population Recovery, and Metapopulation Dynamics
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Research Article

Cougar Exploitation Levels in Utah: Implications for Demographic Structure, Population Recovery, and Metapopulation Dynamics

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Abstract

*Currently, 11 western states and 2 Canadian provinces use sport hunting as the primary mechanism for managing cougar (*Puma concolor*) populations. Yet the impacts of sustained harvest on cougar population dynamics and demographic structure are not well understood. We evaluated the effects of hunting on cougar populations by comparing the dynamics and demographic composition of 2 populations exposed to different levels of harvest. We monitored the cougar populations on Monroe Mountain in south-central Utah, USA, and in the Oquirrh Mountains of north-central Utah from 1996 to 2004. Over this interval the Monroe population was subjected to annual removals ranging from 17.6–51.5% (mean ± SE = 35.4 ± 4.3%) of the population, resulting in a >60% decline in cougar population density. Concurrently, the Oquirrh study area was closed to hunting and the population remained stationary. Mean age in the hunted population was lower than in the protected population (*$F = 9.0$*; df = 1, 60.3;* $P = 0.004$*), and in a pooled sample of all study animals, females were older than males (*$F = 13.8$*; df = 1, 60.3;* $P < 0.001$*). Females from the hunted population were significantly younger than those from the protected population (3.7 vs. 5.9 yr), whereas male ages did not differ between sites (3.1 vs. 3.4 yr), suggesting that male spatial requirements may put a lower limit on the area necessary to protect a subpopulation. Survival tracked trends in density on both sites. Levels of human-caused mortality were significantly different between sites (*$\chi^2 = 7.5$*;* $P = 0.006$*). Fecundity rates were highly variable in the protected population but appeared to track density trends with a 1-year lag on the hunted site. Results indicate that harvest exceeding 40% of the population, sustained for ≥4 years, can have significant impacts on cougar population dynamics and demographic composition. Patterns of recruitment resembled a source–sink population structure due in part to spatially variable management strategies. Based on these observations, the temporal scale of population recovery will most likely be a function of local harvest levels, the productivity of potential source populations, and the degree of landscape connectivity among demes. Under these conditions the metapopulation perspective holds promise for broad-scale management of this species.* (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1588–1600; 2006)

Key words

connectivity, cougar, demographics, hunting, metapopulation, population dynamics, Puma concolor, *radiotelemetry, refuge, source–sink dynamics, Utah.*

Across western North America sport harvest is the primary mechanism for the population-scale management of *Puma concolor* (Pierce and Bleich 2003). Management regimes vary from public safety and depredation control only in California, to a year-round open season in Texas (Nowell and Jackson 1996). In order to balance hunting opportunities with protection of big game and livestock, most states manage cougar populations at some intermediate level. However, cougars are secretive, long-lived, and utilize large home ranges, making them difficult to manage with precision (Ross et al. 1996). At present, there are no widely accepted methods for the enumeration of cougars across diverse habitat types and climatic regimes (Anderson et al. 1992, Ross et al. 1996). Most techniques (e.g., track counts, scent stations, probability sampling) have limitations that render them marginally useful (Choate et al. 2006) or capable of detecting only large and rapid changes in population size (Van Sickle and Lindzey 1992, Beier and Cunningham 1996). Additionally, cougars occur at low population densities relative to their primary prey, making them sensitive both to bottom-up (e.g., prey declines; Logan and Sweanor 2001, Bowyer et al. 2005) and top-down (e.g., overexploitation; Murphy 1998) perturbations. Assessing cougar population trends is complicated by annual removals of varying intensity. Changes in population size and composition are generally indexed through harvest data and are therefore confounded by nonrandom sampling biases, further hindering reliable trend estimation (Wolfe et al. 2004).

Cougar management in Utah is spatially organized, with 4 broad ecoregions subdivided into 30 different hunting units. Each unit is managed independently in order to apply harvest pressure according to local priorities, which can include density reductions aimed at increasing survival in mule deer (*Odocoileus hemionus*) or bighorn sheep (*Ovis canadensis*) populations. Cougars are therefore managed at 2 different spatial scales. Locally, they are either managed conservatively as a trophy species or liberally as a limiting factor in the population dynamics of native ungulates. The statewide population, however, is managed for sustainable

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hunting opportunities and persistence across its currently occupied range (Mason et al. 1999).

Cougar hunting in Utah is conducted by means of pursuit with trained hounds. The hunting season extends from mid-December to early June, but approximately 75% of the kill occurs during December to March, when snow cover facilitates tracking and pursuit (Mason et al. 1999). Prior to 1998 the sport harvest of cougars occurred under a Limited Entry (i.e., lottery) system in which the number of permits for individual units is restricted. The long-term mean hunter success for this system is 64%. Beginning with the 1997–1998 season the Harvest Objective (i.e., quota) system was introduced for some units. This system employs an unlimited availability of permits to achieve a prescribed level of kill. Hunters are required to report their kill within 48 hours and the unit is closed once the quota is reached. Typically 74% of the quota is achieved, but instances of overharvest do occur. Between 1995 and 2003 legal harvest accounted for 90.0% of the total statewide cougar kill (Hill and Bunnell 2005). The remaining known mortality was distributed among animals killed in response to livestock depredation (6.2%) and other human-caused mortality, including roadkill and accidental trappings (3.8%). Additional unreported mortality such as incidental take during big game hunting seasons and illegal snaring occurs, but the magnitude of this impact is probably small relative to legal harvest. Individual cougars involved in livestock depredation are managed by the Wildlife Services Division of the United States Department of Agriculture, who may employ foot-hold snares as well as hounds to remove offending individuals. Nuisance cougars are defined as animals in urban settings that constitute a potential threat to human safety. These animals are generally controlled by Utah Division of Wildlife Resources (UDWR) personnel using lethal or nonlethal means, as circumstances warrant.

Little is known about both the immediate and long-term effects of sustained harvest on cougar populations (Anderson 1983, Ross et al. 1996). Numerous studies have been conducted on exploited populations (Murphy 1983, Barnhurst 1986, Logan et al. 1986, Ross and Jalkotzy 1992, Cunningham et al. 2000), including 2 removal experiments (Lindzey et al. 1992, Logan and Sweanor 2001), but few of these studies directly addressed the questions of: 1) how harvest affects the demographic structure of a population, and 2) what the long-term implications are for persistence and recovery of exploited populations within a metapopulation context. Moreover, habitat configuration and connectivity are important factors influencing cougar recruitment patterns, but with few exceptions (Beier 1993, 1995, Maehr et al. 2002) this relationship has been largely overlooked.

Recent years have seen the emergence of the idea of managing cougars as a metapopulation based on the effects of natural habitat patchiness (Sweanor et al. 2000, Laundré and Clark 2003) or anthropogenic fragmentation (Beier 1996, Ernest et al. 2003). Because metapopulations transcend administrative boundaries, understanding population response to sustained harvest is vital in order to manage for persistence across landscapes exhibiting varying degrees of natural and human-caused fragmentation.

We assessed the impacts of exploitation on cougar population dynamics by comparing demographic characteristics between an exploited and a semiprotected population. Specific objectives of this study were: 1) determine how harvest levels might influence the dynamics and demographic structure of individual populations, 2) identify the factors that may influence the rate of population recovery, and 3) assess how the distribution of harvest impacts might affect recruitment within a metapopulation context.

Study Area

Cougar habitat in Utah is geographically fragmented, being broadly associated with mesic regions between 1500 m and 3000 m. The Wasatch Mountains and associated high plateaus form the core habitat, longitudinally bisecting the state, whereas the Colorado Plateau and Great Basin ecoregions consist primarily of desert ecosystems, with suitable habitat sparsely distributed among insular mountain ranges (Fig. 1). We selected Monroe Mountain and the Oquirrh Mountains as study areas for this research (Fig. 1). Although differences existed between these sites in terms of size and plant community composition, they were located within 190 km of each other, making them climatically and ecologically similar in a broad sense, but far enough apart to be treated demographically as independent populations. The most pronounced difference between these populations was the level of exploitation to which each was subjected.

Exploited Area

Monroe Mountain comprises part of the Sevier Plateau in the Southern Mountains ecoregion of south-central Utah (38.5°N, 112°W). The site is a high volcanic plateau extending 75 km in a north–south orientation and lies within a west–east geologic transition from basin and range topography to the Colorado Plateau. Hydrologically, Monroe is part of the Great Basin, but climatically and biologically it is more closely associated with other high-elevation regions of the Colorado Plateau and southern Rocky Mountains. The study site covered approximately 1,300 km^2 and encompassed the central unit of the Fishlake National Forest, southeast of Richfield. Other landholders included the Bureau of Land Management (BLM), State of Utah, and various private interests.

The terrain is mountainous with elevations ranging from 1,600–3,400 m. Annual precipitation ranged from 15–20 cm at lower elevations to 60–120 cm on the plateaus above 2,700 m. Approximately 60% of the annual precipitation occurred as snow in January and February, with most of the remainder derived from summer thunderstorms (Ashcroft et al. 1992). Snowpack typically persisted until mid-June at elevations >3,000 m. Mean monthly temperatures ranged from −4.6° C in January to 18.7° C in July (Ashcroft et al. 1992).

Plant communities were diverse and varied with elevation and aspect (Edwards et al. 1995). Piñon-juniper woodlands

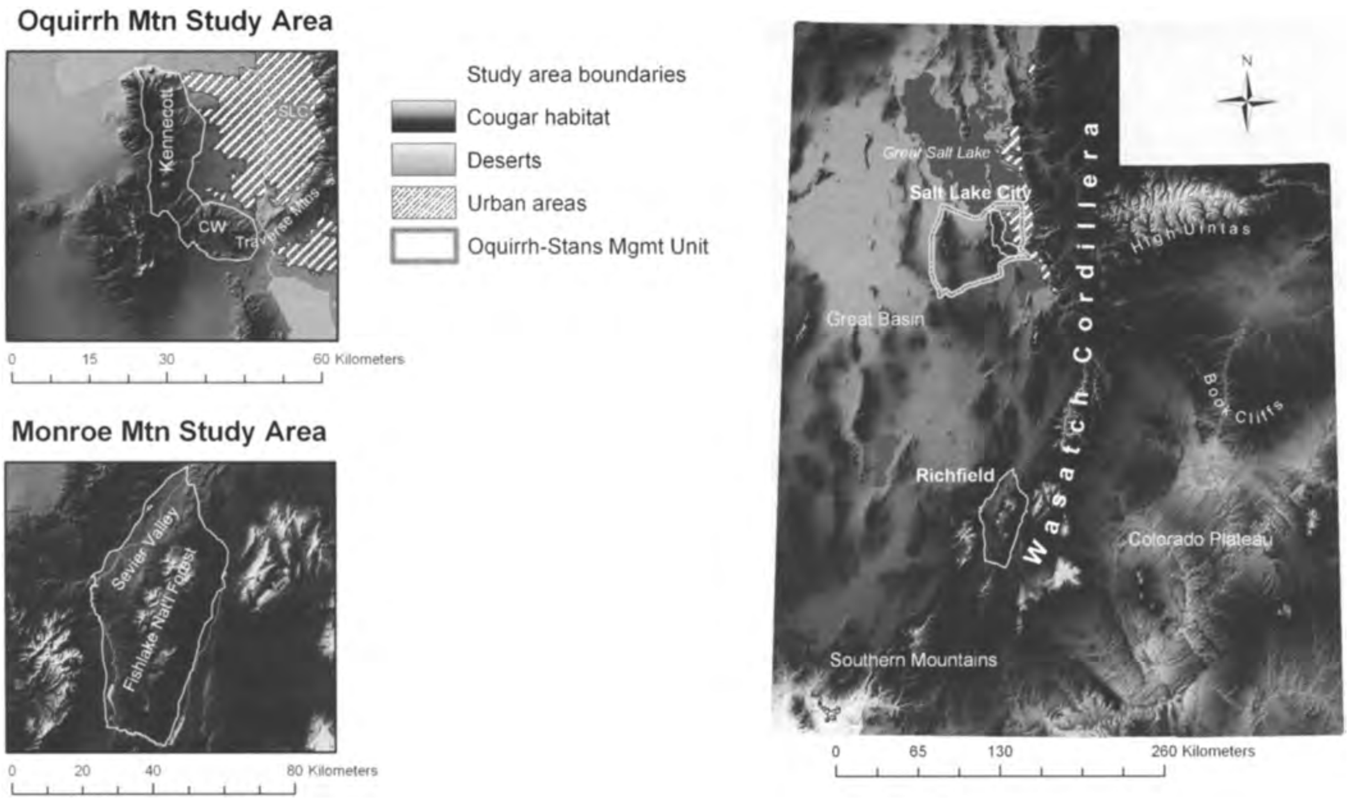

Figure 1. Study-area locations and cougar habitat across Utah, USA, 1996–2004.

(*Pinus edulis, Juniperus scopulorum, Juniperus osteosperma*) comprised the single largest vegetation type covering approximately 44% of the area. Mixed conifer and aspen (*Populus tremuloides*) stands occurred at higher elevations, with gambel oak (*Quercus gambelii*), mountain shrub (e.g., *Cercocarpus ledifolius, Rosa woodsii, Purshia tridentata*), and mixed sagebrush (*Artemisia tridentata*) –grassland meadows interspersed throughout.

Resource exploitation included livestock grazing, logging, and recreation. The UDWR classified Monroe Mountain as Cougar Management Unit 23. Mule deer and elk (*Cervus elaphus*), the primary cougar prey species on this site, were also managed for annual harvests. Human densities around the site varied from 73/100 km^2 to 382/100 km^2 (U.S. Census Bureau), with most of the population scattered among small agricultural communities in the Sevier Valley on the northwestern boundary of the study site.

Protected Area

The Oquirrh-Traverse Mountains complex (hereafter the Oquirrhs) extends 55 km in a north–south orientation on the eastern edge of the Great Basin ecoregion in north-central Utah (40.5°N, 112.2°W). The Oquirrhs are typical of other mountain ranges within this ecoregion in that they form islands of high productivity relative to the surrounding desert basins (Brown 1971) and thus represented the majority of cougar habitat in this area.

The total area of the Oquirrhs measures approximately 950 km^2, but we conducted fieldwork primarily on the northeastern slope of the range on properties owned and managed by the Utah Army National Guard (Camp Williams, Traverse Mountains, 100 km^2) and the Kennecott Utah Copper Corporation (Oquirrh Mountains, 380 km^2). The site was situated at the southern end of the Great Salt Lake, abutting the southwestern side of the greater Salt Lake metro area. Ownership on the southern and western portions of the Oquirrhs was a conglomeration of BLM, grazing associations, and small mining interests, with approximately 45% of the range residing in private ownership.

Elevations on the site vary from lake level at 1,280 m up to 3,200 m. The Traverse Mountains run perpendicular to the Oquirrhs, and range in elevation from 1,650 m to 2,100 m. Annual precipitation ranged from 30–40 cm in the Salt Lake and Tooele valleys to 100–130 cm on the highest ridges and peaks. Most precipitation fell as snow between December and April, with approximately 25% occurring in the form of summer thunderstorms. Mean monthly temperatures ranged from −2.4° C in January to 22.2° C in July (Ashcroft et al. 1992).

Gambel oak and sagebrush were the predominant vegetation on the site. Also prevalent were Utah juniper in the foothills, and canyon maple (*Acer grandidentatum*) in the drainages at low elevations, and across broader areas above 1,800 m. Mountain mahogany (*Cercocarpus spp.*) was present, but relegated to well-drained soils along ridges. North-facing slopes above 2,200 m supported localized montane communities of aspen and Douglas fir (Edwards et al. 1995).

Mining activities have dominated the Kennecott property for >100 years (Roylance 1982), and the site included 2 large open pit mines and attendant infrastructure. Camp Williams was used for military training activities, and consequently exhibited brief fire return intervals. All prominent peaks on the study site supported commercial radio and television transmitters with associated access roads. A limited amount of livestock grazing occurred seasonally. Mule deer and elk were present on this study area as well; however deer were not hunted, whereas elk were subject to intensive management through annual harvests and active translocation projects. The study site was part of the Oquirrh-Stansbury Cougar Management Unit 18, but both of these properties were closed to the public and cougar hunting was prohibited. Human density adjoining the study area varied from 232/100 km^2 in rural Tooele County to 47,259/100 km^2 in urban Salt Lake County (United States Census Bureau).

Methods

We monitored cougar populations within the 2 study areas simultaneously from early 1997 to December 2004. We estimated demographic parameters for each population based on radiotelemetry data collected between 1996 and 2004 on Monroe and from 1997 and 2004 on the Oquirrhs. We calculated estimates of life-history parameters for cougars on the Oquirrh site during 1997 and 1998 from raw data presented in Leidolf and Wolfe (Utah State University, unpublished data). We performed statistical comparisons with the use of SAS (V.8) software. We report all descriptive statistics as mean ± SE unless otherwise noted.

Radiotelemetry and Harvest

We conducted intensive capture efforts during winter (Nov–Apr) each year of the study. We captured cougars by pursuing them into trees, culverts, cliffs, or mine shafts with trained hounds (Hemker et al. 1984). We immobilized each animal with a 5:1 combination of ketamine HCl and xylazine HCl (Kreeger 1996) at a dose of 10 mg ketamine plus 2 mg xylazine/kg of body weight. We administered immobilizing drugs with a Palmer CO_2 pistol (Powder Springs, Georgia), jab stick, or hand-held syringe. We collected tooth (vestigial premolar, P2) samples for age determination by counts of cementum annulations. We sexed, aged, weighed, measured, tattooed with a unique identifier, and equipped with a radiocollar (Advanced Telemetry Solutions, Isanti, Minnesota) and a microchip (AVID Co., Norco, California) every adult animal captured. We checked adult females for evidence of lactation during handling. We tattooed, microchipped, and released all kittens too small to wear a radiocollar. We conducted all procedures in accordance with Utah State University Institutional Animal Care and Use Committee standards (Approval No. 937-R).

We relocated all radio-collared cougars with the use of aerial and ground-based telemetry techniques (Mech 1983). We conducted telemetry flights bimonthly on both sites as weather conditions permitted. We also relocated cougars opportunistically with ground-based telemetry by plotting radiotriangulated locations on United States Geological Survey 7.5′ topographic quads with the use of Universal Transverse Mercator coordinates (zone 12, North American Datum 1927). We stored all locations in a Geographic Information Systems (GIS) database (ArcView, ESRI Products, Redlands, California).

Over the course of the study, radiocollared cougars on Monroe Mountain were not protected from harvest beyond normal legal stipulations outlined in the UDWR hunting proclamations. Annual hunter-kill was regulated by apportionment of a limited number of hunter permits, issued by the UDWR on the decision of the State Wildlife Board. The Camp Williams and Kennecott properties were closed to hunting throughout the study; however, radiocollared cougars leaving those properties were considered legal take on adjacent private and public lands within Unit 18 during the 1997–2001 hunting seasons. Radiocollared cougars on that unit were protected after 2002.

Demographic Parameters

Density.—We measured cougar density as the total number of adult and subadult cougars/100 km^2 present during winter. Our a priori goal was to capture and collar as many individuals as possible. In this sense, we attempted to conduct a census of the population during winter, but during no year were we able to capture all independent cougars. To derive a conservative estimate of the number of unmarked animals on the site, we used 2 methods. First, because males and females can generally be differentiated by track size (Fjelline and Mansfield 1989), we considered multiple track sets of same-sexed animals encountered in the same watershed one individual. Given the large ranges of cougars, we felt that the primary watersheds on the site ($n = 4$; mean ± SD = 361 ± 95 km^2, range = 237–462 km^2) provided a practical threshold for differentiating individuals, as these basins approximated the size of a male home range. This does not negate the possibility that some individuals were double-counted; however, the effect of this error on the population estimate was small due to the number of animals that fell into this category annually. Second, we backcalculated birthdates of radiocollared cougars from age estimations based on tooth wear and counts of cementum annulations and used this information to assess our estimates of uncollared individuals from track evidence and hunter harvest. We excluded males backdated in this manner from the population estimate when they were <3 years old because of the likelihood that they were recent immigrants. Because females tend to be philopatric (Sweanor et al. 2000), we included them in the population estimate as resident subadults at the backcalculated age of 1–2 years. Although there are exceptions to these arbitrary dispersal rules, they provide a reasonable cutoff point for population estimates based on known cougar behavior (Beier 1995, Sweanor et al. 2000). We summed the total number of animals detected (from all means: capture, deaths, tracks) in June at the end of the capture and hunting seasons. This number most accurately represented the population during the period June to December of the preceding year (Choate et al. 2006).

Road densities were high across both study areas. In addition to using 4-wheel-drive vehicles, we conducted winter tracking efforts on horseback and snowmachine in order to reduce bias associated with different levels of access. Using multiple methods also helped to reduce bias in terms of the social classes most vulnerable to detection due to frequent road crossings or small home ranges (Barnhurst 1986). Snow conditions influenced our ability to detect tracks, and therefore dry winters may have some bias associated with population counts; however, this bias was likely consistent between sites, as both study areas are subject to similar weather patterns.

We based study-area boundaries on major roads surrounding the site; therefore we used ecologically relevant vegetative and topographic features to delineate and quantify habitat within the study-site perimeter. We used the criteria of Laing and Lindzey (1991), which excluded valley bottoms and landcover types dominated by urban and agricultural uses. Maps represent geographical area on the planar surface and do not account for slope differences in mountainous terrain where actual surface area is greater. This discrepancy in area calculation leads to an increasing overestimation of population density as the ruggedness of the terrain increases. In order to increase the accuracy of the density estimates we used GIS software (ArcView surface to area ratio extension, Jenness Enterprises, Flagstaff, Arizona) to calculate the surface areas of habitat within study-site perimeters.

Age structure.—We determined age at the time of capture by visual inspection of tooth wear and gumline recession (Ashman et al. 1983, Laundré et al. 2000). In a few cases we used counts of cementum annulations (Matson's Lab, Milltown, Montana). To test for age differences among treatment groups (site and sex combinations), we used a 2-way factorial analysis of variance in a completely randomized design with unequal variances. We adjusted significance levels for pairwise mean comparisons to control experimentwise Type I error with the Tukey-Kramer method.

Cause-specific mortality.—We determined causes of mortality through visual inspection and necropsy of carcasses. When we could not determine cause of death in the field, we submitted the carcass to the Utah State University Veterinary Diagnostics Lab for detailed analysis. We calculated mortality by tallying cause of death among radiocollared animals and unmarked animals found opportunistically during tracking sequences. We pooled all human-related causes by site and tested for proportional differences with the use of chi-square (χ^2) tests.

Survival.—We calculated survival annually for all radiocollared adult and subadult animals from each population. To account for staggered entry and censoring due to the additions and losses of radiocollared animals to the sample, we used a Kaplan-Meier product limit estimator (Kaplan and Meier 1958). We estimated annual survival by defining the start of sample intervals as 1 December of each year. By beginning the sampling interval prior to the beginning of the hunting season (15 Dec), we ensured that human-related mortality is accounted for only once during a single nonoverlapping period in each year. We calculated measures of precision for the computed survival rates from procedures described by Cox and Oakes (1984; cited in Pollock et al. 1989). We compared survival curves between sites with the use of the log-rank test (Pollock et al. 1989).

Fecundity.—We measured fecundity as the proportion of sexually mature females detected with litters-of-the-year (kittens <1 yr) on site during winter. We counted litters during snow tracking and capture efforts. We checked all females taken in the hunt for signs of lactation, which helped account for otherwise undocumented reproduction. Kittens >3 months old are only found with their mothers 20–43% of the time (Barnhurst 1986), but we tracked many female cougars on multiple occasions, thereby increasing the probability of detecting kittens, if present. We did not attempt any analyses on the actual number of kittens born per litter, because of the difficulty in determining the actual number of kittens when ≥2 track sets were found. There are 2 potential sources of error in this estimate. First, it is possible that some maternal females experienced whole-litter loss prior to the winter tracking season, and therefore a proportion of nonlactating females or those without kittens may actually have been reproductively active that season. Second, kittens <2 months old are not mobile, and so this cohort would also have been missed through track-based counts. Consequently, both the number of kittens per litter and the proportion of reproductively active females are biased low. The minimum percentage of females caring for young provided an annual estimate of productivity for each population (Barnhurst 1986). We used paired t-tests to detect differences in mean fecundity rates pooled over the entire study interval.

Dispersal.—We tattooed the ears of all kittens handled on the Oquirrh mountain site in the event that they were recaptured as adults. For the Oquirrh Mountain animals, we were able to calculate several crude estimates of dispersal distance and direction opportunistically based on harvest returns of animals marked as kittens. In addition, we monitored subadults captured as transients on Monroe via radiotelemetry for extrasite movements, thus providing some information on coarse-scale movement patterns. We calculated distances as a straight line between capture site and death site or the center of the home range.

Landscape Configuration

We used measures of landscape configuration to assess the overall degree of connectivity of the study sites to surrounding habitats within their respective ecoregions. Connectivity is defined here as "the degree to which the landscape facilitates or impedes [animal] movement among resource patches" (Taylor et al. 1993). We used descriptions provided by Laing and Lindzey (1991) to delineate potential connective habitats between the study areas and neighboring patches. In assessing connectivity for cougars we used only easily quantifiable landscape variables and did not consider potential psychological barriers, although there is some evidence that outdoor lighting may function as such (Beier 1995). We derived the following metrics: size (km^2), shape (perimeter–area ratios), greatest interpatch distance, percent of perimeter connected to neighboring habitat patches, width of connective habitat, and percent of perimeter impermeable to cougar movement. Impermeability refers to landscape features that prohibited, filtered, or redirected animal movement (Ernest et al. 2003, Forman et al. 2003), such as the Great Salt Lake, interstate highways, and urban areas. Some of these features may not form absolute barriers, but they can act as an impediment to animal movement. Perimeter-area ratios are a unitless metric that provided a relative measure of how circular (or how much edge) one study area had relative to the other. We derived these measures in ArcView using the spatial analyst extension and a 30-m digital elevation model of the state of Utah.

Results

Radiotelemetry and Harvest

Capture.—We captured and marked 110 individual cougars on the 2 study sites, representing 145 capture events (Table 1). In addition, we found one dead cougar opportunistically during tracking on the Oquirrh site. We conducted captures on Monroe Mountain from January 1996 to March 2004 and on the Oquirrh site from February 1997 to March 2004. Rugged terrain and frequent animal use of culverts, mine shafts, and lava tubes hindered the collection of ground-based telemetry observations. Consequently most telemetry data were derived from aerial surveys. Monitoring times for Monroe cougars averaged 758 days (range = 2–3140 days) for females, and 194 days (range = 3–662 days) for males. On the Oquirrh site we monitored females for a mean of 810 days (range = 14–2674 days) and males for 399 days (range = 76–1173 days). Differences between sexes reflected the smaller sample of males, their greater tendency to emigrate, and shorter residence times.

Monroe Mountain cougar harvest.—For the period 1990–1995, prior to initiation of this study, a mean of 15.6 (range = 14–19) hunting permits were issued annually, corresponding to a mean kill of 8.7 cougars per year (range = 6–12), and a mean hunter success of 54.0% (range = 40.7–64.9%). In 1996, the number of permits issued increased 33.7% over the 1990–1995 mean. In 1997, the number of permits increased 40% over 1996 levels and 151% over the 1990–1995 mean. Between 1999 and 2000, the number of permits issued decreased to 1990–1995 mean levels and was again decreased for the 2001 season. During the years of heavy harvest (1996–2001), mean per-capita hunting pressure (i.e., the proportion of the population that was legally harvestable) was 87% (range = 68.5–100%). During the years of reduced harvest (2002–2004) mean per-capita hunting pressure was 25.7% (range = 22.7–29.4%; Table 2). During the study 164 permits were issued, 79 cougars were killed (51 M, 28 F), and total hunter success was 48.1%, whereas mean annual hunter success was 46.5% (1996–2001) and 73.3% (2002–2004; Hill and Bunnell 2005). The general decline in the number of hunting tags issued over time was partially in response to preliminary study results.

Table 1. Number of cougars captured according to age and sex classes, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

Age and sex	Monroe	Oquirrhs
Adults		
F	16	20
M	12	7
Subadults		
F	14	2
M	15	3
Kittens		
F	2	9
M	1	9
Totals	60	50

Oquirrh Mountain cougar harvest.—From 1996 to 2001 radiocollared animals on Unit 18 were considered legally harvestable. Cougars on the Camp Williams and Kennecott properties were protected, but these areas were surrounded by private and public lands open to hunting, making any study animal found offsite legal quarry. Beginning in 2002, all radiocollared animals on the unit were protected by law regardless of property ownership to facilitate a concurrent study. During our study 5 radiocollared cougars were killed just outside the study site boundaries (4 M, 1 F). Of these, the 4 males were legally harvested, whereas the female was taken after the 2002 moratorium on radiocollared study animals.

Demographic Parameters

Density.—Estimated high densities (cougars/100 km^2) were similar between sites (Oquirrhs, 2.9; Monroe, 3.2); however, trends in this parameter differed markedly (Fig. 2). Density on Monroe showed a consistent decline during the years of heavy harvest (1997–2001), which leveled off when permits were reduced by 80%, averaging 2.0 ± 0.3 (2002–2004). Oquirrh density showed minimal variation over the study interval averaging 2.8 ± 0.1 (Fig. 2).

Age structure.—Age estimates determined upon initial capture were pooled by sex and site for the entire study period (Table 1). Sexually mature cougars from the Monroe population ($n = 57$) averaged 3.4 ± 0.2 years (F = 3.7 ± 0.4; M = 3.1 ± 0.3). Adult cougars from the Oquirrh population ($n = 33$) averaged 4.6 ± 0.3 years (F = 5.9 ± 0.5; M = 3.4 ± 0.4; Fig. 3). Mean cougar ages differed both by study site (Monroe cougars < Oquirrh cougars; $F = 9.0$, df = 1,60.3, $P = 0.004$) and by sex (F > M; $F = 13.8$; df = 1, 60.3; $P < 0.001$). Further, we found evidence of an interaction between sex and site ($F = 5.31$; df = 1, 60.3; $P = 0.025$). Within the Monroe population male and female mean ages did not differ ($t = 1.21$; df = 54.6; $P = 0.625$), whereas Oquirrh females were significantly older than their male counterparts ($t = 3.70$; df = 30.2; $P = 0.003$). Between sites, Oquirrh females were older than Monroe females ($t =$

Table 2. Cougar harvest characteristics from Monroe Mountain (Unit 23), Utah, USA, 1996–2004.

Hunting season	Estimated population[a]	Permits issued	Cougars killed[b]	% hunter success	% F	% population	
						Hunted[c]	Killed
1995–96	35	24	14	58.3	42.9	68.5	40.0
1996–97	42	40	17	42.5	47.1	95.2	40.5
1997–98	33	30	15	50.0	26.7	90.9	45.5
1998–99	26	25	7	28.0	28.6	96.1	26.9
1999–00	21	15	9	60.0	44.4	71.4	42.9
2000–01	15	15	6	40.0	33.3	100.0	40.0
2001–02	17	5	3	60.0	33.3	29.4	17.6
2002–03	20	5	4	80.0	00.0	25.0	20.0
2003–04	22	5	4	80.0	25.0	22.7	18.2
Mean	25.6	18.2	8.8	55.4	31.2	66.6	32.4
SE	3.0	4.1	1.8	17.5	5.0	10.8	3.8

[a] Estimated number of adults and independent subadults from winter capture and tracking efforts.

[b] Legal sport harvest only (Hill and Bunnell 2005).

[c] Per capita hunting pressure, i.e., the ratio of the number of permits issued to the estimated population size (column 3/column 2).

-3.53; df $= 38.8$; $P = 0.004$), but male ages did not differ between sites ($t = -0.54$; df $= 22.5$; $P = 0.949$).

Cause-specific mortality.—Mortality on the Monroe site was predominantly human caused (74%), with legal harvest accounting for 81% of human-caused ($n = 26$) and 60% of total mortality ($n = 35$) (Fig. 4). Causes of mortality on the Oquirrh site varied (Fig. 4). All human causes (including roadkill) comprised 53% of the total mortality ($n = 17$) and of this, legal harvest accounted for 44% of all human-caused mortality ($n = 9$) but only 24% of the total. Levels of human-caused mortality differed between sites ($\chi^2 = 7.5$; $P = 0.006$). Various forms of poaching (neck snares, illegal hunter-kill) occurred sporadically on both sites (Monroe, $n = 2$; Oquirrhs, $n = 1$), though alone, this did not represent a significant source of mortality for radio-collared animals.

The second leading cause of death on both sites was intraspecific predation, comprising 17% ($n = 6$) and 18% ($n = 3$) of total mortality on the Monroe and Oquirrh sites, respectively. During the years of high per-capita harvest pressure on Monroe, all victims of intraspecific aggression were resident adult females ($n = 4$), whereas during the period of light harvest all victims were subadult males ($n = 2$). On the Oquirrhs, 1 victim was a predispersal subadult male and 2 were adult females. Notably, one of these instances was an adult female cannibalizing another female with dependent young. Two years later, the survivor in this encounter was killed by an unidentified cougar. Cause of death could not be determined in three cases (2 F, 1 M), but did not appear to be human-related.

In addition to direct mortality, ≥ 11 kittens from 5 different litters on Monroe were orphaned when their mothers were killed during the winter hunt ($n = 10$) or during summer depredation control actions ($n = 1$). We confirmed the death of one orphaned litter (2 kittens, approx. 6 months old) due to dehydration and malnutrition. On the Oquirrhs, one male kitten was orphaned at the estimated age of 9 months when its mother was killed by an automobile. This animal survived 6 weeks before being taken in a depredation control action on a small ranch just outside of Salt Lake City. A litter of 3 4-month-old kittens died following the disease-related death of their mother. One other male kitten was marked at the age of 7 months following the poaching-related death of its mother in January 2002. It survived at least 2 months before radio contact was lost. Aside from this individual, no other orphans were detected following the deaths of their mothers or as adults on either study area in subsequent years.

Survival.—Adult survival varied between sites and among years (Fig. 5). On Monroe, survival tracked harvest

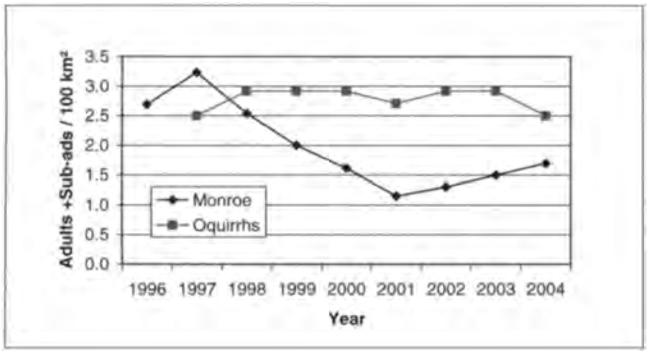

Figure 2. Annual nonjuvenile cougar density as determined from capture, tracking, and harvest, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

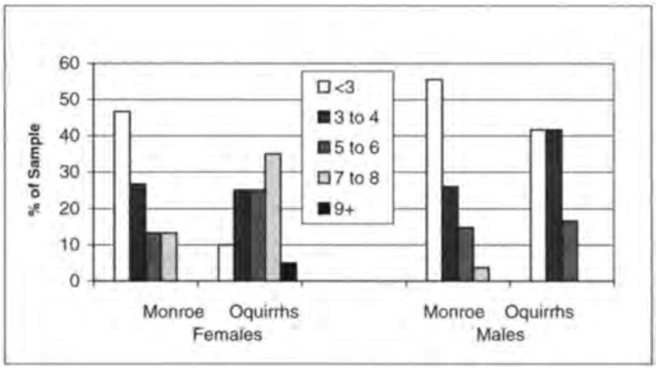

Figure 3. Age distribution of radiocollared cougars by sex, Monroe ($n = 57$) and Oquirrh ($n = 30$) Mountain study sites, Utah, USA, 1996–2004.

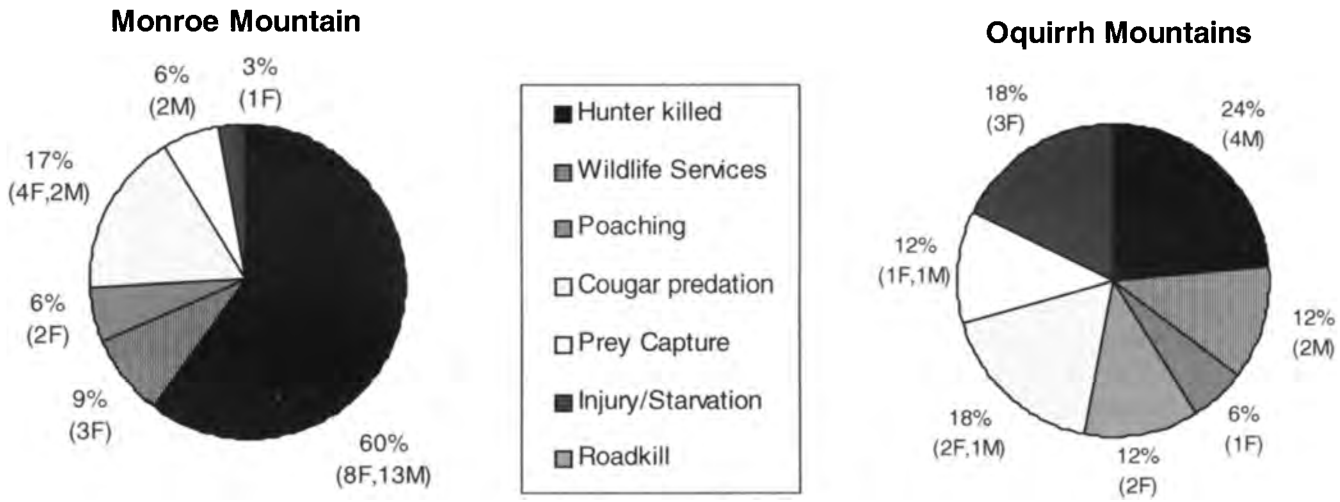

Figure 4. Cause-specific mortality among radiocollared cougars from the Monroe ($n = 35$) and Oquirrh Mountain ($n = 17$), study sites, Utah, USA, 1996–2004.

intensity, ranging from a high of 1.0 in 1996, just prior to the initiation of the treatment period, and declining to a low of 0.36 ± 0.33 (95% CI) in 2001, the end of high per-capita hunting pressure. Survival on the Oquirrhs showed moderate variation, ranging from 0.63 ± 0.28 to 0.91 ± 0.17. Trends in survival mirrored those of density on both sites, averaging 0.64 ± 0.07 (± SE) on Monroe and 0.76 ± 0.04 on the Oquirrhs. Analysis of trends over the entire interval suggested a difference in survival between sites ($\chi^2 = 3.41$; df = 1, $P = 0.068$).

Fecundity.—Reproduction varied between sites and years (Fig. 6). The number of litters detected annually ranged from 0–9 on Monroe and from 1–5 on the Oquirrhs, averaging 0.24 ± 0.04 (Monroe) and 0.34 ± 0.05 (Oquirrhs) litters per sexually mature female. Although rates did not differ statistically between sites ($t = -1.23$; df = 7; $P = 0.258$), fecundity on Monroe tracked the population decline and included a zero detection rate in 2002, the year following the lowest population estimate. At that time there were ≥ 5 sexually mature females present. The lowest fecundity estimate for the Oquirrh population was recorded the year after a 50% reduction in elk numbers. These animals were removed for reintroductions in other states. The removal was conducted over 2 years and was comprised primarily of cows and calves, the sex and age classes most vulnerable to cougar predation (Murphy 1998). The number of resident females on the Oquirrh site was smaller ($\bar{x} = 9.6$/yr) than on Monroe ($\bar{x} = 15.7$/yr), which may have influenced the variability in fecundity. Litter sizes averaged 1.7 and 1.9 kittens per litter on Monroe and the Oquirrhs, respectively. Based exclusively on the Oquirrh site using only kittens handled and marked (4–10 months post partum), the sex ratio was even (9 F, 9 M).

Dispersal.—Several animals were captured and marked either just prior to, or during dispersal. Four cougars (1 F, 3 M) moved from Monroe to neighboring mountain ranges 19–55 km distant. Two of these (1 F, 1 M) established residency in habitat adjacent to the study area; one was recaptured and his collar removed (fate unknown); and one was harvested 42 km northeast on the Fishlake Plateau (Fig. 7).

Seven dispersals were documented on the Oquirrh site (2 F, 5 M), ranging in distance from 13 to 85 km (Fig. 7). Of these, 3 (1 F, 2 M) settled elsewhere in the Oquirrh Mountains; 1 female moved to the Simpson-Sheeprock Mountains; 2 males moved to the Stansbury Mountains where they were hunter-killed as transients; and 1 male dispersed to the Mt. Timpanogos region of the southern

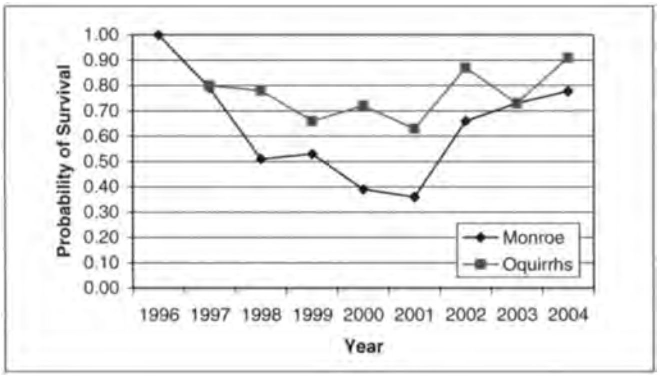

Figure 5. Estimated annual survival rates for radiocollared cougars, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

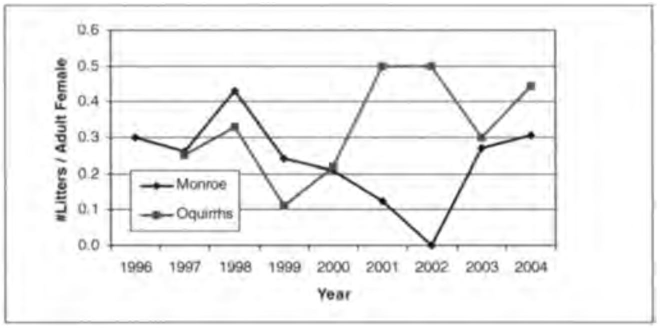

Figure 6. Annual fecundity rates for adult cougars on the Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

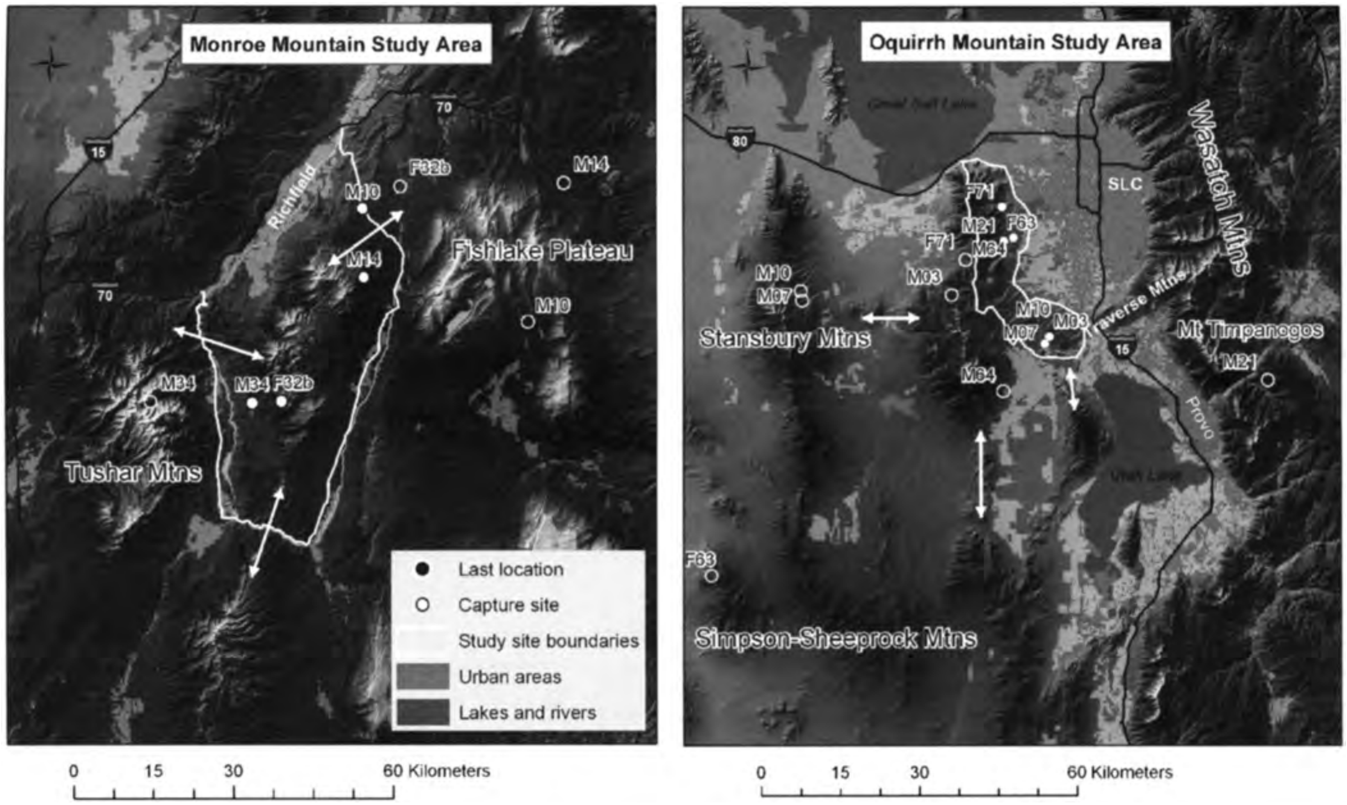

Figure 7. Dispersal patterns and landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004. Arrows represent points of habitat connectivity.

Wasatch Mountains, crossing a 6-lane interstate and ≥5 km of city streets to get there.

Landscape Configuration

The study sites exhibited similar perimeter-area indices, but notable differences in connectivity and perimeter permeability (Table 3). During the study, no substantial movement barriers existed along the perimeter of Monroe Mountain, and in general, the unit was well connected to other habitats of similar quality within the Southern Mountains ecoregion (Fig. 7).

In contrast, only 5% of the Oquirrhs' perimeter was connected to neighboring habitat and approximately 40% was nearly impermeable to cougar movement. Movement barriers included the southern shore of the Great Salt Lake (7 km), the Salt Lake metro area (50 km), and a heavily traveled segment of Interstate 15 (2 km), which bisected the Traverse Mountains (Fig. 7). The remaining 55% graded into salt desert scrub communities offering little vegetative cover or surface water (West 1983). Additionally, residential development emanating from the Salt Lake–Provo metropolitan corridor was much greater around the Oquirrh site.

Overall, the Oquirrhs exhibited much thinner and more tenuous connectivity to neighboring patches of generally poorer quality (i.e., lower primary production), a pattern typical of basin and range topography (Fig. 1). This topographic fragmentation combined with anthropogenic fragmentation in the foothills and valleys around the site rendered this area susceptible to isolation (see Beier 1995).

Discussion

Influence of Harvest on Cougar Populations

Demographic differences between study populations reflected the prevailing management strategies. Cougar removal on Monroe Mountain ranged from 17.6–54.5% of the adult population exceeding 40% for 4 of the 5 years of high per-capita hunting pressure. Females comprised 32% of the harvest but 100% of depredation control and poaching mortality. Under this regime the population declined by >60%, whereas the Oquirrh Mountain population remained stationary. Moreover, the Oquirrh population had a significantly higher mean age among females and a smaller proportion of subadults. Age structure of males did not differ between sites, suggesting either: 1) males and females had a fundamentally different age distribution in the general population, or 2) the unhunted portion of the Oquirrhs was too small to adequately protect males. Density, survival, and fecundity were all negatively associated with sustained high per-capita hunting pressure on Monroe Mountain, whereas, with the exception of fecundity, these measures remained relatively constant over the same interval on the Oquirrh site. Though humans represented the single greatest source of mortality for animals traveling outside the Oquirrh study site, the absence of harvest within the study area suggests that the Camp Williams–Kennecott properties collectively acted as a functional refuge. Resident females were the primary beneficiaries of this protection. On the Monroe site, the prevalence

Table 3. Measures of landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

Landscape metrics	Monroe	Oquirrhs
Perimeter (km)	178	150
Area (km^2)	1300	950
Perimeter:area	0.137	0.157
Greatest interpatch distance (km)	7	25
Perimeter impermeable (%)	0	40
Perimeter connected (%)	33	5
Width connective habitat (km)	7–21	2–4.5

of human-caused mortality, lack of starvation as a mortality cause, and moderately stable prey populations (UDWR, unpublished data) suggest that this level of mortality was largely additive. Annual harvests exceeding 30% of the adult population consisting of 42% females, carried out continuously for >3 years, can reduce density, fecundity, and skew age structure.

The consequences of sustained exploitation may not be limited to numeric population changes. Fecundity rates on Monroe tracked per-capita harvest pressure with a 1-year lag. We did not observe compensatory reproduction under increased harvest levels, as has been noted for some monogamous carnivores (Knowlton 1972, Frank and Woodroffe 2001). Smuts (1978), Knick (1990), and Wielgus and Bunnell (2000) reported analogous findings for hunted populations of African lions (*Panthera leo*), bobcats (*Lynx rufus*), and brown bears (*Ursus arctos*), respectively. One hypothesized function of male territoriality among polygynous carnivores is to increase offspring survival by excluding nonsire males from the natal range (Bertram 1975, Ross and Jalkotzy 1992), thereby reducing infanticide and optimizing fitness (Packer and Pusey 1984, Swenson 2003). Cougars are known to exhibit this behavior (Hornocker 1970, Hemker et al. 1986, Pierce et al. 1998) suggesting that hunted populations may experience increased levels of infanticide (Swenson 2003). On Monroe heavy harvest and subsequent social instability may have reduced the reproductive capacity of the population and therefore its ability to compensate losses.

Factors Influencing the Rate of Population Recovery

From 2002 to 2004 per capita hunting pressure on Monroe Mountain was reduced to <30%, during which survival and fecundity increased. Nevertheless, following 3 seasons of light harvest the population had only recovered to 52.4% of its 1997 levels, with nearly equal sex ratios and reproduction lagging behind resident replacement.

Lindzey et al. (1992) in Utah and Logan and Sweanor (2001) in New Mexico conducted controlled removals to examine the demographic mechanisms and time scales of population recovery. These authors noted that female recruitment was achieved via philopatric behavior or diffuse dispersal, whereas male recruitment was solely the product of immigration. Further, they suggested that recovery from 27–58% population reductions could be attained within 2–3 years under complete protection. However, those removals spanned only a single season and large sanctuaries (>1,000 km^2) buffered the treatment areas. In contrast, the Monroe population had only a 7-month annual reprieve from hunting pressure and was surrounded by units subjected to similar levels of exploitation.

The degree of landscape connectivity can mediate demographic connectivity, and is thus an important factor in population recovery or persistence (Beier 1993). Strong connectivity is the most likely reason we detected transients on Monroe each winter. These animals buffered population declines (Brown and Kodric-Brown 1977) but may have contributed to social instability. It has been hypothesized that the removal of resident males may induce a "vacuum effect" in which multiple transients vie for a vacant home range, potentially leading to an increase in population density (Shaw 1981, Logan et al. 1986). Our results lend only limited support to this argument. We observed an increase in the relative proportion of subadult males subsequent to removal of resident males, whereas the overall population declined. In general, males tend to disperse farther than females, remain transient longer, and are less tolerant of other males (Cunningham et al. 2001, Logan and Sweanor 2001, Maehr et al. 2002). Conversely, females often exhibit philopatric behavior, reproduce at an earlier age than males, and tolerate spatial overlap with other females (Murphy 1998, Pierce et al. 2000). Therefore, the transient segment of the cougar population is likely to be male biased (Hansson 1991). Removal of resident males provides territory vacancies that may be contested by multiple immigrants, thereby temporarily increasing the proportion of males in the population but not the overall density of males in the general population. Based on preliminary data from the post-treatment period, we hypothesize that following sustained disturbance, population recovery will proceed in 2 general phases: numerical and functional. Functional recovery implies not simply increases in absolute density but rather stabilization of social relationships and decreases in the variability of vital life-history rates. Female-biased sex ratios, low male turnover rates, and higher per-capita productivity may be used as relative indices of functional recovery.

Harvest Dynamics and the Regional Metapopulation

The metapopulation concept has been proposed as a framework for large-scale management of cougars (Beier 1996, Sweanor et al. 2000, Laundré and Clark 2003). In the strictest sense, a metapopulation is the composite of numerous spatially discrete subpopulations exhibiting independent behavior over time. The dynamics of the metapopulation are the net result of the shifting balance between local extinctions and recolonizations facilitated by intermittent dispersal events. The latter quality defines the classic metapopulation (Levins 1969, Hanski and Simberloff 1997).

The source–sink model provides a mechanism for metapopulation dynamics by emphasizing recruitment patterns within and among populations. The more general definition describes a sink as a net importer and a source as a net exporter of individuals over time (Pulliam 1988). Demographically, the Monroe and Oquirrh populations approximate the sink–source archetypes, respectively, albeit as a result of exploitation levels rather than habitat quality (e.g., Novaro et al. 2000). When harvest and its apparent impacts are considered, the Monroe population exhibited sink-like mortality. Notwithstanding low kitten production, each winter new animals, primarily subadult males, were captured on the site. Some of these individuals may have been resident progeny but mammalian dispersal patterns tend to be male-biased (Greenwood 1980). Low productivity and high immigration rates are the essence of a sink population.

In contrast, the Oquirrh population exhibited static density and emigration of resident progeny. No marked female kittens were detected as adults on the site. Indeed, 5 tattooed kittens (2 F, 3 M) were later killed elsewhere in the Oquirrhs or on neighboring mountain ranges up to 85 km distant. Solely based on age (4 yr) the female emigrants could have raised one litter to independence, whereas the males were killed immediately upon leaving their natal ranges, thereby subsidizing the harvest in adjacent units. On the Oquirrh site female dispersal appeared to be related to the saturation of available habitat, suggesting a source-like population structure.

When the prevailing harvest rate is considered a component of habitat quality, then a spatially clumped harvest distribution can promote source–sink dynamics. This may result in an immigration gradient directed toward patches such as Monroe Mountain, where strong connectivity coupled with low population density create an ecological trap (i.e., a productive habitat that displays sink-like mortality patterns, e.g., Bailey et al. 1986, Kokko and Sutherland 2001). These sites represent examples of populations exhibiting different dynamics simultaneously within a metapopulation. Importantly, source–sink characteristics may be dynamic and interchangeable depending on how prevailing management interacts with habitat productivity and connectivity. For example, the Monroe population illustrates the potential consequences of overharvest, yet is situated within a large semicontiguous tract of habitat spanning the state with extensions into Colorado, Idaho, and Arizona. Conversely, the Oquirrh population appears demographically stable, but lies within an ecoregion defined by weak connectivity among sparsely distributed desert ranges. Under different objectives, conservative management could render the Monroe population a source, whereas the Oquirrh population should be managed under the small population paradigm (Caughley 1994).

Management Implications

At the scale of the local population or management unit, annual harvests exceeding 40% of the nonjuvenile population for ≥ 4 years can not only reduce density but may also promote or maintain a demographic structure that is younger, less productive, and socially unstable. At an ecoregional scale the difficulties of reliably delineating discrete populations (Pierce and Bleich 2003) and their respective sizes (Choate et al. 2006) emphasize the importance of managing cougars in a metapopulation context. That said, source–sink characteristics may be more amenable to field evaluation than the extinction and recolonization events that define classic metapopulations. Numeric recovery of overexploited populations may initially depend more on immigration than in situ reproduction. Under moderate to heavy exploitation this tack may require: 1) an assessment of habitat connectivity between identified sources and sinks, and 2) the presence of truly functional source populations, most readily managed through the establishment of refugia.

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Literature Cited

Anderson, A. E. 1983. A critical review of literature on puma (*Felis concolor*). Colorado Division of Wildlife, Special Report No. 54, Denver, USA.

Anderson, A. E., D. C. Bowden, and D. M. Kattner. 1992. The puma on the Uncompahgre Plateau, Colorado. Colorado Division of Wildlife, Technical Publication No. 40, Denver, USA.

Ashcroft, G. L., D. T. Jensen, and J. L. Brown. 1992. Utah climate. Utah Climate Center, Utah State University, Logan, USA.

Ashman, D. L., G. C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wickersham. 1983. The mountain lion in Nevada. Nevada Department of Wildlife, Carson City, USA.

→ Bailey, T. N., E. E. Bangs, M. F. Portner, J. C. Malloy, and R. J. McAvinchey. 1986. An apparent overexploited lynx population on the Kenai Peninsula, Alaska. Journal of Wildlife Management 50:279–290.

Barnhurst, D. 1986. Vulnerability of cougars to hunting. Thesis, Utah State University, Logan, USA.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:94–108.

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59:228–237.

Beier, P. 1996. Metapopulation models, tenacious tracking, and cougar conservation. Pages 293–323 *in* D. R. McCullough, editor. Metapopulations and wildlife conservation. Island, Covelo, California, USA.

Beier, P., and S. C. Cunningham. 1996. Power of track surveys to detect changes in cougar populations. Wildlife Society Bulletin 24: 540–546.

Bertram, B. C. R. 1975. Social factors influencing reproduction in wild lions. Journal of Zoology, London 177:463–482.

Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pages 342–361 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island, Covelo, California, USA.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Naturalist 105:467–478.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Choate, D. M., M. L. Wolfe, and D. C. Stoner. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34: 782–799.

Cox, D. R., and D. Oakes. 1984. Analysis of survival data. Chapman & Hall, New York, USA.

Cunningham, S. C., W. B. Ballard, and H. A. Whitlaw. 2001. Age structure, survival, and mortality of mountain lions in southeastern Arizona. Southwestern Naturalist 46:76–80.

Edwards, T. C., C. G. Homer, S. D. Bassett, A. Falconer, R. D. Ramsey, and D. W. Wight. 1995. Utah gap analysis: an environmental information system. Utah Cooperative Fish and Wildlife Research Unit, Technical Report 95–1. Utah State University, Logan, USA.

Ernest, H. B., W. M. Boyce, V. C. Bleich, B. May, S. J. Stiver, and S. G. Torres. 2003. Genetic structure of mountain lion (*Puma concolor*) populations in California. Conservation Genetics 4:353–366.

Fjelline, D. P., and T. M. Mansfield. 1989. Method to standardize the procedure for measuring mountain lion tracks. Pages 49–51 *in* R. H. Smith, editor. Proceedings of the Third Mountain Lion Workshop. Arizona Game and Fish Department, Phoenix, USA.

Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter. 2003. Road ecology—science and solutions. Island, Covelo, California, USA.

Frank, L. G., and R. Woodroffe. 2001. Behavior of carnivores in exploited and controlled populations. Pages 419–442 *in* J. L. Gittleman, S. M. Funk, D. MacDonald, and R. K. Wayne, editors. Carnivore conservation. University of Cambridge, United Kingdom.

Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behavior 28:1140–1162.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 *in* I. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic, San Diego, California, USA.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42:89–103.

Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. Journal of Wildlife Management 48:1275–1284.

Hemker, T. P., F. G. Lindzey, B. B. Ackerman, and A. J. Button. 1986. Survival of cougar cubs in a non-hunted population. Pages 327–332 *in* S. D. Miller and D. D. Everett, editors. Cats of the world: biology, conservation, and management. National Wildlife Federation, Washington, D.C., USA.

Hill, H., and K. Bunnell. 2005. Utah Cougar harvest report, 2001–2002 to 2004–2005. Utah Department of Natural Resources, Publication No. 05-39. Salt Lake City, USA.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:1–39.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 108:1–42.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369–382.

Kokko, H., and W. J. Sutherland. 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evolutionary Ecology Research 3:537–551.

Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals, Inc., Fort Collins, Colorado, USA.

Laing, S. P., and F. G. Lindzey. 1991. Cougar habitat selection in south-central Utah. Pages 27–37 *in* C. S. Braun, editor. Proceedings of the mountain lion–human interaction workshop. Colorado Division of Wildlife, Denver, USA.

Laundré, J., and T. W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. Animal Conservation 6:159–170.

Laundré, J., L. Hernández, D. Streubel, K. Altendorf, and C. A. López-González. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Cougar population response to manipulation in southern Utah. Wildlife Society Bulletin 20:224–227.

Logan, K. A., L. L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648–654.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma—evolutionary ecology and conservation of an enduring carnivore. Island, Washington, D.C., USA.

Maehr, D. S., E. D. Land, D. B. Shindle, O. L. Bass, and T. S. Hoctor. 2002. Florida panther dispersal and conservation. Biological Conservation 106:187–197.

Mason, J., D. Peay, K. Robinson, R. Danvir, B. Bateman, M. Bodenchuk, M. Wolfe, L. Shirley, B. Bates, L. Cornicelli, B. Giunta, S. Cranney, J. Karpowitz, and J. Grandison. 1999. Utah cougar management plan. Utah Department of Natural Resources, Salt Lake City, USA.

Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota, Minneapolis, USA.

Murphy, K. M. 1983. Relationships between a mountain lion population and hunting pressure in western Montana. Thesis, University of Montana, Missoula, USA.

Murphy, K. M. 1998. The ecology of the cougar (*Puma concolor*) in the northern Yellowstone ecosystem: interactions with prey, bears, and humans. Dissertation, University of Idaho, Moscow, USA.

Novaro, A. J., K. H. Redford, and R. Bodmer. 2000. Effect of hunting in source–sink systems in the neotropics. Conservation Biology 14:713–721.

Nowell, K., and P. Jackson, editors. 1996. Puma, *Puma concolor* (Linnaeus 1771). Pages 131–137 *in* Wild cats: status survey and conservation action plan. International Union for the Conservation of Nature. Burlington, Cambridge, United Kingdom.

Packer, C., and A. E. Pusey. 1984. Infanticide in carnivores. Pages 31–42 *in* G. Hausfater and S. B. Hrdy, editors. Infanticide—comparative and evolutionary perspectives. Aldine, New York, New York, USA.

Pierce, B. M., and V. C. Bleich. 2003. Mountain lion. Pages 744–757 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation.

Second edition. The Johns Hopkins University, Baltimore, Maryland, USA.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land tenure system regulate population size? Ecology 81:1533–1543.

Pierce, B. M., V. C. Bleich, C. B. Chetkiewicz, and J. D. Wehausen. 1998. Timing of feeding bouts of mountain lions. Journal of Mammalogy 79:222–226.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417–426.

Ross, P. I., M. G. Jalkotzy, and J. R. Gunson. 1996. The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24: 490–494.

Roylance, W. J. 1982. Utah: a guide to the state. Utah Arts Council, Salt Lake City, USA.

Shaw, H. G. 1981. Comparison of mountain lion predation on cattle on two study areas in Arizona. Pages 306–318 *in* L. Nelson Jr. and J. M. Peek, editors. Proceedings of the wildlife–livestock relationships symposium. Forest, Wildlife, & Range Experiment Station, University of Idaho, Moscow, USA.

Smuts, G. L. 1978. Effects of population reduction on the travels and reproduction of lions in Kruger National Park. Carnivore 2:61–72.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.

Swenson, J. E. 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171–189 *in* M. Festa-Bianchet and M. Apollonio, editors. Animal behavior and wildlife management. Island, Washington, D.C., USA.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Van Sickle, W. D., and F. G. Lindzey. 1992. Evaluation of road track surveys for cougars (*Felis concolor*). Great Basin Naturalist 52:232–236.

West, N. E., editor. 1983. Intermountain salt-desert shrubland. Pages 375–397 *in* Temperate deserts and semi-deserts. Vol. 5: Ecosystems of the world. Elsevier, Amsterdam, Netherlands.

Wielgus, R. B., and F. L. Bunnell. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. Biological Conservation 93:145–154.

Wolfe, M. L., D. M. Choate, and D. C. Stoner. 2004. USU/UDWR statewide cougar study—final report. Utah Division of Wildlife Resources, Salt Lake City.

Associate Editor: Ruggiero.

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Research Article

Evaluation of Harvest Indices for Monitoring Cougar Survival and Abundance

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ABSTRACT Harvest indices are used by state wildlife management agencies to monitor population trends and set harvest quotas for furbearer species. Although harvest indices may be readily collected from hunters, the reliability of harvest indices for monitoring demography and abundance of the harvested species is rarely examined, particularly amongst large carnivores. The overall objective of this study was to assess whether cougar (*Puma concolor*) harvest statistics collected by wildlife managers were correlated with changes in cougar demography, mainly survival rates and abundance. We estimated key demographic parameters for 2 cougar populations in Utah over 17 years during which we monitored 235 radio-collared cougars. We then compared these demographic parameters to harvest statistics provided by the Utah Division of Wildlife Resources over the same time period for the Oquirrh-Stansbury (lightly harvested population) and Monroe (heavily harvested population) harvest management units. In the Oquirrh-Stansbury unit, the percent of harvested cougars >6 years old was positively correlated with annual survival, indicative of a population experiencing several years of high survival resulting in an older age structure. Percent of permits filled and cougar abundance were also significantly correlated, suggesting higher hunting success with increased density. In the Monroe management unit, the annual percent of permits filled was correlated with changes in overall annual survival and male and female annual survival. Of utmost importance, pursuit success (cougars treed/day) increased with the number of cougars on the unit suggesting that pursuit indices may be an informative metric for wildlife managers to determine cougar population trends. Because both management units were subjected to contrasting mortality regimes, results provided by this assessment could potentially be applied to additional management areas sharing similar ecological characteristics and harvest metrics. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS abundance, competing risks, exploitation, harvest statistics, management, mortality, *Puma concolor*, survival.

Knowledge of the status of a carnivore population is essential for the development and implementation of an effective management plan (Ginsberg 2001, Pollock et al. 2012). Carnivores are often managed through regulated sport hunting to maintain viable populations (Sillero-Zubiri and Laurenson 2001, Keefover-Ring 2005), and reduce impacts of predation on their principal prey species and domestic livestock (Treves and Karanth 2003, Anderson et al. 2010, Loveridge et al. 2010). Management agencies often face the difficulty of opposing demands for more effective carnivore control to protect human safety, big game populations, and domestic livestock, and the demand for additional carnivore-hunting opportunities by sportsmen and outfitters and even societal demands for protection from exploitation (Sillero-Zubiri and Laurenson 2001, Anderson et al. 2010, Funston et al. 2013).

Given their large spatial requirements, low densities, and elusiveness, the management of large carnivores is often challenging because of the difficulties in estimating vital rates and population abundance (Gese 2001, Pollock et al. 2012). Cougar (*Puma concolor*) management nevertheless depends on the ability to monitor demographic responses to changing policies and management actions (Anderson et al. 2010). Unfortunately, state and provincial wildlife agencies are often required to make management decisions without the demographic information needed to monitor and maintain sustainable cougar population levels from one harvest season to the next (i.e., adaptive harvest management) because this information is often unavailable. Frequently, harvest

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composition statistics (e.g., age structure and sex composition) are used in lieu of measured demographic variables of population performance and abundance (Whittaker and Wolfe 2011). Harvest data alone is not sufficient for estimation of population size but rather should be used in conjunction with additional demographic data such as annual survival rates (Erickson 1982, Kolenosky and Strathearn 1987, Lindzey 1987, Rolley 1987, Chilelli et al. 1996). The question arises as to whether harvest statistics and harvest composition are reasonable approximations of changes in demographic performance (e.g., survival) and population abundance over time.

Of all demographic estimates, wildlife managers are most interested in monitoring animal abundance because annual changes in abundance measure the net balance among births, immigrants, deaths, and emigrants (BIDE), and indicate whether there is a surplus that can be sustainably harvested from year to year. Because a complete census is never possible, abundance must be estimated using appropriate methods that can account for imperfect detection and even multiple counting of individuals. Indeed, a number of approaches have been proposed for estimating cougar abundance and associated densities (Van Dyke et al. 1986, Smallwood and Fitzhugh 1995, Choate et al. 2006), but all have logistic limitations and statistical assumptions that are difficult to meet in a field setting.

When abundance becomes too difficult to accurately estimate, attention is sometimes transferred to the BIDE vital rates that determine abundance to monitor population trends rather than abundance per se. Immigration and emigration may play a large role in the change of male cougar abundance (Robinson et al. 2008), but in the female-limiting component of the population attention should be focused on reproductive success and survival (Lambert et al. 2006). Regardless of whether the focus is on the male or female component, cause-specific mortality analyses can provide deeper insight into the factors underlying management-relevant changes in survival and population dynamics (e.g., hunting vs. vehicle collisions).

The Utah Division of Wildlife Resources (UDWR) currently uses harvest rate, percent females in the harvest, and number of cougars treed per day to set the following years harvest quotas (Utah Cougar Advisory Group 2011). The cougars treed per day can be thought of a catch-per-unit-effort estimator (Choate et al. 2006). Although there was no significant relationship between cougars treed/day and the size of 2 cougar populations monitored for 6 years (Choate et al. 2006), the UDWR incorporates this index in their formula to determine harvest levels. We calculated estimates of key demographic parameters from 2 cougar populations that were intensively monitored in Utah for 17 years, and compared these estimates to harvest statistics provided by the UDWR over the length of the study period. Cougars in the Oquirrh-Stansbury cougar management unit (OSCMU) were primarily exposed to non-hunting anthropogenic sources of mortality and cougars in the Monroe cougar management unit (MCMU) were mostly influenced by hunting mortality. Our objective was to assess the correlations between currently used harvest statistics and independently derived population parameters within the OSCMU and MCMU.

STUDY AREA

We examined cougar populations on the OSCMU and MCMU, located in the Great Basin and Colorado Plateau ecoregions, respectively, in Utah. Mountain ranges in these ecoregions were surrounded by desert basins and formed a basin and range landscape. Annual precipitation ranged from 60 cm to 120 cm in the higher elevations to 15–20 cm in the desert basin regions with most of the precipitation arriving as snow in January and February (Moller and Gillies 2008). The Oquirrh-Traverse Mountains were dominated by Gambel oak (*Quercus gambelii*), sagebrush (*Artemisia* spp.), and Utah juniper (*Juniperus osteosperma*), whereas Monroe Mountain was dominated by pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) woodlands.

The OSCMU was located in north-central Utah on the eastern edge of the Great Basin (40.5°N, 112.2°W). The Oquirrh Mountains measured >950 km^2, but the study area was focused on a 500-km^2 area encompassing the northeastern slope on properties owned and managed by the Utah Army National Guard (Camp Williams) and the Kennecott Utah Copper Corporation. The site was bounded on the north by the Great Salt Lake and on the east by the Salt Lake Valley. Approximately, 55% of the study area was under the jurisdiction of the Bureau of Land Management (BLM), with the remainder held by individuals, grazing associations, mining companies, and the military. The study area was situated within the larger OSCMU, but both properties (Camp Williams and Kennecott) were closed to the public and cougar hunting was prohibited. Although radio-collared cougars leaving those properties were legally protected within the management unit, they were susceptible to poaching, depredation control, trapping, and road kill. Thus, this population was considered to be semi-protected.

Monroe Mountain comprised part of the Sevier Plateau in south-central Utah (38.5°N, 112°W). The study area measured approximately 1,300 km^2, and formed the central part of the Fishlake National Forest. Additional landholders included the BLM, the State, and various private interests. The study area was within the MCMU, where cougars were managed for sustainable hunting opportunities. Other carnivores present included bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), which were both subject to trapping pressure. Resource use included livestock grazing (cattle, sheep), logging, fossil fuel exploration, and off highway vehicle recreation (e.g., all terrain vehicles). Stoner et al. (2006) provide a more detailed description of the study areas.

METHODS

Cougar Harvest in Utah

Nearly all cougars harvested in Utah are taken with the aid of dogs (Utah Cougar Advisory Group 2011). An individual hunter is restricted to holding either a limited entry permit or a harvest objective permit per season, and must wait 3 years to reapply once they acquire a limited-entry permit. The bag limit is 1 cougar/season, and kittens and females accompanied by young are generally protected from harvest. Currently, the cougar hunting season runs from late November through late May on both limited entry and most harvest objective units. Some units are open year-round and some have earlier or later opening dates. Pursuit (chase or no-kill) seasons provide additional recreational opportunities over most of the state. The pursuit season generally follows the hunting season, but specific units have year-round pursuit and a few units are closed to pursuit (Utah Cougar Advisory Group 2011).

We used information covering 1996–2012 that was published in the most recent Utah Cougar Annual Report (Utah Division of Wildlife Resources 2012), which collated information for a number of harvest and pursuit statistics used by UDWR managers from the OSCMU and MCMU; reporting of each cougar harvested is legally mandated. We first focused on the 3 indices used to monitor cougar population trends and guide management in Utah: percent females in harvest, number of cougars treed per day, and number of cougars harvested annually. We examined additional harvest indicators that were specific to each sex (i.e., annual no. harvested males, % of males in the harvest) and harvest indicators that pertained to age (i.e., proportion of cougars that were ≥ 6 years of age in the harvest, the mean age of harvested animals each year). Finally, we examined statistics related directly to harvest regulations (i.e., % of hunting permits filled each year, no. sport-harvested cougars, no. harvest permits allotted, including all limited entry, conservation, and conventional permits; Utah Division of Wildlife Resources 2012).

Field Methods

From January 1996 to June 2012, we conducted capture efforts during winter (Dec to Apr). We pursued cougars with trained hounds, and then immobilized each cougar with a combination of ketamine hydrochloride (10 mg/kg) and xylazine hydrochloride (2 mg/kg; Fort Dodge Animal Health, Fort Dodge, IA) following recommendations in Kreeger (1996). We sexed, weighed, measured, ear tattooed, and microchipped (AVID, Norco, CA) each individual. For aging the animal, we extracted a vestigial premolar (P2) for aging with cementum annuli, a field estimate of age using gum-line recession (Laundré et al. 2000), and tooth wear (Ashman et al. 1983). We fitted all adult (>24 months) and sub-adult (12–24 months) cougars with a very high frequency (VHF) radio-collar (Advanced Telemetry Systems, Isanti, MN) or a global positioning system (GPS) collar (i.e., Televilt Simplex, Lindesberg, Sweden; LoTek 4400S, Newmarket, Ontario, Canada). We located cougars with a VHF collar twice a month with aerial or ground telemetry (Mech 1983); we attempted to acquire locations of cougars with a GPS collar every 3 hours. We marked kittens (0–12 months) that were too small to wear a radio-collar with a microchip (AVID) and tattooed their ears with a unique identification number. We released all animals at the capture site. For each population, data collection was based on radio-telemetry information collected between 1 January 1996 and 30 June 2012. Animal capture and handling procedures were conducted in accordance with Utah State University Institutional Animal Care and Use Committee standards (approval no. 937-R).

The Utah cougar hunting season commenced in mid-November and continued to the end of May each year. However, most of the harvest occurred during a 4-month period when snow was on the ground (Dec to Mar). We used individual locations within the MCMU collected after 1 March 1996, directly after the harvest season, so we would not split a harvest season across an analysis year and to maximize use of available data (the first individuals were marked in Jan 1996); similarly, the study began in the OSCMU on the 1 March 1997.

The fate of most marked individuals was known with the exception of 11 cases for which we could not ascertain an emigration or death status. We ascertained emigration status and radio-collar failures for 35 and 47 individuals in the OSCMU and the MCMU, respectively (Table 1). Kittens that did not survive to age 1 were not included in the analyses because their fates were dependent on the fate of their mothers. However, kittens that survived to their first birthday and remained in the unit where they were initially marked were included in the analyses; through left-truncation, we included such individuals from age 1 onward in all analyses.

We determined the causes of mortality through visual inspection and necropsy of carcasses (Stoner et al. 2006). When we could not determine cause of death in the field, we submitted the carcass to the Utah Veterinary Diagnostics Lab (Logan, Utah) for a detailed necropsy. Precision of mortality dates varied: with GPS-collared and hunter-harvested animal mortality, dates were known to within 1 day, whereas we estimated dates for animals wearing conventional VHF radio-collars using the midpoint between the last live signal and the detection date of the first mortality signal (+/− 15 days).

Demographic Analyses

Classical survival models used in human demography (Kleinbaum and Klein 2005) are appropriate for estimating survival trajectories when individuals are followed from entrance into the study until death (Murray et al. 2010, Aubry et al. 2011, Sandercock et al. 2011). Various extensions to the non-parametric Kaplan–Meier (Kaplan and Meier 1958) estimator, such as the Cox Proportional Hazard model (CPH; Cox 1972), further allow identification of the measurable (i.e., observed) covariates associated with patterns in survival trajectories. We used semi-parametric CPH models because they do not require assumptions about the shape of the underlying mortality hazard (the force of mortality) over life. Rather, each covariate within the model is assumed to act multiplicatively (i.e., proportionally) on the baseline mortality hazard at each time step (Bradburn et al. 2003): $h_i(t) = h_0(t)^* \exp(\beta_i X_i)$ such as where h_0 refers to the baseline hazard (i.e., the hazard's value when all covariate values are null), X denotes a vector of

Table 1. Sex- and location-specific deaths by cause of mortality for radio-collared cougars in the Oquirrh-Stansbury Cougar Management Unit (OSCMU), 1997–2012, and in the Monroe Cougar Management Unit (MCMU), 1996–2012, Utah, USA.

	OSCMU						MCMU					
	Total		Females		Males		Total		Females		Males	
Mortality cause	*n*	% of total mortality	*n*	% of total mortality	*n*	% of total mortality	*n*	% of total mortality	*n*	% of total mortality	*n*	% of total mortality
1 Hunting	16	32.0	5	17.2	11	52.4	72	67.9	28	53.8	44	81.5
2 Poaching	1	2.0	1	3.4	0	0.0	6	5.7	4	7.7	2	3.7
3 Depredation control	1	2.0	0	0.0	1	4.8	7	6.6	5	9.6	2	3.0
4 Road kill	3	6.0	3	10.3	0	0.0	0	0.0	0	0.0	0	0.0
5 Capture mortality	1	2.0	1	3.4	0	0.0	4	3.8	3	5.8	1	1.8
6 Intra-specific strife	11	22.0	6	20.7	5	23.8	12	11.3	8	15.4	4	7.4
7 Predation attempt	5	10.0	3	10.3	2	9.5	3	2.8	2	3.8	1	1.8
8 Injury, starvation	12	24.0	10	34.5	2	9.5	2	1.9	2	3.5	0	0.0
Total mortality	50		29		21		106		52		54	
Anthropogenic (1–5)	22	44.0	10	34.5	12	57.1	89	83.9	40	76.9	49	90.7
Harvest (1)	16	32.0	5	17.2	11	52.4	72	67.9	28	53.8	44	81.5
Natural only (6–8)	28	56.0	19	65.5	9	42.9	17	16.0	12	23.1	5	9.3

covariates such as $X = (X_1, X_2, \ldots X_i)$, and t denotes time (in our case, time elapsed since marking; Murray and Patterson 2006). We conducted all analyses in R (version 2.15.0, Development Core Team 2012).

Standard survival estimators consider the elapsed time from some origin until the occurrence of death or failure. If ≥ 1 type of end point is of interest, these end points are called competing risks (Geskus 2011). With radio-telemetry data, a competing risk analysis can be used to attain unbiased estimates of cause-specific mortality, whereas standard tabular presentations of percentage representations for cause-of-death data are inherently biased (Heisey and Patterson 2006) but can nevertheless be useful to visualize the cause of death data. Because specific causes of mortality might be more reliable indicators of harvest statistics used to guide cougar management, we considered 2 dichotomies in mortality estimates. We estimated annual cause-specific mortality at each study area for human harvest versus all other causes of death, or all anthropogenic causes of mortality (i.e., harvest, poaching, depredation control, road kill, capture-related mortality) versus natural mortality agents (i.e., intra-specific strife, injury during predation attempt) using the R package wild1 (Sargeant 2011, Wolfe et al. 2015). For the purpose of this assessment, we were specifically interested in estimating annual mortality from hunting exclusively (i.e., the harvest rate $\hat{h}_t$) because it should be most closely linked to harvest statistics if such relationships exist.

We used a minimum abundance index or population estimate for each management unit that included the number of adults and independent sub-adults (i.e., no longer with their mother) based on all captures, radio-telemetry, tracking, and mortality data (Logan and Sweanor 2001, Choate et al. 2006, Cooley et al. 2009). We also calculated corresponding densities based on the size of each unit (adult and independent sub-adult cougars per 100 km^2).

We used Spearman's rank correlation coefficient (r) to examine the relationships between the harvest indices collected by the UDWR and the independently derived demographic rates (Zar 1999). Correlation coefficients range from -1 (i.e., perfect negative correlation) to $+1$ (i.e., perfect positive correlation), where a correlation of 0 indicates there is no relationship between the 2 variables. We used the standard error of a correlation coefficient to determine the confidence intervals around a true correlation of 0, and t-tests to test the null hypothesis that the true correlation was 0 (Zar 1999). For each analysis, we reported the correlation coefficient and associated P-value and considered correlation coefficients with P-values ≤ 0.10 significant.

RESULTS

Overall, demographic analyses were based on 235 marked individual cougars (MCMU: $n = 148$, 66 M and 82 F, 37 sub-adults and 111 adults; OSCMU: $n = 87$, 32 M and 55 F, 24 sub-adults and 63 adults). Seventeen individuals died of natural mortality and 89 of anthropogenic causes in MCMU. In the OSCMU, 28 individuals died of natural death versus 22 of anthropogenic causes (Table 1). In the MCMU, 72 individuals were harvested and 34 individuals died of non-harvest mortality (i.e., all other causes of death). Within the OSCMU, 16 individuals were harvested and 34 individuals died of other causes (Table 1). An additional 82 cougars were right-censored because they were still alive at the end of the study or because they emigrated from the management unit (47 in MCMU and 35 in OSCMU; i.e., the data they provided while on the study area was used until they emigrated out of the study area).

We calculated an abundance index akin to a minimum population abundance estimate for each unit (Fig. 1). In the OSCMU, this index fluctuated between 10 and 20 adults and independent subadult cougars over time, with a corresponding density that ranged from 2 to 4 adult and independent subadult cougars/100 km^2 (Fig. 1). In the MCMU, this index ranged from 10 to 40 adult and independent subadults, for a corresponding density of 1 to 3.5 adult and independent subadult cougars/100 km^2 (Fig. 1).

Unit-Specific Demographic Estimates and Harvest Statistics

Annual survival fluctuated over time in the OSCMU (Fig. 2A) and MCMU (Fig. 2B). Notably, in 1999 and 2012

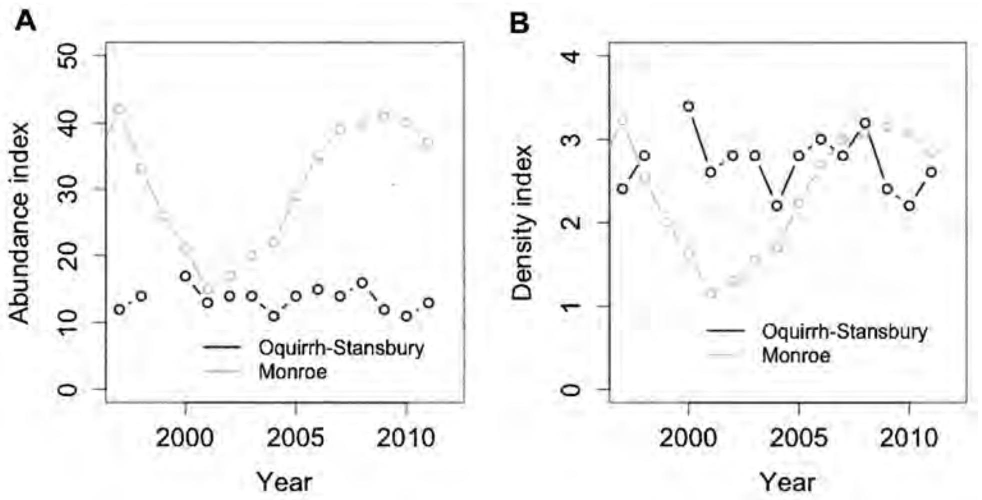

Figure 1. Changes in A) cougar abundance and B) associated density index (cougars/100 km^2), for adult and independent subadult cougars on the Oquirrh-Stansbury (1997–2012) and the Monroe (1996–2012) study areas, in Utah, USA.

annual survival in the MCMU was low (Fig. 2B). Male survival was consistently lower than female survival in both units, and survival was higher in the OSCMU compared to MCMU (Fig. 2).

In the OSCMU, the primary cause of death in males was harvest (Table 1, Fig. 3), and natural causes (injury, starvation) in females (Table 1). Intra-specific strife was also an important influence of overall mortality, equally distributed between females and males (Table 1). Individuals between ages 2 and 6 primarily died from harvest mortality or other sources of anthropogenic mortality (e.g., car collision, Wildlife Services removals). For individuals that died of non-harvest mortality, females died at a later age on average than males (Wolfe et al. 2015). Over the span of the MCMU, 67% of all individuals that died were harvested (Table 1, Fig. 3). All age-classes were subjected to harvest and non-harvest causes of mortality, and more individuals died between 2 and 4 years of age compared to any other age class.

Generally, in the OSCMU we observed a decrease in harvest indices over time. In the MCMU, however, we observed an increase in harvest indices over the last few years of the study. Specifically, increases were observed in the total harvest and in the percentage of harvest permits filled since 2006, along with an increase in the percentage of cougars harvested that were >6 years old and in the number of females harvested since 2009. The number of cougars treed/day (i.e., pursuit statistic) and mean age at harvest fluctuated over time with an increase in the pursuit statistic and harvest pressure since 2004 in the MCMU.

Correlation of Demographic Estimates and Harvest

We found significant correlations between several harvest statistics and demographic estimates for the OSCMU (Table 2) and MCMU (Table 3). In the OSCMU, we found the percent of permits filled and the minimum abundance index were positively correlated (Fig. 4A, Table 2). Further, the percent of individuals in the harvest

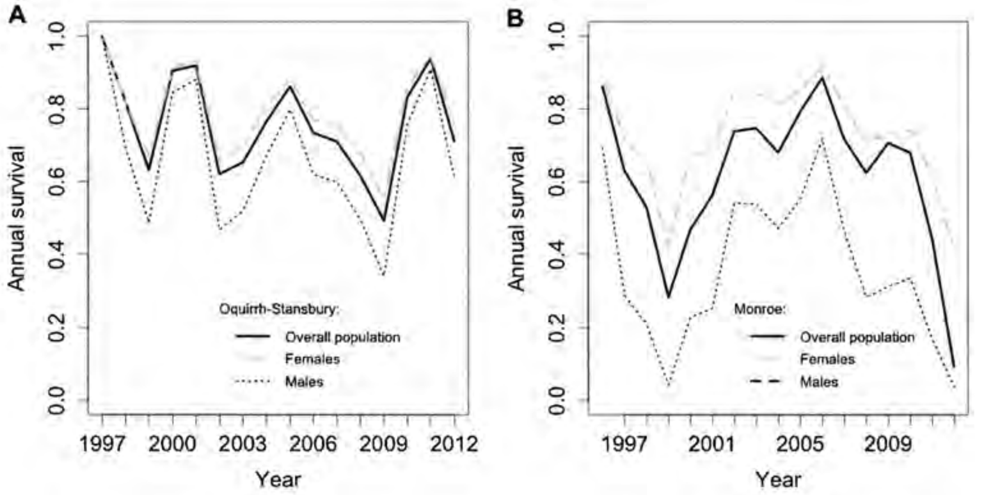

Figure 2. Changes in overall and sex-specific annual survival for radio-collared cougars in the A) Oquirrh-Stansbury and B) Monroe study areas in Utah, USA from 1997 to 2012 and 1996 to 2012, respectively.

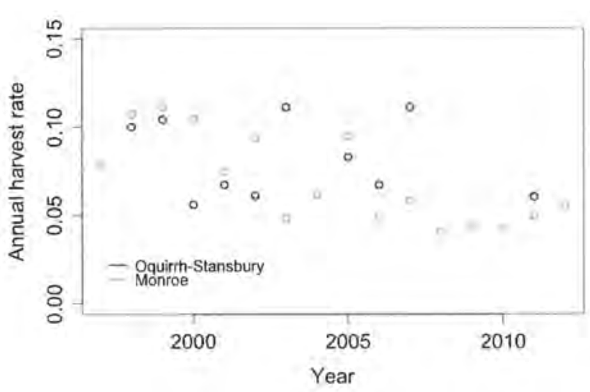

Figure 3. Changes in annual harvest mortality estimates over time in the Oquirrh-Stansbury and Monroe study areas Utah, USA from 1997 to 2012 and 1996 to 2012, respectively.

>6 years old was positively correlated with annual survival, annual male survival, and annual female survival (Fig. 4B–D, Table 2). In the MCMU, which experienced greater hunting pressure, overall annual harvest mortality was principally influenced by male annual harvest mortality (Fig. 5A, Table 3). We also observed a negative relationship between the annual number of females in the harvest and annual survival (Fig. 5B, Table 3). Additionally, we found a negative correlation between the annual proportion of females in the harvest and annual survival (Fig. 5F, Table 3). Further, percentage of permits filled each year was positively correlated with overall annual survival, annual male survival, and annual female survival (Fig. 5, Table 3). We detected a positive relationship between the number of cougars treed/day and the annual abundance index (Fig. 5G, Table 3), suggesting that pursuit success increased with the number of cougars on the unit.

DISCUSSION

Monitoring survival and determining the abundance of large carnivores is a daunting task for many wildlife agencies. Being able to use indirect measures of abundance to monitor changes in population size and survival (i.e., harvest) has routinely been used for large carnivores and cougars in particular, for several decades (Beausoleil et al. 2008, Whittaker and Wolfe 2011). However, knowing the relationships between these indirect measures or harvest indices and actual demographic parameters such as survival and population abundance requires long-term data collected with consistent field methodologies.

Even though intense harvest in the MCMU was a potential concern for sustainable management of cougars in this region, cougar densities assessed from the marked population indicated that densities rebounded and have been maintained at 3 adult cougars/100 km^2 over the last few years (Fig. 1). Immigration was a factor that we were not able to quantify, but the age structure indicated that an influx of cougars since 2006 has likely compensated for increased removal of cougar residents through hunting. Additional data on cougar movement in and out of the study area would be needed to quantify this influx, and the role immigration plays in maintaining stable dynamics (Sweanor et al. 2000, Robinson et al. 2008, Cooley et al. 2009). Abundance estimates obtained from the results of genetic mark-recapture procedures (Long et al. 2008, Kelly et al. 2012), and more sophisticated analytical methods such as dead recovery multi-state analysis (Koons et al. 2014) could help improve abundance estimates in the future. However, the question of whether a density of 3 adult cougars/100 km^2 is the target density that state wildlife agencies should manage for remains unresolved.

Densities ranged from 2 to 4 adult and independent subadult cougars/100 km^2 in the OSCMU and 1 to 3.5 adult and subadult cougars/100 km^2 in the MCMU (Fig. 1). According to the 2009–2021 Utah Cougar Management Plan (Utah Cougar Advisory Group 2011), high quality habitat was assigned a density range of 2.5–3.9 adult and subadult cougars/100 km^2, medium quality habitat was 1.7–2.5 adult and subadult cougars cougars/100 km^2, and low quality habitat was 0.26–0.52 adult and subadult cougars cougars/100 km^2. According to these standards, the OSCMU and MCMU cougar populations would be classed as high quality habitat. Because cougars have large home ranges, these numbers would be valid in locations where cougar home ranges are not constrained by human development and encroachment. This is not the case in the OSCMU, and might not hold true in the MCMU either.

Table 2. Correlations matrix between demographic parameters and harvest statistics in the Oquirrh-Stansbury Cougar Management Unit, 1997–2012, Utah, USA. Significant correlations ($P < 0.1$) are indicated with an asterisk.

		Harvest statistics							
Demographic parameter		**Sport harvest**	**Male sport harvest**	**Female sport harvest**	**% permits filled**	**% harvest >6 years**	**% females harvested**	**No. cougars treed/day**	**Mean age of harvest**
Annual survival	*r*	0.192	0.052	0.329	0.063	0.552*	0.313	−0.093	0.267
	P	0.475	0.847	0.213	0.816	0.026*	0.237	0.742	0.318
Annual male survival	*r*	0.131			0.013	0.546*	0.307	−0.123	0.286
	P	0.627			0.961	0.028*	0.248	0.663	0.282
Annual female survival	*r*	0.132			0.029	0.550*	0.293	−0.099	0.268
	P	0.625			0.913	0.027*	0.271	0.726	0.315
Annual abundance index	*r*	0.218	0.284	0.104	0.600*	−0.199	−0.337	0.260	−0.358
	P	0.453	0.325	0.723	0.023*	0.496	0.238	0.390	0.209
Annual harvest mortality	*r*	−0.435	−0.393	−0.396	−0.433	−0.441	−0.002	0.062	−0.460
	P	0.209	0.261	0.258	0.211	0.202	0.996	0.864	0.181

Table 3. Correlations matrix between demographic parameters and harvest statistics in the Monroe Cougar Management Unit, 1996–2012, Utah, USA. Significant correlations ($P < 0.1$) are indicated with an asterisk.

		Harvest statistics							
Demographic parameter		**Sport harvest**	**Male sport harvest**	**Female sport harvest**	**% permits filled**	**% harvest >6 years**	**% females harvested**	**No. cougars treed/day**	**Mean age of harvest**
Annual survival	*r*	−0.237	0.035	−0.419*	0.630*	0.034	−0.453*	0.058	0.056
	P	0.359	0.893	0.094*	0.009*	0.896	0.067*	0.836	0.831
Annual male survival	*r*	−0.275			0.659*	−0.065	−0.370	−0.193	−0.050
	P	0.275			0.050*	0.804	0.144	0.490	0.849
Annual female survival	*r*	−0.262			0.679*	0.030	−0.374	−0.131	0.041
	P	0.310			0.004*	0.908	0.139	0.641	0.875
Annual abundance index	*r*	0.308	0.249	0.248	−0.013	0.038	0.017	0.747*	0.149
	P	0.246	0.353	0.353	0.961	0.888	0.951	0.002*	0.581
Annual harvest mortality	*r*	0.370	0.463*	0.119	−0.393	−0.040	−0.046	−0.355	−0.289
	P	0.144	0.061*	0.648	0.132	0.880	0.861	0.193	0.260

Specifically, dispersing cougars are potentially exposed to car collisions and Wildlife Services removal. Also, demographic stochasticity alone could lead to small populations of cougars in both locations. We suggest that the UDWR consider re-examining their density and habitat quality indices for future cougar management, and the size of management units for a species whose populations are predominantly regulated by source-sink dynamics (Robinson et al. 2008, Cooley et al. 2009).

The most intuitive finding of our analysis was the positive correlation between the percentage of permits filled and the minimum abundance index in the OSCMU. This was a fairly simple relationship indicating that hunters were more successful when cougars were more abundant. The fraction of females in the harvest is arguably the statistic most widely used by managers to monitor changes in cougar populations (Cooley et al. 2011). However, our analysis revealed no significant correlation between this metric and either annual female survival or annual abundance in the OSCMU, possibly because this index combines a variable fraction of non-reproductive sub-adult females with adult females. Anderson and Lindzey (2005) noted that the sex ratio of harvested cougars alone is of limited value in identifying population change, but when combined with age structure, both provide a more reliable index to population change. This was substantiated by our findings that at least for the OSCMU population, the percent of the harvest >6 years was positively correlated with annual female survival. However, this metric generally served as a proxy for the age structure of the population and was likely indicative of a population that has experienced several years of high survival and a greater proportion of more fecund females in the population.

In the MCMU, overall annual harvest mortality was principally influenced by male annual harvest mortality, suggesting that males were more heavily targeted than females in the MCMU. We further observed a positive correlation between the percentage of permits filled and annual survival overall but also independently for both female

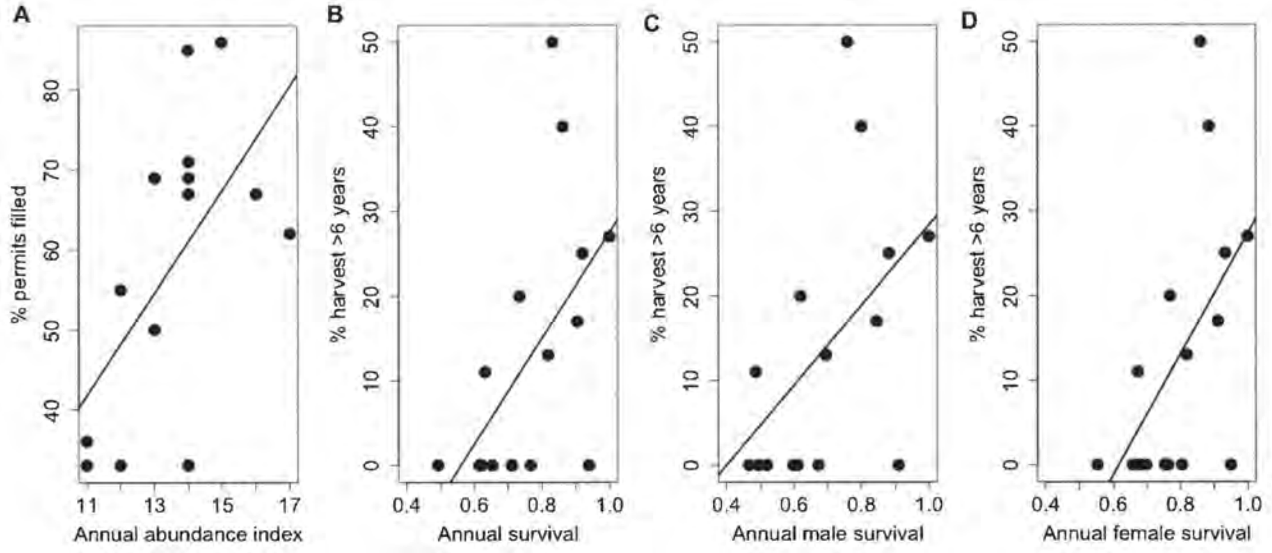

Figure 4. Significant correlations between A) % permits filled and annual abundance, B) % of harvested cougars >6 years old and overall annual survival, C) % of harvested cougars >6 years old and annual male survival, and D) % of harvested cougars >6 years old and annual female survival, for the Oquirrh-Stansbury Cougar Management Unit, 1997–2012, Utah, USA.

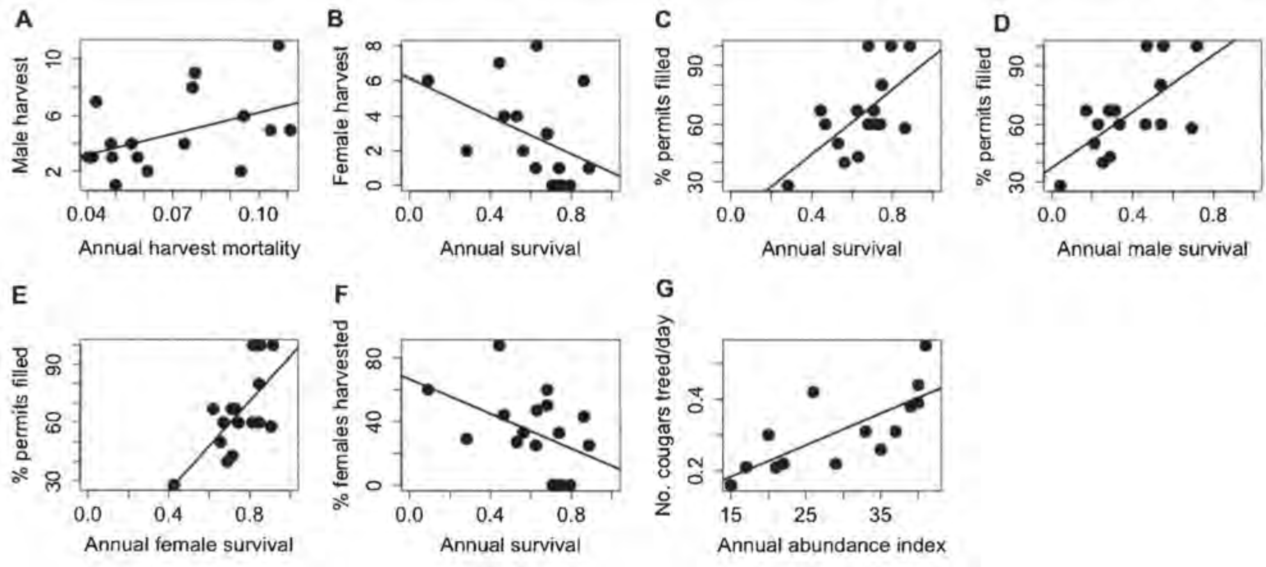

Figure 5. Significant correlations between A) male harvest rate and annual harvest mortality, B) female harvest and annual survival, C) % permits filled and overall annual survival, D) % permits filled and annual male survival, E) % permits filled and annual female survival, F) % females in the harvest and annual survival, and G) no. cougars treed/day and annual abundance for the Monroe Cougar Management Unit, 1996–2012, Utah, USA.

and male survival. This relationship indicates that hunters were more successful when annual cougar survival was high for the population as a whole, but also for females and males separately. The number of females harvested and the fraction of females in the harvest were negatively correlated with annual survival, suggesting that in this management unit, both statistics are relevant and their use is justified as the most widely used harvest index to monitor changes in cougar populations (Cooley et al. 2011). One of the more surprising results was the strong positive relationship between the number of cougars treed per day during the pursuit-season and the index of minimum annual cougar abundance on the MCMU. This index was arguably independent from harvest data because it is derived from the success of non-lethal pursuit permits. Choate et al. (2006) reported a weak ($P = 0.13$) correlation from the same unit that was derived in the same manner but for a much shorter time span (6 years). As discussed by Whittaker and Wolfe (2011), this pursuit index is a catch-per-unit-effort estimator, and although easily obtained, this index is subject to several assumptions including demographic and geographic independence and constant catchability throughout the period of data collection. The latter assumption may be unrealistic because it implies that cougars do not learn to avoid capture. Despite these limitations, the relatively low cost of obtaining this index via phone surveys of sportsmen warrants further investigation and refinement.

MANAGEMENT IMPLICATIONS

Using harvest statistics that are already commonly collected from hunters in the state of Utah to determine harvest quotas for cougars was justified by our analyses. Specifically, the total number of females harvested and the fraction of females in the harvest were negatively correlated with annual survival; managers are right to pay particular attention to these harvest statistics for monitoring cougar populations. In the MCMU, the percentage of permits filled was also a good proxy to changes in annual survival, annual female survival, and annual male survival. The highest correlation between cougars treed/day and the annual abundance of cougars suggests that pursuit indices may be an informative metric for wildlife managers to determine cougar population trends in intensely harvested management units. These harvest statistics may be suitable for cougar management units that have a similar hunting management regime as MCMU, with hunting being the predominant source of mortality.

In the OSCMU, the percentage of cougars in the harvest >6 years of age was correlated to overall annual survival, annual female, and male survival making them useful for monitoring changes in the demographics of cougar management units where harvest is not the only dominant cause of death (Wolfe et al. 2015). In such units, the percentage of permits filled tracked changes in annual cougar abundance, suggesting that this metric is a good indicator of population abundance in units that are not under intense harvest pressure.

Ideally, managers should also keep track of change in demographic rates, specifically survival and abundance, in key harvest management units that display contrasting harvest and mortality regimes. Our results illustrate the value of long-term data collection and suggest the possibility of expanding the scope of such comparisons to additional management units. Because the OSCMU and MCMU were subjected to contrasting mortality regimes (Wolfe et al. 2015), our results could be expanded to additional management units that share either the OSCMU or the MCMU characteristics. Ultimately, we suggest this analytical framework be extended to other harvested carnivore species for which harvest indices are available. When demographic information is available for certain harvest management units, correlations between harvest indices and demographic rates can be used to assess which harvest indices are better proxies to changes in survival, abundance, and population dynamics.

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LITERATURE CITED

Anderson, C., and F. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildlife Society Bulletin 33:179–188.

Anderson, C. R., F. Lindzey, K. H. Knopff, M. G. Jalkotzy, and M. S. Boyce. 2010. Cougar management in North America. Pages 41–54 *in* M. Hornocker and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Ashman, D. L., G. C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wickersham. 1983. The mountain lion in Nevada. Nevada Department of Wildlife, Carson City, USA.

Aubry, L. M., E., Cam, D. N. Koons, J.-Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. Journal of Animal Ecology 80:375–383.

Beausoleil, R. A., D. Dawn, D. A. Martorello, and C. P. Morgan. 2008. Cougar management protocols: a survey of wildlife agencies in North America. Pages 204–242 *in* D. Toweill, S. Nadeau, and D. Smith, editors. Proceedings of the 9th Mountain Lion Workshop, Idaho Game and Fish Department, Boise, USA.

Bradburn, M. G., T. G. Clark, S. B. Love, and D. G. Altman. 2003. Survival analysis Part II: Multivariate data analysis: an introduction to concepts and methods. British Journal of Cancer 89:431–436.

Chilelli, M. E., B. Griffith, and D. J. Harrison. 1996. Interstate comparisons of river otter harvest data. Wildlife Society Bulletin 24:238–246.

Choate, D. M., M. L. Wolfe, and D. C. Stoner. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34:782–799.

Cooley, H. S., K. D. Bunnell, D. C. Stoner, and M. L. Wolfe. 2011. Population management: cougar hunting. Pages 111–134 *in* J. A. Jenks, editor. Managing cougars in North America. Berryman Institute, Utah State University, Logan, Utah, USA.

Cooley, H. S., R. B. Weilgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society B Series 34:187–220.

Erickson, D. W. 1982. Estimating and using furbearer harvest information. Pages 53–65 *in* G. C. Sanderson, editor. Midwest furbearer management. Proceedings of 43rd Midwest Fish and Wildlife Conference, Wichita, Kansas, USA.

Funston, P. J., R. J. Groom, and P. A. Lindsey. 2013. Insights into the management of large carnivores for profitable wildlife-based land uses in African savannas. PloS One 8(3):e59044.

Gese, E. M. 2001. Monitoring of terrestrial carnivore populations. Pages 373–396 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, United Kingdom.

Geskus, R. B. 2011. Cause-specific cumulative incidence estimation and the fine and gray model under both left truncation and right censoring. Biometrics 67:39–49.

Ginsberg, J. R. 2001. Setting priorities for carnivore conservation: what makes carnivores different? Pages 498–523 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, United Kingdom.

Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. Journal of Wildlife Management 70:1544–1555.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Keefover-Ring, W. J. 2005. Mountain lions, myths, and media: a critical reevaluation of The Beast in the Garden. Environmental Law 35:1083–1095.

Kelly, M. J., J. Betsch, C. Wultsch, B. Mesa, and L. S. Mills. 2012. Noninvasive sampling of carnivores. Pages 47–69 *in* L. Boitani and R. A. Powell, editors. Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, United Kingdom.

Kleinbaum, D. G., and M. Klein. 2005. Survival analysis: a self-learning approach, second edition. Springer, New York, New York, USA.

Kolenosky, G. B., and S. M. Strathearn. 1987. Black bear. Pages 444–454 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wildlife furbearer management and conservation in North American. Ontario Ministry of Natural Resources, Toronto, Canada.

Koons D. N., R. F. Rockwell, and L. M. Aubry. 2014. Effects of exploitation on an overabundant species: the lesser snow goose predicament. Journal of Animal Ecology 83:365–374.

Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals Inc., Fort Collins, Colorado, USA.

Lambert, C. M., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

Laundré, J. W., L. Hernández, D. Streubel, K. Altendorf, and C. L. González. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

Lindzey, F. 1987. Mountain lion. Pages 657–668 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wildlife furbearer management and conservation in North American. Ontario Ministry of Natural Resources, Toronto, Canada.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Long, R. A., P. MacKay, W. J. Zielinski, and J. C. Ray, editors. 2008. Noninvasive survey methods for carnivores. Island Press, Washington, D.C., USA.

Loveridge, A. J., S. W. Wang, L. G. Frank, and J. Seidensticker. 2010. People and wild felids: conservation of cats and management of conflicts. Pages 161–195 *in* D. W. Macdonald and A. J. Loveridge, editors. Biology and conservation of wild felids. Oxford University Press, Oxford, United Kingdom.

Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, USA.

Moller, A. L., and R. R. Gillies. 2008. Utah climate. Second edition. Utah Climate Center Utah State University Research Foundation, Logan, USA.

Murray, D. L., and B. R. Patterson. 2006. Wildlife survival estimation: recent advances and future directions. Journal of Wildlife Management 70:1499–1503.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

Pollock, K. H., J. D. Nichols, and K. U. Karanth. 2012. Estimating demographic parameters. Pages 169–187 *in* L. Boitani and R. A. Powell, editors. Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, United Kingdom.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, H. S., R. B. Weilgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Rolley, R. R. 1987. Bobcat. Pages 672–681 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wildlife furbearer management and conservation in North American. Ontario Ministry of Natural Resources, Toronto, Canada.

Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology 80:244–258.

Sargeant, G. A. 2011. Wild1: R tools for wildlife research and management. R package version 2.15.0. Geological Survey Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA.

Sillero-Zubiri, C., and M. K. Laurenson. 2001. Interactions between carnivores and local communities: conflict or co-existence? Pages 282–312 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, United Kingdom.

Smallwood, K. S., and E. L. Fitzhugh. 1995. A track count for estimating mountain lion *Felis concolor californica* population trend. Biological Conservation 71:251–259.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.

Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management world-wide. Conservation Biology 17:1491–1499.

Utah Cougar Advisory Group. 2011. Utah Cougar Management Plan V.2.1. Utah Division of Wildlife Resources, Salt Lake City, USA.

Utah Division of Wildlife Resources. 2012. Utah Cougar Annual Report. Utah Division of Wildlife Resources, Salt Lake City, USA.

Van Dyke, F. G., R. H. Brocke, and H. G. Shaw. 1986. Use of road track counts as indices of mountain lion presence. Journal of Wildlife Management 50:102–109.

Whittaker, D. and M. L. Wolfe. 2011. Assessing cougar populations. Pages 71–110 *in* J. A. Jenks, editor. Managing cougars in North America. Berryman Institute Utah State University, Logan, USA.

Wolfe, M. L., D. N. Koons, D. C. Stoner, P. Terletzky, E. M. Gese, D. M. Choate, and L. M. Aubry. 2015. Is anthropogenic cougar mortality compensated by changes in natural mortality? Insight from long-term studies. Biological Conservation 182:187–196.

Zar, J. H. 1999. Biostatistical analysis, fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Associate Editor: Barbara Zimmermann.

FINAL REPORT

Federal Aid in Wildlife Restoration Project W-131-R

A STUDY OF BLACK BEAR ECOLOGY IN NEW MEXICO WITH MODELS FOR POPULATION DYNAMICS AND HABITAT SUITABILITY

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EXECUTIVE SUMMARY

During the late 1980's and the early 1990's, interpretation of New Mexico black bear (*Ursus americana*) harvest data was stymied by the realization that increasing, stable, and decreasing population trend were all plausible explanations for observed changes in harvest data. Various interest groups, favoring different interpretations of population trend, argued for liberalizing or limiting hunting regulations as justified by the data. Clearly, additional information was needed to interpret these data and to determine the status of New Mexico bear populations.

In 1991, responding to this need for more scientific information, the New Mexico State Game Commission instructed the New Mexico Department of Game and Fish (NMDGF) to conduct a black bear study with funding from the NMDGF and the Federal Aid in Wildlife Restoration program. Research was initiated in 1992 with an overall goal to study the ecology and population dynamics of black bears for developing methods and analytical tools to help estimate and predict trends in population size and structure in New Mexico, as influenced by human-caused mortality and environmental variation.

The study involved 2 related efforts: field investigations and population modeling including harvest data evaluation. The first component was an 8-year, field-based investigation of bear ecology within 2 distinct study areas situated in prime bear habitat. To specifically address the effect of hunting on population dynamics, 1 study area was closed to hunting for the majority of the study period. Primary objectives of the field study were to estimate black bear reproductive and survival rates, especially as related to mast production and human-caused mortality. Another primary objective was to validate the cementum annuli method for aging bears in New Mexico. Secondary objectives were to examine patterns of denning, home range, movements, habitat use, and population density between study areas and among sex-age categories. Combining all relevant data, the final objective was to extrapolate study area characteristics to identify suitable habitat across New Mexico using a Geographic Information System.

The second component involved analyses of existing NMDGF harvest data and development of an analytical tool for understanding bear population dynamics. Primary objectives were to determine relationships between the harvest sample and the sex-age composition of study populations, and to determine relationships among weather variables, mast production, and bear population characteristics. Using all relevant information, the final objective was to develop a population/environmental/hunt model and to integrate the model into management application.

This report chronicles results of this 8-year study, which represents the first concerted effort to understand New Mexico black bear ecology. We also

discuss applications of the existing tools and the new tools based on this research to black bear management in New Mexico.

We conducted field investigations on 2 study areas. The Northern Study Area (NSA) was located in the Sangre de Cristo Mountains of northern New Mexico. The NSA was approximately 310 km^2 and was comprised of private and state lands. It was adjacent to the towns of Eagle Nest and Ute Park, and about 6 km from Cimarron. The Southern Study Area (SSA) was located in the Mogollon Mountains of west-central New Mexico. The SSA was approximately 423 km^2 and was encompassed within the Gila National Forest. It was remote, with the closest towns of Reserve, Glenwood, and Mogollon, located 3-16 km away.

Field data were collected using capture, den investigation, and radio-telemetry techniques. We captured bears using foot snares or culvert traps and chemically immobilized most individuals. Approximate age of bears was estimated from dental characteristics and size. A vestigial premolar tooth was extracted from bears ≥1 year old for age determination using cementum annuli counts. We marked each bear with numbered, colored eartags and tattooed the same number on an inner, upper lip. We placed radio-transmitters on all females, on adult males as needed to maintain a sample of about 10 individuals, and on younger bears as needed for assessing population attributes. We monitored radio-transmittered bears from fixed-wing aircraft on a 14-day schedule during the active season. We visited dens of radio-transmittered bears to ascertain their reproductive status and change or refit collars as necessary. Weights and other measurements were obtained from all bears when possible.

Between September 1992 and June 2000, we captured 300 bears (103 females, 195 males, 2 unknown sex) 517 times, and observed 339 bears in dens (178 females, 137 males, 24 unknown sex) on 680 occasions. We placed 409 radio-transmitters on 316 bears (181 females, 135 males), and obtained 5,723 radio-telemetry locations.

Reproductive data were obtained during 268 den investigations of 80 female bears 4-27 years old. The minimum observed age of first litter production was 4 years old. Mean age at production of the first litter was 5.7 years and most females (73%) produced their first litter either at age 5 or 6 years. Natality of female bears ≥4 years old was 0.77 cubs/female/year and percent of females with cubs was 43%. Among previously reproductive females, natality was 1.4 cubs/female/year and percent of females with cubs was 77% (n = 112). Litter size ranged from 1-3 cubs and mean litter size was 1.8 cubs (n = 115). Observed litter interval ranged from 1-3 years and mean litter interval was 1.8 years (n = 69). Overall cub survival rate for 148 individual cubs from 82 litters was 55%. Recruitment of females ≥5 years old was 0.40 yearlings/female/year and percent of females with yearlings was 27% (n = 232). Recruitment of previously reproductive females was 0.53 yearlings/female/year and percent of females with yearlings was 35% (*n* = 175).

Reproductive success was evaluated on the basis of mast production by 10 surveyed species. Acorn (*Quercus* spp.) crop failure had the greatest influence on reproduction and juniper (*Juniperus* spp.) berry failure had a secondary effect. Mast failure was associated with decreased natality, cub survival, and recruitment. Neither natality nor recruitment varied following poor to good mast production, suggesting only a minimum threshold of quality food is needed for successful reproduction. Documenting annual mast production, especially the occurrence and frequency of oak failures, may be an effective index to bear reproductive success. During 1999-2000, NMDGF officers subjectively evaluated mast production statewide. Evaluations were highly correlated with our survey results, indicating subjective criteria were adequate to distinguish variation in mast production.

Observed annual survival rates for adult and subadult females were above 90%, and rates of adult and subadult males were above 80% (*n* = 591 bear-years). Most mortality of adults and subadults was human-caused, including hunter kills, depredation kills, illegal kills, and automobile kills. Observed yearling survival was variable, ranging from 75%-97% by sex and study area (*n* = 72). Among yearlings, most mortality was from natural causes, but human-caused mortality also was observed.

Among 179 bears observed on both study areas, observed den entrance dates ranged from 25 September-7 February. The majority of bears entered dens between mid October and mid November. Mean entrance date of pregnant females was 29 October, while that of all other bears was 6 November. Among 177 bears, observed den emergence dates ranged from 21 March-5 June. Adult males emerged earliest (mean date = 18 April); females with yearlings, lone females, and subadult males emerged next (mean date = 28 April); and females with cubs emerged the latest (mean date = 7 May). Comparing study areas, the schedule of denning dates was approximately 2 weeks earlier for den entrance and 2 weeks later for emergence on the NSA than the SSA.

Bear home range and movement patterns differed by sex, age class, season, and annual mast production. Males bears had significantly larger home ranges and activity radii than female bears. For both sexes, mean activity radii and percent of long-range movements increased during the mast season, when foraging for acorns and other mast dominated activity. During years of oak failure, mean activity radii were larger than during other years. Dispersal away from natal areas was observed for 4 males monitored until age 4, but none was observed for 8 females. Nuisance and depredation activity was associated with availability of human-related foods, especially garbage. Monitoring of translocated nuisance bears indicated subadult bears, particularly males, were less likely to exhibit homing behavior than adult bears.

Bear density appeared to be higher on the NSA (17.0/100km^2) than the SSA (9.4/100km^2), but the sex-age composition was very similar for the 2 study areas. Adult females constituted approximately 30% of study populations and adult males accounted for 15-19%. Annually, relative proportions of yearlings and subadult males appeared to vary the most.

Using the habitat model, we predicted suitable black bear habitat across approximately 58,939 km^2 (14.6 million acres), of which 75% was comprised of primary cover types. Nearly 50% of the predicted suitable bear habitat was managed by the U. S. Forest Service, 33% was under private ownership, and tribal lands comprised about 10% of the area. Statewide, 17% of predicted bear habitat was within 5 km of human-populated areas. Although currently based on relatively coarse data, the model was constructed so that future, more resolved information can be easily incorporated to update model predictions.

Extrapolating observed density estimates to areas of primary habitat yielded a statewide population estimate of 5,947 bears ≥1 year old. This estimate was similar to the independent estimate of 5,200 derived from population modeling for the state (excluding the Zuni, Mt. Taylor, Sandia/Manzano, and Chuska regions). These estimates refute the previous estimate of 3,000 bears used by the NMDGF, however they do not suggest a doubling of the bear population in the past decade. Rather, these estimates are based on better information and, as such, are more reliable.

Analyses of harvest data from 1985-1999 indicated bear hunters in New Mexico consistently harvested more males than females. The female proportion of annual statewide harvest ranged from 29 to 46%. Total annual bear kill by hunters was affected by many factors including season timing, hunter effort, hunter method, and mast production, as well as underlying population composition. Hunters aided with dogs had higher success rates and harvested 4 times as many female bears per hunter as those not using dogs. Later fall seasons were associated with lower total harvest and lower proportions of females in the harvest, compared to earlier fall seasons and spring seasons. Failures in oak production were associated with increases in hunter effort, hunter success, and the proportion of females in the kill.

Accuracy and consistency of the cementum annuli aging technique appeared adequate for assessing the age composition of annual hunter-killed bears and reporting of sex appeared to be accurate. However, analyses indicated harvest data were incomplete, underestimating the annual bear kill by as much as 7%.

The bear population model was designed to simulate a black bear population through time, with biological realism, hunting, and environmental influences. Using observed reproductive and survival rates, modeling indicated study populations were either stable or slightly increasing. Future utility of the model will depend on continued input of data in the form of annual harvest records and annual surveys of mast production. Use of the model will allow for interpretation of recent demographic trends in New Mexico bear populations, a timely indication of potential overharvest, and predictive scenarios useful for selecting from several management options.

The outcomes of this research will significantly improve understanding of black bear ecology and management in New Mexico. Using the new tools provided by this study, as well as the existing tools, managers can evaluate the results and consequences of numerous management alternatives and assess past, current, and future trends in bear populations. The existing tools consist of hunter-kill records and the hunter mail-in survey. The validity of those tools has been verified to supply useful input to hunt regulation assessment and regional management decisions. The new tools include the bear population model, the model to predict suitable bear habitat, a simple annual mast survey, and the research report as a compilation and archive of these tools.

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PREFACE

In the early part of the 20th century, the science of wildlife management was in its infancy, but public and government interest in this discipline intensified as the need for protection of wildlife species became apparent. Across North America, unregulated hunting had reduced or eliminated wildlife populations once plentiful. In 1914, the last passenger pigeon died, bringing the extinction of a species, once so numerous as to blacken the skies with their multitudes. In the Southwest, Merriam's elk were eradicated, and several carnivore species, including black bears, grizzly bears, cougars, and Mexican wolves, were facing unprecedented mortality from predator control programs.

Amidst these extraordinary events, New Mexico joined only a handful of other states in granting game status to black bears and grizzly bears in 1927. Conservation measures came too late for grizzly bears, but black bear populations rebounded. Today, evidence indicates black bears inhabit the same range in New Mexico as they did prior to European settlement. They tread the same mountains, consume the same foods, and possibly slumber in the very dens used by their ancestors for thousands of years.

How did these historic events come about? The answer is as relevant today as it was in 1927. The decision to protect bear populations, by setting legal hunting regulations, arose from participation of the public, the legislature, and the New Mexico Department of Game and Fish. Without involvement from each of these 3 entities, conservation of black bears might also have come too late. With this in mind, it seems fitting that the black bear was selected as the symbol of the Department of Game and Fish. Black bears may well have been the first wildlife management success story in New Mexico.

As human populations increase in the 21st century, management of black bears will only become more challenging. Creative solutions to bear-human conflict will be necessary, as well as sensible management strategies for hunting and habitat quality. But with continued public involvement and sound management based on science, existence of black bears in New Mexico can continue to be a success story for generations to come.

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Use of brand or trade names throughout this report acknowledges the product’s application to our research but does not constitute agency or cooperator endorsement of those products.

Photo credits for the cover are: Cecily Costello for Gambel oak acorns, F506 yearling in tree, F536 in den, and Baldy Meadows in fall; Robert Inman for Southern Study Area (Gila) ridges from airplane, and Gerry Lamarre for black bear on rock.

CHAPTER 1

INTRODUCTION

RATIONALE FOR STUDY

The black bear (*Ursus americanus*) is an important species in New Mexico, valued both as a big game animal and an embodiment of the southwestern wilderness. Throughout history, bears have been both revered and scorned by humankind. Management of this species must balance the positive aspects of bear-human interactions, including wildlife viewing and hunting, with negative aspects, such as nuisance problems, crop and livestock depredation, and bear-inflicted human injuries. With expanding human populations, management of these bear-human interactions will only become more challenging.

The New Mexico Department of Game and Fish (NMDGF) is responsible for managing the wildlife and fish populations of New Mexico, including black bears. Their mission is to "provide and maintain an adequate supply of wildlife and fish within the state of New Mexico by utilizing a flexible management system that provides for their protection, propagation, regulation, and conservation; and for their use as a public recreation and food supply." The NMDGF primarily manages bear populations through hunting regulations and resolution of nuisance and depredation problems.

Wildlife management is essentially governed by knowledge of the status and trend of populations. However, monitoring black bear population status is a difficult job. The solitary nature of bears, coupled with the dense habitats they generally use, prevent use of survey methods commonly used for other big game species such as elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), or pronghorn antelope (*Antilocapra americana*). As in many states, the primary foundation for black bear management in New Mexico is information obtained from hunter-killed bears. Since 1978, the NMDGF has collected annual records of harvested bears through a mandatory reporting program. Beginning in 1985, utility of these data was improved with the requirement of proof of sex and collection of a premolar tooth for aging with the cementum annuli method. Since 1986, the NMDGF also has conducted hunter surveys to obtain data on hunter effort and methods to be used in conjunction with harvest records.

Managers often make inferences about status and trend of populations based on the sex and age composition of harvested bears. However, harvest data are not necessarily representative of actual bear populations because of differences in vulnerability and hunter selectivity between sex and age groups (Miller 1990, Garshelis 1991). One common circumstance, subject to misinterpretation, is an observed increase in the percentage of young bears in the harvest sample. Is this increase due to previous overharvest of mature individuals or an increase in reproductive success?

During the late 1980's and the early 1990's, interpretation of New Mexico black bear harvest data was stymied by these very circumstances. Increasing, stable, and decreasing population trend were all plausible explanations for the observed changes in the harvest data. The lack of conclusive evidence for any trend did little to alleviate the growing controversy over future hunting regulations. Many guides, outfitters, and hunters favored the interpretation of an increasing trend, arguing that hunting regulations could be less restrictive. But other hunters and environmental groups defended the interpretation of a declining trend, and advocated more conservative hunting regulations. Clearly, additional information was necessary to interpret these data and to determine the true status and trend of New Mexico bear populations.

In 1991, responding to this need for more scientific information, members of the New Mexico State Game Commission instructed the NMDGF to conduct a black bear study. With funding from the NMDGF and the Federal Aid in Wildlife Restoration program (U. S. Fish and Wildlife Service) research was initiated in 1992. This 8-year study involved the NMDGF and three contracting organizations: Hornocker Wildlife Institute (HWI), Ecosystem Modeling (EM), and the New Mexico Cooperative Fish and Wildlife Research Unit (NMCFWRU) at New Mexico State University. The overall goal was to study the ecology and population dynamics of black bears for developing methods and analytic tools to help estimate and predict trends in population size and structure in New Mexico, as influenced by human-caused mortality and environmental variation.

STUDY OBJECTIVES

The study involved 2 related efforts. The first job was an 8-year, field-based investigation of bear ecology. Research was conducted within 2 distinct study areas situated in prime bear habitat. To specifically address the effect of hunting on population dynamics, 1 study area was closed to hunting for the majority of the study period. Research involved use of radio-telemetry transmitters on free-ranging bears, and although our primary objectives were related to population characteristics, use of telemetry permitted investigation of other ecological questions. Objectives of the field study were:

1. To document black bear population characteristics and dynamics, focusing on natality; cub survival; yearling survival; and adult/subadult survival relative to human-caused mortality.

2. To document black bear foraging habits and identify key foods, especially mast-producing species.

3. To quantify annual variation in production of important mast species for evaluation of its influence on reproductive success and survival.

4. To validate the premolar cementum annuli aging technique for New Mexico bears.

5. To document den entrance and emergence dates for comparison among sex/age categories and between study areas.

6. To investigate den site selection and use of elevation and habitat by denning bears.

7. To document home range characteristics, seasonal patterns of movement, subadult dispersal, and general habitat use.

8. To determine density and sex-age composition of study populations annually and with all years combined.

9. To extrapolate study area habitat characteristics to identify suitable bear habitat across the state using a Geographic Information System (GIS).

A second job involved analyses of NMDGF harvest and hunter survey data and development of a black bear population model using data collected during the field study. Primary objectives were:

1. To determine relationships between the harvest sample and the sex-age composition of study populations.

2. To determine relationships among weather variables, mast production, and bear population characteristics.

3. To develop a population/environmental/hunt model based on existing knowledge, and refined by rates observed in the field study.

4. To integrate the model into management application.

This report chronicles the results of this 8-year study, which represents the first concerted effort to understand New Mexico black bear ecology. Prior to 1992, only 2 research efforts had been conducted on New Mexico black bears. With funding from the NMDGF, Zager and Beecham (1982) conducted a preliminary investigation of food habits and habitat ecology in north-central, west-central, and southeast New Mexico. In 1988, a radio-telemetry study was initiated by a NMDGF District Officer to investigate bear-human conflicts, particularly on Philmont Scout Ranch (Jones 1991). That investigation acted as a springboard for establishment of the Northern Study Area for this study.

Further, this study and the resulting report supplements NMDGF data on hunter-killed black bears with information on vital rates, relationships with annual environmental variation, live population structure, and habitat use. The population model will provide managers with a tool for integrating harvest data with biological and environmental information to make inferences about bear population status consistent with all available information. Although uncertainty about black bear population resources will remain a challenge to bear management, the knowledge available to managers has been significantly improved.

CHAPTER 2

LIFE HISTORY AND MANAGEMENT HISTORY IN NEW MEXICO

This chapter describes the general ecology of black bears. It provides background for understanding the design, implementation, outcomes, and interpretations of this research.

TAXONOMY

Bears are members of the Family Ursidae, in the Order Carnivora, in the Class Mammalia. Other families found within the Carnivora include the Canidae (dogs), Felidae (cats), Mustelidae (weasels), and Procyonidae (raccoons). The Ursidae family is of recent origin, believed to have diverged from the Canidae approximately 20-25 million years ago (McLellan and Reiner 1994). Black bears are 1 of 8 ursid species worldwide.

At least 2 million years ago, after radiating to North America from Asia, a small forest-adapted ancestor (probably *Ursus abstrusus*) gave rise to the modern American black bear (Stirling and Derocher 1989). Despite climatic changes and competition with various species, the black bear adapted to survive to the present day virtually unchanged from 1 million years ago (Stirling and Derocher 1989). Within their evolutionary history, black bears have coexisted with several other ursid species, including the extinct short-faced bear (*Arctodus simus*) and the extinct North American spectacled bear (*Tremarctos floridanus*). The brown bear (*Ursus arctos*), which coexists with black bears in northwestern regions today, radiated into North America only about 100,000 years ago, and probably reached the Southwest about 13,000 years ago. Since then, black and grizzly bears inhabited New Mexico and probably shared similar distributions. However, grizzly bears were extirpated from New Mexico by the late 1930's.

DISTRIBUTION AND STATUS

Throughout their evolutionary history, the distribution of black bears has been basically defined by the extent of forested habitat in North America. Black bears have inhabited eastern deciduous forests from Florida to Maine, boreal forests from Newfoundland to Alaska, and montane forests from Alberta to Mexico. Fossil evidence indicates black bears were never commonly found in open habitats, such as the Great Plains, the Great Basin, or the arctic tundra, possibly due to competition with larger ursids, such as short-faced bears and brown bears (Stirling and Derocher 1989).

During modern times, black bear distribution has been most affected by deforestation, unlimited hunting, and use of poisons following European settlement of North America. Beginning in the 19th century, black bears were eliminated or greatly reduced in several U.S. states, including Illinois, Ohio, Kentucky, Florida, Alabama, Louisiana, Arkansas, Missouri, and Texas (Servheen 1989). However, during the last century, reforestation, legal limits on hunting, and restrictions on the use of poisons have allowed population recovery in many regions. The bear population in Arkansas, and subsequently Missouri and Louisiana, also were augmented with bears transplanted from Minnesota in the 1950's. Today, black bear distribution is expanding and is known to include 32 U.S. states, 11 Canadian provinces or territories, and 6 Mexican states (Servheen 1989, Carrera 1993). Throughout their current distribution, bears are variously protected by game, threatened, or endangered status.

In New Mexico, evidence indicates black bear populations were greatly reduced by the early 1900's due to unlimited hunting and use of poisons (NMDGF 1926, Bailey 1932, Brown 1985). Much of the mortality was the result of government sponsored anti-predator programs, aimed at eliminating loss of livestock to grizzly bears, black bear, wolves, and other carnivores (Brown 1985). In 1924, the U. S. Forest Service (USFS) estimated only 1,500 black bears inhabiting the national forests of New Mexico, Arizona, southern Colorado, and southern Utah, combined (Brown 1985). In 1925, the New Mexico population estimate was 660 black bears (NMDGF 1926). Responding to public and legislative support for protection of bears, the NMDGF classified the black bear as a big game species in 1927, and set a bag limit of 1 bear/season (10-31 October). Black bear, deer (*Odocoileus* spp.), and turkey (*Meleagris gallopavo*) were included in a single big game license and this regulation remained until 1981. This protection had significant results, and the bear population appeared to rebound by the 1940's. In 1941, more than 3,500 bears were estimated to reside in the national forests of the southwest (Brown 1985). By 1967, the black bear population in New Mexico was estimated at 3,000 and stable (Lee 1967). In 1971, a regulation was adopted prohibiting the harvest of young less than 1 year of age or females accompanied by young. In 1978, a mandatory hide-tagging program was instituted and 2 further requirements were added in 1985: proof of sex and collection of premolar teeth for cementum aging. In 1982, facilitated by the separate black bear hunting license, the NMDGF initiated a survey of randomly selected license holders.

Since the first bear hunting seasons were set in 1927, timing and duration of seasons have varied. By the late 1970's, bear seasons encompassed 7-8 months each year, including parts of April, May, June, August, September, October, November, December, and January. In 1992, due to concerns about potential overharvest, NMDGF eliminated the spring bear season and reduced the fall season to 1 September-31 October. The fall season was again changed to 15 October-15 December in 1998 and 1 October-15 December in 1999.

Current distribution of black bears in New Mexico is associated with the forested mountain ranges. Bears inhabit areas ranging from the low elevation pinyon-juniper woodland and oak scrub habitats to the high elevation mixed conifer and spruce-fir forests (See Chapter 11).

LIFE HISTORY

Although taxonomically carnivores, black bears are, in fact, omnivorous. Throughout North America, diets of black bears are dominated by plant matter (Hatler 1972, Beeman and Pelton 1980, Graber and White 1983, MacHutcheon 1989, Raine and Kansas 1990). Diets of black bears in New Mexico also are dominated by plant material (see Chapter 5).

To an herbivorous black bear incapable of digesting cellulose, winter represents a time of food shortage, especially in northern regions. It is believed bear hibernation evolved primarily as a response to this seasonal scarcity of food (Pelton 1982). In most regions of North America, hibernation is a central component of the annual cycle of black bear activity, and the timing and duration of all other activities might be viewed as evolutionary consequences of this unique process. Although different from hibernation among smaller mammals, the physiological state attained by bears is generally considered true hibernation (Folk et al. 1976, Hellgren 1998), and some argue it is the most refined response to starvation of any mammal (Nelson 1980). For periods up to 7 months, a hibernating bear does not eat, drink, defecate, or urinate (Folk et al. 1976, Nelson 1980, Hellgren 1998). In all hibernators, metabolic activity is generated from energy stored in the form of fat, but small hibernators must arouse periodically to feed. Bears are capable of recycling the waste products of fat metabolism into lean body mass, while other hibernators must arouse and eliminate wastes through urination or suffer toxemia (Nelson et al. 1973, Hellgren 1980). Bears, like other hibernators, achieve energy savings by reducing their heart rate from 40-50 beats per minute (bpm) to 8-10 bpm, and lowering their metabolic rate by 27-50% (Hellgren 1998). However, concurrent with these other declines, black bear body temperature drops from 37-38^{o}C to only 31-35^{o}C compared to temperatures less than 10^{o}C in other hibernators (Hellgren 1998). Bears can achieve energy savings equal to small hibernators without dramatic changes in body temperature, because of their lower surface-area to volume ratio. This maintenance of near normal body temperature also allows bears to arouse quickly in response to disturbance.

Female black bears give birth in winter dens, and in addition to their own metabolic requirements must fulfill the energetic demands of gestation and lactation during the hibernating phase. Timing of breeding season may be tied to hibernation. Although mating occurs during spring or summer, fetal development does not begin until late fall, due to the process of delayed implantation. Following fertilization, eggs divide until the blastocyst stage (about 300 cells) and remain within the fallopian tubes for several months. In late fall, the blastocyst migrates down the fallopian tubes and implants in the uterine wall, at which time gestation begins (Wimsatt 1963). Actual gestation length is approximately 30-90 days and cubs generally are born during late January or early February (Alt 1983, Hellgren et al. 1991). Black bear litter sizes are known to range from 1-5, but litter sizes observed during this study ranged only from 1-3 (see Chapter 6).

Delayed implantation may be adaptive in bears for 2 primary reasons. First, it allows breeding to occur early in the active season when it would not interfere with the prolonged fall foraging necessary to build up fat stores for hibernation. Secondly, even after mating occurs, it is postulated that delayed implantation may allow females, with fat stores insufficient for gestation and lactation, to forego reproduction by not implanting the blastocyst. No hard evidence of this process had been found, however lack of litter production has been linked to poor nutritional status (Kolenosky 1990, Noyce and Garshelis 1994, Samson and Huot 1995).

Like most other members of the Carnivora, black bears can be classified as k-selected species, characterized by slow maturation, low reproductive potential, and long life spans (Caughley 1977). Throughout North America, female black bears reach reproductive maturity and mate at ages ranging from 1-5 years, with most over 3 years. In New Mexico, the youngest females observed in estrus were 3 years old, and the youngest females observed to give birth were 4 years old (see Chapter 6).

Breeding season typically ranges from May to September with peaks in June or July. Evidence from New Mexico indicates the peak of breeding occurs in June. Prolonged dependence of offspring on their mother sets the minimum successful birth interval at 2 years. Bears have been observed to give birth in the presence of yearlings (Alt 1981) and to give birth to newborn cubs after fall separation from the previous year's cubs (LeCount 1983). Nonetheless, these events appear to be extremely rare, and we found no evidence of their occurrence in New Mexico.

Cubs remain with their mothers for approximately 16-18 months, denning with them during their second winter. Following den emergence in the spring, yearling bears generally become independent between May and July, at which time the female is usually receptive to mating. Despite independence, occasional socialization between mothers and offspring probably occurs for several months to years. Numerous studies, including this one, have documented temporary reuniting of mothers and offspring. Bear species exhibit a high degree of female philopatry. Subadult female bears often remain in the vicinity of their mother's home range and establish their own home range adjacent to their mother. Conversely, most male offspring disperse away from natal areas at ages ranging from 1-3 years old. Finding of this study concur with these general trends (see Chapter 9).

Natural life expectancy of black bears probably varies regionally, but bears living in excess of 20 years are common. During this study, the oldest female bear age documented using cemetum annuli counts was 27 years and the oldest male was 23 years. The highest age recorded for litter production was 22 years and was observed for 2 bears.

CHAPTER 3

STUDY AREAS

Research was conducted on 2 study areas in New Mexico. The Northern Study Area (NSA) was located in the Sangre de Cristo Mountains of northern New Mexico (Figure 3-1). The study area was approximately 310 km^2 and was bounded by U.S. Highway 64 to the south and Moreno Valley to the west. The area encompassed private and state lands, including Philmont Scout Ranch, the Colin Neblett State Wildlife Area (CNWA) and the Elliot Barker State Wildlife Area (EBWA), Cimarron Canyon State Park, and several private ranches. It was adjacent to the towns of Eagle Nest and Ute Park, and about 6 km from Cimarron. It was bordered by a 2-lane highway, which received fairly high use year-round. It also enclosed numerous gravel roads, dirt roads, and trails. During the study period, recreation and cattle ranching were the primary land uses. Philmont Scout Ranch hosted up to 20,000 scouts during 3 months each summer. Access to private lands was limited and vehicular access to the CNWA was restricted to the highway.

In addition to presence of highways and towns, the primary human influences on the landscape included excavation, logging, and construction of dirt tanks. Scattered mines and dredge tailings remained from gold and copper mining activities that lasted from the late 19th to the mid 20th century. Most forests within the study area were second-growth, following selective logging, clearing for pasture, and forest fires. During the 1960's, an elaborate network of dirt roads was constructed on the CNWA to provide access for selective logging. Public driving access to the roads was restricted, allowing most roads to become overgrown. Occasional man-made dirt tanks were scattered within the area, primarily on private lands.

Topography and vegetation were diverse. Elevations range from 2,073 m (6,800 ft) on the east side of the study area to 3,793 m (12,441 ft) on Baldy Mountain. At the lower elevations, dominant habitat types included pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands, and oak-mountain mahogany (*Quercus* spp.-*Cercocarpus* spp.) scrub. Middle elevations were dominated by ponderosa pine (*Pinus ponderosa*), mixed conifer (*Pseudotsuga menziesii-Abies concolor*), and aspen (*Populus tremuloides*) forests. Meadows of fescue (*Festuca* spp.), mountain muhly (*Muhlenbergia Montana*), grama (*Bouteloua* spp.), and bluegrass (*Poa* spp.) existed throughout the wooded habitats at lower and mid elevations. Spruce-fir (*Picea engelmannii-Abies lasiocarpa*), and bristlecone pine-limber pine (*Pinus aristata-Pinus flexilis*) forests dominated the higher elevations. An alpine tundra community, consisting of sedge (*Carex* spp.), alpine avens (*Geum rossii*), mountain current (*Ribes montigenum*), shrubby cinquefoil (*Potentilla fruticosa*), and grounsel (*Senecio* spp.) surrounded the scree and talus slopes at the highest elevations. Further description of these vegetation communities is provided by Dick-Peddie (1993).

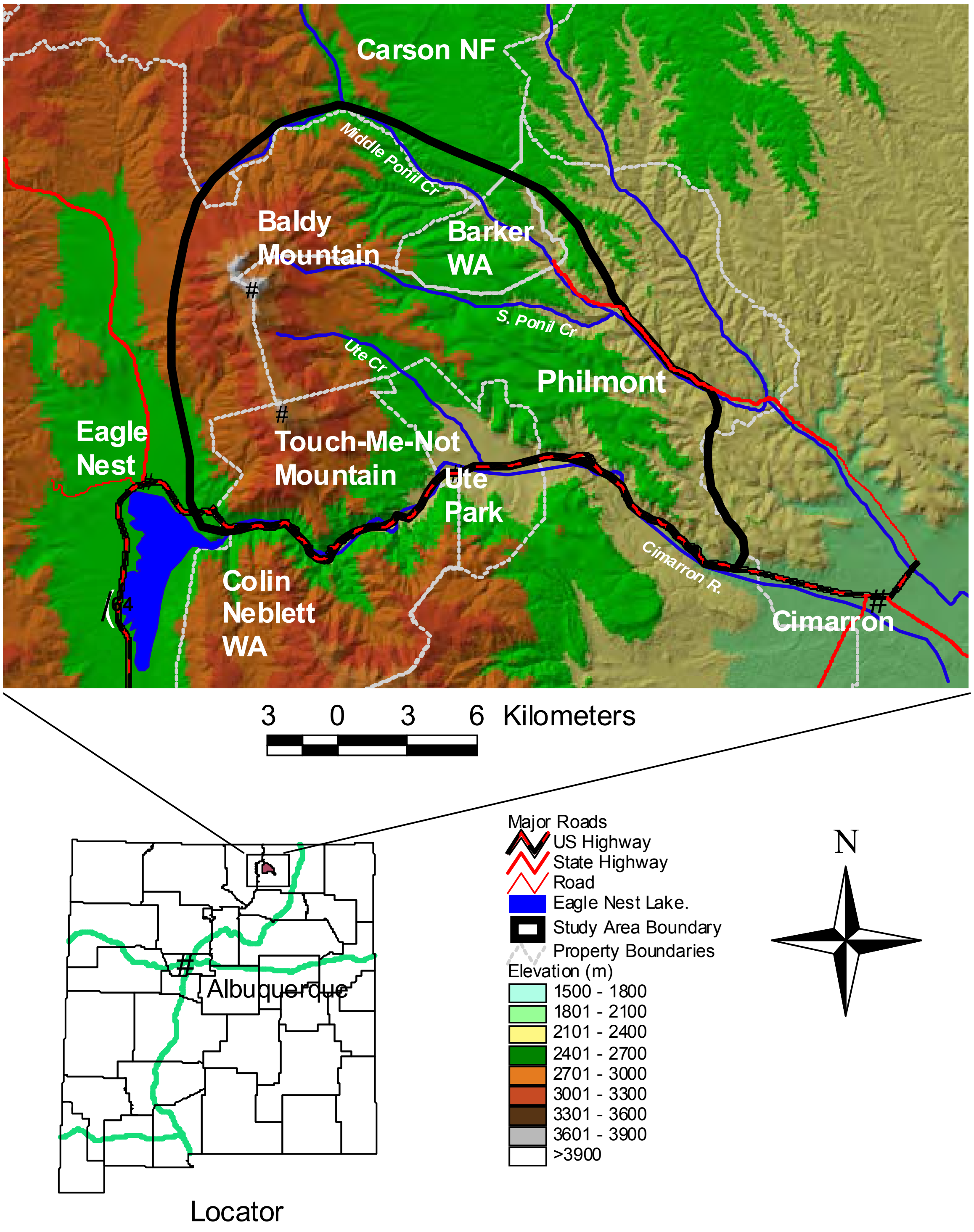


Figure 3-1. Location of the Northern Study Area of the Black Bear Study in New Mexico showing relationship to major roads, towns, and terrain.

The area included numerous permanent streams draining into the Cimarron River, including Willow Creek, California Creek, Ute Creek, Dean Creek, and Ponil Creek. Most of the smaller streams draining into these larger streams also were permanent.

Climate varied by elevation within the study area (Table 3-1). Mean January temperatures were at or below freezing and snowfall was high in the upper elevations. July temperatures were generally mild with most rainfall occurring during July-August.

Table 3-1. Climate variables recorded at weather stations close to the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1939-2000.

	NSA		SSA	
Parameter	Eagle Nest (2506 m[a])	Cimarron (1939 m)	Beaverhead (2023 m)	Glenwood (1432 m)
Mean Jan temperature (^{0}C)	-7	0	-1	5
Mean Jul temperature(^{0}C)	16	21	19	24
Frost -free season (days)	70-120	145-190	110-155	180-230
Annual precipitation (cm)	37.8	41.4	37.6	40.4
Monthly snowfall Dec-Mar (cm)	25.4	15.0	10.5	4.0
Monthly rainfall Jul-Aug (cm)	6.9	7.0	6.6	6.8

[a] Elevation of weather station

The area was located in Game Management Unit (GMU) 55. Prior to the study, bear hunting intensity varied within the study area. The CNWA and EBWA were closed to bear hunting since the late 1980's. Levels of bear hunting varied on private land, but were probably moderate to high throughout the area. With cooperation of private landowners, the area was closed to bear hunting so population dynamics could be studied in the absence of hunting. This closure was in effect from 1992 until 1998 when hunting was reestablished on some private land within the study area.

The Southern Study Area (SSA) was located in the Mogollon Mountains of west-central New Mexico (Figure 3-2). The area was approximately 423 km^2 and was bounded by U. S. Forest Service Road 141 to the north and Mineral Creek to the south. The area was encompassed within the Gila National Forest (Reserve Ranger District), but included some private parcels. It was remote, with the closest towns of Reserve, Glenwood, and Mogollon, located 3-16 km away. A 2-lane, partially paved loop road provided the main access into the study area. Numerous gravel roads, dirt roads, and trails were found on the study area, and access was usually unrestricted.

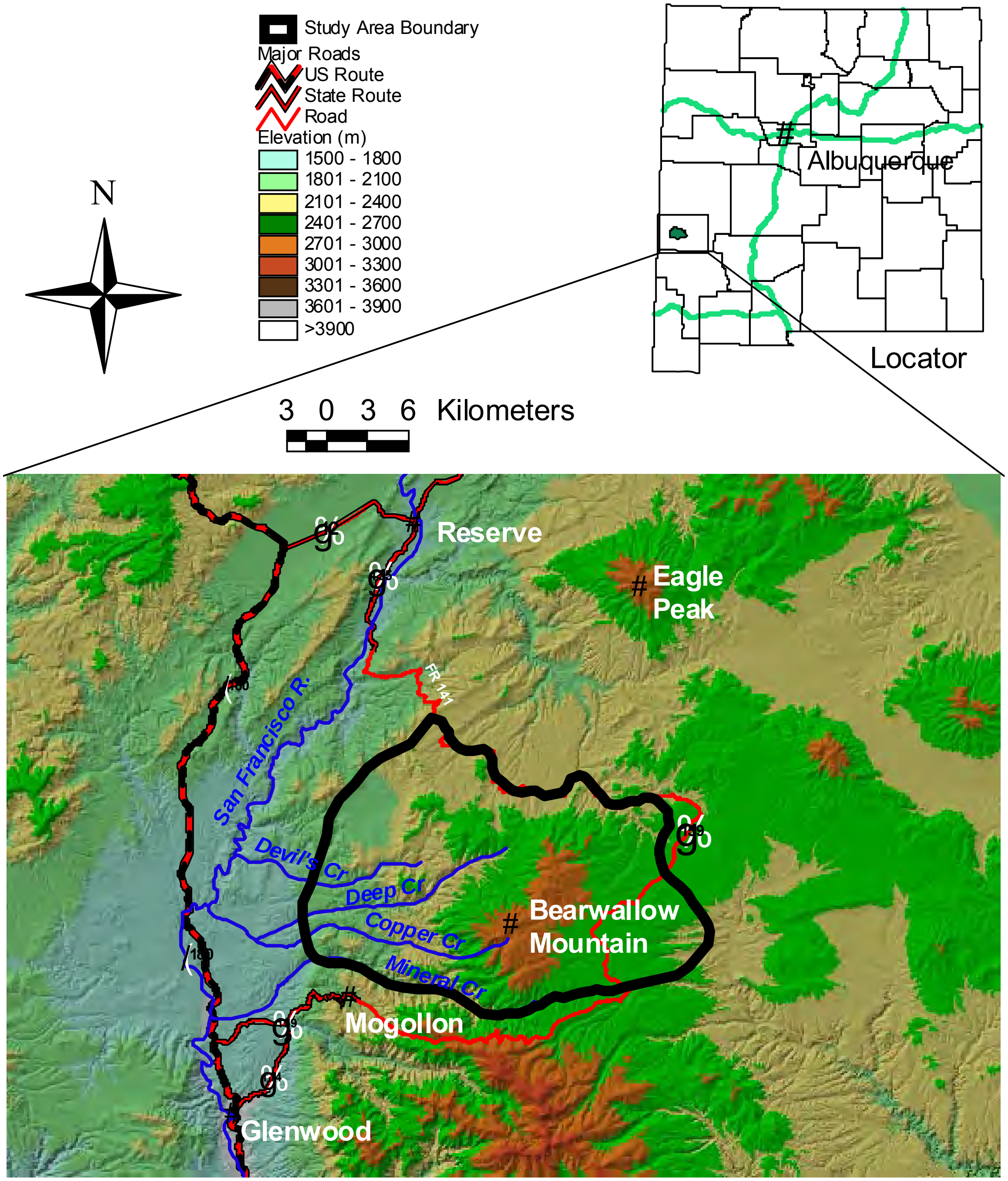


Figure 3-2. Location of the Southern Study Area of the Black Bear Study in New Mexico showing relationship to major roads, towns, and terrain.

During the study period, cattle grazing and recreation were the primary land uses. Historically, logging was also a dominant land use in this area, but during the 1990's, timber harvest was very limited within the study area. It consisted of 1 commercial timber sale on Corner Mountain and limited firewood cutting. Prior to the 1990's, much of the forested area was selectively logged or cleared for pasture, therefore most forests were second-growth. Some old-growth forests persisted, especially in steeper canyons. Numerous constructed dirt tanks were found within the area, providing permanent or seasonal water for cattle and wildlife.

Topography was diverse on the SSA, but elevations were lower than the NSA. Elevations ranged from approximately 1,750 m (5,740 ft) on the west side of the study area to 3,035 m (9,954 ft) on Bearwallow Mountain. Dominant habitat types coincided with those described for the NSA, with some variation in species composition. The high elevation bristlecone pine-limber pine forest and alpine community of the NSA were not present on the SSA.

The area included numerous permanent streams draining into the San Francisco River, including Devils Creek, Deep Creek, Copper Creek, and Mineral Creek. Many of the smaller streams on the area were ephemeral, drying out annually or in drought years.

Climate varied by elevation within the study area (Table 3-1). Mean January temperatures were below freezing at upper elevations, but above freezing at lower elevations. Snowfall was lower than that of the NSA. July temperatures were generally mild, but warmer than the NSA. Most rainfall occurred during July-August and rates were similar to the NSA.

The SSA was located within GMU 16A, and was open to bear hunting throughout the study period. Historically, hunting intensity in the region was moderate to high.

CHAPTER 4

CAPTURE OUTCOMES AND PHYSICAL CHARACTERISTICS

The objectives of the field study required us to capture a large sample of black bears and place radio-transmitters on many individuals. As a prelude to later chapters, we report the methods for our field investigations, including trapping efforts, den investigations, and radio-telemetry monitoring. We also include information on physical characteristics of bears obtained during these activities.

METHODS

Throughout the study period, our trapping efforts were primarily focused on the capture of previously unmarked females, to meet a target of 25 radio-transmitter equipped females monitored each year for reproductive success. During later years, much of the trapping effort was aimed at recapture of individuals requiring refitting or removal of their radio-collar.

Throughout the active season (primarily May-October), we captured bears using foot snares and culvert traps. Traps were examined by 1200 hours each day to prevent excessive stress to captured animals. All snared bears and most culvert-trapped bears were chemically immobilized and handled, however some recaptured bears caught in culvert traps were released without handling. Immobilizing drugs were administered using syringe poles. Captured bears were immobilized using 1 of 2 mixtures of immobilizing agents. Most often, we used a 2:1 mixture of ketamine hydrochloride (Ketaset, Fort Dodge Animal Health, Overland Park, Kansas) and xylazine hydrochloride (Rompun, A. H. Robins Co., Richmond, Virginia) at a combined dosage rate of 6.6 mg/kg (3mg/lb) estimated body weight (Addison and Kolenosky 1979). Under some circumstances, we used tiletamine hydrochloride + zolazepam hydrochloride (premixed as Telazol, A. H. Robins Co., Richmond, Virginia) at a dosage rate of 5.5 mg/kg (2.5mg/lb) estimated body weight (Gibeau and Paquet 1991). Use of Telazol was not ideal for our trapping regime because the protracted recovery period, characteristic of this drug, limited our ability to handle multiple bears per day.

We monitored respiration, pulse, and body temperature during immobilization. Ointment was applied to the eyes of bears to inhibit drying. Blindfolds were used and loud sounds were minimized to reduce unnecessary disrupting stimulus. We remained with immobilized bears until recovery was observed.

Sex of captured bears was determined from external genitalia. Black or brown color phase was noted for each bear, based on the color of the guard hairs and the underfur. Coat condition was rated as good or poor/shedding. For all bears, we recorded chest girth, body length, neck circumference, foot pad length/width, and weight (when possible). For female bears, we noted vulval swelling, teat length/width, teat color, occurrence of lactation, evidence of suckling (swollen teats or hair matting), and presence of offspring.

Approximate age of bears was estimated from tooth eruption/wear (Jonkel 1993) and size. A vestigial premolar tooth was extracted from bears ≥1 year old for age determination using cementum annuli counts (Stoneberg and Jonkel 1966, Willey 1974). Age class was assigned as follows: cub (<1 year), yearling (1 year), subadult (2-4 years), and adult (≥5 years).

We marked each bear with numbered, colored eartags (Allflex USA, Dallas, TX) and we tattooed the same number on an inner, upper lip. We placed radio-transmitters on all females captured, except during 1999-2000 when our target sample size of 25 had been met. We placed radio-transmitters on adult males as needed to maintain a sample of approximately 10 individuals each year. During the first year of the study, most subadult males were also given radio-transmitters. The practice of collaring captured subadult males was terminated after 1993, in favor of placing transmitters on yearling males and females in the den. Adult-sized collars (mod-500 or mod-505, Telonics, Tempe, Arizona) were placed on bears weighing over 23 kg (50 lbs). Bears weighing less than 23 kg were fitted with Telonics mod-400 collars, expandable subadult collars (Ursus Technologies, Williamsburg, Virginia), or ear-tag transmitters (Advanced Telemetry Systems, Isanti, Minnesota). Collars were fitted to allow for growth and cotton spacers were attached to ensure collars would fall off in the event of transmitter failure (Hellgren et al. 1988).

We visited dens of radio-transmittered adult females each year to ascertain their reproductive status. If offspring were present, we attempted to handle all bears in the den, however inaccessibility sometimes prevented it. If offspring were not present, females were usually handled only if necessary to change or refit collars. Dens of males and subadult females were visited annually or biannually to change or refit collars as necessary. Adult, subadult, and yearling bears requiring handling were immobilized using Telazol. We elected to use Telazol for den work because of its reduced tendency to depress heart rate and respiration compared to Ketaset/Rompun. Cubs were handled without immobilization. Typically, we did not remove adult bears from dens, unless it was necessary to reach their head or to reach offspring, however yearlings and cubs were removed from dens for handling. Weights and other measurements were obtained from all bears when possible. Den investigations were conducted between January and April, however we limited handling of cubs to March and April when our handling would have negligible impact on their survival.

We monitored radio-collared bears from fixed-wing aircraft on a 14-day schedule during the active season (weather permitting). During fall and spring months, we attempted to increase the flight schedule to 7-10 days for obtaining den entrance and den emergence data. During winter months, monitoring of bears was reduced while the bears remained in their dens. We recorded locations using Universal Transverse Mercator (UTM) grid coordinates to the nearest 0.1km, on United States Geological Survey (USGS) 7.5-minute maps. We estimated aerial telemetry error by comparing locations obtained by telemetry to actual locations verified by ground investigation. These locations included those of shed transmitters, bear mortalities, and blind tests.

RESULTS AND DISCUSSION

Trapping Success, Den Investigations, and Monitoring

Between September 1992 and June 2000, we captured 300 bears (103 females, 195 males, 2 unknown sex) 517 times. Individual bears were captured 1-9 times with a mean of 1.5 captures/bear. First-time captures, total captures, and capture success were similar between study areas (Table 4-1). History and circumstances of all bears handled are described in Appendix A.

Table 4-1. Black bear trapping success on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-2000.

			No. Captures		Capture Success (trap-nights/bear)	
Area	Category	No. Trap-nights	First-time	Total	First-time	Total
NSA	Snare	1338	64	116	20.9	11.5
	Culvert	1564	76	162	21.7	9.7
	Total	2902	140	278	20.7	10.4
	Females		49	73	59.2	31.9
	Males		91	204	39.8	14.2
SSA	Snare	1552	79	116	19.6	13.4
	Culvert	2230	81	123	27.5	18.1
	Total	3782	160	239	23.6	15.8
	Females		54	73	70.0	51.8
	Males		104	164	36.4	23.1

Between January 1993 and April 2000, we handled or observed 339 bears (178 females, 137 males, 24 unknown sex) in dens 680 times. Individual bears were handled or observed 1-8 times with a mean of 2.0 observations/bear. Successful den investigations included 282 individual adults (233 females, 49 males), 99 subadults (65 females, 34 males), 95 yearlings (45 females, 44 males, 6 unknown sex) and 204 cubs (94 females, 91 males, 19 unknown sex). In addition to these successful den investigations, we attempted to visit the dens of 24 other bears, but were unsuccessful because of inaccessibility of dens (n = 14), and prior emergence from the den (n = 10).

During 1992-1999, we placed 409 radio-transmitters on 316 bears (181 females, 135 males). Transmitters included 287 adult-sized collars, 27 subadultsized collars, 55 expandable subadult collars, and 40 ear-tag transmitters. We obtained 5,723 radio-telemetry locations.

Telemetry error was estimated from 105 locations verified with ground investigation. On the NSA, error ranged from 50-1,100 m with a median of 200 m, and a mean of 285 m (n = 23). On the SSA, error ranged from 50-3,780 m, with a median of 505 m and a mean of 784 m (n = 82).

Physical Characteristics

Color phase was recorded for 471 bears on 918 occasions. Most bears (75%) were brown-phase. Confidently assigning a bear to a color phase was sometimes difficult, due to color differences in underfur, especially when coats were shedding. Black-phase bears were identified by their black guard hairs, but often had gray to brown underfur. Within the brown-phase, we observed hues ranging from blonde to cinnamon to dark chocolate or liver color. Due to bleaching and shedding, the hue of brown-phase individuals was observed to vary, depending on season. Many bears with light-colored coats during spring and summer were observed with dark brown coats in the fall or winter. Color phase has been described as changing for an individual (Beck 1991), but we found no definitive evidence of such change. We believe any recorded changes in color phase were due to seasonal changes in hair condition (shedding, bleaching), different conditions during observation (time of day, lighting), and differences in observers.

Percent color phase did not differ by sex (X^2 = 0.03, df = 1, P = 0.85, n = 471), but differed by study area (X^2 = 35.5, df = 1, P < 0.001, n = 471). On the NSA, 83% of females and 84% of males were brown phase. On the SSA, 58% of females and 64% of males were brown phase.

Coat condition varied throughout the year. Almost all bears (98%) had good coat condition during fall months (September-October, n = 132) and during the denning period (January-early April, n = 326). During May-August, we observed shedding or poor coat condition on 18-40% of bears (n = 267), with the highest proportion in July.

We obtained active-season weights or measurements for 280 individuals on 333 occasions. Weights and measurements differed among sex and age categories (Table 4-2). Mean weight of males increased significantly between cub age and 6-7 years, when mean weight appeared to level off (Figure 4-1). Mean weight of females increased between cub age and 2-3 years, when a gradual increase in weight was observed by age. A significant difference in male and female weights was observed by the ages of 2-3 and this deviation increased with age. Means for all other measurements showed similar trends (Figure 4-2).

Table 4-2. Mean and range for weights and measurements, by age category, of black bears recorded during the trapping season (May-October) on the Northern and Southern Study Areas, New Mexico, 1992-1999.

Measurement	Sex	Age	*n*	Mean	Range
Weight (kg)	Female	Cub	3	20.9	17 - 25
		Yearling	13	23.0	11 - 36
		2-3 years	33	46.2	21 - 71
		4-5 years	17	52.9	36 - 84
		6-7 years	10	64.1	52 - 82
		8-10 years	14	68.9	50 - 114
		>10 years	11	73.1	53 - 107
	Male	Cub	2	20.0	18 - 22
		Yearling	19	29.3	14 - 48
		2-3 years	71	62.8	27 - 105
		4-5 years	33	84.9	50 -130
		6-7 years	16	117.1	75 -178
		8-10 years	20	117.3	77 -159
		>10 years	23	110.2	70 -146
Chest girth (cm)	Female	Cub	3	51	48 - 53
		Yearling	14	52	45 - 63
		2-3 years	36	70	52 - 86
		4-5 years	21	75	62 - 97
		6-7 years	12	77	69 - 93
		8-10 years	16	83	75 - 103
		>10 years	14	84	69 - 98
	Male	Cub	2	54	47 - 61
		Yearling	19	60	45 - 83
		2-3 years	83	79	45 - 108
		4-5 years	38	92	70 - 120
		6-7 years	25	102	84 - 127
		8-10 years	25	104	86 - 124
		>10 years	27	105	88 - 124
Length (cm)	Female	Cub	3	105	100 - 108
		Yearling	14	117	96 - 142
		2-3 years	35	137	107 - 160
		4-5 years	21	148	110 - 162
		6-7 years	11	152	140 - 162
		8-10 years	16	154	139 - 175
		>10 years	13	159	146 - 170
	Male	Cub	1	104	
		Yearling	19	119	103 - 142
		2-3 years	82	153	115 - 184
		4-5 years	35	171	146 - 193
		6-7 years	22	177	161 - 205
		8-10 years	24	177	125 - 194
		>10 years	27	178	164 - 193

Measurement	Sex	Age	*n*	Mean	Range
Neck circumference (cm)	Female	Cub	3	32	29 - 34
		Yearling	14	32	27 - 38
		2-3 years	34	42	27 - 55
		4-5 years	21	46	40 - 54
		6-7 years	12	47	42 - 51
		8-10 years	16	50	44 - 58
		>10 years	13	50	42 - 59
	Male	Cub	1	31	
		Yearling	19	36	28 - 49
		2-3 years	81	48	36 - 69
		4-5 years	36	57	35 - 73
		6-7 years	24	64	22 - 78
		8-10 years	25	66	50 - 76
		>10 years	27	65	49 - 79
Front pad width (mm)	Female	Cub	3	76	73 - 79
		Yearling	14	81	73 - 85
		2-3 years	33	94	80 - 115
		4-5 years	21	99	93 - 108
		6-7 years	12	101	90 - 110
		8-10 years	16	104	90 - 120
		>10 years	14	106	95 - 116
	Male	Cub	1	82	
		Yearling	18	89	70 - 110
		2-3 years	78	108	75 - 135
		4-5 years	36	120	100 - 139
		6-7 years	24	125	110 - 149
		8-10 years	21	125	96 - 140
		>10 years	24	126	102 - 153
Rear pad length (mm)	Female	Cub	3	96	90 - 100
		Yearling	14	108	89 - 122
		2-3 years	34	123	103 - 143
		4-5 years	21	129	102 - 147
		6-7 years	12	135	120 -150
		8-10 years	16	138	124 - 153
		>10 years	14	135	122 - 150
	Male	Cub	3	112	108 - 117
		Yearling	18	119	103 - 140
		2-3 years	77	142	103 - 172
		4-5 years	37	156	140 - 187
		6-7 years	24	157	106 - 184
		8-10 years	20	161	140 - 190
		> 10 years	25	163	146 - 185

We obtained den-season weights or measurements for 183 cubs or yearlings on 238 occasions (Table 4-3). At approximately 4-8 weeks of age, mean weight of cubs was 2.0 kg, and mean weight did not differ by sex (t = -0.5, df = 165, P = 0.64, n = 167). At approximately 12-14 months, mean weight of yearlings was 20.8kg, and it did not differ by sex either (t = -0.5, df = 36, P = 0.63, n =38).

Table 4-3. Mean and range for weights and measurements of cub (<1 year) and yearling (1 year old) black bears, recorded during the den season (January-April) on the Northern and Southern Study Areas, New Mexico, 1992-1999.

Measurement	Age	*n*	Mean	Range
Weight (kg)	Cub	167	2.0	1.0 - 3.8
	Yearling	38	20.8	9.1 - 38.6
Chest girth (cm)	Cub	87	27	19 - 36
	Yearling	65	54	34 - 74
Length (cm)	Cub	44	46	36 - 60
	Yearling	49	105	82 - 134
Neck circumference (cm)	Cub	49	18	12 - 23
	Yearling	51	33	22 - 40
Front pad width (mm)	Cub	7	36	31 - 43
	Yearling	18	75	50 - 91
Rear pad length (mm)	Cub	7	43	38 - 47
	Yearling	18	101	80 - 140

We observed 1 unusual bear on the NSA, first captured as a 3-year-old and monitored for 3 years. This bear exhibited male and a female external genitalia. It was not clear whether this hermaphrodite was reproductively functional as either sex. The bear was not observed to produce cubs, but it was once observed in the company of a marked female bear during the mating season. Its size was also more closely aligned with that of males. Because of the lack of offspring and its large size, we treated this individual as a male for most analyses, such as survival and home range.

Research-related Injury, Mortality, and Den Disturbance

During 517 captures, bears sustained 1 mortality (0.2%) and 10 injuries (1.9%). The mortality was sustained by a snared subadult female killed by another bear, and 1 injury (severed toe and claw) was sustained by a snared adult male as he defended himself from another bear. The other 9 injuries were the result of bears chewing their snared foot and severing toes and/or part of the main pad. Two incidents occurred during 1992 on the NSA, and 7 occurred during 1993 or 1995 on the SSA. During 1993 on the SSA, trapping teams sometimes separated to examine snares and, after meeting up, returned to sites where bears were captured. We suspect this action may have contributed to some of the first incidents of foot chewing on the SSA, and this practice was immediately discontinued when snares were used. It appeared most other incidents occurred when function of the swivel mechanism was inhibited, however cause could not be identified in all cases. Factors contributing to loss of swivel action included: use of stacked log cubbies; use of small, but live plant materials as part of the cubby; and failure to remove small shrubs from the area reachable by the snared bear. We discontinued use of stacked-log cubbies and only used dry, brittle material in cubby construction. Complete elimination of these factors after 1995 resulted in no further incidents of foot chewing. The addition of bungee cords and hood springs to snares during 1995-1997 also may have reduced injuries.

In traps and dens, we immobilized 762 bears and experienced 3 handling mortalities (0.4%). We believe an adult male died from reaction to the immobilizing drugs because a necropsy revealed the bear had sustained internal injuries prior to capture and it also had a congenital heart defect. An adult female with a debilitating case of sarcoptic mange died during den handling. Probably as a result of the infection and blindness, she was very emaciated and weak. The dose of immobilizing drug was appropriate for a healthy bear, however it may have been too much for a bear in her poor condition. Another adult female died when her radio-collar blocked her airway when she became immobile in the den. The problem was not observed quickly enough, and her breathing and heartbeat stopped. Cardio-pulmonary resuscitation was attempted for 35 minutes, however she was not revived.

In 369 uses of radio-collars, 8 uses (2.2%) resulted in severe subdermal injury when bears outgrew the collar. One injury involved an adult male wearing an adult-sized collar. Another injury involved a maturing female wearing an adult -sized collar. The 6 other injuries occurred when juvenile bears were fitted with expandable collars. Injuries occurred both when collars expanded as designed (*n* = 3) and when collars failed to expand (*n* = 2). Four of 6 injuries resulted from collars worn >2 years because we were prevented from removing them by inaccessible dens, unsuccessful trapping, and loss of signal.

During 414 den visits, there were 33 instances when bears fled dens upon our approach. Nine of these instances (27%) involved adult females with offspring (5 with cubs, 4 with yearlings). Following our disturbance, 4 of 5 females with cubs were believed to have returned to their dens. One female abandoned a single cub, which was removed from the den and cross-fostered with another adult female with cubs. When disturbed, 3 of 4 females with yearlings fled without their offspring, while 1 of 4 fled along with her single yearling. One of the 3 females that fled without their yearlings returned to the den, while 2 did not return. It was unknown if 1 of these females reunited with her offspring, but the other was handled in a second den and her yearlings were not with her. One female on the NSA fled her den each time we visited it, including 4 times when we immobilized her as she fled the den. This bear accounted for 4 of the 9 incidents described above (3 with cubs, 1 with yearlings).

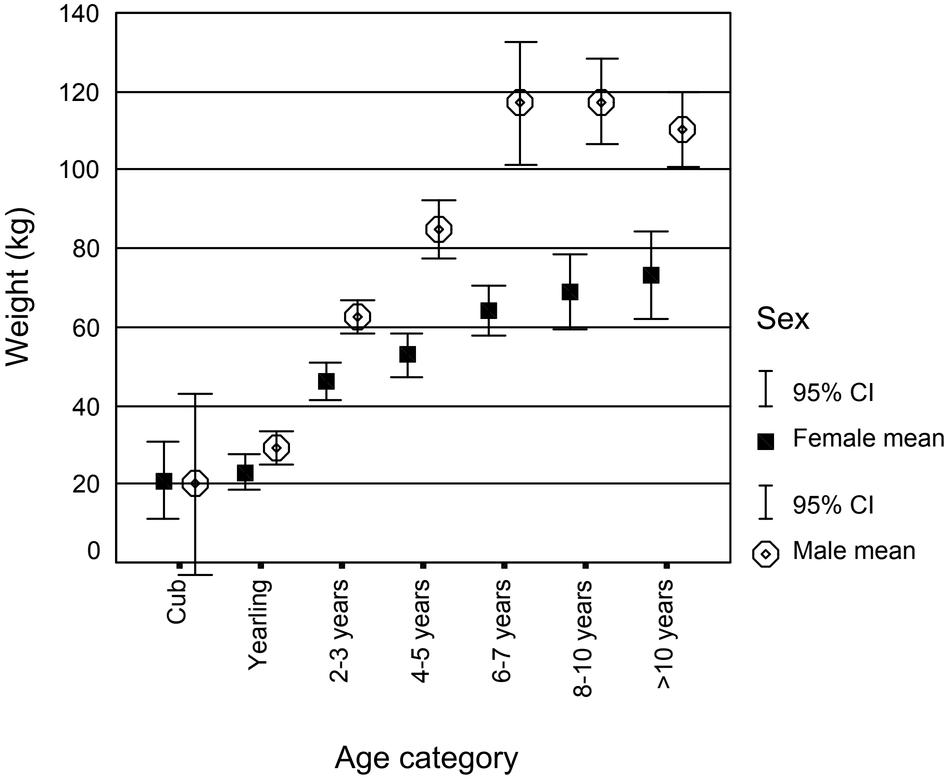


Figure 4-1. Mean and 95% confidence interval for weight (kg), by age category, of female and male black bears, recorded during the trapping season (May-October) on the Northern and Southern Study Areas, New Mexico, 1992-1999.

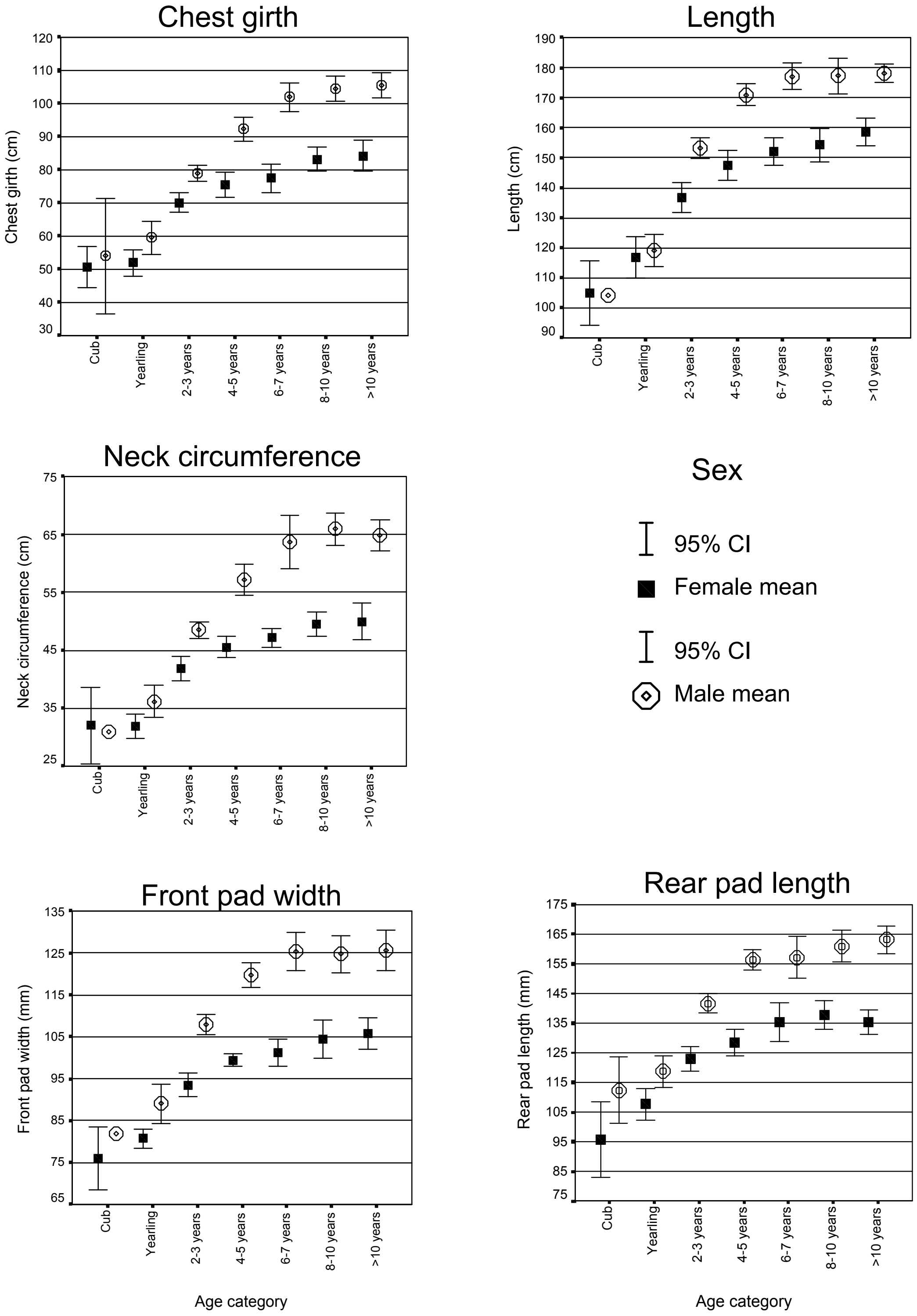


Figure 4-2. Mean and 95% confidence interval for measurements, by age category, of female and male black bears, recorded during the trapping season (May-October) on the Northern and Southern Study Areas, New Mexico, 1992-1999.

CHAPTER 5

VARIATION IN MAST PRODUCTION

A positive correlation between food abundance and black bear reproductive success has been widely reported, based on annual variability in foods (Jonkel and Cowan 1971, Rogers 1976, Eiler et al. 1989, Elowe and Dodge 1989, McLaughlin et al. 1994, Miller 1994), geographic variability in foods (Schwartz and Franzmann 1991, McLaughlin et al. 1994, Miller 1994) and differential feeding behaviors among bears (Rogers 1976, Elowe and Dodge 1989). In most studies, availability of hard mast (e.g., acorns and beechnuts) and soft mast (e.g., huckleberries and blueberries) appeared to have the greatest influence on reproduction. Reproductive success also has been linked to female nutritional condition (Kolenosky 1990, Noyce and Garshelis 1994, Samson and Huot 1995).

A first step in understanding New Mexico black bear ecology and population dynamics was to verify use and availability of mast species. We investigated bear foraging habits and variation in mast production on the 2 study areas during 1993-2000. Our objectives were to: (1) identify important mast species consumed by New Mexico black bears; (2) document annual variation in mast production of these species; (3) determine relationships between weather parameters and mast production; and (4) evaluate the feasibility of implementing statewide mast production surveys.

METHODS

Foraging Habits

We quantified bear foraging habits from scat analysis and observation. During 1992-1995, we collected scats incidental to field work. In addition, we visited selected ground locations identified from aerial telemetry to collect scats and observe bear sign. We recorded approximate date of deposition, location, and habitat descriptions for each scat. Data on other bear sign and activity also were noted. We analyzed scats using methods described by Hatler (1972) and visually estimated percent volume of each food item. We summarized scat contents during 3 seasons: premast (den emergence-20 July), early mast (21 July-15 September), and late mast (16 September-den entrance). During 1995-1996, we documented general trends in foraging habits by recording observations of bear sign and identifying primary contents of scats in the field.

Study Area Mast Surveys

We conducted mast production surveys to quantify annual variation in food abundance on the 2 study areas. Surveys were limited to species contributing most to bear diets, based on scat analysis, field observations, and previous studies in the Western U.S. On the NSA, surveyed species included Gambel oak (*Quercus gambelii*), wavyleaf oak (*Q. undulata*), pinyon (*Pinus edulis*), Rocky Mountain juniper (*Juniperus scopulorum*), one-seed juniper (*J. monosperma*), and chokecherry (*Prunus virginiana*). On the SSA, surveyed species included Gambel oak, gray oak (*Q. grisea*), pinyon, alligator juniper (*J. deppeana*), Utah juniper (*J. osteosperma*), and orange gooseberry (*Ribes pinetorum*). Timing of surveys coincided with the period just prior to peak ripening (mid August to mid September), to ensure most fruit were fully formed, but losses to wildlife were minimal.

We established mast survey routes across study areas designed to encompass variation in elevation and aspect. Survey routes followed roads, jeep trails, or foot trails, and ranged from approximately 0.8-8.0 km (0.5-5.0 mi), depending on the extent of appropriate habitat. On each transect, we designated 2-10 survey sites at predetermined intervals of 0.2-1.6 km (0.1-1.0 mi). At each site, we walked 10 paces away from the road and classified production for the closest 1-10 (usually 5) plants of each species. The same survey routes and sites were revisited each year, with the same number of plants classified at each site. One hundred individual plants were classified for oaks, junipers, pinyon, and gooseberry. Forty individual plants were classified for chokecherry. All species, except for chokecherry, were surveyed on 2-5 separate survey routes.

Ratings were assigned as described by Graves (1980): no visible fruit = 0; fruit visible after very close inspection = 2; fruit readily visible, but not covering entire plant = 4; or fruit readily visible and covering entire plant = 8. This sequence of numbers was chosen because it roughly represented a minimum ratio of fruit/plant among the 4 classifications.

Analyses were performed using SPSS statistical software (SPSS, Chicago, Illinois). Mean ratings were calculated for each species by year. Because the rating data were ordinal, the Kruskal-Wallis (KW) rank procedure was used to test for annual differences, by species and genera. The Student-Newman-Keuls (SNK) test was then used to detect differences among mean ranks and identify homogenous subsets (pool years). We used mean ratings of homogenous subsets to characterize mast production by species or genera, with the following ranges of values as guidelines: 0.0 - 1.4 = failure; 1.5 - 2.4 = poor; 2.5 – 3.9 = moderate; 4.0 – 4.9 = good; 5.0 – 6.0 = excellent. These ranges of values were flexible under certain circumstances. For example, if the mean rating of subset A was 1.6 and the mean rating of subset B was 2.4, subset B might be designated as “moderate” to differentiate it from subset A.

Relationship with Weather Variables

Forward and backward stepwise linear regressions, using S-PLUS 2000 statistical software (Insightful Corporation, Seattle, Washington), were performed using average oak mast index as the response variable. Explanatory environmental variables considered included temperature, last frost date, seasonal rainfall, and seasonal Palmer Drought Stress Index, all varying both between study areas and from year to year on each study area. Additional statewide variables, which differed from year to year but were the same for both study areas each year, were annual total wildland fire acres, winter El Nino state estimated by NOAA (coded as +1 for warm El Nino conditions, -1 for cold or La Nina conditions, and 0 for neutral). One-year time lags were considered. Analyses were run using 1993-1999 mast observations, to be tested with 2000 observations, and also with 1993-2000 mast observations.

District Mast Surveys

During 1999-2000, we distributed simplified mast survey forms to New Mexico Department of Game and Fish officers whose districts included bear habitat. For these surveys, mast production was assessed at the genera level for oaks, junipers, and pinyon. Officers were asked to observe mast production any time during September, coincident with other field activities, and answer the following questions for each genera (no specific training given to officers):

(a) What percentage of plants had fruit? (circle one)
< 25% = 1; 25-50% = 2; 51-75% = 3; > 75% = 4

(b) In general, of plants bearing fruit, how would you characterize the number of fruit per plant? (circle one or two)
scarce = 2; moderate = 3; abundant = 4; super abundant = 5

(c) How would you characterize overall fruit production? (circle one)
mast failure = 1; poor = 2; moderate = 3; good = 4; bumper crop = 5

For summarizing data, the subjective criteria were substituted with numerical variables, as shown above. Numerical values to questions (a) and (b) were multiplied to produce a mast production “score”. Numerical answers to question (c) were used as mast production "assessment". Officer surveys were summarized on a regional basis. Mean scores and assessments were calculated for each of the following mountain regions (see Chapter 11):

San Juan complex (San Juan and Jemez Ranges, Navajo Dam area)
Sangre de Cristo complex
Central (Sandia, Manzano, Zuni, and San Mateo ranges)
Gila complex (Mogollon, Tularosa, Mimbres, Gallinas, and Animas ranges)
Southeast (Sacramento, Capitan, and Guadalupe ranges)

We used Spearman’s rank correlation procedure to compare our mast survey results to scores and assessments provided by officers from the 2 Districts encompassing the study areas.

Follow-up Telephone Survey

We conducted a follow-up telephone survey during October-December 1999. Personnel from NMDGF were asked several questions regarding the ease of the survey, the time spent on the survey, and their willingness to participate in the survey on an annual basis.

RESULTS

Foraging Habits

Analysis of scats collected during 1993-1995, indicated most of the annual diet was plant matter on both study areas (Table 5-1). Diets during the pre-mast season (den emergence – 20 July) were dominated by grasses and forbs. On the NSA, most of diet was grasses, including *Poa*, *Festuca*, and *Muhlenbergia*. On the SSA, grasses and sedges were most dominant, including *Poa*, *Festuca*, *Muhlenbergia, Piptochaetium* and *Carex.*, Forbs appeared to be more important on the SSA, and included vetch (*Vicia* spp.), peavine (*Lathyrus* spp.), and golden pea (*Thermopsis rhombifolia*). Blossoms of New Mexico locust (*Robinia neomexicana*) also were consumed. On both study areas, ants (Formicidae) constituted a significant portion of the pre-mast season diet. Unlike the NSA, soft mast was a significant portion of the pre-mast diet for bears on the SSA. Mast species consumed included alligator juniper, Utah juniper, squawroot (*Conopholis alpina*), gooseberry (*Ribes* spp.), and hawthorn (*Crataegus* sp.).

Mast species became more dominant in the diets of bears on both study areas during the early mast season (21July – 15 September), and consumption of vegetation and ants was reduced. On the NSA, acorns of Gambel oak and wavyleaf oak were most common, comprising 56% of the scat volume. Other mast species consumed included chokecherry, squawroot, and gooseberry. On the SSA, important species consumed included juniper berries, acorns, pinyon nuts, gooseberries, prickly pear fruit (*Opuntia* spp.), and squawroot.

During the late mast season (16 September – den entrance), mast was the dominant food on both study areas. On the NSA, 88% of the scat volume was mast, with acorns comprising 87%. On the SSA, 82% of the diet was mast, with acorns accounting for 36%. Other species included juniper and prickly pear.

Observations and field examination of scats during 1995-2000 concurred with scat analysis findings reported above. On the NSA, grasses and insects were the most commonly observed pre-mast foods. During the early and late mast seasons, observations indicated acorns were the primary food sought by bears. However, consumption of 5 other soft mast species, not found during 1992-1995, were recorded. During the early mast season bears were observed to forage on squawbush (*Rhus trilobata*), wild plum (*Prunus americana*), and kinnikinnick (*Arctostaphylos uva-ursi*), and during the late mast season bears were observed to forage on Rocky Mountain juniper and one-seed juniper. Most juniper scats were encountered at den sites, indicating this food was primarily consumed during the late fall, just prior to den entry.

Table 5-1. Percent volume and percent frequency (in parentheses) of food items identified from black bear scats collected on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-1995.

	NSA			SSA		
Item	Pre-Mast Season[a] (*n* = 44)	Early Mast Season[b] (*n* = 20)	Late Mast Season[c] (*n* = 50)	Pre-Mast Season (*n* = 53)	Early Mast Season (*n* = 145)	Late Mast Season (*n* = 56)
Vegetation						
Poaceae / Cyperaceae	78 (89)	11 (30)	2 (10)	33 (60)	17 (34)	4 (16)
Forbs	2 (5)			9 (19)	3 (9)	5 (7)
Conopholis spp.		5 (5)		6 (6)	4 (6)	Tr [d] (4)
Robinia neomexicana				5 (6)		
Prosopis glandulosa					3 (5)	
Hard and Soft Mast						
Quercus spp.		56 (60)	87 (98)	1 (6)	7 (10)	36 (43)
Juniperus spp.				2 (6)	32 (46)	36 (52)
Pinus edulis					11 (17)	2 (4)
Opuntia spp.					4 (10)	6 (11)
Ribes spp.		5 (5)		1 (4)	10 (21)	
Prunus virginiana		5 (5)	1 (2)			
Crataegus sp.				3 (4)		
Actea arguta	1 (2)					
Rhamnus sp.					Tr (1)	
Juglans sp.						Tr (2)
Sambucus sp.					Tr (1)	
Unidentified		3 (5)				2 (4)
Insect						
Formicidae	15 (48)	9 (15)	5 (6)	23 (66)	3 (13)	Tr (11)
Vespidae				Tr (4)	1 (4)	
Coleoptera	Tr (2)			1 (8)	Tr (3)	
Orthoptera			2 (2)			
Unidentified larvae	Tr (2)	3 (10)			Tr (1)	Tr (2)
Fungi	0	0	0	0	Tr (3)	2 (4)
Mammal						
Ursus americanus		Tr (5)	Tr (32)		Tr (6)	Tr (14)
Urocyon cinereoargenteus	1 (2)					
Cervidae			2 (8)			
Sciuridae	1 (2)					
Unidentified	Tr (7)			2 (2)	2 (6)	

[a] Den emergence-20 July
[b] 21 July-15 September
[c] 16 September-den entrance
[d] Trace amounts

On the SSA, observations during 1996-2000 also concurred with findings from scat analysis, with 1 possible exception. During 1997 and 1999, we observed bears feeding on juniper berries throughout the active season, beginning as early as April. These observations indicated juniper berries constituted more than 10% of the spring and summer diet as observed from scat analysis. Consumption of 2 other soft mast species, Wright silktassel (*Garrya wrightii*) and squawbush), was noted during 1996-2000.

Study Area Mast Surveys

Mast production varied annually for all species on both study areas ($P < 0.001$). Production of Utah juniper was most variable of the species surveyed, with crops ranging from failure to excellent (Table 5-2). Production of Gambel oak, gray oak, alligator juniper, and orange gooseberry also was variable, with crops ranging from poor to excellent or failure to good. Production of wavyleaf oak, Rocky Mountain juniper, and pinyon was generally low, with only 1 of 8 years exceeding a poor rating on either study area. Although production of one-seed juniper varied among years, all production was rated as failure.

Within most years on each study area, mast production varied by species or genera. With the exceptions of 1997 (NSA) and 2000 (SSA), at least 1 species produced mast in excess of poor each year. We observed only 1 year of outstanding mast production, when production of all species was at least moderate. This occurred on the SSA in 1998. Production of combined oak varied annually on both study areas. Combined juniper production varied greatly on the SSA, but juniper failure occurred every year on the NSA.

Relationship with Weather Parameters

Mast patterns differed between the study areas. The SSA had a higher correlation among species, but more variability within species over time. Analysis focused on environmental associations with oak mast, because oak had a consistent relationship to parturition (see Chapter 6).

For the NSA for 1993-1999, the best regressions with average oak mast used last frost date and El Nino state. Both a regression with frost date alone and a regression with both variables predicted good mast for 2000, as observed, but the regressions were not usable. The single variable model was not significant ($P = 0.185$) and the independent variables were negatively correlated (-0.60) in the model with both variables. For the NSA for 1993-2000, reasonable models were found with a single variable (last frost date) and 2 variables (last frost date and winter El Nino: Table 5-3). With the addition of the year 2000 data points, the correlation between frost date and El Nino (0.07) was eliminated. Both models leave much of the variation in oak mast unexplained, and neither correctly predicts the single NSA mast failure in 1993.

Table 5-2. Mast production survey results for 10 woody plant species examined on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-2000.

			Mast Production Rating by Year							
Area	Species	N	1993	1994	1995	1996	1997	1998	1999	2000
NSA	Gambel Oak	100	1.2[a] P[b]	3.4 M	1.6 P	3.3 M	2.3 P	3.5 M	1.5 P	5.9 E
	Wavyleaf Oak	100	0.6 F	3.3 M	2.4 P	1.9 P	2.3 P	2.8 P	2.4 P	2.0 P
	Combined Oaks	200	0.9 F	3.4 M	2.0 P	2.6 P	2.3 P	3.2 M	1.9 P	4.0 M
	Rocky Mtn. Juniper	100	2.6 M	0.3 F	0.1 F	0.6 F	1.6 P	1.7 P	0.8 F	1.0 F
	One-seed Juniper	100	0.1 F	0.8 F	0.2 F	0.02 F	0.8 F	0.3 F	0.9 F	0.04 F
	Combined Junipers	200	1.4 F	0.5 F	0.1 F	0.3 F	1.2 F	1.1 F	0.9 F	0.5 F
	Pinyon	100	2.4 M	0.5 F	1.2 P	2.2 P	0.3 F	1.4 P	1.8 P	0.4 F
	Chokecherry	40	---	2.9 M	2.4 M	1.6 P	0.6 F	3.9 M	3.1 M	---
SSA	Gambel Oak	100	1.6 F	1.3 F	2.1 P	1.1 F	3.5 M	4.6 G	0.7 F	1.5 F
	Gray Oak	100	2.5 M	1.1 F	4.1 G	0.6 F	1.6 P	4.4 G	0.1 F	0.0 F
	Combined Oaks	200	2.1 P	1.2 F	3.1 M	0.9 F	2.5 P	4.5 G	0.4 F	0.7 F
	Alligator Juniper	100	---	0.5 F	0.5 F	0.5 F	1.8 P	4.6 G	0.5 F	0.4 F
	Utah Juniper	100	---	4.4 G	4.9 G	2.2 P	4.6 G	5.9 E	1.8 P	0.8 F
	Combined Junipers	200	---	2.5 M	2.7 M	1.3 F	3.2 M	5.2 E	1.1 F	0.6 F
	Pinyon	100	1.3 F	0.2 F	1.1 F	0.8 F	0.4 F	3.6 M	0.1 F	0.1 F
	Orange Gooseberry	100	4.4 G	1.7 P	0.2 F	3.3 M	2.2 P	3.6 M	3.4 M	---

[a] Individual plants were visually rated using the following criteria and mean ratings are shown: no visible fruit = 0; fruit visible after very close inspection = 2; fruit readily visible, but not covering entire plant = 4; or fruit readily visible and covering entire plant = 8.

[b] Letters refer to the following relative scale for mast production: F = Failure, P = Poor, M = Moderate, G = Good, or E = Excellent. For each species, annual estimates designated with distinct letters were different based on the Kruskal-Wallis rank sum and Student-Newman-Keuls tests ($P \leq 0.10$).

For the SSA, good regressions with average oak mast were found with either winter El Nino state or average April temperature for 1993-2000 (Table 5-3). Models for 1993-1999 were nearly identical. El Nino and April temperature are strongly negatively correlated (-0.76 for 1993-1999 and –0.80 for 1993-2000), so the 2 models are related. The El Nino model correctly predicts the mast failures in 1996, 1999, and 2000, but not in 1994. The April temperature model correctly predicts the mast failures in 1996 and 2000, but not in 1994 or 1999.

Table 5-3. Regressions predicting average oak mast production from weather parameters for the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-2000.

Area	Model	Variable	Coefficient	*t*-value	*Model* R^2	Model *P*
NSA	1-variable	Intercept	12.4215	3.5	0.56	0.03
		Date of last 28°F frost	-0.0844	-2.8		
	2-variable	Intercept	12.1190	3.6	0.67	0.07
		Date of last 28°F frost	-0.0818	-2.8		
		Winter El Nino state	-0.3455	-1.3		
SSA	1-variable	Intercept	1.9250	6.8	0.72	<0.008
		Winter El Nino state	1.2833	3.9		
	1-variable	Intercept	18.3257	3.2	0.58	0.03
		Average April temperature	-0.3325	-2.9		

District Mast Surveys

Combining all genera, mast scores and evaluations were highly correlated (Spearman’s *r* = 0.82, *P* < 0.001, *n* = 58), indicating both criteria (Question a*b vs. Question c) produced similar relationships. On the 2 study areas, scores were highly correlated with survey results (Spearman’s *r* = 0.0.72, *P* = 0.008, *n* = 12), as were assessments (Spearman's *r* = 0.76, *P* = 0.004, *n* = 12), but scores displayed less variation at the lower levels.

Summarizing data for the 5 mountain regions, mast production was either failure or poor for all genera (Table 5-4). However, a few districts reported moderate and good production of oak and juniper. Some districts also reported moderate pinyon production, but none reported good production.

Phone Survey

Twenty-two NMDGF officers were interviewed in the follow-up phone surveys, but 3 (14%) did not complete mast surveys in their districts. One respondent thought the survey pertained only to an adjacent district; 1

respondent felt there was only marginal bear habitat in his district, therefore a survey was not necessary; and 1 respondent said he did not have time to participate.

Nineteen (86%) of the 21 NMDGF officers interviewed completed mast surveys in their districts. Summary of responses to 6 questions indicated that most respondents (94%) said it was easy to evaluate mast production using the criteria provided, while 1 respondent (5%) said it was moderately difficult. More than half of respondents (67%) said it was easy to evaluate their entire district, while several respondents (28%) said it was moderately difficult, and 1 respondent (6%) said it was difficult.

Similarly, more than half of respondents (64%) did not believe their districts needed to be subdivided for this survey, while several respondents (36%) believed districts should be subdivided. Two NMDGF personnel subdivided their districts by Game Management Unit (GMU) for the mast survey, and several respondents also suggested this option during the phone surveys. One respondent identified 4 separate sections of bear habitat within a district, but said these areas did not correspond with GMU boundaries. One other respondent suggested adding a section on the form for a description of the areas surveyed.

Almost all respondents (95%) said they were able to complete the surveys in the course of their usual duties; only 1 respondent (5%) said he had to devote specific time to the survey, but he added that it was not a large time commitment. All respondents agreed mast survey information is important for bear management, but several respondents voiced concern over how data would be used, or whether the surveys were detailed enough to be useful. All respondents (100%, n = 20) said they would be willing and able to participate in the survey on an annual basis. One respondent suggested the survey period be extended into October, since mast is still available, and officers spend many hours patrolling during that month.

DISCUSSION

Oak production was highly variable on both study areas, especially that of Gambel oak and gray oak. On the NSA, only 1 oak failure was recorded in 8 years of study, however 4 oak failures were recorded on the SSA in the same period. Continuation of mast surveys may allow us to determine if these observed frequencies of oak failure are consistent within the 2 regions of the state. Production was highly variable for Utah and alligator juniper, but was consistently low for Rocky Mountain and one-seed-juniper. If further surveys indicate a consistent trend, the lack of abundant juniper berries throughout northern New Mexico, where Utah and alligator juniper are largely absent, may have important implications for bear population dynamics. According to popular thought, abundant pinyon production occurs only once every 7 years. Results of our surveys concur with that belief, in that there was only 1 year of moderate production on each study area in 8 years. Results of statewide mast surveys showed, in most areas, mast production was relatively low in both 1999 and 2000.

The variables correlated with oak production were temperature and El Nino winter state, suggesting that a combination of moisture and temperature conditions for the winter and spring influence mast conditions in the following fall. Each of the oaks surveyed were species that flower and fruit within the same year, and we observed oak flowering from mid May-early June. Models for the NSA and SSA used different variables, and no useful relationship was found that applied to both areas. All of the models failed to predict at least 1 mast failure year; none predicted mast failure when no failure was observed.

MANAGEMENT IMPLICATIONS

Environmental cues did not provide a prediction of mast conditions adequate for bear management needs. Results of simplified surveys conducted by NMDGF officers were highly correlated with our more intensive survey results, indicating subjective criteria were adequate to distinguish variation in mast production. Results were most consistent with a score of relative numbers of fruit/plant and relative numbers of plants bearing fruit. Most officers indicated the criteria were reasonably easy to use and said they were able to complete the surveys in the course of their usual duties. Although most NMDGF officers were comfortable making assessments for their entire districts, others felt subdivision of their district into sections or Game Management Units made the assessments more realistic. Quality assessments of regional mast production will always be improved with higher sample sizes, therefore subdivision of districts may be preferable to district-wide surveys.

Table 5-4. Results of mast production surveys conducted by New Mexico Department of Game and Fish District Officers, New Mexico, 1999-2000[a].

		1999			2000		
Genera	Region / District	a*b	c	Rating	a*b	c	Ratings
Oak	San Juan complex						
	Aztec				4	3	P
	Chama				8	4	M
	Jemez Springs	2	1	F			
	Navajo Dam	1	1	F			
	Tres Piedras (GMU 51)	4	3	P			
	Tres Piedras (GMU 52)	12	4	G			
		4.8	**2.4**	**P**	**6.0**	**3.5**	**P**
	Sangre de Cristo						
	Cimarron	4	3	P	12	4	G
	Mora	4	3	P	4	3	P
	Pecos				1	2	F
	Penasco	1	2	F	1	2	F
	Raton	1	2	F	9	4	M
	Santa Fe	2	2	F			
		2.4	**2.4**	**F**	**5.4**	**3.0**	**P**
	Central						
	Belen	1	1	F	1	2	F
	Gallup	3	2	F	3	2	F
	Grants				1	2	F
	Grants (GMU 9)	9	4	M			
	Grants (GMU 10)	2	2	F			
	Grants (GMU 13)	3	3	F			
	Moriarty	1	2	F			
		2.8	**2.1**	**F**	**1.7**	**2**	**F**
	Gila complex						
	Quemado	1	2	F			
	Reserve	1	2	F	1.5	2	F
	Silver City	1	2	F	1	2	F
	Socorro				6	2	P
	T or C	1	2	F	4	3	P
		1.0	**2.0**	**F**	**3.1**	**2.3**	**F**
	Southeast						
	Alamagordo	3	2	F	1	2	F
	Carlsbad	1	1	F			
	Mayhill				9	4	M
	Mountainaire				2	2	F
	Ruidoso	4	3	P			
		2.7	**2.0**	**F**	**4.0**	**2.7**	**P**
Juniper	San Juan complex						
	Aztec				9	4	M
	Chama				4	3	P
	Jemez Springs	2.5	1	F			
	Navajo Dam	1	2	F			
	Tres Piedras (GMU 51)	4	3	P			
	Tres Piedras (GMU 52)	9	4	M			
		4.1	**2.5**	**P**	**6.5**	**3.5**	**P**
	Sangre de Cristo						
	Cimarron	4	3	P	2	2	F
	Mora	4	3	P	6	3	P
	Pecos				1	2	F

		1999			2000		
Genera	Region / District	a*b	c	Rating	a*b	c	Ratings
	Penasco	12	4	G	4	2	P
	Raton	1	2	F	6	3	P
	Santa Fe	12	4	G			
		6.6	**3.2**	**P**	**3.8**	**2.4**	**P**
	Central						
	Belen	1	2	F	1	2	F
	Gallup	4	2	P	10	4	M
	Grants				4	3	P
	Grants (GMU 9)	4	3	P			
	Grants (GMU 10)	3	2	F			
	Grants (GMU 13)	3	2	F			
	Moriarty	2	3	F			
		2.8	**2.5**	**F**	**5.0**	**3.0**	**P**
	Gila complex						
	Quemado	1	2	F			
	Reserve	4	2	P	1.5	1	F
	Silver City	4	3	P	9	4	M
	Socorro				1	1	F
	T or C	4	3	P	2	2	F
		3.2	**2.5**	**F**	**3.4**	**2.0**	**F**
	Southeast						
	Alamagordo	1	1	F	1	1	F
	Carlsbad	3	3	F			
	Mayhill				9	4	M
	Mountainaire				6	3	P
	Ruidoso	6	3	P			
		3.3	**2.3**	**F**	**5.3**	**2.7**	**P**
Pinyon	San Juan complex						
	Aztec				4	3	P
	Chama				4	3	P
	Jemez Springs	2	1	F			
	Navajo Dam	6	3	P			
	Tres Piedras (GMU 51)	4	3	P			
	Tres Piedras (GMU 52)	9	4	M			
		5.3	**2.8**	**P**	**4.0**	**3.0**	**P**
	Sangre de Cristo						
	Cimarron	6	3	P	1	2	F
	Mora	3	3	F	2	2	F
	Pecos				1	1	F
	Penasco	1	2	F	1	2	F
	Raton	1	2	F	2	2	F
	Santa Fe	4.5	3	P			
		3.1	**2.6**	**F**	**1.4**	**1.8**	**F**
	Central						
	Belen	4	3	P	1	1	F
	Gallup	6	4	P	6	3	P
	Grants				1	1	F
	Grants (GMU 9)	9	4	M			
	Grants (GMU 10)	6	3	P			
	Grants (GMU 13)	9	4	M			
	Moriarty	4	3	P			
		6.3	**3.5**	**P**	**2.7**	**1.6**	**F**
	Gila complex						

Genera	Region / District	1999 a*b	1999 c	1999 Rating	2000 a*b	2000 c	2000 Ratings
	Quemado	1	2	F			
	Reserve	1	2	F	1	1	F
	Silver City	1	2	F	9	4	M
	Socorro				1	1	F
	T or C	1	2	F	1	2	F
		1.0	**2.0**	**F**	**3.0**	**2.0**	**F**
	Southeast						
	Alamagordo	1	1	F	1	1	F
	Carlsbad	1	1	F			
	Mayhill				9	4	M
	Mountainaire				4	3	P
	Ruidoso	6	3	P			
		2.7	**1.7**	**F**	**4.7**	**2.7**	**P**

[a] Officers assessed production of oak, juniper, and pinyon production using the following subjective criteria: mean number of fruit/plant on a scale of 1-4 (a), percent of plants bearing fruit on a scale of 1-4 (b), and overall production on a scale of 1-5 (c). Scores (a*b) were highly correlated with more intensive surveys conducted concurrently (Spearman's *r* = 0.0.72, *P* = 0.008, *n* = 12), and ratings were calculated using the equation of the line. Letters refer to the following relative scale for mast production: F = Failure, P = Poor, M = Moderate, G = Good, or E = Excellent.

CHAPTER 6

REPRODUCTION AND CUB SURVIVAL

Maintenance and growth of wildlife populations are closely tied to reproductive output. Collectively, bear species exhibit some of the lowest reproductive rates among terrestrial mammals (Bunnell and Tait 1981). In many previous bear studies, a positive correlation between food abundance and black bear reproduction has been reported, based on annual variability in foods (Jonkel and Cowan 1971, Rogers 1976, Eiler et al. 1989, Elowe and Dodge 1989, McLaughlin et al. 1994, Miller 1994), geographic variability in foods (Schwartz and Franzmann 1991, McLaughlin et al. 1994, Miller 1994), and differential feeding behaviors among bears (Rogers 1976, Elowe and Dodge 1989). Reproductive success also has been linked to female nutritional condition (Kolenosky 1990, Noyce and Garshelis 1994, Samson and Huot 1995). Understanding the reproductive rates of black bears in New Mexico, as well as the factors that influence success, is important for monitoring population trend. On an annual basis, collection of actual data on bear reproduction would probably be labor-intensive and cost-prohibitive. However, documentation of annual variation in food abundance may serve as an index to bear reproductive success.

We investigated black bear reproductive success on the 2 New Mexico study areas during 1993-2000. Our objectives were to (1) document black bear reproductive parameters, including age of primiparity, natality, cub survival, recruitment, and litter interval; and (2) investigate relationships between mast production and reproductive parameters.

METHODS

Data on natality, litter size, and recruitment were collected during annual den investigations of radio-collared bears. We visited dens of adult females each year to ascertain their reproductive status. Dens of 2- or 3-year-old bears were visited annually or biannually to change or refit collars as necessary. We obtained cub survival data by revisiting dens of females whose cubs were handled or observed the previous year. Cubs were assumed to have died if they were absent from the den as yearlings, or if their mother died prior to 1 July in their birth year. Cubs whose mother died after 1 July and cubs whose fate was unknown (due to mother shedding collars, lost signals, inaccessible dens, etc.) were excluded from analyses.

We estimated mean age when the first litter is produced (age of primiparity) by constructing a cumulative table of ages for bears that had never give birth versus ages of bears when they first produced cubs.(Garshelis et al. 1998). The minimum age of primiparity was judged to be 4 years old, because no 1-, 2-, or 3-year-old bear was observed with cubs in the den (*n* = 76), and no

1- or 2-year-old bear was observed in estrus when captured between May and September (*n* = 21). We constructed the cumulative table by first including all bears whose reproductive status was verified during annual den investigations beginning at age 4 (*n* = 36). We also included females captured at age 4, whose reproductive status was judged from teat measurements, weight, lactation, or observation of cubs (*n* = 11). Among females captured at age 5, we included bears judged to never have given birth from teat measurements and weight, but entered them into the table only for later den investigations (*n* = 2). To backdate them to age 4 or include them for the year of capture would bias the sample against bears captured with their first cubs, because we could not distinguish first litters from subsequent litters for bears captured at ages >4 years. We used the same procedure to estimate mean age of primiparity relative to mast production during the previous fall (year-1).

We tested for variation in reproductive success relative to mast production using Mann-Whitney (MW), Kruskal-Wallis (KW), Chi-square, and Student-Newman-Keuls (SNK) tests. We report specific p-values associated with any differences declared. Annual reproductive events for the same female were treated as independent observations, as were offspring from the same female. When possible, we separated females into distinct subsets to lessen effects of any potential lack of independence. Variation in reproductive parameters was investigated relative to mast production during the previous fall (year-1) and relative to fall mast production 2 years previous (year-2). Mast production categories included combined oaks, combined junipers, pinyon, and softmast (chokecherry or gooseberry).

To construct a sample for estimating mean litter interval, we first included all bears whose interval was verified during annual den investigations (*n* = 63). We also included females whose interval was known from observation of offspring at capture (*n* = 2), and bears whose incomplete interval was known to be at least 3 years (*n* = 7). We included these latter bears in the analyses because long intervals were more difficult to document than short intervals. Reproductive status must be documented for at least 3 consecutive years to document a successful 3-year interval and at least 4 years for an unsuccessful 3-year interval. During this study, reproductive status was documented <3 times for 38% of individual bears (*n* = 64), reducing the likelihood of documenting longer intervals.

RESULTS

Age of First Birth

Age at birth of first litter was documented for 31 bears between 1992 and 2000, and mean age from this sample was 5.5 years. However, age(s) prior to primiparity were documented for another 18 bears aged 4-6. Ultimate age of primiparity was not documented among this sample because of collar removals at the end of the study (n = 6), collar removal due to a wound (n = 1), mortalities (n = 4), shed transmitters (n = 4), and lost signals (n = 3).

Among bears observed at each age that had not produced litters previously, only 9% of 4-year-old bears produced their first litters, while 40% of 5-year-olds, 67% of 6-year-olds, 75% of 7-year-olds, and 100% of 9-year-olds produced their first litters (Table 6-1). Proportions differed among ages (X^2 = 27.1, df = 5, $P < 0.001$, n = 97), with 4-year-old females having the most significant residual. When this age was excluded, proportions did not differ among other ages (X^2 P= 0.21, n = 51). Proportions did not differ between study areas within any age (X $P \geq 0.47$). Accounting for the proportion of previously non-reproductive bears in the population at each age, analysis indicated 9% of bears produced their first litter at age 4, 37% at age 5, 36% at age 6, 14% at age 7, and 5% at age 9. The mean age of primiparity calculated from these percentages was 5.7 years. Mean age of primiparity was 5.8 years on the NSA and 5.7 years on the SSA. Although age of primiparity varied by 5 years among the entire sample, analyses indicated most bears (73%) produced their first litter either at age 5 or 6.

Table 6-1. Observed percent of previously non-reproductive female black bears (by age) that produced first litters, on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-2000.

	Age (years)[a]						Mean
Area	4	5	6	7	8	9	age
NSA							
n	28	19	8	3	1	1	
% of *n* with first litters	11	37	63	67	0	100	
Cumulative % with first litter	11	44	79	93	93	100	
Incremental % with first litter	11	33	35	14	0	7	5.8
SSA							
n	19	11	6	1			
Percent of *n* with first litters	5	46	67	100			
Cumulative % with first litter	5	48	83	100			
Incremental % with first litter	5	43	40	17			5.6
Combined							
n	47	30	14	4	1	1	
Percent of *n* with first litters	9	40	64	75	0	100	
Cumulative % with first litter	9	45	80	95	95	100	
Incremental % with first litter	9	36	35	15	0	5	5.8

[a] Proportions of previously non-reproductive bears that produced first litters were different among ages ($P < 0.001$), but were not different within ages between study areas ($P > 0.45$). Mean age at birth of first litter was calculated using incremental percentages.

Mean age of primiparity appeared to differ by oak production during the previous fall, however mean testing was not possible using this method. Mean age of primiparity following oak failure was 6.3 years. Mean age of primiparity following poor, moderate, and good oak production was 5.7 years, 5.7 years, and 5.8 years, respectively.

Natality

Between 1993 and 2000, reproductive data were obtained during 268 den investigations of 80 female bears aged 4-27 years. We estimated natality (cub production) using observations from all females. In addition, we separated the sample into 2 categories: non-reproductive females (those never having produced cubs prior to the current observation) and eligible reproductive females (those having produced cubs prior to the current observation). We considered all bears unaccompanied by yearlings "eligible" for cub production.

Overall natality of female bears ≥ 4 years old was 0.77 cubs/female/year and parturition rate (percent of females with cubs) was 43% ($n = 268$). Overall there was no difference (0.85 vs. 0.67, MW, $Z = -1.4$, $P = 0.15$) in natality on the NSA versus the SSA (Table 6-2). Parturition rate also did not differ by study area (X^2 $P = 0.32$). Among previously non-reproductive females, natality was 0.53 cubs/female/year and parturition rate was 33% ($n = 87$). Neither rate differed by study area (MW $P = 1.0$, X^2 $P = 0.81$). Among previously reproductive females, natality was 1.4 cubs/female/year and parturition rate was 77% ($n = 112$). Natality among these female bears was higher on the NSA (1.6 vs. 1.2, MW, $Z = -2.3$, $P = 0.02$), as was parturition rate (62% vs. 37%, $X^2 = 4.8$, df = 1, $P = 0.04$).

Table 6-2. Natality and recruitment of female black bears determined from den investigations on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-2000. Females were considered eligible for cub production if unaccompanied by yearlings in the den. Rates denoted by asterisks differed from others by reproductive history or study area ($P \leq 0.15$).

Area/	Natality (all females)			Natality (eligible females)			Recruitment (all females)		
Category of female	n	Rate[a]	%[b]	n	Rate[a]	%[b]	n	Rate[c]	%[d]
NSA	155	0.9	46	118	1.1*	60	133	0.4	27
SSA	112	0.7	39	85	0.9	52	98	0.4	27
Combined	267	0.8	43	203	1.0	57	231	0.4	27
Previously non-reproductive	45	1.0	64	35	1.3*	83	42	0.3	21
Previously reproductive	153	1.0	56	101	1.6	85	152	0.5	34

[a] No. cubs/female/year

[b] Percent of females with cubs

[c] No. yearlings/female/year

[d] Percent of females with yearlings

Within all categories of females, natality and parturition rate were positively associated with oak production during the previous year (Table 6-3). For all females and for reproductive females, natality was lower in years following acorn failures than all other years (KW $P < 0.001$, SNK $P = 0.05$), as was parturition rate (X^2 $P < 0.001$). Neither natality nor parturition rate differed relative to poor, moderate, or good oak production during the previous fall (KW $P \geq 0.37$, X^2 $P \geq 0.23$). Among previously non-reproductive females, natality varied by oak production (KW $P = 0.08$), however no distinct subsets were identified (SNK $P > 0.15$). Parturition rate was positively associated with oak production (X^2 $P = 0.10$), with the lowest rate associated with oak failure. However, among the previously non-reproductive females, strength of the test was limited by an age bias in the sample. Of the 18 previously non-reproductive females observed following oak failure, 13 (72%) were 4-year-olds, and 5 (28%) were aged 5 or 6. Following poor, moderate, and good oak production, 4-year-old females comprised 29% ($n = 45$), 40% ($n = 15$), and 0% ($n = 7$) of the sample, respectively. When 4-year-old bears were analyzed alone, natality was positively but weakly associated with oak production. Natality was 0.2 cubs/female/year following moderate oak production, but 0.0 following oak failure and poor production (KW, $X^2 = 4.3$, $P = 0.12$, $n = 32$, SNK $P = 0.15$). Parturition rate was higher following moderate oak production (0% vs. 17%, $X^2 = 4.4$, $P = 0.11$, $n = 32$). When non-reproductive bears >4 years old were examined, neither natality nor parturition rate varied significantly by oak production during the previous fall (KW $P \geq 0.77$, X^2 $P = 0.91$). Within all categories of females, neither natality nor parturition rate was positively associated with juniper, pinyon, or softmast production during the previous year.

In years following oak failures, natality was lowest when the failure was preceded by poor oak production, among all females and among eligible reproductive females (KW $P \leq 0.09$, SNK $P = 0.05$). When the failure was preceded by moderate or good oak production, 73% of eligible reproductive females produced cubs. However, none produced cubs when the failure was preceded by a poor oak crop ($X^2 = 10.0$, df = 2, $P = 0.007$, $n = 19$). This association was possibly observed for juniper production. During 1993, no juniper survey was completed on the SSA. However, scat analysis and bear weight data indicated juniper production was relatively low. If we assume a juniper failure, or even a poor juniper crop occurred in that year, then natality was positively associated with juniper production during the fall 2 years previous. However, the low oak and juniper production, prior to oak failure, occurred simultaneously, therefore it was not possible to ascertain which genera exerted more of an influence on natality.

Litter Size

A total of 115 litters were handled or observed in dens during 1993 - 2000. Litter size ranged from 1-3 cubs and mean litter size was 1.8 cubs (Table 6-4). Two-cub litters were most common (71%), followed by 1-cub litters (24%).

Three-cub litters were rare, accounting for only 5% of observations. Mean litter size on the NSA (1.9) did not differ ($Z = -1.6$, $P = 0.11$) from that on the SSA (1.7). Observed frequencies of 1-, 2-, and 3-cub litters did not differ by study area ($X^2 = 2.6$, df = 2, $P = 0.27$).

Table 6-3. Black bear reproductive parameters associated with variable oak production on 2 New Mexico study areas, 1993-2000. Natality (cubs/female/year) and parturition rates (percent of females with cubs) were analyzed relative to oak production during the previous fall (year-1). Following oak failure, rates were also analyzed relative to fall oak production 2 years previous (year-2). Recruitment rate (yearlings/female/year) and percent of females with yearlings were analyzed relative to fall oak production 2 years previous (year-2). Asterisks indicate distinct subsets differing from other observations within the category, with corresponding *P*-values provided.

Parameter / Category of females	Observations included	Mast year	*n*	Oak production rating[a] F	P	M	G	KW[b] *P*	SNK[c] *P*	X^2 *P*
Natality										
All (age ≥ 4)	All	Year – 1	262	0.3 *	0.9	1.0	0.7	<0.001	0.05	
	Year-1 = F	Year – 2	52		0 *	0.4	0.5	0.09	0.15	
Previously non-reproductive	All	Year – 1	85	0.1	0.6	0.5	0.9	0.08		
Eligible[d] reproductive	All	Year – 1	108	0.7 *	1.6	1.6	2.0	<0.001	0.05	
	Year-1 = F	Year – 2	19		0 *	1.5	1.3	0.01	0.05	
Percent with Cubs										
All (age ≥ 4)	All	Year – 1	262	16 *	47	59	40			<0.001
	Year-1 = F	Year – 2	52		0 *	20	32			0.08
Previously non-reproductive	All	Year – 1	85	11	38	33	57			0.10
Eligible reproductive	All	Year – 1	108	35 *	84	90	100			<0.001
	Year-1 = F	Year – 2	19		0 *	75	72			0.007
Recruitment										
All (age ≥ 5)	All	Year – 2	214	0.1 *	0.4	0.6	0.6	0.003	0.10	
Reproductive	All	Year – 2	157	0.2 *	0.6	0.7	0.7	0.009	0.05	
Percent with Yearlings										
All (age ≥ 5)	All	Year – 2	214	7 *	28	42	38			0.001
Reproductive	All	Year – 2	157	10 *	40	51	46			0.003

[a] F = Failure, P = Poor, M = Moderate, G = Good

[b] Kruskal-Wallis test

[c] Student-Newman-Keuls test

[d] Females were considered eligible for cub production if unaccompanied by yearlings in the den.

First litters were smaller than subsequent litters (1.6 vs. 1.9, $Z = -2.7$, $P = 0.008$, $n = 115$) and frequencies of 1-, 2-, and 3-cub litters also varied ($X^2 = 7.18$, df = 2, $P = 0.03$). Specifically, frequency of 1-cub litters was higher among first litters than among subsequent litters. Litter size did not vary by mast production of any species among all litters, first litters, or subsequent litters (KW $P \geq 0.24$).

Table 6-4. Size (range, mean, and relative frequency) of black bear litters observed on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-2001.

Area/Litter order	*n*	Range (cubs/litter)	Mean[a] (cubs/litter)	Relative frequency[a]		
				1-cub	2-cub	3-cub
NSA	71	1 – 3	1.9	20%	75%	5%
SSA	44	1 – 3	1.7	32%	66%	2%
Combined	115	1 – 3	1.8	25%	71%	4%
First litters	29	1 – 2	1.6*[*]	41%*[*]	59%	
Subsequent litters	86	1 – 3	1.9*[*]	19%*[*]	76%	6%

[a] Means and frequencies denoted by asterisks were different by litter order ($P < 0.10$).

Cub Survival

Cub survival was documented for 148 individual cubs from 82 litters handled or observed in dens between 1993 and 2000. Overall cub survival rate was 0.55, and observed rates did not differ by study area (X^2 $P = 0.22$) or sex (X^2 $P = 0.30$). Among litters observed, 45% experienced no mortality, 20% experienced partial mortality, and 35% were completely lost. Observed frequencies of litter fate did not differ by study area (X^2 $P = 0.53$).

Cub survival was lower among first litters than subsequent litters (38% vs. 60%, $X^2 = 4.9$, df = 1, $P = 0.03$, $n = 148$). Similarly, frequency of whole litter loss was higher among first litters than subsequent litters (57% vs. 30%, $X^2 = 5.7$, df = 2, $P = 0.06$, $n = 84$). Based on these findings, cubs were separated into these 2 categories for further analyses.

Among all litters and first litters, cub survival varied positively with juniper and pinyon production during the previous fall (X^2 $P \geq 0.10$), but no differences were found among subsequent litters (X^2 $P \geq 0.34$). The most significant residual corresponded to 100% cub survival ($n = 5$) observed in 1999, following the single most outstanding year of juniper, pinyon, and oak production on the SSA. Cub survival within the cohort born following 1998 was higher than within the combined cohorts born following years of lower production (100% vs. 56%, $X^2 = 3.9$, df = 1, $P = 0.07$, $n = 133$). When this cohort was excluded from analyses, cub survival no longer differed by juniper or pinyon production during the previous fall (X^2 $P \geq 0.55$). Instead, cub survival appeared to be weakly associated with oak production during the birth year (X^2 $P \geq 0.14$). The most significant residual was associated with cohorts born during years of oak failure. Their survival rate was lower than the rate observed for cohorts born during years of poor to good oak production (33% vs. 57%, $X^2 = 3.1$, df = 1, $P = 0.08$, $n = 136$). The association of low cub survival and oak failure during the birth year was masked when the 1999 cohort was included in analyses. Although this cohort was born during a year of oak failure, it experienced 100% survival, possibly owing to the super abundance of food produced in 1998. Field observations indicated mast of oak, pinyon, and especially juniper remained available long into the spring and summer of 1999, perhaps compensating for the lack of new production.

To account for the interacting effects of mast production during the previous fall and mast production during the birth year, we produced mast indices combining genera over the 2 periods. Cub survival was most significantly associated with an index of juniper production (during the previous fall) and oak production (during the birth year). For these analyses, we presumed juniper failure on the SSA during 1993 (as described above). Low cub survival was associated with mast failure by oak and juniper; intermediate cub survival was associated with poor to moderate production by oak and/or juniper; and high cub survival was associated with good to excellent production by oak and/or juniper. These patterns in survival were observed among all litters (13% vs. 54% vs. 76%, $X^2 = 9.7$, df = 2, $P = 0.008$, $n = 138$) and among subsequent litters (13% vs. 60% vs. 83%, $X^2 = 10.1$, df = 2, $P = 0.006$, $n = 108$). Among first litters, no cubs were born in years when both genera failed, however, higher cub survival was associated with good to excellent production (29% vs. 67%, $X^2 = 3.8$, df = 2, $P = 0.10$, $n = 30$).

Cub survival varied annually on the SSA within all categories (X^2 $P \leq 0.08$). On the NSA, cub survival did not vary annually within any category (X^2 $P \geq 0.13$). The uniform cub survival observed on the NSA was associated with consistent poor to moderate combined mast production. The variable cub survival on the SSA (13% vs. 63% vs. 76%, $X^2 = 9.9$, df = 2, $P = 0.007$, $n = 48$) was positively associated with all 3 levels of mast production. When all observations from the NSA were compared to the SSA observations associated with poor to moderate mast production, no difference was found in the cub survival rate ($P = 0.45$).

Cause of death was rarely documented among cubs, because they were not fitted with radio-transmitters. However, cause of death was documented for 8 cubs, all on the NSA. Two sibling female cubs were killed in August 1993 by an automobile when they attempted to cross a 2-lane highway in Ute Park, adjacent to a campground. These cubs, as well as their mother, frequently obtained food from visitors to the campground and from unsecured garbage containers. In February 1997, a dead female cub was found at the entrance of her den. Her mother and female sibling were hibernating within the den. The position and condition of the carcass indicated she had died at least 6 weeks prior to our discovery and that she had been dragged from the den chamber (probably by her mother). Examination of the carcass indicated a broken pelvis, suggesting she may have died from internal injuries, but cause of the injuries was unknown. This family resided in a part of the study area characterized by very steep slopes adjacent to a 2-lane highway, therefore the injuries may have been sustained in a fall or an automobile collision. Five cubs in 2 litters presumably died from predation, along with their mothers. Although no cub remains were found, evidence indicated their mothers had been killed by predators, possibly bears. The first incident occurred in May 1995 and the second incident occurred in April 1999.

Recruitment

We estimated recruitment using observations from all females ≥5 years old and observations of reproductive females only. Overall recruitment of females ≥5 years old was 0.40 yearlings/female/year and 27% of 232 females were accompanied by yearlings in the den. Rates did not differ by study area (MW $P \geq 0.78$, Table 6-2). Recruitment of previously reproductive females was 0.53 yearlings/female/year and percent of females with yearlings was 35% (n = 175). These rates did not differ by study area either (MW $P \geq 0.79$).

Within both categories, recruitment was positively associated with fall oak production 2 years previous (KW $P \leq 0.09$, SNK $P \leq 0.10$). Specifically, recruitment was lower 2 years after oak failures than all other years (Table 6-3). Percent of females with yearling also was lower 2 years after oak failures than all other years ($P \leq 0.003$). Neither rate differed relative to poor, moderate, or good oak production 2 years previous ($P \geq 0.43$), nor did they differ by production of juniper, pinyon, or softmast production 2 years prior ($P \geq 0.49$).

Litter Interval

We documented 65 complete litter intervals and 7 incomplete intervals known to be at least 3 years, occurring between 1992 and 2001 (Table 6-5). Incomplete intervals ranged from 3-5 years. However 3 of the 7 incomplete intervals (two 3-year intervals and one 5-year interval) were documented for bears believed to have reached reproductive senescence at 16, 24, and 25 years of age, respectively. Because it was likely these bears would not complete the intervals, these 3 observations were excluded from analyses. In fact, the diseased 16-year-old female did not survive to complete her interval.

Observed litter interval ranged from 1-3 years. One-year intervals occurred when entire litters were lost and bears bred again. Two- and 3-year intervals occurred both when litters were lost and cubs survived, but 3-year intervals included an additional year when the bear failed to produce a litter. Mean litter interval was 1.8 years and it was slightly lower on the NSA than the SSA (1.7 vs. 1.9, $Z = -1.7$, $P = 0.09$, n = 69). However, relative frequencies of 1-, 2-, and 3-year intervals were not different between study areas (X^2 $P = 0.15$). Unsuccessful intervals (when entire litters were lost) ranged from 1-3 years with a mean of 1.3 years (n = 27). For unsuccessful intervals, neither mean interval nor frequencies of 1-, 2-, and 3-year intervals differed by study area (X^2 $P > 0.44$). Successful intervals (when some or all cubs survived) ranged from 2-3 years with a mean of 2.1 years (n = 42). Among successful intervals, frequency of 3-year intervals was lower on the NSA (X^2 $P = 0.07$), resulting in a lower mean successful interval (2.0 vs. 2.2, $Z = -1.9$, $P = 0.05$).

Table 6-5. Ranges, means, and relative frequencies of black bear litter intervals observed on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-2001.

Interval type/Area	*n*	Range (years)	Mean[a] (years)	Relative frequency[a] 1-year	2-year	3-year
All intervals						
NSA	44	1 - 3	1.7*	34%	61%	5%
SSA	25	1 - 3	2.0*	20%	64%	16%
Combined	69	1 - 3	1.8	29%	62%	9%
Successful intervals						
NSA	25	2 - 3	2.0*		96%*	4%*
SSA	17	2 - 2	2.2*		77%*	23%*
Combined	42	2 - 3	2.1		88%	12%
Unsuccessful intervals						
NSA	19	1 - 3	1.3	79%	16%	5%
SSA	8	1 - 2	1.4	63%	37%	
Combined	27	1 - 3	1.3	74%	22%	4%

[a] Means and frequencies denoted by asterisks were different by study area (X^2 $P < 0.10$).

Within unsuccessful 2- and 3-year intervals, and within successful 3-year intervals, bears failed to produce cubs at 1 or 2 reproductive opportunities. We observed 14 failed reproductive opportunities, and 71% coincided with oak failures during the previous fall, while 29% coincided with poor to good oak production. Conversely, within 1-year intervals and successful 2-year intervals, bears reproduced at the first reproductive opportunity. We observed 52 successful reproductive opportunities, and only 14% coincided with oak failures, while 84% coincided with poor to good oak production. These observed ratios of failed to successful opportunities varied by oak production ($X^2 = 19.8$, df = 3, $P < 0.001$, $n = 66$).

DISCUSSION

The influence of mast production on age of first production of cubs was not entirely clear. Mean age of first litter appeared to increase in years following oak failure. However, production of first litters did not appear to decline, except among 4-year-old bears. This result was possibly due to the small sample size of previously non-reproductive bears aged >4 years observed during years following oak failure. Among females that had produced multiple litters, a higher frequency of skipped reproductive opportunities occurred following oak failure. Therefore, it would be expected that reproduction of potential first litters would also decline. However, production of first litters may not be determined solely by mast production during the previous year. Instead, a bear's ability to produce her first litter may be influenced by mast production throughout her developing years. Noyce and Garshelis (1994) postulated age at birth of first litter may be more closely tied to cub growth rates and hence the condition of the mother. The more important influence of mast production may be the onset of first estrus. Of 3-year-old females handled between May and September (*n* = 18), only 11% showed signs of estrus, indicating most 4-year-old bears would not reproduce regardless of mast abundance. Even among non-reproductive bears aged 4-6 (*n* = 14), only 43% handled during the mating season appeared to be in estrus.

The influence of oak production, especially acorn failures, on bear reproductive success appeared to be strong. Natality, and subsequently recruitment, was reduced by more than 50% following years of oak failure. Rates were reduced to zero when oak failure was preceded by poor oak production. Availability of hard mast has been tied to reproductive success in several regions (Eiler et al. 1989, Elowe and Dodge 1989, McLaughlin et al. 1994). Neither natality nor recruitment varied following poor, moderate, or even good oak production. Following poor to good production, 94% of eligible reproductively experienced females produced cubs, and no increase in litter size was observed when oak production was high. This suggests only a minimum threshold of high quality food is needed for successful reproduction.

Juniper production possibly had a secondary effect on natality, when oak production failed. Natality rates were zero when oak failure was preceded by poor juniper production. However this poor juniper production coincided with poor oak production, making it impossible to ascertain which genera may have exerted the greater influence on natality. Given the primary effect oak had on reproductive success, it is probable that oak also exerted the greater secondary effect.

Juniper production probably had more of an impact on cub survival than natality. From our observations, juniper berries began to ripen from September to October and remained on the tree through late fall. Berries began to drop during winter and early spring. We observed consumption of significant quantities of juniper berries by bears during fall, spring, and summer (unpublished data). Therefore, more than any other mast genera, juniper could continue to affect the nutritional condition of bears and their cubs long after emergence from the den. Comparing study areas, consumption of juniper berries appeared to be related to production. Juniper production failed each year on the NSA, and only limited consumption of juniper berries was observed, primarily during late fall. The lack of this important spring food, combined with no occurrence of good or excellent fall oak production, resulted in consistent, but low cub survival on the NSA. On the contrary, juniper production varied greatly on the SSA, with crops ranging from failure to excellent. Juniper berries were a significant food item in the spring and summer diets of bears on this area (see Chapter 5). The variable cub survival observed on the SSA was associated with varied levels of juniper and oak production.

No positive association was found between pinyon production and reproductive success. On each study area, pinyon production was better than poor during only 1 year. Unfortunately, on the SSA, the moderate pinyon crop coincided with a good oak crop and an excellent juniper crop in 1998. These simultaneous events did not allow us to assess the effect of pinyon alone on reproductive success. On the NSA, moderate pinyon production occurred in 1993, when both oak and juniper production failed. Nonetheless, natality and recruitment was zero following this production, indicating a moderate supply of pinyon nuts did not compensate for the lack of acorn production. This result may be due to the timing of availability. Pinyon cones mature and open approximately 6 to 8 weeks after the ripening of acorns, possibly limiting the foraging opportunities of bears readying for hibernation. More study is needed to determine the influence of pinyon production on bear reproduction, especially in the absence of other foods.

Production of chokecherries and gooseberries did not appear to influence reproductive success. Compared to the other species surveyed, these soft mast species were more limited in distribution, and were probably available to only a fraction of the bear population. Analyses of foraging habits indicated these species also accounted for <10% of scat volume during the fall (see Chapter 5).

In their study comparing body condition to reproductive success, Noyce and Garshelis (1994) concluded black bears respond to declining nutrition by modifying reproductive performance in the following sequence: (1) litter size, (2) age of primiparity, (3) cub survival, and (4) litter frequency. Our analyses indicated the sequence may be exactly opposite in New Mexico. The greatest influence of mast failure on bears in New Mexico appeared to be a reduction in the number of females producing litters, hence an increase in litter interval. Second, cub survival appeared to decline associated with mast availability. Third, mast failure was associated with a decrease in the percent of bears producing first litters and a resulting increase in the age of primiparity. Litter size did not appear to be associated with availability of mast, among first litters or subsequent litters.

MANAGEMENT IMPLICATIONS

Documenting annual mast production, particularly occurrence and frequency of mast failures, may be an effective tool for monitoring black bear reproductive success in New Mexico. Continuation of the statewide mast surveys, as conducted by NMDGF officers during 1999-2000 (see Chapter 5), will provide valuable data for all regions of bear habitat. These data will be useful for analyzing population trend and interpreting harvest data with the bear population model.

Chapter 7

SURVIVAL RATES AND CAUSES OF MORTALITY

As in many states, the primary foundation for black bear management in New Mexico is information obtained from hunter-killed bears. Fluctuations in the sex and age composition of kills are seen as signals of changing population trends. However, trends in kill data can sometimes be misleading (Garshelis 1991). Therefore, interpretation of kill data is often aided by supporting information about bear population characteristics, especially survival rates, and associated cause-specific mortality rates.

We investigated black bear survival on 2 New Mexico study areas. To better understand the effects of hunting on black bears, a hunting closure was instituted on 1 study area that remained in effect from 1992-1997. Our objective was to document survival and cause-specific mortality rates by sex and age category.

METHODS

We estimated adult (≥5 years old), subadult (2-4 years old), and yearling (1 year old) survival rates using data from bears equipped with radio-transmitters. We monitored radio-collared bears from fixed-wing aircraft on a 14-day schedule during the active season (weather permitting). Radio-collars were constructed to emit a "mortality" signal when they remained stationary for more than 2 hours. We ground-tracked all collars emitting a mortality signal to determine whether the signal was a mortality or a dropped collar. We determined approximate date and cause of mortality (when possible).

Hunting mortalities of marked bears were recorded through the New Mexico Department of Game and Fish (NMDGF) mandatory pelt tag program. Personnel of the Colorado Division of Wildlife (CDOW) and the Arizona Department of Game and Fish (ADGF) also reported hunting mortalities. Depredation mortalities and relocations of marked bears were reported by the NMDGF and the CDOW.

Survival rates were calculated using the staggered entry method (Pollock et al. 1989). Rates were estimated separately for each study area by year, within 26 quarter-monthly intervals from May 1 – November 15. Mortality rates for specific causes of death were calculated as 1– survival rate estimated with deaths from other causes treated as censors. Annual rates over 1993-1999 were averaged with years weighted equally; annual confidence intervals were pooled (N.S. Urquhart, personal communication.)

We used data from all bears with working transmitters monitored for ≥1 day during the active season. Bears whose signals were not heard for periods exceeding 45 days were censored from analyses beginning on the last day of contact. If contact was re-established, bears re-entered the analyses on the day the first signal was heard. If contact was not re-established, bears did not re-enter the analysis.

Radio-telemetry contact was permanently lost for numerous bears during the study period. Some signal loss was probably attributable to premature transmitter failure, transmitter battery expiration, or long-range movements made by bears. However, we suspect other signal loss was due to deliberate destruction of transmitters following human-caused mortality. Signal loss also may have been due to transmitter damage caused by predation. To account for these possibilities in our survival estimates, we identified a portion of the missing bears as possible mortalities.

Assignment of potential mortality for each bear was based on transmitter type, expected battery life left on its transmitter, known failure rate for that transmitter type, and information on subsequent recapture, observation, or mortality. Signal loss was attributed to battery expiration if it occurred at $\geq$70% of battery life. Signal loss was attributed to known failure if transmitters were recovered or observed not functioning or not functioning properly (timer failure of eartag transmitters). Signal loss was attributed to possible signal failure when bears were later captured or killed by hunters not wearing transmitters. Signal loss was attributed to possible damage or weak signal if temporary signal loss occurred $\geq$3 times or if signal loss occurred during the time the bear was denned. Signal loss not attributed to any of these causes was considered possible mortalities. We also reclassified 1 handling mortality as a possible natural mortality due to the poor condition of the bear. Possible survival rates were then calculated including known and suspected mortalities.

RESULTS

Possible Mortalities from Signal Loss

Known and possible failure rates were only 1% and 2% for Telonics and Ursus Technologies (UT) radio-collars, respectively (Table 7-1). However, known failure rate for the Advanced Telemetry Systems (ATS) eartag transmitters was 13%. Due to this high rate of known failure among ATS transmitters, and an even higher number of unexplained signal losses (32%), no missing bears wearing ATS eartags were considered possible mortalities. Eight missing bears wearing Telonics or UT radio-collars were considered possible mortalities due to unexplained signal loss.

Known and Possible Survival Rates

Observed adult female survival rates were very similar for the 2 study areas and were above 90% (Table 7-2). Most mortality of adult females was human-caused, including hunter kills, depredation kills, and illegal kills (Table 7-3). Surprisingly, female hunting mortality rates were fairly similar for the 2 study areas, despite the hunting closure from 1992-1997 on the NSA. Of 4 adult female bears killed by hunters on the NSA, 1 (25%) was taken after the closure was lifted, 2 (50%) were known to be taken outside of the closure area, and 1 (25%) was reported as taken outside of the hunting closure area, however examination of her movements suggest this may not have been true. Depredation mortalities (*n* = 2) were observed only on the NSA, while illegal kills (*n* = 2) were observed only on the SSA. The 2 illegal kills occurred during the hunting season but no carcasses were found (only cut collars), therefore they may have been unreported legal kills. Of 4 mortalities of unknown cause, 3 (75%) occurred during the hunting season and may have been associated with hunting. However, we found no evidence confirming this due to the condition of the carcasses. The other mortality of unknown cause occurred during August. Despite finding an almost intact carcass, we could not identify the cause of death, but it did not appear to be human-caused.

Table 7-1 . Signal loss from radio-telemetry transmitters fitted on black bears on the Northern Study Area and Southern Study Area, New Mexico, 1992-1999.

	Telonics Radio-Collars	UT Radio-Collars	ATS Eartag Transmitters
Transmitters Used	287	55	38
Total Signal Loss	**20 (7%)**	**9 (16%)**	**24 (63%)**
Known or Probable Battery Expiration	9 (3%)	4 (7%)	7 (18%)
Known Failures	1 (0.3%)	1 (2%)	5 (13%)
Possible Failures with Known Fate	4 (1%)	0	0
Possible Damage or Weak Signal	0	2 (4%)	0
Unexplained Losses	6 (2%)	2 (4%)	12 (32%)

Two known natural mortalities occurred on the NSA and both appeared to be predation. Both females killed had new cubs and the predation occurred during spring. Evidence for the first mortality indicated the bear was killed in a struggle with another bear. Evidence for the second mortality was not conclusive, but bear sign in the area suggested the predator may have been a bear. A possible mortality was observed on the NSA and involved an adult female with a severe case of sarcoptic mange. Her mortality was actually a result of our handling in the den. However she was extremely emaciated and essentially blind (from callousing over her eyes), and we suspect she would not have survived through spring.

Known and possible survival rates of subadult females also were similar between study areas. Known survival rates were very similar to adult females; however possible rates appeared to be somewhat lower. Most mortality of subadult females also was human-caused. Again, hunting mortality rates were fairly similar for the 2 study areas, despite the hunting closure. The single subadult female killed by a hunter on the NSA was reported as taken outside of the hunting closure area, however examination of her movements suggest this may not have been true. Again, depredation mortality (*n* = 1) was observed only on the NSA. The 2 mortalities of unknown cause were observed on the SSA. Although no cause of death could be identified, timing and locations of these mortalities did not suggest they were human-caused.

Table 7-2. Observed survival rates and 95% confidence intervals (in parenthesis) of adult (≥ 5 years old), subadult (2-4 years old), and yearling (1 year old) black bears monitored on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-1999. Rates were obtained using the staggered entry method. Known rates included documented mortalities, while possible rates included known and suspected mortalities. Sample size is reported in bear-years.

	NSA			SSA			Combined	
	n	Known	Possible	*n*	Known	Possible	Known	Possible
Female								
Adult	131	0.93 (0.81-1.0)	0.92 (0.79-1.0)	119	0.90 (0.73-1.0)	0.90 (0.73-1.0)	0.92 (0.81-1.0)	0.91 (0.80-1.0)
Subadult	67	0.94 (0.72-1.0)	0.86 (0.58-1.0)	54	0.91 (0.71-1.0)	0.89 (0.68-1.0)	0.93 (0.78-1.0)	0.88 (0.70-1.0)
Yearling	19	0.75 (0.56-0.86)	0.75 (0.56-0.86)	19	0.97 (0.84-1.0)	0.97 (0.84-1.0)	0.85 (0.63-1.0)	0.85 (0.63-1.0)
Male								
Adult	77	0.89 (0.69-1.0)	0.89 (0.69-1.0)	80	0.91 (0.68-1.0)	0.82 (0.53-1.0)	0.91 (0.75-1.0)	0.87 (0.71-1.0)
Subadult	27	0.94 (0.73-1.0)	0.94 (0.73-1.0)	36	1.0 (1.0-1.0)	0.97 (0.83-1.0)	0.95 (0.73-1.0)	0.92 (0.67-1.0)
Yearling	21	0.90 (0.68-1.0)	0.87 (0.59-1.0)	13	0.82 (0.30-1.0)	0.76 (0.24-1.0)	0.86 (0.55-1.0)	0.83 (0.47-1.0)

Unexplained signal loss occurred for 3 subadult females, 2 on the NSA and 1 on the SSA, and these losses were identified as possible illegal kills. Two (67%) signals were last heard just before the start of hunting seasons, suggesting bears may have been unreported legal kills.

Observed yearling female survival was lower on the NSA than the SSA, but sample sizes were relatively small. On the NSA, all mortalities (*n* = 3) were of natural causes. One bear appeared to have died of starvation after emerging from the den with low weight. One bear appeared to have been preyed on by a mountain lion. One bear may have been preyed on by a bear. However, no clear evidence of predation was found, other than the fact the carcass was fed on by a bear. It should be noted the 2 mortalities attributed to predation might have been affected by our research activities. During 1994, larger collars were put on young bears and the burden of these large collars may have affected their survival. Since that time, we have used smaller, expandable collars on yearling and subadult bears in an effort to reduce our influence on survival. On the SSA, one mortality of a subadult female was attributed to illegal kill. This mortality occurred during the hunting season but no carcass was found (only a cut collar); therefore it may have been an unreported legal kill.

Table 7-3. Cause-specific mortality rates of adult (≥ 5 years old), subadult (2-4 years old), and yearling (1 year old) black bears monitored on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-1999. Rates were obtained using the staggered entry method. Known rates included documented mortalities, while possible rates included known and suspected mortalities.

			NSA		SSA		Combined	
Sex	Age class	Cause	Known	Possible	Known	Possible	Known	Possible
Female	Adult	Hunt	0.04	0.04	0.07	0.07	0.05	0.05
		Depredation	0.01	0.01	-	-	<0.01	<0.01
		Illegal kill	-	-	0.01	0.01	<0.01	<0.01
		Natural	0.01	0.02	-	-	0.01	0.03
		Unknown	0.01	0.01	0.02	0.02	0.02	0.02
		Total	**0.07**	**0.08**	**0.10**	**0.10**	**0.08**	**0.09**
	Subadult	Hunt	0.05	0.05	0.04	0.04	0.04	0.04
		Depredation	0.02	0.02	-	-	0.01	0.01
		Illegal kill	-	0.08	-	0.02	-	0.05
		Unknown	-	-	0.05	0.05	0.02	0.02
		Total	**0.06**	**0.14**	**0.09**	**0.11**	**0.07**	**0.12**
	Yearling	Natural	0.25	0.25	-	-	0.13	0.13
		Illegal kill	-	-	0.03	0.03	0.02	0.02
		Total	**0.25**	**0.25**	**0.03**	**0.03**	**0.15**	**0.15**
Male	Adult	Hunt	0.02	0.02	0.07	0.07	0.05	0.05
		Depredation	0.03	0.03	-	-	0.01	0.01
		Illegal kill	0.03	0.03	-	0.10	0.02	0.05
		Automobile	0.03	0.03	-	-	0.02	0.02
		Hunt (Arizona)	-	-	0.02	0.02	0.01	0.01
		Total	**0.08**	**0.08**	**0.09**	**0.18**	**0.09**	**0.13**
	Subadult	Depredation	0.06	0.06	-	-	0.06	0.06
		Illegal kill	-	-	-	0.03	-	0.02
		Total	**0.06**	**0.06**	**-**	**0.03**	**0.05**	**0.08**
	Yearling	Illegal kill	0.10	0.10	-	-	0.07	0.07
		Natural	-	-	0.08	0.14	0.02	0.02
		Unknown	-	0.03	0.10	0.10	0.05	0.09
		Total	**0.10**	**0.13**	**0.18**	**0.24**	**0.14**	**0.17**

Known adult male survival rates were very similar for the 2 study areas and were above 90%. However, including possible mortalities, the possible survival rate dropped to 82% on the SSA. Specific causes of death were different between study areas, however all were human-caused. Mortality sources for adult males included hunting, illegal kill, depredation kill, and automobile collision. As expected, male hunting mortality was lower on the NSA than on the SSA, and the single adult male killed by hunters on the NSA was taken after the hunting closure was lifted. One adult male captured on the SSA was killed in Arizona during their hunting season. On the NSA, 2 adult males were illegally killed outside of the hunting season. Radio-collars of these males were disposed of in Eagle Nest Lake and in the Cimarron River. On the NSA, 2 adult males appeared to have died from collisions with automobiles on U. S. Highway 64 in Cimarron Canyon.

Unexplained signal loss occurred for 3 adult males on the SSA, and these losses were identified as possible illegal kills. None of these possible mortalities occurred during the hunting season, suggesting they were not unreported legal kills. Although these mortalities cannot be verified, the documented occurrence of illegal kills of adult males on the NSA, coupled with documented occurrence of illegal kills of other bears on the SSA, indicate a high probability for illegal kill of adult males on the SSA. Inclusion of these possible mortalities doubled the mortality rate of males on the SSA.

Observed survival rates of subadult males were high on both study areas, and no hunting mortality was documented. The single documented mortality was a depredation kill following an incident on Philmont Scout Ranch when the bear entered a camp and scratched a scout inside a tent.

Unexplained signal loss occurred for 1 subadult male on the SSA, and this loss was also identified as a possible illegal kill. This possible mortality occurred during the bear hunting season, suggesting it may also have been an unreported legal kill.

Observed male yearling survival appeared lower on the SSA than the NSA. The single mortality documented on the NSA was an illegal kill during the bear season (the carcass was found). On the SSA, 1 yearling male mortality was due to predation by another bear. Cause of death was not known for the other 2 mortalities, but locations and dates did not suggest they were human-caused.

One SSA yearling bear never left the den following our den investigation. We suspect he may have died as a result of our handling, therefore this bear was censored in analysis of the known survival rates. However, the bear may have also died from natural causes, therefore it was included in analysis of possible mortality. Inclusion of this mortality increased the observed total mortality rate on the SSA from 18% to 24%. Unexplained signal loss occurred for 1 yearling male on the NSA, and this loss was attributed to an unknown cause. The signal was lost from this bear only weeks out of the den, and it was unlikely the possible death was human-caused.

DISCUSSION

Although not statistically distinct, survival rates appeared to differ among sex-age categories during this study. Among adult and subadult bears of both sexes, human-caused mortality was most common. Among yearling bears, most mortality was from natural causes, but human-caused mortality was also observed. Mortality from hunting was lower on the NSA and this difference was probably attributable to the hunting closure in effect from 1992-1997. However, even during the years of closure, hunting mortality was observed on the NSA. Most mortalities occurred outside of the closed area, indicating it was not large enough to allow complete protection for resident bears. However, we suspect 2 of the hunt mortalities occurred within the area of the hunt closure, indicating a possible source of illegal activity. Other sources of human-caused mortality included illegal kill, depredation kill, and automobile collisions. These sources of mortality were substantial, especially on the NSA, where they accounted for as much as 10% mortality.

Within the Southwest, observed adult female survival rates from this study were similar to those reported in Colorado (0.96: Beck 1991) and Mexico (0.94, Doan-Crider and Hellgren 1996), but higher than those reported in Arizona (0.85: LeCount 1990). Observed adult male survival rates were slightly higher than those reported in Arizona (0.85: LeCount 1990) and substantially higher than those reported in Colorado (0.70: Beck 1991).

The lack of documented hunting mortality among subadult males was surprising, given the substantial proportion of subadult males observed in hunter harvests. Relative to adults, and even subadult females, sample sizes were low for subadult males; therefore these results should be interpreted with caution. Our observed subadult male survival was higher than that observed in Colorado (0.76: Beck 1991), but our observed subadult female survival was similar to Colorado (0.94: Beck 1991).

Yearling survival rates appeared lower than those of adults and subadults, however much of the documented mortality was due to natural causes. Due to the small sample sizes associated with this ageclass, these results should also be interpreted with caution. Yearling survival rate was lower than the rate reported for Colorado (0.94: Beck 1991).

MANAGEMENT IMPLICATIONS

Among adult and subadult bears, most mortality was human-caused. In addition to hunting, illegal kills and depredation kills were significant sources of mortality for these bears. Illegal kills were documented on both study areas, and many of the unexplained losses were probably due to illegal kills followed by destruction of the transmitters. We were unable to verify any of these possible mortalities, therefore these possible rates should be viewed as maximum rates. Depredation mortality was only documented on the NSA. The proximity of the NSA to several towns, as well as the inclusion of Philmont Scout Ranch within its boundaries, increased the likelihood of bear-human interactions.

It is important to recognize that there was no legal hunting on the NSA during 1992 through 1997. Therefore the hunting mortality rates observed may not reflect actual mortality of bears from hunting in northern New Mexico. The possibility of total mortality exceeding the rates we observed must be considered when interpreting harvest data and output from the population model.

CHAPTER 8

DENNING CHRONOLOGY AND DEN SITE SELECTION

As omnivores, New Mexico black bears are faced with reduced foraging opportunities during winter, primarily due to a lack of new plant growth, desiccation of existing plant matter, and accumulation of snow. Like bears throughout most of their range, New Mexico bears respond to this limited food supply by hibernating. Use of dens or shelters during this extended period of immobility provides both security from predators and protection from extreme weather (Nelson and Beck 1984, Beck 1991).

Timing of den entry and emergence is widely variable among populations and between individuals within a population. Typically, female bears enter dens earlier and emerge from dens later than male bears across North America (Tietje and Ruff 1980, Beecham et al. 1983, LeCount 1983, O'Pezio et al. 1983, Beck 1991, Schooley et al. 1994, Weaver and Pelton 1994, Oli et al. 1997). The prolonged denning period of females is usually most pronounced for adults giving birth during that period. Knowledge of the denning chronology of New Mexico black bears may facilitate more effective management of hunting. In many states and provinces, patterns of differential denning chronology afford wildlife managers an opportunity to regulate the demographic composition of bear harvests (Troyer 1961, Lindzey 1981). In addition, interpretation of hunter-kill data also is enhanced with an understanding of the denning behavior of populations (Alt 1977, O'Pezio et al. 1983).

Knowledge of den site characteristics is also valuable. Energetic properties and level of security of the physical site of hibernation may play a role in the success of bear populations. Where quality den sites are limited, forest management practices can be adjusted to increase their availability (Weaver and Pelton 1994, Oli et al. 1997).

Our objectives were to (1) document den entrance and emergence dates by sex-age category and study area, and (2) document den site characteristics by sex and study area.

METHODS

Denning Chronology

We estimated dates of den entrance and den emergence using aerial telemetry data. During appropriate months (1 October–15 December and 15 March–30 May), we intensified our flight schedule in an effort to locate each radio-collared bear once per 7-10 days (weather permitting). We did not attempt to determine exact dates of den entry or emergence by observation because of the possibility of disturbance.

Studies have shown bears often concentrate their movements around den sites days or weeks before den entry, and bears often remain in the den vicinity after emergence in the spring (Lindzey and Meslow 1976, LeCount 1980, Tietje and Ruff 1980, Beecham et al. 1983, Kolenosky and Strathearn 1987). Our observed telemetry error prevented us from distinguishing very small movements associated with a specific den location. Therefore, we defined denning dates as those when bears were in the den vicinity, not dates of actual movement into or out of the den cavity.

For each consecutive location, we assigned active or denned status based on its proximity to the previous location or its proximity to the actual den site (documented during a den visit). Other relevant information, particularly observer notes and "mortality" signal status, also were considered. Denning occurred when a bear was found in the "same" location during 2 or more consecutive flights, or when a bear was located at its documented den site. Locations were considered the same if they were within the median aerial telemetry error radius of 505 m. Bears were considered active the first time they were located more than 505 m from the den site in the spring.

We defined the fall den entry date as the midpoint between the last active location and the first denned location. Similarly, we defined the spring den emergence date as the midpoint between the last denned location and the first active location (O'Pezio et al 1983). For den entry, we limited our analyses to those observations when the period between relevant locations was $\leq$15 days; and for den emergence, we limited the period to $\leq$20 days. These criteria allowed us to use approximately 50% of our data. To eliminate the potential bias of our research activities, we excluded den emergence observations when the first active location occurred following our den visit.

We used analysis of variance (ANOVA) to determine differences in den chronology among the following sex-age categories: pregnant females (with cubs at den emergence), females with yearlings, other females, adult males, and subadult males. We used t-tests to determine differences within distinct categories between study areas.

We determined total denning period for bears with entrance and emergence dates as defined above. Differences in denning period was tested among sex-age categories using ANOVA and tested between study areas using *t*-tests. All analyses were performed using SPSS software (Chicago, Illinois); where appropriate because of variance differences, degrees of freedom are expressed as decimals.

Den Characteristics

We documented den characteristics, site features, and habitat variables during all visits to winter dens. Den type, number of entrances, types of bedding material, and prior use were recorded. Prior use was known when previous visits to the same den were made. Prior use was judged probable based on characteristics such as vegetation growth on the dirt berm of an excavated den, soil compaction of the berm, and old claw marks on hollow trees. We recorded elevation, topographic position, slope, and aspect of each den site. Habitat type was assigned following Brown (1982). We estimated canopy cover above 0.9 m (3 ft), and ground cover at 0-0.3 m (0-1 ft) and 0.3-0.9 m (1-3 ft) in the following categories: 1-5%, 6-25%, 26-50%, 51-75%, 76-100%. For analysis of aspect at the den site, aspect was classified into 9 categories: N, NE, E, SE, S, SW, W, NW, and flat (no aspect).

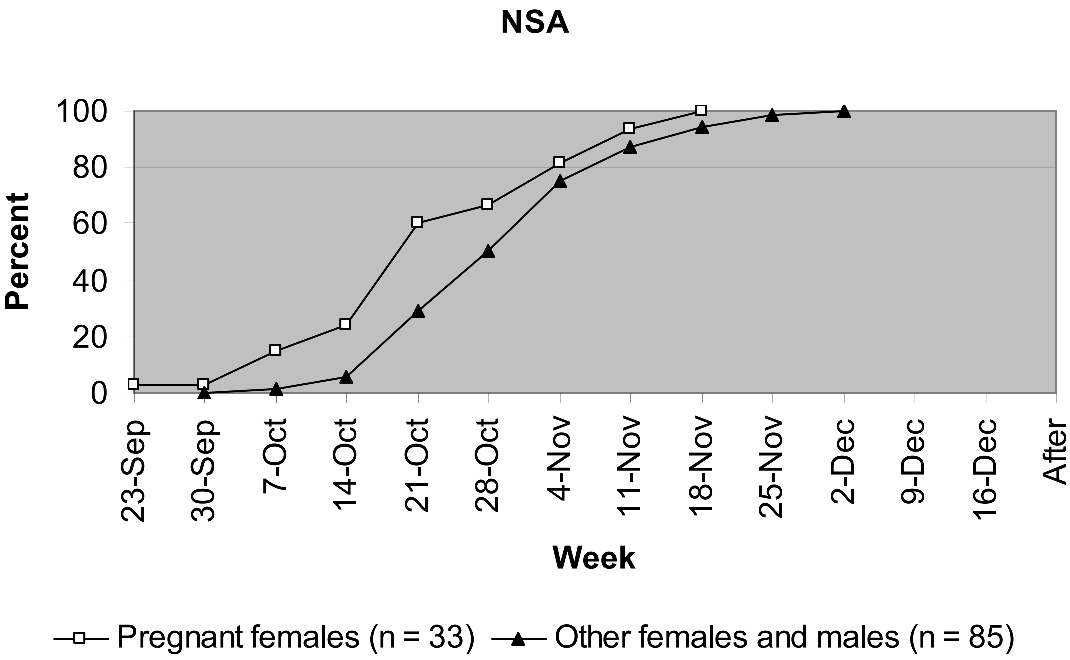
RESULTS

Denning Chronology

Among all bears on both study areas, observed den entrance dates ranged from 25 September-7 February (*n* = 179). Range of den entrance dates differed among sex-age categories and between study areas (Table 8-1). Among males, the first observed den entrance date was 18 October, while the latest was 29 December. Among females, the first observed den entrance date was 25 September, while the latest was 7 February. Among both sexes, the majority of bears entered dens between mid October and mid November (Figure 8-1).

Table 8.1. Ranges and means of black bear den entrance dates, by sex-age category, observed on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992–1999.

Area	Sex-age Category	*n*	Earliest	Latest	Mean
NSA	Pregnant females	33	25 September	21 November	26 October
	Females with yearlings	18	12 October	8 December	3 November
	Other females	27	7 October	28 November	2 November
	Adult males	27	18 October	21 November	3 November
	Subadult males	13	19 October	24 November	2 November
SSA	Pregnant females	10	29 October	15 November	11 November
	Females with yearlings	7	3 November	27 January	28 November
	Other females	31	20 October	7 February	8 November
	Adult males	8	29 October	29 December	18 November
	Subadult males	5	2 November	10 December	11 November



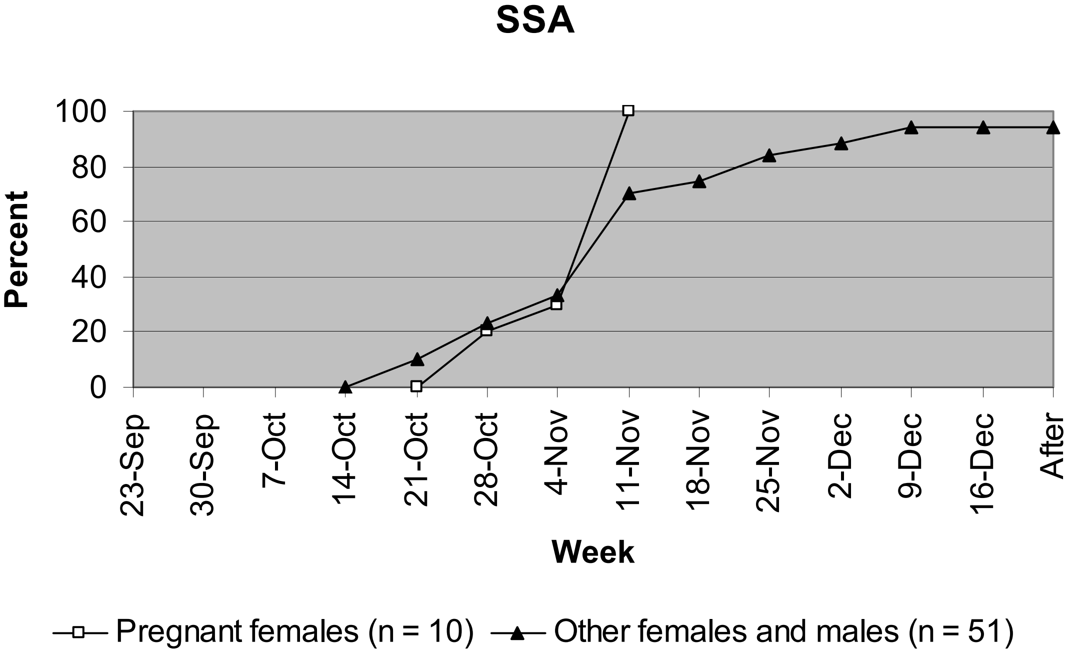


Figure 8-1. Cumulative percent of black bears that entered dens, by week, on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-1999.

Mean den entrance date differed among the 5 sex-age categories (F = 2.5; df = 4,174; *P* = 0.05), but subsets were not distinct. When observations were divided into 3 categories (pregnant females; females with yearlings; other females and males), 2 distinct subsets were identified (SNK, *P* = 0.05). Mean entrance date of pregnant females was 29 October, while that of all other bears was 6 November. Comparison of 95% confidence intervals indicated pregnant females entered dens approximately 1-15 days earlier than all other bears.

Within both groups, mean den entrance date also differed between study areas. Pregnant females entered dens approximately 4-25 days earlier on the NSA (26 October vs. 10 November, *t* = -4.3, df = 27.9, *P* < 0.001). Other bears entered dens about 2-19 days earlier on the NSA (3 November vs. 13 November, *t* = -3.0, df = 68.3, *P* = 0.003).

On the SSA, mean den entry date differed by oak production for the group of other females and subadult males (F = 3.4, df = 2,40, *P* = 0.04, *n* = 42) and for pregnant females (*t* = -4.1, df = 2.0, *P* = 0.05, *n* = 9). Other females and subadult males entered dens later during the years of good oak production than all other years (30 November vs. 8 November, SNK *P* = 0.05). Pregnant females entered dens later during years of good oak production than during years of poor production (15 November vs. 31 October). Mean den entry date did not differ significantly by oak production on the NSA.

Among all bears on both study areas, observed den emergence dates ranged from 21 March-5 June (*n* = 177). Range of emergence dates was similar for males and females (Table 8-2). Among males, the earliest observed date was 21 March, while the latest was 20 May. Among females, the first observed den emergence date also was 21 March, while the latest was 5 June. Among both sexes, the majority of bears emerged from dens during April (Figure 8-2).

Table 8.2. Ranges and means of black bear den emergence dates, by sex-age category, observed on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993–1999.

Area	Sex-age Category	*n*	Earliest	Latest	Mean
NSA	Females with cubs	40	9 April	5 Jun	10 May
	Females with yearlings	19	13 April	19 May	4 May
	Other females	31	1 April	23 May	1 May
	Adult males	20	21 March	20 May	21 April
	Subadult males	7	29 March	20 May	30 April
SSA	Females with cubs	10	28 March	29 April	24 April
	Females with yearlings	3	21 March	6 May	15 April
	Other females	28	21 March	31 May	21 April
	Adult males	12	23 March	6 May	14 April
	Subadult males	7	6 April	6 May	24 April

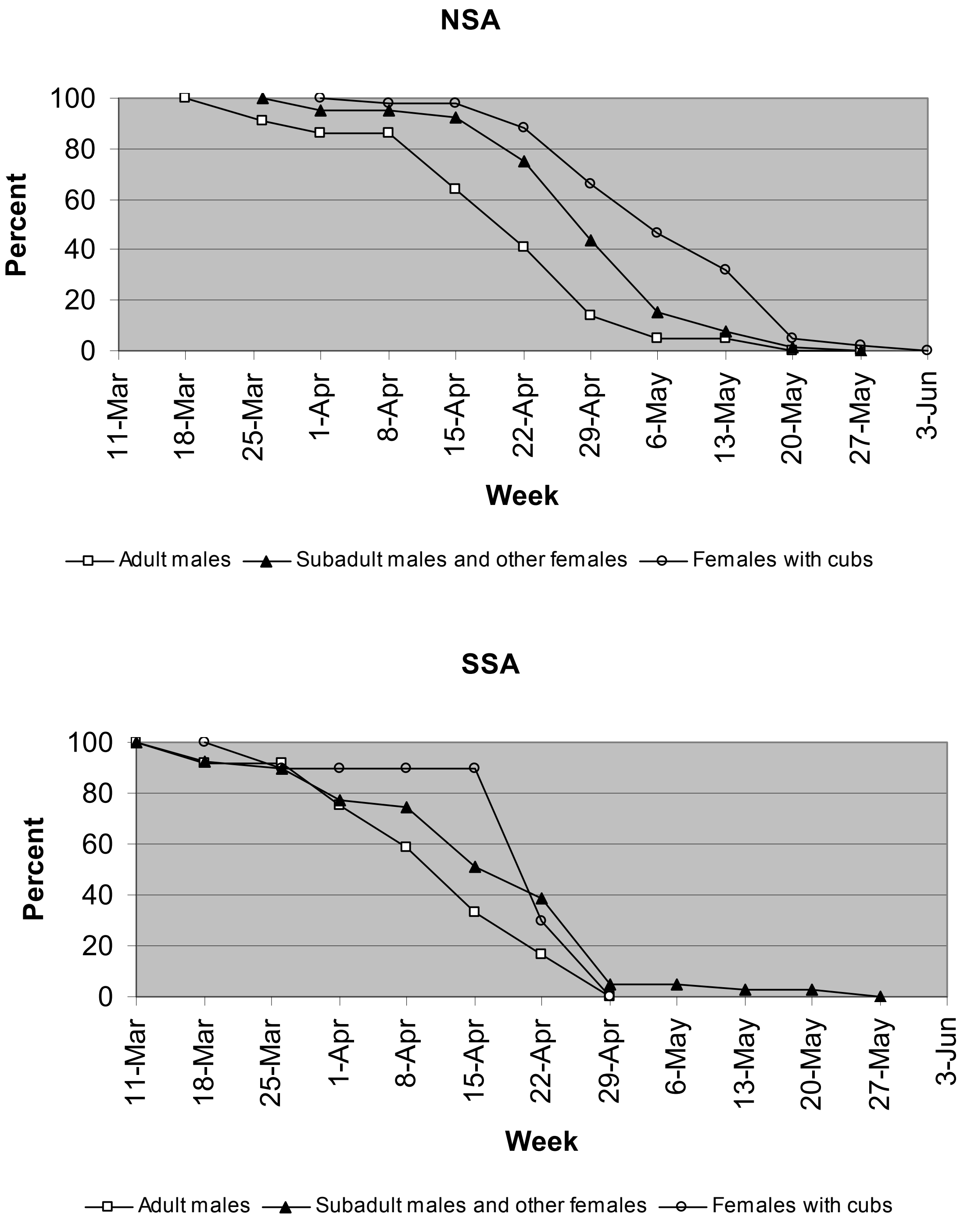


Figure 8-2. Decreasing percent of black bears remaining in dens, by week, on the Northern Study Area (NSA) and southern Study Area (SSA), New Mexico, 1993-1999.

Mean den emergence date differed among the 5 sex-age categories (F = 9.8; df = 4, 172; *P* < 0.001). Using a SNK test, females with yearlings, other females, and subadult males constituted a homogenous subset. When this combined group was compared to females with cubs and adult males, all 3 categories were different (SNK, *P* = 0.05). Adult males emerged earliest with a mean date of 18 April. The mean date for combined group was 28 April. Females with cubs emerged the latest, with a mean date of 7 May.

Comparing these groups between study areas, we observed some differences in mean date. Among the combined group of other females and subadult males, bears emerged about 2-19 days earlier on the SSA (21 April vs. 2 May, *t* = 3.8, df = 93, *P* < 0.001). Females with cubs emerged from dens about 6-27 days earlier on the SSA (24 April vs. 10 May, *t* = 4.4, df = 48, *P* < 0.001). Mean date did not differ between areas for adult males (19 April, *t* = 1.6, df = 32, *P* = 0.12).

Total denning period for 83 individuals varied significantly among the 5 sex-age categories (F = 2.6; df = 4, 78; *P* = 0.04), however homogenous subsets overlapped (Table 8-3). Denning period of adult males was different from all other bears combined. Denning period of adult females with cubs also differed from all other bears combined. Combining all sex-age categories, mean denning period was shorter on the SSA than the NSA (165.6 vs. 178.0 days, *t* = 2.4, df = 81, *P* = 0.02).

Table 8.3. Ranges and means of black bear total denning period (days), by sex-age category, observed on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993–1999.

Area	Sex-age Category	*n*	Minimum	Maximum	Mean
NSA	Females with cubs	16	165	229	187.1
	Females with yearlings	10	145	201	172.4
	Other females	13	145	216	173.8
	Adult males	8	155	203	173.8
	Subadult males	3	162	197	178.0
SSA	Females with cubs	3	171	181	174.3
	Females with yearlings	2	151	163	157.0
	Other females	19	42	198	170.6
	Adult males	6	98	170	142.7
	Subadult males	3	171	185	180.3

Den Characteristics

Over 64% of 390 dens visited during 1993-2000 were associated with rock structure, including excavations under rock (35%) and natural rock cavities (30%). Den types associated with tree structure were used to a lesser degree (a total of 31%), with 20% of dens excavated under trees and 11% in natural tree cavities.

Use of den types differed by sex and study area (X^2 = 96.1, df = 18, $P <$ 0.001, n = 387). Females and males on the NSA used dens excavated under rocks more than bears on the SSA (Table 8-4). Females on the SSA used tree cavity dens and dens excavated under trees more than any other group. Males on the SSA used rock cavity dens more than any other group.

Table 8-4. Relative use of den types by female and male bears on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-2000.

	NSA		SSA	
Den type	Females (*n* = 173)	Males (*n* = 53)	Females (*n* = 132)	Males (*n* = 29)
Rock cavity	0.25	0.32	0.24	0.69
Tree cavity	0.06	0	0.24	0
Excavated under rock	0.43	0.60	0.17	0.24
Excavated under tree	0.21	0.08	0.27	0.03
Excavated into ground	0.03	0	0.06	0.03
Ground nest	0.01	0	0.01	0
Other	0.01	0	0	0

Bears denned in a variety of habitats (Table 8-5). The most commonly used habitats were mixed conifer forests (45%), pinyon-juniper woodlands (21%), spruce-fir forests (13%), ponderosa pine forests (9%), and oak shrublands (8%). Other den-site habitats included aspen forests (3%), bristlecone and limber pine forests (2%), desert shrubland (<1%), and subalpine-plains grassland (<1%). On each study area, bears denned most frequently in mixed conifer habitat. Bears of the NSA used pinyon-juniper habitat secondarily, while SSA bears used pinyon-juniper and oak habitats secondarily.

Denning habitat differed by sex and study area (X^2 = 63.5, df = 24, $P <$ 0.001, n = 380). Males denned in scrub oak habitat more frequently than females on both study areas (Table 8-5). Females on the NSA denned in spruce-fir habitat more frequently than other groups and SSA females denned in mixed conifer habitat more frequently than other groups. Use of pinyon-juniper and ponderosa habitats did not differ between sexes on either study area.

Certain den types were more closely associated with specific habitats. Over 95% of tree cavity dens were located in mixed conifer or spruce-fir habitat (n = 42), with the vast majority (83.3%) located in mixed conifer habitat. Over 82% of dens associated with tree structure were located in mixed conifer or spruce-fir habitats (n = 120). All dens located in scrub oak habitat (n = 28) and

88% of dens located in pinyon-juniper habitat (*n* = 69) were rock cavity dens or dens excavated under rocks.

Table 8-5. Relative use of habitat types for denning by female and male bears on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-2000.

	NSA		SSA	
Habitat type	Females (*n* = 174)	Males (*n* = 50)	Females (*n* = 126)	Males (*n* = 27)
Grassland	0.01	0	0	0
Oak shrubland	0.01	0.20	0.08	0.26
Pinyon -juniper woodland	0.22	0.24	0.13	0.22
Ponderosa pine forest	0.10	0.06	0.10	0.07
Aspen forest	0.02	0.02	0.02	0.07
Mixed conifer forest	0.41	0.36	0.57	0.33
Spruce-fir forest	0.20	0.10	0.09	0.04
Bristlecone-limber pine forest	0.03	0.02	0	0

Elevation at den sites ranged from 1,636 - 3,576 m (5,400 - 11,800 ft). Elevation differed by study area (t = 7.5, df = 385, P < 0.001, n = 385); elevation at NSA den sites averaged 2,657 meters (8,768 feet) whereas SSA den sites averaged 2,427 meters (8,010 feet). Elevation differed by sex on each study area. Males on the NSA denned at lower elevations than females (2,485 vs. 2,706 m, t = 4.0, df = 222, P < 0.001, n = 224), as did males on the SSA (2,332 vs. 2,448 m, t = 2.4, df = 159, P = 0.02, n = 161).

Aspect at den site differed by sex and study area (X^2 = 51.1, df = 24, P = 0.001, n = 390) and the significant differences were primarily among females. Female bears on the NSA selected dens with SW aspects more frequently and dens with NW aspects less frequently than other bears. Female bears on the SSA selected dens with NW aspects more frequently and dens with S or SE aspects less frequently than other bears. There was no difference between study areas in use of aspect by male bears (X^2 = 4.7, df = 7, P = 0.70, n = 82).

Slope at den sites ranged from 0^o – 90^o and the mean was 28^o (n = 386. Only 1 den site had a slope of 90^o. It was a natural rock cavity den used by a subadult male on the SSA, situated on a sheer cliff face with a narrow path to the entrance. There was no difference in slope at the den site between study areas (P = 0.173). However, there was a difference between the sexes, with males using steeper slopes than females (31^o vs. 27^o, P = 0.006).

Bears denned at all categories of topographic position, however few den sites were located on ridge-tops (5%) or bottoms (3%). Most den sites were located at the upper portion of slopes (42%), the mid portion of slopes (37%), or the lower portion of slopes (13%). Bears on the NSA denned most frequently at mid-slope (43%), while SSA bears denned most frequently on the upper slope (48%).

The number of useable entrances into a den ranged from 1 to 4, but most dens had only 1 entrance (94%, *n* = 390). Twenty-one dens had 2 entrances (5%), 2 dens had 3 entrances (1%), and 1 den had 4 entrances (<1%). Eighteen of 24 (75%) dens with more than 1 entrance were natural rock cavity dens. Only 7% of den entrances were blocked with bedding material (*n* = 381), and this frequency did not differ by study area or sex ($P \leq 0.11$). Snow covered 22% of den entrances (*n* = 377); this frequency did not differ by study area or sex ($P = 0.67$). Snow cover ranged from approximately 15cm to 1.2m. Typically, there was a small hole in the snow (5-15cm diameter) that was kept open by heat generated from within the den.

Bedding material was found in 93% of all bear dens (*n* = 360) and was common to all sex and age categories. Percent of dens with beds was high on both study areas, however SSA females used beds most frequently and NSA females used beds least frequently (98% vs. 89%, $X^2 = 7.5$, df = 3, $P = 0.06$, $n = 357$). Common bedding materials found in 351 dens were pine needles (48%), twigs (42%), leaves (39%), and grass (37%). Other materials included conifer boughs, duff , bark, bracken fern (*Pteridium* spp.), yucca (*Yucca* spp.), beargrass (*Nolina microcarpa*), conifer cones, lichen, moss, agave (*Agave* spp.), silktassel (*Garrya* spp.), and remains of rodent midden. An earthen floor, sometimes strewn with stones, characterized dens lacking a bed.

Of 390 dens visited on both study areas, 10% were definitely used in years prior to the visit, and an additional 26% likely were used in years prior to the visit. There was a difference in the frequency of den re-use by study area ($X^2 = 14.8$, df = 1, $P < 0.001$, $n = 387$). Definite or probable re-use occurred at 43% of the NSA den sites, but only 24% of the SSA den sites. On the SSA, males denned in sites believed to have been previously used more often than females (38% vs. 21%, $X^2 = 4.0$, df = 1, $P = 0.06$, $n = 161$). Rates of probable re-use did not differ by sex on the NSA ($P = 0.27$). Several bears on the NSA were observed to use the same den 2-5 times during the study period. Use of the same den by different individuals also was observed.

DISCUSSION

Johnson and Pelton (1980b) proposed that 2 factors interact to ensure optimal timing of hibernation and denning of black bears. The primary factor is a genetically controlled hormonal response to photoperiod, or day length. This factor is modified by annually variable elements such as weather and food supply. These factors interact to provide the final stimulus to den.

Erickson and Youatt (1961) reported that prolonged feeding delayed denning of captive bears, but when feeding was terminated, denning occurred promptly. Delayed den entrance by wild black bears has been documented during years of greater fall food availability in Maine (Hugie 1982, Schooley et al. 1994), Alberta (Tietje and Ruff 1980), Tennessee (Johnson and Pelton 1980b), and Idaho (Beecham et al. 1983). In Ontario, bears that fed on acorns, a food with high fat and carbohydrate content (Eagle and Pelton, 1983), denned significantly later than bears not feeding on acorns (Kolenosky and Strathearn 1987). Shorter denning periods observed in mild climates has led to the theory that bears forage until they encounter a decreasing or negative energy return per unit of search effort (Lindsey and Meslow 1976, Johnson and Pelton 1980b).

Timing of den entrance also has been reported to be influenced by various weather factors including snowfall (Jonkel and Cowan 1971), temperature (Johnson and Pelton1980b, Rogers 1987), and precipitation (Lindzey and Meslow 1976, Johnson and Pelton 1980b). However, Schwartz et al. (1987) and Schooley et al. (1994) reported that variation in den entry was not strongly associated with weather patterns during autumn. Bears have the physical capability to survive brief periods of hostile weather, and onset of hibernation is probably not controlled by changes in weather. Rather, inclement weather typically coincides with decreased food availability, and tends to compound the negative energy return of a dwindling food supply by increasing the foraging effort required to obtain food. In the case of snow cover, food is exponentially more difficult to find and retrieve per unit effort of search.

On average, we observed bears entering dens 1-2 weeks later than usual during a single year of outstanding food production on the SSA. Two females without offspring were observed to delay den entrance until January and February. That year of outstanding mast production also was characterized by mild weather and little snowfall, allowing for increased foraging opportunities. Dates of den entrance were not different among years of oak production ranging from failure to moderate. Overall, our results lend support to the theory of negative energy return and that food availability is the primary proximate cause of black bear den entry. We hypothesize that years of mast failure do not result in earlier den entrance because the endogenous rhythm has not yet prepared bears to den. Weather factors are likely a secondary proximate cause of den entrance.

Smith et al. (1994) summarized denning chronology results of 25 black bear research projects and concluded that populations of more northern latitudes and higher elevations tend to enter dens earlier, remain denned longer, and emerge later. Our data suggest this pattern may exist within New Mexico. Mean entrance dates of the SSA population were very similar to those of central Arizona (LeCount 1983), and were approximately 2 weeks later than those observed on the NSA. Entrance dates of NSA bears were more similar to those of Colorado (Beck 1991) and Idaho (Beecham et al. 1983). Bears inhabiting mountain ranges in New Mexico of lower elevations than our study areas may display this trend to a greater degree. With uniform hunting seasons for black bears throughout New Mexico, regional differences in denning chronology will likely affect the demographic composition of the harvest and interpretation of population sex and age structure from harvest data.

Differential denning dates among demographic segments of black bear populations has been widely reported in such regions as the Southwest (LeCount 1983, Beck 1991), the Pacific Northwest (Lindzey and Meslow 1976, Schwartz et al.1987, Smith et al. 1994), the intermountain west (Tietje and Ruff 1980, Beecham et al. 1983), the Northeast (O'Pezio et al. 1983, Schooley et al. 1994), and the Southeast (Johnson and Pelton 1980b, Weaver and Pelton 1994, Oli et al. 1997). Typically, females enter dens earlier than males. Pregnant females enter dens earlier than any other group, and adult males enter dens latest. The reverse sequence is commonly observed at den emergence. Subadult entrance and emergence appears to be more random and has not exhibited the definitive patterns apparent between sex and reproductive groups. Bears of New Mexico exhibited these same demographic variations and fit the overall pattern documented with other research projects. Mean den entrance date for pregnant females was earlier than all other bears on both study areas. The weekly cumulative percentage of pregnant females having entered dens was 5-30% greater than for all other bears on the NSA during peak entrance in October; den entry by pregnant females on the SSA probably was similar but sample size was too small to document this pattern. Den emergence patterns in New Mexico also fit the general pattern of other research findings. Adult male bears on both study areas emerged earliest and females with cubs emerged latest. Mean emergence dates differed by 10-20 days between these groups. The weekly cumulative percentage of adult males that had departed the den vicinity was 20-50% greater than for females with cubs during peak emergence in April and May.

Bears of New Mexico exhibited these same demographic variations and fit the overall pattern documented with other research projects. Mean den entrance date for pregnant females was earlier than all other bears on the NSA and the SSA. Also, the weekly cumulative percentage of pregnant females that had entered the den was 5-30% greater than for all other bears on the NSA during October; den entry by pregnant females on the SSA probably was similar but sample size was too small to assess this pattern . These differences generally agree with other documented populations.

Emergence from dens in New Mexico also fit the general pattern of other research findings. Adult male bears on both study emerged earliest, females with cubs emerged latest; average emergence dates differ by 10 to 20 days between those groups. Also, the weekly cumulative percentage of adult males that had departed the den vicinity was 20-50% greater than for females with cubs during peak emergence in April and May. However this emergence schedule was about 20 days later on the NSA than the SSA. These differences generally agree with other documented populations.

We found that male and female black bears selected different types of den sites and den structure, and that trends were similar between regions in New Mexico. In general, males denned at lower elevations, on steeper slopes, in oak habitats, and in rock dens. Females used dens associated with trees with greater frequency than males and denned at higher elevations, on more moderate slopes, and in spruce-fir and mixed conifer habitats. While some of the variation in the aforementioned den characteristics may be inter-related (primarily site-characteristics), much of the differences that we observed in New Mexico can, in large part, be explained by differing needs of the sexes and the adaptive significance they afford each sex.

Black bears den for periods up to 6 months long and can lose 14-34% of their body weight during the denning period (Hock 1960, Erickson and Youatt 1961, Tietje and Ruff 1980). Females nursing cubs may lose an additional 9% above the 25% that other females lose during denning (Tietje and Ruff 1980). In addition, factors other than metabolic expenditure also influence energy conservation during the denning period. Bears have been documented changing dens within a winter apparently by natural causes (LeCount 1980, Weaver and Pelton 1994). Abandonment of a den site was estimated to cause a doubling of over-winter weight loss (Tietje and Ruff 1980). Considering the intense physiological demands of denning, lactation, and the generally poor forage conditions available to bears upon emergence, the need for den types that favor energy conservation during this period is obvious.

The insulating capacity of snow is well known and of great significance to bears of more northern regions where accumulations are deep enough to cover dens and mid-winter thawing is not frequent (Tietje and Ruff 1980). We found that 22% of dens in New Mexico were covered with snow at our visit date. We did not detect any difference in the frequency with which male and female dens were covered with snow. Interestingly, there also was no difference in frequency of snow-covered dens between study areas even though the NSA was farther north and included areas of higher elevation. Bears on the SSA, particularly females, used NE slopes more frequently which may account for this lack of difference. Female use of higher elevations on both study areas may represent an inclination to use more insulated dens.

Use of tree cavity dens by black bears may result in energetic conservation in regions where snow accumulations are not significant, mid-winter rains occur, or intermittent flooding occurs (Johnson and Pelton 1980b, Weaver and Pelton 1994, Oli et al. 1997). Johnson et al. (1978) simulated winter heat loss of denned black bears and concluded that enclosed tree cavity dens accounted for a 15% energy savings compared to open ground dens. However, Thorkleson and Maxwell (1974) suggested while dens afford protection from conductive, convective, and radiant heat loss, the increased air circulation can greatly reduce their thermal efficiency. Because of its latitudinal position and range of elevations, New Mexico falls somewhere between the typical northern bear habitats and those with less severe winters. The fact that only 22% of dens were covered with an insulating blanket of snow indicates that thermally insulated dens may have great importance for bears in New Mexico. The need for more thermally efficient dens may be greater for females and younger bears due to their higher surface area to volume ratio. Observed use of tree dens was higher on the SSA, where snow accumulation was more limited. Although male bears have been observed to use hollow trees for denning in other regions (C. Godfrey, pers. commun., 1998), no use of tree cavity dens by males was observed during this study. It is possible that availability of large cavities suitable for adult males is limited in New Mexico.

In addition to energetic conservation, security is another factor of importance related to den type. Predation of denned black bears by wolves (Rogers and Mech 1981), man (Erickson 1964), and other bears (Rogers 1977, Tietje and Ruff 1980, Alt 1984) has been reported. Security of the den site is affected by inaccessibility, defensibility, and cover. Females may seek tree den types because of a greater need for security, due to their smaller size and the vulnerability of cubs. Bears that den in hollow tree cavities above the ground are less accessible to potential predators than those in other den types. During this study, no elevated tree cavity dens were abandoned at our approach, supporting previous contentions that bears denned in trees were less vulnerable to human disturbance than those using ground (Johnson and Pelton 1981, Weaver and Pelton 1994). Den types other than elevated tree cavities appear to be less secure, but similarly inaccessible and defensible to each other. Ninety-four percent of the dens we examined had only 1 entrance. Although lethargic and approachable while denned, bears remain capable of defending themselves. Cover would appear to function for security purposes by reducing the odds that a den could be located, and, as we often found during the research effort, by functioning as an auditory alarm system. Undetected approaches to dens were difficult to achieve in thick scrub oak and mountain mahogany vegetation and/or steep terrain covered with loose rocks.

Craighead and Craighead (1972) suggested grizzly bear use of northern aspects for den sites reduced the likelihood of a flooded den as the result of a mid-winter thaw. Cub mortality from hypothermia and drowning, associated with flooding of dens, has been observed (Alt 1984, Hayes and Pelton 1994, Weaver and Pelton 1994). Although SSA females appeared to favor dens with NW aspects, NSA females tended to avoid this aspect, selecting sites with SW aspects instead. Snowmelt on south-facing slopes was relatively common on both study areas. We observed flooding of a maternal den on the NSA during a den visit in late March. The den was beneath a rock ledge where snow was melting through the roof of the den. The female, her 2 cubs, and all of the bedding material were extremely wet, however the female remained lethargic. Fearing for the survival of the cubs, we dried them, put fresh bedding under them, and attempted to redirect the snowmelt. Fortunately, the bears moved from the den within 2 days after the den visit. It is unknown if the bears would have moved without our disturbance. On the SSA, females may have selected north-facing slopes to avoid frequent snowmelts that may reduce cub survival; however other factors, such as availability of large tree dens, may have caused them to select these sites.

Relatively high levels of den reuse have been documented in other regions, particularly in western states, such as Colorado (Beck 1991), Idaho (Beecham et al. 1983), and Alaska (Smith et al. 1994). Methodologies used to determine rates of den reuse differed widely among studies, making comparison difficult. Lindzey and Meslow (1976) documented a high degree of den reuse (90% of all bears reused dens) and attributed it to reduced den site availability following logging. Schwartz et al. (1987) documented competition among bears for den sites. The wide variety of den types observed during this study suggested availability of dens was not limiting.

MANAGEMENT IMPLICATIONS

The verified differential in den entry and emergence dates among sex and age groups has application to setting bear hunting seasons to accomplish various objectives. However, den entry and emergence dates are highly variable and generally span a period exceeding 2 months. We observed variation relative to mast production; other factors undoubtedly play a role influencing the timing from year to year. No single timing scenario is appropriate for every use. This information also is valuable for interpreting past and future harvest composition relative to season timing and region. These interpretations are especially important for selecting information to be used in the Population Model as a management tool.

Dens that facilitate security and energy conservation during hibernation period are of significant value to black bears, and female bears exhibit a tendency to select tree cavity dens when available. Retention of large diameter live trees, large snags, and large fallen logs may be a valuable goal to benefit black bears in all forest management plans and programs.

CHAPTER 9

HOME RANGE, MOVEMENTS, AND HABITAT USE

Relative to most North American game species, black bears exhibit very large home ranges, and are known to travel great distances to reach abundant food sources (Amstrup and Beecham 1976, Lindzey an Meslow 1977, Garshelis and Pelton 1981, Warburton and Powell 1985, Smith and Pelton 1990, Wooding and Hardisky 1994). A thorough understanding of the movement patterns of bears may help agencies identify and manage distinct subpopulations within a state, and work with neighboring states to manage inter-state populations. Information about dispersal rates may aid in interpreting hunter-kill data, as it relates to emigration and immigration. Knowledge of the sources of bear-human conflict and effectiveness of translocation may aid in management of nuisance and depredation complaints.

We investigated black bear home range and movements on 2 New Mexico study areas during 1992-2000. Our objectives were to (1) document black bear home range size by sex and study area; (2) investigate seasonal movement patterns by sex and age category; (3) investigate general habitat use patterns on each study area; (4) examine dispersal of subadult males and females; (5) examine patterns of nuisance and depredation activities by sex and study area; and (6) compare movements of translocated bears by sex and age category.

METHODS

For analysis of home range and movements, we used aerial telemetry locations, capture and recapture locations, den locations, and locations of mortalities (including hunter kill or depredation kill locations). Locations were classified by season: den, premast (den emergence to 20 July), and mast (21 July to den entry). To eliminate autocorrelation of locations, we excluded recapture locations if the bear was captured more than once at the same trapsite during the same trap period. When the interval between 2 locations was <5 days, we excluded the second location if the distance between the 2 locations was <1000 m for females or <1500 m for males.

Numerous studies of black bears have documented extensive movements to abundant food sources, especially during the fall foraging period. Although these distant locations are a significant part of a bear's lifetime home range, we wished to discriminate them from the locations representing areas of concentrated, multi-annual use. For each bear, we selected den locations and locations from the premast season. For each location, we determined the distance to its nearest neighbor. For each bear, we multiplied the maximum distance by 1.5, and this became our critical value. Any mast season location exceeding this critical distance from any den or premast location was considered a long-range movement. If the maximum distance was ascribed to an outlier among the den and premast locations and the maximum distance was more than 2 times the second longest distance, we usually reclassified the outlier as a long-range movement, and reanalyzed based on the second longest nearest neighbor distance. In most of these circumstances, the outliers appeared to be associated with movements to summer foods (mostly during July) or return movements from distant den locations (mostly during February to April). For the few subadult bears determined to be dispersing as described below, we used the above criteria only for locations when the bears were resident in their natal range. During years of active dispersal, we did not classify any locations as long-range movements.

Home Range

Multi-annual total home ranges were estimated using all locations, while multi-annual primary home ranges were estimated excluding long-range movements. Home range was estimated using the 100% minimum convex polygon (MCP) method (Mohr 1947) and the 95% fixed kernel (FK) method with the least squares cross validation procedure as the smoothing parameter (Silverman 1986). Estimates were calculated using the Animal Movements extension (P. Hooge, USGS-BRD, Alaska Biological Science Center) developed for use with ArcView software (Environmental Systems Research Institute, Redlands, California). A minimum sample size of 30 locations was required for bears to be included in home range analyses. Mean home range size was compared by sex and study area using *t*-tests.

Movements

We estimated the center of each primary home range using the arithmetic mean. We then calculated an “activity radii” for each bear location as the distance between the location and the home range center (Dice and Clark 1953). To determine the effect of sample size on our ability to estimate the home range center, and thus activity radii, we calculated incremental mean activity radii for each bear by sample size, starting with the first 3 premast locations. We then calculated the percent change in the mean activity radius as sample size increased. Minimum sample size was achieved when the mean percent change fell below 5%. Bears with sample sizes below this number were excluded from analyses using activity radii. Differences in mean activity radius by sex, ageclass, season, and study area were tested using *t*-tests and analysis of variance (ANOVA), with individual bears as a random factor.

Habitat Use

We defined habitats using land cover data obtained from the New Mexico Gap Analysis Project (NMGAP, Thompson et al. 1996). These data included 42 land cover types, primarily based on dominant vegetation and canopy cover. For analysis of general use, we reclassified these land cover types into 6 broad categories: closed forest/closed woodland, open forest, open woodland, open shrubland, open grassland/tundra, and other land cover.

We used bear location data compiled for home range analyses to document use of these habitat types by the bear populations on each study area. For these analyses, locations outside of New Mexico were excluded. For each bear location, a scan area was created with a radius corresponding to the median telemetry error for each study area (NSA = 200 m, SSA = 505 m). Scan areas were overlaid onto the NMGAP map and habitats found within the buffer area were determined. When more than 1 habitat type was found within a scan area, use was weighted by the inverse of the number of types within the scan area (ranging from 1-3). Percent use was defined by percent of locations within each habitat type by season.

We determined availability of habitat types using composite home range data. We created composites of the 100% MCP and the 95% FK total home ranges for all radio-transmittered bears, excluding the locations outside of New Mexico as described above. We also excluded the single long-range movement to Elephant Butte Lake (observed for a male on the SSA), because this single location would have greatly inflated the available habitat area. Relative distribution of habitat types within the composite home ranges was determined by assigning habitat type to random points generated at approximately 1 point/km^2. Patterns of selection versus avoidance of habitat types were estimated using use versus availability analyses (Neu et al. 1974).

Dispersal

We estimated dispersal rates using 2 samples of radio-transmittered juvenile bears. The first sample consisted of bears whose natal range was known (those handled as cubs or yearlings in the den). The second sample consisted of bears whose natal range was not verified (those captured as yearlings or subadults). Dispersal was determined by examining annual changes in premast movements. We considered a bear dispersed when it moved from 1 premast range to a second premast range (with no overlap).

Nuisance or Depredation Activity and Post-translocation Movements

We identified areas of potential human conflict for bears on each study area. We restricted analyses to areas of predictable potential food sources, including towns, public campgrounds, and other known sources of garbage or food. Areas of unpredictable potential food sources, such as backcountry campsites, were not assessed. We determined percent of all MCP home ranges of bears >1 year old that overlapped these areas of potential human conflict. In addition, nuisance and depredation complaints reported to NMDGF were recorded for marked study bears. Percent of each study population involved in these complaints was determined by sex.

During the study period, several radio-collared study bears were translocated by NMDGF personnel due to nuisance or depredation activities. We documented post-translocation movements of radio-collared bears to determine rate of return.

RESULTS

Home Range

Mean total and primary home range size was larger for males than females (*P* < 0.001) on both study areas (Table 9-1). Total home range size varied greatly by individual, especially using the MCP method. Total MCP home range size ranged from 104.8 km^2 to 3,343.8 km^2 for males. Variation in FK home range size was not as great, but still notable. The largest home range size was that of a SSA adult male (M380) that made a single long-range movement to the vicinity of Elephant Butte Lake. Although this home range size greatly exceeded those of other males, it may actually reflect the potential areas used by SSA bears. Of 8 SSA males with estimated home ranges, 7 (88%) were not found for 1-4 periods exceeding 45 days, indicating many long-range movements were not documented. The single SSA male bear that was consistently located (M326) had a total MCP home range size of 847.1 km^2 and a FK home range size of 213.4 km^2. On the NSA, only 3 of 10 (30%) bears were missing for 1-3 periods exceeding 45 days. Therefore, home ranges were probably more accurately documented for NSA males than SSA males. No significant differences were found between NSA and SSA male total home ranges (*P* ≥ 0.39), however the higher frequency of missing bears on the SSA may indicate total home ranges were larger.

Total MCP home range size ranged from 10.2 km^2 to 866.7 km^2 for females. Among females, the largest total home range size was that of a SSA adult female (F804) that appeared to have 2 distinct primary home ranges. One range was located within the study area, while the other was located within the Gila Wilderness. Most of the large sizes of other female total home ranges were attributable to isolated long-range movements. Mean total home range size was not significantly different by study area (*P* ≥ 0.25). On the SSA, 15 of 26 (58%) female bears were not found for 1-2 periods exceeding 45 days, but only 4 of 35 (11%) females were missing for a single period exceeding 45 days on the NSA. This may indicate total home ranges were larger on the SSA.

Mean primary home range size estimates were approximately 3-5 times larger for males than females (*P* ≤ 0.01) on both study areas (Table 9-1). Among males, ranges and means of primary home range size were very similar between study areas, and no differences were found (*P* ≥ 0.96). Mean primary home range size estimates of SSA females were nearly twice as large as estimates for NSA females. The difference was significant for the MCP estimates (*t* = -2.1, df

= 27.0, $P = 0.05$) and slightly significant for the FK estimates ($t = -1.7$, df = 24.6, $P = 0.10$).

Table 9-1. Size (km^2) of multi-annual minimum convex polygon and 95% fixed kernel home ranges for black bears monitored on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-2000. All estimates differed by sex within study areas ($P < 0.001$) and estimates of primary home range differed between areas for females ($P \leq 0.003$).

				Minimum Convex Polygon		Fixed Kernel	
			n^a	Mean	Range	Mean	Range
Total[b]	NSA	Female	35	123.3	10.2 - 482.0	70.2	17.2 - 509.1
		Male	11	417.8	104.8 - 855.3	370.1	112.0 - 800.1
	SSA	Female	26	172.4	17.4 - 866.7	116.6	16.4 - 1001.7
		Male	8	769.8	180.6 - 3343.8	383.8	213.4 - 967.9
Primary[c]	NSA	Female	28	24.0	7.2 - 50.4	27.6	10.6 - 45.2
		Male	10	132.1	46.6 - 266.6	162.1	56.4 - 307.7
	SSA	Female	25	43.1	10.7 - 222.7	55.8	13.7 - 430.9
		Male	4	130.1	74.6 - 180.1	163.4	102.3 - 231.4

[a] Sample included individuals with ≥30 locations
[b] Total home ranges included all locations
[c] Primary home ranges excluded long-range movements

Movements

Mean activity radius around home range centers was smaller during the premast season than during the mast season for all sex-age categories, except yearling females and SSA male yearlings ($P \leq 0.05$, Table 9-2). On both study areas, mean activity radii were larger for adult and subadult males than all other sex-age categories during the premast season and during the mast season ($P < 0.001$).

Among adult and subadult males, mean activity radius did not differ between study areas during either season ($P \geq 0.28$). Among all females and yearling males, mean activity radius was larger on the SSA than the NSA during the premast season ($t = -5.1$, df = 775.2, $P < 0.001$), but not during the mast season ($t = -0.3$, df = 1899.0, $P = 0.79$).

Mean activity radius was larger during years of oak failure than all other years for adult and subadult males on the NSA (16.2 vs. 9.1 km, $P < 0.001$) and the SSA (19.3 vs. 9.5 km, $P < 0.001$). The same was observed for all females and yearling males on the SSA (5.4 vs. 3.9 km, $P = 0.001$), however no difference was observed for that group on the NSA ($P = 0.21$).

On both study areas, mean activity radii of male bears displayed a gradual increase throughout the premast season, while mean activity radii of female bears remained relatively constant (Figure 9-1). On the NSA, both sexes appeared to increase movements during mid-August and continue to move until early October. On the SSA, both sexes increased movements during late August and continued to move widely through late October. Peaks of fall movements appeared to occur earlier for males on both study areas. Peaks also appeared to occur earlier on the NSA than the SSA.

Table 9-2. Activity radii (km) around home range centers for black bears monitored on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-2000. Mean activity radius differed by season and sex for all age classes, except yearling males (*P* = 0.05).

			Premast (den emergence - 20 July)			Mast (21 July - den entry)		
			n	Mean	Range	*n*	Mean	Range
NSA	Female	Adult	561	1.9	0.03 - 23.1	649	4.8	0.08 - 41.4
		Subadult	229	1.6	0.2 - 7.2	298	6.1	0.08 - 35.7
		Yearling	47	1.1	0.04 - 4.7	55	2.1	0.1 - 22.0
	Male	Adult	384	5.3	0.2 - 40.5	382	11.6	0.2 - 53.5
		Subadult	99	3.9	0.2 - 63.2	88	9.7	0.6 - 46.1
		Yearling	53	1.7	0.04 - 5.3	57	4.5	0.2 - 28.1
SSA	Female	Adult	400	2.6	0.09 - 57.1	561	4.5	0.1 - 55.4
		Subadult	137	2.2	0.03 - 10.8	205	4.2	0.04 - 27.5
		Yearling	25	2.2	0.03 - 6.3	50	5.2	0.6 - 17.2
	Male	Adult	174	7.6	0.2 - 59.1	180	14.5	0.3 - 134.9
		Subadult	74	6.1	0.4 - 28.6	82	14.1	0.2 - 75.8
		Yearling	21	4.6	0.8 - 24.9	28	3.1	0.5 - 6.5

Percent of all locations considered long movements (outside of primary home ranges) also increased during the fall mast season (Figure 9-2). On the NSA, from late August until early October, over 40% of male locations and over 30% of female locations were long-range movements. On the SSA, over 25% of female locations were long-range movements from late August to late October. For SSA males, sample sizes were smaller than other categories, therefore that group exhibited more variation, but in general more than 20% of male locations were long-range movements between mid August and late October.

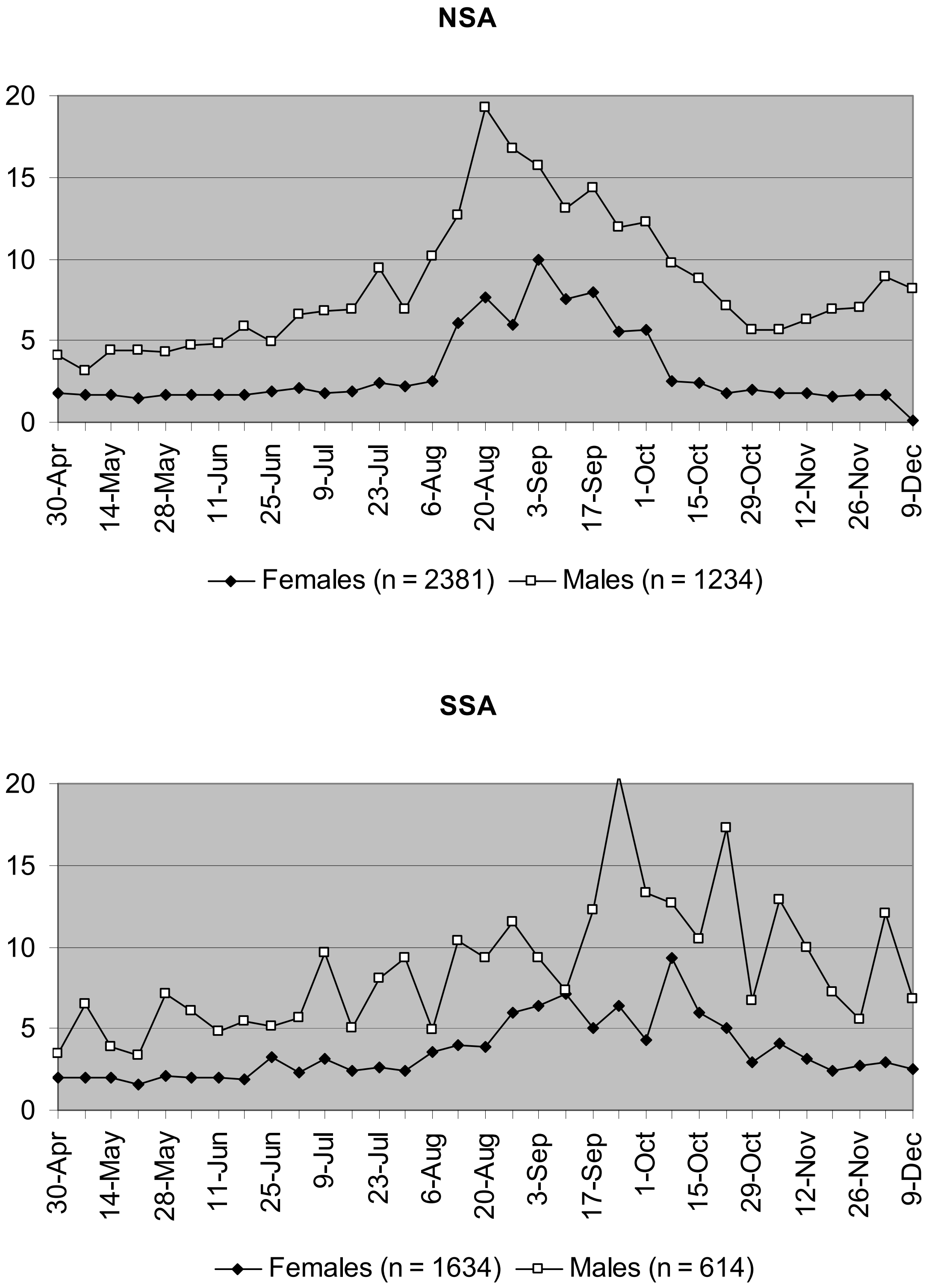


Figure 9-1. Mean activity radius (km) around home range centers, by week, for male and female black bears monitored on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-2000.

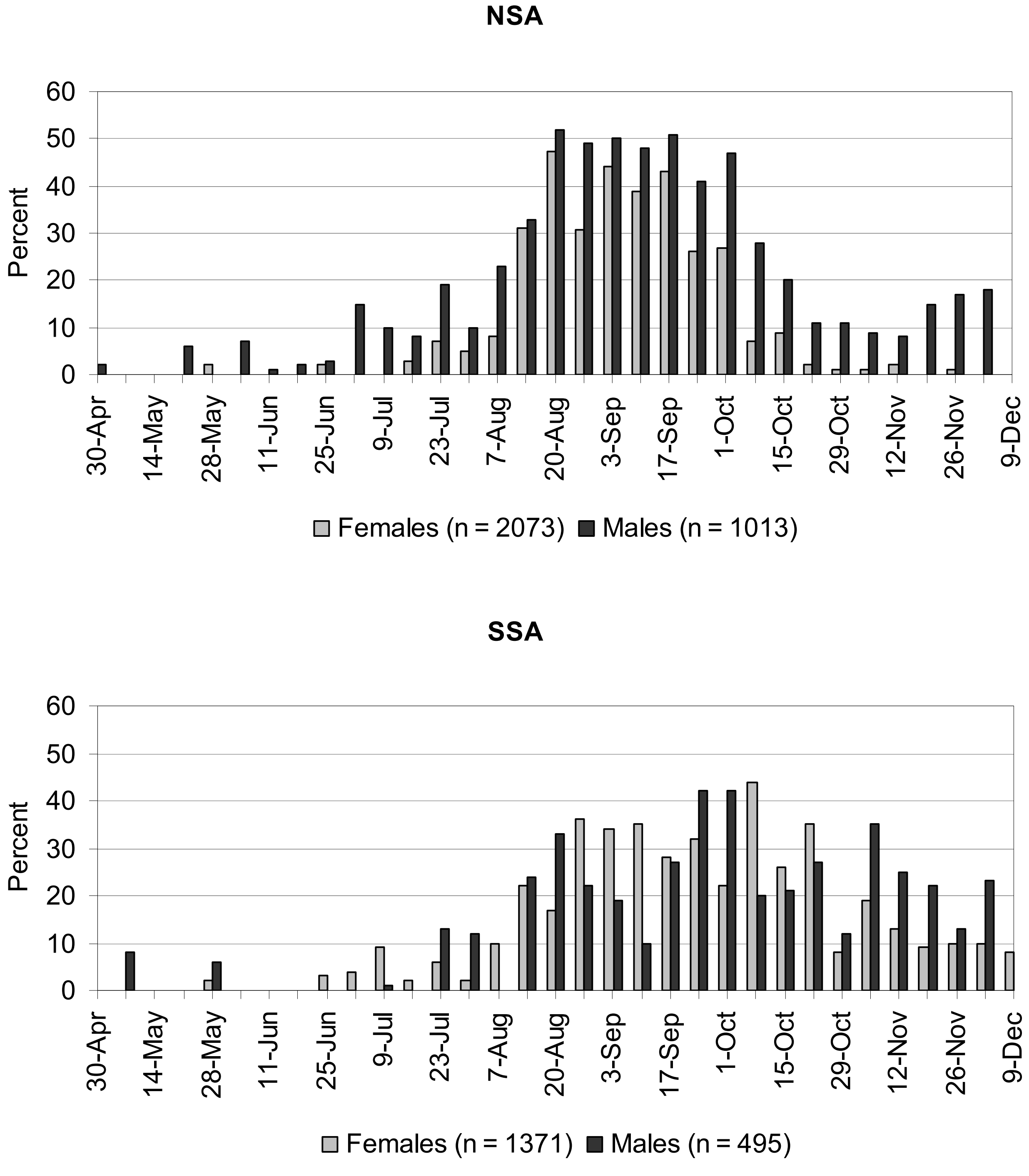


Figure 9-2. Percent of black bear locations considered long-range movements (outside of primary home ranges), by week, on the Northern Study Area (NSA) and the Southern Study Area (SSA), New Mexico, 1992-2000.

Habitat Use

Patterns of habitat use were very similar between the 2 study areas. On both study areas, analyses indicated bears were highly selective of the closed forest and woodland habitat types during all seasons, with >80% of locations occurring in these types (Table 9-3). Areas of open shrubland also were selected, but use and availability of this type was more limited. Areas of open woodland and open grassland were avoided, and most locations (96%, *n* = 460) within these habitats occurred within 500 m of the edge of closed-canopy habitats.

Table 9-3. Observed use versus availability of habitat types by black bears on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-2000.

		Observed percent use by season			Percent in composite home range		
Area	Habitat type	All year	Premast season	Mast season	MCP	95K	Result $P < 0.001$
NSA	Closed forest/ woodland	90	92	87	79	77	Selected
	Open woodland	4	3	4	4	5	Avoided[a]
	Open shrubland	3	2	3	2	1	Selected[b]
	Open grassland	3	3	4	16	16	Avoided
	Agricultural land	0	0	0	1	1	
	n	3085	1883	1203			
SSA	Closed forest/ woodland	85	86	84	76	71	Selected
	Open woodland	3	2	4	11	13	Avoided
	Open shrubland	6	7	6	1	2	Selected
	Open grassland	7	6	7	12	14	Avoided
	n	2444	1176	1015			

[a] Not significant relative to MCP composition

[b] Not selected during premast season

Habitat use patterns differed slightly by sex during the premast season on both study areas, but closed forest and woodland habitats still accounted for >85% of use for both sexes. On the NSA, more male locations were found in open grassland habitats (4% vs. 2%) and agricultural lands (1% vs. 0%) than females ($X^2 = 13.1$, df = 4, $P = 0.01$, $n = 1883$). On the SSA, more male locations were found in open woodland habitats (3% vs. 1%) and open shrubland habitats (6% vs. 3%) than females ($X^2 = 24.0$, df = 4, $P < 0.001$, $n = 1170$).

Dispersal

No dispersal was observed among female bears whose natal range was known, however dispersal was observed among male bears (Table 9-4). Radio-telemetry monitoring ended prior to dispersal for most males (76%), due to shed transmitters, collar removal, mortality, or lost contact. Of males monitored until age 4, 100% dispersed from their natal range. Five dispersal movements were documented. Two males (40%) dispersed during fall of their yearling year, 2 males (40%) dispersed during fall of their second year, and 1 male dispersed during the spring of his third year (20%). Dispersal distance ranged from approximately 25-60 km. Interestingly, 2 littermates dispersed at the same time to the same area and made similar movements to fall mast.

In addition to these known dispersal observations, we also documented the probable dispersal of a male bear captured as a subadult. This bear appeared to disperse during late summer of its third year, when it moved approximately 45 km from its previous range and established a new home range. This individual was known to maintain this home range until fall of his fifth year.

Table 9-4. Rate of dispersal, by age, for juvenile black bears monitored with radio telemetry on the Northern and Southern Study Areas, New Mexico, 1993-2000.

	Age	*n*	Percent Dispersed[a]	Details
Females	1	21	0	
	2	9	0	
	3	8	0	
	4	2	0	
	5	2	0	
Males	1	17	0	
	2	13	15	2 bears left natal range in fall of yearling year
	3	4	100	1 bear left natal range in fall of second year 1 bear left natal range in spring of third year

[a] By end of premast season (20 July)

Nuisance or Depredation Activity and Post-translocation Movements

On the NSA, radio-telemetry data was obtained for 52 females bears and 41 male bears >1 year old. Primary MCP home ranges of 81% of females and 90% of males overlapped areas of potential human conflict. The most common area of overlap was Philmont Scout Ranch, used by 65% of females and 90% of males. Public campgrounds were found within 10% of female and 34% of male home ranges. The towns of Eagle Nest, Ute Park, or Cimarron, or the Eagle Nest Reintegration Center were found within 15% of female and 39% of male home ranges.

On the SSA, radio-telemetry data were obtained for 41 females and 35 males >1 years old. Primary MCP home ranges of 3 (7%) females and 4 (11%) males overlapped areas of potential human conflict. Areas of overlap included 2 public campgrounds at Willow Creek and Snow Lake. None of the home ranges of SSA bears overlapped towns.

On the NSA, 14% of females and 20% of males >1 year old were known or suspected of potential nuisance or depredation activity (*n* = 158), but only 2% of females and 1% of males on the SSA were involved in these activities (*n* = 154, Table 9-5). Of 28 NSA bears involved in nuisance or depredation activities, half (50%) were attracted to towns with unsecured garbage or other available foods. Garbage was made available to bears most often by the use of open dumpsters lacking bear-resistant lids. Foods associated with homes included hummingbird feeders, pet foods, deer feed, and garbage. Nuisance activities of 7 bears (25%) were associated with Philmont camps and activities of 5 bears (18%) were associated with public campgrounds. Three depredation complaints (11%) arose from depredation of domestic pigs or apiaries.

Table 9-5. Percent of marked black bears >1 year old known or suspected of nuisance or depredation activities on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992-1999.

Area	Sex	*n*	Percent suspected of nuisance activity	Percent causing nuisance or depredation complaints by management action: Hazed	Translocated	Killed	Total percent
NSA	Females	57	7	2	4	2	14
	Males	101	4	3	8	5	20
SSA	Females	56	0	0	2[a]	0	2
	Males	98	1	0	0	0	1

[a] Both bears were translocated into the study area from outside its boundary

On the SSA, both female bears translocated because of nuisance activity were actually moved onto the study area from outside its boundary. One incident arose at a public campground and the other was associated with a backcountry camp. The single male bear suspected of depredation activity was found shot dead near a cattle carcass. It was unknown if the bear was responsible for the death of the cow.

Post-translocation movements were documented following 11 translocations of 8 bears (Table 9-6). Translocation distances ranged from 26-84 km and overall rate of return was 73%. Return movements took from approximately 1-328 days. Return rate of adult bears was 100%, and each individual appeared to begin return movements immediately following translocation. Return rate of subadult bears was 57%, and 3 of 4 bears that did not attempt return movements were males.

DISCUSSION

Evidence indicated bears on the SSA, in general, moved over larger areas than bears on the NSA. Mean premast activity radii and primary home range size was larger for females on the SSA. Although no differences in male home range size or activity radii were found between study areas, the higher frequency of missing bears on the SSA suggested they may have moved greater distances than documented. Many have postulated home range size is an indication of habitat quality. The premise is when food is abundant and evenly distributed animals do not need to search far for food. When food is scarce and distribution is patchy, animals need to move more widely in search of food. We do not have detailed information on the distribution of food plants on each study area, but examination of habitat data showed that availability of mast-producing habitats did not differ between study areas. However, relative consumption of premast foods did appear to differ between study areas (see Chapter 5). On the NSA, the premast diet was dominated by grasses. On the SSA, the premast diet was characterized by less consumption of grasses, and greater consumption of mast and woody plants. The more arid conditions of the SSA, coupled with livestock grazing, may limit the availability of grasses to bears, and compel individuals to search more widely for other foods, such as juniper berries.

Table 9-6. Rate of return, by sex-age category, for nuisance bears translocated into or away from the Northern and Southern Study Areas, New Mexico, 1993-2000.

Sex	Age class	*n*	Percent Returned	Distance Moved	Details
Female	Adult	2	100%	38-47 km	Both bears previously moved as subadults, both returned
	Subadult	4	75%	25-58 km	The bear that did not return moved to another human development
Male	Adult	2	100%	45 km	One individual moved twice
	Subadult	3	0%	65-85 km	All bears appeared to establish home ranges in new area, no further nuisance activity documented

The fall foraging period lasted for over 2 months. On the NSA, bears ranged widely beginning in early August and ending during early to mid October. On the SSA, fall movements were less well-defined, but ranged from mid August to late October. On both study areas, peaks of male movements appeared to occur earlier than those of females, and initiation of long-range movements was earlier for males on the NSA. Earlier initiation of fall movements to oak stands by male black bears also was observed in Great Smoky Mountain National Park (Garshelis and Pelton 1981).

Increased fall travel distances during years of food shortage have been reported in other bear studies (Garshelis and Pelton 1981, Beck 1991). Mast season activity radii of black bears in New Mexico were significantly larger during years of oak failure for most sex-age categories, indicating bears may have had to travel farther in search of food when oak production failed. The increased movements and unfamiliarity of distant areas may make bears more vulnerable to hunting. Higher bear harvest levels have been associated with shortages of natural foods in Massachusetts (McDonald et al. 1994) and Minnesota (Noyce and Garshelis 1997). This has important ramifications for interpreting and predicting fall harvest of bears.

Analyses of habitat use indicated bear movements were strongly associated with closed forest and closed woodland habitat types. Open habitats, including grasslands and open woodlands, appeared to be avoided, particularly by female bears. Use of the open shrubland habitat was relatively low, but was higher than expected given its low occurrence. Oak species are an important component of many montane shrubland communities in New Mexico, and general observations throughout the study period indicated bears sought these habitats during the fall foraging period. Based on ground knowledge of the study areas, we believe shrubland communities were under-represented in the NMGAP landcover map (Thompson et al. 1996) we used for habitat analysis (see Chapter 11). This probably limited our ability to assess actual use of shrubland habitat. Selection for closed canopy habitats, avoidance of open habitats, and use of edges by black bears have been reported in other black bear studies in the West (Lindzey and Meslow 1977, LeCount and Yarchin 1990).

Overlap of bear home ranges with areas of potential human conflict was very different between the 2 study areas. Most bears on the NSA had 1 or several sources of human-related food within their primary home ranges, but few bears on the SSA had access to predictable human-related foods. Given these circumstances, it is easy to explain the substantial depredation mortality observed on the NSA and the lack of such mortality on the SSA (see Chapter 7).

Despite the potential for conflict on the NSA, most bears did not engage in nuisance or depredation activities. At least 35 female study bears had home ranges partly or entirely within Philmont Scout Ranch, however only 3 of these bears created nuisance problems requiring management action. Likewise, at least 37 male study bears used areas of Philmont, but only 2 were involved in nuisance complaints. Throughout the study period, Philmont maintained strict guidelines for storing foods in established camps and on the trail. These precautions appeared to be effective at minimizing bear-human conflict.

Compared to bears using areas of Philmont, far fewer study bears (9 females and 17 males) had home ranges encompassing towns or campgrounds. However, the majority of documented conflict was associated with these areas. In each of the 3 towns close to the NSA and the Eagle Nest Reintegration Center, garbage disposal was achieved using non bear-resistant dumpsters, often distributed throughout residential areas. These dumpsters were probably the initial attractant drawing bears into human-populated areas. The reward of high-calorie food obtained from dumpsters was probably enough to overcome the natural wariness of bears to humans (Herrero 1989). Human habituation, or loss of innate fear of humans, has been directly associated with use of human-related foods by black and grizzly bears (Hastings et al. 1989, Herrero 1989). In human-populated areas of the NSA, the transition from wariness to human habituation probably fit the circumstances described by Herrero (1989), whereby over time, when use of human-related foods did not result in harm or harassment to the bear, habituation developed. Increased use of other human-related foods, such as hummingbird feeders or pet food, was a predictable outcome of this progression. In the end, bears and humans can be negatively impacted by these events. Mortality of male and female bears was observed on the NSA due to nuisance and depredation problems. In most cases, bears were destroyed because they were considered a threat to human safety. In addition, many incidents of human injury and fatality from black and grizzly bears have been attributed to human habituation (Herrero 1989).

Increases in black bear nuisance problems have been correlated with shortages in natural foods (Rogers 1976, Rogers 1987). The small number of depredation complaints recorded on an annual basis, and the occurrence of only 1 oak failure on the NSA prevented us from drawing any conclusions about the effect of natural food availability on bear problems in New Mexico. However, general observation in the region of the NSA hinted at an association of bear problems with spring and summer periods lacking rainfall. Analyses of bear complaints relative to fall mast production and spring to summer conditions is needed in New Mexico.

Use of translocation as a means of solving nuisance or depredation complaints had variable success. All translocated adult bears returned to their original home range within days or months of their translocation. However, in most cases the time elapsed before their return did allow for immediate resolution of the problem. Some translocations of subadult bears, especially males, were successful in that bears remained in the new area, and did not resume nuisance behavior. This was probably due to behavioral differences between sex-age categories. Subadult male bears may not have attempted return to their previous home range, because of the dispersing behavior characteristic of this age class. On the contrary, adult bears, and even subadult females displayed a high degree of home range fidelity during our study, indicating they would most like show homing behavior following translocation. Homing behavior of translocated bears has been widely reported and an inverse relationship between distance moved and probability of return was evident in all studies (Sauer et al. 1969, Beeman and Pelton 1976, McArthur 1981, Rogers 1986). In general, bears translocated more than 65 km from the capture site were less likely to exhibit homing behavior. Despite some success, translocation is not without cost to bears. Survival rates of translocated bears were found to be only 23% in Virginia and the primary cause of death was automobile collisions (Comly-Gericke and Vaughan 1997).

MANAGEMENT IMPLICATIONS

Analyses of bear movement data and distribution among habitat types on the 2 study areas illustrated the importance of distinguishing how male and female bears use the landscape differently. These analyses also indicate the importance of considering the season and condition of food supply when drawing conclusions about the presence of bears in specific locations.

Three of the largest tracts of bear habitat in New Mexico (the San Juan complex, the Sangre de Cristo complex, and the Gila complex) are contiguous with bear habitat in Colorado or Arizona (see Chapter 11). Two small tracts (the Bootheel region and the Guadalupe region) share habitat with Arizona or Texas. Evidence indicates bears commonly cross state boundaries during fall foraging and dispersal. Therefore, bear management in New Mexico is not independent of these other states. Some understanding of the population trend in these other states is vital for estimating the potential impact of immigration and emigration on New Mexico black bear populations.

Analysis indicated a small percentage of individuals within a bear population engage in nuisance and depredation activities. Most documented bear problems were associated with human-related foods, especially garbage. Efforts to reduce accessibility of human-related foods will be instrumental in reducing the likelihood of bear problems on an annual basis. More information is needed on the relationships of natural food availability and bear problems. Increase in nuisance problems have been associated with food shortage in other regions,. Therefore, during years of low natural food abundance, problems can be expected to increase above the average level in New Mexico.

There is an apparent differential between subadult and adult bears regarding homing after translocation. This difference suggests that choices about relocating nuisance or depredating bears need to consider age and sex of the animal in addition to other factors surrounding the complaint.

CHAPTER 10

POPULATION DENSITY AND SEX-AGE COMPOSITION

For wildlife managers, 2 of the most desirable facts about a wildlife population are a firm estimate of total number of individuals and a tally by sex and age category. Sound wildlife management can be, and most often is practiced in the absence of these data. Nonetheless, population data are invaluable for monitoring population trend, setting hunt regulations, and providing adequate suitable habitat. Estimates of density and sex-age composition are among the most difficult values to obtain for wild populations, and black bears present some special challenges. Their solitary nature, forest-dwelling habit, and low densities make them difficult to enumerate using survey methods common for other big game species. Most often mark-recapture methods have been used to estimate black bear density (LeCount 1982, Beecham 1983, Miller et al. 1987, Garshelis 1992, Clark and Smith 1994).

At the beginning of this study, reliable information on population size and structure was lacking in New Mexico. The NMDGF had a long-standing populations estimate of 3000 bears statewide; however the means by which this estimate was deduced were not available. Our objective was to determine density and sex-age composition of study populations annually and with all years combined. This information would be valuable in estimating statewide and regional population numbers and for comparison of the sex-age composition of the live population to that of hunter-killed bears.

METHODS

Although the number of captures and recaptures were numerous, our trapping effort was primarily designed to capture an increasing sample of unmarked adult females. For this reason, it did not lend itself to a traditional capture-recapture analysis. We used population reconstruction (Eberhardt and Knight 1996), or backdating, to estimate a minimum population size of bears on each study area. This technique simply counts each individual as part of a study population during years when it was known or presumed to be resident, based on knowledge of its age. To translate this count into a density estimate, the critical element becomes the size of the area occupied by the individuals.

We defined a multi-year "effective sampling area" based on distribution of trap sites (Caughley 1977, Clark and Smith 1994). For each sex, we applied a buffer around each trap site equal to the mean activity radius of adult bears. We used the mean activity radius for the time period before most bears began to make long-range movements to fall mast (1 May – 12 August, see Chapter 9). We also restricted trap sites to those trapped within this period. The buffer areas around each trap were merged into a composite, and this became our effective sampling area. On the NSA, sampling areas used were 297.1 km^2 for females and 545.4 km ^{2} for males. On the SSA, areas used were 538.6 km ^{2} for females and 969.2 km ^{2} for males. In essence, size of the area differed by sex, based on observed differences in movement patterns. Because males ranged over larger areas than females, we were able to sample a larger area for males than females using a single trap site.

We constructed a table of bears known alive during each year, by backdating from the last known observation of each study bear. Because no dispersal was observed among females (see Chapter 9), we counted bears as resident during all years if they were captured during the 1 May-12 August season. If they were captured during the mast season, they were counted only if they were known from radio-telemetry monitoring to reside within the effective sampling area. Female offspring of resident females were counted as residents. Due to observed dispersal patterns of males (see Chapter 9), we used different criteria. For males captured as adults, we could not assume they were born on the effective sampling area, therefore we counted them as resident only back to the age of 4 years. For males captured only as subadults and not monitored with radio-telemetry, we counted them as resident only during years when they were captured. For males captured as yearlings, we backdated until birth. Male offspring of resident females were counted as resident only as yearlings or until dispersal was observed through radio-telemetry monitoring.

We determined annual and mean population densities of bears $\geq$1 year old based on these counts. We did not assume we captured all resident bears within the sampling area; therefore these estimates were considered minimum. Because more female bears were monitored with radio-telemetry than male bears, more information on residency and survival was obtained for female bears. Therefore, although we used this method to estimate the sex-age composition of the populations, we recognized it could be biased toward females. Relative proportions of yearlings were also probably underestimated. Because capture probabilities appeared to be lower for this age class, and most bears were captured as adults, bears that did not survive their yearling year would not appear in our analyses.

RESULTS

Estimates of adult and subadult densities remained relatively constant from year to year, on both study areas (Table 10-1). Number of females, particularly adult females, varied little between years. Number of males generally decreased over the years of study; however this decrease may have been due to a reduction in trapping effort rather than an actual change in numbers. Densities of yearlings were more variable. Bear density appeared to be higher on the NSA than the SSA. Mean estimates of adult bears were 45% lower for females on the SSA and 29% lower for males.

Relative proportions of sex-age categories varied annually, with most of the changes observed in the yearling age class. Proportions of subadult males also varied, with peaks observed during 1993-95 on the NSA and 1994-95 on the SSA.

Table 10-1. Density (bears/100 km^2) of adult (≥5 years old), subadult (2-4 years old), and yearling (1 year old) black bears sampled on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-1999[a].

			Year							All
Area	Sex	Age class	1993	1994	1995	1996	1997	1998	1999	years
NSA	Female	Adult	4.7	5.0	5.0	5.4	6.7	7.7	7.4	6.0
		Subadult	3.4	4.0	4.7	3.7	3.4	2.7	2.4	3.5
		Yearling	2.0	1.7	0.7	2.0	0.7	2.4	1.7	1.6
		Total	**10.1**	**10.8**	**10.4**	**11.1**	**10.8**	**12.8**	**11.4**	**11.1**
	Male	Adult	3.3	3.1	3.3	3.9	3.3	2.6	2.2	3.1
		Subadult	2.9	4.6	2.8	1.1	1.3	1.5	0.9	2.1
		Yearling	0.4	0.4	0.0	1.1	0.7	0.9	1.3	0.7
		Total	6.6	8.1	6.1	6.1	5.3	5.0	4.4	5.9
	Grand Total		**16.7**	**18.8**	**16.5**	**17.2**	**16.1**	**17.7**	**15.8**	**17.0**
SSA	Female	Adult	2.6	2.8	2.8	3.5	3.2	3.9	4.1	3.3
		Subadult	2.0	2.2	3.2	2.2	1.9	1.1	1.1	2.0
		Yearling	0.4	1.9	0.6	0.2	1.1	0.7	1.1	0.8
		Total	**5.0**	**6.9**	**6.5**	**5.9**	**6.1**	**5.8**	**6.3**	**6.1**
	Male	Adult	2.7	2.6	2.4	3.1	2.0	2.0	0.7	2.2
		Subadult	0.3	1.7	1.9	0.7	0.4	0.4	0.4	0.8
		Yearling	0.1	0.3	0.0	0.0	0.9	0.4	0.7	0.4
		Total	**3.1**	**4.5**	**4.2**	**3.8**	**3.3**	**2.8**	**1.9**	**3.4**
	Grand Total		**8.1**	**11.4**	**10.7**	**9.8**	**9.4**	**8.5**	**8.2**	**9.4**

[a] Estimates were derived using population reconstruction within an effective sampling area based on distribution of traps.

Population sex-age composition was very similar for the 2 study areas (Table 10-2). Adult females constituted approximately 35% and adult males accounted for 18-23% of study populations. Relative proportions of yearlings varied annually.

DISCUSSION

Although this method had limitations, we believe the estimates derived were relatively accurate, particularly for adult and subadult bears. The raw numbers of individuals counted within the sampling areas were similar for the 2 study areas, as expected considering the nearly equal trapping success (see Chapter 4). The primary factors contributing to differences in density estimates were observed difference between study areas in activity radius and the differences between study areas in total area sampled. The smaller activity radii observed on the NSA, coupled with the more restricted study area boundary, resulted in smaller effective sampling areas, thus higher densities. The activity radius values used to generate the effective sampling error appeared to be fairly accurate, based on comparisons with the composite primary MCP home ranges (see Chapter 9) for the individuals counted as residents (Figures 10-1 and 10-2). For females, the composite home range areas were only 5-6% larger than the effective sampling area, and most individual home ranges were well within its boundary. For males, the composite home range area was 28-59% larger, but most individual home ranges were still contained within the sampling area. A high degree of home range overlap was observed between individuals, especially males. Therefore, the composite home range areas would likely contain more unsampled individuals, especially on the outer edges, well away from trap sites.

Table 10-2. Estimated proportions of adults (≥5 years old), subadults (2-4 years old), and yearlings (1 year old) within black bear populations sampled on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993-1999[a].

			Year							All
Area	Sex	Age class	1993	1994	1995	1996	1997	1998	1999	Years
NSA	Female	Adult	0.28	0.27	0.31	0.31	0.42	0.44	0.47	0.35
		Subadult	0.20	0.21	0.29	0.22	0.21	0.15	0.15	0.20
		Yearling	0.12	0.09	0.04	0.12	0.04	0.13	0.11	0.09
		Total	**0.60**	**0.57**	**0.63**	**0.65**	**0.67**	**0.72**	**0.72**	**0.65**
	Male	Adult	0.20	0.17	0.20	0.22	0.21	0.14	0.14	0.18
		Subadult	0.18	0.24	0.17	0.06	0.08	0.08	0.06	0.13
		Yearling	0.02	0.02	0.00	0.06	0.05	0.05	0.08	0.04
		Total	**0.40**	**0.43**	**0.37**	**0.35**	**0.33**	**0.28**	**0.28**	**0.35**
SSA	Female	Adult	0.32	0.24	0.26	0.36	0.33	0.46	0.50	0.35
		Subadult	0.25	0.20	0.29	0.23	0.20	0.13	0.14	0.21
		Yearling	0.05	0.16	0.05	0.02	0.12	0.09	0.14	0.09
		Total	**0.62**	**0.60**	**0.61**	**0.61**	**0.65**	**0.67**	**0.77**	**0.64**
	Male	Adult	0.33	0.23	0.22	0.32	0.21	0.23	0.09	0.23
		Subadult	0.04	0.14	0.17	0.07	0.04	0.05	0.05	0.09
		Yearling	0.01	0.03	0.00	0.00	0.10	0.05	0.09	0.04
		Total	**0.38**	**0.40**	**0.39**	**0.39**	**0.35**	**0.33**	**0.23**	**0.36**

[a] Estimates were derived using population reconstruction within an effective sampling area based on distribution of traps.

Although density estimates were quite different by study area, estimates of sex-age composition were remarkably similar. Given similar survival rates observed on the 2 study areas (see Chapter 7), our estimates of density and composition appear relatively accurate. However, densities observed on the NSA may have been higher than in similar habitat where hunting was not restricted. Our data are not sufficient to rigorously assess that question.

Figure 10-1. Size of the effective sampling area used for estimating black bear density, relative to primary minimum convex polygon home ranges of resident bears on the Northern Study Area, New Mexico, 1992-2000.

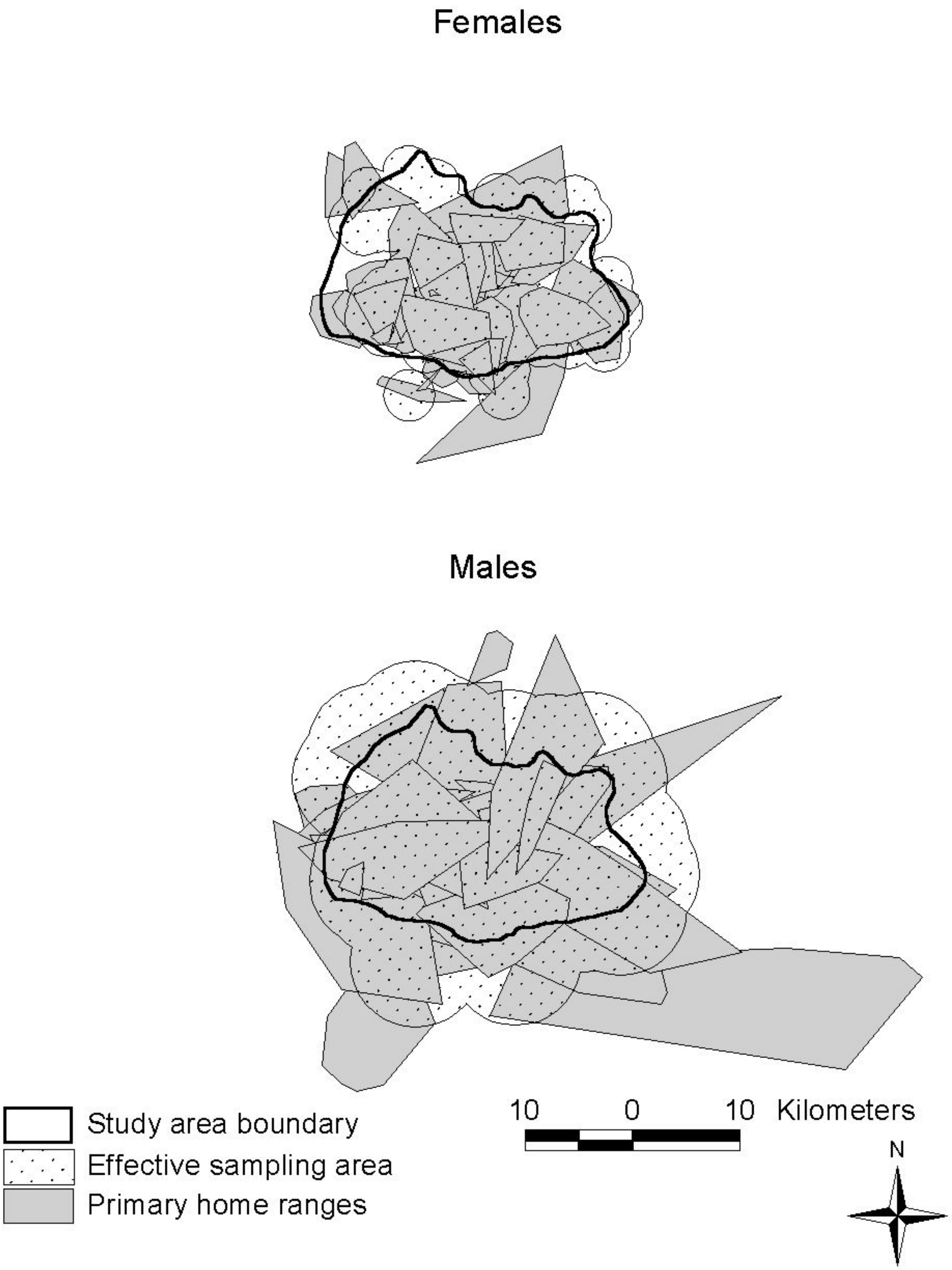


Figure 10-2. Size of the effective sampling area used for estimating black bear density, relative to primary minimum convex polygon home ranges of resident bears on the Southern Study Area, New Mexico, 1992-2000.

Densities and proportions of yearlings were quite variable among years. For each study area, the years of lowest yearling density (1995 on the NSA, 1996 on the SSA) corresponded to years following oak failure (see Chapter 6). On both study areas, the densities and proportions of yearlings were lower for males than for females. We suspect this was a product of the sampling and estimation method, and did not accurately reflect true values. In any given year, most yearlings counted within the sampling area were offspring of resident females, not trapped bears. Because the male sampling area was larger than the female's, there were likely unsampled females within it. Because we could not count their offspring, the resulting density estimates for male yearlings were lower than those of females. The density estimates for females in these age classes were probably more accurate.

Black bear density has been estimated in many regions of North America, primarily using mark-recapture or mark-resight methods. The variability of these estimates is tremendous, with densities as low as 1.8 bears/100 km ^{2} in the Snowy Mountains of southeast Wyoming (Grogan and Lindzey 1999) to 149 bears/km^2 on a coastal island in Washington (Lindzey and Meslow 1977). Within the Southwest, density estimates have ranged from 12-16 bears/100 km^2 in west-central Colorado (Beck 1991) to 71 bears/100 km^2 in north-central Arizona (LeCount 1987). Our density estimates appeared reasonable in the context of these other studies.

MANAGEMENT IMPLICATIONS

The density estimates obtained for the study areas can be used in conjunction with habitat data (see Chapter 11) to estimate statewide and regional population sizes. However, these estimates must be used with caution. Arguably, our study was conducted within some of the most productive bear habitat in New Mexico, particularly the NSA. Direct extrapolation of these density values to all areas of bear habitat would not be realistic.

The sex-age composition estimated for the study areas also can be compared to the structure of hunter kill data and simulated population structures generated using the bear population model (see Chapter 14). These analyses may aid in current and future interpretation of bear population trend, as reflected in the harvest data.

CHAPTER 11

A MODEL OF STATEWIDE HABITAT SUITABILITY AND POPULATION SIZE

Understanding the population status and trend of large carnivores, such as bears, over large landscapes is constrained by limited by availability of detailed empirical data and few approaches to analysis and display of spatial information (Merrill et al. 1999). Habitat analysis using GIS technologies has proven useful for management of wildlife in general (Scott et al. 1993, Horino and Miura 2000) and black bears in particular (Clark et al 1993, van Manen and Pelton 1997). These approaches can be useful to forecast future impacts of human population growth or habitat alteration. Van Manen et al. (1997) considered forecasting capabilities fundamental to the management process.

In this chapter, we describe the New Mexico landscape from the perspective of bear habitat suitability. Specifically, we make spatial predictions as to potential availability of mast species and the potential for human interaction. Our objectives were to: (1) predict suitable black bear habitat in New Mexico, (2) derive associated statewide and regional population estimates, and (3) analyze potential human influences on bear habitat. These objectives involved GIS analyses of bear habitat associations based on habitat use and movements observed on the 2 study areas. These associations were applied to a land cover map of New Mexico and other spatial criteria to depict predicted suitable bear habitat. Factors (roads, human population density, hunter kills) known to affect bear populations were overlaid with suitable habitat to develop spatially explicit perspectives on potential hunting mortality and bear-human conflict.

Information gathered from these exercises should help managers better understand the status of black bears across the state and serve as the basis for black bear management. The bear habitat model is a tool that identifies where bears have the potential to occur, the spatial boundaries of distinct populations, the degree of isolation between populations, and whether landscape characteristics differ among populations. These perspectives can aid in forecasting bear management needs and challenges.

METHODS

Habitat Model Development

A spatial model predicting the extent of suitable black bear habitat was developed using a rule-based system with GIS technologies, based on the New Mexico Gap Analysis (NMGAP) land cover map (Thompson et al. 1996) and biological information derived from field studies during 1992-2000. The habitat model was developed using ESRI Arc/View script language. The NMGAP land cover map includes 42 cover classes, described by dominant vegetation and canopy cover. Each of these cover classes was assigned to 1 of 4 categories of relative suitability for bears based on habitat use observed on the 2 study areas (see Chapter 9) and cover type descriptions. Suitability was rated as primary, secondary, edge use, and no use (Table 11-1). Cover classes rated as primary included all closed-canopy forest and woodland types, because more than 80% of bear locations were found within these types. Cover classes rated as secondary included shrubland types used more than expected, but accounting for <10% of total use. Cover classes rated as edge use included open woodland and grassland types used less than expected. Analyses indicated these types were used by bears, but usually in close proximity to more suitable habitats. Cover classes associated with humans, such as agriculture or urban, were rated as no use. Desert cover types also were classified as no use.

Each land cover class also was assigned to 1 of 3 categories of relative mast production potential, based on cover type descriptions (Thompson et al. 1996) and occurrence of oak, juniper, or pinyon species within cover classes. Categories were high, poor, and no mast production potential.

The habitat model first selected all land cover classes classified as primary. Secondary types were then selected only if they were adjacent to a primary type. Edge use types were then selected if they were adjacent to a primary type, and only that portion within a 500 m buffer from the primary type was included in predicted habitat.

When these areas were identified, we used GIS analyses in the model determine the area of each contiguous tract of suitable habitat (regardless of its habitat suitability score). Tracts >300 km^2 were selected as suitable habitat. This size represented the approximate area supporting 50 individual bears based on density data from the NSA (see Chapter 10), and we deemed this a “minimum sustainable population”. Also, tracts >20 km^2 (large enough to support 1-2 bears based on home range data) were selected only if they were within 15 km of a habitat tract large enough for a minimum sustainable population.. All other tracts were considered too small or too isolated to be included in the final model.

The model was designed to allow users to vary the habitat scores for each land cover class, minimum tract size for a sustainable population, minimum tract size for a single individual, and maximum distance that an individual must be from viable population before it is considered too isolated from the population. Predictions of bear habitat reported here were based on values described above.

The model was designed to generate 2 maps of black bear habitat. The first was the detailed map described above. The second was a generalized distribution map that identified major regions of bear habitat. To develop this map, internal, unselected polygons were absorbed and the boundaries were simplified by expansion and shrinking of the boundary. This eliminated much of the reticulation and complexity of the polygon boundary. We found that doing this process twice resulted in a better generalization.

Table 11-1. Habitat suitability and mast potential assignments used in the statewide black bear habitat model for New Mexico; land cover classes are from Thompson et al. (1996).

NMGAP Code	Description	Suitability	Mast potential
1111	Rocky Mountain Alpine Graminoid Tundra	EdgeUse	None
1112	Rocky Mountain Alpine Forb Tundra	EdgeUse	None
2111	Subalpine Conifer Forest	Primary	None
2112	Subalpine Broadleaf Forest	Primary	None
2121	Rocky Mountain Upper Montane Conifer	Primary	Poor production
2122	Rocky Mountain Lower Montane Conifer	Primary	High production
2211	Madrean Lower Montane Conifer Forest	Secondary	High production
3111	Upper Montane Open Conifer Woodland	EdgeUse	None
3121	Rocky Mnt/Great Basin Closed Conifer	Primary	High production
3122	Rocky Mnt/Great Basin Open Conifer	EdgeUse	None
3211	Madrean Closed Conifer Woodland	Primary	High production
3222	Madrean Open Oak Woodland (Encinal)	Secondary	High production
4110	Rocky Mountain Montane Scrub & Interior	Secondary	High production
4111	Rocky Mountain Montane Deciduous Scrub	Secondary	High production
4121	Broadleaf Evergreen Interior Chaparral	Secondary	High production
4131	Plains-Mesa Broadleaf Sand-Scrub	None	High production
4211	Great Basin Microphyllous Desert Scrub	None	None
4212	Great Basin Broadleaf Deciduous Desert	None	None
4220	Chihuahuan Desert Scrub	None	None
4221	Chihuahuan Broadleaf Evergreen Desert	None	None
4222	Chihuahuan Broadleaf Deciduous Desert	None	None
5110	Rocky Mountain Subalpine and Montane	EdgeUse	None
5121	Short Grass Steppe	EdgeUse	None
5122	Mid-Grass Prairie	EdgeUse	None
5123	Tall Grass Prairie	None	None
5211	Great Basin Foothill-Piedmont Grassland	EdgeUse	None
5212	Great Basin Lowland/Swale Grassland	None	None
5220	Chihuahuan Desert Grassland	EdgeUse	None
5221	Chihuahuan Foothill-Piedmont Desert	EdgeUse	None
5222	Chihuahuan Lowland/Swale Desert	None	None
6110	Rocky Mountain Montane Forested/Shrub	Secondary	None
6120	Southwest & Plains Forested/Shrub Wetland	Secondary	None
6131	Arroyo Riparian Scrub	None	None
6210	Persistent Emergent Wetlands	Secondary	None
6211	Graminoid Wetlands	EdgeUse	None
9110	Dryland Agriculture	None	None
9120	Irrigated Agriculture	None	None
9210	Barren	None	None
9220	Mine/Quarries	None	None
9230	Rock Outcrop	None	None
9310	Urban	None	None
9320	Urban Vegetated	None	None
9410	Riverine/Lacustrine	None	None
9420	Basin/Playa	None	None

Estimates of statewide and regional black bear population size were derived by extrapolating mean density estimates from the 2 study areas (see Chapter 9) to areas of primary habitat. Density estimates from the NSA were used to estimate population size on the San Juan and Sangre de Cristo complexes. Density estimates from the SSA were used for all other regions.

GIS data and related metadata (Appendix B) and the habitat model (Appendix C) are included on a CD associated with this report. The habitat model is written in ESRI Arc/View script language and this package, with Spatial Analyst is needed for its use. The script language used for the New Mexico bear habitat model is contained in a file on the CDs associated with this report.

Hunter-Kill Locations

We used locations (UTM coordinates reported to the nearest 1000 m) recorded for hunter-killed bears obtained from the NMDGF harvest data (see Chapter 13) to compile a point file of bear kill locations. Accuracy of data was verified by comparing the recorded GMU with the recorded location, and obvious mistakes were corrected. Records for which the numeric portion of the GMU did not match with valid coordinates were discarded from analyses.

A total of 3,047 records of hunter-killed bears were available for the years 1990-1999, but 420 records (14%) were discarded due to a lack of UTM coordinates or UTM coordinates inconsistent with the GMU recorded. Examination of relative numbers of discarded records by year and GMU did not indicate any bias in the remaining sample of 2,627 records.

Human Interface

We created a coverage depicting total road length within the mean activity radius for female and male bears during the fall season (1 September-den entry, see Chapter 9). Mean activity radii were calculated for bears on both study areas, and a radius of 7.0 km was used for females and 12.0 km was used for males. A coverage depicting New Mexico roads was obtained from the U.S. Census Bureau (http://www.uscensus.gov). Road length was tabulated for each region. Analysis of total length of secondary roads within female (7 km) and male (12 km) fall activity radii was designed to estimate the potential length of road a bear might encounter during months of fall hunting. These data were derived by calculating the length of roads within 7-km or 12-km radii of points distributed at 1-km intervals across all of New Mexico.

A coverage of U.S. census blocks was used to evaluate distribution of bear habitat relative to human populations. Population blocks with human residential density >1 person/ha and >5 households were identified. Buffers created around these population centers represented areas within 5-20 20 km.

Conceptually, we viewed human activity relative to potential effect on the bear population. Bear hunters pose the greatest relative direct effect on a bear population, therefore we tried to obtain available information on distribution and magnitude of bear hunting activity statewide. Secondly, human activity on the landscape can cause significant indirect and direct influence on bear distribution and mortality (e.g., interaction with or avoidance of recreationists, bear mortality to depredation complaints or vehicle collision). In addition to bear mortality, interactions with humans can be highly visible events. We sought spatial data that would identify the degree of human use (not including recreationists) on the landscape. Recreationists were considered a separate group. Their interactions with bears are varied but generally present seasonal and dispersed effects. Residential and recreational uses were conceptually separated not only because of their effect on the bear population but to the social aspects of management. A nuisance bear is different to a resident versus a recreationist regarding the type of mitigation possible.

With this conceptual framework we searched for data to develop indices of human use of the landscape. We directed our search toward data that were statewide in scope. NMDGF harvest survey data were obtained, compiled, and linked to GMU coverages to depict relative hunter occurrence on the landscape. Similarly, angler survey data obtained from NMDGF were linked to a coverage of New Mexico fishing waters. We anticipated that these data will represent areas of possible hunter/angler-bear interaction. We also made attempted to obtain United States Forest Service (USFS) Lands spatial data as they contain a significant portion of bear habitat in New Mexico. We looked for spatially explicit measures of use and locations of facilities. We acquired recreation data from the USFS including limited recreation user days data and point locations of recreation facilities. In addition, we acquired recreation user days data from the New Mexico State Parks and the National Park Service.

RESULTS

Predicted Suitable Habitat

The habitat model prediction depicted prospective distribution of suitable black bear habitat (Figure 11-1) across approximately 58,939 km^2 (5.9 million hectares or 14.6 million acres). Simplification of the boundaries identified 10 distinct regions of predicted black bear habitat: 4 large regions including the San Juan complex, the Sangre de Cristo complex, the Gila complex, and the Sacramento region; 3 smaller, relatively isolated tracts including the Zuni region, Mt. Taylor region, and Sandia/Manzano region; and 3 small regions connected to larger range outside New Mexico, including the Chuska region, Bootheel region, and the Guadalupe region. The simplification process did not distinguish the San Juan complex and the Sangre de Cristo complex. We artificially separated these complexes, with the boundary defined as the Rio Grande. All applicable summaries reported here use this stratification of the state.

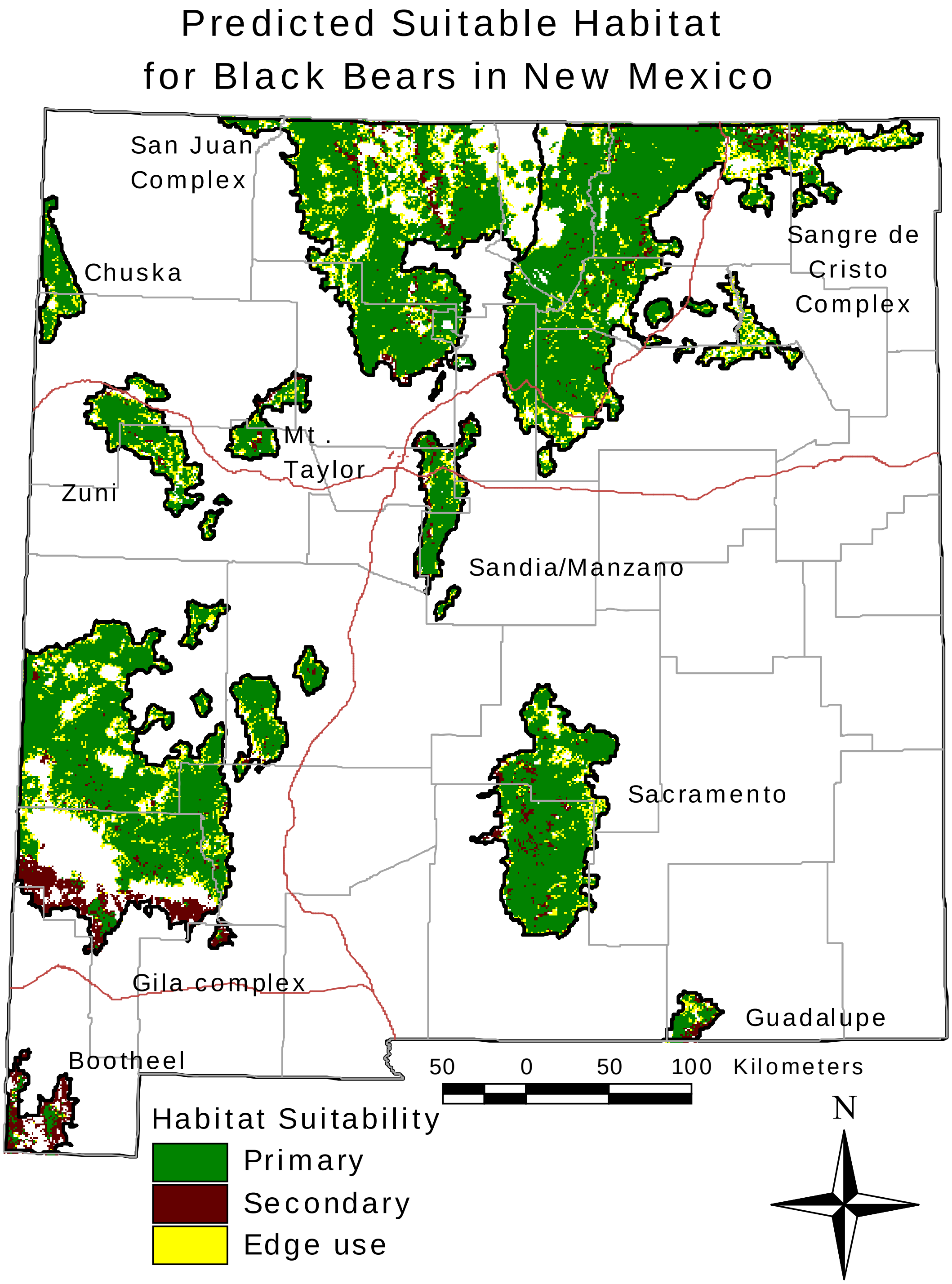


Figure 11-1. Map of predicted suitable habitat for black bear in New Mexico.

Of the 5.9 million ha of suitable habitat, 75% was comprised of primary cover types, 7% was comprised of secondary cover types, and 18% was comprised of edge use cover types (Table 11-2). Relative proportions of these types varied among regions. Most notably, the Bootheel region was comprised of relatively little primary habitat. Among the 4 large regions, the Gila complex had less primary habitat and more secondary habitat (Table 11-2).

Mast potential within suitable bear habitat showed some variability among regions (Figure 11-2). Areas of poor mast production potential were associated with higher elevations, especially in the San Juan complex, the Sangre de Cristo complex, the Gila complex, and the Sacramento region. When primary habitat was overlaid with mast production potential, only 280 km^2 was found to be >7.0 km from areas of high mast production potential. This distance corresponds to the observed mast season activity radius of female bears. That limited area with no mast production potential was located within the highest elevations of the Pecos Wilderness in the Sangre de Cristo complex.

Land ownership differed among the regions (Table 11-2). Nearly half of the predicted suitable bear habitat was managed by the USFS (Figure 11-3). Private landowners were the second most predominant stewards bear habitat, with about one third of all lands under private ownership. Tribal lands comprised about 10% of bear habitat, but it was concentrated in 3 regions. All of the Chuska range was situated within the Navajo Reservation, and large portions of the San Juan complex and the Sacramento region were found within the Jicarilla Apache and Mescalero Reservations, respectively. State lands and Bureau of Land Management properties constitute a relatively small portion of New Mexico bear habitat (Figure 11-3).

Human Interface

Locations of hunter-killed bears overlaid with the predicted habitat indicated strong corroboration of the habitat model predictions of habitat distribution (Figure 11-4). Significant tracts with no recorded bear kills were tribal lands and the Guadalupe and Bootheel regions. The Sandia range found within the north part of the Sandia/Manzano region also lacked records of bear kills. Overall, 95% (*n* = 2,488) of the bear kills occurred within the regional boundaries of predicted bear habitat. Of the 5% occurring outside boundaries, most were located north of the Gila complex. Bear kills are expected outside of predicted habitat because of occurrence of transient bears and slight errors in the predictive model.

Total road length within a female activity radius was highly variable statewide (Figure 11-5), but relatively uniform for a male activity radius (Figure 11-6). Approximately 40% of the bear habitat had >120 km of road within a female activity radius, while greater than 80% of the habitat had >120 km of road within a male activity radius.

Table 11-2. Summary of habitat model predictions and bear population estimates statewide and by region in New Mexico (see text and Figure 11-1 for description of regions).

	Statewide	Sangre de Cristo complex	San Juan complex	Gila complex	Sacramento region	Zuni region	Mt Taylor region	Sandia / Manzano region	Bootheel region	Chuska region	Guadalupe region
Predicted habitat (km^2)											
Total range	70,680	19,350	16,006	19,594	7,123	2,584	988	1,969	1,363	1139	564
Suitable habitat	58,939	16,960	12,495	15,472	6,642	2,242	887	1,788	895	1,060	499
Type of suitable habitat (%)											
Primary	75.10	79.74	77.70	71.25	80.21	68.86	64.85	72.66	21.29	75.79	53.31
Secondary	6.95	2.08	4.02	11.26	5.90	2.84	9.15	8.19	74.96		28.83
Edge use	17.96	18.18	18.28	17.49	13.89	28.29	26.00	19.15	3.75	24.21	17.86
Mast potential of suitable habitat (%)											
None	21.93	26.34	24.33	18.47	14.35	28.29	26.61	19.88	3.75	24.74	17.86
Poor	11.84	19.47	10.19	8.16	13.47	0.25	2.42	8.83		5.81	
High	66.23	54.19	65.48	73.37	72.19	71.46	70.97	71.29	96.25	69.45	82.14
Stewardship of suitable habitat (%)											
USFS[a]	49.89	27.32	49.19	82.86	45.05	50.72	50.60	40.77	23.22		58.49
Private	31.60	62.88	22.57	10.15	22.03	19.23	35.84	47.03	55.22		5.19
Tribal	10.61	2.14	20.30		27.01	15.97	1.57	7.35		100.00	
BLM[b]	3.79	1.98	5.38	4.22	2.67	4.14	11.79	0.86	15.25		9.12
State	3.18	5.55	1.04	2.75	2.93	1.55	0.20	3.89	6.31		3.58
NPS[c]	0.61	0.03	0.76	0.01		6.31					23.62
DOE[d]	0.15		0.72								
DOD[e]	0.12				0.31	2.09		0.10			
USFWS[f]	0.03	0.10									
BOR[g]	0.01	0.00	0.06								
Population estimate (bears ≥1 year old)											
Total bears	5947	2299	1651	1047	506	147	55	123	18	76	25

[a] U.S. Forest Service
[b] Bureau of Land Management
[c] National Park Service
[d] Department of Energy
[e] Department of Defense
[f] U. S. Fish and Wildlife Service
[g] Bureau of Reclamation

Predicted Mast Production Potential in Black Bear Habitat

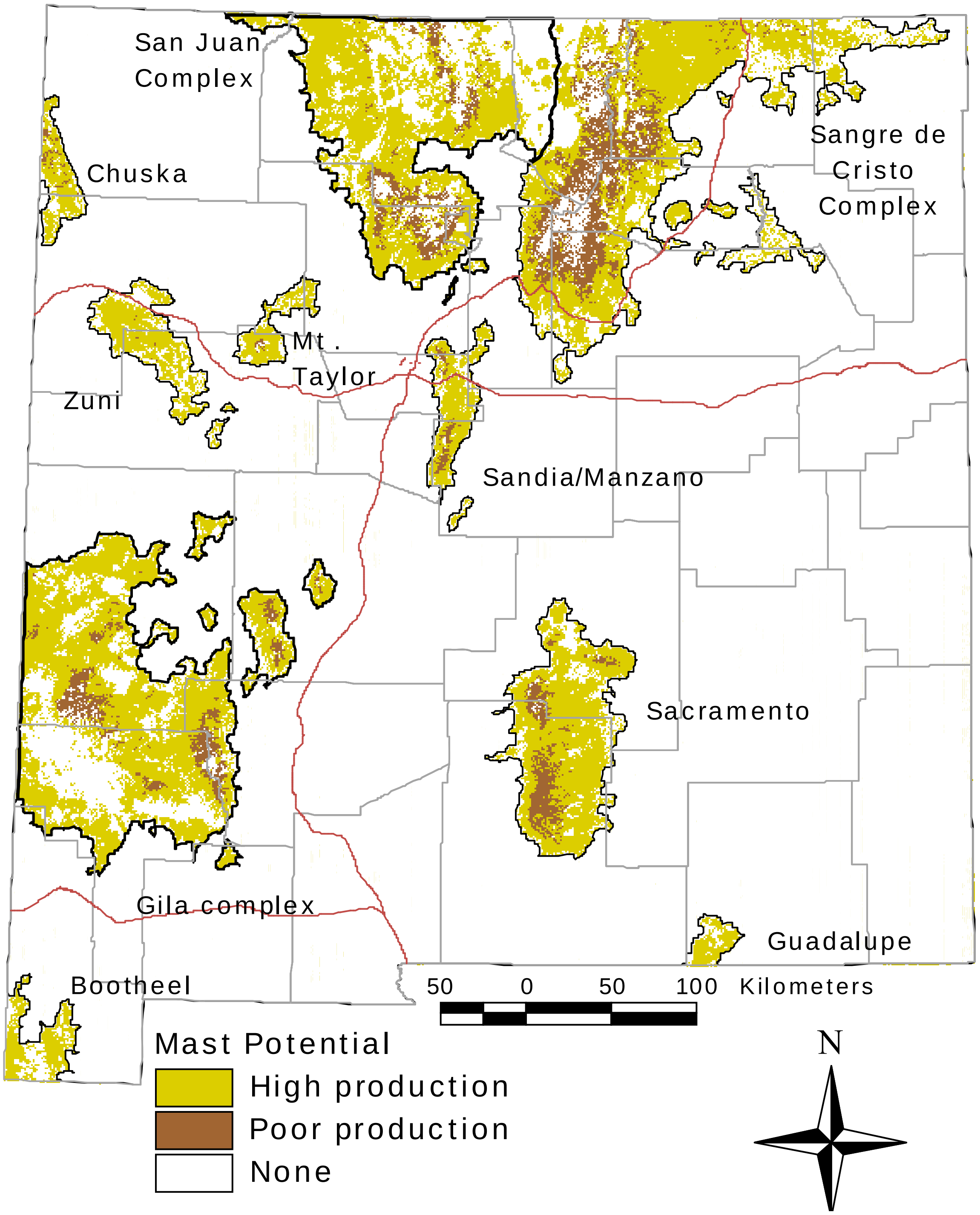


Figure 11-2. Distribution of mast production within predicted black bear suitable habitat.

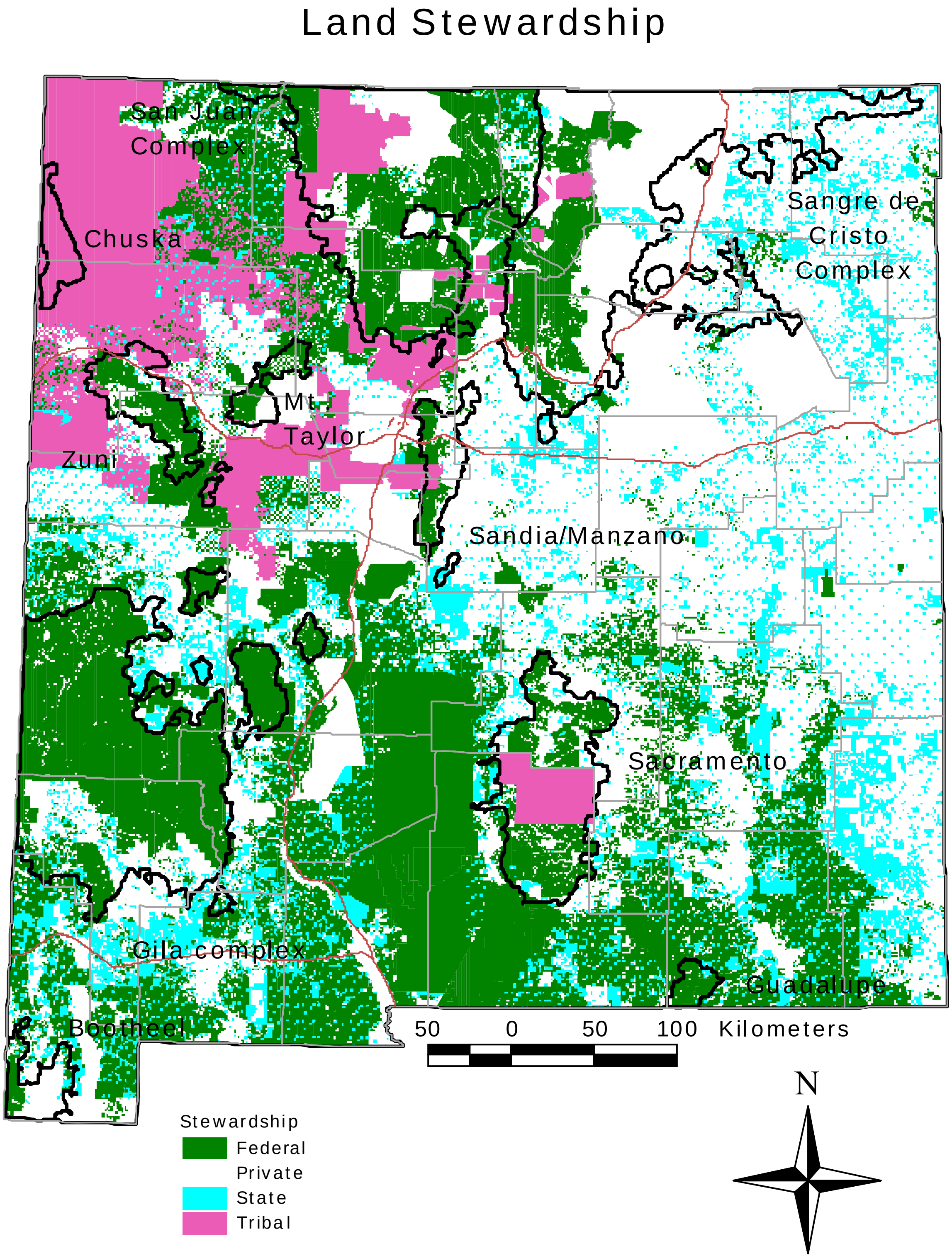


Figure 11-3. Federal, state, tribal, and private land stewardship (ownership) relative to predicted suitable black bear habitat in New Mexico.

Location of Bear Kills by Hunters 1990-1999

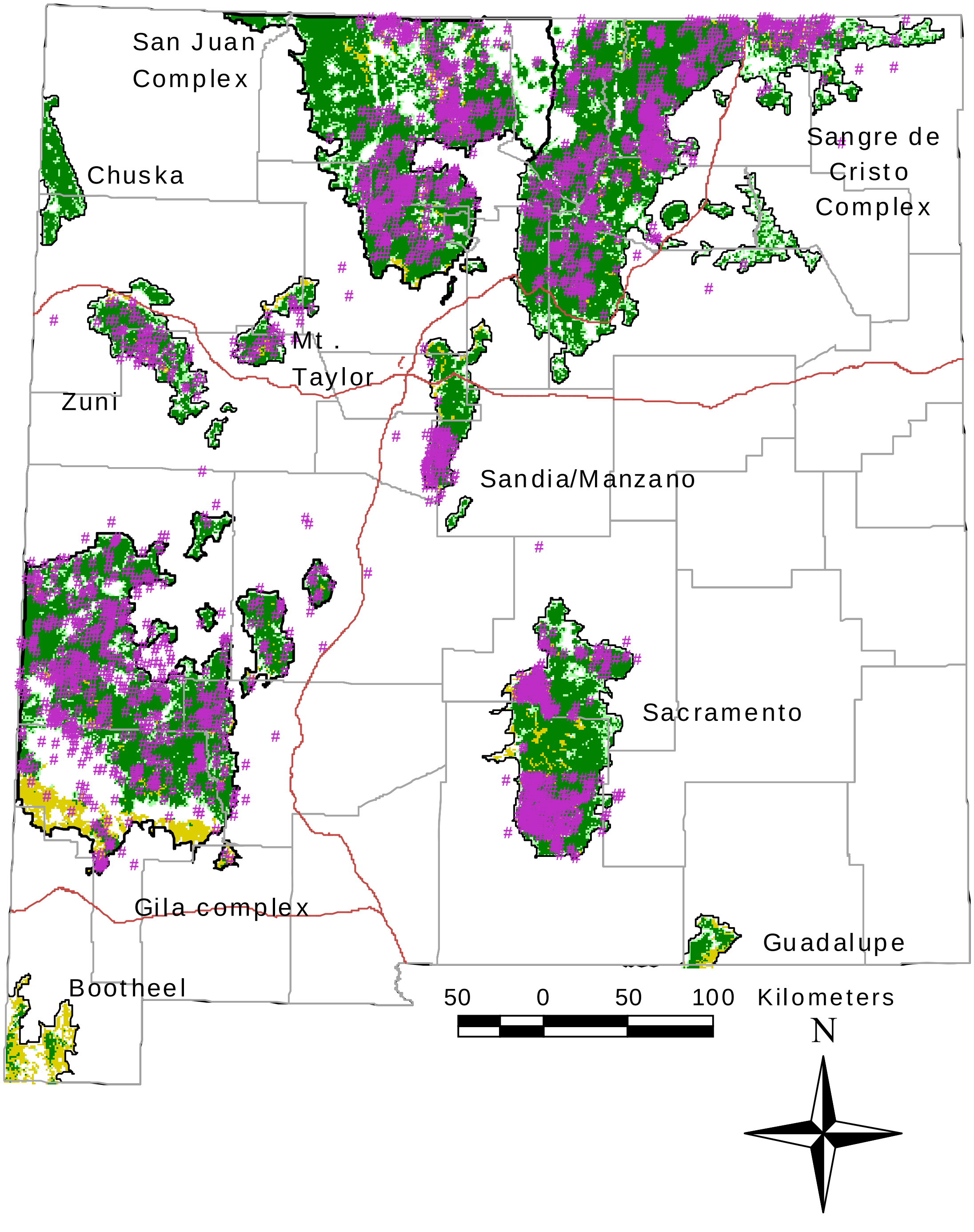


Figure 11-4. Distribution of reported bear kills by hunters from 1990 to 1999.

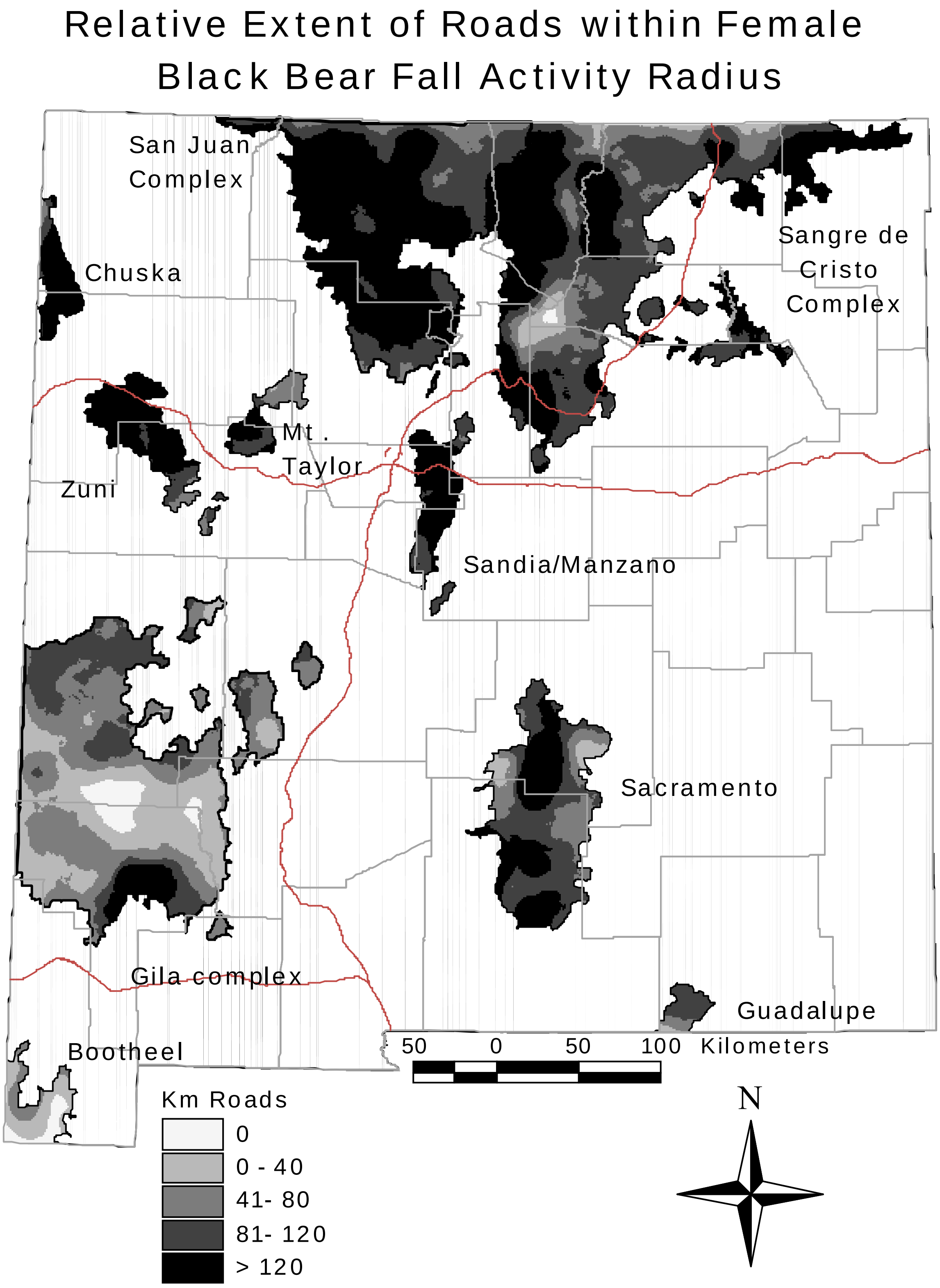


Figure 11-5. Extent of secondary roads within a female black bear fall activity radius (7 Km) in New Mexico.

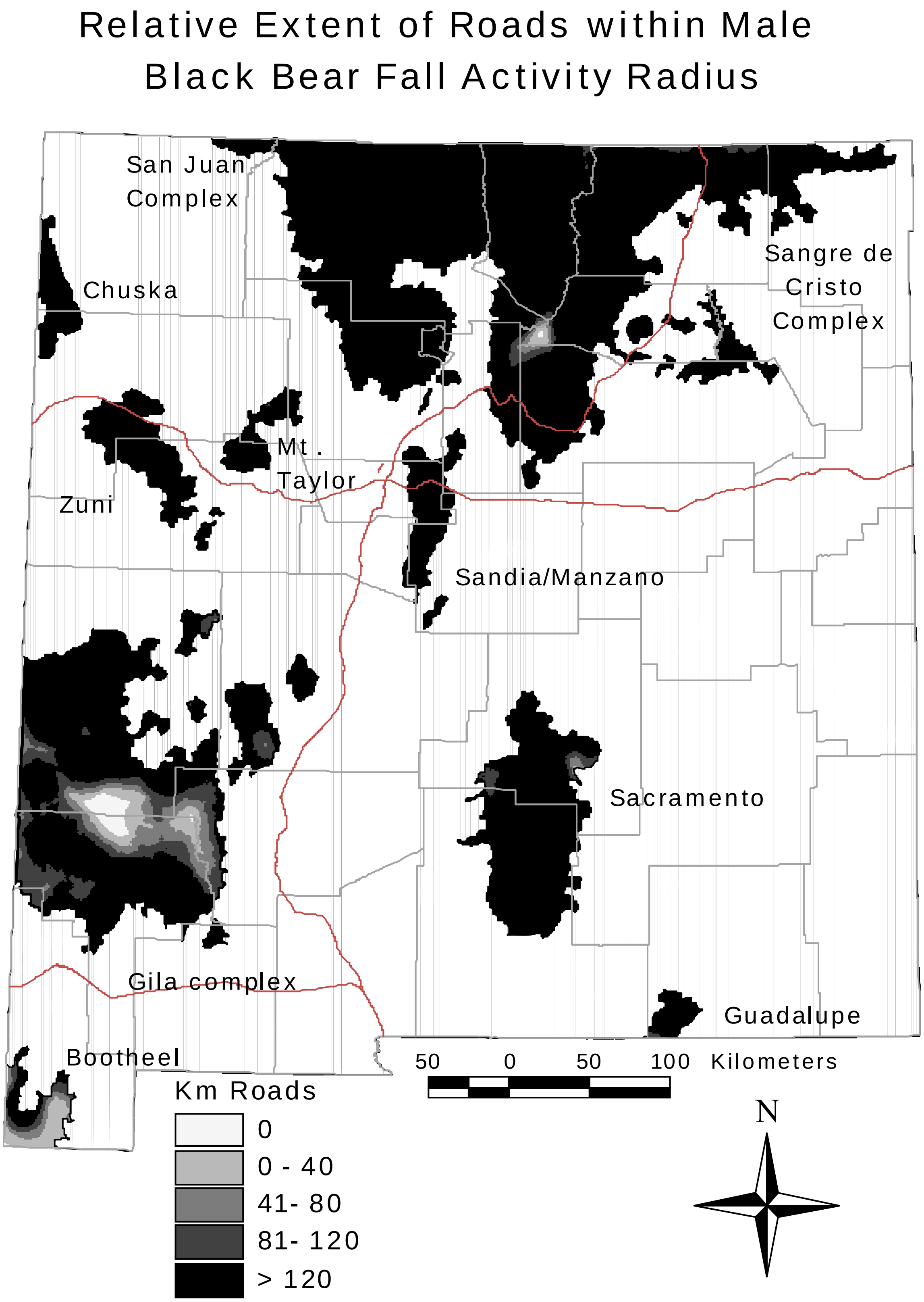


Figure 11-6. Extent of secondary roads within a male black bear fall activity radius (12 km) in New Mexico.

All predicted regions of bear habitat displayed areas that were in proximity to human populations (Figure 11-7). Statewide, 17% of bear habitat was within 5 km of human populated areas. Percent of bear habitat within proximity to human populations differed regionally, with the highest proportions observed in the Sandia/Manzano region, the Sacramento region, and the Sangre de Cristo complex (Table 11-3). Within the Guadalupe region and the Bootheel region, more than 60% of bear habitat was >20 km from human populated areas.

Table 11-3. Percent of predicted suitable black bear habitat within 0 to 20 km of human-populated areas (> 1 person/ha and > 5 households) in New Mexico, based on 2000 U.S. Census Bureau block data and sorted by area of bear habitat.

Region	Area (km^2)	< 5 km	< 10 km	< 15 km	< 20 km	>20 km
Sangre de Cristo	16,960	23.16%	48.77%	66.66%	80.15%	19.85%
Gila	15,472	6.49%	19.69%	36.47%	53.98%	46.02%
San Juan	12,495	14.96%	38.71%	60.96%	75.35%	24.65%
Sacramento	6,642	28.15%	57.50%	74.82%	87.77%	12.23%
Zuni	2,242	17.73%	45.29%	69.15%	86.19%	13.81%
Sandia/Manzano	1,788	50.76%	79.79%	95.63%	98.68%	1.32%
Chuska	1,060	10.30%	43.39%	79.03%	94.64%	5.36%
Bootheel	895	0.89%	4.89%	9.63%	14.18%	85.82%
Mt Taylor	887	1.47%	14.59%	38.16%	60.88%	39.12%
Guadalupe	499	0.10%	5.37%	17.27%	34.38%	65.62%

Predictions for proximity to secondary roads and proximity to human populations did not necessarily coincide. Some areas with relatively higher length of road within activity radii were situated in areas of low human populations, particularly private and USFS lands in the Gila complex and private and tribal lands in the San Juan complex.

Our compilation of various coverages and data sets regarding distribution of human recreation produced information of varied completeness, quality, and spatial resolution. We judged that these data in current form were insufficient to perform detailed analyses relative to distribution of bear habitat and population estimates. Nonetheless,. we anticipate that these data, if further compiled with specific objectives in mind, can be used to depict areas of possible human-bear interactions. Thus, we provide these data digitally (see Appendix C) for future users of this report and the associated modeling tools. Those data include consolidated NMDGF hunter and angler survey results for hunt year 1990-1991 through 1999-2000 (hunt year generally is April-March). We were unable to collect spatially explicit results for small game and birds (except turkey). The finest spatial resolution available for all hunts is the GMU. Because some data are missing, care must be taken not to make literal interpretations of absolute hunter days from these data. However, this data set can provide a fair indication of the spatial distribution of hunting activities in New Mexico with further editing.

Distance of Predicted Black Bear Habitat to Human-Populated Areas

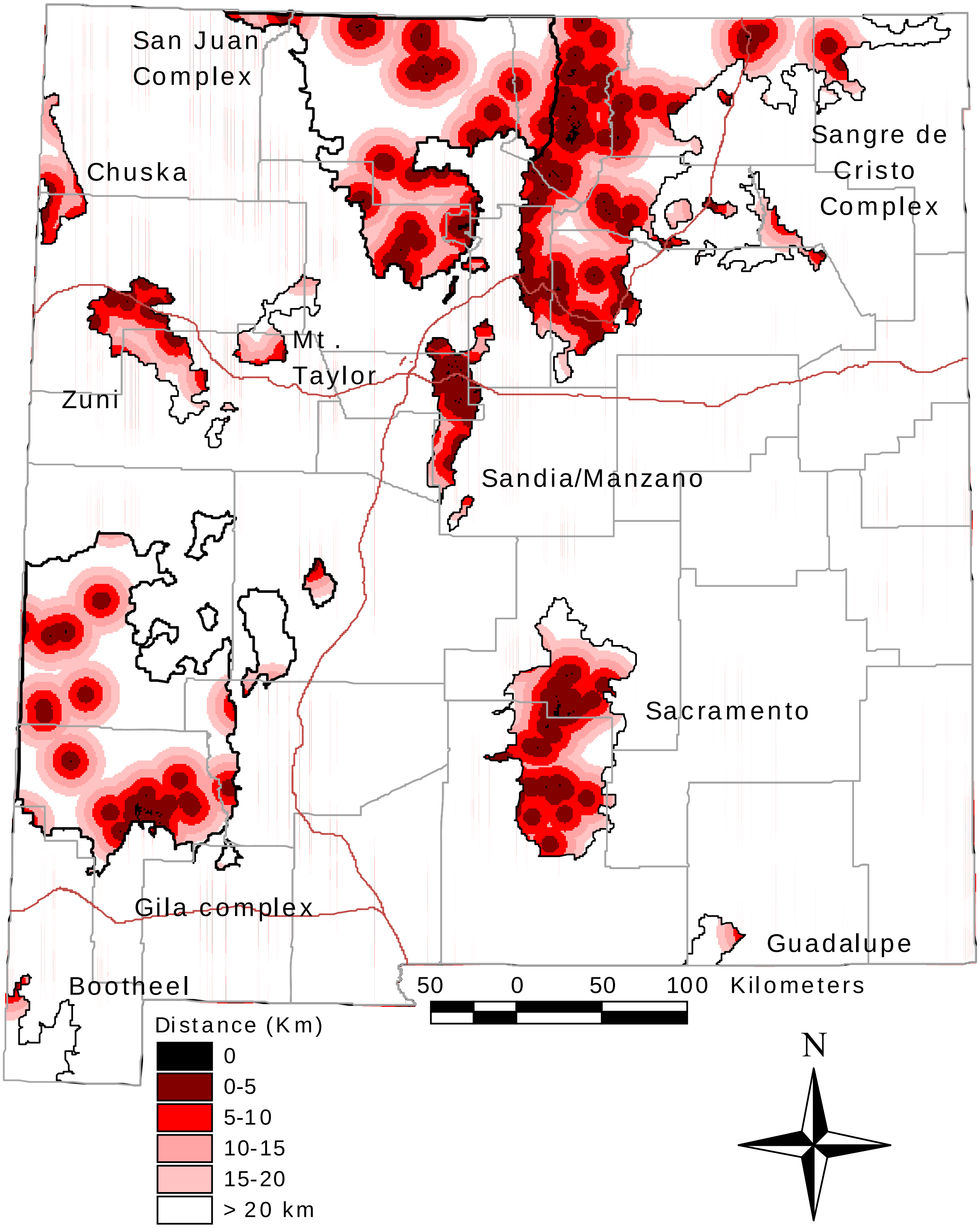


Figure 11-7. Distance of predicted black bear habitat to human-populated areas (>1 person per hectare and >5 households) in New Mexico.

Bear Population Estimate

Extrapolating observed density estimates (see Chapter 10) to areas of primary habitat yielded a statewide population estimate of 5,947 bears >1 year old, pertaining to the premast season (Table 11-2). Regional estimates ranged from 18 bears in the Bootheel region to 2,299 bears in the Sangre de Cristo complex. The small populations (<50 bears) estimated for the Bootheel and Guadalupe regions reflect areas of contiguous habitat with Arizona and Texas

DISCUSSION

In the NMGAP methodology (Thompson et al. 1996), prediction of suitable habitat for a species was based on the premise that a species distribution was all suitable land cover categories within that species general range. Other ancillary variables, such as elevation or soil classification also were included in the habitat modeling when those values were represented on spatially-registered maps. This methodology has proven useful for developing landscape and regional scale maps of species occurrence (Edwards et al. 1996). Another approach is to assign a numeric score to habitat rather than assignment to categories (Boyce and McDonald 1999, Kliskey et al. 1999). In constructing the statewide black bear habitat model for this study , we enriched the modeling process by classifying suitable habitat into multiple categories (e.g., primary, secondary , edge, and no use) rather than the Boolean response (suitable or not) used in NMGAP (Thompson et al. 1996). Our more enriched approach provided greater realism in identifying occupied habitat.

As with all modeling exercises, our habitat prediction results were a compromise between realism, practicality, and data limitations. The largest impediment to a “true” habitat map was the size and scale of this objective. Scaling is probably the most difficult aspect of landscape ecology and the subject of intense research. Large, mobile animals function at a relatively larger scale (Wiens, 1982). Scale is also not independent of spatial pattern (O’Neill et al. 1988). Changing of scale can greatly change perceived landscape patterns. When inappropriate scales are used, true biological relations can become masked or false patterns can emerge (Scott et al. 1996).

Our model was limited to data available as of summer 2001. To our knowledge, NMGAP is the only statewide coverage of land cover (42 themes at 2-100 ha resolution) that exists. There are other vegetation coverages that are more detailed in thematic and spatial resolution but they are not statewide in scope. For example, databases and digital vegetation coverages developed by the USDA Forest Service may provide more comprehensive information appropriate for analysis of black bear habitat quality. Although not statewide, these data would provide insight into a majority of the bear habitat in New Mexico. However, although the data are publicly accessible, at present they are not complied in a single archive to our knowledge.

Bear reproduction is inherently stochastic with its variability tied to mast crop variability, particularly oaks. Our ability to define this variability statewide was limited because there is no temporal variability in the land cover map. In addition, the land cover map does not differentiate on the basis of subdominant species in each land cover class. Most oak species in New Mexico exist as understory species in several different cover types, therefore the actual abundance of these species cannot be predicted using the current data. Although general predictions of mast potential were developed, more detailed data would be necessary to assess actual habitat productivity between regions.

We were purposely careful to identify suitable habitat and this map should be considered potential habitat rather than actual bear distribution on any given day or in a single year. It is very important to recognize that bears (e.g., transients) can occur in New Mexico outside of the predicted habitat areas. The key consideration is that we modeled conditions on the landscape that are considered to be reliably associated with routine occurrence of reproductively sustaining bear population.

As the human population increases, human-bear interactions have the potential for increase. This raises the value of human-bear interface data. These data serve as a tool to increase the ability of a game/land manager to predict areas of interactions between bears and humans. Spatial data provide a means to “visualize” these areas of interaction on the landscape.

The study area density estimates were derived in productive bear habitat that arguably represents some of the best habitat within their prospective regions. These values may not be applicable to areas of low quality habitat. However, some of this difference was accounted for in the habitat suitability analysis, where secondary habitat was identified. Because the population estimate was derived by extrapolating to primary habitat only, lower quality habitat did not unduly influence the population estimate.

MANAGEMENT IMPLICATIONS

The statewide estimate of 5,947 bears derived from habitat-density extrapolation is similar to the independent estimate derived from population modeling (see Chapter 14). That estimate of 5,200 bears was for the state, excluding the Zuni, Mt. Taylor, Sandia/Manzano, and Chuska regions. Both estimates are for the pre-mast season (May-early August) and excluded cubs of the year.

Statewide population estimates derived from this study refute previous estimates. Our estimates indicate a statewide population of approximately twice the long-standing estimate of 3,000 bears previously used by the NMDGF. However, these estimates do not suggest a doubling of the bear population in the past decade. Rather, these estimates are based on better information including demographics, density, and habitat extent.

Annual trends in black bear reproductive success were highly influenced by fall mast crops, especially the abundance of acorns. Within predicted bear habitat, mast producing land cover types were found within 7 km (female activity radius) of primary habitat throughout New Mexico except for about 300 km^2 in the Sangre de Cristo complex. This indicates that nearly all bears have access to habitat with potential for producing important mast producing species. However, the actual abundance of oak, juniper, and pinyon within different regions remains unknown. In the future, incorporation of more detailed data, especially on distribution of oak species, may provide valuable insight into the relative productivity of habitats throughout the regions of New Mexico.

Estimated statewide bear habitat encompasses approximately 14.6 million acres, of which 75% is primary habitat. Primary habitat represents about 13.5% of the state. Approximately 17% of bear habitat is situated within 5 km of human populations. These dimensions clearly illustrate the extent of bear exposure to human influences. More detailed analyses of the dataset provided can be used to target bear conflict and nuisance reduction efforts.

The modeling algorithm is intentionally constructed to alter the criteria so managers can examine different habitat assumptions and land management scenarios. Further, the modeling approach allows incorporation of future, improved spatial data sets (e.g., more resolved land cover) with minimal adaptation or cross-walking of habitat categorizations. Accordingly, it will be interesting and wise to perform sensitivity analyses of conclusions based on this coverage and future modifications.

CHAPTER 12

RELIABILITY OF HARVEST DATA

INTRODUCTION

In New Mexico, as in many states, interpretation of black bear population trend is based primarily on harvest data. Annual harvest data include the total number of hunter-killed bears and sex-age composition in the kill. Given the complexities associated with documenting population trend (Miller 1990, Garshelis 1991), determining the accuracy and consistency of current methods is important.

Age composition of NMDGF harvest data is determined using the cementum annuli aging technique on teeth collected from each bear. This method involves counting the layers of cementum deposited in teeth. Each year, 2 types of cementum are produced which are visible when stained. The first layer is a dark narrow band deposited during the winter months. The second layer appears broad and lightly-stained and is produced during the growth seasons of spring, summer, and fall (Harshyne et al. 1998). When a thin cross-sectional segment of the tooth is viewed, these layers can be counted as an estimate of the animal's age, similar to growth rings on a tree. This method was first developed using canine teeth collected from hunter-killed bears (Sauer et al. 1966, Stoneberg and Jonkel 1966). The technique was further refined by use of the small vestigial premolar tooth, which can be collected from live animals as well as hunter-killed bears (Willey 1974). Accuracy of the cementum annuli aging technique has been tested in only a few locations across North America (McLaughlin et al. 1990, Harshyne et al. 1998). Diet and variability in food supplies are known to affect deposition of cementum layers, therefore accuracy rates from other regions may have no bearing on New Mexico bears. Our objective was to determine the accuracy and consistency in estimating age using teeth from New Mexico black bears. A second objective was to determine the comprehensiveness of the NMDGF harvest data and to document any error with regard to reporting of sex.

METHODS

Harvest-data

We tested the completeness and accuracy of reported sex for the NMDGF hunter-kill (pelt tag) harvest records. These records were tested by comparing them to known hunter-kills of study bears, verified by radio-telemetry monitoring and direct reports from NMDGF personnel.

Cementum Annuli Data

An upper premolar tooth was extracted from most study bears ≥1 year of age during initial capture, and a second tooth was collected from some bears during recapture or den investigations, particularly during the final year of fieldwork (see Chapter 4). For hunter-killed study bears, a second tooth also was collected by NMDGF as part of the mandatory check program (see Chapter 11). During 1993, NMDGF personnel removed 2 teeth from each hunter-killed black bear specifically for examining consistency in aging black bear teeth.

All collected teeth, from study bears and hunter-killed bears, were processed by Matson Laboratory (Milltown, Montana) for age determination using cementum annuli counts. Pairs of teeth from the same bears were assigned different numbers to create a blind sample. Date of extraction, sex of bear, and comments relevant to tooth condition (e.g., broken or rotten) were reported to Matson's Laboratory for most tooth samples.

Matson's Laboratory provided us with age estimates with corresponding accuracy limits. These accuracy limits were based on the determined age of the bear and the condition of the tooth sample. In general, they found that error increased with age. Thus, determined ages were grouped into 1-7 years, 8-15 years, and ≥16 years. "Certainty codes", based on tooth condition, were superimposed on these age groupings. Assigned certainty codes were (A) result nearly certain, (B) some error possible, and (C) error likely. The combination of the tooth age grouping and the certainty code resulted in an age estimate with a corresponding range of error in years.

We tested the consistency of the aging technique by comparing 2 or more age estimates obtained for a single individual. Two samples were used for consistency analysis: (1) paired teeth collected from hunter-killed bears on the same day, and (2) pairs of teeth collected from study bears on different dates (often years apart). We tested accuracy of the aging technique by obtaining age estimates from known-age study bears. The sample of known-age bears consisted of individuals handled as cubs or yearlings in the den, and individuals confidently aged from tooth eruption when captured as cubs or yearlings.

Using Chi-square tests and Pearson's correlation, we evaluated consistency relative to estimated age class (or mean age class of pairs), sex, tooth condition, certainty code, and season of extraction (den = January-April, active = May-October). Probability levels are reported for all test outcomes reported.

RESULTS

Harvest Data

From 1992-1999, 42 marked study bears were known harvested by hunters, including 16 radio-transmittered bears and 26 marked bears. Three bears (7%) were not included as records in the NMDGF harvest database. In all instances, the bears were known to have been checked by a NMDGF officer, however record of the kill was not present in the central database. Sex was accurately recorded for all study bears present in the harvest database.

Cementum Annuli Aging

Age estimates were obtained for 236 pairs of teeth collected by NMDGF personnel in 1993. All teeth were collected during the mast season. Most age estimates (83%, n = 472) were assigned a certainty code of A (result nearly certain), while 16% were assigned as B (some error possible) and 1% were assigned C (error likely). Among the 96 teeth that were broken (20% of total), most were assigned a certainty code of B (61%), while 32% were assigned as A and 6% were assigned as C.

Teeth were consistently aged for 74% of pairs (n = 236). Among pairs inconsistently aged (n = 96), discrepancies ranged from 1-6 years, with a mean of 1.6 years. Percent inconsistency among pairs differed by certainty code (X^2 = 28.7, df = 2, n = 236). Among pairs with both age estimates assigned A, 83% of pairs were consistently aged (n = 168). Only 52% and 33% of pairs were consistently aged when ≥1 assignment was B (n = 62) or C (n = 6), respectively.

Discrepancy in estimated age, in years, was positively associated with mean estimated age of the pair (Pearson r = 0.51, P = 0.001, n = 236). Compared to intermediate groups, percent inconsistency was significantly lower (9%) for pairs with a mean estimated age of 1 and significantly higher (46%) for pairs with a mean estimated age of ≥5 (X^2 = 34.7, df = 4, n = 236).

Percent consistency also was lower when teeth were broken (50% vs. 83%, X^2 = 27.8, df = 1, n = 236), however percent tooth breakage was positively associated with estimated age class (X^2 = 29.3, df = 5, n = 472) and with higher certainty codes (X^2 = 214.4, df = 2, n = 472). Only 8% of ages designated with A (n = 392) were broken, while 88% and 100% of ages designated with B (n = 62) or C (n = 6) were broken.

Percent consistency differed by sex (X^2 = 6.6, df = 1, n = 231). Percent consistency was 65% for females and 80% for males. However, mean estimated age of tooth pairs was higher for females than for males (t = 4.8, df = 174, P < 0.001, n = 231).

Extraction of improper teeth (e.g., molars, incisors) did not appear to affect consistency, however sample size was very low. Inconsistency in estimated ages was 33% for these teeth (*n* = 6), however the patterns of inconsistency relative to estimated age and certainty codes appeared similar to other teeth.

The observed inconsistencies in aging did not appear to affect the estimated age composition of the harvest (Table 12-1). Comparing the 2 blind samples (obtained independently), estimated age composition of the harvest did not differ statewide (X^2 = 1.4, df = 5, *P* = 0.92, *n* = 472) or for any region (*P* ≥ 0.55).

Table 12-1. Estimated age composition of hunter-killed black bears, by region, using the cementum annuli technique applied to 2 blind samples of premolar teeth in New Mexico, 1993.

			Percent composition by age category[a]					
Region	Sample	*n*	Cub	1 year	2 years	3 years	4 years	≥5 years
Statewide	1	236	0	14	26	13	5	42
	2	236	0	14	28	12	6	41
San Juan	1	55	0	11	26	18	7	38
complex	2	55	0	13	24	18	11	35
Sangre de Cristo	1	77	0	14	22	9	3	52
complex	2	77	0	14	23	8	3	52
Zuni and Mt.	1	20	0	10	20	0	0	70
Taylor regions	2	20	0	10	20	10	0	60
Sandia/Manzano	1	10	0	20	0	0	20	60
region	2	10	0	20	0	0	20	60
Gila complex	1	29	3	14	35	14	3	31
	2	29	0	17	35	14	3	31
Sacramento	1	56	0	16	29	14	5	36
region	2	56	0	14	34	11	5	36

[a] Percent composition did not differ between samples for any region (*P* ≥ 0.55).

We obtained age estimated for 61 pairs of teeth from study bears (actual ages not known). Most age estimates (85%, *n* = 122) were assigned a certainty code of A, while 11% were assigned as B and 3% were assigned C. Among the 20 teeth that were broken (16% of total), most were assigned a certainty code of A (80%), while 10% were assigned as B and 10% were assigned as C. Pairs of teeth were extracted 0-9 years apart, with a mean of 4.0 years (*n* = 61).

Teeth were consistently aged for only 46% of pairs (*n* = 61). Among pairs inconsistently aged (*n* = 33), discrepancies ranged from 1-12 years, with a mean of 2.8 years. Percent inconsistency among pairs did not differ by certainty code (X^2 = 1.0, df = 2, n = 61). Discrepancy in estimated age, in years, was positively associated with mean estimated age of the pair (Pearson r = 0.50, P < 0.001, n = 61).

Percent consistency was lower when teeth were broken (46% vs. 80%, X^2 = 5.4, df = 1, P = 0.04, n = 61), however percent tooth breakage was positively associated with higher certainty codes (X^2 = 21.9, df = 3, n = 122). Only 13% of ages designated with A (n = 103) were broken, while 21% and 100% of ages designated with B (n = 14) or C (n = 4) were broken. Percent consistency was lower for tooth pairs when 1 or both teeth were removed in the den (34% vs. 62%, X^2 = 4.5, df = 1, P = 0.04, n = 61). Percent consistency did not differ by sex (X^2 = 1.0, df = 1, P = 0.40, n = 61).

For 26 of 31 (84%) inconsistent pairs of teeth extracted during different years, the age estimate from the tooth extracted at an older age was lower than the age estimate for the tooth extracted at a younger age (accounting for the difference in years). In other words, compared to earlier ages estimated, older ages were underestimated most of the time.

Accuracy Analyses

We obtained age estimates for 29 known-age bears, including 15 yearlings, 10 subadults, and 4 adults. Twenty-eight of 29 age estimates (97%) were assigned a certainty code of A, and 1 age estimate (3%) was assigned B. No teeth were broken among this sample.

Most of these teeth (83%) were accurately aged (n = 29). Among age estimates designated with A, 86% were accurate, but the single age estimate designated with B was inaccurate. Difference between estimated age and actual age ranged from 1-2 years, with a mean of 1.2 years (n = 5). All inaccurate age estimates were underestimates.

Percent accuracy differed by age class (X^2 = 6.9, df = 2, P = 0.03). All yearlings were aged accurately, while 60% of subadults and 75% of adults were aged accurately. Percent accuracy did not differ by sex (X^2 = 0.08, df = 1, P = 1.0).

Accuracy of age estimates differed by season (X^2 = 13.4, df = 1, P = 0.001). Estimates from teeth extracted during the active season were 100% accurate, while estimates from those extracted during the den season were only 55% accurate, however only sub-adult and adult teeth were extracted during the den season.

DISCUSSION

Harvest Data

Results revealed both negative and positive aspects regarding usefulness of the harvest data obtained by the NMDGF. Our analyses indicated the harvest data were incomplete, underestimating the annual bear kill by as much as 7%. This proportion not only limits the usefulness of these data for monitoring total kill, but also hinders reliable estimation of sex-age composition of the kill.

On the other hand, analyses indicated age estimates using the cememtum annuli method were relatively accurate and consistent for New Mexico bears. Accuracy and consistency were negatively associated with age and tooth breakage, however these 2 factors were correlated. These results supported earlier findings that consistency and accuracy declined with age (Willey 1974, McLaughlin 1990, and Harshyne et al. 1998). Sauer et al. (1966) suggested cementum annuli were more difficult to count in older teeth because annuli become thinner as the tooth ages.

Differences in the patterns of annuli deposition have been noted for male and female black bears (Coy and Garshelis 1992). Cross-sections of male teeth have displayed dark accessory lines that can be confused with annuli, especially in late summer and fall. On teeth from female bears, narrow bands associated with cub rearing can make distinction of adjacent annuli difficult to observe, leading to miscounts. Despite these potential differences, our analyses did not indicate sex affected accuracy or consistency of aging, and these findings were consistent with Harshyne et al. (1998). Although female teeth were less consistently aged in the sample of study bears, evidence indicated age was the factor likely causing the difference.

Accuracy and inconsistency were also affected by season. Age estimates from teeth extracted in the den were less consistent than those from teeth extracted during the active season. When the den-extracted teeth were removed from the known-age sample, accuracy improved to 100%. This may have been due to the fact that black bears deposit annuli during the winter and new annuli may not appear visibly until late spring (Sauer et al.1966, Coy and Garshelis 1992).

MANAGEMENT IMPLICATIONS

Accuracy and consistency of the cementum annuli method appeared adequate for estimating age of New Mexico black bears. Among adult bears, our findings indicated the cementum annuli method was not precise enough to identify specific age cohorts. However, accuracy and consistency was relatively high for bears with known or estimated ages <5 years old. Identification of specific cohorts is only required for these younger age classes, therefore the method appeared adequate to classify bears into age classes and to estimate the age composition of the kill.

According to Matson Laboratory, 2 types of tooth breakage occurred. The first occurred when the root tip was broken off during extraction. The second occurred when the tooth was removed intact, but the tools used for extraction damaged the cementum annuli. Breakage probably cannot be completely avoided, especially when extracting teeth from older bears. However, extra care in tooth extraction, use of proper tools, and improved training of personnel responsible for tooth extraction will aid in the consistency of aging teeth.

CHAPTER 13

PATTERNS IN HARVEST DATA

INTRODUCTION

New Mexico has more than 2 decades of black bear harvest data, a rich information resource. Harvest data document harvest numbers and provide a historical perspective on new information accumulating year by year. Relationships among harvest, regulations, effort, and environmental conditions provide valuable insight for managers that is useful for regulating harvest numbers and composition.

Black bear harvest data alone do not provide a window onto populations; changes in harvest size and composition do not indicate trends in the living resource population (Garshelis 1990). This study provides an opportunity for limited comparisons of live populations and harvests.

Our objective in this chapter is to describe relationships between the harvest sample and the sex-age composition of study populations. We do this from the standpoint of hunter supplied information, kill records, and results of field investigations.

METHODS

Harvest Data

Tagging of bear pelts and reporting of all hunter-killed bears has been mandatory in New Mexico since 1978. NMDGF officers have recorded proof of sex and collected a tooth for estimating age of bears since 1985. Other information recorded included date and Game Management Unit (GMU) of kill, use or nonuse of dogs, and use or nonuse of guides. Pelt tag records were complete through 1999.

A card survey has been mailed to all licensed bear hunters with usable mailing addresses since 1990. Information requested included whether they hunted, used guides or used dogs, days hunted in up to 3 different GMUs, killed a bear, and sex and GMU location of kill. Statewide effort and success projections by hunt method were based on individual responses with use or nonuse of guides and dogs reported. For the 1994 survey, use of guides and use of dogs could not be separated, so projections were made for using aids (guides or dogs or both) and no aids (neither).

Hunt regulations and license costs were obtained from annual NMDGF Proclamations. Numbers of licenses sold were obtained from NMDGF fiscal records.

Regional summaries were compiled for contiguous game management units including mountain ranges. The Gila complex, containing the SSA, consists of GMUs 13, 15-17, 21-24, 26, and 27. The Sangre de Cristo complex, containing the NSA, consists of GMUs 41-49 and 53-58.

Years in summary tables are calendar years of hunting seasons, not fiscal year or license year designations. Harvest numbers in summaries are derived from pelt tag reports, considered more reliable than projections from the hunter card survey. Correlation coefficients were calculated from annual statewide total harvest numbers and license sales.

Effort, Success, and Hunting Method

Estimates of hunter success were based on reported numbers of hunters and kills by GMU from card survey returns for each year. Hunters reporting days in multiple GMUs were included in each unit reported. Unit hunter and bear harvest numbers using guides, dogs, both, or neither, were summed over GMUs for regional totals. Success by year and method was calculated as total reported harvest divided by total reported hunters for each region.

Proportions of hunters or harvests by hunting method were based on the subset of records with hunting methods known. Numbers of hunters or harvests by hunting method were calculated as the product of total hunters or harvests and calculated proportions. Most pelt tag and hunter card survey records contained information on hunting methods used.

Regional harvests and resident study populations were compared for 1993-1997; later years are excluded because hunt regulations and effort changed substantially in 1998, potentially confounding any change in the relationship of live and harvest sample composition. We looked at age composition of females only, because reproductive females are important to population trends, and migrant subadult males may confound male age structure and sex ratios. Study area live population proportions were recalculated excluding cubs, because cubs do not appear in harvest data. We examined proportions of yearlings of all females, yearlings and subadults of all females, and subadults of all females aged ≥2 years.

Years of mast failure were determined from combined oak mast index measured on the study areas (see Chapter 5).

Age and Sex Composition

Ages of hunter-killed bears were based on cementum annuli analysis of collected teeth (see Chapter 12). Age class proportions were calculated only from records with age estimates. For total numbers by age class, the un-aged subset was prorated among age classes using the proportions derived from the aged subset for each sex. Most pelt tag records had associated age estimates. Year of birth for hunter-killed bears was calculated from age estimates. Virtually all pelt tag records included sex of kill.

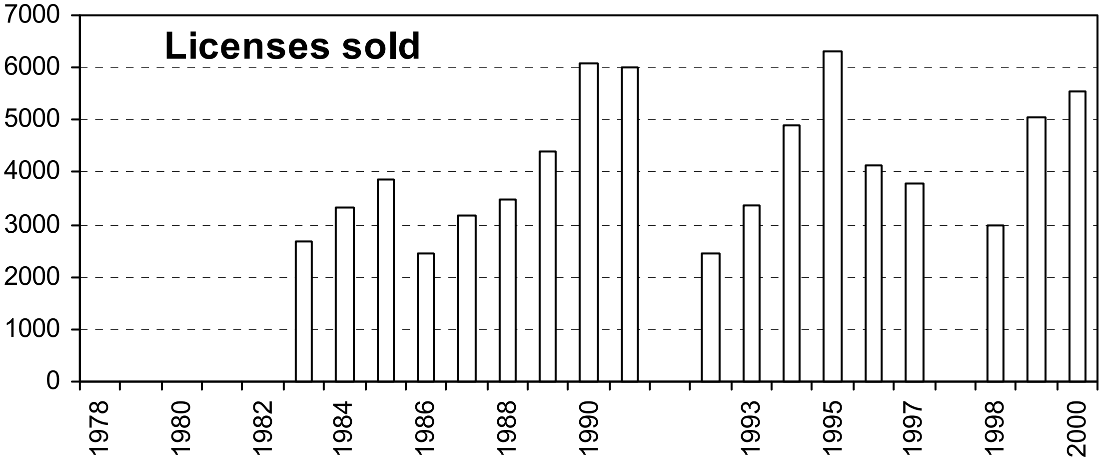
Age and sex composition of study area live populations was based on population reconstructions (see Chapter 10). Year of birth for study area bears aged ≥1 year was known from den observations or calculated from tooth age estimates. Sex was known for all study area bears.

Relative numbers of bears by year of birth were compared for the study area populations and hunter-killed bears from the surrounding regions. From live population data, bears were counted by cohort year. All study bears observed at age ≥1 were included, regardless of age at first observation, date of capture, or den observation. Individual study bears were counted only once, regardless of frequency of observation. For harvest data, bears from a cohort year were represented by kills during the 3 hunt years following the birth year of the cohort. Proportions of 1, 2, or 3-year-olds of all-aged hunter-killed bears were calculated for the appropriate hunt year, to eliminate distortion from annual variation in total harvests. An index of harvest abundance for each cohort was calculated as the sum of its representative year class proportions at ages 1-3. For example, the index for bears born in 1991 was the sum of the proportion of 1-year-olds in the 1992 harvest, 2- year-olds in the 1993 harvest, and 3-year-olds in the 1994 harvest.

RESULTS

Patterns in Harvest, Effort, and Success

Statewide bear harvest fluctuated (Figure 13-1). The largest annual number of hunter kills for both sexes was reported in 1994, with declining numbers in each of the following 4 years. Year to year variation in statewide harvest numbers was similar for the sexes. Detailed statewide and regional information from pelt tag reports and card survey projections is presented in the Pelt Tag Notebook (Appendix D) that describes black bear harvest data history through 1999. Fall and spring hunts occurred in New Mexico from 1978-1991. Early fall hunts, beginning by 1 September and ending 31 October, occurred from 1992-1997. Late fall hunts, beginning 1 or 15 October and ending 15 December, occurred from 1998-2000.



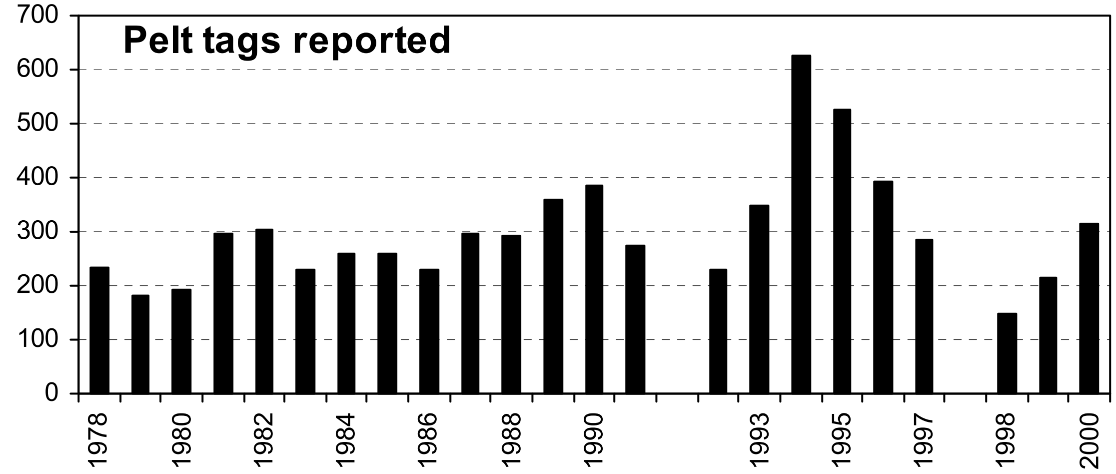


Figure 13-1. Numbers of black bear hunting licenses sold and pelt tags reported in New Mexico for years with both spring and fall hunts (1978-1991), early fall hunts only (1992-1997), and late fall hunts only (1998-2000).

License sales and statewide harvests increased during the 1990s (Table 13-1). Average license sales and average total females harvested for 1990-2000 were 38% greater than for 1983-1989. Because of the peak harvest in 1994, average harvests increased out of proportion to license sales for 1994-1997 compared to previous 4-year averages, both regional and statewide. Average harvests decreased for 1998-2000 because of the shift to late fall hunt dates.

Table 13-1. Average license sales and harvest reports for female (F) and male (M) black bears in New Mexico for 1978-2000.

		Harvests reported					
		Statewide		Sangre de Cristo complex		Gila complex	
Years	Licenses sold statewide	F	M	F	M	F	M
1978-1981[a]	not available	87	139	33	57	19	43
1982-1985	3290[b]	99	162	31	49	23	41
1986-1989	3381	98	195	33	63	27	65
1990-1993	4471	123	185	39	63	26	43
1994-1997	4782	188	267	51	75	50	71
1998-2000	4529	70	154	22	56	20	29

[a] 4-year averages make long-term changes easier to see;
[b] averaged over 1983-1985

Bear hunters in New Mexico consistently harvested more males than females (Table 13-2). The female proportion of annual statewide harvest ranged from 29 to 46%. The proportion of females averaged 37% during the years of combined spring and fall hunts, 41% during early fall hunts, and 36% for late fall hunt years.

Harvest patterns differed by region (Figure 13-2). Harvests in the Gila and Sangre de Cristo complexes fluctuated, but Gila numbers were more variable. The 1994 female harvest in the Gila complex was 4 times the average from previous years, and more than twice the harvest from any other year. In contrast, Sangre de Cristo regional female harvests were elevated for 1993-1995, at about twice the average from previous years.

From 1983-2000, annual statewide license sales varied more than 2-fold (Appendix D, Table 2). License sales decreased in years with regulation or cost changes. License sales dropped 36% and total black bears harvested dropped 11% in 1986, when spring season dates were shifted 1 month earlier and the fall season was closed during elk firearm hunts. License sales decreased 59% and total harvest decreased 17% in 1992, when spring hunting was discontinued and the fall season was shortened to September and October only. License sales decreased 35% and harvest decreased 25% in 1996, when license cost for residents increased from $10 to $30. License sales decreased 22% and total harvest decreased 52% in 1998, when the fall season dates were shifted 6 weeks later and no licenses were sold after the hunting season began.

Table 13-2. Numbers and mean ages of female (F) and male (M) black bears harvested statewide and in 2 regions of New Mexico where study areas were located, 1985-1999.

	Statewide				Sangre de Cristo complex				Gila complex			
	No. kills		Mean age		No. kills		Mean age		No. kills		Mean age	
Year	F	M	F	M	F	M	F	M	F	M	F	M
1985	94	160	5.2	4.4	21	49	5.4	3.5	27	39	5.0	5.4
1986	84	145	5.5	4.6	28	72	6.3	4.8	22	26	6.0	4.8
1987	104	192	5.6	4.6	43	62	5.8	4.8	27	68	5.8	4.8
1988	101	188	5.0	4.2	39	62	5.6	4.8	24	49	4.8	4.6
1989	103	254	6.2	5.0	21	57	5.3	5.8	36	115	7.5	5.5
1990	151	232	5.9	5.3	40	67	5.9	6.3	47	64	6.9	4.9
1991	99	176	6.4	5.9	26	62	5.3	5.5	23	47	7.7	7.1
1992	91	137	6.4	4.8	29	55	7.0	4.6	16	30	6.9	5.0
1993	152	196	6.3	4.0	61	67	6.9	4.1	18	30	5.8	3.7
1994	259	364	7.0	5.3	60	75	6.3	5.3	103	138	6.8	5.9
1995	213	313	7.0	5.0	62	114	6.7	5.0	39	49	8.4	6.1
1996	171	216	6.7	5.7	43	72	6.2	5.5	36	50	8.0	6.1
1997	110	175	6.3	5.6	38	52	7.0	5.3	22	48	5.9	6.3
1998	51	97	5.3	4.4	20	50	5.8	4.0	10	12	7.4	7.4
1999	60	150	6.1	4.5	20	59	5.4	5.8	14	26	7.1	2.4

Total hunt effort influenced total harvest. Correlations between statewide annual total legal kills and total licenses sold were 0.68 for 1983-1991 with both spring and fall seasons, 0.82 for 1992-1997 with early fall seasons, and 0.90 for 1998-2000 with late fall seasons.

Success rates for all black bear license buyers were relatively low, ranging from 5-9% for years with spring and fall hunts, from 7-10% for early fall hunts except for 13% in 1994, and from 4-6% for late fall hunts. The exceptional success rate in 1994 coincided with the largest statewide annual harvest.

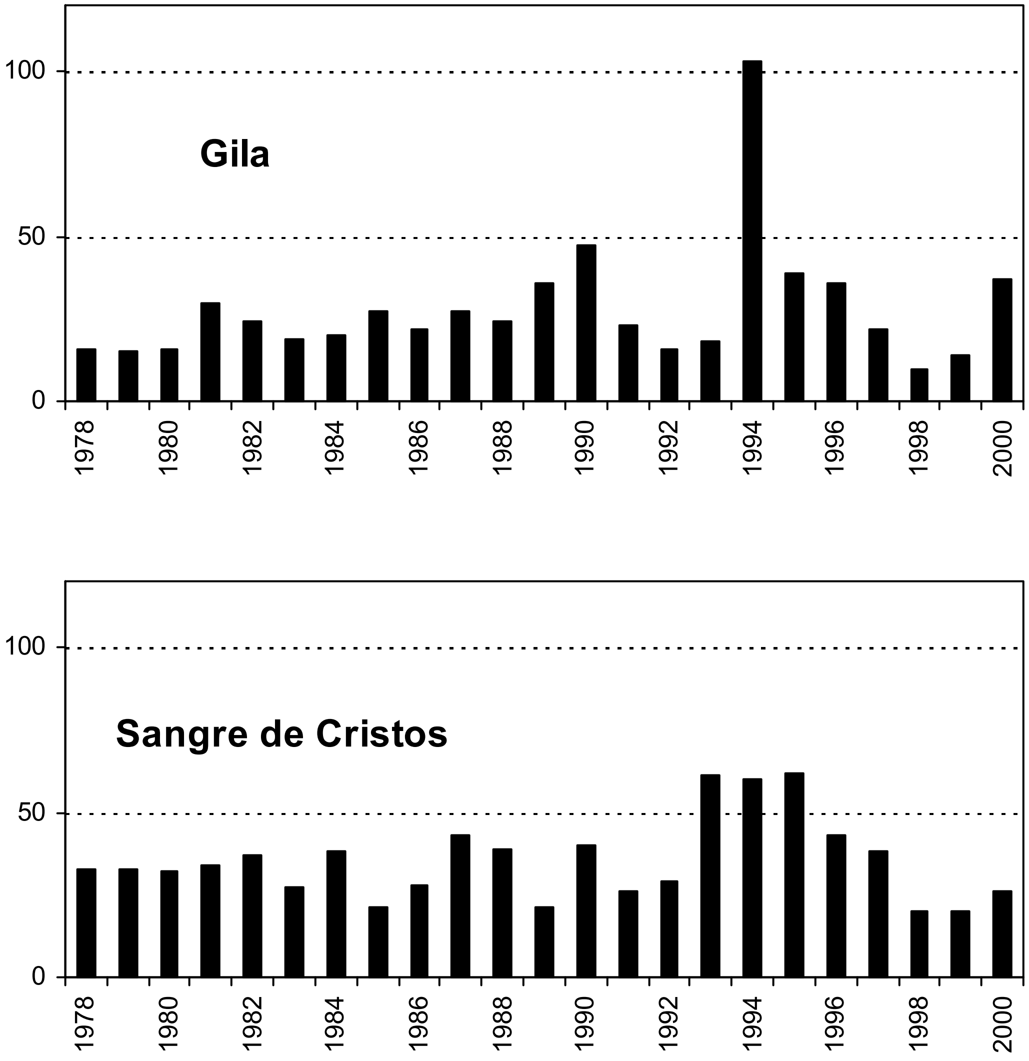


Figure 13-2. Number of female hunter-killed black bears reported from the Gila and Sangre de Cristo complexes of New Mexico, 1978 – 2000.

Patterns by Hunting Method and Season Timing

Hunters using dogs were about 3 times as successful as hunters not using dogs (Table 13-3). Using dogs doubled success for unguided hunters, and increased success 2 to 5 fold for guided hunters. Using dogs increased success more in spring and late fall hunts than in early fall hunts.

Table 13-3. Average annual participation and hunter success by hunting method and season timing from card survey data and pelt tag reports from black bear hunting in New Mexico, 1990-1999.

	Hunt season timing			
Comparison by hunting method	Spring 1990-1991	Early fall 1990-1993 1995-1997	Early fall 1994	Late fall 1998-1999
Percent of hunters using each method, from hunter card survey				
Guides and dogs	17	8		7
Guides only	2	4		10
Dogs only	19	10		10
Neither	63	78	73	74
Percent success by method, from hunter card survey				
Dogs	22	28		21
No dogs	3	9		6
Percent of females in harvest by method, from pelt tag reports				
Dogs	23	46	40	35
No dogs	22	37	43	30

Fall season hunters using dogs took a higher proportion of females than hunters not using dogs, except for 1994 when hunters not using dogs took an unusually high proportion of females (Table 13-3). Hunters using dogs took about 4 times as many female bears per hunter as hunters not using dogs (Table 13-4).

Most hunting effort was without dogs (Table 13-3). In fall hunts, an average of 18% of all hunters used dogs; in spring, 36% used dogs. However, hunters using dogs took 45% of the female bears killed during fall hunts and 71%

of the few females killed during spring hunts, because of higher success rates and higher percentages of females taken with dogs.

The proportion of females in early fall hunter kills was double that in spring kills. Overall, 41% of early fall harvests, 32% of late fall harvests, and 21% of spring harvests were female. The same pattern held for all hunting methods (Table 13-3).

For all hunting methods, success rates were higher for early fall hunts than for late fall or spring hunts (Table 13-3). Overall success from card survey reports was 13% for early fall hunts (except for 1994 with 48% success reported), 11% for spring hunts, and 9% for late fall hunts.

Table 13-4. Relationships of hunting method and season timing to female black bear harvest in New Mexico, 1990-1999.

	Hunt season timing			
Comparison by hunting method	Spring 1990-1991	Early fall 1990-1993 1995-1997	Early fall 1994	Late fall 1998-1999
Average no. females killed / 100 hunters / year				
Guides and dogs	7.7	21.6		11.2
Guides only		7.8		3.1
Dogs only	2.1	7.2		4.2
Neither	0.8	3.3	17.2	1.8
Dogs	4.8	12.9		7.4
No dogs	1.1	3.3		1.8
Average percent of all F bear kills taken by each method				
Guides and dogs	59	32		28
Guides only		6		11
Dogs only	18	13		15
Neither	23	48		47
Dogs	71	46		45
No dogs	29	54		55

Patterns by Mast Availability

The NSA did not experience a mast failure during the late fall season hunt years 1998-2000, and experienced only a single year of mast failure during the early fall hunt season years from 1993-1997. The SSA experienced mast failure in 2 of the 5 early fall hunt season years and in 2 of the 3 late fall hunt season years.

In the Gila complex, more bears were killed in years of mast failure during early and late fall seasons (Table 13-5). This pattern was observed with or without guides and dogs. In the Sangre de Cristo complex early fall hunts, the proportion of females in the total harvest was higher during the mast failure year. In the Gila complex, hunters using dogs or guides killed the same proportion of females in mast failure years as other years. However, on average 78% of the hunting effort in the Gila complex was by hunters not using aids, who took a higher proportion of females in mast failure years. Statewide, the largest bear harvest in early fall hunts occurred in 1994, and the largest harvest in late fall hunts occurred in 2000, both probably years of widespread mast failure.

Table 13-5. Hunter success, sex composition, and total harvest of black bears in New Mexico by hunting method for years with and without mast failures, 1993-1999.

	Early fall hunts				Late fall hunts	
	Sangre de Cristo complex		Gila complex		Gila complex	
Parameter	Oak on NSA		Oak on SSA		Oak on SSA	
by hunting method	Fail	Not fail	Fail	Not fail	Fail	Not fail
Average percent hunter success from card survey						
Guides or dogs or both	46	34	24	18	12[a]	5
No aids	13	14	16	10	4[1]	4
Average percent females in harvest from pelt tag reports						
Guides or dogs or both	54	42	44	44	40	56
No aids	44	36	37	33	27	38
Average annual bear kills from pelt tag reports						
Guides or dogs or both	48	61	57	34	29	9
No aids	80	68	106	34	34	13
Total	**128**	**129**	**163**	**68**	**63**	**22**
Years included	1993	1994 1995 1996 1997	1994 1996	1993 1995 1997	1999 2000	1998

[a]Value for 1999 only; card survey projections for 2000 not yet available

For the Gila complex, the contrast in average harvest was exaggerated by an exceptionally high harvest in the mast failure year 1994 (with 242 bears reported), and an exceptionally low harvest in the non-failure year 1998 (with 22 pelts reported) when regulations changed significantly and effort and harvest decreased statewide.

Live Population and Harvest Age Composition

More individual bears born in 1991 were captured on both study areas than bears born in 1990 or 1992; bears born in 1988-1990 were observed less frequently than those born in 1987 or 1991. A similar pattern occurred in hunter-killed bears from the surrounding regions (Figure 13-3). The 1994 cohort in the SSA and Gila region, and the 1995 cohort in the NSA and Sangre de Cristo complex, were relatively small in harvests and live captures. No yearlings were observed in dens from the 1992 and 1994 cohorts on the NSA, and only 1 yearling was observed from the 1993-1995 cohorts on the SSA (Table 13-6).

Table 13-6. Yearlings per adult female (F, aged ≥5 years) from den observations on the Northern Study Area (NSA) and Southern Study Area (SSA) in New Mexico, 1993-2000.

		NSA		SSA	
Year of observation	Cohort year	No. adult F dens observed	Yearlings / adult F	No. adult F dens observed	Yearlings / adult F
1993	1992	5	0		
1994	1993	8	0.63	6	0
1995	1994	12	0	9	0.11
1996	1995	16	0.63	15	0
1997	1996	23	0.22	15	0.67
1998	1997	27	0.48	18	0.33
1999	1998	23	0.59	19	0.58
2000	1999	21	0.52	16	0.56

In both live study populations, adults comprised 54% of resident females ≥1 year old on average (Table 13-7). Adults comprised 58% of female harvests in the Sangre de Cristo complex and 70% of female harvests in the Gila complex on average for 1993-1999 (Table 13-7). Both live populations averaged 65% females of all resident bears, with little annual variation, from 1993-1999.

Regional harvests varied from 26 to 48% females in the Sangre de Cristo complex, and from 31 to 48% female in the Gila complex.

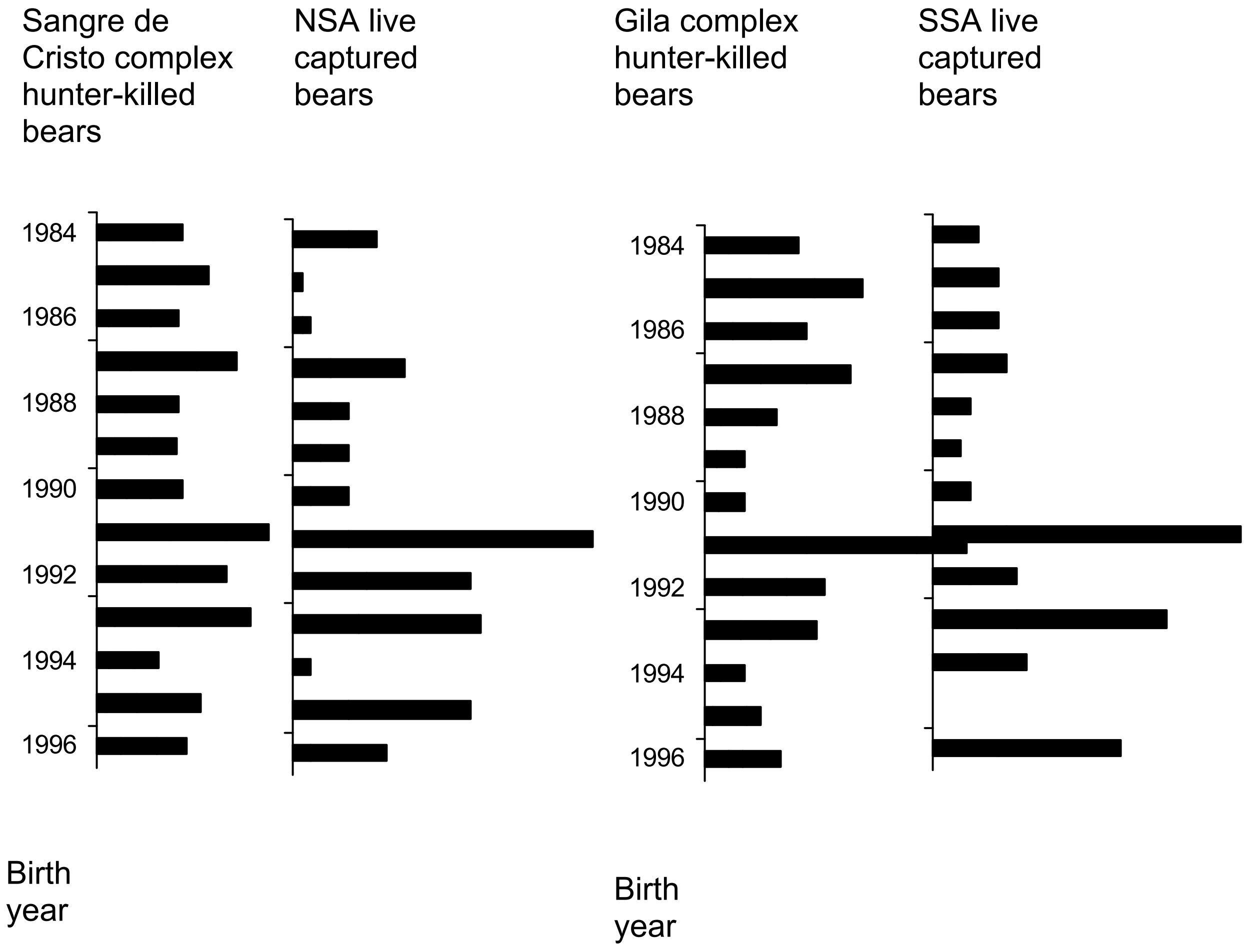


Figure 13-3. Relative numbers of black bears born in the indicated years and subsequently killed by hunters at ages 1-3 in the Sangre de Cristo and Gila complexes of New Mexico, 1985-1999, or captured live at any age on the New Mexico black bear study areas within the regions, 1993-1999.

Yearling proportions of females were higher in study area live populations than in early fall season harvests from the surrounding regions. From 1994-1997 subadults comprised 42% of live population resident females aged ≥2 years on the NSA and 44% on the SSA. In contrast, subadults comprised 38% of reported female hunter kills aged ≥2 in the Sangre de Cristo complex, but only 27% in the Gila complex, during the same years. In 1993, the NSA live population had 43% subadults, but the Sangre de Cristo harvest had only 24%; both SSA and the Gila harvest had 44% subadults.

Table 13-7. Proportions of adults (≥5 years old), subadults (2-4 years old), and yearlings (1 year old) in black bear harvests from the Sangre de Cristo and Gila complexes of New Mexico, 1993-1999.

			Year							All
Region	Sex	Age class	1993	1994	1995	1996	1997	1998	1999	Years
Sangre de Cristo	F	Adult	0.32	0.25	0.18	0.21	0.25	0.14	0.10	0.21
		Subadult	0.12	0.16	0.16	0.14	0.12	0.09	0.13	0.13
		Yearling	0.04	0.02	0	0.02	0.01	0.05	0.03	0.02
		Total	0.48	0.43	0.34	0.37	0.39	0.28	0.26	0.36
	M	Adult	0.18	0.32	0.24	0.29	0.32	0.23	0.33	0.27
		Subadult	0.24	0.20	0.39	0.33	0.23	0.33	0.30	0.29
		Yearling	0.11	0.05	0.04	0.01	0.07	0.16	0.11	0.08
		Total	0.52	0.57	0.66	0.63	0.61	0.72	0.74	0.64
Gila	F	Adult	0.18	0.28	0.29	0.30	0.21	0.48	0.26	0.28
		Subadult	0.16	0.12	0.14	0.12	0.06	0	0.06	0.10
		Yearling	0.02	0.05	0	0.01	0.03	0	0.03	0.02
		Total	0.36	0.44	0.43	0.44	0.31	0.48	0.35	0.40
	M	Adult	0.18	0.26	0.29	0.34	0.45	0.38	0.10	0.28
		Subadult	0.36	0.22	0.27	0.21	0.19	0.10	0.26	0.23
		Yearling	0.11	0.08	0.01	0.01	0.05	0.05	0.29	0.09
		Total	0.64	0.56	0.57	0.56	0.69	0.52	0.65	0.60

DISCUSSION

Harvest Patterns

In 1994, statewide harvest jumped to a record peak, and then dropped steadily during the following 4 years. Harvests for 1994-1998 differed from the fluctuating, but gradually increasing, pattern of harvests from previous years. Such a dramatic change should get the attention of managers. We cannot determine from harvest data alone whether the 1994-1998 numbers reflect overharvest and subsequent population decline. Examination of factors associated with the pattern can illuminate the information that is embedded in harvest data.

Higher harvests in the 1990s than the 1980s were associated with increased license sales. The record harvest in 1994 was not a statewide phenomenon, but derived from an anomalous harvest from the Gila complex, large enough to affect the statewide total. Return to a normal harvest size in the Gila complex in 1995 accounted for most of the decrease in statewide harvest for that year. License sales were lower in 1996-1997 than in 1994-1995, probably accounting for some of the reduction in total harvest. The decrease in statewide harvest in 1998 likely resulted from a change in hunt season from early to late fall, and an associated reduction in license sales. While these observations do not rule out a population change as the reason for decreasing bear harvests, they do suggest reasonable alternative explanations.

Harvest data history for the Gila complex implied that the impact of the 1994 hunt on the black bear population was unusual, but its effect on the population trend is not known. The high number of females removed from the population is a significant management consideration. The harvest data can provide useful indicators for managers, even without providing certainty about populations.

Why was the 1994 harvest in the Gila complex so large? Regional hunter numbers were not unusual, but success rates were extraordinary. Cub survival on the SSA was very low in 1994, and many adult females may not have been accompanied by cubs, thus not protected from hunting. Oak mast failed in 1994, and a dry summer and wildfires may have increased food stress. Bears moved longer distances during years of oak failure (see Chapter 9), and may have been more likely to encounter hunters as a result. Average annual harvest totals, hunter success rates, and percent of females harvest by unaided hunters were higher in years of oak mast failure in the Gila complex during both early and late fall hunt seasons. The proportion of females in the total harvest was also higher during the mast failure year in the Sangre de Cristo early fall hunts. Hunter success, percent of females in the kill, and mean age of females killed were inversely related to fall food abundance in Minnesota (Noyce and Garshelis 1997). Higher harvest levels also were associated with shortages of natural foods in Massachusetts (McDonald et al. 1994).

Patterns of harvest over time differed by mountain range region for New Mexico. Environmental conditions may not be uniform statewide in any given year. Harvest data should be examined by region, and regional differences in management objectives and strategies are appropriate.

The timing of hunt seasons influenced the size and composition of the harvest. Early fall hunts in New Mexico resulted in higher effort, success, and proportion of females in the harvest compared to late fall or spring hunts, and produce larger total harvests and female harvests.

Hunters using dogs harvested more bears per hunter, and proportionally more female bears, than hunters not using dogs. Most hunters in New Mexico did not use dogs. In early fall hunts, about 20% of hunters used dogs, but took almost 50% of the females harvested. The influence of hunting method on harvest depends on the combination of effort, success, and proportion females taken by different hunting methods, and is not simple to predict.

Live Population and Harvest Comparisons

In the study design, we planned to relate the live population sample represented by study bears to the killed sample represented by harvests, to explore what harvests could indicate about populations. This proved difficult in practice. Ideally, the size and composition of harvests from the study populations would be compared to the size and structure of the study populations over time. However, too few study bears were killed by hunters for meaningful comparisons.

As an alternative, harvests from the mountain range regions surrounding the study areas were used for the killed samples. The study area populations were used to represent the population structures for the larger regions, a problematic assumption. The unhunted status of the NSA during much of the study weakened its comparison with the hunted Sangre de Cristo complex. During the record high 1994 harvest in the Gila complex, no SSA hunting mortalities were observed, suggesting that hunting on the study area was not typical of hunting in the larger surrounding region. These limitations apply to the remaining discussion.

Relative Cohort Sizes

Examination of year classes of hunter-killed bears over time revealed striking and persistent differences in relative numbers by year of birth. Some cohorts were virtually absent from the harvest records. Bears born in 1988-1990 were relatively scarce in New Mexico harvest data, reflective of the decrease in proportion of subadults in the early 1990s and part of the concerns that prompted this study.

Age distributions from harvests (killed samples) and study area captures (live samples) showed similar variation in apparent cohort size from year to year (Figure 13-3). Because live captures began in 1993, cohorts born in earlier years were represented on the study areas only by older survivors and residents, and more recent cohorts were exaggerated in number compared to earlier ones in the live samples. Because harvest age collection began in 1985, pelt tag records contained information on cohorts born since 1984.

Apparent cohort size variation suggested underlying reproductive variation. A pattern of alternating larger and smaller cohorts appeared in the harvest data for the 1980s and 1990s, and from the live sample for the 1990s, consistent with moderately synchronized reproduction. In both the NSA and SSA samples, the alternating year pattern failed in 1989, with a small cohort where a larger one would be expected. The cohorts from 1988-1990 were smaller than the 1987 and 1991 cohorts. This combination suggested that bear reproduction may have been lower than normal during the late 1980s.

Correspondence between apparent relative cohort size and natality can be examined for the years of the study. The 1992 NSA cohort and the 1993 SSA cohort were missing in den observations (Table 13-6) but not in study live captures or regional harvests. The discrepancy may be attributable to the very small sample sizes for natality observations for the first year on each study area. Cohorts on the NSA from 1994 and 1996 appeared small relative to 1993 and 1995 in den observations, live captures, and harvests. The same was observed for cohorts on the SSA from 1994 and 1995 compared to 1996. For years with higher sample sizes, study natality data were consistent with apparent cohort size differences in the harvest.

The relative proportions of bears from different birth years in harvest data appeared to reflect the relative proportions of bears from different birth years in the study area live populations. The patterns of variation do not imply the causes of variation. Cohorts may appear relatively large when they are not absolutely large if mortality in adjacent cohorts was high. But absence of a cohort in harvest records for several years may indicate low reproductive success for that birth year. A missing cohort is a flag indicating possible poor reproduction; other evidence such as associated mast abundance must be considered. Missing cohorts in harvest data records are more useful for interpreting historical records than for evaluating current populations, because several years of data collection are needed to detect the differences in cohort representations in the harvest.

MANAGEMENT IMPLICATIONS

Harvest patterns and environmental conditions differ among mountain range regions in New Mexico. Analysis of harvest data and related factors on a regional basis is appropriate.

Changes in black bear populations cannot be detected from harvest data alone. However, patterns in harvest data may flag areas of concern to managers. Missing cohorts and associated decreases in proportions of subadults in the harvest over several years suggest poor reproduction. Other evidence such as mast availability should be examined, and the possible population consequences can be factored into management considerations.

Hunting method appears to affect proportion of females in the kill. During 1990-1999, hunters using dogs were 3 times more successful and took 4 times as many female bears per hunter than those not using dogs. However, the impact of hunting with dogs on the total harvest for a region depends on the proportion of hunters using dogs.

Timing of hunting seasons influences the total black bear harvest and the proportion of females in the harvest. During 1990-1999, later fall seasons were associated with lower total harvest and lower proportions of females in the harvest, compared to earlier fall seasons and spring seasons.

Environmental conditions can influence the effect of a hunt on harvest magnitude and composition. During 1993-1999, failures in oak production were associated with increases in hunter effort, hunter success, and the proportion of females in the kill.

CHAPTER 14

THE BLACK BEAR POPULATION MODEL

Our objective in this chapter is to develop and describe the bear population model as a tool for integrating harvest and biological information, and forming interpretations that are consistent with existing knowledge. This approach is intended to help managers to interpret harvest data in the context of bear population biology, make inferences about bear population size and status consistent with available harvest and biological information, and evaluate consequences of management options to bear populations. The model is designed to simulate population behaviors that are realistic for conditions in New Mexico.

CONCEPTUAL BACKGROUND

Information available to managers about black bears in New Mexico has traditionally been limited to data from hunter-killed bears. This study augments management information with biological data on New Mexico's black bear populations, improved understanding of the influence of annual variation in mast abundance, and estimates of potential bear density in different habitats. How can a manager use this diverse information to make inferences about the status of regional black bear populations and the potential consequences of harvest regulations? The population model is the tool for integrating harvest numbers, vital rates, and environmental relationships into a coherent whole.

Models of bear populations have been used for estimating population parameters, projecting population trends from vital rates, determining upper limits on sustainable mortality, and demonstrating various relationships between population and harvest composition. Treatment of biological detail and temporal variability has differed, depending on modeling objectives and information available.

Taylor et al. (1987) developed the ANURSUS model for estimating natality rates for polar bear populations from age specific litter size and family group observations. They emphasized the importance of accounting for the effect of whole litter loss on reproductive eligibility and litter intervals for animals with multi-year reproductive cycles.

Whether a population is increasing or decreasing, and why, are more important to management than population size (Eberhardt and Knight 1996). Assessment of population trends for Yellowstone grizzlies has been approached though comparison of female survival before and after sexual maturity, age of first reproduction, and reproductive rates, rather than through direct population size estimation (Eberhardt 1990, Eberhardt et al. 1994). These models use detailed biological information, and infer trends from average rate estimates. For small populations, perturbations of age and sex structure influence dynamics for many years (Knight and Eberhardt 1985). Such perturbations can affect estimates of and projections from vital rates.

A simple model with detailed reproduction (average age of first reproduction, litter size, breeding interval) and constant mortality was described by Bunnell and Tait (1981). They related maximum sustainable mortality to reproductive characteristics for several documented populations of grizzly, polar, and black bears, and aided other insights into bear population dynamics.

Consequences of food related variation in natality, particularly synchronized or alternating reproductive schedules, were modeled by McLaughlin (1998). He imposed patterns of variable parturition on an individual based, stochastic simulation model with detailed reproductive biology and density dependent mortality, and found a substantial impact on sustainable mortality rates for females.

Population viability assessment models (e.g., Weigand et al. 1998) and other stochastic, individual based models (Knight and Eberhardt 1985) are useful for small or endangered populations where chance is a significant contributor to population variability and probability of extinction is a management concern.

Abundant, detailed biological information is not available to many bear managers, but almost all have harvest data. However, inferring population trend from harvest data alone is nearly impossible (Bunnell and Tait 1980, Garshelis 1991, Miller 1990). A stable age and sex composition in both the live population and the harvest can occur when the live population is stable, but also when it is increasing or declining (Miller 1990). A predominantly male harvest is possible from a predominantly female population (Bunnell and Tait 1980). The erroneous assumption of a constant harvest mortality rate can lead to misinterpretation of harvest data (Garshelis 1991). However, models can be used to demonstrate counterintuitive relationships between simulated populations and harvest data, warning managers of the possibility of drawing false conclusions from pelt data.

Modeling with constant rates can provide useful insights on the boundaries of possible bear population behavior. However, vital rates are variable in real populations, and the particular patterns of variation influence population structure for long time periods. Stochastic modeling provides implicit variation in vital rates over time, but the time pattern of the variation is not related to observed habitat conditions, cohort size, or harvest numbers. Selected general patterns of cohort variation have been examined. The consequences of hypothetical variation in survival over time to population age structure have been used to demonstrate problems in relating harvest data to population status. However, bear models have rarely dealt with the implications of specific population histories. The perils of population assessment from harvest data alone are well documented. Modeling tools for integrating harvest data, biological information, and population history are needed.

METHODS

The bear population model was designed to simulate a black bear population through time, with biological realism, hunting, and environmental influences. Choices for population structure and for life history events accommodated population concerns, hunting patterns, and age of first reproduction for New Mexico. Input requirements were based on information anticipated from the field study for vital rates and bear densities, information routinely collected by NMDGF from hunters on effort and kills, and readily obtained environmental information important to bears. Outputs were chosen to track changes in population numbers and composition, as well as realized mortality rates and harvest predictions for comparison with observations. A set of functions with vital rates as arguments was developed to describe annual births, deaths, and age shifts. Additional functions related annual vital rate changes to environment (mast index, den entry timing) and hunting (effort and season timing). Functions for migration and population size constraints were added last.

Sets of vital rates from the study areas and regional pelt tag (hunter-kill) records were developed and stored with the model. A library of regional history simulations and teaching (hypothetical) model scenarios was developed.

Model software was programmed in APL (Array Processing Language, APL2000 APL+Win version 3.6) with a user interface in Windows Graphic User Interface (GUI) format. Installation is from CDDOM, programmed with Install Shield Express version 2.13. Automated output graphics are displayed using Microsoft Excel (version from Office 97 or later).

The model is implemented in a Windows Graphics User Interface (GUI) program, with a user shell to facilitate inputs, outputs, and scenario saves. Outputs are in both table and graphic formats. The model installation program is provided on CDROM with this report. The model CDROM also contains a library of scenarios, user manual, and documentation for the core model calculations.

The model user interface provides an assortment of aids to choosing input values, including stored characteristic rate sets for geographic regions of New Mexico, and hunt season and pelt tag (hunter-kill) report historic data sets.

RESULTS

Conceptual Model Structure

Overview. The bear population model (Appendix E) simulates a hunted bear population, tracking changes in numbers and sex-age composition over time based on births, deaths, and migrants (Figure 14-1). The initial population, characteristic vital rates, and annual variation in environment and hunting are inputs to the model. The core model equations are a calculation engine to change population numbers based on varying rates over time (Appendix F). Details of bear reproductive biology are incorporated into the model calculations. The model extrapolates population changes based on the conditions described by the full set of model inputs. Outputs are detailed population and harvest numbers and realized total mortality rates over time.

Vital rates are age and sex specific, and vary from year to year in response to environment and hunting. Vital rates are not explicit functions of density dependence or social structure. Migration of subadult males is optional and depends on threshold population sex proportions. Optional upper limits on total population and total adult females approximate density dependence at high population levels.

Population composition. The model's population age structure has separate age classes for each year from cub through 4 years, and an adult class containing ages 5 and above combined. Each age class also is separated by sex. Adult females are partitioned into groups with cubs, with yearlings, and with no offspring.

Scale. The modeled population should represent a large geographic area with a reasonably well-defined bear population, such as a mountain range. The model is not suitable for very small areas or small population subsets. Model runs typically simulate a population for 20 years or longer.

Annual variation. Mast availability index and den entry timing represent annual variation in environmental conditions. Hunting occurs in the fall, with annual variation in effort and season start dates. Fall mast index (poor, fair, or good) may be input for each year, or randomized based on input frequencies for each index level. Annual den entry is input as normal or late for each year. Hunt season dates may be loaded from historic data files; annual low, average, or high effort must be input for each year. Although the model is deterministic, it allows for unlimited patterns of variation over time.

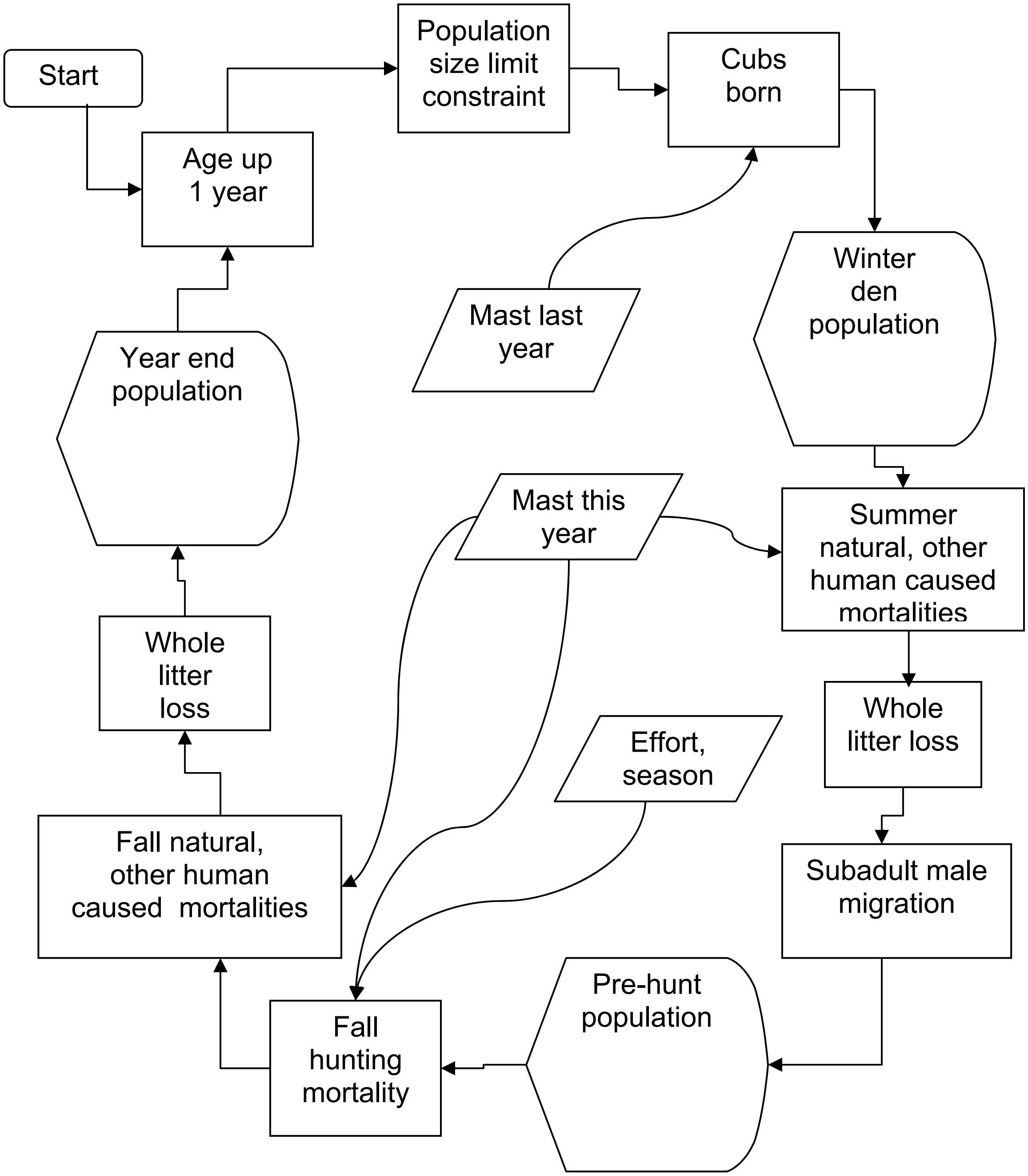


Figure 14-1. Schematic of sequence of events for a simulated year in the bear population model, New Mexico Black Bear Study, 1993-2000.

Natality. Parturition and cub survival rate inputs are step functions of poor, fair, and good mast availability and characteristic of the population being modeled. Fall mast each year determines cub survival rate for cubs born the previous winter and parturition rates for eligible adult females the following winter. Adult females with yearlings in dens do not give birth. Parturition rate is applied only to eligible adult females, defined as adult females without yearlings in dens. Cohort size variation and synchronized alternate year reproduction can be simulated. Calculated cub numbers are based on number of eligible mothers, parturition rate, and litter size frequency. Whole litter loss prior to hunting and prior to the following denning season is based on litter size frequency and cub survival. Whole litter loss in either time period classifies an adult female as eligible to give birth the next year, corresponding to the estimation of parturition rates for all adult females without yearlings in dens in this study.

Mortality. Long-term average mortality rate inputs characteristic of the population being modeled are age and sex specific, and partitioned into natural, hunting, and other human causes. Rates are additive. Hunting mortality varies as the characteristic rate is modified each year by hunt effort, season timing in relation to den entry, and mast conditions. Annual realized mortality rates, or characteristic rates modified by environmental factors, are an explicit output.

Hunting. The model can be run with hunt mortality rates as inputs, and hunter kills or pelt numbers as outputs. Alternatively it can be run with tagged pelt numbers as inputs, and the associated hunt mortality rates as outputs. The choice can be made separately for each year in the simulation. Forcing harvest numbers is useful for simulating unusual events such as the large 1994 harvest. Forcing harvest also makes explicit use of the NMDGF’s long-term ongoing harvest pelt tag report data collection (see Chapter 13). Regional harvest data history files are stored with the model. Only fall hunts, the current NMDGF practice, have been implemented; a spring hunt could be added to a later version of the population model.

Scenarios. A scenario is the complete set of inputs for a model run. Scenarios may be saved and restored. Data interpretation using the model should be based on sets of scenarios, not on single runs. Sets of scenarios bracketing the range of uncertainty for inputs of interest or concern produce a set of outputs representing a plausible range of outcomes.

DISCUSSION

Limitations and Advantages of the Model

The New Mexico bear population model is deterministic. It is not suitable for assessing extinction probabilities or for modeling very small populations where chance is a significant influence. A set of runs with varied inputs is necessary to achieve a range of plausible outcomes. The model is intended for simulation of viable, hunted populations, not endangered ones.

The model does not predict vital rates or environmental variation, although it allows variation in environment to modify realized rates over time. The influence of habitat quality can be expressed by choice of characteristic vital rates. Inputs are detailed, a disadvantage when biological information is sparse, but an advantage for simulating the particular conditions experienced by a real population. Annual mast index is an explicit input, allowing use of observations when available. Mast variation can also be randomized, based on frequencies characteristic of the geographic area being modeled.

The influence of bear social structure on population dynamics is not modeled explicitly. Migration of 3-year-old males in or out of the population can be included, activated by selected threshold population sex ratios. However, interpretation of the results of simulations allowing subadult male migrants should include the plausibility of an external population source for immigrants. An upper limit on adult females and on total bears can approximate density dependence and habitat carrying capacity. The model is sensitive to upper limits, so choices should be based on habitat types and potential densities where possible.

Reproductive biology is modeled in detail. Females with cubs and probability of whole litter loss are tracked for reproductive eligibility and for hunting vulnerability. There are not separate age classes for adult females and parturition rates are average for all adult females, not age specific, because age specific reproductive rate data will not be generally available for New Mexico populations. Age at first reproduction is effectively 5 years, the approximate average for New Mexico. However, reduced parturition in mast failure years is equivalent to older age of first reproduction under poor environmental conditions. Parturition rate is not affected by adult sex ratios, since depressed reproduction due to scarce males is not a problem in New Mexico. However, no cubs are produced if there are no adult males in the simulated population.

Hunt season timing or closure and hunting effort are inputs, allowing management options to be explicit inputs for simulations. The current version allows hunting only in the fall, the current practice in New Mexico. The addition of a spring hunt option would expand the utility of the model.

The New Mexico bear model is designed to facilitate a synthesis of harvest data, population biology, and information on environmental variability. Resulting inferences about bear populations are consistent with all available information. The model cannot provide certainty, but it can rule out nonsense.

When good information is available on annual mast availability, harvest numbers with sex and age, and an upper limit or carrying capacity number of adult females for a population, in conjunction with the vital rate estimates from this study, model results can be of considerable use to managers. Scenarios with population constraints are more sensitive to the combination of harvest numbers, mast failure frequency, and carrying capacity than to rate estimates. Mast, harvest, and carrying capacity can indicate potential over harvest; vital rates can indicate potential for recovery.

Some Strategic Uses of the Model

Real population status. Use of the model to assess population status requires criteria for recognizing a plausible simulation. The criteria will combine best available information for rates and environmental inputs, and information on historic harvests to compare with outputs. To establish criteria for an acceptable simulation, (1) determine reasonable harvest and total mortality rates for the region and time period, (2) use measured mast indices, or any other indicators of mast availability for each year, or use a reasonable frequency of mast failure and randomize mast index over time, (3) note hunt season start dates and identify years with unusually low or high hunter effort, (4) from pelt records, calculate the average numbers of harvests by sex for the time period, and identify years of unusually low or high harvests, and (5) find indications of cohort size variation from harvest data records or independent observations. Run the model using the most plausible rate, environment, and hunt condition inputs. If necessary, make additional runs, varying the initial population numbers until the predicted average female harvest agrees with the observed average, to ensure a plausible initial population size. Then evaluate other outputs against criteria for a plausible simulation. Check predicted variations in cohort size and total harvest for agreement with observed patterns over time. If harvest numbers were forced (inputs) for some years, check the realized hunting and total mortality rates for those years for plausibility. A simulation with plausible inputs and with outputs consistent with observation provides a plausible assessment of population size and trend, consistent with available information.

Hypothetical population behavior. To investigate bear population behavior in general, use an arbitrary initial population with a reasonable age and sex composition, and vary characteristic rates or environmental conditions while leaving the initial population unchanged. Compare patterns in outputs over time, rather than numbers, to see how populations and harvest size and composition respond to different conditions. For example, change mast failure frequency to see the impact on population growth and harvest composition. Increase characteristic harvest and total mortality rates to find levels of over-harvest associated with population reproductive rates, and observe how harvest number and composition predictions change at the same time. Or simulate different hunting regimes over time for comparison, and include environmental variation for realism.

Examples from literature. The model can also be used to reproduce cautionary examples derived from technical literature concerning the problems of relating population status to harvest composition. An example is the counterintuitive finding that a predominantly female population is consistent with a predominantly male harvest, or that population and harvest age and sex composition can remain stable while population size is increasing, stable, or decreasing. The model user can thus be educated about the difficulties of interpreting harvest data, and avoid unwarranted deductions.

Reasonable Input Values

Characteristic vital rates. Estimating vital rates with minimal uncertainty is difficult for bear populations. Allowing rates to vary with environment and hunting is more important to model interpretations than getting average rates exactly right. The field study has produced reproductive and mortality rate estimates for New Mexico, although measured hunting mortalities are suspected to be low in some cases, providing the basis for reasonable input values for the population model (Tables 14-1 and 14-2).

Table 14-1. Black bear population model inputs for characteristic natality rates based on field study observations, New Mexico Black Bear Study 1993-2000.

Litter size frequency			Mast index frequency			
No. cubs	NSA	SSA	Model label	Mast classification	NSA	SSA
single	14	13	Poor	Fail	1	4
twins	43	24	Fair	Poor	4	2
triplets	4	1	Good	Medium or better	3	2

Mast index		Parturition rate		Cub survival	
Model label	Mast classification	NSA	SSA	NSA	SSA
Poor	Fail	0	0.39	0.50	0.43
Fair	Poor	0.71	0.67	0.50	0.85
Good	Medium or better	0.78	0.77	0.50	0.85

Choices for characteristic rate inputs have significant impact on model outputs, reflecting realistic uncertainty about bear population dynamics. Sets of simulations with different characteristic rates are needed to assess the impact of uncertainty on population inferences, and to bracket a range of plausible inferences.

Table 14-2. Observations and reasonable ranges for characteristic mortality rate inputs to the population model for female (F) and male (M) black bears on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico Black Bear Study 1993-2000.

	Hunt mortality rate			Total mortality rate		
Population category	NSA	SSA	Reasonable range	NSA	SSA	Reasonable range
F Yearling	0	0	0.02 - 0.03	0.25	0.03	0.10 -0 .30
F Subadult	0.05	0.04	0.04 -0.08	0.06 - 0.14	0.09 - 0.11	0.05 - 0.15
F Adult	0.04	0.07	0.04 - 0.08	0.07 - 0.08	0.10	0.08 - 0.20
M Yearling	0	0	0.02 - 0.05	0.10 - 0.13	0.24	0.10 - 0.30
M Subadult	0	0	0.07 - 0.10	0.05	0 - 0.03	0.08 - 0.25
M Adult	0.02	0.07	0.07 - 0.10	0.08	0.09 - 0.18	0.10 - 0.25

Choices for characteristic rates can be used to describe conditions for a particular population. Natality rates can be adjusted to represent habitat quality differences. Mortality rates can be increased for areas with many roads or other disturbances.

The model allows for characteristic natality rates associated with 3 levels of mast abundance. Study results indicate that only 2 levels, failure or not, are significant (see Chapters 5 and 6). To reconcile the model structure and the study findings, use the model category of poor mast abundance for failure conditions, and assign the same rates to the fair and good model categories for non-failure conditions, taking care to indicate the correct frequencies for the failure and non-failure categories. Alternatively, assign a 0 frequency to the good mast category in the model, and use the poor and fair categories to represent failure and non-failure conditions.

Initial population numbers. The model addresses changes in populations over time. Each simulation or model run requires a starting population as an input. When vital rate and environmental inputs are reasonable, but model outputs of pelt numbers or realized total mortalities are not consistent with observations, then the simulated population is not plausible, and the initial population input should be changed.

Where possible, use GIS habitat extent, quality and associated bear home range size to estimate total male and female numbers, and use those as inputs. Partition the totals by age using default proportions or use extrapolated study area population structure as a guide.

If habitat based estimates are not available, consider a manager's informed estimate of total bears in the region as a starting point. Using the model will provide a check on the plausibility of such estimates.

When there is no other basis for selecting an initial population size, the model can be used to generate ballpark initial populations from harvest data, with the following steps: (1) Select and load a set of characteristic vital rates based on geography from rates stored with the model. (2) Set mast values to average for all years, so that reproductive rates will be steady at average values. (3) Start with an arbitrary total of 1000 bears, and run the model for 20 years. (4) Use the final population from that simulation, which will have age and sex proportions consistent with the vital rates, as the initial population for the next run. This step eliminates the influence of unstable population age structure on average harvest. (5) Run the model again, and compare the average total pelts and female pelts to pelt tag observations. (6) Adjust the initial total numbers up or down until predicted average pelts are similar to observed average harvest. Then use that initial population for simulations with variations in environment and hunting.

One use of the model is testing a range of population sizes for plausibility in light of past harvest history and mast availability by repeated runs varying only initial population totals. Take care to avoid other input constraints that may invalidate the population size interpretation.

Application outside of New Mexico. The model can be applied to black bear populations in other locations by suitable choices of characteristic vital rates, litter size frequencies, and mast frequencies and mast step function values. The input details allow considerable opportunity for simulating particular conditions. In this version, simulated hunting is limited to a single fall season.

Modeling study population viability

The model was used to investigate the implications of observed natality and total mortality rates from both study areas. Natality rates from Table 14-1 were used as model inputs. Calculation of long term averages weighted by frequencies shows the NSA had an average parturition rate for eligible adult females of 0.65, and average litter size of 1.84. The SSA had lower average reproductive rates, with 0.51 for parturition rate and 1.68 average litter size. Observed total mortality rates for the study areas from Table 14-2 were entered as characteristic natural mortality, with other human and hunting mortality rates set to zero, for correct total realized mortality. Where the total mortality estimate was a range (excluding or including probable deaths), the mid point of the range was used for the input value.

Initial population age and sex composition were based on history scenarios previously developed for the surrounding mountain ranges, but total numbers were rounded to the nearest 1000 for simplicity. This analysis considers proportional population changes rather than absolute numbers, so the initial total numbers used do not affect the interpretations.

Some simulations were made with mast set to average for all years, to produce constant average natality rates. Additional runs were made with randomized mast values, using the frequencies characteristic of the study areas, so that cub production varied. Cub survival varied with mast, but total mortality rates for older bears were constant at input rates. For each study area, 1 run used mast index set to observed levels for 1993-2000. Since observed mortalities on the study areas appear unrealistic for female yearlings on both areas and subadult males on the SSA, simulations were also run with total mortalities set to the minimum, middle, and maximum of the reasonable ranges for each population category. Changes in adult female numbers from beginning to end of the simulations varied from 199% increase to 84% decrease, depending on the combination of mast conditions and mortality rates used (Table 14-3).

The interpretation of simulation results will focus on adult females, because their numbers determine the reproductive potential of the populations. Our observations of subadult male total mortality are unrealistically low, skewing the simulated male numbers and the simulated population sex composition.

These simulations are not realistic, because constant rates over time are not realistic, but they reveal the population trends implied by the observed average rates. Both populations have a built in tendency to increase, based on observed rates. The unhunted NSA has lower mortality for subadult and adult females, and higher potential reproduction because of its low frequency of mast failures, and so has potential to increase faster than the SSA.

The potential for increase is overestimated if total mortality for females has been underestimated. For both study areas, the average annual female total mortality is 10%. Model simulations with the same total mortality rate for all female age classes and average observed natality rates show that the NSA population would begin to decrease with average total female mortality above 12.5%, and the SSA population would begin to decrease with average total female mortality of 11.5%, well within the range of uncertainty for the observed rates.

Table 14-3. Percent changes in adult female numbers from bear population model runs using study area vital rates and mast observations for the Northern Study Area (NSA) and Southern Study Area (SSA), Black Bear Study in New Mexico 1993-2000.

Time frame	Constant average mortality rate	Mast	NSA female population change	SSA female population change
20 years	Study area observations	Constant at average	+117%	+49%
20 years	Study area observations	Randomized	+39 -128%	+40 - 86%
1992-2000	Study area observations	Study observations	+23%	+14%
20 years	Minimum of reasonable range	Constant at average	+199%	+129%
20 years	Middle of reasonable range	Constant at average	-16%	-34%
20 years	Maximum of reasonable range	Constant at average	-79%	-84%

The simulations with observed mast abundance indicate that both study populations have increased during the study. There were no marked bears killed from the SSA population during 1994, the year of record harvests for both sexes in the surrounding Gila region, but marking began only in 1993. If unmarked females resident on the SSA were killed in 1994, the study population may not have increased.

The pattern of mast abundance over time strongly affects simulated population trends, with all other inputs left unchanged. Routine observation of mast abundance would greatly enhance utility of the model and assessment of population status.

Modeling Pelt Tag Data Histories

In workshops held in 1998 and 1999, NMDGF area managers used the population model to assess black bear populations in 4 mountain range regions comprising most of the state's bear habitat (Table 14-4). Simulations used vital rates and mast observations from the study areas for the Gila and Sangre de Cristo complexes, and similar rates for the San Juan complex and Sacramento region with adjustments based on area managers' knowledge of local conditions. Simulations were run for 1981-1998. Outputs were evaluated for plausibility based on comparisons with observed average pelts tagged by sex for 1989-1998, timing of peak harvests, and proportions of subadults. Scenarios with reasonable matches to observed patterns provide interpretations of bear population status that are consistent with both pelt tag observations and field study findings.

Table 14-4. Regional black bear population status interpretations based on population model simulations and harvest observations in New Mexico, 1989-1998.

Region	Rough population estimate	Trend	Observed average no. bear kills 1989-1998		Model average no. bear kills 1989-1998		Pelt tag numbers forced	Scenario name
			F	M	F	M		
Sangre de Cristo complex	1500	Slow increase	40	67	41	56	none	SANG99D
San Juan complex	1000 hunted + 700 unhunted?	Slow increase	26	44	25	35	none	SNJN99C
Gila complex	1000	Stable	35	58	37	43	1989, 1994	GILA99B
Sacramento region	1000	Increasing	24	33	23	35	1994, 1995	SE99B

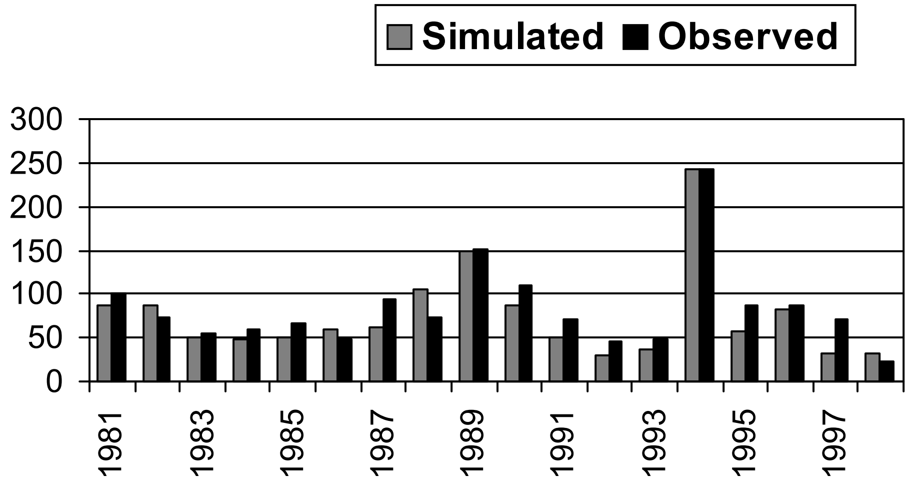
Sangre de Cristo complex. Scenarios were based on NSA rates, but with higher adult hunting and total mortality rates, because most of the region is hunted (although the study area was not). A scenario with constant hunt effort and observed mast pattern for the study years produced a slowly increasing population with reasonable harvest patterns but low average numbers, and a peak in kills for 1994. Initial population was increased to raise average pelt tag numbers, and hunt effort was specified as low for 1992 and high for 1995, consistent with card survey results. The final scenario showed a gradual increase in the live population total. Scenario average pelt numbers for males were lower than observed, suggesting that the hunt component of male mortality may have been underestimated.

San Juan complex. Scenarios were based on NSA rates, but with higher adult hunting and total mortality rates, because part of the region is hunted (although the study area was not). . Mast index inputs were based on knowledge of local conditions, not northern study area observations. Runs with slightly increasing population and a reasonable match for observed female pelt tag reports had lower male pelt tag numbers than observed. The large areas of this region protected from hunting may be a source of some of the males killed by hunters.

Gila complex. Southern study area vital rates were used, except that a higher subadult female hunt mortality (same as for adult females) was needed to match the observed proportions for subadults of females in pelt tag reports. High harvest numbers for 1989 and 1994 were forced because simulations did not produce the observed peaks. For 1994, with the harvest forced to match the high observed pelt tag report numbers, realized total mortality for the year was 22% for females, 35% for adult males, and 42% for subadult males; area managers interpreted the high mortality values as reasonable for the unusually harsh conditions of 1994. In a scenario that produced a good match to observed pelt tag numbers and proportions for females, the 1994 harvest reduced the pool of adult females in the model population, so that the population fluctuated around initial 1981 population numbers without much change over time (Figure 14-2). Scenarios that matched observed female pelts predicted too few male pelts. The discrepancy could be reduced by assuming substantial immigration of subadult males from Arizona, or by shifting all subadult male mortality from other causes into hunting, or by a higher total population with much lower female hunting mortality.

Sacramento region. A population scenario with fast turnover, both natality and mortality near the high end of reasonable ranges, is consistent with the observed high proportions of subadults in pelt tag reports. With the large 1994 and 1995 pelt tag observations forced, a scenario with a slowly increasing population predicts harvests that agree with both observed numbers and proportions. There is no likely source of immigrant subadult males for this population, and the scenario does not need 1 because these mountain ranges are isolated from sources of immigrants.

Total harvest



Simulated population

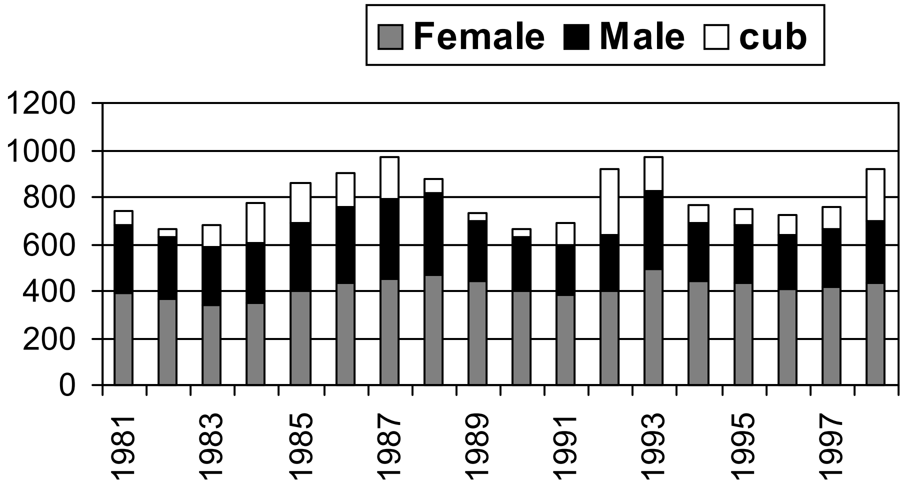


Figure 14-2. Black bear population and harvest numbers simulation

Statewide. The steady decrease in statewide hunter-killed bears from 625 in 1994 to 148 in 1998 raises concern about over-harvest. That pattern was exaggerated by the large harvest in the Gila complex in 1994; although present, the pattern is much less marked in other regions. Harvests increased again in 1999 and 2000. License sales decreased steadily from 1995 through 1998, and the 1998 season was 6 weeks later than previous years. Model population simulations with field study rates indicate that the peak harvests likely resulted from mast failure combined with an abundance of available subadults born in the early 1990s, and subsequent decreases were likely related to decreasing hunter numbers rather than to a rapid drop in bear populations.

Pelt tag reports show a higher proportion of males than do simulations based on vital rates observed during field study. The difference may result from difficulty in documenting male bear mortality rates, or from inclusion of immigrant subadult males in harvest reports, or both. Focusing on the female segment of the population for interpreting population changes avoids the problem.

Model Application to Management

Simulations used for the following model application discussions are included with the population model software in the scenario library (Table 14-5).

How fast can a population change? In simulations with all mortality rates at the high end of reasonable ranges based or study, model populations disappear in 2 or 3 decades. The persistence of bears is evidence against the plausibility of the long-term maximum mortality rate simulations. Populations with average natality like the SSA would decrease by 61 – 79% in 10 years and by 85 – 96% in 20 years with constant annual mortality rates of 20 – 25% for all population categories. Populations with average natality like the NSA would decrease by 56 – 75% in 10 years and by 80 – 94% in 20 years.

Minimum mortality simulations, while not realistic, identify an upper limit on bear population growth rates in New Mexico. Unless limited by habitat capacity, southern populations might double in 20 years, and northern populations might triple, if mortality were minimal and the pattern of mast availability remained normal. Since most New Mexico populations are hunted, the fastest population increase possible with persistent low mortality would be doubling in 20 years. With occasional years of greater mortality, population increases are reasonably expected to be slower.

Average statewide hunter kills for 1994 and 1995 were double the average for 1991-1993. This increase must be interpreted as increased hunting mortality rate, and not as a proportional increase in total population with unchanged harvest mortality, because the population could not have doubled during that time frame. Similarly, the decrease in total pelts tagged from 625 in 1994 to 148 in 1998 cannot be interpreted as evidence of a 75% reduction in population in 5 years, because such a rapid drop would be highly unlikely. Instead, other factors should be considered along with the possibility of a less rapid population decrease.

Table 14-5. Scenarios used for the black bear population model application discussion and stored in the scenario library, Black Bear Study in New Mexico, 1993-2000.

Scenario library name	Description of scenario	Interpretation section
NSAOBS01	Constant mast, NSA characteristic vital rates	Study population viability
SSAOBS01	Constant mast, SSA characteristic vital rates	Study population viability
CUBVAR1	Population varying slightly around a stable total	Synchronous reproduction
OVER0	Baseline stable population with annual variations	Characteristics of over harvest
OVER1*x*	Persistent mast and reproductive failure	Characteristics of over harvest
OVER2*x*	Increased hunt mortality	Characteristics of over harvest
OVER3*x*	Increased nonhunt mortality	Characteristics of over harvest
SANG99D	Sangre de Cristo pelts, NSA rates	Pelt tag histories
SNJN99C	San Juan pelts, modified NSA rates	Pelt tag histories
GILA99B	Gila pelts, SSA rates	Pelt tag histories
SE99B	Southeast pelts, modified SSA rates	Pelt tag histories

Cohort variation, synchronized reproduction, and pelt age composition. The baseline scenario simulates a hypothetical population varying slightly around a stable total for 20 years. Mast index and the associated natality and cub survival rates vary annually. The population age composition changes over time as variable size cohorts age. Hunt effort is held constant so that realized total mortality rates for yearling, subadult, and adult bears remain constant. Predicted hunter kills or pelt tag numbers vary slightly with population size and composition over time. The proportions of subadults in the pelts vary from 35 to 53%, with several large drops over a few years; however, total population size is essentially stable (Figure 14-3). This simulation demonstrates that shifting proportions of subadults in hunter-killed bears may indicate, and lag, cohort variations, but do not necessarily indicate population size change.

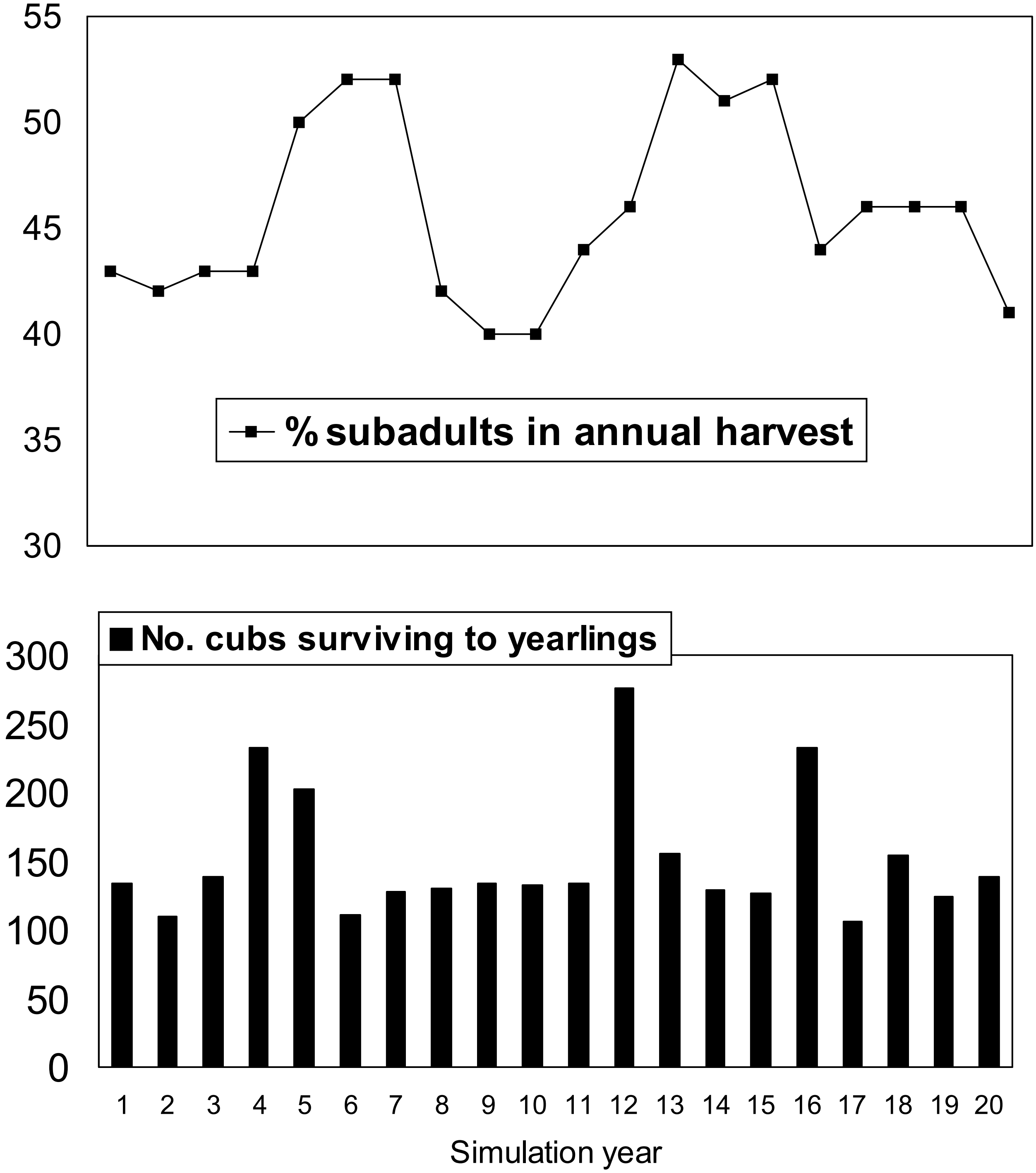


Figure 14-3. Simulation of black bear cohort size variation and its influence on harvest age composition in a 20 year stable population simulation for data applicable to black bears in New Mexico.

Synchronized reproduction can be simulated. Constant rate scenarios provide a basis for examining synchrony, by following the impact of a single mast failure over time. One year of mast failure in a simulation with NSA natality rates and otherwise all fair mast produces almost no cubs in the year following the mast failure, a very large cohort in the second year, and a smaller than normal cohort the third year. Variations continue for several more years, but with differences too small to be noticeable. A similar pattern occurs with SSA natality rates, except that the initial mast failure produces 2 cohorts about half average size since the mast failure reduces survival for cubs already born as well as parturition for the next year's cohort. A single mast failure affects cohort size for 3 or 4 years. Any single year's observation of population composition may misrepresent the longer time scale pattern. Averages over 2 to 4 years are useful for examining patterns over long time periods.

Characteristics of over-harvest. The model was used to investigate potential indicators of over-harvest and declining populations. A 20 year simulation of a hypothetical population fluctuating around a steady mean, with annual variations in mast index and 2 years each of high and low hunt effort, was used as a baseline. Declining populations were simulated by mast and reproductive failure, increased non-hunt mortality, and increased hunt mortality. For each cause of decline, runs were made with hunt mortality determining pelt numbers and with pelt numbers specified resulting in increasing hunt mortalities in the second decade. The hypothetical scenarios used for this discussion are stored in the model scenario library.

In the baseline simulation, pelt numbers fluctuated from year to year with cohort and hunt effort variations, but remained stable on average. The proportion of females varied in the range of 46-51%, and the proportion of subadults varied in the range of 34 – 44%, with no trends over time.

In all of the declining population simulations without forced pelt tag numbers, simulated harvest numbers fluctuated, but relative peaks decreased and averages clearly dropped over time. In the stable population simulation, harvest numbers were steady on average. In other simulations with increasing populations, pelt numbers increased on average. Trends in harvest numbers should indicate population trends if hunting effort remains reasonably constant and if harvest numbers are related to bear numbers, that is if hunting mortality rate has some reasonable upper limit. The problem with depending on pelt tagging report numbers as a population indicator lies in the assumptions. In New Mexico, changes in hunt season dates and substantial variation in numbers of hunters produce variations in hunt effort, so that patterns in pelt numbers must be interpreted in conjunction with patterns in hunter numbers and seasons. A persistent decrease in total pelts over 4 years or more without a related decrease in hunting effort should be investigated as a potential indication of a population decline.

Simulations with forced pelt tag numbers can represent cases of harvest numbers not related to bear numbers, so that hunt mortality increases until hunters take all bears. If hunters can kill the same numbers of bears at high and low bear population levels, then pelt number patterns are not a reliable indicator of live population trends.

The age and sex composition of pelts from populations declining due to increased mortality rates did not differ noticeably from the baseline stable population simulation. In the simulation with persistent reproductive failure, the proportion of subadults in pelts decreased by half in 6 years, and then remained low but stable. In the reproductive failure case, independent information on persistent mast failures would alert managers to a probable population decline before pelt age changes could become obvious. Changes in pelt sex and age composition are not useful indicators of population size trends. Age and sex of pelts does provide useful information on relative cohort sizes and impacts on the pool of reproductive females, however.

In the simulations of populations declining from increased hunt or nonhunt mortality rates, the population declines could be stopped or reversed by reducing hunt mortality. In the simulation of population decline from reproductive failure, the rate of the decline was slowed with reduced hunt mortality.

Declining populations are hard to recognize from pelt tag data alone. Decreased pelt numbers without decreased hunt effort would indicate a declining live population, but would take perhaps a decade to become apparent. The bear model provides a context for interpreting pelt numbers; interpretations are considerably strengthened by the incorporation of other information such as mast observations, hunter numbers, and season timing.

Focus on female harvests. Initial experiments with the model are likely to produce frustration with the difficulty of forming definitive conclusions in the face of uncertainty about vital rates. Further experience with a variety of simulations will indicate that the pool of reproductive females is critical to population trends, an outcome that is not surprising. In New Mexico there is good information on harvest numbers. Even though female mortality rates are not known with certainty, unusually high female harvest numbers (well above averages from other years) can be recognized from pelt data, and imply unusually high female mortality for the year. In New Mexico there is a well-documented relationship between mast crop success or failure and reproductive success or failure (see Chapter 6). Continuing observations of fall mast will provide a good indication of annual variation in reproduction, and the associated variability in cohort size should be detectable from pelt ages. The model provides the capability of simulating the population consequences of the real pattern of female harvest and reproduction over several years, key to assessing the potential for over-harvest. High female harvest numbers combined with poor reproduction need management attention.

MANAGEMENT IMPLICATIONS

The bear population model is a tool for integrating harvest and biological information, and forming interpretations that are consistent with existing knowledge. It helps managers to:

- Interpret harvest data in the context of bear population biology, including reproductive patterns and the influence of environmental conditions on vital rates, such as parturition and survival

- Make inferences about bear population size and status that are plausible and consistent with available harvest and biological information

- Evaluate the consequences of management options to bear populations

“Knowledge in, knowledge out” is the philosophy of bear model use. Inputs are the characteristics of the particular population to be modeled and the year-to-year changes in the conditions that affect that population. Outputs are predicted year-to-year changes in numbers and in age and sex composition of the live population and of hunter-killed bears. Model calculations link the outputs to the inputs based on knowledge of bear population dynamics. Model predictions are consistent with the inputs. Greater confidence in inputs means greater confidence that simulated population behavior is realistic.

The model simulates population behaviors that are realistic for conditions in New Mexico. There will always be considerable uncertainty in information about black bears. Because of this uncertainty, managers will not be able to use the population model for simple predictions of legal kills or population trends. The model will be useful for gaining insight about how bear populations can behave, and for discriminating between reasonable and unreasonable explanations of observed harvest trends.

The New Mexico bear model can incorporate variation in vital rates over time based on real population histories, through annual mast observations for natality variation, and annual harvest numbers for mortality variation. The consequent perturbations in live population structure and harvest composition can then be simulated and taken into account for population status interpretation.

The black bear population model can be a useful tool for understanding bear population dynamics, and educating the intuition of managers. Sufficient practice with the model is essential to appropriate interpretation.

Experimentation with the impacts of small changes in different inputs, or sensitivity analysis, will provide insight into the relative importance of different kinds of input information, allowing effort to focus on the most important variables.

When good input information is available, the black bear population model can be a useful tool for assessing population status. Continuing collection of hunt effort information though the hunter card survey and information on the number, sex, age, and location of hunter-killed bears through mandatory pelt tagging reports will be useful. Routine observation of fall mast abundance will be useful. Attention to habitat suitability, using GIS tools, will be useful.

Black bear population status appears to vary among mountain regions in New Mexico. Hunting regulations that vary among regions make sense from a population biology perspective.

Focusing the interpretation on bear population status on the female segment is useful, because the pool of adult females is critical to population maintenance. Annual variation in male harvest numbers is harder to interpret because subadult males may be migrants.

Be cautious in interpreting bear model predictions for conditions outside the range of experience from the bear study, including poorer habitats, different hunt regimes, and other climate conditions.

CHAPTER 15

MANAGEMENT TOOLS AND APPLICATIONS

It is vital that readers of this report and its appendices recognize that they are a tool for future management investigation and decision-making. Using the study results, the population and habitat models, and data collected annually by NMDGF, managers can explore the results and consequences of many management options. This product does not provide answers to all management questions; it provides the means to answer questions when used with reliable and up-to-date information.

EXISTING TOOLS

Hunter-Kill Data Records

Since 1978, the NMDGF has collected annual records of harvested bears through a mandatory tagging and reporting program. Beginning in 1985, utility of these data was improved with the requirement of proof of sex and collection of a premolar tooth for age determination with the cementum annuli method. This data set, known as the pelt tag records, also includes information on date, location, and method of kill.

Hunter Survey

Since 1989, the NMDGF also has conducted mail-in surveys of all buyers of bear hunting licenses to obtain data on hunter effort and methods to be used in conjunction with harvest records. These records, known as the card survey data, are collected and analyzed by the NMDGF Division of Wildlife.

NEW TOOLS

Bear Population Model

An important product of this study is a black bear population model that directly incorporates reproductive and survival rates observed during 8 years of field study, along with harvest data routinely collected by the New Mexico Department of Game and Fish. Utility of the model depends on continued input of data in the form of (1) annual hunter-kill (pelt tag) records and (2) annual observations of regional mast production.

Habitat Model

Another important product of this study is a model of predicted suitable habitat for black bears in New Mexico. This model is a relatively simple predictive algorithm that incorporates land cover classes (habitat types), land cover class suitability for bears, mast production potential, and distance of isolated habitat tracts from primary habitat types. The model allows for examination of bear habitat with respect to other landscape features such as roads, distribution of hunter-killed bears, proximity to human population, and other factors that a resource manager may choose to evaluate. The model is designed to incorporate and integrate with new ecological and socioeconomic information as it becomes available.

Annual Mast Survey

The mast production survey implemented during this project is a procedure conducted by NMDGF personnel using categorical criteria to distinguish annual variation in mast production. Study results indicate that documenting annual mast production, particularly occurrence and frequency of mast failures, will be an effective tool for predicting future black bear reproductive success. In addition, knowledge of mast failure may aid in interpreting harvest data, because mast failure appeared to influence amount and composition of hunter harvests.

Research Report and Data sets

The Final Report and associated data sets (on CDs) provide extensive archiving of bear project data and interpretation of that information. Some of this information is supplemental to specific uses in the bear population model and habitat model. The report materials in total are a foundation for asking additional questions about managing black bears in New Mexico and describe uses of all of the tools mentioned here.

UNDERSTANDING THE TOOLS

Hunter-Kill Data

Hunter kill data provide information only from successful hunters. Continued collection of pelt tag report data is essential for estimating population trends using the bear population model. Analyses indicate ages of hunter-killed bears, estimated using the cementum annuli method, are sufficiently accurate to support interpretation of pelt tag data. Use of the bear population model requires age-specific data on bears aged 1-4 years, and distinguishing subadult from adult bears killed by hunters. Our analysis indicated the currently used age determination technique is most accurate and consistent for young bears. Procedural improvements, such as minimizing breakage and extracting the correct tooth, also will increase accuracy.

Analysis of pelt tag records from marked study bears indicated as many as 7% of hunter-killed bears reported to NMDGF are missing from finalized pelt tag data. Improvement in the flow of data from field personnel through area offices to the Santa Fe office is necessary to ensure the most accurate data possible. Also, it is essential that UTM coordinates for locations of bear kills recorded on the pelt tag record be accurate and consistent with the GMU to maximize abilities to plot bear kill data with respect to habitat model output.

Hunter Survey

The hunter card survey collects information from unsuccessful as well as successful hunters, allowing estimation of effort and success rates. Continued collection of mail survey data is essential for knowledge of the geographic distribution of hunting effort, not available from statewide license sales or pelt tag records. Archiving raw survey response data will facilitate analysis beyond the routinely reported annual projections.

Projections of total hunter effort and harvest from card survey responses depend on total statewide license sales numbers. Because the state fiscal year is different from the regulation year, and license sales records are maintained for fiscal use, careful attention to appropriate total license numbers is important to card survey projections.

Surveys are mailed to all license holders with usable mailing addresses. Archiving mailing lists and noting undeliverable returns would improve knowledge of response rates, allow comparison of response rates by region, and facilitate follow up surveys of nonrespondents to assess bias.

Annual Mast Survey

Results of simplified surveys conducted by NMDGF officers were highly correlated with more intensive survey results, indicating quantified subjective criteria are adequate to distinguish variation in mast production. Most officers found the criteria were reasonably easy to use and could be completed during routine duties. In the future, an effort to establish general survey routes, revisited each year, may reduce unnecessary variability and ensure quality data.

Bear Population Model

The bear population model is a tool for (1) interpreting past or present conditions using real time series observations of harvest and mast, and (2) investigating demographic outcomes from hypothetical information based on realistic biological conditions and management actions. Model input variables are reproductive rates, survival rates; and mast production; outputs are predicted population composition and harvest composition. The inputs appear to be simple, but the user must be educated to the influences of factors such as hunt timing, methods, and regional differences in productivity and mortality. Information in the Final Report and interpretations from GIS habitat modeling are important resources for judging inputs for the bear population model.

Reliable information is essential for using the bear population model and interpreting its output. Continuing collection of hunt effort information though the hunter card survey and information on the number, sex, age, and location of hunter-killed bears through mandatory pelt tagging reports will be important for future management. Continued mast survey data are also essential inputs for the bear population model, because vital rates are deterministic functions of mast index in the model.

Information from this study indicated mean age of females at birth of first cubs was 5.7 years for study bears, and only 9% of 4-year-old bears produced first litters. Use of the population model assumes the adult segment of the bear population in New Mexico is bears ≥5 years old.

Sufficient practice with the model is essential to appropriate interpretation. Sensitivity analysis, or experimentation with the impacts of small changes in different inputs, will provide insight into the relative importance of different kinds of input information, allowing efforts to focus on the most important variables. Focusing interpretation of bear population status on the female segment is useful because the pool of adult females is critical to population maintenance. Annual variation in male harvest numbers is harder to interpret because subadult males may be migrants.

Caution is necessary in interpreting bear model predictions for conditions outside the range of experience from the bear study, including poorer habitats, different hunt regimes, and other climate conditions.

Habitat Model

At present, restrictions on availability of comprehensive, detailed, statewide information layers limit detailed analysis of habitat quality and potential effects of humans on bear survival. However, the model was constructed so that future, more resolved information can be easily incorporated to update model predictions. Such new data integration also applies to analytical uses of the habitat model to assess proximity to human-populated areas and other evidence of prospective human interaction with bears (e.g., traffic, recreation). The habitat model also may be useful in developing or verifying inputs to the bear population model, especially upper limits for modeled populations.

APPLYING THE TOOLS

Population Monitoring and Interpreting Hunter-Kill Data

Use of the bear population model, with the inputs described above, will (1) allow for interpretation of recent demographic trends in New Mexico bear populations, (2) provide a timely indication of potential overharvest, and (3) provide predictive scenarios useful for selecting from several management options.

Although status and trends in black bear populations cannot be detected from harvest data alone, patterns in harvest data may flag areas of concern to managers. For example, missing cohorts and associated reduction in proportions of subadults in the harvest over several years may suggest poor reproduction.

Model vital rates are deterministic functions of mast index, which can be randomized with realistic frequencies, or matched to observations. Series of scenarios with different mast patterns or characteristic vital rates can be set up easily and run in a short time by NMDGF wildlife managers and researchers investigating further and future questions about bear population management. Outputs of interest must be recorded and organized for comparison; the model does not compare results of differing scenarios automatically.

Among adult and subadult bears, most mortality was human-caused. In addition to hunting, illegal kills and depredation kills were significant sources of mortality for these bears. Illegal kills were documented on both study areas, and many of the unexplained losses were probably due to illegal kills followed by destruction of the transmitters. We were unable to verify any of these possible mortalities, therefore these possible rates should be viewed as maximum rates.

Interpretation of population trend also will be improved by actual data on bear mortalities resulting from depredation and nuisance situations. Currently, NMDGF data are incomplete and do not represent a concerted effort to assess the impact of these actions on bear populations.

Because reproductive success and recruitment are determined largely by mast production, people primarily alter black bear population growth through human-caused mortality of adult and subadult bears. Use of the bear population model with reproductive and survival rates observed during this study indicated study populations were stable (SSA) or slightly increasing (NSA) with a likely annual population increment of no more than 2-4% growth per year on average. If management goals are to maintain bear population levels, strategies that emulate demographic rates observed during this project are appropriate. If management goals are to accomplish strategic changes in numbers or redistribution of bears (e.g., reduce or increase total population, different regional population objectives), then management strategies will call for altering mortality rates up or down from those observed during this study. Options related to those goals can be explored using capabilities of the bear population model.

If annual mast surveys are continued long-term, in addition to providing annual information necessary for model inputs, they also will provide valuable information on the relative frequency of mast failures within different regions of

New Mexico. This information will be useful for determining the growth potential of distinct bear populations within the different regions of New Mexico.

Population Estimation

Two independently derived population estimates (bear population model and habitat extrapolation) put the New Mexico statewide bear population at approximately 5200-6000 bears. These estimates were for the pre-mast season (May-early August) and excluded cubs of the year.

Statewide population estimates derived from this study refute previous estimates. Our estimates indicate a statewide population of approximately twice the long-standing estimate of 3,000 bears previously used by the NMDGF. However, these estimates do not suggest a doubling of the bear population in the past decade. Rather, these estimates are based on better information including demographics, density, and habitat extent.

Population estimates must be used advisedly because each method of population estimation has intrinsic limitations and firm numbers can never be achieved. Furthermore, population estimates derived from the field study represent density in good habitat, and little is known about the relative density of bears found in less suitable habitat. With this new information NMDGF has additionally recognized latitude in bear management, but should proceed with caution regarding adjustment of harvest goals near the upper limit of new estimates without further testing of the model and predictive scenarios.

Estimates of black bear density and total population provide a reasonable estimate of the upper limit of New Mexico bear populations. As an input into the bear population model, this information is intended as a planning figure. While it is not exact, it illustrates that there is an upper limit to the possible statewide bear population and ensures a level of reality prohibiting predictions of unlimited population growth.

Hunt Management

Annual bear kill by hunters was affected by many factors including season timing, hunter effort, hunter method, and mast production, as well as underlying population composition. Hunters aided with dogs had higher success rates and harvested 4 times as many female bears per hunter as those not using dogs. Harvest was positively associated with hunter effort (higher harvest with greater effort), while harvest was negatively associated with mast production (higher harvests with lower mast abundance). Knowledge of these relationships may aid the NMDGF in selecting among various hunt management options.

During the intensive fall foraging period, study bears commonly increased activity patterns and made frequent long-range movements outside of their primary home ranges. Differences in movement patterns were observed between regions and among different sex and age categories. Movement patterns also differed relative to availability of mast, primarily acorns. Knowledge of these movement patterns may allow the NMDGF to set fall seasons at times most appropriate to accomplish various harvest objectives.

Bears entered dens as early as September and as late as February. Differences in den entry dates were observed between pregnant female and other bears and between regions of New Mexico, however much overlap occurred between sexes and varied annually. Knowledge of these differences will allow the NMDGF to influence the sex and age composition of the harvest to achieve desired management objectives, such as protection of adult females as the reproductive segment of the population. Analysis of pelt tag records indicates later timing of fall seasons reduced harvest of female bears.

Bears emerged from dens as early as March and as late as May. Slight differences in den emergence dates were observed between male and female bears, indicating careful timing of an early spring season could reduce vulnerability of female bears, especially those with new cubs. Analysis of pelt tag records showed spring harvests were dominated by male bears. However, immobility of cubs immediately following den emergence increases the potential for separation of cubs from their mothers (preventing identification of females with cubs), thus orphaning and inevitable cub mortality. Considering both factors, it appears that any spring hunting season will have the potential for reducing cub survival.

Knowledge of black bear denning dates is useful for interpreting sex and age composition of the harvest. The verified differential in den entry and emergence dates among sex and age groups has application to setting bear hunting seasons to accomplish various objectives. However, den entry and emergence dates are highly variable and generally span a period exceeding 2 months. We observed variation relative to mast production; other factors undoubtedly play a role influencing the timing from year to year. No single timing scenario is appropriate for every use.

It is important to recognize that there was no legal hunting on the NSA during 1992 through 1997. Therefore the hunting mortality rates observed may not reflect actual mortality of bears from hunting in northern New Mexico. The possibility of total mortality exceeding the rates we observed must be considered when interpreting harvest data and output from the bear population model.

Habitat Considerations

Estimated statewide bear habitat encompasses approximately 14.6 million acres, of which 75% is primary habitat. Primary habitat represents about 13.5% of the state.

Within predicted bear habitat, mast producing land cover types were found within 7 km (female mast season activity radius) of primary habitat throughout New Mexico except for about 300 km^2 in the Sangre de Cristo complex. This indicates that nearly all bears have access to habitat with important mast-producing species. However, actual abundance of oak, juniper, and pinyon is unknown within bear habitat because current data are not adequate to assess detailed distribution of potential mast production. Better information on actual mast-species abundance may allow for better interpretation of habitat quality and its potential for bear productivity.

Dens that facilitate security and energy conservation during hibernation period are of significant value to black bears, and female bears exhibit a tendency to select tree cavity dens when available. Retention of large diameter live trees, large snags, and large fallen logs may be a valuable goal in all forest management plans and programs.

Nuisance and Depredation Resolution

Approximately 17% of bear habitat is situated within 5 km of human populations. Availability of garbage and other human-related foods is associated with increased nuisance and depredation activity by bears. Despite the significant potential for conflict, analyses indicated only a minority of bears engaged in nuisance or depredation activities. Nonetheless, kills resulting from bear-human conflict represent a significant mortality factor within the bear population. Efforts to reduce accessibility of human-related foods will be instrumental in reducing the likelihood of bear problems in areas with human populations.

Translocation of bears, as a means of solving depredation and nuisance problems, has shown variable success. Observed homing behavior of adult bears indicates translocation of adult bears is merely a short-term solution, particularly if attractants are not removed from the original site. However, short- and long-term settlement was observed among translocated subadult bears, indicating relocation of subadult bears into remote areas, with little potential for human conflict, may be an effective management tool. Nonetheless, translocation of problem bears should not be done without associated attempts to eliminate or reduce accessibility to human-related attractants (e.g., garbage, pet foods, wildlife feeding, bee hives) where such attractants exist.

LITERATURE CITED AND OTHER REFERENCES

Addison, E. W., and G. G. Kolenosky. 1979. Use of ketamine hydrochloride to immobilize black bears (*Ursus americanus*). Journal of Wildlife Diseases 15:253-258.

Alt, G. L. 1977. Home range, annual activity patterns, and movements of black bears in northeastern Pennsylvania. M.S. Thesis, Pennsylvania State University, College Station, Pennsylvania. 67 pp.

Alt, G. L. 1981. Reproductive biology of black bears of northeastern Pennsylvania. Transactions of the North American Wildlife and Natural Resources Conference 38:88-89.

Alt, G. L. 1983. Timing of parturition of black bears (*Ursus americanus*) in northeastern Pennsylvania. Journal of Mammalogy 64:305-307.

Alt, G. L. 1984. Black bear cub mortality due to flooding of natal dens. Journal of Wildlife Management 48:1432-1434.

Alt, G. L. 1989. Reproductive biology of female black bears and early growth and development of cubs in northeastern Pennsylvania. Ph.D. Dissertation, West Virginia University, Morgantown. 111pp.

Amstrup, S. C., and J. J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. Journal of Wildlife Management 40:340-348.

Bailey, V. 1932. Mammals of New Mexico. North American Fauna 53:1-412.

Beck, T. D. I. 1991. Black bears of west-central Colorado. Colorado Division of Wildlife Technical Publication No. 39. 86pp.

Beck, T. D. I. 1995. Development of black bear inventory techniques. Colorado Division of Wildlife Federal Aid Progress Report W-153-R8. Fort Collins, CO, USA.

Beecham, J. J. 1983. Population characteristics of black bears in west central Idaho. Journal of Wildlife Management 47:405-412.

Beecham, J. J., D. G. Reynolds, and M. G. Hornocker. 1983. Black bear denning activities and den characteristics in west-central Idaho. International Conference on Bear Research and Management 5:79-86.

Beeman, L. E., and M. R. Pelton. 1976. Homing of black bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 3:87-95.

Beeman, L. E., and M. R. Pelton. 1980. Seasonal foods and feeding ecology of the black bears in the Smoky Mountains. International Conference on Bear Research and Management 4:141-147.

Boyce, M.S., and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268-272

Brown, D. E., editor. 1982. Biotic communities of the American Southwest – United States and Mexico. Desert Plants 4(1-4):1-342.

Brown, D. E. 1985. The grizzly in the Southwest. University of Oklahoma Press, Norman. 274pp.

Bunnell, F .L. and D. E. N. Tait. 1980. Bears in models and reality – implications to management. International Conference on Bear Research and Management 4:15-23.

Bunnell, F .L. and D. E. N. Tait. 1981. Population dynamics of bears – implications. Pages 75-98 *in* C.W. Fowler and T.D. Smith, eds. Dynamics of Large Mammal Populations. John Wiley & Sons, New York. 477pp.

Bunnell, F. L. and D. E. N. Tait. 1985. Mortality rates of North American bears. Arctic 38(4):316-323.

Bureau of Business and Economic Research. 1997. New Mexico Population Projections by the Bureau of Business and Economic Research. Released April 1997. University of New Mexico, Albuquerque, NM.

Carrera, J. A. 1993. Status report: Coahuila, Mexico. Pages 35-35 *in* J. A. Keay, editor. Proceeding of the Fourth Western Black Bear Workshop. U.S.D.I. Technical Report NPS/NRWR/NRTR-93/12.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons Ltd, Chichester, United Kingdom. 234 pp.

Clark, J. D., and K. G. Smith. 1994. A demographic comparison of two black bear populations in the interior highlands of Arkansas. Wildlife Society Bulletin 22:593-603.

Clark, J.D., J.E. Dunn, and K.G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57:519-526.

Comly-Gericke, L. M., and M. R. Vaughan. 1997. Survival and reproduction of translocated Virginia black bears. International Conference on Bear Research and Management 9:113-117.

Coy, P. L and D. L. Garshelis. 1992. Reconstructing reproductive histories of black bears from incremental layering in dental cementum. Canadian Journal of Zoology 70:2150-2160.

Craighead, F. C., and J. J. Craighead. 1972. Grizzly bear prehibernation and denning activities as determined by radiotracking. Wildlife Monographs 32:1-35.

Dice, L. R., and P. J. Clark. 1953. The statistical concept of home range as applied to the recapture radius of the deermouse (*Peromyscus*). Laboratory of Vertebrate Biology Contribution Number 62, University of Michigan, Ann Arbor.

Dick-Peddie, W. A. 1993. New Mexico vegetation past, present and future. University of New Mexico Press, Albuquerque. 244 pp.

Doan-Crider, D. L., and E. C. Hellgren. 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. Journal of Wildlife Management 60:398-407.

Eagle, T. C., and M. R. Pelton. 1983. Seasonal nutrition of black bears in the Great Smokey Mountains National Park. International Conference on Bear Research and Management 5:94-101.

Eberhardt, L.L. 1990. Survival rates required to sustain bear populations. Journal of Wildlife Management 54:587-590.

Eberhardt, L.L. and R.R. Knight. 1996. How many grizzlies in Yellowstone? Journal of Wildlife Management 60:416-421.

Eberhardt, L.L., B.M. Blanchard, and R.R. Knight. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Canadian Journal of Zoology 72:360-363.

Edwards, T. C., Jr., E. T. Deshler, D. Foster, and G. G. Moisen. 1996. Adequacy of wildlife habitat relation models for estimating spatial distributions of terrestrial vertebrates. Conservation Biology 10:263-270.

Eiler, J. H., W. G. Wathen, and M. R. Pelton. 1989. Reproduction in black bears in the southern Appalachian Mountains. Journal of Wildlife Management 53:353-360.

Elowe, K. D, and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962-968.

Erickson, A. W. 1964. An analysis of black bear kill statistics for Michigan. Michigan State University Research Bulletin 4:68-102.

Erickson, A. W., and W. G. Youatt. 1961. Seasonal variations in the hematology and physiology of black bears. Journal of Mammalogy 41:198-203.

Ewer, R.F. 1973. The carnivores. Cornell University Press, Ithaca, New York, 494 pp.

Folk, G. E., Jr., A. Larson, and M. A. Folk. 1976. Physiology of hibernating bears. International Conference on Bear Research and Management 3:373-380.

Free, S. L., and E. McCaffrey. 1972. Reproductive synchrony in the female black bear. International Conference on Bear Research and Management 2:199-206.

Garshelis, D. L. 1991. Monitoring effects of harvest on black bear populations in North America: a review and evaluation of techniques. Proceedings of the Eastern Workshop on Black Bear Research and Management 10:120-144.

Garshelis, D. L. 1992. Mark-recapture density estimation for animals with large home ranges. Pages 1098-1111 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001:populations. Elsevier Applied Science, London, UK.

Garshelis, D. L., and M. R. Pelton. 1981. Movements of black bears in the Great Smoky Mountains National Park. Journal of Wildlife Management 45:912-925.

Garshelis, D. L., K. V. Noyce, and P. L. Coy. 1998. Calculating average age of first reproduction free of the biases prevalent in bear studies. Ursus 10:437-447.

Gibeau, M. L., and P. C. Paquet. 1991. Evaluation of telazol for immobilization of black bears. Wildlife Society Bulletin 19:400-402.

Goldman, D., P. R. Giri, and S. J. O'Brien. 1989. Molecular genetic-distance estimates among the Ursidae as indicated by one- and two-dimensional protein electrophoresis. Evolution 43:282-295.

Graber, D. M., and M. White. 1983. Black bear food habits in Yosemite National Park. International Conference on Bear Research and Management 5:1-10.

Graves, W. C. 1980. Annual oak mast yield from visual estimates. Pages 270-274 *in* Proceedings of the Symposium on the Ecology, Management, and Utilization of California Oaks. U.S. Department of Agriculture Forest Service General Technical Report PSW-44.

Grenfell, W. E., and J. J. Brody. 1983. Black bear habitat use in Tahoe National Forest, California. International Conference on Bear Research and Management 6:65-72.

Grogan, R. G., and F. G. Lindzey. 1999. Estimating population size of a low-density black bear population using capture-resight. Ursus 11:117-122.

Harris, R. B., and L. H. Metzgar. 1987. Estimating harvest rates of bears from sex ratio changes. Journal of Wildlife Management 51: 802-811.

Harshyne, W. A., D. R. Diefenbach, G. L. Alt, and G. M. Matson. 1998. Analysis of error from cementum-annuli age estimates of known-age Pennsylvania black bears. Journal of Wildlife Management 62:1281-1291.

Hastings, B. C., B. K. Gilbert, and D. L. Turner. 1989. Effect of bears eating camper's food on human-bear interactions. Pages 15-18 *in* M. Bromley, ed. Bear-people Conflicts: Proceedings of a Symposium on Management Strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

Hatler, D.F. 1972. Food habits of black bears in interior Alaska. Canadian Field Naturalist 86:17-31.

Hayes, S. G., and M. R. Pelton. 1994. Habitat characteristics of female black bear dens in northwestern Arkansas. International Conference on Bear Research and Management 9:411-418.

Hellgren, E. C. 1998. Physiology of hibernation in bears. Ursus 10:467-477.

Hellgren, E. C., and M. R. Vaughan. 1987. Home range and movements of winter-active black bears in the Great Dismal Swamp of Virginia and North Carolina. International Conference on Bear Research and Management 7:227-234.

Hellgren, E. C., D.W. Carney, N.P. Garner, and M.R. Vaughan. 1988. Use of breakaway cotton spacers on radio-collars. Wildlife Society Bulletin 16:216-218.

Hellgren, E. C., M. R. Vaughan, F. C. Gwazdauskas, B. Williams, P. F. Scanlon, and R. L. Kirkpatrick. 1991. Endocrine and electrophoretic profiles during pregnancy and nonpregnancy in captive female black bears. Canadian Journal of Zoology 69:892-898.

Herrero, S. 1989. The role of learning in some fatal grizzly bear attacks on people. Pages 9-14 *in* M. Bromley, ed. Bear-people Conflicts: Proceedings of a Symposium on Management Strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

Hock, R.J. 1960. Seasonal variation in physiological functions of arctic ground squirrels and black bears. Pages 155-171 *in* C.P. Lyman and A.R. Dawe, editors. Mammalian hibernation I. Harvard University Press, Cambridge, Massachusetts.

Horino, S, M, and S. Miura 2000. Population viability analysis of a Japanese black bear population. Population Ecology 42: 37-44.

Hugie, R. D. 1982. Black bear ecology and management in the northern conifer-deciduous forests of Maine. Ph.D. Dissertation, University of Montana, Missoula. 203 pp.

Irwin, L. L., and F. M. Hammond. 1985. Managing black bear habitats for food items in Wyoming. Wildlife Society Bulletin 13:477-483.

Johnson, K. G., and M. R. Pelton. 1980a. Prebaiting and snaring techniques for black bears. Wildlife Society Bulletin 8:46-54.

Johnson, K. G., and M. R. Pelton. 1980b. Environmental relationships and the denning period of black bears in Tennessee. Journal of Mammalogy 61:653-660.

Johnson, K. G., and M. R. Pelton. 1981. Selection and availability of dens for black bears in Tennessee. Journal of Wildlife Management 45:111-119.

Johnson, K. G., D. O. Johnson, and M. R. Pelton. 1978. Simulation of winter heat loss for a black bear in a closed tree den. Proceedings of the Eastern Workshop on Black Bear Management and Research 4:155-166.

Jones, D. 1991. Philmont bear project – final report. New Mexico Department of Game and Fish, Santa Fe. 11pp.

Jonkel, J. J. 1993. A manual for handling bears for managers and researchers. Office of Grizzly Bear Recovery, U. S. Fish and Wildlife Service, Missoula, Montana, USA. 175pp.

Jonkel, C. J., and I. McT. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monograph 27. 57pp.

Kasworm, W. F., and T. J. Thier. 1994. Adult black bear reproduction, survival, and mortality sources in northwest Montana. International Conference on Bear Research and Management 9:223-230.

Kliskey, A.D., E.C. Lofroth, W.A. Thompson, S. Brown, and. H. Schreier. 1999. Simulating and evaluating alternative resource-use strategies using GIS-based habitat suitability indices. Landscape and Urban Planning 45: 163-175

Knight, R.R. and L.L. Eberhardt. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:323-334.

Kolenosky, G. B. 1990. Reproductive biology of black bears in east-central Ontario. International Conference on Bear Research and Management 8:385-392.

Kolenosky, G. B., and S. M. Strathearn. 1987. Winter denning of black bears in east-central Ontario. International Conference on Bear Research and Management 7:305-316.

LeCount, A. L. 1980. Some aspects of black bear ecology in the Arizona chaparral. International Conference on Bear Research and Management 4:175-179.

LeCount, A. L. 1982. Characteristics of a central Arizona black bear population. Journal of Wildlife Management 46:861-868.

LeCount, A. L. 1983. Evidence of wild black bears breeding while raising cubs. Journal of Wildlife Management 47:264-268.

LeCount, A. L. 1987. Characteristics of a northern Arizona black bear population - a final report. Arizona Game and Fish Department. 26pp.

LeCount, A. L. 1990. Characteristics of an east-central Arizona black bear population. Arizona Game and Fish Department Technical Report No. 2. 26pp.

LeCount, A. L., and J. C. Yarchin. 1990. Black bear habitat use in east-central Arizona. Arizona Game and Fish Department Technical Report Number 4. 42pp.

Lee, L. 1967. Bears in New Mexico wildlife management. New Mexico Department of Game and Fish, Santa Fe. 250pp.

Lindzey, F. G. 1981. Denning dates and hunting seasons for black bears. Wildlife Society Bulletin 9:212-216.

Lindzey, F. G., and E. C. Meslow. 1976. Winter dormancy in black bears in southwestern Washington. Journal of Wildlife Management 40:408-415.

Lindzey, F. G., and E. C. Meslow. 1977a. Home range and habitat use by black bears in southwestern Washington. Journal of Wildlife Management 41:413-425.

Lindzey, F. G., and E. C. Meslow. 1977b. Population characteristics of black bears on an island in Washington. Journal of Wildlife Management 41:408-412.

MacHutchon, A. G. 1989. Spring and summer food habits of black bears in the Pelly River Valley, Yukon. Northwest Science 63:116-118.

McArthur, K. L. 1981. Factors contributing to effectiveness of black bear transplants. Journal of Wildlife Management 45:102-110.

McDonald, J. E., D. P. Fuller, J. E. Cardoza, and T. K. Fuller. 1994. Influence of hunter effort and food abundance on Massachusetts black bear harvest. Eastern Workshop on Black Bear Research and Management 12:159.

McLaughlin, C.R. 1998. Modeling effects of food and harvests on female black bear populations. Ph.D. Dissertation, University of Maine, Orono. 263pp.

McLaughlin C. R., G. J. Matula Jr., R. A. Cross, W. H. Halteman, M. A. Caron, and K. I Morris. 1990. Precision and accuracy of estimating age of Maine black bears by cementum annuli. International Conference on Bear Research and Management 8:415-419.

McLaughlin, C. R., G. J. Matula, Jr., and R. J. O’Connor. 1994. Synchronous reproduction by Maine black bears. International Conference on Bear Research and Management 9:471-479.

McLellan, B., and D. C. Reiner. 1994. A review of bear evolution. International Conference on Bear Research and Management 9:85-96.

Merrill, T., D.J. Mattson, R.G. Wright, and H.B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears *Ursus arctos* in Idaho. Biological Conservation 87:231-248.

Miller, S. 1990. Population management of bears in North America. International Conference on Bear Research and Management 8:357-373.

Miller, S. D. 1994. Black bear reproduction and cub survivorship in south-central Alaska. International Conference on Bear Research and Management 9:263-273.

Miller, S. D. and S. M. Miller. 1988. Interpretation of bear harvest data. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration Project W-22-6, Job 4.18R. 65pp.

Miller, S. D., E. F. Becker, and W. B. Ballard. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. International Conference on Bear Research and Management 7:23-35.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223-249.

Nelson, R. A. 1980. Protein and fat metabolism in hibernating bears. Federation Proceedings 39: 2955-2958.

Nelson, R. A., and T. D. Beck. 1984. Hibernation adaptation in the black bear: implication for management. Proceedings of the Eastern Workshop on Black Bear Management and Research 7:48-53.

Nelson, R. A., H. W. Wahner, J. D. Jones, R. D. Ellefson, and P. E. Zollman. 1973. Metabolism of bears before, during, and after winter sleep. American Journal of Physiology 224:491-496.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541-545.

New Mexico Department of Game and Fish. 1926. Report for the fiscal years 1925-1926. New Mexico Department of Game and Fish, Santa Fe.

Noyce, K. V., and D. L. Garshelis. 1994. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. International Conference on Bear Research and Management 9:481-496.

Noyce, K. V., and D. L. Garshelis. 1997. Influence of natural food abundance on black bear harvest in Minnesota. Journal of Wildlife Management 61:1067-1074.

Oli, M. K., H. A. Jacobson, and B. D. Leopold. 1997. Denning ecology of black bears in the White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 61:700-706.

O'Neill, R.V., B.T. Milne, M.G. Turner, and R.H. Gardner. 1988. Resource utilization scales and landscape pattern. Landscape Ecology 2:63-69.

O'Pezio, J., S. H. Clarke, and C. Hackford. 1983. Chronology of black bear denning in the Catskill region of New York. International Conference on Bear Research and Management 5:87-94.

Pelton, M. R. 1982. Black bear (*Ursus americanus*). Pages 504-514 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America: biology, management, and economics. The Johns Hopkins University Press, Baltimore, Maryland.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.

Raine, R. M., and J. L. Kansas. 1990. Black bear food habits and distribution by elevation in Banff National Park, Alberta. International Conference on Bear Research and Management 8:297-304.

Reynolds, D. G., and J. J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. International Conference on Bear Research and Management 4:181-190.

Rogers, L. L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Transactions of the North American Wildlife and Natural Resources Conference 41:431-438.

Rogers, L. L. 1977. Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. Ph.D. Dissertation, University of Minnesota, Minneapolis. 194 pp.

Rogers, L. L. 1986. Homing by radio-collared black bears, *Ursus americanus*, in Minnesota. Canadian Field-Naturalist 100:350-353.

Rogers, L. L. 1987. Effect of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 97:1-72.

Rogers, L. L., and L. D. Mech. 1981. Interactions of wolves and black bears in northeastern Minnesota. Journal of Mammalogy 62:434-436.

Samson, C., and J. Huot. 1995. Reproductive biology of female black bears in relation to body mass in early winter. Journal of Mammalogy 6:68-77.

Sauer, P. R., S. Free, and S. Browne. 1966. Age determination in black bears from canine tooth sections. New York Fish and Game Journal 13:125-139.

Sauer, P. R., S. L. Free, and S. D. Browne. 1969. Movement of tagged black bears in the Adirondacks. New York Fish and Game Journal 16:205-223.

Schooley, R. L., C. R. McLaughlin, G. J. Matula, Jr., and W. B. Krohn. 1994. Denning chronology of female black bears: effects of food, weather, and reproduction. Journal of Mammalogy 75:466-477.

Schwartz, C. C., and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monograph 113. 58pp.

Schwartz, C. C., S. D. Miller, and W. W. Franzmann. 1987. Denning ecology of three black bear populations in Alaska. International Conference on Bear Research and Management 7:281-291.

Scott, J.M., F. Davis, B. Csuti, R. Noss, B.C. Butterfield, C. Groves, H. Anderson, S. Caicco , F. D’Erchia, T.C. Edwards, Jr. J. Ullman, and R.G. Wright. 1993. Gap: Analysis: A geographic approach to protection of biodiversity. Wildlife Monographs 123:1-41.

Scott, J. M., T. H. Tear, and F. W. Davis. 1996. Gap analysis – A landscape approach to biodiversity planning. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland. 320 pp.

Servheen, C. 1989. The status and conservation of bears of the world. International Conference on Bear Research and Management Monograph Series Number 2. 32pp.

Shields, G. F., and T. D. Kocher. 1991. Phylogenetic relationships of North American ursids based on analysis of mitochondrial DNA. Evolution 45:218-221.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, U. K., 175pp.

Smith, M. E., J. L. Hetchel, and E. H. Follman. 1994. Black bear denning ecology in interior Alaska. International Conference on Bear Research and Management 9:513-522.

Smith, T. R., and M. R. Pelton. 1990. Home range and movements of black bears in a bottomland hardwood forest in Arkansas. International Conference on Bear Research and Management 8:213-218.

Stirling, I., and A. E. Derocher. 1989. Factors affecting the evolution and behavioral ecology of the modern bears. International Conference on Bear Research and Management 8:189-204.

Stoneberg, R.P., and C.J. Jonkel. 1966. Age determination of black bears by cementum layers. Journal of Wildlife Management 30:411-414.

Taylor, M., F. Bunnell, D. DeMaster, R. Schweinsburg, and J. Smith. 1987. ANURSUS: a population analysis system for polar bears (*Ursus maritimus*). International Conference on Bear Research and Management 7:117-125.

Thompson, B. C., P. J. Crist, J. S. Prior-Magee, R. A. Deitner, D. L. Garber, and M. A. Hughes. 1996. Gap analysis of biological diversity conservation in New Mexico using geographic information systems. Research completion report, New Mexico Cooperative Fish and Wildlife Research Unit, Las Cruces. 93 pp. + 21 app.

Thorkleson, J., and R.K. Maxwell. 1974. Design and testing of a heat transfer model of a raccoon (*Procyon lotor*) in a closed tree den. Ecology 55:29-39.

Tietje, W. D., and R. L. Ruff. 1980. Denning behavior of black bears in boreal forest of Alberta. Journal of Wildlife Management 44:858-870.

Troyer, W. A. 1961. The brown bear harvest in relation to management on the Kodiak Islands. Transactions of the North American Wildlife and Natural Resources Conference 26:460-467.

Van Manan, F.T., and M.R. Pelton. 1997. A GIS model to predict black bear habitat use. Journal of Forestry 95(8): 6-12.

Warburton, G. S., and R. A. Powell. 1985. Movements of black bears on the Pisgah National Forest. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 39:351-361.

Weaver, K. M., and M. R. Pelton. 1994. Denning ecology of black bears in the Tensas River Basin of Louisiana. International Conference on Bear Research and Management 9:427-433.

Weigand, T., J. Naves, T. Stephan, and A. Fernandez. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. Ecological Applications 68:539-570.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Willey, C. H. 1974. Aging black bears from first premolar tooth sections. Journal of Wildlife Management 38:97-100.

Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66:13-21.

Wilson, K. R., and D. R. Anderson. 1985. Evaluation of a density estimator based on a trapping web and distance sampling theory. Ecology 66:1185-1194.

Wimsatt, W. A. 1963. Delayed implantation in the Ursidae, with particular reference to the black bear, *Ursus americanus*. Pages 69-77 *in* A. C. Enders, editor. Delayed implantation. University of Chicago Press, Chicago, Illinois.

Wooding, J. B., and T. S. Hardisky. 1994. Home range, habitat use, and mortality of black bears in north-central Florida. International Conference on Bear Research and Management 9:349-356.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Zager, P., and J. Beecham. 1982. New Mexico black bear studies, report for contract number 516-7-28. New Mexico Department of Game and Fish, Santa Fe. 174pp.

APPENDICES

This section contains and references a variety of more lengthy context information regarding the black bear investigation in New Mexico. This section also identifies information in various digital formats and indicates how that information is delivered in final form.

In some cases, digital information are on CDs that reside with New Mexico Department of Game and Fish and U.S. Fish and Wildlife Service Division of Federal Aid. CDs are not provided with every copy of the final report that is printed and distributed.

APPENDIX A: BEAR HANDLING HISTORY, DENNING DATES, AND LOCATION DATA

This appendix represents a tabulation of field data regarding capture and handling histories of individual study bears (StudyBearHistory), den entry and emergence data (DenningDates), and bear locations derived from telemetry monitoring (BearLocations). This appendix is 3 extensive Excel spreadsheets with metadata that are included as data files on a CD-ROM deposited with NMDGF and USFWS as part of the electronic deliverables. A brief example of the file formats for each of the 3 files follows:

StudyBearHistory file format

Age Class	Age	Date	Event	Transmitter Status	Reproductive Status
SA	4	9/24/1992	Capture	New collar	
SA	4	9/26/1992		Shed collar	
SA	3	9/1/1992	Began monitoring	Collar OK	
SA	4	1/13/1993	Handled in den	New collar	No offspring
AD	5	3/22/1994	Observed in den	Collar OK	No offspring
AD	6	3/27/1995	Handled in den	New collar	2 cubs (F690, F691)
AD	7	2/19/1996	Handled in den	Collar OK	1 yearling (F691)
AD	8	3/23/1997	Handled in den	New collar	2 cubs (M284, F674)
AD	9	3/22/1998	Observed in den (inaccessible)	Collar fit unknown	2 yearlings (M284, F674)
AD	9	8/20/1998	Recapture	Collar OK	
AD	10	3/22/1999	Handled in den	New collar	2 cubs (F656, F657)
AD	11	2/18/2000	Handled in den	Removed collar	2 yearlings (F656, F657)
AD	8	9/1/1992	Began monitoring	Collar OK	
AD	9	3/11/1993	Handled in den	New collar	2 cubs (F513, F601)
AD	10	2/7/1994	Handled in den	Collar OK	1 yearling (F513)
AD	10	6/9/1994	Recapture	Collar OK	
AD	10	9/17/1994	Mortality (hunter kill)	Collar OK	
AD	8	9/1/1992	Began monitoring	Collar OK	
AD	9	3/13/1993	Handled in den	New collar	1 cub (M201)
AD	10	2/5/1994	Observed in den	Collar OK	1 yearling (M201)
AD	11	3/17/1995	Handled in den	New collar	2 cubs (M296, M297)
AD	12	2/20/1996	Handled in den	Collar OK	1 yearling (M296)
AD	12	9/2/1996	Mortality (hunter kill)	Collar OK	
AD	10	9/1/1992	Began monitoring	Collar OK	
AD	11	3/15/1993	Handled in den	New collar	3 cubs (M135, M136, F514)
AD	12	2/9/1994	Handled in den	Collar OK	3 yearlings (M135, M136, F514)
AD	13	3/23/1995	Handled in den	New collar	3 cubs (M295, F692, F693)
AD	13	5/12/1995	Mortality (possibly killed by bear)	Collar OK	
SA	3	9/1/1992	Began monitoring	Collar OK	

DenningDates file format

BEAR	YEAR	AREA	SEX	MAXACT	MINDEN	ENTRY DATE	DAYS1	MAXDEN	MINACT	EMERGE DATE	DAYS2	TDAYS
F502	1993	NSA	F	10/26/1992	11/6/1992	11/1/1992	11	4/12/1993	4/21/1993	4/17/1993	9	166
F502	1994	NSA	F	11/4/1993	11/9/1993	11/7/1993	5	3/24/1994	4/7/1994	4/1/1994	14	145
F502	1996	NSA	F					4/26/1996	5/5/1996	5/1/1996	9	
F502	1997	NSA	F	10/31/1996	11/11/1996	11/6/1996	11	4/27/1997	5/10/1997	5/4/1997	13	178
F502	1998	NSA	F					4/30/1998	5/9/1998	5/5/1998	9	
F502	2000	NSA	F	10/14/1999	10/21/1999	10/18/1999	7					
F503	1993	NSA	F	10/14/1992	10/26/1992	10/21/1992	12	4/5/1993	4/12/1993	4/9/1993	7	169
F503	1994	NSA	F	11/4/1993	11/9/1993	11/7/1993	5	4/18/1994	5/2/1994	4/26/1994	14	170
F504	1993	NSA	F	10/14/1992	10/26/1992	10/21/1992	12	4/30/1993	5/14/1993	5/8/1993	14	198
F504	1994	NSA	F	10/15/1993	10/22/1993	10/19/1993	7	5/2/1994	5/13/1994	5/8/1994	11	201
F504	1995	NSA	F	10/14/1994	10/28/1994	10/22/1994	14					
F504	1996	NSA	F					4/26/1996	5/5/1996	5/1/1996	9	
F505	1994	NSA	F	10/8/1993	10/15/1993	10/12/1993	7	4/7/1994	4/18/1994	4/13/1994	11	183
F506	1993	NSA	F					5/24/1993	6/2/1993	5/29/1993	9	
F506	1994	NSA	F	11/4/1993	11/9/1993	11/7/1993	5	3/24/1994	4/7/1994	4/1/1994	14	145
F506	1995	NSA	F	10/14/1994	10/28/1994	10/22/1994	14					
F506	1996	NSA	F	11/7/1995	11/14/1995	11/11/1995	7	5/5/1996	5/12/1996	5/9/1996	7	180
F506	1997	NSA	F	10/24/1996	11/2/1996	10/29/1996	9					
F506	1998	NSA	F					5/9/1998	5/28/1998	5/19/1998	19	
F510	1994	NSA	F	11/9/1993	11/18/1993	11/14/1993	9	4/18/1994	5/2/1994	4/26/1994	14	163
F510	1995	NSA	F	10/14/1994	10/28/1994	10/22/1994	14					
F510	1996	NSA	F	11/7/1995	11/14/1995	11/11/1995	7	5/5/1996	5/12/1996	5/9/1996	7	180
F510	1997	NSA	F	10/10/1996	10/24/1996	10/18/1996	14	5/28/1997	6/12/1997	6/5/1997	15	229
F510	1998	NSA	F					4/30/1998	5/9/1998	5/5/1998	9	
F511	1994	NSA	F					4/18/1994	5/2/1994	4/26/1994	14	
F512	1994	NSA	F	10/15/1993	10/22/1993	10/19/1993	7	5/13/1994	5/31/1994	5/23/1994	18	216
F512	1995	NSA	F	10/14/1994	10/28/1994	10/22/1994	14	5/4/1995	5/20/1995	5/13/1995	16	203
F512	1996	NSA	F	11/7/1995	11/19/1995	11/14/1995	12	5/5/1996	5/12/1996	5/9/1996	7	177
F512	1997	NSA	F					4/27/1997	5/10/1997	5/4/1997	13	
F516	1995	NSA	F	11/4/1994	11/10/1994	11/8/1994	6					
F516	1996	NSA	F					4/26/1996	5/5/1996	5/1/1996	9	
F516	1998	NSA	F					5/9/1998	5/28/1998	5/19/1998	19	
F516	1999	NSA	F					5/6/1999	5/22/1999	5/15/1999	16	
F516	2000	NSA	F	10/14/1999	10/21/1999	10/18/1999	7					
F517	1995	NSA	F					5/4/1995	5/20/1995	5/13/1995	16	
F517	1996	NSA	F	11/7/1995	11/14/1995	11/11/1995	7	4/26/1996	5/5/1996	5/1/1996	9	172
F517	1997	NSA	F					5/10/1997	5/28/1997	5/20/1997	18	
F517	1998	NSA	F	11/17/1997	11/30/1997	11/24/1997	13	4/30/1998	5/9/1998	5/5/1998	9	162
F517	1999	NSA	F					5/13/1999	5/22/1999	5/18/1999	9	

BearLocations file format

AREA	BEAR	SEX	DATE	YEAR	AGE	AGECL	LANDMARK	EAST	NORTH	LOCSTAT
NSA	F502	F	10/2/1992	1992	3	SA	Atmore Ranch	488000	4048200	I
NSA	F502	F	10/26/1992	1992	3	SA	Colin Neblett	486400	4047400	A
NSA	F502	F	1/1/1993	1993	4	SA		488200	4049900	DV1
NSA	F502	F	2/1/1993	1993	4	SA	Maxwell Camp	486300	4050600	D2
NSA	F502	F	4/21/1993	1993	4	SA	Colin Neblett	486300	4047500	A
NSA	F502	F	4/30/1993	1993	4	SA	Maxwell Camp	486200	4051100	A
NSA	F502	F	5/14/1993	1993	4	SA	Maxwell Camp	486200	4051100	A
NSA	F502	F	5/24/1993	1993	4	SA	California Creek	486600	4049400	A
NSA	F502	F	6/2/1993	1993	4	SA	W Atmore Ranch	486700	4049300	A
NSA	F502	F	6/8/1993	1993	4	SA	Maxwell Camp	485700	4050200	A
NSA	F502	F	6/15/1993	1993	4	SA	Maxwell Camp	486000	4050700	A
NSA	F502	F	6/23/1993	1993	4	SA	California Creek	487200	4047800	A
NSA	F502	F	6/30/1993	1993	4	SA	W Atmore HQ	487400	4048900	A
NSA	F502	F	7/9/1993	1993	4	SA	Atmore HQ	489100	4049200	A
NSA	F502	F	7/19/1993	1993	4	SA	Atmore HQ	486100	4049000	A
NSA	F502	F	7/29/1993	1993	4	SA	Maxwell Camp	485100	4049800	A
NSA	F502	F	8/5/1993	1993	4	SA	W of Atmore	485600	4049100	A
NSA	F502	F	8/24/1993	1993	4	SA	Maxwell Camp	486500	4050200	A
NSA	F502	F	9/1/1993	1993	4	SA	N Dean Canyon	504200	4045800	A
NSA	F502	F	9/16/1993	1993	4	SA	S Horseshoe Canyon	504200	4048700	A
NSA	F502	F	9/21/1993	1993	4	SA	Chase Canyon	505500	4048400	A
NSA	F502	F	10/1/1993	1993	4	SA	W Atmore HQ	487400	4049200	I
NSA	F502	F	10/8/1993	1993	4	SA	Chase Canyon	504900	4048500	A
NSA	F502	F	10/15/1993	1993	4	SA	W Johns Pond	487900	4047400	A
NSA	F502	F	10/22/1993	1993	4	SA	E Ute Creek Ranch	492100	4047700	A
NSA	F502	F	11/4/1993	1993	4	SA	E Ute Creek Ranch	491100	4049600	A
NSA	F502	F	1/1/1994	1994	5	AD		491900	4048300	DV
NSA	F502	F	4/7/1994	1994	5	AD	NE Ute Creek Ranch	491300	4048700	A
NSA	F502	F	4/18/1994	1994	5	AD	W Santa Claus Camp	491100	4049800	A
NSA	F502	F	5/2/1994	1994	5	AD	W Johns Pond	488100	4047900	A
NSA	F502	F	5/13/1994	1994	5	AD	E Ute Creek	487100	4051100	A
NSA	F502	F	5/25/1994	1994	5	AD	W Atmore HQ	486600	4048800	A
NSA	F502	F	5/31/1994	1994	5	AD	Ute Creek	487300	4049600	A
NSA	F502	F	6/17/1994	1994	5	AD	California Creek	487700	4047600	A
NSA	F502	F	6/30/1994	1994	5	AD	S California Creek	485500	4046300	A
NSA	F502	F	7/11/1994	1994	5	AD	N California Creek	487100	4047900	A
NSA	F502	F	7/29/1994	1994	5	AD	TMN Mountain	485400	4049200	A
NSA	F502	F	8/18/1994	1994	5	AD	N California Creek	488500	4047800	A
NSA	F502	F	8/26/1994	1994	5	AD	Johns Pond	488700	4047800	A

APPENDIX B. GIS AND DATA FILE LISTING AND METADATA

This is an index to the GIS coverages and data files that have been compiled for use in the bear project. The metadata for these files consists of the listing in this appendix and metadata records included with the GIS coverages or individual files identified. Metadata for GIS coverages are designed to meet Federal Geographic Data Committee standards and format. The data and metadata are available on a CD-ROM on file with NMDGF and USFWS as part of final electronic deliverables. The following table describes the directory and file structure for accessing coverages and data files.

Folder	Description	Files	File Description	FGDC Metadata Record
ArcView	ArcView projects and files			
		Model2.apr	Programming for habitat model	
		bearfigs.apr	Arc/View programming for Chapter 11 figures	
		studysites.apr	Arc/View programming for study site figures	
		fig11-x.wmf	Chapter 121 figures	

Residents	Census data			
		blk00.dbf	2000 Census block Boundaries	..\Residents\blk00.htm
		grp00.mdb	2000 Census Block-Group boundaries	..\Residents\grp00.htm
		tract00.dbf	2000 Census Tract Boundaries	..\Residents\tract00.htm
		PlaceNames.shp	Names and locations of physical and cultural geographic features located within New Mexico.	..\Residents\PlaceNames.htm
		distopop	Distance (m) to nearest human population center	..\Residents\distopop.htm
		Census2000	Tables associated with 2000 census and population projections by county	
HabitatModel	Files associated with bear habitat model.			
		statemodel2	Predicted habitat suitability for Black bear.	..\HabitatModel\statemodel2.htm
		Range2	Predicted extent (range) of black bear occurrence	..\HabitatModel\Range2

		vegattr.dbf	Habitat and Mast scores by Land cover classification	
		popcodes.dbf	Description of black bear range assignments	
HuntingFishing	Files associated with hunter and fisherman use statistics and areas of use.			
		HuntingAnglingEffort.mdb	Access files containing hunter use data by game management unit, or antelope management unit, angler survey data, and New Mexico fishing waters data. Also contains a file with metadata.	
		amu.shp	Shapefile showing boundaries of New Mexico Game and Fish antelope management units for use with antelope harvest survey data.	..\HuntingFishing\amu.htm
		fishingwaters.shp	Shapefile coverage of waters in New Mexico used by fishermen, for use with angler survey data.	..\HuntingFishing\fishingwaters.htm
		gmu98.shp	Shapefile showing boundaries of New Mexico Game and Fish game management units, for use with harvest survey data.	..\HuntingFishing\gmu98.htm
		beartag	Pont locations of bear kills in New Mexico	..\HuntingFishing\beartag.htm
Landcover	Land cover coverage			
		gaplandcover	GAP landcover file.	..\landcover\gaplandcover.htm
Metadata	Metadata for bear project			
		BearPrjMetadata.xls	This file, excel file containing bear project index and metadata.	
		citation.dbf	Citations used in metadata.	
		contact.dbf	Table of contacts used in	

			metadata.	
Ownership	Stewardship of New Mexico lands			
		PLSS	Shape file depicting stewardship of lands in New Mexico	..\landownership\PLSS.htm
Roads	Files with road locations			
		AllRoads.shp	Shapefile roads coverage containing major and minor New Mexico roads.	..\Roads\AllRoads.htm
		cfccodes.xls	Excel file explaining codes used in allroads coverage.	
		nmroads.shp	Shapefile containing major roads in New Mexico	..\Roads\nmroads.htm
		distord	Distance to nearest secondary road	..\Roads\distord.htm
		rddens7k	Total Length of road within 7k radius (female activity radius)	..\Roads\rddens7k.htm
		rddens12k	Total length of road within 12k radius (male fall activity radius)	..\Roads\rddens12k.htm
StudyData	Files specific to bear project			
		nsabounds.shp	Shapefile showing boundary of northern study area.	..\StudyData\nsabounds.htm
		nsabuff.shp	Shapefile showing buffer around northern study area.	..\StudyData\nsabuff.htm
		nsadem	Digital elevation model for northern study area.	..\StudyData\nsadem.htm
		nsahillshade	Hillshade file for use with northern study area digital elevation model.	..\StudyData\nsahillshade.htm
		ssabounds.shp	Shapefile showing boundaries of southern study area.	..\StudyData\ssabounds.htm
		ssabuff.shp	Shapefile showing buffer around southern study area.	..\StudyData\ssabuff.htm
		ssadem	Digital elevation model for southern study area.	..\StudyData\ssadem.htm
		ssahillshade	Hillshade file for use with southern study area digital	..\StudyData\ssahillshade.htm

			elevation model.	
		DenningDates	Den Entry and Emergence Information	
		BearLocations	Geographic coordinates of bear locations by date	
		StudyBearHistory	Identity and status of bears captured and handled during project.	

APPENDIX C. HABITAT MODEL AND ASSOCIATED COVERAGES

This appendix contains GIS coverages and data files associated with the habitat model generated for black bears in New Mexico and related analyses in context with human interests and population on the landscape.

The files are located on a CD-ROM and are also identified in Appendix B for file reference and metadata access.

APPENDIX D. PELT TAG NOTEBOOK

This appendix contains a year by year summary of pelt tag and hunter card survey data as they pertain to demographic modeling and simulation. This information was compiled by Katherine Green-Hammond. The appendix is included as digital files on a CD-ROM on file with NMDGF and USFWS as a final electronic deliverable.

See the following pages for an example of the Notebook format

CHANGES BEGINNING IN THE 1998 VERSION

The Central mountain range region was split into the Zuni region (units 9 and 10) and the Manzano region (units 8 and 14). Unit 18 was dropped since it is closed to bear hunting.

Ages defining adults and subadults have been changed for all data summaries. Age 4 bears have been reclassified from adults to subadults consistent with the bear study finding that age 5 is the earliest age at which females give birth in New Mexico populations. Consequently, subadults are defined as bears ages 1 to 4, and adults are defined as bears ages 5 and above, for both sexes.

Most of the interpretive comments have been removed from this notebook. Interpretations will be revised in a future revision of the notebook.

CHANGES IN THIS VERSION

Card survey results from the 1997 season, and pelt tags from the 1998 season have been added; ages are not yet available for the 1998 season pelts.

1998 AND 1999 SEASON DIFFERENCES

Prior to 1998, fall hunting began September 1 or earlier. Both 1998 and 1999 fall hunts were late, beginning and ending later than in previous years.

For the 1998 hunting season, major regulation changes were made. The season dates were October 15 - December 15, a change from the previously standard September 1 - October 31. Also, for 1998 only, hunters could not buy bear licenses after the bear hunting season began. The total bear pelt tags reported for 1998 were 148, the lowest statewide total since pelt tag record keeping began in 1978. The numbers of 1998 hunt season licenses sold, 2969, was lower than all years since 1983 except for 1986 (when bear hunting was closed during elk hunting) and 1992 (when license fees doubled for nonresidents).

In 1999, hunting season dates were October 1 - December 15, and licenses could be purchased during the hunt season. Total pelts increased to 213.

WHAT PELT DATA SUGGEST ABOUT NM BEAR POPULATIONS

Bear populations have gradually increased statewide in the last 30 years. Very high harvests in 1994 and 1995, especially of females, probably interrupted the increasing trend.

The total harvest and, presumably, the hunting mortality rate on bears, were unusually high during 1989 - 1990 and 1993 -1996, possibly because dry environmental conditions increased vulnerability to hunting.

Total statewide harvest peaked in 1994, dropped steadily through 1998, and increased again in 1999. The very low harvest in 1998 can be attributed to the change to a late fall season and very low license sales.

The high numbers and proportions of adult females harvested in recent years may represent the beginning of a period of excessive harvesting, and should be watched.

IMPORTANCE OF HARVEST DATA

Information on bears is very hard to get. Harvest data provide the only information on bears statewide and over time.

Complete pelt tag data (mandatory reporting) substantially reduces the uncertainty about bear harvests, for a reasonable cost.

Tooth age data (one tooth from each pelt) is essential for identifying subadults. Identifying subadults allows pelt data to provide information on good and bad reproductive years, and allows more useful interpretation of changes in total pelt tag numbers.

The bear hunter card survey provides the only information on the geographic distribution of hunting effort and success.

CAUTIONS ABOUT CARD SURVEY DATA

Statewide bear card survey returns number in the hundreds, but there are very few responses reporting hunting or killing a bear in many of the individual game management units. Consequently projections by unit, which are summed for the regional numbers included in this notebook, may be based on unacceptably small sample sizes. The card survey provides the only available information on geographic distribution of hunting effort, so the unit analysis results have been used in spite of the sample size problem.

The projected total statewide bear kills from the card surveys are usually higher than reported pelt tags, sometimes substantially higher. This may be a consequence of higher return rates from successful than from unsuccessful hunters (we are in the process of testing this hypothesis). Because pelt tag reports are mandatory, the pelt tag numbers are considered to be a more reliable estimate of bear kills than the survey projections. Consequently, survey results are used only for estimates of number of hunters (hunting effort) in this notebook. Number of kills, either reported directly or used in calculations of success rate, are based on pelt tag reports.

TABLE 1. Bear pelt tag numbers over time, ranked by total pelts recorded from 1978 through 1997.

Unit	Total Pelts 1978 - 1997	Annual Average # Pelts 1978 - 1992	Annual Average # Pelts 1993 - 1997
16	662	28	48
6	598	25	45
55	575	32	20
34	558	23	43
45	349	14	27
36	308	13	23
15	274	13	15
48	229	10	16
4	228	9	18
54	203	8	15
51	192	7	17
57	186	6	18
14	184	7	15
49	178	7	13
21	177	10	7
22	146	6	10
23	120	4	11
37	117	6	5
24	115	5	8
53	113	5	6
17	112	6	6
5	107	4	8
44	105	4	8
10	97	3	11

REGION	Total Pelts 1978 - 1997	Annual Average # Pelts 1978 - 1992	Annual Average # Pelts 1993 - 1997
Sangre de Cristos	1996	90	129
Gila	1631	73	107
San Juan	1188	48	92
Southeast	989	42	72
Zuni + Manzanos	340	12	31
Statewide	6195	268	435

APPENDIX E. CD-ROM WITH BEAR POPULATION MODEL SOFTWARE, SCENARIO LIBRARY, AND USER MANUAL

This appendix consists of model software and other tools associated with preparation and use of the Bear Population Model as compiled by Katherine A. Green Hammond. The information in final form is a set of electronic files on CD-ROM on file with NMDGF Santa Fe state office and USFWS Division of Federal Aid in Albuquerque.

See the following pages for an example of the format of the User Manual.

This information also is on a CD-ROM distributed with selected copies of the completion report

APPENDIX F. BEAR POPULATION MODEL CORE EQUATIONS DOCUMENTATION

This appendix contains the mathematical background for the Bear Population Model. The appendix was compiled by Katherine Green-Hammond and is contained on a CD-ROM provided as a final electronic deliverable.

An example of the text of this documentation is presented on the following pages. It is presented in Times New Roman font to preserve the format as prepared in original form. The version on the CD must be accessed for full understanding and use.

BEAR MODEL CORE EQUATIONS

POPULATION / ENVIRONMENT / HUNT MODEL DESIGN

The bear model tracks changes in population numbers and age and sex composition over time based on computed births, deaths, and migrants. Initial population, characteristic vital rates, and annual variations in mast conditions, den entry timing, and hunting regulations and effort are inputs. An upper limit on population size is optional.

Parturition and cub survival rates vary annually, as a function of mast conditions. Characteristic or average mortality rates are specified for yearlings, subadults, and adults of both sexes. Rates from natural causes, legal hunting, and other human causes are specified separately and are additive. Legal hunting mortality can vary annually, with the characteristic rate modified by hunting effort or increased by poor mast conditions. Hunting mortality for late hunting seasons (beginning in October) is also a function of den entry timing.

Birth and mortality rates are not explicit functions of density dependence or social structure in this model. Optional upper limits on total population and total adult females approximate density dependence at high population levels. Since a hunted population is being modeled, natural mortality rates will be low and hunting mortality is additive rather than compensatory. If there is a need to model long time periods without hunting, natural mortality rates in the absence of hunting should be modified. Migration is treated as a net gain or loss of 3 year old (subadult) males, and is a function of the proportions of males and females in the prehunt population. Immigration occurs when the proportion of males is below a specified threshold. Migration occurs when the proportion of males exceeds a specified threshold.

The model should be applied to a geographic area that is meaningful to bears and managers, from a game management unit to a mountain range. Migration of subadults applies to the modeled area and its surroundings, not movements within the modeled area.

The model bear population structure tracks females and males separately in age classes of cubs, yearlings, subadults (2, 3, and 4 year olds are separate age classes), and all adults (ages 5 and up) lumped. The age structure allows the influence of strong and weak cohorts to be expressed over time, and tracking of recruitment to breeding age. No maximum age is imposed or tracked in simulations; long term average total annual mortality rates determine model population longevity.

The adult female category is divided into groups with cubs, with yearlings, and with no offspring in dens. The birth rate model includes the alternate year breeding pattern of black bears; adult females with yearlings in dens are not eligible to produce cubs. The phenomenon of synchronized breeding can be simulated by the model under appropriate conditions. Adult females with cubs in the fall are partially vulnerable to legal hunting.

The effectiveness of the regulation protecting females with cubs from hunting mortality is a variable.

The model biological year has 3 parts, denning, active season spring and summer, and active season fall. Births take place during denning. Natural and other human caused mortalities occur during both active seasons. Hunting mortality occurs only during the fall season in the current model version. A spring hunting season may be added in a later version.

CORE MODEL RELATIONSHIPS: CALCULATION ENGINE

Timing and Sequence of Events

The initial population is post hunt numbers by sex and age category at the time of den entry at the end of the fall active season. The bear model year is a calendar year and begins with the winter denning season.

For age tracking throughout a simulation run, all birthdays occur at the beginning of the year, in dens, but before births. Each model year, including the first, begins with age updating; cubs at den entry become yearlings, and adult females with cubs at den entry are reclassified as adult females with yearlings at the beginning of the simulation year, and are not eligible to produce cubs that year. Bears aged 1, 2, 3, and 4 the previous year become ages 2, 3, 4 and adult (all yearlings become subadults, some subadults become adults); adults aged 5+ remain adults. New age 5 females are classified as adult females with no offspring in the den, and are eligible to produce cubs. Adult females with yearlings at the end of the previous fall are reclassified as adult females with no offspring, and are eligible to produce cubs. Adult females with no offspring at the end of the previous fall remain adult females with no offspring, and are eligible to produce cubs.

At the beginning of the year, with updated ages, there are no adult females with cubs, and the male and female cub categories are empty. All births, but no mortalities, occur during the denning season. All mortalities, but no births, occur during the early and late active seasons.

Environmental variation

The environmental condition variables of mast index, hunt effort, hunt season start date (or hunt closure), and den entry timing are inputs which may change from year to year. All vital rates are simple functions of the environmental variables modifying an underlying rate treated as a population characteristic. Variation in the environmental variables results in variation of the vital rates.

Vital rates: Characteristic rates with variation

Parturition rates and cub survival rates have input characteristic values associated with poor, fair, and good mast conditions, as well as values for special cases and long term average values. Fall mast condition (or special case or average values) is an input which may vary by year, forcing parturition and cub survival to vary by year correspondingly. Functions of mast condition involve time lags; mast index for a year influences cub survival for the same year, and parturition rate for the next year. Mortality rates have characteristic values for each combination of age, sex, and cause, which are constant and specified as inputs. Variation in mortality rates from year to year is handled by multiplying the characteristic rates by factors which are functions of mast condition, hunt effort, hunt regulations, and den entry timing.

Notation for Representing Population Numbers

F0, F1, F2, F3, F4, AF	number of females of age 0 (cubs), 1, 2, 3, 4, adult
M0, M1, M2, M3, M4, AM	number of males of age 0 (cubs), 1, 2, 3, 4, adult
CUBS = F0 + M0	number of cubs
YF = F1, **YM** = M1	numbers of yearlings for each sex
SF = F2 + F3 + F4	number of subadult females
SM = M2 + M3 + M4	number of subadult males
AFnone	number of adult females without cubs or yearlings
AFcubs	number of adult females with cubs
AFyrl	number of adult females with yearlings

AF = AFnone + AFcubs + AFyrl

CONTINUED IN THE APPROPRIATE FILE ON THE CD

U.S. Fish and Wildlife Service

Estimating Black Bear Density in New Mexico Using Noninvasive Genetic Sampling Coupled with Spatially Explicit Capture-Recapture Methods

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Cooperator Science Series # 120-2016

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The Cooperator Science Series was initiated in 2013. Its purpose is to facilitate the archiving and retrieval of research project reports resulting primarily from investigations supported by the U.S. Fish and Wildlife Service (FWS), particularly the Wildlife and Sport Fish Restoration Program. The online format was selected to provide immediate access to science reports for FWS, state and tribal management agencies, the conservation community, and the public at large.

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Estimating Black Bear Density in New Mexico Using Noninvasive Genetic Sampling Coupled with Spatially Explicit Capture-Recapture Methods

Federal Aid in Wildlife Restoration Project W93 R56 2.0

Final Report to The New Mexico Department of Game and Fish

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EXECUTIVE SUMMARY

During the 2004–2005 to 2015–2016 hunting seasons, the New Mexico Department of Game and Fish (NMDGF) estimated black bear abundance (*Ursus americanus*) across the state by coupling density estimates with the distribution of primary habitat generated by Costello et al. (2001). These estimates have been used to set harvest limits. For example, a density of 17 bears/100 km^2 for the Sangre de Cristo and Sacramento Mountains and 13.2 bears/100 km^2 for the Sandia Mountains were used to set harvest levels. The advancement and widespread acceptance of non-invasive sampling and mark-recapture methods, prompted the NMDGF to collaborate with the New Mexico Cooperative Fish and Wildlife Research Unit and New Mexico State University to update their density estimates for black bear populations in select mountain ranges across the state.

We established 5 study areas in 3 mountain ranges: the northern (NSC; sampled in 2012) and southern Sangre de Cristo Mountains (SSC; sampled in 2013), the Sandia Mountains (Sandias; sampled in 2014), and the northern (NSacs) and southern Sacramento Mountains (SSacs; both sampled in 2014). We collected hair samples from black bears using two concurrent non-invasive sampling methods, hair traps and bear rubs. We used a gender marker and a suite of microsatellite loci to determine the individual identification of hair samples that were suitable for genetic analysis. We used these data to generate mark-recapture encounter histories for each bear and estimated density in a spatially explicit capture-recapture framework (SECR). We constructed a suite of SECR candidate models using sex, elevation, land cover type, and time to model heterogeneity in detection probability and the spatial scale over which detection probability declines. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank and select the most supported model from which we estimated density.

We set 554 hair traps, 117 bear rubs and collected 4,083 hair samples. We identified 725 (367 M, 358 F) individuals; the sex ratio for each study area was approximately equal. Our density estimates varied within and among mountain ranges with an estimated density of 21.86 bears/100 km^2 (95% CI: 17.83 – 26.80) for the NSC, 19.74 bears/100 km^2 (95% CI: 13.77 – 28.30) in the SSC, 25.75 bears/100 km^2 (95% CI: 13.22 – 50.14) in the Sandias, 21.86 bears/100 km^2 (95% CI: 17.83 – 26.80) in the NSacs, and 16.55 bears/100 km^2 (95% CI: 11.64 – 23.53) in the SSacs. Overall detection probability for hair traps and bear rubs, combined, was low across all study areas and ranged from 0.00001 to 0.02. We speculate that detection probabilities were affected by failure of some hair samples to produce a complete genotype due to UV degradation of DNA, and our inability to set and check some sampling devices due to wildfires in the SSC. Ultraviolet radiation levels are particularly high in New Mexico compared to other states where NGS methods have been used because New Mexico receives substantial amounts of sunshine, is relatively high in elevation (1,200 m – 4,000 m), and is at a lower latitude. Despite these sampling difficulties, we were able to produce density estimates for New Mexico black bear populations with levels of precision comparable to estimated black bear densities made elsewhere in the U.S.

Our ability to generate reliable black bear density estimates for 3 New Mexico mountain ranges is attributable to our use of a statistically robust study design and analytical method.

There are multiple factors that need to be considered when developing future SECR-based density estimation projects. First, the spatial extent of the population of interest and the smallest average home range size must be determined; these will dictate size of the trapping array and spacing necessary between hair traps. The number of technicians needed and access to the study areas will also influence configuration of the trapping array. We believe shorter sampling occasions could be implemented to reduce degradation of DNA due to UV radiation; this might help increase amplification rates and thereby increase both the number of unique individuals identified and the number of recaptures, improving the precision of the density estimates. A pilot study may be useful to determine the length of time hair samples can remain in the field prior to collection. In addition, researchers may consider setting hair traps and bear rubs in more shaded areas (e.g., north facing slopes) to help reduce exposure to UV radiation. To reduce the sampling interval it will be necessary to either hire more field personnel or decrease the number of hair traps per sampling session. Both of these will enhance detection of long-range movement events by individual bears, increase initial capture and recapture rates, and improve precision of the parameter estimates. We recognize that all studies are constrained by limited resources, however, increasing field personnel would also allow a larger study area to be sampled or enable higher trap density.

In conclusion, we estimated the density of black bears in 5 study areas within 3 mountains ranges of New Mexico. Our estimates will aid the NMDGF in setting sustainable harvest limits. Along with estimates of density, information on additional demographic rates (e.g., survival rates and reproduction) and the potential effects that climate change and future land use may have on the demography of black bears may also help inform management of black bears in New Mexico, and may be considered as future areas for research.

INTRODUCTION

Setting sustainable harvest limits for game species is one of the main duties of state wildlife management agencies. To this end, state agencies spend a large portion of their annual budget on population surveys to estimate abundance and population trends of game animals. Survey methodologies for large ungulates are well developed and can provide relatively robust estimates of common game species such as deer (*Odocoileus* spp.) and elk (*Cervus canadensis*). In contrast, estimating the abundance or density of large carnivores like American black bears (*Ursus americanus*), which are cryptic and occur at low densities is more difficult because their behavior makes the survey methods used for ungulates ineffective, e.g., assuming perfect detection probability (Miller 1990, Obbard et al. 2010). Historically, many state agencies set harvest limits for carnivores based on harvest data (Hristienko and McDonald 2007), including sex ratio and age structure of the harvested animals, which, along with other analytical approaches, can be used to infer harvest effects on a population (Garshelis 1990). Yet, hunter selectivity and sex-specific vulnerability may influence harvest composition (Miller 1990, Beston and Mace 2012). Thus, additional information provided by abundance and density estimates generated from robust statistical methods can aid in setting harvest limits for black bear populations.

New Mexico's most recent black bear density estimates were derived from a comprehensive, decade-long study on black bear ecology in the 1990s in which researchers estimated study area specific density using population reconstruction (Downing 1980), or backdating, to estimate the minimum population size during the study and then divided that estimate by the effective trapping area (ETA; Costello et al. 2001) to obtain a minimum density estimate. The ETA is an estimate of the actual area used by identified individuals to account for home ranges that straddle the study area boundary and may bias abundance estimates (Dice 1938, Wilson and Anderson 1985). Costello et al. (2001) estimated the ETA using the distribution of live-capture trap sites buffered by the mean activity radius of adult bears. Their minimum density estimate for the more northern, mesic, and presumably more productive Sangre de Cristo Mountains was 17.0 bears/100 km^2 (310 km^2 study area) while their estimate for the more southern, xeric, and presumably less productive Mogollon Mountains was 9.4 bears/100 km^2 (423 km^2 study area). It is important to note that backdating a population fails to account for undetected individuals or provide measures of uncertainty in estimates, thereby producing only a minimum population estimate. They extrapolated these minimum density estimates to similar black bear habitat throughout New Mexico assigning areas with habitat conditions in between the Sangre de Cristo Mountains and Mogollon Mountains a density equal to the mean of the two minimum density estimates (i.e., 13.2 bears/100 km^2). Costello et al. (2001) estimated the statewide minimum population by multiplying minimum density by the area of statewide primary habitat identified through their habitat suitability analysis, which introduces another source of uncertainty that was not quantified. Along with the density estimates, Costello et al. (2001) provided the NMDGF with a population model that incorporated the new density estimates, harvest data, mast survey data, and the relationship between mast production and reproductive success to model abundance and trend of black bear abundance in each Bear Management Zone (BMZ). These model-based abundance estimates, coupled with yearly harvest and mast survey data, have been the basis for establishing black bear harvest limits in New Mexico (Rick Winslow, NMDGF, personal communication). Although live-capture provides a wealth of information on age, dispersal, fecundity, health, home range size, and mortality rates, it is still inferentially limited due to small sample sizes. While Costello et al. (2001) was a progressive and highly informative study on New Mexico black bears, the capabilities of the technology at that time limited their ability to estimate abundance and density.

Capture-recapture (CR) is a common method for estimating abundance and density of animals and associated parameter uncertainty (Williams et al. 2002). Abundance estimates using CR are determined by comparing the ratio of uniquely marked individuals to unmarked individuals captured each sampling occasion in live capture studies (Pollock et al. 1990). Gould and Kendall (2013) summarize CR methodology and recent advances. Low capture probabilities and sample sizes inherent with species that typically reside at the low densities characteristic of carnivore populations hinders management agencies from utilizing traditional CR techniques for some species (Mills et al. 2000, Settlage et al. 2008). Noninvasive genetic sampling (NGS) revolutionized CR research by providing the ability to use remotely collected DNA samples to identify individuals (Waits and Paetkau 2005). Consequently, NGS enabled researchers to estimate population parameters for carnivores by increasing detection probability, increasing sample size of individuals detected, increasing the size of the study area, decreasing tag loss, and decreasing invasiveness compared to live capture studies (Woods et al. 1999, Mills et al. 2000). However, density estimators using traditional non-spatial CR methods are often less reliable because of the ad hoc and arbitrary estimate of the ETA, which introduces an unquantifiable error (Wilson and Anderson 1985, Parmenter et al. 2003).

Spatially explicit capture-recapture (SECR) models remedy this issue by estimating the number of home range centers within the study area, and subsequently density, directly, using a spatial point process (Efford 2004, Gopalaswamy 2013). By using SECR models, accounting for edge effects has been rooted in statistical theory and incorporated into the modeling process thereby eliminating the need to estimate ETA. Furthermore, integrating the distribution and location of sampling devices into the model eliminates individual heterogeneity related to unequal trap exposure (Borchers 2012). To date, SECR methods have shown improved parameter estimation compared to non-spatial methods with simulated datasets (Ivan et al. 2013, Whittington and Sawaya 2015) and similar or lower density estimates in empirical comparisons (Obbard et al. 2010, Stetz et al. 2014, Whittington and Sawaya 2015), particularly when distance to edge and sampling effort are not included in CR models. Although the accuracy of any density estimate is unknown, use of statistically robust estimation methods yields greater confidence in a management agency's ability to set defensible management objectives that will help ensure the long-term viability of harvested animal populations.

In light of advances in sampling (Woods et al. 1999) and statistical methods (Efford 2004), NMDGF began a collaborative project with the New Mexico Cooperative Fish and Wildlife Research Unit (NMCFWRU) and New Mexico State University (NMSU) to update their density estimates for New Mexico black bear populations. These estimates will then be used by NMDGF to set harvest limits in the respective study areas. Our (NMCFWRU and NMSU) objectives were to estimate the density of black bears ≥1 year of age in primary bear habitat within 7 of the 14 BMZs located within the Sangre de Cristo (BMZs 3, 4, and 5), Sandia (BMZ 8), and Sacramento Mountains (BMZs 11, 12, 13), New Mexico. We used non-invasive genetic samples from hair traps and bear rubs in combination with SECR models to estimate density for each study site.

STUDY AREA

We conducted our research in the Sangre de Cristo, Sandia, and Sacramento Mountains, New Mexico constituting 5 study areas: northern (NSC; 6,400 km^2) and southern Sangre de Cristo Mountains (SSC; 3,525 km^2), Sandia Mountains (300 km^2), and northern (NSacs; 925 km^2) and southern Sacramento Mountains (SSacs; 2,775 km^2). Interstate 25 and Interstate 40 separated the 3-mountain ranges. The sampling area for each study area was limited to primary habitat identified by Costello et al. (2001; Figure 1). Costello et al. (2001) used the New Mexico Gap Analysis land cover map (NMGAP, Thompson et al. 1996) to classify primary habitat as all closed-canopy forest and woodland types. All 5 study areas were managed as multiple-use forests encompassing portions of 4 National Forests (Carson, Cibola, Lincoln, and Santa Fe), 6 wilderness areas (Columbine-Hondo, Latir Peak, Pecos, Sandia Mountain, Wheeler Peak, and White Mountain), and 25 private landowners. Maximum elevation was 4,011 m, 3,254 m, and 3,649 m for the Sangre de Cristo, Sandia, and Sacramento Mountains and minimum elevations were approximately 1,900 m, 1,700 m, and 1,500 m, respectively. The Southern Rocky Mountains floristic district characterizes the Sangre de Cristo Mountains while the Sandia and Sacramento Mountains are characterized by the Mogollon floristic district (McLaughlin 1992). Dominant vegetation types in the study areas include: oak–mountain mahogany (*Quercus* spp. – *Cercocarpus* spp.) scrublands; piñon pine (*Pinus edulis*) - juniper (*Juniperus* spp.) woodlands; ponderosa pine (*P. ponderosa*), white pine (*P. monticola*), Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), Engleman spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) mixed-forest, and bristlecone (*P. aristata*) and limber (*P. flexilis)* pine forests (Costello et al. 2001). Important mast-producing species include oak, piñon pine, juniper, algerita (*Berberis haematocarpa*), chokecherry (*Prunus virginiana*), gooseberry (*Ribes* spp.), bear corn/squawroot (*Conopholus alpina*), cactus fruits (*Opuntia* spp.) and sumac (*Rhus* spp.; Kaufmann et al. 1998, Costello et al 2001).

METHODS

Field Sampling

We used hair traps (Woods et al. 1999) and bear rubs (Kendall et al. 2008) concurrently to sample black bear populations (Sawaya et al. 2012, Stetz et al. 2014). We sampled the black bear populations by systematically distributing a grid of 5-km x 5-km cells, with a randomly determined origin, across the landscape. A 5-km x 5-km cell size allowed us to place 4 hair traps within the average fixed kernel female home range in the Sangre de Cristo Mountains (27.6 km^2; Costello et al. 2001). We then set hair traps across primary habitat in areas most likely to encounter bears (Figure 2, 3, 4; Costello et al. 2001). We chose trap site locations based on suspected travel routes, occurrence of seasonal forage (e.g., green grass and ripe soft and hard mast), and presence of bear sign. We set hair traps and bear rubs across 4 sampling occasions in the NSC (22 April – 5 September 2012) and SSC (29 April - 9 September 2013) and across 6 sampling occasions in the Sandias, NSacs, and SSacs (5 May – 6 August 2014). Due to logistical constraints, a sampling occasion in the NSC and SSC lasted 4 weeks whereas the sampling occasion for the Sandias, NSacs, and SSacs was 2 weeks.

A hair trap consisted of a single strand of barbed wire wrapped around ≥3 trees with a lure pile constructed from woody debris, rocks, pine needles, and leaves at the center (Woods et al. 1999). During each sampling occasion in the NSC and SSC, 1 of 4 non-consumable lures (cow blood/fish emulsion mixture, anise oil, fatty acid scent tablet, or skunk tincture/lanolin mixture) was randomly selected and applied to the lure pile to attract bears into the exclosure and increase the novelty of hair traps to increase recapture rates. In the Sandias, NSacs, and SSacs we randomly selected and applied 1 of 2 non-consumable lures (cow blood/fish emulsion mixture or skunk tincture/lanolin mixture) each occasion. Based on our judgement in the field, we eliminated anise oil and fatty acid scent tablets because their scent duration and dispersal distance was inferior compared to the other two lures. Therefore, we believe the cow blood/ fish emulsion and skunk tincture/lanolin mixtures provided a better opportunity to attract bears over a longer period of time and greater distance. When a bear passed over or under the wire to investigate the lure pile, a barb snagged a tuft of hair from the individual. We assumed that cubs of the year were too small to be sampled by the barbed wire based on the size of cubs photographed at hair traps by trail cameras. Thus, sub-adults and adults were our sampled population. A sample consisted of all hair caught in one barb, and we used our best judgement to define hair samples collected from the lure pile. We deposited each hair sample in a separate paper coin envelope. We sterilized the barbed wire with a propane torch to ensure we removed any remaining hair to prevent false recaptures during the next sampling occasion. Hair traps were moved (100 m – 2.5 km) each occasion to help increase novelty and recapture rates (Boulanger and McLellan 2001, Boulanger et al. 2004, Boulanger et al. 2008).

Bears rub on trees, power poles, barbed-wire fences, wooden signs, and road signposts (Burst and Pelton 1983, Green and Mattson 2003). We opportunistically identified and collected hair from bear rubs along trails used to navigate to hair traps. We identified bear rubs by evidence of rubbing behavior such as a smoothed surface and snagged hair on the surface (Kendall et al. 2008, 2009). We attached 3-short strands of barbed wire vertically to the rub structure in order to collect discrete, higher quality hair samples (Kendall et al. 2008, 2009, Stetz et al. 2014). Rubs were identified at varying time intervals across sampling occasions, however, once established they were checked concurrently with nearby hair traps. We collected hair samples only from the barbed wire to ensure that the samples collected were from individuals that visited the rub during the sampling occasion and we sterilized the barbed wire to prevent false recaptures (Kendall et al. 2009). All hair samples were stored in an airtight container on silica desiccant at room temperature.

Genetic Analysis

We identified individuals by comparing multilocus genotypes generated for hair samples using 8 polymorphic microsatellite loci (G1D, G10B, G10L, G10M [Paetkau et al. 1995]; G10H, G10J, G10U [Paetkau et al. 1998]; MU59 [Taberlet et al. 1997]). We used the amelogenin or ZFX/ZFY markers to identify the sex of the individual (Paetkau 2003, 2004; Yamamoto et al. 2002; Durin et al. 2007). We selected specific markers for individual identification by ensuring that the mean expected heterozygosity for each marker was between 0.70 and 0.80 (Paetkau 2003, 2004). These markers were determined from an initial subsample from the NSC population in 2012. Because NGS-collected samples may contain low quantity and quality DNA (e.g., hair vs. tissue), genotyping errors may create or delete individuals, which may bias estimates (Mills et al 2000, Lukacs and Burnham 2005). Paetkau (2003) suggested that the largest source of genotyping error resulted from human error when identifying alleles at a locus, which only training and experience could reduce. Therefore, we sent our genetic samples to Wildlife Genetics International (WGI), which is a genetics laboratory that specializes in strict laboratory and error-checking methods that reduce genotyping errors that may arise from poor quality or small quantities of DNA (Paetkau 2003, Kendall et al. 2009). The laboratory has conducted over

2,000 projects including successfully identifying 653 samples without error during a blind sample test (Kendall et al. 2009). Thus, WGI has established a reputation for integrity and high quality work.

First, we eliminated samples that contained insufficient genetic material for analysis (no root, ≤ 1 guard hair, or < 5 underfur hairs) or appeared to be from heterospecifics. Next, we used either the G10J or ZFX/ZFY marker as a prescreen to remove low quality hair samples that were likely to fail during the multilocus genotyping phase. After the prescreen, we amplified the 9 candidate markers for each sample. We eliminated samples that failed to amplify at ≥ 3 loci or that amplified ≥ 3 alleles at 1 marker because they indicated a mixed sample from 2 individuals. We reanalyzed the samples that failed at < 3 loci resulting in either a full 9-locus genotype or a discarded sample. We examined pairs of samples that were mismatched at 1 or 2 markers (1MM pairs or 2MM pairs) for evidence of amplification or human error. We then reamplified and resequenced the mismatched pair for these samples under the assumption that genotyping error may have created the similarity between the two samples (Paetkau 2003). If a 1MM or 2MM pair remained between samples, then we considered the two samples to be from separate individuals, otherwise, we identified and corrected the genotyping error and we concluded that the two samples were from the same individual. We assigned individual ID to each sample with a unique multilocus genotype based upon the first sample to identify the individual's genotype. We calculated the expected and observed heterozygosity for the Sangre de Cristo, Sandia, and Sacramento Mountains using program GENEPOP (Genepop on the Web, Raymond and Rousset, 1995). Detailed laboratory methods may be found in Paetkau (2003, 2004).

Density Estimation

We used genotypes of individual samples to generate capture-recapture encounter histories for each uniquely identified black bear. We then used these capture histories to estimate density using spatially explicit capture-recapture (SECR) models (Efford 2004, Efford et al. 2009a, Efford et al. 2013) with the R package "secr" (Efford 2013). We used SECR to estimate 3 parameters: density (D), detection probability (g0), and the spatial scale over which the detection probability declines (σ; Efford et al. 2004). We used a half-normal detection function for our observation model, which represents the probability of detecting an individual as a function of the individual's home range location relative to the detection device (Efford et al. 2009a). We then specified a homogeneous Poisson distribution as our state model to represent the spatial distribution of animals across the sampling grid. We only included primary habitat as identified by Costello et al. (2001) for black bears in New Mexico for our habitat mask. The habitat mask identifies the area of habitat/non-habitat within and buffered around the trapping grid. We estimated the state space (i.e., the trapping grid and all individuals potentially exposed to capture outside the trapping grid) using the secr function suggest.buffer for each study area. However, this buffer is not to be confused with the ad hoc method of identifying a buffer using the ETA. Instead, the suggested buffer is the area of integration and includes all animals with a non-zero probability of detection (Ivan et al. 2013). Habitat may extend beyond the mask but individuals outside the buffer have a negligible probability of encounter (Borchers and Efford 2008, Royle et al. 2014). Derived from the capture data using suggest.buffer, we set the habitat mask buffer for the NSC, SSC, Sandias, NSacs, and SSacs as 18.75 km, 25.40 km, 13.23 km, 14.84 km, and 11.03 km, respectively. Variability in sampling effort may negatively bias density estimates and reduce the ability to explain variation in detection probability (Efford et al. 2013). We accounted for variable sampling effort by using the number of days each hair trap and bear rub was active (Kendall et al 2009, Sawaya et al 2012, Efford et al. 2013).

We tested for variation due to time (t), sex, elevation (elev), detector type (type; hair trap versus bear rub), and land cover classification (veg) as predictors of g0, and σ. Elevation was standardized prior to analyses by subtracting the mean and dividing by the standard deviation (Gelman and Hill 2007). We did not consider behavioral models because we did not provide a food reward. We modeled D only using sex because we did not expect bear density to vary by time, land cover type, or elevation. We entered sex into our models as a session covariate. We modeled g0 and σ concurrently by fitting 4 models that varied by time, sex, land cover type, and elevation. We also included models that varied by temporal variation for g0 and land cover for σ, temporal variation for g0 and elevation for σ, land cover for g0 and temporal variation for σ, and elevation for g0 and temporal variation for σ. We chose temporal variation and sex as covariates because multiple studies have reported that detection probability and movement patterns fluctuate over the course of the sampling period and differ between males and females (Kendall et al. 2009, Sawaya et al. 2012, Stetz et al. 2014, Ciucci et al. 2015). We selected elevation and land cover to represent the spatial heterogeneity of food resources exploited by black bears. We hypothesized that this heterogeneity could influence g0 and σ depending on the presence or absence and distribution of food on the landscape. However, we did not include both land cover type and elevation in the same model due to concerns of multicollinearity. We also constructed models with temporal variation for g0 and σ in addition to additive variation with either elevation or land cover. We included additive effects because we hypothesized that g0 and σ are likely to vary because of the black bear mating season, hyperphagic foraging behavior during late summer and early fall, and the temporally variable distribution of food resources on the landscape.

We extracted the elevation for each detector using the National Elevation Dataset 30 m resolution digital elevation model. We extracted land cover using the Interagency Landfire Project (www.landfire.gov; Rollins 2009) land cover classification at 30 m spatial resolution. We combined 6 Landfire land cover classifications into 5 categories: aspen – conifer, mixed conifer (combination of Douglas fir and white pine), piñon pine – juniper, ponderosa pine, and spruce – fir. Variability in abundance and distribution of each land cover classification across study areas resulted in a different number of categories and, consequently, number of parameters in each model among study areas. Aspen-conifer and spruce-fir were only included in the NSC and SSC. Mixed-conifer was included in all study areas except the Sandia Mountains. Piñon-juniper and ponderosa pine were included in all study areas. We extracted elevation and assigned the dominant land cover classification surrounding the location of each detector using ArcGIS 10.2.1 (Environmental Systems Research Institute, Inc. [ESRI], Redlands, California, USA). Each model serves as a hypothesis modeling the heterogeneity in the data for each estimable parameter. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank our final model set (Akaike 1973, Hurvich and Tsai 1989). We used the difference in AIC_c score (ΔAIC_c) between the top-ranked model and competing models to compare relative support, and we provide the AIC_c weights (w_i) to show the proportional support for each model (Burnham and Anderson 2002). We used model averaging to account for model selection uncertainty when the top ranked model in the final model set garnered less than 0.90 of the model weight (Burnham and Anderson 2002).

We conducted our study with authorization under Convention on International Trade in Endangered Species Export Permits 12US86417A/9, 13US19950B/9, and 14US43944B/9, and New Mexico Department of Game and Fish Authorization for Taking Protected Wildlife for Scientific and/or Education Purposes Permit 3504. All procedures were approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocol number 2011-027).

RESULTS

Field Sampling

We set 557 hair traps that were open for 57,010 trap days and we collected 3,825 hair samples. In addition, we identified and sampled 112 bear rubs, which yielded 258 hair samples over 7,007 trap days (Figure 2, 3, and 4; Tables 1 and 2). Sampling effort varied across study areas and was dependent on the number of hair traps and bear rubs set, the length of a sampling occasion for each study area (4 weeks vs. 2 weeks), and the accessibility of areas due to stochastic weather events and wildfire. The number of hair traps that collected ≥1 hair sample ranged from 28% to 42% with most traps collecting a hair sample in 1 – 2 sampling occasions. The number of hair samples collected during a particular occasion increased over the course of the summer and decreased towards the conclusion of sampling with peak collection during June and July (Table 2).

Genetic Analysis

The mean observed heterozygosity for our suite of genetic markers was 0.73 (Table 3). The number of individuals that were mismatched at 1 or 2 markers was extremely low with 3, 0, 0, and 0 observed 1MM-pairs and 0, 4, 0, and 4 observed 2MM-pairs and 3, 0, 0, and 0 for the NSC, SSC, Sandias, and Sacramento Mountains, respectively. Excluding the NSC, the observed mismatched pairs fell within the expected mismatch distribution for each population (Paetkau 2003). The deviation from expectation observed in the NSC was likely due to chance (D. Paetkau, WGI, personal communication). From the 4,083 total hair samples collected, we eliminated 27.7% from the genotyping process. Reasons for excluding hair samples included: the sample contained insufficient genetic material for analysis (26.1%), was not of black bear origin (1.49%), or contained DNA from more than one individual (0.17%). We attempted to genotype 2,950 (72.3%) hair samples but were only able to generate a full 9-loci genotype for 49.6% of the eligible samples and identified 726 (368 M: 358 F) individuals (Table 4). The observed sex ratio for each study area was approximately equal. Genotyping success varied across study areas (43% - 60%), but overall, our success rates were lower than the 75% success rate observed in similar studies (D. Paetkau, WGI, personal communication). Contrary to our prediction, when we shortened the length of the sampling occasion from 4 weeks (NSC and SSC) to 2 weeks (Sandias, NSacs, and SSacs), we increased the percentage of successful genotypes by 4%.

Density Estimation

We detected the majority (61% – 85%) of individuals in each study area only once with similar average number of detections of males (1.19 – 1.67) and females (1.14 – 1.56; Table 5). The number of unique individuals detected during each occasion for the NSC, NSacs, and SSacs increased over the course of sampling, peaking mid-summer, and subsequently decreasing towards the end of the season (Figure 5); this pattern was similar to the total number of hair samples collected per sampling occasion (Table 3). However, the number of unique individuals detected continued to increase over the course of the summer reaching its highest point during the last sampling occasion for both the SSC and the Sandias. Mean maximum recapture distance for males ranged from 4.23 to 12.46 km with a maximum distance of 52 km by one individual in the NSC (*n* = 3 – 33). Mean maximum recapture distance for females ranged from 0.38 to 4.59 km with a maximum distance of 47 km by one individual, also in the NSC (*n* = 4 - 23; Table 5). Three individuals were detected in two study areas. The first two detections were males we detected in the NSC in 2012 and then again in the SSC in 2013, and the third was a female we detected in the SSC in 2013 and then again 90 km away in the Sandias in 2014.

The most supported model for the NSC received all model weight and suggested that time and land cover type were important covariates explaining both g0 and σ (Table 6). The top model (w_i = 0.87) for the SSC included time and elevation, whereas the second highest-ranking model (w_i = 0.13) included time and land cover type (Table 7). The top model (w_i = 0.96) for the Sandias indicated that both g0 and σ varied by sex (Table 8). The highest-ranking model (w_i = 0.96) for the NSacs included time and land cover type for both g0 and σ (Table 9). There was higher model selection uncertainty for the SSacs than any other site, but the most supported model (w_i = 0.50) included land cover type for both g0 and σ (Table 10). The second and third ranked models included time and land cover, and time and elevation, respectively; these three top-ranked models contained all of the model weight (Table 15). For the NSC, we were able to fit all models except when g0 and σ were modeled concurrently with elevation (i.e., g0 ~ elev, σ ~ elev), concurrently with time and elevation (i.e., g0 ~ t + elev, σ ~ t + elev), independently with elevation (i.e., either g0 ~ elev, σ ~ constant; or g0 ~ constant, σ ~ elev), independently with time and elevation (i.e., either g0 ~ t + elev, σ ~ constant; or g0 ~ constant, σ ~ t + elev), and with time and elevation for different parameters (i.e., either g0 ~ t, σ ~ elev; or g0 ~ elev, σ ~ t) because of computational limitations. For the NSacs, we did not fit a model using detector type to predict g0 and σ concurrently because only one bear rub was set.

Detection probability (g0) was highest for the Sandias (g0 = 0.02), but overall, g0 was low across all study areas (Table 11). The final model for all study areas, except the Sandias, did not support a sex effect. Despite having the highest g0 relative to the other study areas, the precision of the Sandias density estimate was the lowest; whereas, the NSC density estimate was the most precise despite a low g0 (Table 11). Mean density estimates varied within and between mountain ranges (range 16.55 to 21.86 bears/100 km^2) and were model averaged for the SSC and SSacs (Table 11).

DISCUSSION

Our study provided the most current density estimates for multiple New Mexico black bear populations in over a decade (Costello et al. 2001). Our results suggest that densities are similar (SSacs) to or higher (NSC, SSC, Sandia, and NSacs) than the previous estimates used by NMDGF (17 bears/100 km^2 and 13.2 bears/100 km^2) to manage New Mexico black bear populations. The differences in estimated density could be a result of an increasing black bear population, simple variation in population density due to time, a difference in the state of environmental conditions, or different sampling and analytical methods. For example, Costello et al. (2001) did not account for uncollared individuals in their density estimation approach and thus likely underestimated the density of the population by not accounting for imperfect detection. Furthermore, their abundance and density estimates provided no measure of uncertainty because their estimation technique was not statistically based and did not provide a measure of uncertainty. As a result, Costello et al. (2001) used minimum abundance to derive their density estimates, which may explain at least some of the difference in our density estimates given we estimated mean density. Regardless, unless populations are extremely stable, we would expect density of a population to vary across space and with time.

The relative importance of the covariates we selected for modeling parameters was similar across study areas. The top model for all study areas held density constant suggesting an equal sex ratio in each population. Time of the detection event and the land cover type or elevation at which the detector was deployed were helpful covariates in modeling heterogeneity in both g0 and σ for all study areas except the Sandia Mountains, which included sex of the individual detected as an important explanatory variable. The importance of temporal variability is likely a result of seasonal reproductive and foraging behaviors (Alt et al. 1980, Garshelis and Pelton 1981, Costello et al. 2003). Black bear mating season begins with den emergence, which can be as early as late March, peaks in June, and typically ends by July (Costello et al. 2001). During this period, males move more as they traverse their home range searching for receptive females (Young and Ruff 1982, Costello 2008, Lewis and Rachlow 2011). Mast season begins in July, with peak masting occurring during late summer and early fall (Costello 2008). At this time, bears begin to enter a hyperphagic state when they increase daily caloric intake from 8,000 kcal to 15,000 – 20,000 kcal to build up fat stores for hibernation and reproduction in females (Nelson et al. 1980). Bear home range size and distance between sequentially recorded movements increases as bears travel outside their core area to exploit the spatially and temporally variable mast (Ostfeld et al. 1996, Costello 2008), which is an important food source and highly correlated with black bear reproductive output in New Mexico (Costello et al. 2003). Increased movement rates and enlarged home range size during mating and hyperphagia would likely affect trap exposure rates on the landscape, thus affecting g0 and σ.

The influence of land cover and elevation is likely a function of black bears responding to spatio-temporal changes in food abundance (Costello and Sage 1994, Costello et al. 2001, Mazur et al. 2013, McCall et al. 2013). Using scat surveys, Costello et al. (2001) reported that grasses, forbs, and ants tend to dominate bear diets during the pre-mast season (den emergence – 20 July). As the summer progresses, early mast season (21 July – 15 September) diets included soft mast species including chokecherry, squawroot (*Conopholis alpina*), and gooseberry as well as acorns (56% of scat volume). Diets during the late mast season (15 September – den entrance) are dominated by acorns (87% of scat volume) and supplemented with juniper berries (Costello et al. 2001). Mid-elevation land cover types (i.e., mixed conifer) are likely to contain a higher abundance of pre-mast species (grass and forbs) due to earlier snowmelt (compared to higher elevations) and moist conditions near riparian areas compared to dry, lower elevations. As snow melts, grasses and forbs will increase in abundance and distribution. With the arrival of monsoonal rains, soft mast will begin to ripen at lower elevations. Once oak acorns ripen in late summer/early fall, black bears begin to shift their attention towards vegetation types containing abundant acorns.

The main challenge we faced was genetic samples failing to produce a reliable genotype (i.e., not generating an individual ID for a particular hair sample). The inability to assign a reliable genotype to half of our genetic samples (44% - 61%) reduced the number of unique individuals and spatial recaptures (i.e., recapture of individuals at different traps) available for analysis. Consequently, this led to low detection probability and likely affected estimation of σ inducing larger standard errors and less precise density estimates (Efford et al. 2004, Sollmann et al. 2012, Sun et al. 2014). The relatively more precise NSC density estimate, despite a low g0, may be a result of a greater number of unique individuals and recaptures, which provided sufficient data for the model to predict unobserved movement distances (Table 5; Sollmann et al. 2012, Sun et al. 2014). Interestingly, despite having the highest estimated g0 among all study areas, the density estimate for the Sandias was the least precise, which may have been influenced by a low number of recaptures for both sexes, a low g0 for males, a large individual heterogeneity in male movement patterns, and/or an over-partitioning in data due to estimating sex specific detection parameters (i.e., g0 and σ). However, we believe the greatest factor affecting the density estimate is the number of individuals detected. Detecting fewer individuals results in less data to estimate the model parameters. Consequently, small sample size coupled with few recaptures can result in wider confidence intervals (Sun et al. 2014), which is likely the case for the Sandia density estimate. Our second highest-ranking model for the Sandias estimated density as 18.4 bears/100 km^2, which is still higher than the current density estimate used to manage the population (13.2 bears/100 km^2). Replicative sampling may help provide more information on the density of the Sandias.

In the SSC, we likely lost hair samples due to two forest fires, the Tres Lagunas and Jaroso Fires (Figure 6). The Tres Lagunas Fire started 30 May 2013 and burned 4,135 ha just below the southern boundary of the Pecos Wilderness. The Jaroso Fire started 10 June 2013 and burned 4,511 ha in the northwest corner of the Pecos Wilderness. We suspect these fires contributed to a less precise density estimate for the SSC. These fires affected 450 km^2 (12.7%) of the trapping grid and prevented us from checking hair traps located in close proximity to the fire primarily during the second and third sampling occasions (3–13% of total hair traps). Moreover, many of the fire-affected traps were in relatively high quality bear habitat where we would expect higher bear abundance. Anecdotally, post-fire these hair traps consistently yielded more hair samples than hair traps located in some areas that were unaffected by the fires. The inability to collect samples in this area may have reduced the number of new individuals detected, and, more importantly, most likely reduced the number of recaptures necessary for more precise parameter estimates. The limited access also prevented us from identifying more bear rubs across the SSC, restricting our ability to utilize multiple sampling methods and hindering our ability to minimize the impacts of capture heterogeneity (e.g., age, sex, reproductive status) caused by any one survey method (Boulanger et al. 2008). The use of hair traps and bears rubs concurrently has also been shown to increase the precision of parameter estimates compared to those generate by hair traps alone (Sawaya et a. 2012, Stetz et al. 2014), and likely aided our ability to generate more precise density estimates given our low amplification rates. We also hypothesize that the presence of fire on the landscape increased movements of individuals (Cunningham and Ballard 2004) as seen by our estimate of σ for the SSC, which is 3x – 24x larger than the other study areas.

Overall, a net loss in sampling occasions and hair samples reduced the amount of data available for the SSC analysis. The few individuals we recaptured in each occasion and the large number of unique bears identified in the last occasion, after the fires were extinguished or contained, support our argument that the fires in the SSC affected our model parameter estimates. Ideally, as a population is sampled the number of unique individuals captured declines over time (i.e., fewer unmarked individuals are encountered). Yet, in the SSC we captured 34% of all unique individuals during the last sampling occasion. While the number of individuals detected the last occasion in the NSC is still high (20%), it seems that the fires in the SSC influenced our ability to detect bears in this area as compared to the NSacs and SSacs (both 10%; Figure 5). Limited access to these hair traps during the fires led to longer sampling occasions and greater exposure to environmental conditions (i.e., exposure increased from 4 weeks to ≥8 weeks), subjecting hair samples to longer periods of environmental exposure, particularly to ultraviolet radiation (UV).

We suspect that for all study areas UV radiation is the main factor explaining failure of hair samples to produce a complete genotype (Stetz et al. 2015). Ultraviolet radiation causes DNA degradation by the formation of chemical compounds known as dimers. Dimers form by the binding of two adjacent, pyrimidine-nucleotide bases (cytosine and thymine) on a single strand of the double helix instead of binding between cross-strand partners (Jagger 1985). This fusion forms a bulge in the chemical structure of the DNA preventing DNA polymerase from progressing past the dimer and correctly duplicating the sequence, which prevents further amplification of the DNA molecule resulting in an incomplete genotype. Consequently, we suspect that the inability to assign an identity to a large portion of the genetic samples may have reduced the number of unique individuals and recaptures across all study areas. Multiple factors influence UV levels and, subsequently, its effects on DNA degradation including cloud cover, elevation, latitude, time of day, time of year, length of exposure, season, ozone depletion, and atmospheric turbidity (Piazena 1996, Stetz et al. 2015). For example, UV radiation increases with decreasing cloud cover, increases with elevation (9.0% – 11.0% per 1,000 m), and increases with lower latitude (Blumthaler et al. 1997). New Mexico receives substantial amounts of sunshine (Albuquerque 76% vs. U.S 58% average annual possible sunshine; NOAA 2004), is relatively high in elevation (1,200 m – 4,000 m), and is at a lower latitude than other geographic areas where NGS methods have been used to estimate bear abundance and density. Collectively, these factors result in UV radiation levels across much of New Mexico being higher than across most of the U.S. Further, we would expect UV radiation levels to be 1% – 26% higher in our study areas compared to those for Albuquerque, NM (Figure 7; NOAA 2015) because our study areas were typically located at higher elevations. Reducing sampling interval length should increase genotyping success, however, when we reduced our sampling interval from 4 to 2 weeks (which is a common time frame used by similar NGS studies), in the Sandias, NSacs, and SSacs we observed only a marginal improvement in genotyping success (4%). Surprisingly, the lowest genotyping success rate was in the SSacs (44%) given sampling occasions in the SSacs were 2 weeks shorter than the NSC and SSC. Thus, we suggest researchers consider conducting a pilot study to determine the optimal sampling interval for reducing UV degradation of DNA within hair samples particularly for study areas in the southwestern U.S.

Despite these sampling difficulties, we were able to produce density estimates with comparable levels of precision as those obtained in black bear studies conducted elsewhere in the U.S. (Table 12). We believe these estimates were possible due to the large extent of our study areas, which allowed us to detect a larger proportion of the population within each mountain range, increased the potential number of recaptures, and buffered the data from the low amplification success rates. In addition, we believe because there was no observable spatial pattern in the collection locations of samples that failed to amplify we were still able to gather an adequate representation of movement of individuals on the landscape due to our sampling intensity and use of multiple survey methods. This allowed us to model unobserved movement distances (Sollmann et al. 2012). However, a small data set affected the Sandias estimate resulting in larger confidence intervals than the other study areas, particularly the NSC. It is likely that precision for these two study areas was influenced by the number of individuals detected (NSC: $n = 379$ vs. Sandias: $n = 18$).

Black bears are naturally difficult to sample due to their cryptic behavior and large home ranges. Furthermore, spatially and temporally stochastic environmental (e.g., masting oak and wildfire; Cunningham et al. 2003, Mazur et al. 2013) and anthropogenic (e.g., recreation and roads; Boyle and Samson 1985, Kasworm and Manley 1988) factors confound black bear detection by influencing the distribution of individuals across the landscape. In New Mexico, the abundance and distribution of masting oak heavily influences black bear fitness and movement patterns as they accrue adequate fat reserves for hibernation and reproduction for females (Costello et al. 2001, Costello et al. 2003, Inman et al. 2007). Under the assumption of a count index, multiple years of low black bear harvest may indicate a declining population while multiple years of high black bear harvest may indicate an increasing population. While observed harvest numbers may be a function of a changing population, the observed changes in harvest could be a product of various factors unrelated to the number of animals harvested. In years with average or above average precipitation levels, acorn and soft mast abundance increases. During these times, black bear movement rates are smaller due to the high availability of food on the landscape. Smaller movement rates reduce black bear exposure to hunters resulting in hunters observing, and subsequently, harvesting fewer individuals (Costello et al. 2001, Fieberg et al. 2010). However, when food crops fail, particularly acorn crops, black bear home range size increases, along with hunter harvest rates, due to the increased movements of black bears searching for food (Costello et al. 2001, Fieberg et al. 2010).

In developing sampling designs for future SECR-based black bear density estimation projects, there are multiple considerations. First, the spatial extent of the population must be determined (Sun et al. 2014). Sollmann et al. (2012) suggested that trapping arrays could be smaller than an average male home range but 1.5x larger than the average female home range. Yet, they cautioned that a small trapping array might not provide an accurate representation of movement patterns necessary to inform σ. A larger trapping array may buffer against stochastic environmental events (e.g., mast crop failure) which may cause individuals to move larger distances (McCall et al. 2013). If trapping arrays are large, there is a reduced chance that individuals will move off of the study area and thus not be detected. Selecting study area boundaries is an important aspect to consider when trying to avoid violating geographic closure of the study area. The spacing between hair traps will also influence the spatial extent of the trapping array. Non-spatial CR literature has suggested a trapping density of 4 traps per individual home range, which we adhered to, however, recent simulation work has suggested only 2 hair traps per individual home range may be required when using SECR models (Sollmann et al. 2012, Sun et al. 2014). We stress that an accurate representation of the smallest average home range size is necessary to prevent traps from being spaced too far apart. When traps are spaced too widely, the number of unique individuals and recaptures declines causing a decrease in the precision of the parameter estimates (Sun et al. 2014). If hair traps can be spaced closer together, then a regular trapping array configuration may be used, however, if they cannot, then a cluster configuration may be preferred with clusters wider than the spacing between hair traps (Sun et al. 2014). Use of fewer traps has the benefit of decreasing the trapping array size, reducing the sampling occasion length reducing environmental exposure, or reducing the number of technicians required for the study potentially saving both time and money. However, depending on the extent of the population, the size of the study area, and available resources it may not be possible to sample all available black bear habitat. In that case, it may be more appropriate to distribute multiple, smaller trapping arrays randomly across the available sampling area instead of one large array (Wilton et al. 2014).

We suggest that future efforts to estimate the density of black bear populations in New Mexico may need to shorten the length of the sampling occasion to reduce DNA degradation via UV radiation, which will increase microsatellite amplification success helping to reduce genotyping errors and increase the number of individual genotypes identified (Stetz et al. 2015). When we decreased sampling occasion length from 4 weeks to 2 weeks the genotype success rate increased by only 4% (Sandia and Sacramento Mountains: 52% vs. SSC: 48%). Thus, a pilot study may be useful to determine the length of time hair samples can remain in the field prior to collection. In addition, researchers may consider setting hair traps and bear rubs in more shaded areas (e.g., north facing slopes) to help reduce exposure to UV radiation. This may help increase the amplification success for hair samples. Increasing the number of personnel would be preferable over fewer hair traps because it would allow for a larger study area or a denser trapping array to be sampled, which should increase detection of long-range movements helping to inform σ, increase recapture rates, and increase the precision of parameter estimates (Sollmann et al. 2012). A larger study area will also place density estimates at the spatial scale at which state agencies make management decisions (Dreher et al. 2007). Personnel should be able to check and reset, on average, 3 – 5 hair traps per day depending on road density. For example, we were able to check more traps in the Sacramento Mountains ($n = 148$) than the SSC ($n = 141$) in half the time (2 weeks vs. 4 weeks, respectively) due to the higher road density in the Sacramento Mountains. Increased seasonal personnel will certainly increase cost, but this cost will be offset by a reduction in total sampling time per season. The other option is to reduce the number of hair traps resulting in a smaller study area or an increased distance between hair traps. A small study area, relative to home range size, will increase the probability that individuals travel off the sampling grid and are unavailable for capture. Individuals will also be unavailable for capture when traps are widely spaced relative to home range size causing some home ranges to fall in between hair traps. Both scenarios will reduce the number of unique individuals identified, the number of recaptures, and ultimately the precision of the parameter estimates (Sollmann et al. 2012, Sun et al. 2014). Careful consideration of these factors must be taken into account when reducing the number of hair traps to ensure a reasonable tradeoff between study area size and the distance between hair traps.

To estimate density, we used SECR models. The SECR analysis may be performed using inverse prediction (Efford 2004), maximum likelihood (ML; Borchers and Efford 2008), or Bayesian based methods (Royle et al. 2009). Inverse prediction was the original constitution of SECR models, but it is applied only to single catch traps (e.g. Sherman-live traps), due to the lack of a ML based single-catch model. Inverse prediction is limited in regards to model selection and the inclusion of parameter covariates (Borchers and Efford 2008). The two prominent statistical paradigms in SECR-based analyses are ML and Bayesian with both methods providing similar density estimates (Borchers and Efford 2008, Royle et al. 2009). The ML framework is advantageous because these models require less computation time compared to Bayesian methods (Noss et al. 2012). Although, we note that larger study areas and finer discretization increases the necessary computation time for a model. Maximum likelihood methods may require less user knowledge compared to the Bayesian because the latter requires a prior distribution be specified and "model warnings" are often prompted if an error has occurred during model fitting (Noss et al. 2012, Efford 2013). However, users should evaluate model output carefully regardless of statistical paradigm chosen. Bayesian models may be preferred in cases where data sets with small sample size are expected (Noss et al. 2012) because ML models rely on asymptotic theory, which requires larger sample sizes in order to approach normality (Gerber and Parmenter 2015). Model output generated by a Bayesian approach may be difficult to decipher due to the mechanisms of the analysis. To interpret model output, a researcher must be able to understand the influence of model priors, the distribution of the MCMC chains, the posterior model output, and other results generated by the model (Noss et al. 2012). Inverse prediction and ML based SECR models may be fitted in either program DENSITY, which offers a Graphical User Interface (GUI), or the R package "secr" (Efford et al. 2004, Efford 2013). The secr package allows a wider range of analyses including modeling density surfaces and telemetry-integrated capture-recapture, and it provides the user greater flexibility in model optimization and processing. Bayesian estimation may be conducted in either program SPACECAP (Gopalaswamy et al. 2012), which offers a GUI, or in Program R using JAGS (Just Another Gibbs Sampler) in the BUGS (Bayesian inference Using Gibbs Sampling) language (Royle et al. 2014). For our study, we chose to estimate density using the ML based approach because the statistical knowledge and expertise of our research laboratory is rooted in ML theory.

In conclusion, we estimated the density of black bears in 5 study areas within 3 mountains ranges of New Mexico. Our estimates will aid the NMDGF in setting sustainable harvest limits. In addition to density estimates, information on demographic rates (e.g., survival rates and reproduction) and the potential effects that climate change and future land use may have on the demography of black bears may also help inform management of black bears in New Mexico, and may be considered as future areas for research.

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LITERATURE CITED

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages. 267–281 in B. N. Petrov, F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.

Alt, G.L., G.J. Matula, Jr., F.W. Alt, and J.S. Lindzey. 1980. Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. Bears: Their Biology and Management 4:131–136.

Apker, J.A., P. Lukacs, J. Broderick, B. Dreher, J. Nao, and A. Vitt. 2009. Non-invasive DNA-based black bear density estimates in Colorado – 2009. Colorado Division of Wildlife, Monte Vista, CO, USA.

Beston, J.A., and R.D. Mace. 2012. What can harvest data tell us about Montana's black bears? Ursus 23:30–41.

Blumthaler, M., W. Ambach, and R. Ellinger. 1997. Increase in solar UV radiation with altitude. Journal of Photochemistry and Photobiology 39:130–134.

Borchers, D. 2012. A non-technical overview of spatially explicit capture recapture models. Journal of Ornithology 152:435–444.

Borchers, D.L. and M.G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385.

Boulanger, J. and B. McLellan. 2001. Closure violation in NDA-based mark-recapture estimation of grizzly bear populations. Canadian Journal of Zoology 79:642–651.

Boulanger, J. B.N. McLellan, J.G. Woods, M.F. Proctor, and C. Strobeck. 2004. Sampling design and bias in DNA-based capture-mark-recapture population and density estimates of grizzly bears. Journal of Wildlife Management 68:457–469.

Boulanger, J., K.C. Kendall, J.B. Stetz, D.A. Roon, L.P. Waits, and D. Paetkau. 2008. Multiple data sources improve DNA based mark-recapture population estimates of grizzly bears. Ecological Applications 18:577–589.

Boyle, S.A., and F.B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: a review. Wildlife Society Bulletin 13:110–116.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Second addition. Springer, New York, USA.

Burst, T.L., and M.R. Pelton. 1983. Black bear mark trees in the Smoky Mountains. Ursus 5:45–53.

Ciucci, P., V. Gervasi, L. Boitani, J. Boulanger, D. Paetkau, R. Prive, and E. Tosoni. Estimating abundance of the remnant Apennine brown bear population using multiple noninvasive genetic data sources. Journal of Mammalogy 96: 206–220.

Costello, C.M. 2008. The spatial ecology and mating system of black bears (*Ursus americanus*) in New Mexico. Dissertation, Montana State University, Montana, USA.

Costello, C.M., and R.W. Sage Jr. 1994. Predicting black bear habitat selection from food abundance under 3 forest management systems. Ursus 9:375–387.

Costello, C.M., D.E. Jones, K.A. Green-Hammond, R.M. Inman, K.H. Inman, B.C. Thompson, R.A. Deitner, and H.B. Quigley. 2001. A study of black bear ecology in New Mexico with models for population dynamics and habitat suitability. Final Report, Federal Aid in Wildlife Restoration Project W-131-R, New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA.

Costello, C.M., D.E. Jones, R.M. Inman, K.H. Inman, B.C. Thompson, and H.B. Quigley. 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. Ursus 14:1–16.

Cunningham, S.C., and W.B. Ballard. 2004. Effects of wildfire on black bear demographics in Central Arizona. Wildlife Society Bulletin 32:928-937.

Dice, L.R. 1938. Some census methods for mammals. Journal of Wildlife Management 2:119–130.

Downing, R. L. 1980. Vital statistics of animal populations. Pages 247–267 in S.D. Schemnitz, editor. Wildlife Techniques Manual. The Wildlife Society, Washington, D.C., USA.

Dreher, B.P., S.R. Winterstein, K.T. Scribner, P.M. Lukacs, D.R. Etter, G.J.M. Rosa, V.A. Lopez, S. Libants, and K.B. Filcek. 2007. Noninvasive estimation of black bear abundance incorporating genotyping errors and harvested bear. Journal of Wildlife Management 71:2684-2693.

Drewry, J.M., F.T. Van Manen, and D.M. Ruth. 2013. Density of and genetic structure of black bears in coastal South Carolina. Journal of Wildlife Management 77:153–164.

Durin, M.E., P.J. Palsboll, O.A. Ryder, D.R. McCullough. 2007. A reliable genetic technique for sex determination of giant panda (*Aliuropoda melanoleuca*) from non-invasively collected hair samples. Conservation Genetics 8:715–720.

Efford, M.G. 2004. Density estimation in live-trapping studies. Oikos 106:598 – 610.

Efford, M.G. 2013. secr: spatially explicit capture-recapture models. R package version 2.9.5. http://CRAN.R-project.org/package=secr.

Efford, M.G., D.K. Dawson, and C.S. Robbins. 2004. DENSITY: software for analyzing capture-recapture data from passive detector arrays. Animal Biodiversity and Conservation 27: 217–228.

Efford, M.G., D.L. Borchers, and A.E. Byrom. 2009*a*. Density estimation by spatially explicit capture-recapture: likelihood-based methods. Pages 255-269 *in* D.L. Thomson, E.G. Cooch, and M.J. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York, New York, USA.

Efford, M.G., D.L. Borchers, and G. Mowat. 2013. Varying effort in capture-recapture studies. Methods in Ecology and Evolution 4:629–636.

Fieberg, J.R., K.W. Shertzer, P.B. Conn, K.V. Noyce, and D.L. Garshelis. 2010. Integrated population modeling of black bears in Minnesota: implications for monitoring and management. PLoS ONE 5:e12114.

Gardner, B., J.A. Royle, M.T Wegan, R.E. Rainbold, and P.D. Curtis. 2010. Estimating black bear density using DNA from hair snares. Journal of Wildlife Management 74:318–325.

Garshelis, D.L. 1990. Monitoring effects of harvest on black bear populations in North America: a review and evaluation of techniques. Eastern Workshop on Black Bear research and Management 10:120–144.

Garshelis, D.L. and M.R. Pelton. 1981. Movements of black bears in the Great Smoky National Park. Journal of Wildlife Management 45:912–925.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.

Gerber, B.D., and R.R. Parmenter. 2015. Spatial capture-recapture model performance with known small-mammal densities. Ecological Applications 25:695–705.

Gopalaswamy, A.M. 2013. Spatially explicit capture-recapture models. Pages 1–11 *in* A. El-Shaarawi and W.W. Piegorsch, editors. Encyclopedia of Environmetrics. Second edition. John Wiley and Sons, Hoboken, New Jersey.

Gopalaswamy, A.M., Royle, J.A., Hines, J.E., Singh, P., Jathanna, D., Kumar, N.S. and Karanth, K.U. 2012. Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. Methods in Ecology and Evolution 3:106–1072.

Gould, W.R. and W.L. Kendall. 2013. Capture-recapture methodology. Pages 1–6 *in* A. El-Shaarawi and W.W. Piegorsch, editors. Encyclopedia of Environmetrics. Second edition. John Wiley and Sons, Hoboken, New Jersey.

Green, G.I., and D.J. Mattson. 2003. Tree rubbing by Yellowstone grizzly bears *Ursus arctos*. Wildlife Biology 9:1–10.

Hristienko, H., and J.E. McDonald Jr. 2007. Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. Ursus 18:72–88.

Hurvich, C.M., and C.L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Inman, R.M., C.M. Costello, D.E. Jones, K.H. Inman, B.C. Thompson, and H.B. Quigley. 2007. Denning chronology and design of effective bear management units. Journal of Wildlife Management 71:1476–1483.

Ivan, J.S., G.C. White, and T.M. Shenk. 2013. Using simulation to compare methods for estimating density from capture-recapture data. Ecology 94:817–826.

Jagger, J. 1985. Solar-UV actions on living cells. Praeger Publishers, New York, NY, USA.

Kasworm, W.F. and T.L. Manley. 1988. Grizzly bear and black bear ecology in the Cabinet Mountains of Northwest Montana. Montana Department of Fish, Wildlife & Parks, Helena, Montana, USA.

Kaufmann, M.R., L.S. Huckaby, C.M. Regan, J. Popp. 1998. Forest Reference Conditions for Ecosystem Management in the Sacramento Mountains, New Mexico. U.S Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Kendall, K.C., J.B. Stetz, D.A. Roon, L.P. Waits, J.B. Boulanger, and D. Paetkau. 2008. Grizzly bear density in Glacier National Park, Montana. Journal of Wildlife Management 72:1693–1705.

Kendall, K.C., J.B. Stetz, J. Boulanger, A.C. Macleod, D. Paetkau, and G.C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. Journal of Wildlife Management 73:3–17.

Lewis, J.S., and J.L. Rachlow. 2011. Activity patterns of black bears in relation to sex, season, and daily movement rates. Western North American Naturalist 71:388–395.

Lukacs, P.M. and K.P. Burnham 2005. Estimating population size from DNA-based closed capture-recapture data incorporating genotyping error. Journal of Wildlife Management 69:396-403.

Mazur, R., A.P. Klimley, and K. Folger. 2013. Implications of the variable availability of seasonal foods on the home ranges of black bears, Ursus americanus, in the Sierra Nevada of California. Animal Biotelemetry 1:16.

McCall, B.S., M.S. Mitchell, M.K. Schwartz, J. Hayden, S.A. Cushman, P. Zager, and W.F. Kasworm. 2013. Combined use of mark-recapture and genetic analyses reveals response of a black bear population to changes in food productivity. Journal of Wildlife Management 77:1572–1582.

McLaughlin, S.P. 1992. Are floristic areas hierarchically arranged? Journal of Biogeography 19:21–32.

Miller, S.D. 1990. Population management of bears in North American. International Conference on Bear Research and Management 8:350–373.

Mills, L.S., J.J. Citta, K.P. Lair, M.K. Schwartz and D.A. Tallmon. 2000. Estimating animal abundance using noninvasive DNA sampling: promise and pitfalls. Ecological Applications 10:283–294.

National Oceanic and Atmospheric Administration [NOAA]. 2004. Ranking of cities based on % annual possible sunshine in descending order from most to least average possible sunshine. <http://www1.ncdc.noaa.gov/pub/data/ccd-data/pctposrank.txt>. Accessed 23 Aug 2015.

National Oceanic and Atmospheric Administration [NOAA]. 2015. UV Index: annual time series <http://www.cpc.ncep.noaa.gov/products/stratosphere/uv_index/uv_annual.shtml>. Accessed 11 Nov 2015.

Nelson, R.A., G.E. Folk, Jr, E.W. Pfeiffer, J.T. Craighead, C.J. Jonkel, and D.L. Steiger. 1980. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. Pages 284–290 *in* Proceedings of the Fifth International Conference on Bear Research and Management, Madison, Wisconsin, USA.

Noss, A.J., B. Gardner, L. Maffei, E. Cuéllar, R. Montaño, A. Romero-Muñoz, R. Sollman, and A.F. O'Connell. 2012. Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del Gran Chaco landscape. Animal Conservation 15:527–535.

Obbard, M., E.J. Howe, and C.J. Kyle. 2010. Empirical comparison of density estimators for large carnivores. Journal of Applied Ecology 47:76–84.

Ostfeld, R.S., C.G. Jones, and J.O. Wolff. 1996. Of mice and mast. BioScience 46:323–330.

Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. Molecular Ecology 12:1375–1387.

Paetkau, D. 2004. The optimal number of markers in genetic capture-mark-recapture studies. Ecological genetic studies of bears using microsatellite analysis. Journal of Wildlife Management 68:449–452.

Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347–354.

Paetkau, D., G.F. Shileds, and C. Strobeck. 1998. Gene flow between insular, coastal, and interior populations of brown bears in Alaska. Molecular Ecology 7:1283–1292.

Parmenter, R.R., T.L. Yates, D.R. Anderson, K.P. Burnham, J.L. Dunnum, A.B. Franklin, M.T. Friggens, B.C. Lubow, M. Miller, G.S. Olson, C.A. Parmenter, J. Pollard, E. Rexstad, T.M. Shenk, T.R. Stanley, and G.C. White. 2003. Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. Ecological Monographs 73: 1–26.

Piazena, H. 1996. The effect of altitude upon the solar UV-B and UV-A irradiance in the tropical Chilean Andes. Solar Energy 57:133–140.

Pollock, K.H., J.D. Nichols, C. Brownie, and J.E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:1–96.

Raymond, M., and F. Rousset .1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Rollins, M.G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. International Journal of Wildland Fire 18: 235–249.

Royle, J.A., K.U. Karanth, A.M. Gopalaswamy, and N.S. Kumar. 2009. Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. Ecology 90:3233–3244.

Royle, J.A., R.B. Chandler, R. Sollmann, and B.Gardner. 2014. Spatial Capture-Recapture. Academic Press, Waltham, Massachusetts, USA.

Sawaya, M.A., J.B. Stetz, A.P. Clevenger, M.L. Gibeau, and S.T. Kainowski. 2012. Estimating grizzly and black bear population abundance and trend in Banff National Park using noninvasive genetic sampling. PLoS ONE 7:e34777.

Settlage, K.E., F.T. Van Manen, J.D. Clark, and T.L. King. 2008. Challenges of DNA-based mark-recapture studies of American black bears. Journal of Wildlife Management 72:1035–1042.

Sollmann, R., B. Gardner, and J.L. Belant. 2012. How does spatial study design influence density estimates from spatial capture recapture models? PLoS ONE 7:e34574.

Stetz, J.B., K.C. Kendall, and A.C. Macleod. 2014. Black bear density in Glacier National Park, Montana. Wildlife Society Bulletin 38:60–70.

Stetz, J.B., T. Seitz, M.A. Sawaya. 2015. Effects of exposure on genotyping success rates of hair samples from brown and American black bears. Journal of Fish and Wildlife Management 6:191–198.

Sun, C.C., A.K. Fuller, and J.A. Royle. 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. PLoS ONE 9:e88025.

Taberlet, P., J.-J. Camarra, S. Griffin, O. Hanotte, L. P. Waits, C. Dubois- Paganon, T. Burke, and T. Bouvet. 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. Molecular Ecology 6:869–876.

Thompson, B.C., P.J. Crist, J.S. Prior-Magee, R.A. Deitner, D.L. Garber, and M.A. Hughes. 1996. Gap analysis of biological diversity conservation in New Mexico using geographic information systems. Research completion report, New Mexico Cooperative Fish and Wildlife Research Unit, Las Cruces.

Tredick, C.A., and M.R. Vaughn. 2009. DNA-based population demographics of black bears in coastal North Carolina and Virginia. Journal of Wildlife Management 72:1031–1039.

Waits, L.P., and D. Paetkau. 2005. Noninvasive genetic sampling tools for wildlife biologists: a review of applications and recommendations for accurate data collection. Journal of Wildlife Management 69:1419–1433.

Whittington, J., M.A. Sawaya. 2015. A comparison of grizzly bear demographic parameters estimated from non-spatial and spatial open population capture-recapture models. PLoS ONE 10: e0134446.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and management of animal populations. Academic Press, New York.

Wilson, K.R., and D.R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66:13–21.

Wilton, C.M., E.E. Puckett, J. Beringer, B. Gardner, L.S. Eggert, and J.L. Belant. 2014. Trap array configuration influences estimates and precision of black bear density and abundance. PLoS ONE 9:e111257.

Woods, J.G., D. Paetkau, D. Lewis, B.N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

Yamamoto, K., T. Tsubota, T. Komatsu, A. Katayama, T. Murase, I. Kita, and T. Kudo. 2002. Sex identification of Japanese black bear, *Ursus thibetanus japonicus*, by PCR based on amelogenin gene. Journal of Veterinary Medical Science 64:505–508.

Young, B.F. and R.L. Ruff. 1982. Population dynamics and movements of black bears in east central Alberta. Journal of Wildlife Management 46:845–86.

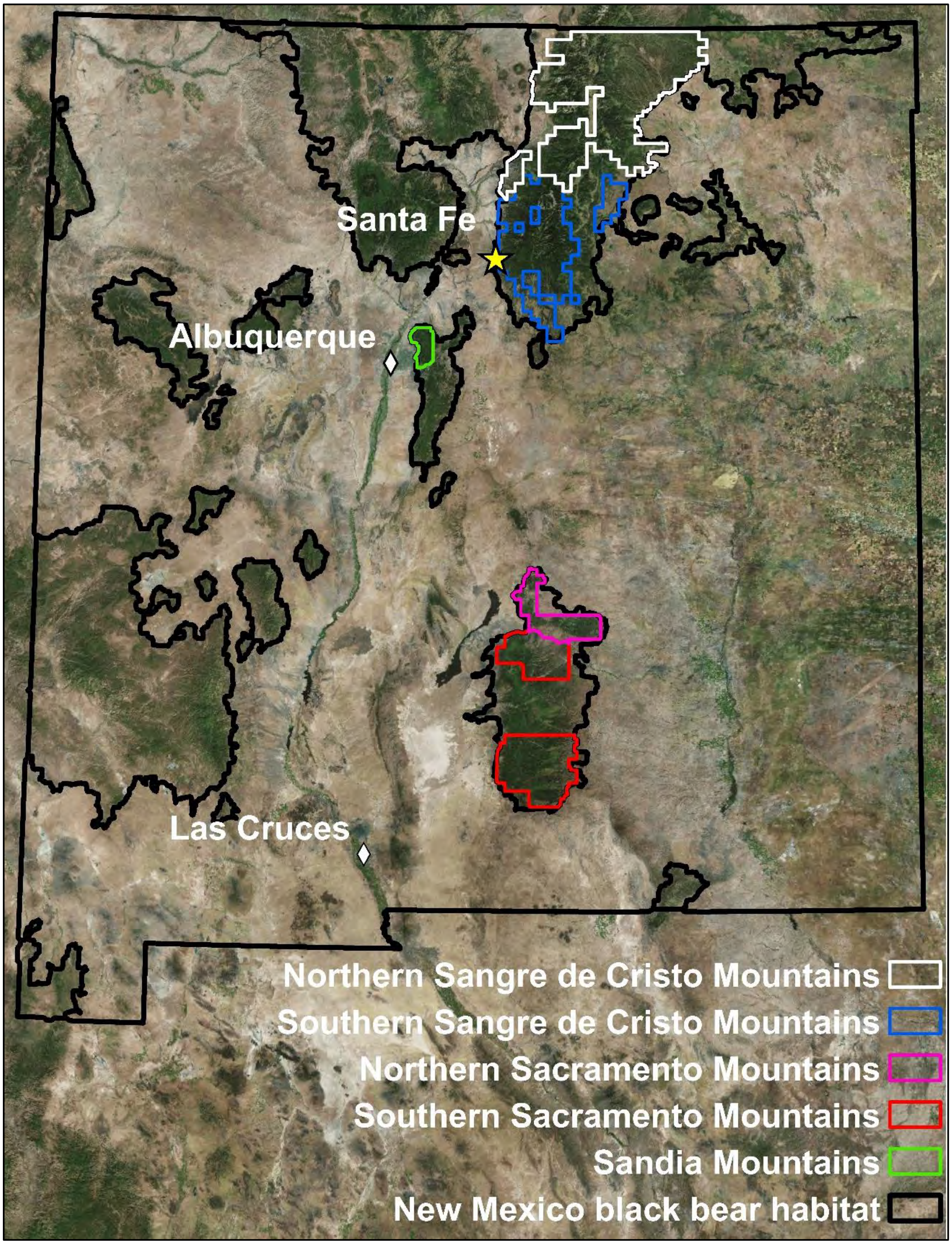


Figure 1. Aerial imagery of black bear habitat in New Mexico highlighting the study areas located within the Sangre de Cristo Mountains, Sandia Mountains, and Sacramento Mountains.

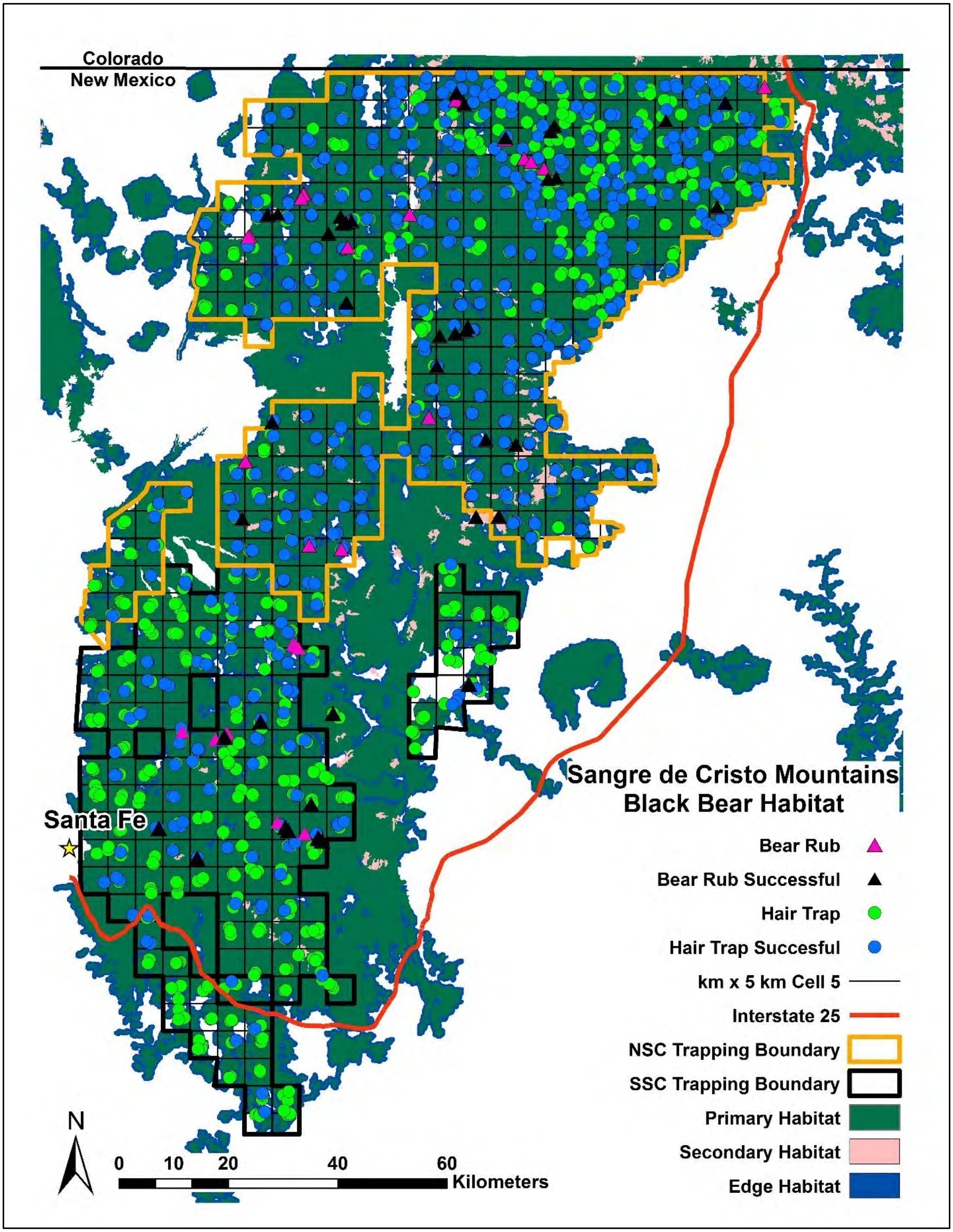


Figure 2. Black bear habitat identified by Costello et al. (2001) overlaid with hair traps and bear rubs set for the northern Sangre de Cristo Mountains, NM in 2012 and 2013.

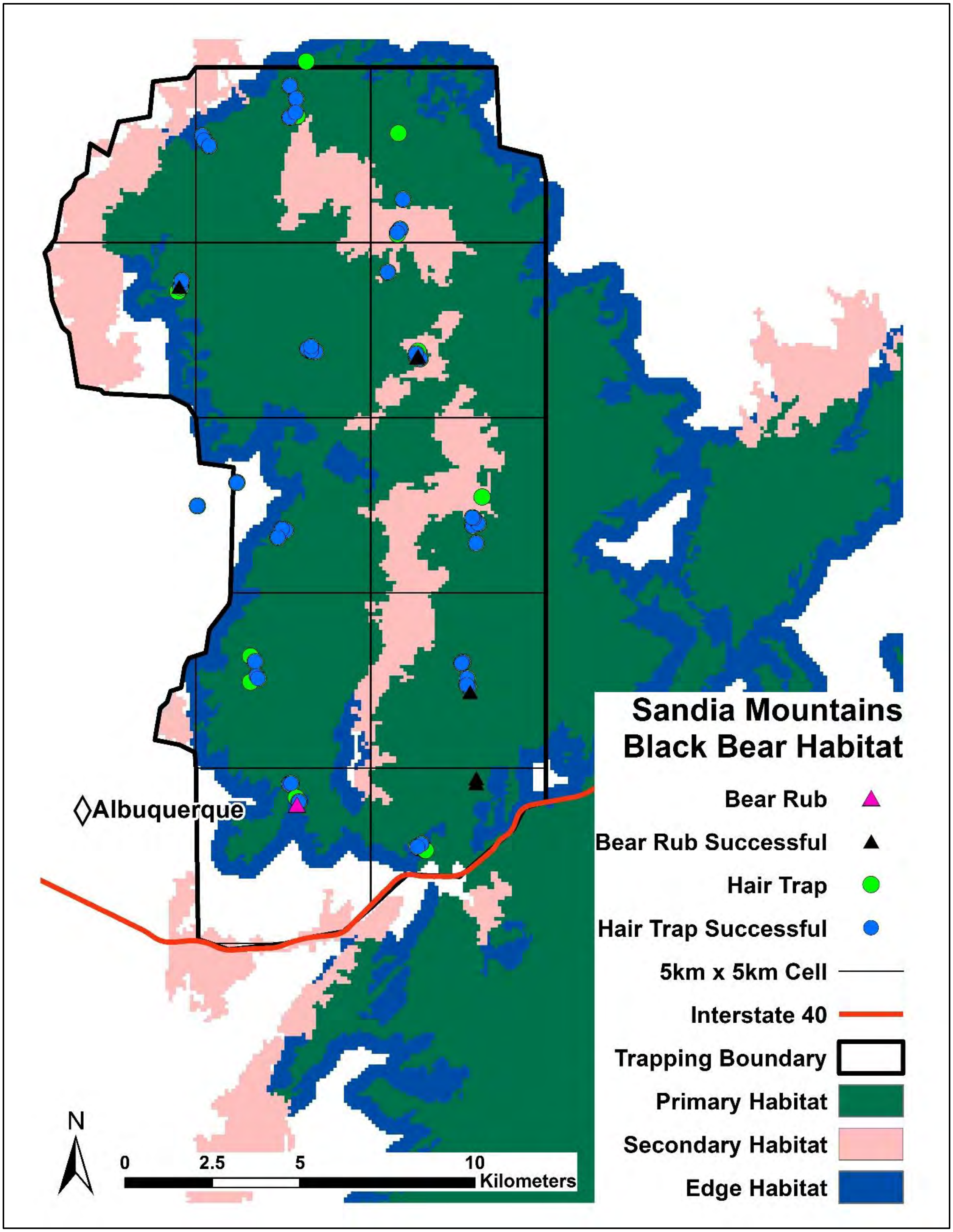


Figure 3. Black bear habitat identified by Costello et al. (2001) overlaid with hair traps and bear rubs set for the Sandia Mountains, NM in 2014.

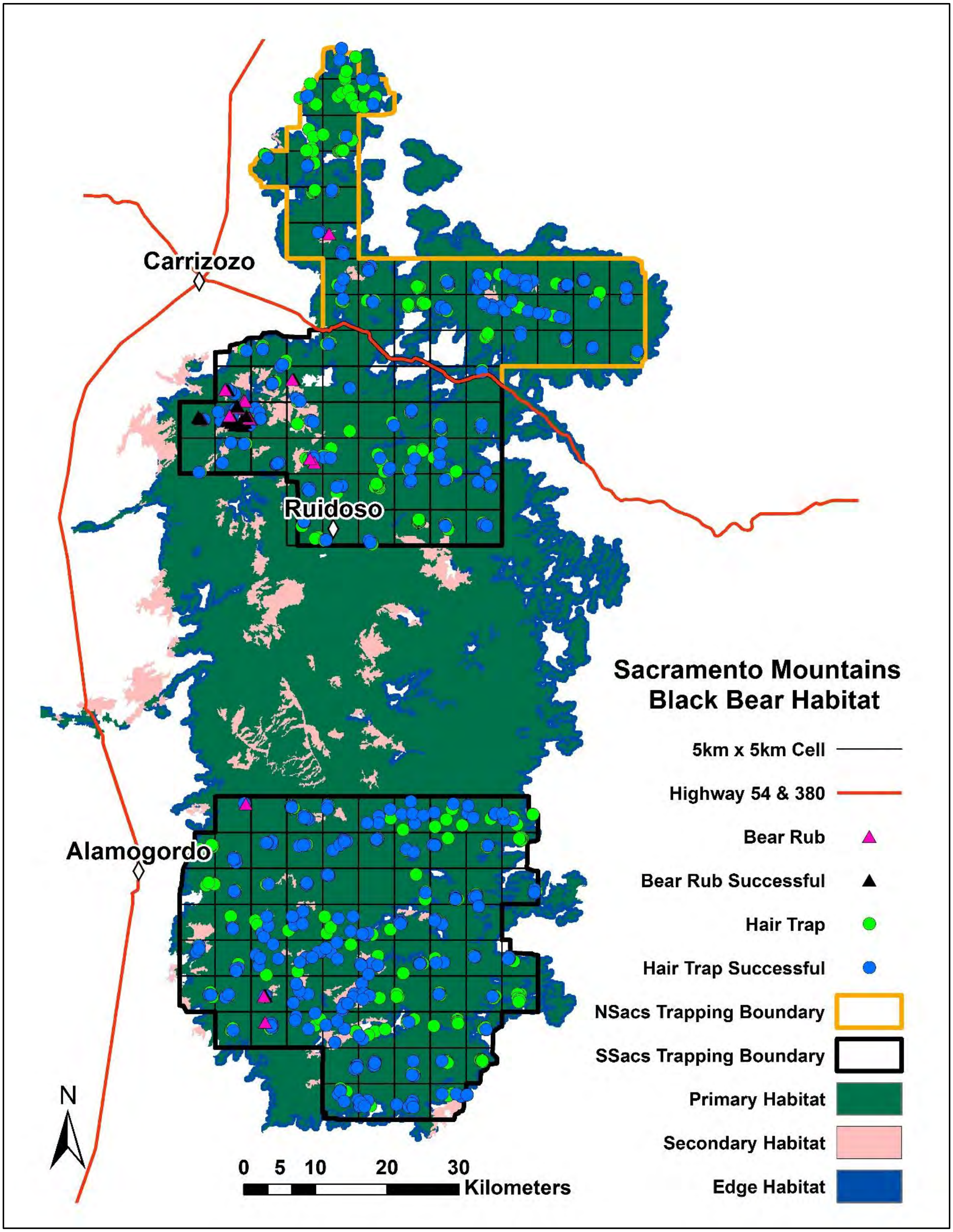


Figure 4. Black bear habitat identified by Costello et al. (2001) overlaid with hair traps and bear rubs set for the Sacramento Mountains, NM in 2014.

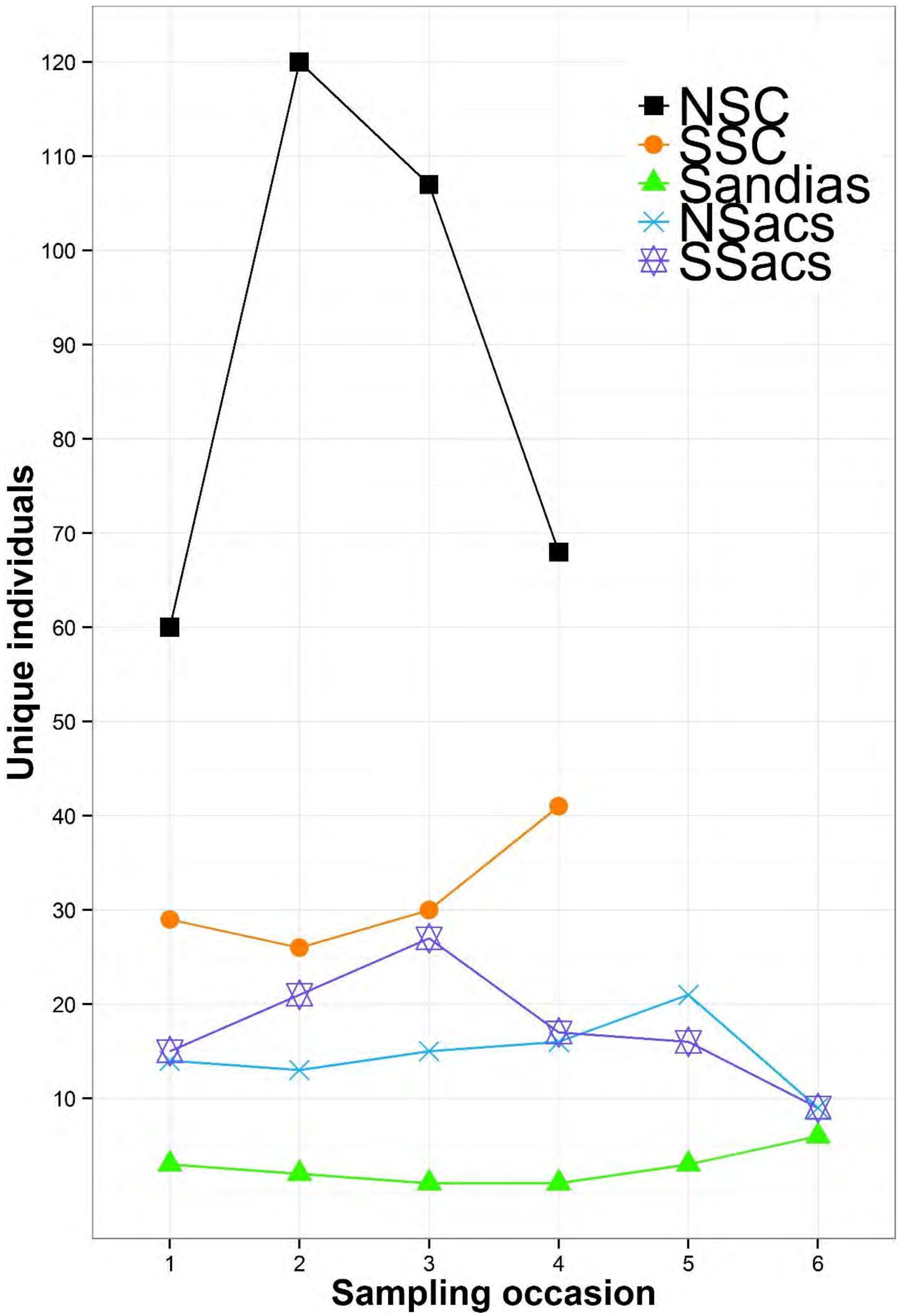


Figure 5. Number of unique individuals detected by hair traps and bear rubs combined for each sampling occasion in the Northern (NSC) and Southern (SSC) Sangre de Cristo, Sandia, and Northern (NSacs) and Southern (SSacs) Sacramento Mountains, NM.

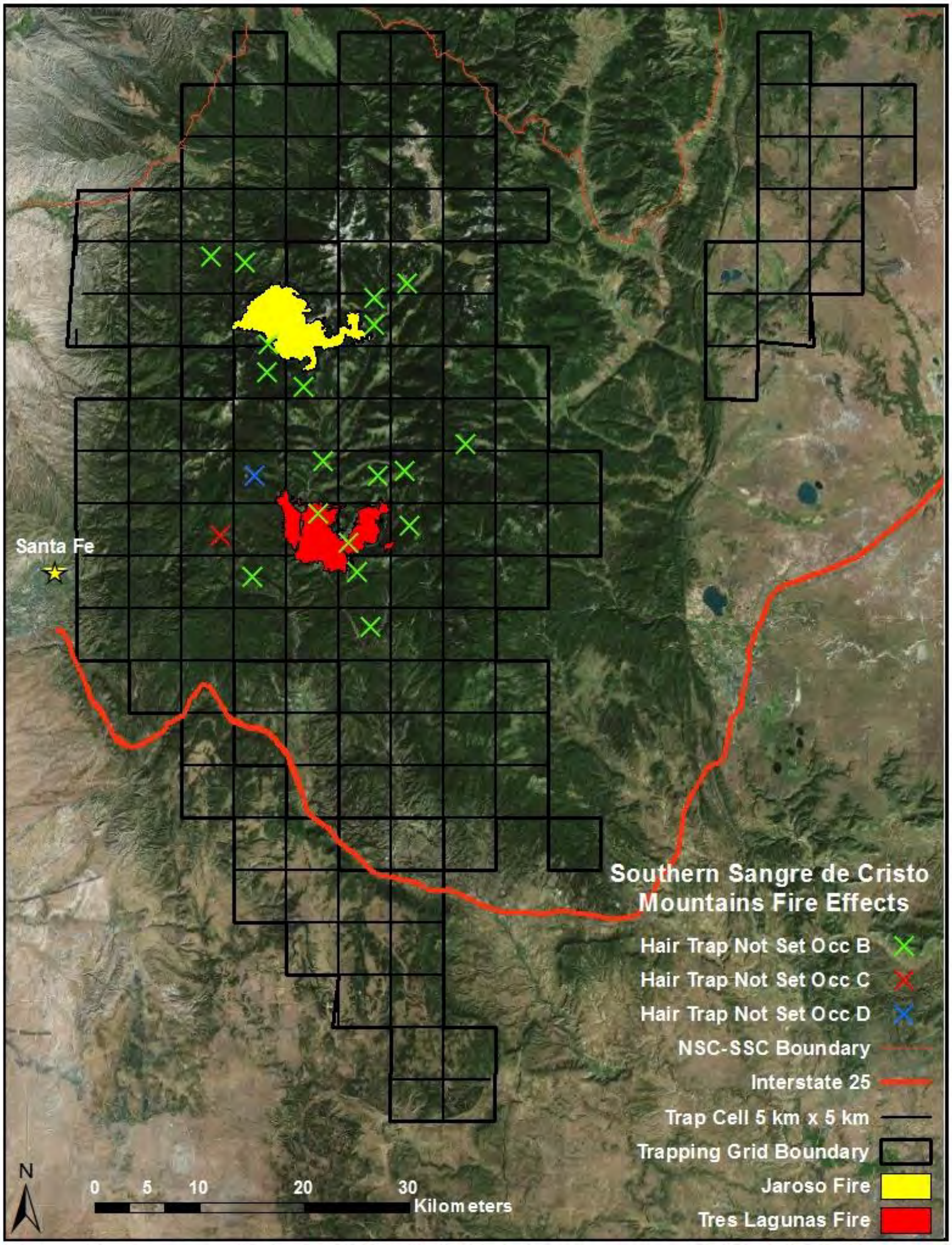


Figure 6. Map of hair traps not deployed due to the Jaroso and Tres Lagunas fires in the southern Sangre de Cristo Mountains, NM in 2013.

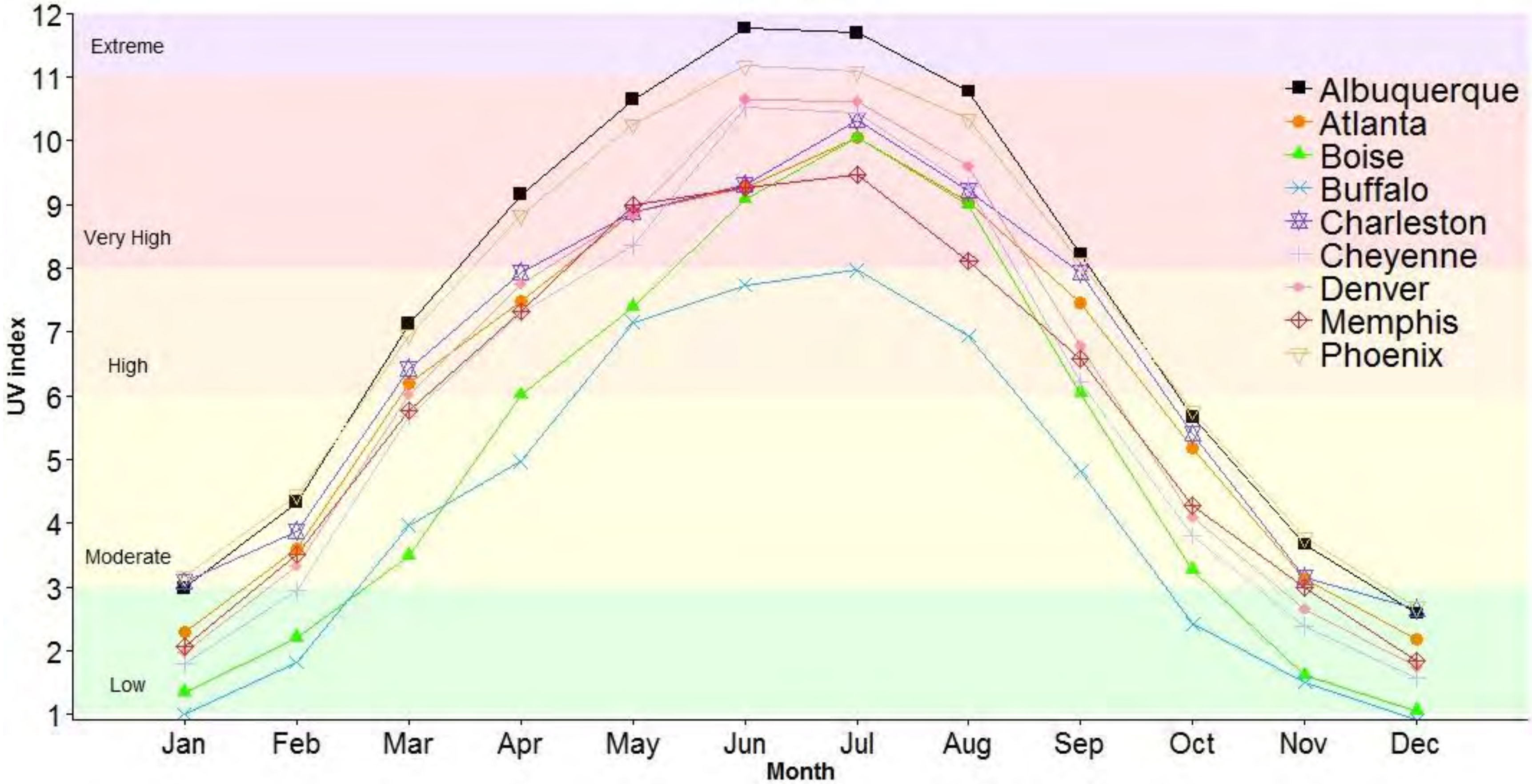


Figure 7. Mean montly ultraviolet index (UVI) generated by the National Oceanic and Atmospheric Administration showing estimated noontime intensity of ulatraviolet radiation coupled with the World Health Organization human health hazard UVI classification for Albuquerque, NM, Atlanta, GA, Boise, ID, Buffalo, NY, Charleston, SC, Cheyenne, WY, Denver, CO, Memphis, TN, and Phoenix, AZ, USA in 2012.

Table 1. Field sampling summary statistics allocated by number of detector types set (hair traps = HR & bear rub = BR), for the Northern (NSC) and Southern (SSC) Sangre de Cristo, Sandia, and Northern (NSacs) and Southern (SSacs) Sacramento Mountains, NM.

Study Area	**HT**[a]	**HT Sites**[b]	**HT Hit**[c]	**HT Effort**[d]	**BR**[a]	**BR Effort**[d]
NSC	256	1018	0.36	28,183	46	3,730
SSC	141	537	0.29	15,768	25	1,816
Sandias	12	69	0.42	979	7	293
NSacs	37	217	0.41	2,990	1	56
SSacs	111	656	0.29	9,090	33	1,112
Total	557	2497	0.33	57,010	112	7,007

[a] Number of sampling detectors set.

[b] Number of sampling detectors cumulatively summed across all sampling occasions.

[c] Number of traps which collected ≥1 hair sample over the all sampling occasions.

[d] Sampling effort represented by the number of days a sampling detector (hair trap & bear rub) was set summed across all detectors and all sampling occasions.

Table 2. The total number of hair samples collected across sampling occasions (1-6) and detector type (hair trap:bear rub) , and the overall total for the Northern (NSC) and Southern (SSC) Sangre de Cristo, Sandia, and Northern (NSacs) and Southern (SSacs) Sacramento Mountains, NM.

Study Area	**1**	**2**	**3**	**4**	**5**	**6**	**Total**
NSC	312 (299:13)	634 (582:52)	597 (571:26)	374 (339:35)	-	-	1917 (1791:126)
SSC	145 (141:4)	125 (124:1)	184 (183:1)	273 (246:27)	-	-	727 (694:33)
Sandias	8 (8:0)	30 (30:0)	23 (19:4)	28 (19:9)	51 (35:16)	37 (31:6)	177 (142:35)
NSacs	49 (49:0)	58 (58:0)	77 (73:4)	75 (73:2)	123 (118:5)	82 (79:3)	464 (450:14)
SSacs	93 (93:0)	143 (143:0)	183 (179:4)	135 (118:17)	129 (118:11)	115 (97:18)	798 (748:50)
Total	607 (590:17)	990 (937:53)	1064 (1025:39)	885 (795:90)	303 (271:32)	234 (207:27)	4083 (3825:258)

Table 3. Number of alleles, expected heterozygosity (H_E), and observed heterozygosity (H_O) for eight microsatellite markers used for individual identification of American black bears in the Sangre de Cristo Mountains, Sandia Mountains, and Sacramento Mountains, NM.

	No. Alleles			**H_E**			**H_O**		
Marker	**Sangres**	**Sandias**	**Sacramentos**	**Sangres**	**Sandias**	**Sacramentos**	**Sangres**	**Sandias**	**Sacramentos**
G10L	8.00	6.00	6.00	0.80	0.81	0.74	0.80	0.78	0.73
G1D	7.00	4.00	5.00	0.76	0.76	0.61	0.76	0.56	0.60
G10H	12.00	6.00	8.00	0.76	0.77	0.63	0.76	0.61	0.60
G10M	6.00	4.00	6.00	0.72	0.73	0.71	0.70	0.72	0.72
G10B	7.00	4.00	4.00	0.72	0.72	0.68	0.72	0.83	0.65
G10J	9.00	6.00	7.00	0.71	0.78	0.73	0.72	0.67	0.72
MU59	10.00	4.00	5.00	0.70	0.49	0.50	0.71	0.50	0.50
G10U	9.00	6.00	6.00	0.65	0.78	0.69	0.66	0.78	0.70
Mean	8.50	5.00	5.88	0.73	0.73	0.66	0.73	0.68	0.65

Table 4. Number of samples collected, number of samples that contained enough genetic material for analysis (samples analyzed), the proportion of samples that produced a successful genotype (Sample Success) and the number of unique individuals identified by each detector type (hair trap only = HT; bear rub only = BR; hair trap and bear rub = HTBR) for the Northern (NSC) and Southern (SSC) Sangre de Cristo, Sandia, and Northern (NSacs) and Southern (SSacs) Sacramento Mountains, NM.

				Unique Individuals		
Study Area	**Samples Collected**	**Samples Analyzed**	**Sample Success**	**M (HT:BR:HTBR)**	**F (HT:BR:HTBR)**	**Total (HT:BR:HTBR)**
NSC	1917	1416	0.49	190 (171:18:1)	189 (179:10:0)	379 (350:28:1)
SSC	727	517	0.48	67 (63:2:2)	64 (61:2:1)	131 (124:4:3)
Sandias	177	115	0.53	9 (5:1:3)	9 (8:1:0)	18 (13:2:3)
NSacs	464	360	0.61	49 (46:0:3)	39 (38:0:1)	88 (54:0:4)
SSacs	798	542	0.44	53 (50:2:1)	57 (53:3:1)	110 (103:5:2)
Total	4083	2950	0.50	368 (335:23:10)	358 (339:16:3)	726 (674:39:13)

Table 5. A summary of the capture history data for both male and female black bears identified by samples collected across the Northern (NSC) and Southern (SSC) Sangre de Cristo, Sandias, and Northern (NSacs) and Southern (SSacs) Sacramento Mountains, NM.

	Males								**Females**							
	N[a]	**Det[b]**	**Avg[c]**	**SD[d]**	**Max[e]**	**R[f]**	**MMR (km)[g]**	**MaxD (km)[h]**	**N[a]**	**Det[b]**	**Avg[c]**	**SD[d]**	**Max[e]**	**R[f]**	**MMR (km)[g]**	**MaxD (km)[h]**
NSC	190	239	1.26	0.43	3	33	7.57	52.03	189	216	1.14	0.35	3	23	3.98	47.41
SSC	67	80	1.19	0.38	3	8	12.46	29.33	64	77	1.20	0.39	2	12	2.53	20.33
Sandias	9	15	1.67	0.46	2	3	8.27	9.84	9	14	1.56	0.73	3	4	0.38	0.69
Nsacs	49	74	1.51	0.74	5	14	9.22	36.18	39	58	1.49	0.72	3	12	2.47	7.05
Ssacs	53	69	1.30	0.41	3	10	4.23	8.02	57	73	1.28	0.54	3	11	4.59	14.88
Total	368	477	1.39	0.48	5	68	8.35	27.08	358	438	1.33	0.55	3	62	2.79	18.07

[a] Number of animals detected.

[b] Total number of detections across all sampling occasions.

[c] Average number of detections per individual detected across all sampling occasions.

[d] Standard deviation for the average number of detections.

[e] Maximum number of detections of a single individual across all sampling occasions.

[f] Number of recaptured individuals across all sampling occasions.

[g] Mean maximum recapture distance.

[h] Maximum distance moved by an individual.

Table 6. The final set of *a priori* spatially explicit capture-recapture models for the Northern Sangre de Cristo Mountains, NM in 2012.

D[a]	**g0**[a]	**σ**[a]	**K**[b]	**AIC_c**[c]	**ΔAIC_c**[d]	**w_i**[e]	**Dev**[f]
constant	t + veg	t + veg	17	3149.15	0.00	1.00	3113.46
constant	t	t	9	3201.03	51.88	0.00	3182.54
constant	veg	veg	11	3216.43	67.28	0.00	3193.71
constant	t	veg	10	3221.75	72.59	0.00	3201.15
constant	veg	t	10	3236.73	87.58	0.00	3216.14
constant	type	type	5	3251.32	102.17	0.00	3241.16
constant	sex	sex	5	3271.17	122.02	0.00	3261.01
constant	constant	constant	3	3271.37	122.22	0.00	3265.31
sex	constant	constant	4	3273.42	124.26	0.00	3265.31

[a] Model parameters a function of: sex; t = time variation; type = detector type, veg = land cover type; + = additive effect; constant = no variation.

[b] Number of model parameters.

[c] Akaike's Information Criterion adjusted for small sample size.

[d] The difference between the top ranked model and the *i*th ranked model.

[e] Model weight.

[f] Model deviance = -2(log-likelihood).

Table 7. The final set of *a priori* spatially explicit capture-recapture models for the Southern Sangre de Cristo Mountains, NM in 2013.

D[a]	g0	σ	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	Dev[f]
constant	t + elev	t + elev	11	1169.98	0.00	0.87	1145.76
constant	t + veg	t + veg	17	1173.85	3.87	0.13	1134.44
constant	veg	t	10	1195.99	26.01	0.00	1174.16
constant	elev	t	7	1197.67	27.69	0.00	1182.76
constant	t	veg	10	1199.07	29.09	0.00	1177.24
constant	t	elev	7	1199.91	29.93	0.00	1185.00
constant	veg	veg	11	1205.12	35.14	0.00	1180.90
constant	t	t	9	1210.10	40.12	0.00	1190.61
constant	elev	elev	5	1210.48	40.50	0.00	1200.00
constant	sex	sex	5	1214.90	44.92	0.00	1204.42
constant	type	type	5	1216.35	46.37	0.00	1205.87
constant	constant	constant	3	1223.86	53.88	0.00	1217.67
sex	constant	constant	4	1225.92	55.94	0.00	1217.60

[a] Model parameters a function of: elev = elevation; sex; t = time variation; type = detector type; veg = land cover type; + = additive effect; constant = no variation.

[b] Number of model parameters.

[c] Akaike's Information Criterion adjusted for small sample size.

[d] The difference between the top ranked model and the *i*th ranked model.

[e] Model weight.

[f] Model deviance = -2(log-likelihood).

Table 8. The final set of *a prior*i spatially explicit capture-recapture models for the Sandia Mountains, NM in 2014.

D[a]	**g0**[a]	**σ**[a]	**K**[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	***w$_i$***[e]	**Dev**[f]
constant	sex	sex	5	209.23	0.00	0.96	194.23
constant	constant	constant	3	216.23	6.99	0.03	208.51
constant	elev	elev	5	219.20	9.97	0.01	204.20
sex	constant	constant	4	219.59	10.36	0.00	208.51
constant	type	type	5	219.84	10.60	0.00	204.84
constant	veg	veg	5	219.97	10.74	0.00	204.97
constant	t	elev	9	235.19	25.96	0.00	194.69
constant	t	veg	9	238.34	29.11	0.00	197.84
constant	elev	t	9	243.24	34.00	0.00	202.74
constant	veg	t	9	243.52	34.29	0.00	203.02
constant	t	t	13	311.75	102.52	0.00	194.75
constant	t + elev	t + elev	15	451.94	242.71	0.00	189.35
constant	t + veg	t + veg	15	461.61	252.38	0.00	191.61

[a] Model parameters a function of: elev = elevation; sex; t = time variation; type = detector type; veg = land cover type; + = additive effect; constant = no variation.

[b] Number of model parameters.

[c] Akaike's Information Criterion adjusted for small sample size.

[d] The difference between the top ranked model and the *i*th ranked model.

[e] Model weight.

[f] Model deviance = -2(log likelihood).

Table 9. The final set of *a prior*i spatially explicit capture-recapture models for the Northern Sacramento Mountains, NM in 2014.

D^a	$g0^a$	σ^a	K^b	$AIC_c{}^c$	$\Delta AIC_c{}^d$	$w_i{}^e$	Dev^f
constant	t + veg	t + veg	17	868.31	0.00	0.96	825.57
constant	veg	t	10	874.86	6.55	0.04	852.01
constant	t	veg	10	880.74	12.44	0.00	857.89
constant	veg	veg	7	883.07	14.76	0.00	867.67
constant	t + elev	t + elev	15	910.39	42.08	0.00	873.72
constant	sex	sex	5	910.45	42.14	0.00	899.71
constant	t	t	13	922.95	54.65	0.00	892.04
constant	elev	elev	5	923.70	55.39	0.00	912.97
constant	t	elev	9	925.73	57.42	0.00	905.42
constant	elev	t	9	928.60	60.30	0.00	908.30
constant	constant	constant	3	951.19	82.88	0.00	944.91
sex	constant	constant	4	952.25	83.94	0.00	943.77

[a] Model parameters a function of: elev = elevation; sex; t = time variation; veg = land cover type; + = additive effect; constant = no variation.

[b] Number of model parameters.

[c] Akaike's Information Criterion adjusted for small sample size.

[d] The difference between the top ranked model and the *i*th ranked model.

[e] Model weight.

[f] Model deviance = -2(log-likelihood).

Table 10. The final set of *a priori* spatially explicit capture-recapture models for the Southern Sacramento Mountains, NM in 2014.

D[a]	g0[a]	σ[a]	K[b]	AIC$_c$[c]	ΔAIC$_c$[d]	w_i[e]	Dev[f]
constant	veg	veg	7	1168.68	0.00	0.50	1153.58
constant	t + veg	t + veg	17	1169.62	0.94	0.31	1128.97
constant	t + elev	t+ elev	15	1170.58	1.90	0.19	1135.47
constant	veg	t	10	1180.23	11.54	0.00	1158.00
constant	type	type	5	1182.05	13.37	0.00	1171.48
constant	elev	elev	5	1182.51	13.83	0.00	1171.93
constant	elev	t	9	1184.24	15.56	0.00	1164.44
constant	t	t	13	1186.59	17.91	0.00	1156.80
constant	t	elev	9	1191.22	22.54	0.00	1171.42
constant	t	veg	10	1193.33	24.65	0.00	1171.10
constant	constant	constant	3	1196.53	27.85	0.00	1190.31
constant	sex	sex	5	1198.08	29.40	0.00	1187.50
sex	constant	constant	4	1198.54	29.86	0.00	1190.16

[a] Model parameters a function of: elev = elevation; sex; t = time variation; type = detector type; veg = land cover type; + = additive effect; constant = no variation.

[b] Number of model parameters.

[c] Akaike's Information Criterion adjusted for small sample size.

[d] The difference between the top ranked model and the *i*th ranked model.

[e] Model weight.

[f] Model deviance = -2(log-likelihood).

Table 11. Density and model parameter estimates, coefficient of variation of the density estimate (CV), detection probability at the activity center (g0), spatial scale over which detection probability declines (σ; km), and their 95% confidence intervals for the Northern (NSC) and Southern (SSC) Sangre de Cristo, Sandia, and Northern (NSacs) and Southern (SSacs) Sacramento Mountains, NM. Competing models for the SSC and SSacs were model averaged. We performed all analyses within a spatially explicit capture-recapture framework.

Study Area	**D**[a]	**g0**[b]	**σ**[c]	$\widehat{D}$[d]	**CV**($\widehat{D}$)	$\widehat{g0}$[e]	$\hat{\sigma}$[f]
NSC	constant	t + veg	t + veg	21.86 (17.83 – 26.80)	0.10	0.00060 (0.000233 - 0.001528)	3.31 (2.09 – 5.25)
SSC	constant	t + elev	t + elev	19.74 (13.77 – 28.30)	0.18	0.00001 (0.000006 – 0.000052)	18.35 (12.73 – 26.46)
	constant	t + veg	t + veg				
Sandias	constant	sex	sex	25.75 (13.22 – 50.14)	0.35	0.02941[g] (0.010779 – 0.077689) 0.00163[h] (0.000480 – 0.005488)	0.76[g] (0.49 – 1.15) 4.99[h] (2.46 – 10.09)
NSacs	constant	t + veg	t + veg	20.17 (15.35 – 26.52)	0.14	0.00266 (0.000580 – 0.012125)	5.42 (2.03 – 14.44)
SSacs	constant	veg	veg	16.55 (11.64 – 23.53)	0.18	0.00318 (0.001087 - 0.009279)	2.67 (1.69 – 4.21)
	constant	t + veg	t + veg				
	constant	t + elev	t + elev				

[a] Final model structure for the secr parameter, density (D).

[b] Final model structure for the secr parameter, detection probability (g0).

[c] Final model structure for the secr parameter, σ, the spatial scale over which detection probability declines.

[d] Black bear density estimate (bears/100 km^2) with the 95% confidence intervals in parentheses.

[e] Detection probability (g0) parameter estimate with the 95% confidence intervals in parentheses.

[f] σ (km) parameter estimate with the 95% confidence intervals in parentheses.

[g] Parameter estimate for female black bears.

[h] Parameter estimate for male black bears.

Table 12. Mean density estimates for black bears (bears/100 km^2) and 95% CIs in parentheses for noninvasive genetic sampling studies conducted in the United States that also used a spatially explicit capture-recapture framework.

State	$\hat{D}$	**Reference**
Ozark Highlands, Missouri	1.7 (1.1 – 2.4)	Wilton et al. 2014
Carver Bay, South Carolina	4.6 (2.4 – 6.7)	Drewry et al. 2013
Southern Black Bear Range, New York	9.1 (7.6 – 11.3)	Sun et al. 2014
Picture Rocks National Lakeshore, Michigan	10.5 (8.5 – 12.7)	Sollmann et al. 2012
Glacier National Park, Montana[a]	12.0 (10.0 – 14.4)	Stetz et al. 2014[a]
Southern Sacramento Mountains, New Mexico	16.5 (11.6 – 23.5)	This Study
Southern Sangre de Cristo Mountains, New Mexico	19.7 (13.8 – 28.3)	This Study
Fort Drum Military Installation, New York	20.0 (15.0 – 26.0)	Gardner et al. 2010
Northern Sacramento Mountains, New Mexico	20.1 (15.3 – 26.5)	This Study
Northern Sangre de Cristo Mountains, New Mexico	21.8 (17.8 – 26.8)	This Study
Sandia Mountains, New Mexico	25.7 (13.2 – 50.1)	This Study
Spanish Peaks, Colorado	44.0 (32.1 – 55.8)	Apker et al. 2009
Lewis Ocean Bay, South Carolina	33.9 (22.9 – 44.8)	Drewry et al. 2013
Alligator River National Wildlife Refuge, North Carolina 2004	37.0 (30.7 – 43.2)	Tredick et al. 2009
Great Dismal Swamp National Wildlife Refuge, North Carolina and Virginia	46.0 (34.6 – 57.3)	Tredick et al. 2009
Alligator River National Wildlife Refuge, North Carolina 2003	57.0 (47.9 – 66.0)	Tredick et al. 2009
Pocosin Lakes National Wildlife Refuge, North Carolina 2002	58.0 (49.1 – 66.8)	Tredick et al. 2009
Pocosin Lakes National Wildlife Refuge, North Carolina 2003	77.0 (65.4 – 88.5)	Tredick et al. 2009

[a] Black bear population sympatric with grizzly bears (*Ursus arctos*).

Update to Bear Habitat Model for the 2016-2020 Rule

Introduction

Black bears are cryptic, mainly solitary animals that prefer areas with dense cover, and therefore cannot be directly counted through aerial or ground surveys. Density estimates are derived through collecting field data on individually marked animals and applying population reconstruction or mark-recapture analyses to the data. Habitat models estimate quantity and location of bear habitat around the state, and bear density estimates generated for mountain ranges or specific habitat types can be extrapolated to similar areas to derive a statewide population estimate. In this paper, we describe the process used to update the original habitat model using the most current technology available.

The original habitat model for black bear population estimation in New Mexico was generated as part of the 9 year Black Bear Ecology Study (hereafter 2001 study, Costello et al. 2001) conducted 1992–2000 (Fig. 1). This habitat model utilized the New Mexico Gap Analysis Program (NM GAP) land cover classification which was designed to predict species distribution based on habitat type. The NM GAP model was used, in conjunction with information gathered from 316 radio-collared bears across 2 study areas and mast production potential by habitat type, to predict primary, secondary, and edge habitat classifications across New Mexico. NM GAP had several data limitations (Costello et al. 2001, p. 109), and the habitat model was intended to be updated as new information became available (Costello et al. 2001, p. 111). Advances in technology such as more detailed and accurate land cover classifications (the Landscape Fire and Resource Management Planning Tools (LANDFIRE) land cover classification), ability to identify individual animals through genetic techniques (Boerson et al. 2003, Lukacs and Burnham 2005), improved spatial data, and more accurate statistical methods provide an opportunity to develop more accurate population estimates.

Improved land cover classification and models are available through the Southwest Regional GAP and the more recently developed LANDFIRE datasets, which improve upon the shortcomings of the NM GAP. The habitat model from the 2001 study depended on the NM GAP dataset because it was the only comprehensive, statewide dataset available at the time. It posed substantial limitations (Costello et al. 2001, p. 109) due to poor classification accuracy (especially for habitat types important to bears) and inability to separate habitat type from cover density. As an example, the NM GAP model accurately predicted Rocky Mountain/Great Basin Open and Closed Conifer habitat types on average 28% and 15%, respectively (Thompson et al. 1996). In comparison, LANDFIRE separated these into multiple vegetation classifications, each with 10 canopy closure classifications, and the resulting model accurately predicted the analogous habitat types approximately 88% and 79% of the time, respectively (Stehman 2012).

Substantial improvements in habitat classification accuracy and the ability to separate habitat type from cover density were important developments in the new LANDFIRE datasets. The number of habitat classifications increased from 42 in NM GAP (Appendix A) to more than 150 in LANDFIRE allowing for fine-scale classification in areas where there were previously few classification options. This allows for greater discrimination across similar habitat types and improved classification accuracies. As an example, the single Rocky Mountain Upper Montane Conifer habitat type from the NM GAP can be compared to 9 habitat types within the LANDFIRE dataset including 6 mixed conifer classifications, 2 riparian classifications, and 1 aspen classification. Cover type classifications have become more standardized, allowing for consistent and repeatable land cover classifications, and a greater depth of information for comparison across years. The updated habitat model (Fig. 2) is based on LANDFIRE data for 2008, 2010, and 2012, which improved the robustness of the final model as it does not depend on a single year of data.

Separating canopy closure from vegetation classification data is another improvement in the LANDFIRE database. For example, NM GAP separates the Rocky Mountain/Great Basin Open and Closed Conifer Woodland classifications based on vegetation type and canopy density within a single dataset. By comparison, LANDFIRE separates vegetation classification and canopy closure into 2 datasets which provides improved discrimination in vegetation classification while maintaining the ability to differentiate by canopy closure. The aforementioned NM GAP classifications are separated in LANDFIRE into at least 4 vegetation classifications and canopy closure classifications in 10% increments.

Advances in genetic laboratory techniques have resulted in more sophisticated bear density estimation methods. The 2001 study captured as many animals as possible and used population reconstruction methods to estimate densities. It was assumed not all resident bears were captured; therefore, population estimates were considered minimum, not average, population sizes (Costello et al. 2001, p. 88). In contrast, hair-snare studies can employ spatial capture-recapture statistics which produce average population estimates and associated confidence intervals, as opposed to the point estimate produced by population reconstruction. Recent developments in statistical models have alleviated some of the uncertainties in classic capture-recapture population models and should provide more accurate estimates (Gardiner et al. 2010). Genetic hair snare studies are currently being employed around New Mexico to estimate bear densities across several mountain ranges, and the results are being used in conjunction with the updated habitat model to provide more accurate bear population estimates.

The advent and increased use of GPS radio-collars has provided insight into movement rates and capabilities of bears. Bears travel longer distances than previously believed, increasing the maximum distance between viable population centers (Liley and Walker 2015). Increased movement capacity, especially by breeding males, also provides more flexibility in the patch size and distance-based metrics of model assumptions because a population can remain sustainable with fewer individuals as long as sufficient breeding is maintained. In addition, larger patches separated by a long distance are often connected through linear patches of habitat (e.g., mesa edges and riparian canyons) that are not typically considered primary bear habitat. These linear patches act as stepping stones for longer distance movements and subsequently improve connectivity across the landscape.

Methods

As a means of incorporating up-to-date and comprehensive landcover data, we employed LANDFIRE datasets to update the bear habitat model. These data result from the partnership between the U.S. Forest Service and Department of the Interior to provide consistent nationwide landcover mapping for fire management and general resource use, and are the most accurate and updated datasets available. These data are based on 30-m Landsat satellite imagery and have a reported accuracy of 0–100% depending on landcover type with forest and woodland landcover types having a user accuracy of 87.8% in the Southwest super zone (Bobbe et al. 2006). Datasets are updated every 2 years, and we acquired the 3 most recent vegetation type datasets (i.e., 2008, 2010, and 2012) from the LANDFIRE website (http://www.landfire.gov/) for this analysis.

We determined suitability of available cover types based on food availability and their use by bears. Cover types and their corresponding values as bear habitat were modified from the 2008 to the 2010 model because cover types were further refined (Appendix B and C). We omitted cover types with <10 cells throughout the original LANDFIRE image if they were of questionable importance to bears. Cover types were classified either as bear habitat or non-bear habitat, and did not specify primary and secondary classifications as in Costello et al. (2001); instead we depended on the selection criteria to determine the primary, secondary, and edge designations. We used the Extract by Attributes tool within the Spatial Analyst extension of ArcGIS to subset the LANDFIRE datasets based on the appropriate cover type value (Appendix B and C). Extracted values were reclassified into a single value and the 3 datasets were added together, keeping only the areas where all 3 datasets agreed.

We used the Aggregate tool in Spatial Analyst to sum across the final dataset by a factor of 7 to generate an output in 210-m-sided (0.0441 km^2) blocks. We selected 7 as the best aggregate factor from a test run across aggregate factors 2–10 based on knowledge of bear use across the state while balancing the smoothing effects of the aggregation. This also accommodated errors within the LANDFIRE dataset by eliminating small areas. We visually inspected the distribution of aggregated values and assigned a cutoff of 25% as an acceptable breakpoint between “edge” and “primary” designations. Areas that fell below the break point were considered edge habitat and were not included in the final model areal calculations. To allow for areal calculations and patch size selection, we converted the model raster to a polygon feature class without simplification.

We created a filter from LANDFIRE 2012 existing vegetation cover data by creating a raster with human-dominated cover types, barren areas, and cover classes <20%. We only used the 2012 dataset as there are concerns about the validity of canopy cover data in earlier LANDFIRE datasets (Scott 2008). We reclassified the appropriate cover classes to the same value (Appendix D), aggregated them to a 210-m cell, and kept the top 75% of cells (to match the habitat classification aggregation). We converted this to a polygon and filtered the model. We converted multipart features to single-part features prior to the selection process, and updated the area calculation. The same filter was used to further discriminate bear habitat in GMU's 10, 12, and 13 except we included cover classes <30%. The GMU 10, 12, and 13 areas were replaced with the 30% model outputs in the final model area calculations.

The Select Layer by Location and Select Layer by Attributes tools were used to set distance-based search criteria and patch size requirements, as follows:

- All features >200 km^2 were selected from the initial data set as main patches based on minimum habitat size needed to support a minimum viable population of 45–50 individuals. Use of a patch size smaller than the 300 km^2 used by Costello et al. (2001) is based on more accurate bear density estimates produced by the current bear density study, and documentation of larger distances moved as provided by GPS radio-collars. Inclusion of parcels 200–300 km^2 defined the Dry Cimarron area in GMU 58 and the Los Pinos Mountains in GMU 18 as bear habitat, both of which are known to sustain sizable bear populations. The Peloncillo Mountains, known to support a bear population, fell just below the 200 km^2 minimum, but were included due to proximity of large patches of bear habitat in Arizona.
- We varied both distance to and minimum patch size within biologically reasonable values, with minimal impact on the resulting habitat model. We selected all features within 30 km of main patches that were >25 km^2 because they included key areas with known populations of bears including the Oscura Mountains in GMU 19, Sierra Grande in GMU 56, and the complex around Mesa Rica in GMU 42. These values are greater than those used in Costello et al. (2001; all features within 15 km of main patches that were >20 km^2) because data showing that bears move larger distances means that they can move between patches spaced more widely apart, and higher bear densities on the landscape mean that smaller patches can support the 1-2 bears necessary to be considered bear habitat.
- All selected parcels included a 2 km buffer because black bears consistently use areas within 2 km of primary bear habitat.
- All holes smaller than 2 km^2 were closed with the Eliminate Polygon Part tool as a means of matching the 2 km "buffer" in the previous step and following a methodology similar to Costello et al. (2001).

We used the Intersect tool to combine the final selection output with the Game Management Unit shapefile. Total area (km^2) for each GMU was generated using the Summary Statistics tool. Areas that did not meet the selection criteria as secondary habitat and areas that fell below the 25% aggregation were classified as edge habitat. We did not include secondary or edge habitats in area calculations, but have included them in the map as areas of potential use by bears (Fig. 1, Table 1). The Python code for the classification and selection process is included in Appendix E.

We verified bear mortality locations from 1994–2014 through spatial location and agreement with the reported GMU. There were 9,852 mortalities in the database, of which 197 (2.0%) had the UTM zone interpolated from the GMU and Easting, 91 (0.9%) were removed for falling outside the geographic bounds of NM, 1,039 (10.8%) were removed due to a disparity between the GMU and the UTM coordinate, and 643 (6.7%) were removed due to lacking or incorrect spatial information. We overlaid the 7,809 spatially-verified mortalities on the new habitat model as a check of model validity (Table 2). Hunter harvest locations (n = 6,863) occurred in primary habitat more often than depredation (n = 676), road kill (n = 239), and other (n = 31) locations. The new model contained 83% of sport-harvest mortalities within primary bear habitat.

We could not directly compare our model validity results with those of the 2001 study (p. 100) due to differences in methodologies. Specifically, our verified sport-harvest location data set was from 1994-2014, as opposed to the 1990-1999 data set used in the 2001 study. Next, although both studies verified mortality locations using some of the same standards, there was not enough detail in the 2001 study report to know if the standards were identical. Differences in standards for which records to include and how modifications were made could lead to very different results. Finally, Costello et al. (2001) did not verify the accuracy of the habitat model. Rather, she created a generalized distribution map identifying major regions of bear habitat (p. 95; e.g. Sangre de Cristo Complex in Fig. 1) which comprise larger land areas than primary habitat predicted by the habitat model. When we overlaid the 1994-2014 verified dataset on the major regions of bear habitat as defined in the 2001 study, 81% of harvest locations fell within those regions, compared with 95% reported for the 1990-1999 dataset. When we overlaid our verified sport-harvest locations on primary habitat produced by the 2015 habitat model, 83% of sport-harvest mortalities were within primary bear habitat, compared with the 2001 model that contained 71% of sport-harvest mortalities. We do not know why there is a discrepancy in the sport-harvest locations found in major regions of bear habitat between the 2 data sets, and reiterate our concern that they were not created using the same standards and therefore none of the model validity results should be compared.

Figure 1. Predicted black bear habitat in New Mexico from Costello et al. (2001).

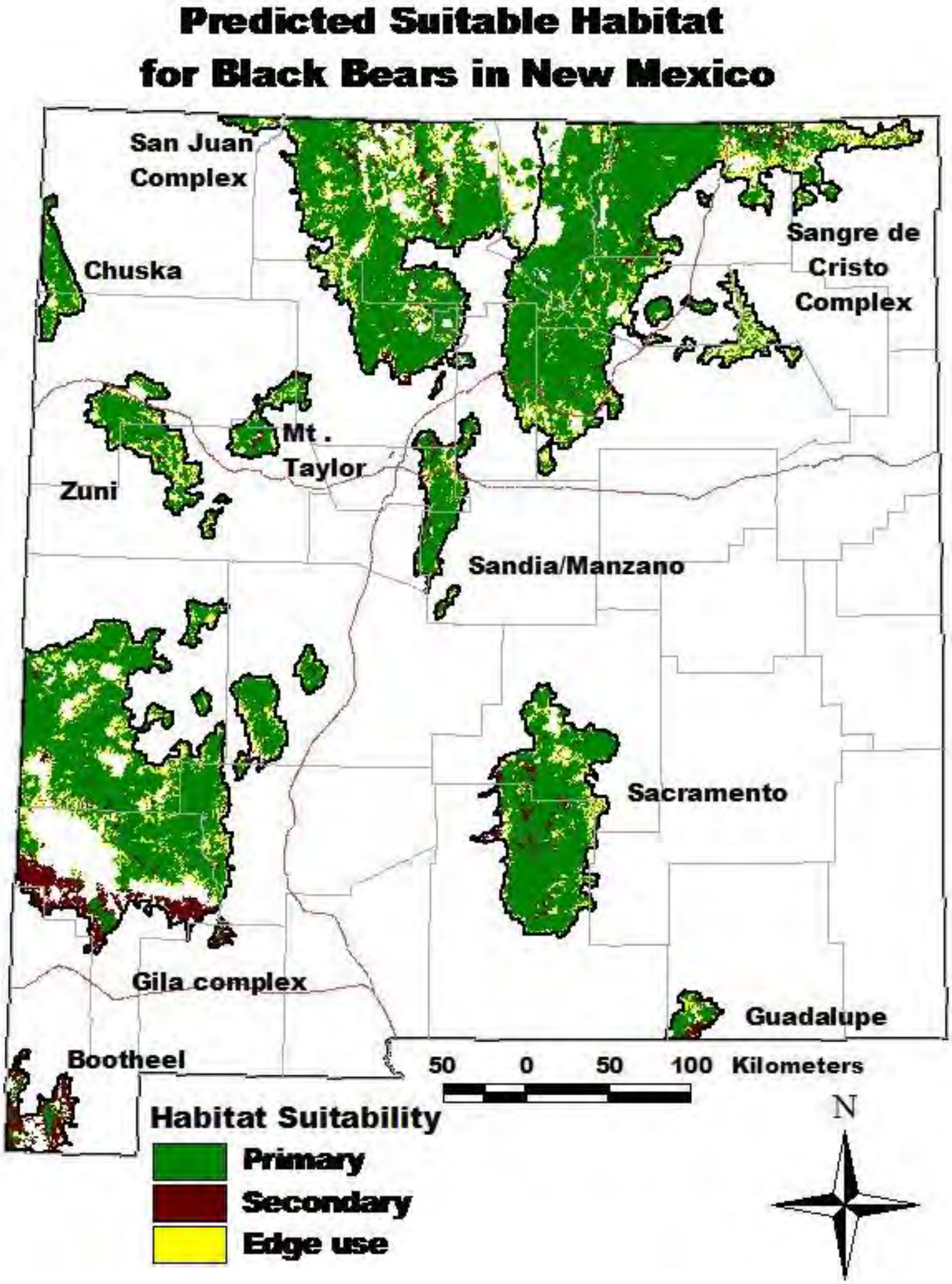


Figure 2. Predicted black bear habitat in New Mexico 2015.

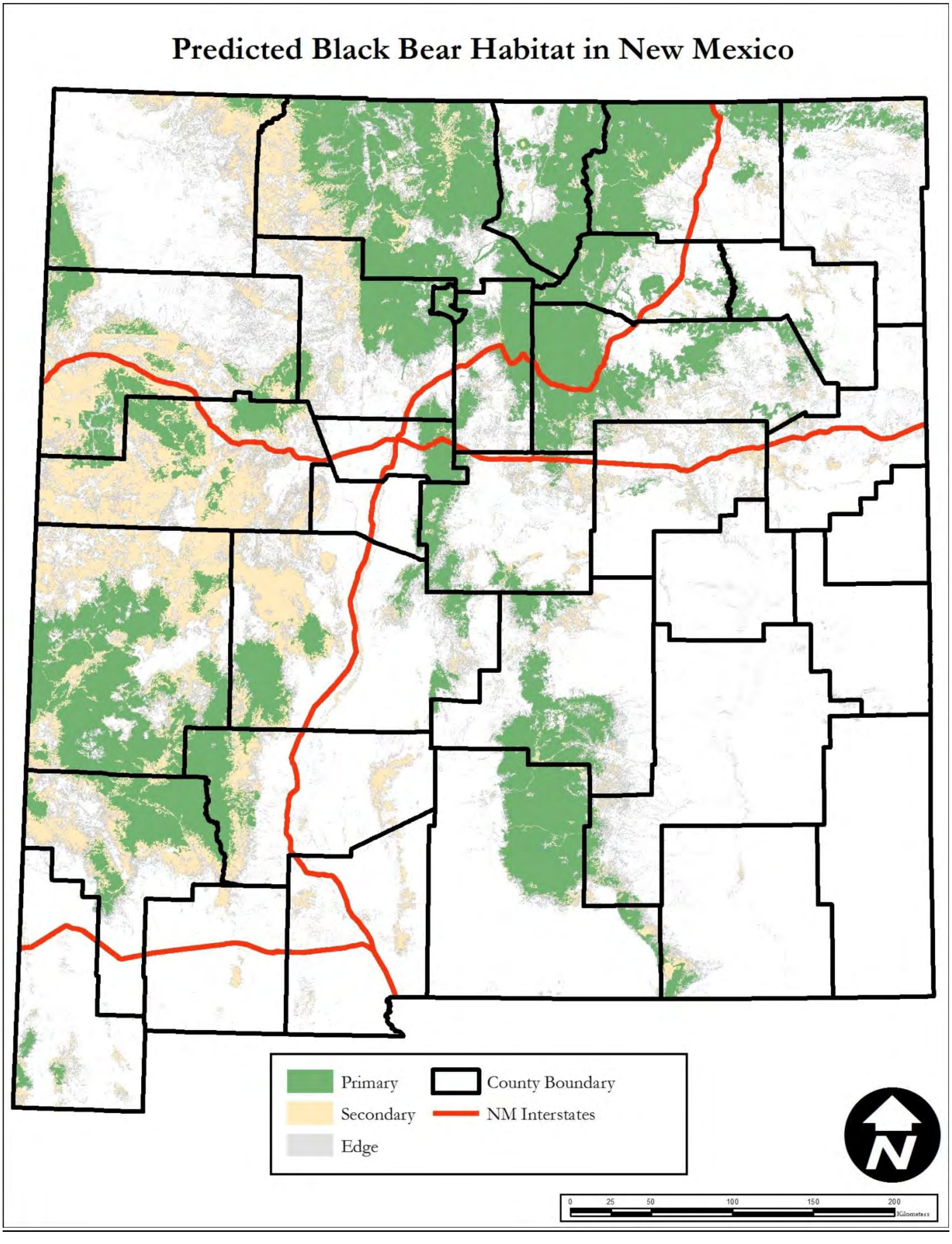


Table 1. Total primary bear habitat as predicted by the model by bear management zone and game management unit.

Zone	GMU	Primary Habitat
Tribal	1	1,505
	3	1,645
	11	706
	35	1,649
		5,505
1	4	1,212
	5	895
	6	4,408
	7	15
	51	2,043
	52	723
		9,296
2	2	**880**
3	49	1,029
	50	533
	53	1,081
		2,642
4	48	388
	45	3,497
	46	1,893
		5,778
5	54	653
	55	3,620
		4,273
6	39	151
	42	1,901
	43	1,954
	47	674
	59	10
		4689
7	56	192
	57	779
	58	674
		1,645
8	8	**719**
9	9	1,255
	10	1,438
		2,693
10	12	61
	13	520
	15	2,549
	16	5,334
	17	1,504
	18	763
	21	1,606
	22	484
	23	1,114
	24	1,310
	26	60
	27	182
		15,488
11	37	1,113
	38	698
		1,811
12	34	**2,428**
13	36	**1,184**
14	14	**1,267**
Total		**60,298**

Table 2. Spatially-verified bear mortality location agreement by type of mortality event and habitat type for our updated 2015 model and the 2001 study (Costello et al.).

Walker et al. Model	Habitat Type					Model Test by Habitat Type			
	Primary	Secondary	Edge	None	Total	Primary	Secondary	Edge	None
Sport Harvest	5,675	501	382	305	6,863	83%	7%	6%	4%
Road Kill	100	33	47	59	239	42%	14%	20%	25%
Depredation	352	117	94	113	676	52%	17%	14%	17%
Other	19	3	1	8	31	3%	0%	0%	1%
Total	6,146	654	524	485	7,809	79%	8%	7%	6%

Costello et al. Model	Habitat Type					Model Test by Habitat Type			
	Primary	Secondary	Edge	None	Total	Primary	Secondary	Edge	None
Sport Harvest	4,848	410	574	1,031	6,863	71%	6%	8%	15%
Road Kill	94	20	20	105	239	39%	8%	8%	44%
Depredation	327	20	77	252	676	48%	3%	11%	37%
Other	17	0	3	11	31	3%	0%	0%	2%
Total	5,286	450	674	1,399	7,809	68%	6%	9%	18%

Literature Cited

Bobbe, T., G. Dillon, D. Ohlen, S. Prisley, M. Reeves, J. L. Smith, S. Stehman, and Z. Zhu. 2006. LANDFIRE product assessment: western milestone super zone analysis and report. LANDFIRE Program, Missoula, Montana, USA.

Boerson, M. R., J. D. Clark, and T. L. King. 2003. Estimating black bear population density and genetic diversity at Tensas River, Louisiana using microsatellite DNA markers. Wildlife Society Bulletin 31:197–207.

Costello, C. M., D. E. Jones, K. A Green Hammond, R. M. Inman, K. H. Inman, B. C. Thompson, R. A. Deitner, and H. B. Quigley. 2001. A study of black bear ecology in New Mexico with models for population dynamics and habitat suitability. New Mexico Department of Game and Fish, Santa Fe, USA.

Gardiner, B., J. A. Royle, M. T. Wegan, R. E. Rainbolt, and P. D. Curtis. 2010. Estimating black bear density using DNA data from hair snares. Journal of Wildlife Management 74:318–325.

Liley, S. G., and R. N. Walker. 2015. Extreme movement by an American black bear in New Mexico and Colorado. Ursus: *In press*.

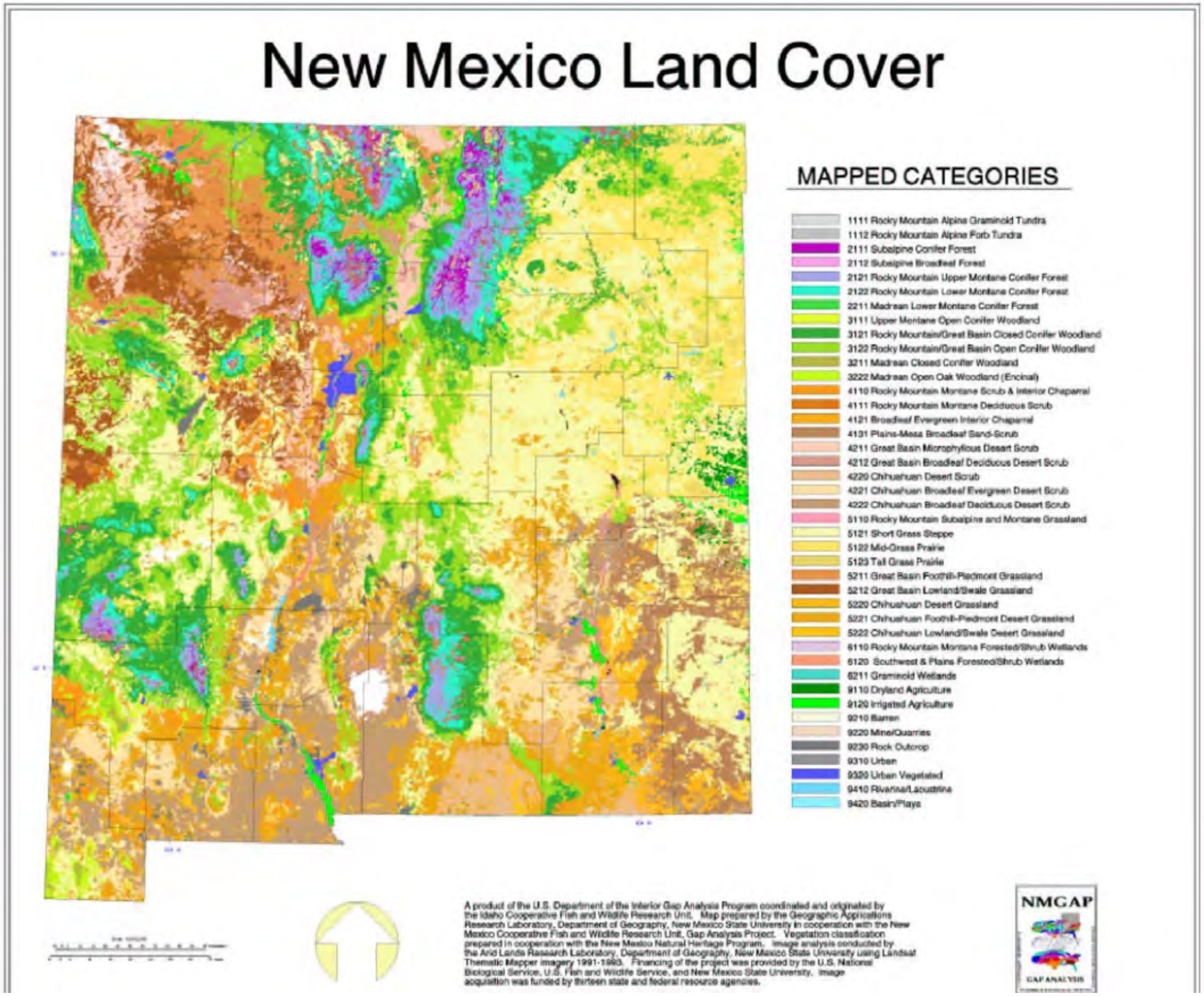
Lukacs, P. M. and K. P. Burnham. 2005. Estimating Population Size from DNA-Based Closed Capture-Recapture Data Incorporating Genotyping Error. Journal of Wildlife Management 69:396–403.

Scott, J. 2008. Review and assessment of LANDFIRE canopy fuel mapping procedures. LANDFIRE Program, Missoula, Montana, USA.

Stehman, S. 2012. Landfire accuracy estimates for the Great Basin superzone: comparison of original estimates with poststratified estimates adjusted for proportion of area in each EVT map class. Landscape Fire and Resource Management Planning Tools (LANDFIRE), www.landfire.gov

Thompson, B. C., P. J. Crist, J. S. Prior-Magee, R. A. Deitner, D. L. Garber, and M. A. Hughes. 1996. Gap analysis of biological diversity conservation in New Mexico using geographic information systems. New Mexico Cooperative Fish and Wildlife Research Unit, Las Cruces, USA.

Appendix A



A product of the U.S. Department of the Interior Gap Analysis Program coordinated and originated by the Idaho Cooperative Fish and Wildlife Research Unit. Map prepared by the Geographic Applications Research Laboratory, Department of Geography, New Mexico State University in cooperation with the New Mexico Cooperative Fish and Wildlife Research Unit, Gap Analysis Project. Vegetation classification prepared in cooperation with the New Mexico Natural Heritage Program. Image analysis conducted by the Arid Lands Research Laboratory, Department of Geography, New Mexico State University using Landsat Thematic Mapper imagery 1991-1993. Financing of the project was provided by the U.S. National Biological Service, U.S. Fish and Wildlife Service, and New Mexico State University. Image acquisition was funded by thirteen state and federal resource agencies.

Appendix B

Value and Classnames from 2008 LANDFIRE dataset defined as black bear habitat.

VALUE	CLASSNAME
2011	Rocky Mountain Aspen Forest and Woodland
2012	Rocky Mountain Bigtooth Maple Ravine Woodland
2016	Colorado Plateau Pinyon-Juniper Woodland
2019	Great Basin Pinyon-Juniper Woodland
2023	Madrean Encinal
2024	Madrean Lower Montane Pine-Oak Forest and Woodland
2025	Madrean Pinyon-Juniper Woodland
2026	Madrean Upper Montane Conifer-Oak Forest and Woodland
2049	Rocky Mountain Foothill Limber Pine-Juniper Woodland
2050	Rocky Mountain Lodgepole Pine Forest
2051	Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland
2052	Southern Rocky Mountain Mesic Montane Mixed Conifer Forest and Woodland
2054	Southern Rocky Mountain Ponderosa Pine Woodland
2055	Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland
2056	Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest and Woodland
2057	Rocky Mountain Subalpine-Montane Limber-Bristlecone Pine Woodland
2059	Southern Rocky Mountain Pinyon-Juniper Woodland
2061	Inter-Mountain Basins Aspen-Mixed Conifer Forest and Woodland
2070	Rocky Mountain Alpine Dwarf-Shrubland
2107	Rocky Mountain Gambel Oak-Mixed Montane Shrubland
2117	Southern Rocky Mountain Ponderosa Pine Savanna
2119	Southern Rocky Mountain Juniper Woodland and Savanna
2155	North American Warm Desert Riparian Forest and Woodland
2159	Rocky Mountain Montane Riparian Forest and Woodland
2160	Rocky Mountain Subalpine/Upper Montane Riparian Forest and Woodland
2208	Abies concolor Forest Alliance
2215	Quercus turbinella Shrubland Alliance
2217	Quercus gambelii Shrubland Alliance

Appendix C

Value and Classnames from 2010 and 2012 LANDFIRE datasets defined as black bear habitat.

VALUE	CLASSNAME
3011	Rocky Mountain Aspen Forest and Woodland
3012	Rocky Mountain Bigtooth Maple Ravine Woodland
3016	Colorado Plateau Pinyon-Juniper Woodland
3019	Great Basin Pinyon-Juniper Woodland
3023	Madrean Encinal
3024	Madrean Lower Montane Pine-Oak Forest and Woodland
3025	Madrean Pinyon-Juniper Woodland
3026	Madrean Upper Montane Conifer-Oak Forest and Woodland
3049	Rocky Mountain Foothill Limber Pine-Juniper Woodland
3050	Rocky Mountain Lodgepole Pine Forest
3051	Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland
3052	Southern Rocky Mountain Mesic Montane Mixed Conifer Forest and Woodland
3054	Southern Rocky Mountain Ponderosa Pine Woodland
3055	Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland
3056	Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest and Woodland
3057	Rocky Mountain Subalpine-Montane Limber-Bristlecone Pine Woodland
3059	Southern Rocky Mountain Pinyon-Juniper Woodland
3061	Inter-Mountain Basins Aspen-Mixed Conifer Forest and Woodland
3070	Rocky Mountain Alpine Dwarf-Shrubland
3107	Rocky Mountain Gambel Oak-Mixed Montane Shrubland
3117	Southern Rocky Mountain Ponderosa Pine Savanna
3119	Southern Rocky Mountain Juniper Woodland and Savanna
3155	North American Warm Desert Riparian Forest and Woodland
3159	Rocky Mountain Montane Riparian Forest and Woodland
3160	Rocky Mountain Subalpine/Upper Montane Riparian Forest and Woodland
3208	Abies concolor Forest Alliance
3215	Quercus turbinella Shrubland Alliance
3217	Quercus gambelii Shrubland Alliance

Appendix D

Value and Classnames for cover classes used to create a filter for the habitat model. The >=20 and < 30% classes were only included in GMU 12 and 13.

VALUE	CLASSNAMES
11	Open Water
12	Snow/Ice
13	Developed-Upland Deciduous Forest
14	Developed-Upland Evergreen Forest
15	Developed-Upland Mixed Forest
16	Developed-Upland Herbaceous
17	Developed-Upland Shrubland
22	Developed - Low Intensity
23	Developed - Medium Intensity
24	Developed - High Intensity
25	Developed-Roads
31	Barren
32	Quarries-Strip Mines-Gravel Pits
61	NASS-Vineyard
63	NASS-Row Crop-Close Grown Crop
64	NASS-Row Crop
65	NASS-Close Grown Crop
68	NASS-Wheat
100	Sparse Vegetation Canopy
101	Tree Cover >= 10 and < 20%
102	Tree Cover >= 20 and < 30%
111	Shrub Cover >= 10 and < 20%
112	Shrub Cover >= 20 and < 30%
121	Herb Cover >= 10 and < 20%
122	Herb Cover >= 20 and < 30%

Appendix E

Python script run to process multiple aggregate factors and select parcels as indicated.

```
# Author:   Ryan Walker, CWB
#           Regional Wildlife Biologist
#           New Mexico Department of Game and Fish
# Date: 30 January 2015
# Tool Description: This tool uses the LANDFIRE datasets to build a black bear (Ursus
  americanus) habitat model.
#

import arcpy

# Specify input raster paths.
raster2012 = arcpy.Raster("Landfire_NM/US_130EVT/us_130evt")
raster2010 = arcpy.Raster("Landfire_NM/US_120EVT/US_120_EVT/us_120evt")
raster2008 = arcpy.Raster("Landfire_NM/US_110EVT/us_110evt")

# LANDFIRE landcover values for the 2010 and 2012 datasets.
newvaluelist = (3011, 3012, 3016, 3019, 3023, 3024, 3025, 3026, 3049, 3050, 3051, 3052, 3054,
  3055, 3056, 3057, 3059, 3061, 3070, 3107, 3117, 3119, 3155, 3159, 3160, 3208, 3215, 3217)

# LANDFIRE landcover values for the 2008 datasets.
oldvaluelist = (2011, 2012, 2016, 2019, 2023, 2024, 2025, 2026, 2049, 2050, 2051, 2052, 2054,
  2055, 2056, 2057, 2059, 2061, 2070, 2107, 2117, 2119, 2155, 2159, 2160, 2208, 2215, 2217)

# Check out the Spatial Analyst Extension.
arcpy.CheckOutExtension("Spatial")

# Extract attributes from the value lists.
bear2012 = arcpy.sa.ExtractByAttributes(raster2012, "VALUE IN(newvaluelist)")
bear2010 = arcpy.sa.ExtractByAttributes(raster2010, "VALUE IN(newvaluelist)")
bear2008 = arcpy.sa.ExtractByAttributes(raster2008, "VALUE IN(oldvaluelist)")

# Specify the range of values to be reclassified within the raster ouputs.
newReclassRange = arcpy.sa.RemapRange([[3011, 3217, 1]])
oldReclassRange = arcpy.sa.RemapRange([[2011, 2217, 1]])

# Reclassify all values to 1.
reclass2012 = arcpy.sa.Reclassify(bear2012, "VALUE", newReclassRange)
reclass2010 = arcpy.sa.Reclassify(bear2010, "VALUE", newReclassRange)
reclass2008 = arcpy.sa.Reclassify(bear2008, "VALUE", oldReclassRange)

# Total the reclassified rasters together and save the output.
```

```
reclassSum = (reclass2012 + reclass2010 + reclass2008)

stateMask = "NMState_NAD83.shp"
raster = arcpy.sa.ExtractByMask(reclassSum, stateMask) # Clips the resulting raster to the NM
 State boundary.

# Set the initial aggregate factor to 2.  An aggregate factor of 1 is simply the summation raster,
 and thus not needed.
aggregate_factor = 3

# Loop through and save aggregate factors 1 to 10 and reclassify the aggregates for all values >
 0.25 of the maximum value.
while aggregate_factor <= 10:
   outAgg = arcpy.sa.Aggregate(reclassSum, aggregate_factor, "SUM")
   maxvalueResult = arcpy.GetRasterProperties_management(outAgg, "MAXIMUM") #
 Retrieve the output result object for the maximum value within a raster.
   maxvalue = maxvalueResult.getOutput(0)  # Retrieve the maximum value from the result
 object.
   reclassmax = (int(maxvalue) / 4)    # Convert the maximum value to an integer and divide by
 4.
   reclassMaxRange = arcpy.sa.RemapRange([[0, reclassmax, "NoData"], [reclassmax,
 maxvalue, 1]])  # Set RemapRange based on 25% breakpoint.
   reclass = arcpy.sa.Reclassify(outAgg, "VALUE", reclassMaxRange) # Reclassify raster with
 all values > 25% of the maximum value being considered "primary".
   outputname = "Reclass_polygon_aggregate_" + str(aggregate_factor)
   arcpy.RasterToPolygon_conversion(reclass, outputname, "NO_SIMPLIFY")    # Convert
 raster to polygon.
   print "Raster conversion for " + str(aggregate_factor) + " completed."

   # Add a new column and populate it with the area in square kilometers.
   arcpy.AddField_management(outputname, "Area", "FLOAT", "", "", 20)
   arcpy.CalculateField_management(outputname, "Area",
 "float(!SHAPE.AREA@SQUAREKILOMETERS!)", "PYTHON")

   # Turn polygon feature into layer to facilitate selection process.
   layername = "layer" + str(aggregate_factor)
   arcpy.MakeFeatureLayer_management(outputname, layername)

   # Selection process.
   # First selection of all parcels > 200 sq. km.
   arcpy.SelectLayerByAttribute_management(layername, "NEW_SELECTION", '"Area" >=
 200')
   layer200 = arcpy.CopyFeatures_management(layername, "Primary_bear_" +
 str(aggregate_factor) + "_area_over_200")

   # Second selection of all parcels within 2 km. of 200 sq. km. parcels.
```

```
    firstDist = "2 KILOMETERS"
    secondDist = "10 KILOMETERS"
    arcpy.SelectLayerByLocation_management(layername, "WITHIN_A_DISTANCE", layer200,
  firstDist, "NEW_SELECTION")
    layer2km = arcpy.CopyFeatures_management(layername, "Primary_bear_" +
  str(aggregate_factor) + "_area_within_2_km")

    # Third selection of all parcels > 25 sq. km. within 30 km. of 200 sq. km. parcels.
    arcpy.SelectLayerByLocation_management(layername, "WITHIN_A_DISTANCE", layer200,
  secondDist, "NEW_SELECTION")
    arcpy.SelectLayerByAttribute_management(layername, "SUBSET_SELECTION", '"Area" >=
  25')
    layer25 = arcpy.CopyFeatures_management(layername, "Primary_bear_" +
  str(aggregate_factor) + "_area_over_25_within_30_km")

    arcpy.Merge_management([layer200, layer2km, layer25], "Primary_bear_" +
  str(aggregate_factor) + "_selection_final")

    print "Aggreate Factor " + str(aggregate_factor) + " processing completed."
    aggregate_factor += 1

# Check in the Spatial Analyst Extension.
arcpy.CheckInExtension("Spatial")
```

Python script run to accommodate changing the selection process and altering the cover filter input (inputs were variable)

```
import arcpy

agnum = "7"
arearestriction = "25"
dist = "30"
covernumber = "20"
agFactor = "Reclass_polygon_aggregate_" + agnum
af_200 = "Primary_bear_" + agnum + "_area_over_200_test"
GMU = "E:/GIS/Boundaries/NM_GMU_no_subunits.shp"
output = "Final_selection_cover_filter_" + covernumber
intersectOut = output + "_GMU_Intersect"
statOut = "Final_selection_cover_filter_" + covernumber + "_summary"
filter = "Cover_filter_less_than_" + covernumber

arcpy.Erase_analysis(agFactor, filter, "Model_cover_filter_" + covernumber)
```

```
arcpy.MultipartToSinglepart_management("Model_cover_filter_" + covernumber, "Model_cover_filter_"
+ covernumber + "_single")
arcpy.CalculateField_management("Model_cover_filter_" + covernumber + "_single", "Area",
"float(!SHAPE.area@SQUAREKILOMETERS!)", "PYTHON")

arcpy.MakeFeatureLayer_management("Model_cover_filter_" + covernumber + "_single", "layer")

arcpy.SelectLayerByLocation_management("layer", "WITHIN_A_DISTANCE", af_200, dist + "
KILOMETERS", "NEW_SELECTION")
arcpy.SelectLayerByAttribute_management("layer", "REMOVE_FROM_SELECTION", '"Area" < ' +
arearestriction)
arcpy.SelectLayerByLocation_management("layer", "WITHIN_A_DISTANCE", "", "2 KILOMETERS",
"ADD_TO_SELECTION")
arcpy.EliminatePolygonPart_management("layer", output, "AREA", "2 SQUAREKILOMETERS")

arcpy.Intersect_analysis([output, GMU], intersectOut)

arcpy.CalculateField_management(intersectOut, "Area",
"float(!SHAPE.area@SQUAREKILOMETERS!)", "PYTHON")
arcpy.Statistics_analysis(intersectOut, statOut, [["Area", "SUM"]], "GMU")
```

Python script run to create “sparse cover” filter

```
import arcpy

arcpy.CheckOutExtension("Spatial")

boundary = "E:/Z_drive/boundaries/NMState_NAD83.shp"

cover = arcpy.sa.Raster("Landfire_NM/US_130EVC/us_130evc")

cover = arcpy.sa.ExtractByMask(cover, boundary)

cover = arcpy.sa.Reclassify(cover, "VALUE", arcpy.sa.RemapRange([[0, 0, "NoData"], [11, 101, 1],
[102, 109, "NoData"], [111, 111, 1], [112, 119, "NoData"], [121, 121, 1], [122, 129, "NoData"]]))

cover = arcpy.sa.Aggregate(cover, 7, "SUM")

cover = arcpy.sa.Reclassify(cover, "Value", arcpy.sa.RemapRange([[0, 12, "NoData"], [13, 49, 1]]))

arcpy.CheckInExtension("Spatial")

polygon = arcpy.RasterToPolygon_conversion(cover, "Cover_filter_less_than_20", "NO_SIMPLIFY")
```

Python script used to create “edge” habitat

```
reclassSum = arcpy.Raster(“summation”)

aggregate_factor = 7

outAgg = arcpy.sa.Aggregate(reclassSum, aggregate_factor, “SUM”)
maxvalueResult = arcpy.GetRasterProperties_management(outAgg, “MAXIMUM”)
maxvlue = maxvalueResult.getOutput(0)
reclassmax = (int(maxvalue) / 4)
reclassMaxRange = arcpy.sa.RemapRange([[0, reclassmax, 1], [reclassmax, maxvalue, “NoDate”]])
reclass = arcpy.sa.Reclassify(outAgg, “VALUE”, reclassMaxRange)
outputname = “Edge_bear_habitat”
arcpy.RasterToPolygon_conversion(reclass, outputname, “NO_SIMPLIFY”)
```

ABSTRACT

We produced three, statewide, inductive habitat suitability models and population estimates for mountain lions for New Mexico. The first two models used a binary logistic regression to produce the linear combination of habitat variables that best predicted the distinction between either (1) mountain lion harvest locations and random points; or, (2) gps collared mountain lion locations and random points. The third model was produced by combining the mapped results of the first two models by adding the "excellent" and "good" habitat from the collar model to the harvest model. The models produced by binary logistic regression were entered into Raster Calculator in ArcGIS to produce maps of habitat suitability state wide. Habitat suitability was simplified to 5 categories (quintiles) using Spatial Analysis, Reclassify, in ArcGIS. Finally, the area of each habitat suitability class for each mountain lion management zone was multiplied by plausible mountain lion densities (derived from the literature) to produce an estimated range of mountain lion population sizes. The harvest, collar, and combined models predicted 8%, 16%, and 60% greater statewide mountain lion population estimates, respectively, than the current New Mexico Department of Game and Fish population estimates based on a deductive model. (Note: The higher population estimate produced by our harvest model is not uniform across mountain lion management zones. Approximately, half of the management zones were predicted to have smaller populations than previously predicted.) Our harvest model is the most conservative of the three and is in close agreement, at the state level, with the deductive model. We suggest that the harvest model be the primary source for guiding an adaptive management approach to mountain lion conservation in New Mexico.

INTRODUCTION

Information on the abundance and distribution of any species is essential for its responsible management. According to the New Mexico Department of Game and Fish Strategic Plan for 2008 through 2012, the mission of the agency is:

"To provide and maintain an adequate supply of wildlife and fish within the state of New Mexico by utilizing a flexible management system that provides for their protection, propagation, regulation, conservation, and for their use as public recreation and food supply."

Meeting these objectives for mountain lions poses significant challenges as these animals are secretive and occur at relatively low densities, making it difficult to conduct population counts. Even the result of such a census may be primarily local in application. However, the density estimates obtained from local studies is a critical starting point in understanding mountain lion population sizes and distribution.

To address these needs in mountain lion management alternative approaches to direct population counts are used. One increasingly useful approach is the use of habitat or niche modeling with GIS technology (Hirzel et al. 2006). The Cougar Management Guidelines Working Group (2005) suggests this technique as a primary means of planning statewide mountain lion management programs. This approach has been used to predict mountain lion habitat dispersal corridors and habitat patches in the Midwest (LaRue and Nielson 2005) as well as mountain lion population distribution and dispersal routes in Riverside County California, and to inform mountain lion management in New Mexico (Negri and Quigley 2010). These models have employed a deductive approach using expert opinion regarding mountain lion habitat preferences. Actual location data may be used to produce more objective, and possibly more accurate models. Location data may come from hunter harvest records or from VHF or GPS collars worn by free roaming mountain lions. The resulting models are inductive, generalizing habitat preferences from a subset of the mountain lion population across a broad geographic area. It should be noted that models built from harvest data may also be biased by hunter distribution and success. Data from collared mountain lions can address some of these biases. Perhaps the greatest utility of these models is that they represent testable hypotheses about the distribution and density of mountain lions that can inform an adaptive management approach.

Our primary goal in this project is to provide a scientifically robust estimate of mountain lion status across the state, based on actual mountain lion locations derived from harvest data and GPS collared mountain lions. Our objectives were to: (1) Identify and map habitat quality, defined by probability of mountain lion occurrence, in five quality categories, excellent, good, moderate, fair, and poor; (2) quantify the total area of each category of habitat quality in square kilometers by game management unit and mountain lion management zone; (3) map the statewide distribution of each habitat type; and, (4) project a statewide mountain lion population estimate, broken down by hunt unit and mountain lion management zone, based on the area and extent of habitat categories and reasonable mountain lion densities derived from the scientific literature.

METHODS

Statistical Approach

We used an inductive model building approach, using mountain lion locations, and their associated habitat characteristics to make generalizations about mountain lion habitat preference and suitability. Specifically, we used a binary logistic regression to produce the linear combination of habitat variables that best distinguished between random locations and mountain lion locations across the state of New Mexico. We made this approach more rigorous by building the model with a subset of locations and then testing the accuracy of the model at identifying the remaining points as either random or mountain lion based on associated habitat characteristics. This linear combination of variables (the model) was then entered into ArcGIS Raster Calculator to produce habitat suitability maps. We actually constructed three models: we used a binary logistic regression to distinguish between harvest locations and random locations to produce one model. We used the same approach to distinguish between random locations and collared mountain Lion locations to produce a separate model. Finally, we combined these models by adding the ‘excellent’ and ‘good’ habitats from the collar model to the harvest model.

Data

In initial model building, we used two sources of mountain location data, (1) harvest and (2) GPS collar, and data on several habitat variables: (3) vegetation type, (4) topographic ruggedness, (5) slope, (6) elevation, (7) snow depth, (8) distance to paved roads, (9) distance to dirt roads, (10) elk distribution, and (11) mule deer distribution.

(1) New Mexico mountain lion harvest data was provided by the New Mexico Department of Game and Fish. Approximately, 1,684 total records from 2001 to 2009 were provided. We georeferenced 1,397 of these records for the model. There are inherent, but unavoidable, biases to harvest data in the construction of harvest data. For example, proximity to roads may seem to be an important quality for suitable mountain lion habitat. When, in fact, it is hunter access that drives the importance of this variable. A second potential source of error is the accuracy of the georeferencing. Caution is warranted in the use and interpretation of models based on harvest data.

(2) We obtained GPS collar data from 10 free roaming mountain lions between 2005 and 2010. GPS locations were taken at night and reflect active habitat use. We used approximately, 13,000 GPS locations for model building. A bias inherent to the use of these data is their restricted geographic application. As all of these mountain lions were in the southcentral portion of New Mexico, below 7,000 ft, the resulting model would not predict that habitat types outside of this region would be suitable mountain lion habitat. (eg mixed coniferous forest). The advantage of these data is that they show mountain lion habitat use outside of areas frequented by hunters.

(3) We simplified vegetation classifications provided by the Southwest Regional GAP Analysis, as described in “Landcover descriptions for the Southwestern Regional GAP Analysis project” compiled by NatureServe, 2004. The relationship between the vegetation categories used for the model and the original SWReGAP categories can be found in Appendix I. For use in the raster calculator, we created a separate raster for each vegetation type, giving pixels a value of either zero (not the specified vegetation type) or one.

(4) We created an index of topographic ruggedness by using the USGS 30 meter National Elevation Dataset for New Mexico available from the RGIS website. (http://rgis.unm.edu/intro.cfm). The following equation was applied: TPI = SQR(FOCALSTD([DEM], CIRCLE, X, where X is the number of pixels in the radius of the circle. In this way we created four rasters of topographic ruggedness at four scales: 120, 240, 480, and 960 meters, respectively.

(5) Slope was derived from the USGS 30m DEM as percentage slope using ArcGIS Spatial Analyst.

(6) Elevation was taken from the USGS 30m DEM

(7) Snow depth was obtained from the National Climatic Data Center which is within the National Oceanic and Atomospheric Administration (NOAA)

(http://hurricane.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl). National data representing average annual snowfall were used for this input.

(8) Distance to Paved Roads was calculated from the TIGER 2008 roads dataset. Roads were obtained from the U.S. Census 2008 TIGER shapefiles website (http://www2.census.gov/cgi-bin/shapefiles/national-files). Paved roads were extracted and distance to roads was calculated using the Euclidean Distance function in Spatial Analyst at a 30 m resolution.

(9) Distance to Dirt Roads was calculated from the TIGER 2008 roads dataset. Dirt roads were extracted and distance to roads was calculated using the Euclidean Distance function in Spatial Analyst at a 30 m resolution.

(10) We calculated a rough index of elk availability by dividing the total allowable harvest of elk for the 2010-2011 season by the area of each hunt unit.

(11) We calculated a rough index of mule deer availability by dividing the total allowable harvest of mule deer for the 2010-2011 season by the area of each hunt unit.

We entered the resulting binary logistic models (one for harvest data and one for collar data) into the ArcGIS Spatial Analyst, Raster Calculator to produce a raster in which each pixel was given a value that corresponded to the inverse odds of mountain lion occurrence. The range of pixel values in each of the resulting rasters was then simplified to 255 values using the Spatial Analysist Reclassify tool. These 255 values were then further simplified to 5 values by grouping the 255 values by quintiles and reclassifying a second time. The result, for each model, was a raster showing 5 categories of mountain lion habitat suitability (probability of mountain lion occurrence).

Next, we used Hawth's Tools, Raster Tools, Thematic Raster Summary by Polygon to calculate the area of each habitat class for each Game Management Unit (GMU). Then we multiplied each habitat type area for each GMU by a range of possible mountain lion densities, supplied by the New Mexico Department of Game and Fish (Table 1).

	Excellent	Good	Moderate	Fair
Density Range (per 100sqKm)	2-3	0.89-1.2	0.4-0.6	0.2-0.3

Table 1. Mountain lion density ranges by habitat category, provided by the New Mexico Department of Game and Fish used in the calculation of mountain lion populations.

RESULTS

In both the harvest and collar models the variables with the most significant predictive value were topographic ruggedness, at the scale of 480m, and vegetation type. The addition of other predictor variables did not significantly improve the models. In the models that follow, the lower the coefficient, the more this variable contributes to suitable mountain lion habitat. The binary logistic regression models were:

> (1) for harvest data:
> Puma = -.0001[TRI480] + 21.844 * [acmesq1] + 21.04 * [acpsdg2] + 21.127 * [agric3] + 22.019 * [badland4] + 21.616 * [barren5] + 22.54 * [ccreosote7] + 42.332 * [cscrub8] + 21.352 * [canyon9] +22.277 * [canmesa10] + 42.322 * [ccdunesd11] + 20.547 * [chaparral12] + 19.583 * [cliffrock13] + 0.065 * [cpshrub14] + 42.399 * [dgrasslnd15] + 22.219 * [dunes17] +21.857 * [gpmesq18] + 42.322 * [gpsndshb19] + 19.088 * [gpfpgrass20] + 42.322 * [gypgrass21] +21.907 * [imgrass22] + 21.9 * [imbshrub23] + 21.539 * [junpgrass25] + 42.332 * [lava26] + 19.9 * [madoak29] + 20.419 * [mixconifer30] + 20.261 * [mongrass32] + 19.962 * [montshrub33] + 42.337 * [water35] +19.681 * [pine36] + 20.529 * [pj37] + 20.27 * [playa38] + 19.486 * [ripwood42] + 20.381 * [sage44] + 22.459 * [sgprairie45] + 21.051 * [urban49]

Certain adjustments to coefficients were made: 0.065 coefficient for cpshrub (Colorado Plateau Shrubland) was unrealistic and resulted from small sample size. Also, the coefficients for [barren5], [playa38], and [urban49] were changed to 43 (meaning low probability of mountain lion occurrence), as breeding populations of mountain lions cannot reasonably be expected to occur in these areas.

This model correctly predicted 85% of test mountain lion harvest locations (Appendix II).

> (2) for collar data:
> Puma = -0.0001 * [TRI_480.img] + 19.708 * [acmesq1] + 18.739 * [acpsdg2] + 20.998 * [agric3] + 43.049 * [badland4] + 43.654 * [barren5] + 20.002 * [ccreosote7] + 19.724 * [cscrub8] + 46.082 * [canyon9] + 22.311 * [ccdunesd11] + 18.515 * [chaparral12] + 17.559 * [cliffrock13] + 19.886 * [dgrasslnd15] + 20.735 * [dunes17] + 42.769 * [gpmesq18] + 42.412 * [gpsndshb19] + 42.409 * [gypgrass21] + 20.603 * [imgrass22] + 22.279 * [imbshrub23] + 46.184 * [jungrass25] + 42.46 * [lava26] + 21.677 * [madoak29] + 25.507 * [mixconifer30] + 43.691 * [mongrass32] + 44.049 * [montshrub33] + 42.489 * [water35] + 21.742 * [pine36] + 19.870 * [pj37] + 19.231 * [playa38] + 1.215 * [ripherb39] + 15.223 * [ripwood42] + 44.265 * [sage44] + 42.479 * [sgprairie45] + 42.496 * [urban49]

This model correctly predicted 99% of test collared mountain lion locations. (Appendix III)

The three resulting models, from harvest data, collar data, and the combination of the two, predict successively larger statewide mountain lion populations respectively. The harvest data model is the most conservative, predicting a statewide population of mountain lions between 2,099 and 3,122 (Table 2, Figure 1). The collar model predicts a statewide population between 2,253 and 3,122 (Table 2, Figure 2). The combined models, in which excellent and good mountain lion habitat predicted by the collar model was added to the harvest model, predicts a statewide population between 3,197 and 4,732 (Table 2, Figure 3). The real number of mountain lions statewide likely lies between the harvest model and harvest + collar population estimates. As the harvest model is the most conservative, we suggest that it be used for management decisions.

Cougar Zone	harvest lo	harvest hi	collar lo	collar hi	harvcol lo	harvcol hi
A	139	207	117	167	169	249
B	96	142	38	56	98	146
C	193	289	58	84	195	291
D	52	76	21	31	56	82
E	168	251	120	171	187	275
F	104	156	45	65	108	161
G	166	247	155	223	209	308
H	54	78	216	318	206	302
I	123	183	146	215	198	295
J	298	445	294	429	436	646
K	151	225	177	262	232	347
L	43	64	137	203	145	216
M	98	146	362	537	376	557
N	51	76	8	12	52	78
O	70	103	51	71	75	109
P	33	49	13	19	33	49
Q	115	170	236	347	268	396
R	87	131	22	33	88	132
S	57	85	37	52	65	95
T						
Total	2099	3122	2253	3294	3197	4732

Table 2. This table compares mountain lion population estimates by mountain lion management unit across the three models, harvest, collar, and harvest and collar (Harvcol) combined. Note that mountain lion population estimates for the “T” (Tribal) areas of the state are not included in the estimate.

For detailed calculations of mountain lion population size by GMU across all three models see Appendix IV.

DISCUSSION

The harvest data model, the most conservative of the three models, predicts a statewide mountain lion population approximately 8% larger than the current NMDGF mountain lion population estimates. It is perhaps most notable, that the two estimates are so similar. The harvest model's higher statewide estimate is not the result of uniformly higher estimates across GMU's. Approximately, half of the units were predicted to have fewer mountain lions by the model than previously predicted by NMDGF. The fact that tribal areas were not included in the statewide population estimate makes the harvest model more conservative.

The accuracy of any model is only as good as the data used to construct the model. There are at least three points of potential issue with the data used for these models.

First, there are inherent biases in both harvest data and GPS collar data. Harvest data may be biased by hunter access (roads) or environmental factors that increase hunter success (snow). The result of this bias is that the model may underestimate the mountain lion population in areas where there are few roads or where there is infrequent, or no, snow fall. Likewise, favored hunting areas with high success may over-estimate mountain lion populations. The GPS collar data is biased in two ways. First, because there was not a statewide distribution of collared mountain lions, the habitat selection of collared lions was limited. For example, because all collared mountain lions were in southcentral New Mexico, below 7,000 ft, obviously suitable habitat types, such as mixed conifer, are not predicted to be suitable mountain lion habitat by this model. This also, would lead to a significant underestimate of statewide populations. Second, collared mountain lions may pass through unsuitable habitat, regularly, to access favored habitats. As a result, unfavorable habitat types, such as creosote flats, may be shown by the model to be moderately suitable to mountain lion populations, causing an overestimation of mountain lion numbers. A solution to the second bias may be addressed by using only prey cache sites from collared mountain lions. Evidence of mountain lions feeding in particular habitats is stronger evidence of habitat suitability than mere location data.

A second source of concern is the accuracy of georeferenced harvest data. Whereas collar data may be accurate to the scale of meters, harvest data may only be accurate to the scale of 100's of meters or even kilometers. The result may be that truly unfavored habitat types appear to be favored. The best remedy for these inaccuracies is sample size. With 1,400 georeferenced records, we can be relatively confident that this is not a significant source of error in these models.

A final area of potential inaccuracy, in calculating population size, is the choice of density ranges. The density of mountain lions has been accurately measured in a number of intensive field studies. However, it is difficult to compare density estimates across studies due to differences in approach. Recently, Quigley and Hornocker (2010) provided a summary of density estimates across several studies, ranging from 0.32 to 7.3 per 100 sqKm. The density estimates used in these models are conservative, ranging from 0.2 to 3 per 100sqKm. Mountain lion densities in New Mexico might exceed this top range in productive habitats. Recently, four resident adult females and two resident adult males were observed frequenting a 100 sqKm camera study area in the eastern piedmont of the Black Range.

The primary utility of population estimate models is to serve as hypotheses to guide adaptive management practices. There are at least two methods for testing the accuracy of these model predictions: (1) remote camera mark-resight population estimates in select habitats and (2) monitoring the sex and age distribution of harvested lions as per the findings of Anderson and Lindzey (2005).

ACKNOWLEDGEMENTS

We would like to thank Rick Winslow and the New Mexico Department of Game and Fish for providing the opportunity to contribute to responsible, science based, conservation of mountain lions in New Mexico. We would also like to thank the NMDGF conservation officers who have diligently collected accurate location data from harvested mountain lions. Special thanks goes to Megan Pitman and Michael Jiang for their many, many hours of tedious georeferencing.

LITERATURE CITED

Anderson, C. R., Jr., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildl Soc Bull 33: 179-188.

Cougar Management Guidelines Working Group. 2005. Cougar management guidelines. WildFutures, Bainbridge Island, WA.

Hirzel, A. H., G. L. Lay, V. Helfer, C. Randin, AND A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences, Ecological Modeling 199:142-152.

LaRue, M. A. and C. K. Nielson. 2008. Modeling potential dispersal corridors for cougars in midwestern North America using least-cost path methods, Ecological Modeling 212:372-381.

Negri, S. and H. B. Quigley. Cougar Conservation *in* Cougar Ecology and Conservation, eds. M. Hornocker and S. Negri. University of Chicago Press, Chicago and London.

Quigley, H. B. and M. G. Hornocker. 2010. Cougar population dynamics *in* Cougar Ecology and Conservation, eds. M. Hornocker and S. Negri. University of Chicago Press, Chicago and London.

APPENDIX I

SWReGAP Original Vegetation Types	Our Model Vegetation Types
Apacherian-Chihuahuan Mesquite Upland Scrub	AC Mesquite
Apacherian-Chihuahuan Piedmont Semi-Desert Grassland and Steppe	ACPSD Grassland
Agriculture	Agriculture
Inter-Mountain Basins Shale Badland	Badland
North American Warm Desert Badland	Badland
Inter-Mountain Basins Playa	Barren
Barren Lands, Non-specific	Barren
Recently Burned	Barren
Inter-Mountain Basins Subalpine Limber-Bristlecone Pine Woodland	Bristle Cone
North American Warm Desert Pavement	C Creosote
Chihuahuan Creosotebush, Mixed Desert and Thorn Scrub	C Creosote
Chihuahuan Succulent Desert Scrub	C scrub
Chihuahuan Mixed Salt Desert Scrub	C scrub
Rocky Mountain Cliff and Canyon	Canyon
Sierra Nevada Cliff and Canyon	Canyon
Inter-Mountain Basins Cliff and Canyon	Canyon
Colorado Plateau Mixed Bedrock Canyon and Tableland	Canyon and Mesa
Chihuahuan Stabilized Coppice Dune and Sand Flat Scrub	CC Dune Sand
Great Basin Semi-Desert Chaparral	Chaparral
Mogollon Chaparral	Chaparral
Coahuilan Chaparral	Chaparral
Rocky Mountain Alpine Bedrock and Scree	Cliff and Rock
Mediterranean California Alpine Bedrock and Scree	Cliff and Rock
Western Great Plains Cliff and Outcrop	Cliff and Rock
North American Warm Desert Bedrock Cliff and Outcrop	Cliff and Rock
Recently Mined or Quarried	Cliff and Rock
Colorado Plateau Blackbrush-Mormon-tea Shrubland	CP Shrub
Southern Colorado Plateau Sand Shrubland	CP Shrub
Chihuahuan-Sonoran Desert Bottomland and Swale Grassland	D Grassland
Chihuahuan Sandy Plains Semi-Desert Grassland	D Grassland
Disturbed, Non-specific	Disburbed
Inter-Mountain Basins Active and Stabilized Dune	Dunes
North American Warm Desert Active and Stabilized Dune	Dunes
Western Great Plains Mesquite Woodland and Shrubland	GP Mesquite
Western Great Plains Sandhill Shrubland	GP sand Shrub

SWReGAP Original Vegetation Types	**Our Model Vegetation Types**
Western Great Plains Foothill and Piedmont Grassland	GPFP Grassland
Chihuahuan Gypsophilous Grassland and Steppe	Gyp Grassland
Inter-Mountain Basins Semi-Desert Grassland	IM Grassland
Inter-Mountain Basins Mat Saltbush Shrubland	IMB Shrub
Inter-Mountain Basins Mixed Salt Desert Scrub	IMB Shrub
Inter-Mountain Basins Semi-Desert Shrub Steppe	IMB Shrub
Inter-Mountain Basins Greasewood Flat	IMB Shrub
Inter-Mountain Basins Wash	IMB Wash
Southern Rocky Mountain Juniper Woodland and Savanna	Juniper Grassland
Inter-Mountain Basins Juniper Savanna	Juniper Grassland
Madrean Juniper Savanna	Juniper Grassland
Inter-Mountain Basins Volcanic Rock and Cinder Land	Lava
North American Warm Desert Volcanic Rockland	Lava
	Layer border
Recently Logged Areas	Logged
Madrean Pine-Oak Forest and Woodland	Madrean Oak
Madrean Encinal	Madrean Oak
Madrean Upper Montane Conifer-Oak Forest and Woodland	Madrean Oak
Rocky Mountain Aspen Forest and Woodland	Mixed Conifer
Rocky Mountain Subalpine-Montane Limber-Bristlecone Pine Woodland	Mixed Conifer
Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	Mixed Conifer
Northern Pacific Mesic Subalpine Woodland	Mixed Conifer
Rocky Mountain Subalpine Mesic Spruce-Fir Forest and Woodland	Mixed Conifer
Rocky Mountain Montane Dry-Mesic Mixed Conifer Forest and Woodland	Mixed Conifer
Mediterranean California Dry-Mesic Mixed Conifer Forest and Woodland	Mixed Conifer
Rocky Mountain Montane Mesic Mixed Conifer Forest and Woodland	Mixed Conifer
Inter-Mountain West Aspen-Mixed Conifer Forest and Woodland Complex	Mixed Conifer
Mediterranean California Red Fir Forest and Woodland	Mixed Conifer
Mojave Mid-Elevation Mixed Desert Scrub	Mojave Scrub
Rocky Mountain Alpine Fell-Field	Montane Grass
Rocky Mountain Subalpine Mesic Meadow	Montane Grass
Southern Rocky Mountain Montane-Subalpine Grassland	Montane Grass
Rocky Mountain Alpine-Montane Wet Meadow	Montane Grass

SWReGAP Original Vegetation Types	**Our Model Vegetation Types**
Temperate Pacific Montane Wet Meadow	Montane Grass
Mediterranean California Subalpine-Montane Fen	Montane Grass
North Pacific Montane Grassland	Montane Grass
Rocky Mountain Bigtooth Maple Ravine Woodland	Mountain Shrub
Rocky Mountain Alpine Dwarf-Shrubland	Mountain Shrub
Rocky Mountain Gambel Oak-Mixed Montane Shrubland	Mountain Shrub
Rocky Mountain Lower Montane-Foothill Shrubland	Mountain Shrub
Inter-Mountain Basins Mountain Mahogany Woodland and Shrubland	Mountain Shrub
Central Mixedgrass Prairie	Odd grass
Invasive Perennial Grassland	Odd grass
Invasive Perennial Forbland	Odd grass
Invasive Annual Grassland	Odd grass
Invasive Annual and Biennial Forbland	Odd grass
Open Water	Open Water
Rocky Mountain Lodgepole Pine Forest	Pine forest
Rocky Mountain Ponderosa Pine Woodland	Pine forest
Sierra Nevada Subalpine Lodgepole Pine Forest and Woodland	Pine forest
Mediterranean California Ponderosa-Jeffrey Pine Forest and Woodland	Pine forest
Rocky Mountain Foothill Limber Pine-Juniper Woodland	Pine forest
Southern Rocky Mountain Pinyon-Juniper Woodland	Pinyon Juniper
Colorado Plateau Pinyon-Juniper Woodland	Pinyon Juniper
Great Basin Pinyon-Juniper Woodland	Pinyon Juniper
Colorado Plateau Pinyon-Juniper Shrubland	Pinyon Juniper
Madrean Pinyon-Juniper Woodland	Pinyon Juniper
Recently Chained Pinyon-Juniper Areas	Pinyon Juniper
North American Warm Desert Playa	Playa
North American Arid West Emergent Marsh	Riparian Herb
Western Great Plains Floodplain Herbaceous Wetland	Riparian Herb
Western Great Plains Saline Depression Wetland	Riparian salt
Rocky Mountain Subalpine-Montane Riparian Shrubland	Riparian Shrub
Rocky Mountain Subalpine-Montane Riparian Woodland	Riparian Woodland
Rocky Mountain Lower Montane Riparian Woodland and Shrubland	Riparian Woodland
North American Warm Desert Lower Montane Riparian Woodland and Shrubland	Riparian Woodland
Western Great Plains Riparian Woodland and Shrubland	Riparian

	Woodland
SWReGAP Original Vegetation Types	**Our Model Vegetation Types**
North American Warm Desert Riparian Woodland and Shrubland	Riparian Woodland
North American Warm Desert Riparian Mesquite Bosque	Riparian Woodland
Great Basin Foothill and Lower Montane Riparian Woodland and Shrubland	Riparian Woodland
Invasive Southwest Riparian Woodland and Shrubland	Riparian Woodland
Sonoran Paloverde-Mixed Cacti Desert Scrub	S Shrub
Sonora-Mojave Creosotebush-White Bursage Desert Scrub	S Shrub
Sonora-Mojave Mixed Salt Desert Scrub	S Shrub
Sonora-Mojave-Baja Semi-Desert Chaparral	S Shrub
Sonoran Mid-Elevation Desert Scrub	S Shrub
Inter-Mountain Basins Big Sagebrush Shrubland	Sagebrush
Great Basin Xeric Mixed Sagebrush Shrubland	Sagebrush
Colorado Plateau Mixed Low Sagebrush Shrubland	Sagebrush
Inter-Mountain Basins Montane Sagebrush Steppe	Sagebrush
Inter-Mountain Basins Big Sagebrush Steppe	Sagebrush
Wyoming Basins Low Sagebrush Shrubland	Sagebrush
Western Great Plains Shortgrass Prairie	SG Prarie
Western Great Plains Sandhill Prairie	SH Prarie
Western Great Plains Tallgrass Prairie	Tallgrass
North American Alpine Ice Field	Tundra
Rocky Mountain Dry Tundra	Tundra
Developed, Open Space - Low Intensity	Urban
Developed, Medium - High Intensity	Urban
North American Warm Desert Wash	WD Wash

APPENDIX II

SPSS Harvest Model Binary Logistic Regression Output

```
LOGISTIC REGRESSION VARIABLES Class
  /SELECT=validate EQ 1
  /METHOD=FSTEP(LR) TRI480 GAP_4
  /CONTRAST (GAP_4)=Indicator
  /SAVE=PRED COOK SRESID
  /PRINT=GOODFIT
  /CRITERIA=PIN(0.05) POUT(0.10) ITERATE(20) CUT(0.5).
```

Logistic Regression

Notes

	Output Created	02-Jun-2010 17:49:27
	Comments	
Input	Data	C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NMDGFhabitatmodel\Data2010\modeldata2b.sav
	Active Dataset	DataSet1
	Filter	Model_ID > 4000 & Class ne 'PC' (FILTER)
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data File	2397
Missing Value Handling	Definition of Missing	User-defined missing values are treated as missing
	Syntax	LOGISTIC REGRESSION VARIABLES Class /SELECT=validate EQ 1 /METHOD=FSTEP(LR) TRI480 GAP_4 /CONTRAST (GAP_4)=Indicator /SAVE=PRED COOK SRESID /PRINT=GOODFIT /CRITERIA=PIN(0.05) POUT(0.10) ITERATE(20) CUT(0.5).
Resources	Processor Time	0:00:00.515
	Elapsed Time	0:00:00.517
Variables Created or Modified	PRE_1	Predicted probability
	COO_1	Analog of Cook's influence statistics
	SRE_1	Standard residual

```
[DataSet1] C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NM
DGFhabitatmodel\Data2010\modeldata2b.sav
```

Case Processing Summary

Unweighted Cases [a]		N	Percent
Selected Cases	Included in Analysis	1684	70.3
	Missing Cases	0	.0
	Total	1684	70.3
	Unselected Cases	713	29.7
	Total	2397	100.0

a. If weight is in effect, see classification table for the total number of cases.

Dependent Variable Encoding

Original Value	Internal Value
PH	0
R	1

Categorical Variables Codings

			Parameter coding					
		Frequency	(1)	(2)	(3)	(4)	(5)	(6)
GAP_4	1	51	1.000	.000	.000	.000	.000	.000
	2	175	.000	1.000	.000	.000	.000	.000
	3	26	.000	.000	1.000	.000	.000	.000
	4	3	.000	.000	.000	1.000	.000	.000
	5	9	.000	.000	.000	.000	1.000	.000
	7	79	.000	.000	.000	.000	.000	1.000
	8	4	.000	.000	.000	.000	.000	.000
	9	4	.000	.000	.000	.000	.000	.000
	10	4	.000	.000	.000	.000	.000	.000
	11	12	.000	.000	.000	.000	.000	.000
	12	16	.000	.000	.000	.000	.000	.000
	13	7	.000	.000	.000	.000	.000	.000
	14	1	.000	.000	.000	.000	.000	.000
	15	2	.000	.000	.000	.000	.000	.000
	17	4	.000	.000	.000	.000	.000	.000
	18	9	.000	.000	.000	.000	.000	.000
	19	13	.000	.000	.000	.000	.000	.000
	20	10	.000	.000	.000	.000	.000	.000
	21	2	.000	.000	.000	.000	.000	.000
	22	52	.000	.000	.000	.000	.000	.000
	23	72	.000	.000	.000	.000	.000	.000
	25	57	.000	.000	.000	.000	.000	.000
	26	2	.000	.000	.000	.000	.000	.000
	29	53	.000	.000	.000	.000	.000	.000
	30	105	.000	.000	.000	.000	.000	.000
	32	24	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(7)	(8)	(9)	(10)	(11)	(12)	(13)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	1.000	.000	.000	.000	.000	.000	.000
	9	.000	1.000	.000	.000	.000	.000	.000
	10	.000	.000	1.000	.000	.000	.000	.000
	11	.000	.000	.000	1.000	.000	.000	.000
	12	.000	.000	.000	.000	1.000	.000	.000
	13	.000	.000	.000	.000	.000	1.000	.000
	14	.000	.000	.000	.000	.000	.000	1.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	20	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(14)	(15)	(16)	(17)	(18)	(19)	(20)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	14	.000	.000	.000	.000	.000	.000	.000
	15	1.000	.000	.000	.000	.000	.000	.000
	17	.000	1.000	.000	.000	.000	.000	.000
	18	.000	.000	1.000	.000	.000	.000	.000
	19	.000	.000	.000	1.000	.000	.000	.000
	20	.000	.000	.000	.000	1.000	.000	.000
	21	.000	.000	.000	.000	.000	1.000	.000
	22	.000	.000	.000	.000	.000	.000	1.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(21)	(22)	(23)	(24)	(25)	(26)	(27)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	14	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	20	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	1.000	.000	.000	.000	.000	.000	.000
	25	.000	1.000	.000	.000	.000	.000	.000
	26	.000	.000	1.000	.000	.000	.000	.000
	29	.000	.000	.000	1.000	.000	.000	.000
	30	.000	.000	.000	.000	1.000	.000	.000
	32	.000	.000	.000	.000	.000	1.000	.000

Categorical Variables Codings

		Parameter coding					
		(28)	(29)	(30)	(31)	(32)	(33)
GAP_4	1	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000
	14	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000
	17	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000
	20	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding	
		(34)	(35)
GAP_4	1	.000	.000
	2	.000	.000
	3	.000	.000
	4	.000	.000
	5	.000	.000
	7	.000	.000
	8	.000	.000
	9	.000	.000
	10	.000	.000
	11	.000	.000
	12	.000	.000
	13	.000	.000
	14	.000	.000
	15	.000	.000
	17	.000	.000
	18	.000	.000
	19	.000	.000
	20	.000	.000
	21	.000	.000
	22	.000	.000
	23	.000	.000
	25	.000	.000
	26	.000	.000
	29	.000	.000
	30	.000	.000
	32	.000	.000

Categorical Variables Codings

			Parameter coding					
		Frequency	(1)	(2)	(3)	(4)	(5)	(6)
GAP_4	33	35	.000	.000	.000	.000	.000	.000
	35	3	.000	.000	.000	.000	.000	.000
	36	266	.000	.000	.000	.000	.000	.000
	37	344	.000	.000	.000	.000	.000	.000
	38	4	.000	.000	.000	.000	.000	.000
	42	21	.000	.000	.000	.000	.000	.000
	44	26	.000	.000	.000	.000	.000	.000
	45	176	.000	.000	.000	.000	.000	.000
	49	11	.000	.000	.000	.000	.000	.000
	50	2	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(7)	(8)	(9)	(10)	(11)	(12)	(13)
GAP_4	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000
	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(14)	(15)	(16)	(17)	(18)	(19)	(20)
GAP_4	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000
	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(21)	(22)	(23)	(24)	(25)	(26)	(27)
GAP_4	33	.000	.000	.000	.000	.000	.000	1.000
	35	.000	.000	.000	.000	.000	.000	.000
	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding					
		(28)	(29)	(30)	(31)	(32)	(33)
GAP_4	33	.000	.000	.000	.000	.000	.000
	35	1.000	.000	.000	.000	.000	.000
	36	.000	1.000	.000	.000	.000	.000
	37	.000	.000	1.000	.000	.000	.000
	38	.000	.000	.000	1.000	.000	.000
	42	.000	.000	.000	.000	1.000	.000
	44	.000	.000	.000	.000	.000	1.000
	45	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding	
		(34)	(35)
GAP_4	33	.000	.000
	35	.000	.000
	36	.000	.000
	37	.000	.000
	38	.000	.000
	42	.000	.000
	44	.000	.000
	45	1.000	.000
	49	.000	1.000
	50	.000	.000

Block 0: Beginning Block

Classification Table[d,e]

			Predicted			
			Selected Cases [a]			Unselected Cases [b,,c]
			Class			Class
Observed			PH	R	Percentage Correct	PH
Step 0	Class	PH	977	0	100.0	420

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. Constant is included in the model.

e. The cut value is .500

Classification Table[d,e]

Observed			Predicted Unselected Cases[b,,c] Class R	Percentage Correct
Step 0	Class	PH	0	100.0

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. Constant is included in the model.

e. The cut value is .500

Classification Table[d,e]

Observed			Predicted Selected Cases[a] Class PH	R	Percentage Correct	Unselected Cases[b,,c] Class PH
Step 0	Class	R	707	0	.0	292
		Overall Percentage			58.0	

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. Constant is included in the model.

e. The cut value is .500

Classification Table[d,e]

Observed			Predicted Unselected Cases[b,,c] Class R	Percentage Correct
Step 0	Class	R	0	.0
		Overall Percentage		59.0

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. Constant is included in the model.

e. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 0	Constant	-.323	.049	42.914	1	.000	.724

Variables not in the Equation[a]

			Score	df	Sig.
Step 0	Variables	TRI480	128.563	1	.000
		GAP_4	420.926	35	.000
		GAP_4(1)	13.155	1	.000
		GAP_4(2)	.007	1	.932
		GAP_4(3)	.697	1	.404
		GAP_4(4)	.752	1	.386
		GAP_4(5)	.684	1	.408
		GAP_4(6)	48.530	1	.000
		GAP_4(7)	5.541	1	.019
		GAP_4(8)	.106	1	.745
		GAP_4(9)	1.794	1	.180
		GAP_4(10)	16.702	1	.000
		GAP_4(11)	1.913	1	.167
		GAP_4(12)	2.214	1	.137
		GAP_4(13)	.724	1	.395
		GAP_4(14)	2.767	1	.096
		GAP_4(15)	1.794	1	.180
		GAP_4(16)	2.263	1	.132
		GAP_4(17)	18.104	1	.000
		GAP_4(18)	4.225	1	.040
		GAP_4(19)	2.767	1	.096
		GAP_4(20)	14.128	1	.000
		GAP_4(21)	20.991	1	.000
		GAP_4(22)	4.854	1	.028
		GAP_4(23)	2.767	1	.096
		GAP_4(24)	14.044	1	.000
		GAP_4(25)	18.535	1	.000
		GAP_4(26)	2.883	1	.090
		GAP_4(27)	7.092	1	.008
		GAP_4(28)	4.153	1	.042
		GAP_4(29)	99.496	1	.000
		GAP_4(30)	25.735	1	.000
		GAP_4(31)	.475	1	.491
		GAP_4(32)	6.698	1	.010
		GAP_4(33)	1.363	1	.243

a. Residual Chi-Squares are not computed because of redundancies.

Variables not in the Equation[a]

			Score	df	Sig.
Step 0	Variables	GAP_4(34)	110.429	1	.000
		GAP_4(35)	.055	1	.815

a. Residual Chi-Squares are not computed because of redundancies.

Block 1: Method = Forward Stepwise (Likelihood Ratio)

Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Step	456.703	35	.000
	Block	456.703	35	.000
	Model	456.703	35	.000
Step 2	Step	26.096	1	.000
	Block	482.799	36	.000
	Model	482.799	36	.000

Model Summary

Step	-2 Log likelihood	Cox & Snell R Square	Nagelkerke R Square
1	1834.339[a]	.238	.320
2	1808.244[a]	.249	.335

a. Estimation terminated at iteration number 20 because maximum iterations has been reached. Final solution cannot be found.

Hosmer and Lemeshow Test

Step	Chi-square	df	Sig.
1	.000	7	1.000
2	19.988	8	.010

Contingency Table for Hosmer and Lemeshow Test

		Class = PH		Class = R		
		Observed	Expected	Observed	Expected	Total
Step 1	1	264	264.000	43	43.000	307
	2	154	154.000	39	39.000	193
	3	33	33.000	11	11.000	44
	4	241	241.000	103	103.000	344
	5	119	119.000	82	82.000	201
	6	71	71.000	99	99.000	170
	7	42	42.000	90	90.000	132
	8	37	37.000	139	139.000	176
	9	16	16.000	101	101.000	117

Contingency Table for Hosmer and Lemeshow Test

		Class = PH		Class = R		
		Observed	Expected	Observed	Expected	Total
Step 2	1	143	151.599	25	16.401	168
	2	140	140.266	27	26.734	167
	3	141	135.651	27	32.349	168
	4	135	123.956	33	44.044	168
	5	116	113.046	52	54.954	168
	6	112	106.290	60	65.710	172
	7	68	83.546	100	84.454	168
	8	62	56.473	106	111.527	168
	9	41	39.734	127	128.266	168
	10	19	26.437	150	142.563	169

Classification Table[d]

			Predicted			
			Selected Cases [a]			Unselected Cases [b,,c]
			Class			Class
Observed			PH	R	Percentage Correct	PH
Step 1	Class	PH	817	160	83.6	350
		R	283	424	60.0	119
		Overall Percentage			73.7	
Step 2	Class	PH	830	147	85.0	358
		R	288	419	59.3	120
		Overall Percentage			74.2	

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. The cut value is .500

Classification Table[d]

			Predicted	
			Unselected Cases[b,,c]	
			Class	
Observed			R	Percentage Correct
Step 1	Class	PH	70	83.3
		R	173	59.2
		Overall Percentage		73.5
Step 2	Class	PH	62	85.2
		R	172	58.9
		Overall Percentage		74.4

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 1[a]	GAP_4			311.527	35	.000	
	GAP_4(1)	21.899	28533.052	.000	1	.999	3.240E9
	GAP_4(2)	20.895	28533.052	.000	1	.999	1.187E9
	GAP_4(3)	21.206	28533.052	.000	1	.999	1.620E9
	GAP_4(4)	21.899	28533.052	.000	1	.999	3.240E9
	GAP_4(5)	21.429	28533.052	.000	1	.999	2.025E9
	GAP_4(6)	22.576	28533.052	.000	1	.999	6.379E9
	GAP_4(7)	42.409	34899.910	.000	1	.999	2.617E18
	GAP_4(8)	21.206	28533.052	.000	1	.999	1.620E9
	GAP_4(9)	22.304	28533.052	.000	1	.999	4.860E9
	GAP_4(10)	42.409	30801.915	.000	1	.999	2.617E18
	GAP_4(11)	20.107	28533.052	.000	1	.999	5.400E8
	GAP_4(12)	19.414	28533.052	.000	1	.999	2.700E8
	GAP_4(13)	.003	49291.073	.000	1	1.000	1.003
	GAP_4(14)	42.409	40272.478	.000	1	.999	2.617E18
	GAP_4(15)	22.304	28533.052	.000	1	.999	4.860E9
	GAP_4(16)	21.899	28533.052	.000	1	.999	3.240E9
	GAP_4(17)	42.409	30633.353	.000	1	.999	2.617E18
	GAP_4(18)	19.008	28533.052	.000	1	.999	1.800E8
	GAP_4(19)	42.409	40272.478	.000	1	.999	2.617E18
	GAP_4(20)	21.928	28533.052	.000	1	.999	3.335E9

a. Variable(s) entered on step 1: GAP_4.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 1[a]	GAP_4(21)	21.962	28533.052	.000	1	.999	3.451E9
	GAP_4(22)	21.453	28533.052	.000	1	.999	2.074E9
	GAP_4(23)	42.409	40272.478	.000	1	.999	2.617E18
	GAP_4(24)	19.619	28533.052	.000	1	.999	3.314E8
	GAP_4(25)	19.934	28533.052	.000	1	.999	4.544E8
	GAP_4(26)	20.107	28533.052	.000	1	.999	5.400E8
	GAP_4(27)	19.819	28533.052	.000	1	.999	4.050E8
	GAP_4(28)	42.409	36778.073	.000	1	.999	2.617E18
	GAP_4(29)	19.414	28533.052	.000	1	.999	2.700E8
	GAP_4(30)	20.356	28533.052	.000	1	.999	6.924E8
	GAP_4(31)	20.107	28533.052	.000	1	.999	5.400E8
	GAP_4(32)	19.414	28533.052	.000	1	.999	2.700E8
	GAP_4(33)	20.395	28533.052	.000	1	.999	7.200E8
	GAP_4(34)	22.529	28533.052	.000	1	.999	6.086E9
	GAP_4(35)	21.023	28533.052	.000	1	.999	1.350E9
	Constant	-21.206	28533.052	.000	1	.999	.000

a. Variable(s) entered on step 1: GAP_4.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 2[b]	TRI480	.000	.000	20.419	1	.000	1.000
	GAP_4			213.860	35	.000	
	GAP_4(1)	21.844	28402.674	.000	1	.999	3.067E9
	GAP_4(2)	21.040	28402.674	.000	1	.999	1.373E9
	GAP_4(3)	21.127	28402.674	.000	1	.999	1.498E9
	GAP_4(4)	22.019	28402.674	.000	1	.999	3.653E9
	GAP_4(5)	21.616	28402.674	.000	1	.999	2.441E9
	GAP_4(6)	22.540	28402.674	.000	1	.999	6.154E9
	GAP_4(7)	42.332	34793.135	.000	1	.999	2.424E18
	GAP_4(8)	21.352	28402.674	.000	1	.999	1.875E9
	GAP_4(9)	22.277	28402.674	.000	1	.999	4.730E9
	GAP_4(10)	42.322	30681.180	.000	1	.999	2.400E18
	GAP_4(11)	20.547	28402.674	.000	1	.999	8.383E8
	GAP_4(12)	19.583	28402.674	.000	1	.999	3.197E8
	GAP_4(13)	.065	49215.716	.000	1	1.000	1.068
	GAP_4(14)	42.399	40171.974	.000	1	.999	2.593E18
	GAP_4(15)	22.219	28402.674	.000	1	.999	4.461E9
	GAP_4(16)	21.857	28402.674	.000	1	.999	3.107E9
	GAP_4(17)	42.322	30511.951	.000	1	.999	2.400E18
	GAP_4(18)	19.088	28402.674	.000	1	.999	1.948E8
	GAP_4(19)	42.322	40180.210	.000	1	.999	2.399E18
	GAP_4(20)	21.907	28402.674	.000	1	.999	3.267E9
	GAP_4(21)	21.900	28402.674	.000	1	.999	3.245E9
	GAP_4(22)	21.539	28402.674	.000	1	.999	2.260E9
	GAP_4(23)	42.332	40180.175	.000	1	.999	2.423E18
	GAP_4(24)	19.900	28402.674	.000	1	.999	4.389E8
	GAP_4(25)	20.419	28402.674	.000	1	.999	7.373E8
	GAP_4(26)	20.261	28402.674	.000	1	.999	6.301E8
	GAP_4(27)	19.962	28402.674	.000	1	.999	4.670E8
	GAP_4(28)	42.337	36676.628	.000	1	.999	2.435E18
	GAP_4(29)	19.681	28402.674	.000	1	.999	3.528E8
	GAP_4(30)	20.529	28402.674	.000	1	.999	8.230E8
	GAP_4(31)	20.270	28402.674	.000	1	.999	6.354E8
	GAP_4(32)	19.486	28402.674	.000	1	.999	2.902E8
	GAP_4(33)	20.381	28402.674	.000	1	.999	7.102E8
	GAP_4(34)	22.459	28402.674	.000	1	.999	5.675E9
	GAP_4(35)	21.051	28402.674	.000	1	.999	1.387E9
	Constant	-21.118	28402.674	.000	1	.999	.000

a. Variable(s) entered on step 1: GAP_4.

b. Variable(s) entered on step 2: TRI480.

Model if Term Removed

Variable		Model Log Likelihood	Change in -2 Log Likelihood	df	Sig. of the Change
Step 1	GAP_4	-1145.521	456.703	35	.000
Step 2	TRI480	-917.170	26.096	1	.000
	GAP_4	-1055.662	303.081	35	.000

Variables not in the Equation

			Score	df	Sig.
Step 1	Variables	TRI480	21.763	1	.000
		Overall Statistics	21.763	1	.000

```
COMPUTE chgdev=SRE_1 ** 2.
EXECUTE.
* Chart Builder.
GGRAPH
  /GRAPHDATASET NAME="graphdataset" VARIABLES=PRE_1 chgdev MISSING=LISTWISE R
EPORTMISSING=NO
  /GRAPHSPEC SOURCE=INLINE.
BEGIN GPL
  SOURCE: s=userSource(id("graphdataset"))
  DATA: PRE_1=col(source(s), name("PRE_1"))
  DATA: chgdev=col(source(s), name("chgdev"))
  GUIDE: axis(dim(1), label("Predicted probability"))
  GUIDE: axis(dim(2), label("chgdev"))
  ELEMENT: point(position(PRE_1*chgdev))
END GPL.
```

GGraph

Notes

	Output Created	02-Jun-2010 17:52:24
	Comments	
Input	Data	C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NMDGFhabitatmodel\Data2010\modeldata2b.sav
	Active Dataset	DataSet1
	Filter	Model_ID > 4000 & Class ne 'PC' (FILTER)
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data File	2397

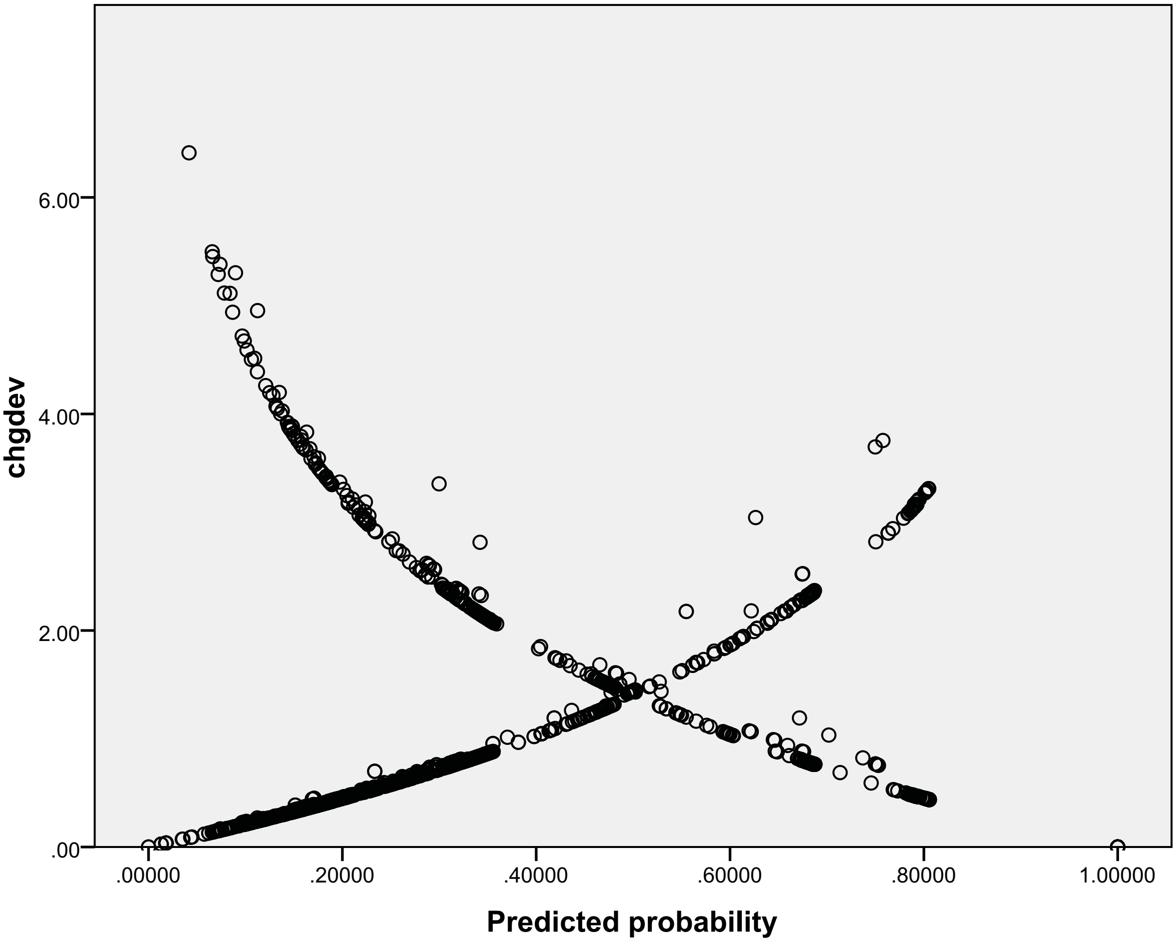
Notes

Syntax

```
GGRAPH
  /GRAPHDATASET NAME="
graphdataset" VARIABLES=PRE_1
chgdev MISSING=LISTWISE
REPORTMISSING=NO
  /GRAPHSPEC SOURCE=INLINE.
BEGIN GPL
  SOURCE: s=userSource(id
("graphdataset"))
  DATA: PRE_1=col(source(s),
name("PRE_1"))
  DATA: chgdev=col(source(s),
name("chgdev"))
  GUIDE: axis(dim(1), label
("Predicted probability"))
  GUIDE: axis(dim(2), label
("chgdev"))
  ELEMENT: point(position
(PRE_1*chgdev))
END GPL.
```

Resources	Processor Time	0:00:00.266
	Elapsed Time	0:00:00.281

```
[DataSet1] C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NM
DGFhabitatmodel\Data2010\modeldata2b.sav
```



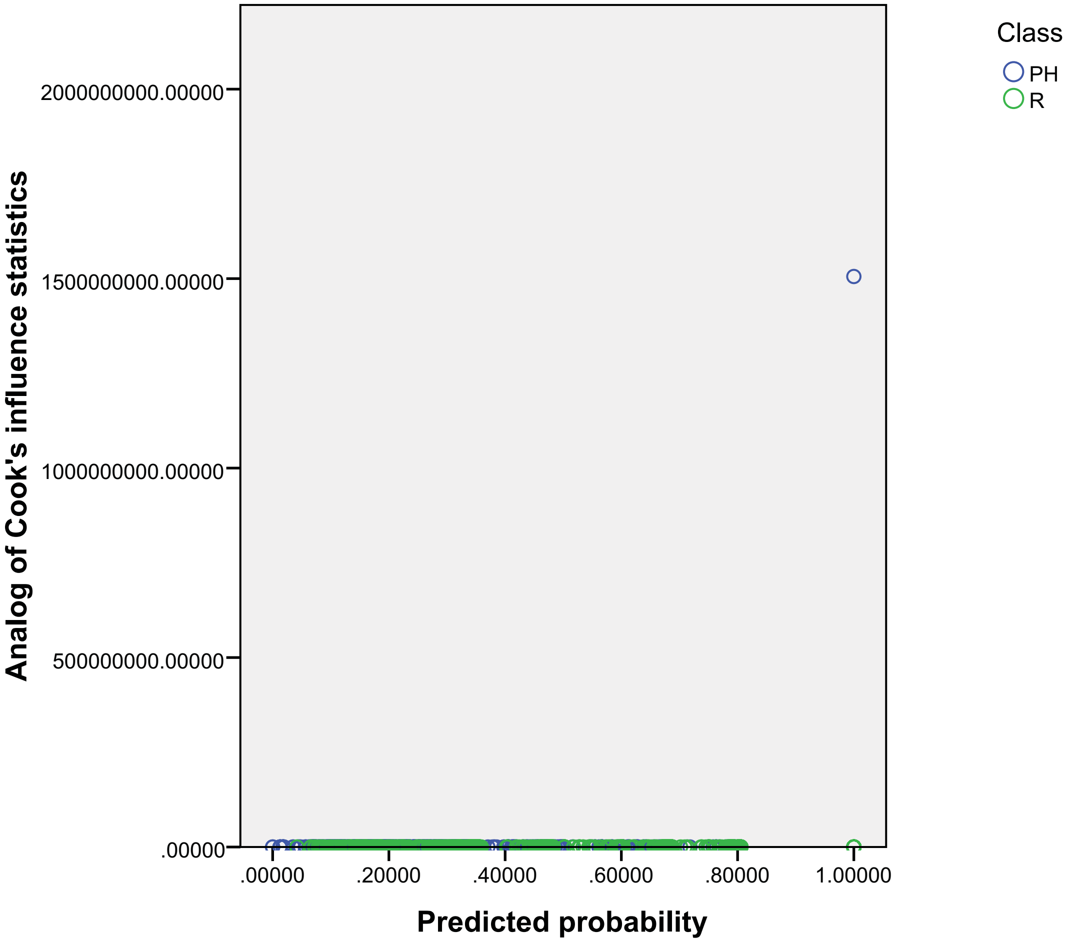
```
* Chart Builder.
GGRAPH
  /GRAPHDATASET NAME="graphdataset" VARIABLES=PRE_1 COO_1 Class MISSING=LISTW
ISE REPORTMISSING=NO
  /GRAPHSPEC SOURCE=INLINE.
BEGIN GPL
  SOURCE: s=userSource(id("graphdataset"))
  DATA: PRE_1=col(source(s), name("PRE_1"))
  DATA: COO_1=col(source(s), name("COO_1"))
  DATA: Class=col(source(s), name("Class"), unit.category())
  GUIDE: axis(dim(1), label("Predicted probability"))
  GUIDE: axis(dim(2), label("Analog of Cook's influence statistics"))
  GUIDE: legend(aesthetic(aesthetic.color.exterior), label("Class"))
  ELEMENT: point(position(PRE_1*COO_1), color.exterior(Class))
END GPL.
```

GGraph

Notes

	Output Created	02-Jun-2010 17:54:44
	Comments	
Input	Data	C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NMDGFhabitatmodel\Data2010\modeldata2b.sav
	Active Dataset	DataSet1
	Filter	Model_ID > 4000 & Class ne 'PC' (FILTER)
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data File	2397
	Syntax	GGRAPH /GRAPHDATASET NAME=" graphdataset" VARIABLES=PRE_1 COO_1 Class MISSING=LISTWISE REPORTMISSING=NO /GRAPHSPEC SOURCE=INLINE. BEGIN GPL SOURCE: s=userSource(id ("graphdataset")) DATA: PRE_1=col(source(s), name("PRE_1")) DATA: COO_1=col(source(s), name("COO_1")) DATA: Class=col(source(s), name ("Class"), unit.category()) GUIDE: axis(dim(1), label ("Predicted probability")) GUIDE: axis(dim(2), label("Analog of Cook's influence statistics")) GUIDE: legend(aesthetic (aesthetic.color.exterior), label ("Class")) ELEMENT: point(position (PRE_1*COO_1), color.exterior (Class)) END GPL.
Resources	Processor Time	0:00:00.312
	Elapsed Time	0:00:00.296

```
[DataSet1] C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NM
DGFhabitatmodel\Data2010\modeldata2b.sav
```



```
SORT CASES BY COO_1 (D).
USE ALL.
COMPUTE filter_$=(Model_ID > 4000 & Class ne 'PC' & COO_1 < 2.0).
VARIABLE LABEL filter_$ "Model_ID > 4000 & Class ne 'PC' & COO_1 < 2.0 (FILTE
R)".
VALUE LABELS filter_$ 0 'Not Selected' 1 'Selected'.
FORMAT filter_$ (f1.0).
FILTER BY filter_$.
EXECUTE.
LOGISTIC REGRESSION VARIABLES Class
  /SELECT=validate EQ 1
  /METHOD=FSTEP(LR) TRI480 GAP_4
  /CONTRAST (GAP_4)=Indicator
  /SAVE=PRED COOK SRESID
  /PRINT=GOODFIT
  /CRITERIA=PIN(0.05) POUT(0.10) ITERATE(20) CUT(0.5).
```

Logistic Regression

Notes

	Output Created	02-Jun-2010 17:57:31
	Comments	
Input	Data	C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NMDGFhabitatmodel\Data2010\modeldata2b.sav
	Active Dataset	DataSet1
	Filter	Model_ID > 4000 & Class ne 'PC' & COO_1 < 2.0 (FILTER)
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data File	2394
Missing Value Handling	Definition of Missing	User-defined missing values are treated as missing
	Syntax	LOGISTIC REGRESSION VARIABLES Class /SELECT=validate EQ 1 /METHOD=FSTEP(LR) TRI480 GAP_4 /CONTRAST (GAP_4)=Indicator /SAVE=PRED COOK SRESID /PRINT=GOODFIT /CRITERIA=PIN(0.05) POUT(0.10) ITERATE(20) CUT(0.5).
Resources	Processor Time	0:00:00.453
	Elapsed Time	0:00:00.452
Variables Created or Modified	PRE_2	Predicted probability
	COO_2	Analog of Cook's influence statistics
	SRE_2	Standard residual

```
[DataSet1] C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NM
DGFhabitatmodel\Data2010\modeldata2b.sav
```

Case Processing Summary

Unweighted Cases [a]		N	Percent
Selected Cases	Included in Analysis	1683	70.3
	Missing Cases	0	.0
	Total	1683	70.3
	Unselected Cases	711	29.7
	Total	2394	100.0

a. If weight is in effect, see classification table for the total number of cases.

Dependent Variable Encoding

Original Value	Internal Value
PH	0
R	1

Categorical Variables Codings

			Parameter coding					
		Frequency	(1)	(2)	(3)	(4)	(5)	(6)
GAP_4	1	51	1.000	.000	.000	.000	.000	.000
	2	175	.000	1.000	.000	.000	.000	.000
	3	26	.000	.000	1.000	.000	.000	.000
	4	3	.000	.000	.000	1.000	.000	.000
	5	9	.000	.000	.000	.000	1.000	.000
	7	79	.000	.000	.000	.000	.000	1.000
	8	4	.000	.000	.000	.000	.000	.000
	9	4	.000	.000	.000	.000	.000	.000
	10	4	.000	.000	.000	.000	.000	.000
	11	12	.000	.000	.000	.000	.000	.000
	12	16	.000	.000	.000	.000	.000	.000
	13	7	.000	.000	.000	.000	.000	.000
	15	2	.000	.000	.000	.000	.000	.000
	17	4	.000	.000	.000	.000	.000	.000
	18	9	.000	.000	.000	.000	.000	.000
	19	13	.000	.000	.000	.000	.000	.000
	20	10	.000	.000	.000	.000	.000	.000
	21	2	.000	.000	.000	.000	.000	.000
	22	52	.000	.000	.000	.000	.000	.000
	23	72	.000	.000	.000	.000	.000	.000
	25	57	.000	.000	.000	.000	.000	.000
	26	2	.000	.000	.000	.000	.000	.000
	29	53	.000	.000	.000	.000	.000	.000
	30	105	.000	.000	.000	.000	.000	.000
	32	24	.000	.000	.000	.000	.000	.000
	33	35	.000	.000	.000	.000	.000	.000
	35	3	.000	.000	.000	.000	.000	.000
	36	266	.000	.000	.000	.000	.000	.000
	37	344	.000	.000	.000	.000	.000	.000
	38	4	.000	.000	.000	.000	.000	.000
	42	21	.000	.000	.000	.000	.000	.000
	44	26	.000	.000	.000	.000	.000	.000
	45	176	.000	.000	.000	.000	.000	.000
	49	11	.000	.000	.000	.000	.000	.000
	50	2	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(7)	(8)	(9)	(10)	(11)	(12)	(13)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	1.000	.000	.000	.000	.000	.000	.000
	9	.000	1.000	.000	.000	.000	.000	.000
	10	.000	.000	1.000	.000	.000	.000	.000
	11	.000	.000	.000	1.000	.000	.000	.000
	12	.000	.000	.000	.000	1.000	.000	.000
	13	.000	.000	.000	.000	.000	1.000	.000
	15	.000	.000	.000	.000	.000	.000	1.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	20	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000
	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000
	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(14)	(15)	(16)	(17)	(18)	(19)	(20)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	1.000	.000	.000	.000	.000	.000	.000
	18	.000	1.000	.000	.000	.000	.000	.000
	19	.000	.000	1.000	.000	.000	.000	.000
	20	.000	.000	.000	1.000	.000	.000	.000
	21	.000	.000	.000	.000	1.000	.000	.000
	22	.000	.000	.000	.000	.000	1.000	.000
	23	.000	.000	.000	.000	.000	.000	1.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000
	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000
	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(21)	(22)	(23)	(24)	(25)	(26)	(27)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	20	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	1.000	.000	.000	.000	.000	.000	.000
	26	.000	1.000	.000	.000	.000	.000	.000
	29	.000	.000	1.000	.000	.000	.000	.000
	30	.000	.000	.000	1.000	.000	.000	.000
	32	.000	.000	.000	.000	1.000	.000	.000
	33	.000	.000	.000	.000	.000	1.000	.000
	35	.000	.000	.000	.000	.000	.000	1.000
	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(28)	(29)	(30)	(31)	(32)	(33)	(34)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	20	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000
	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000
	36	1.000	.000	.000	.000	.000	.000	.000
	37	.000	1.000	.000	.000	.000	.000	.000
	38	.000	.000	1.000	.000	.000	.000	.000
	42	.000	.000	.000	1.000	.000	.000	.000
	44	.000	.000	.000	.000	1.000	.000	.000
	45	.000	.000	.000	.000	.000	1.000	.000
	49	.000	.000	.000	.000	.000	.000	1.000
	50	.000	.000	.000	.000	.000	.000	.000

Block 0: Beginning Block

Classification Table[c,d]

Observed			Predicted			
			Selected Cases[a]			Unselected Cases[b]
			Class			Class
			PH	R	Percentage Correct	PH
Step 0	Class	PH	976	0	100.0	419
		R	707	0	.0	292
		Overall Percentage			58.0	

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Constant is included in the model.

d. The cut value is .500

Classification Table[c,d]

Observed			Predicted	
			Unselected Cases[b]	
			Class	
			R	Percentage Correct
Step 0	Class	PH	0	100.0
		R	0	.0
		Overall Percentage		58.9

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Constant is included in the model.

d. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 0	Constant	-.322	.049	42.625	1	.000	.724

Variables not in the Equation[a]

			Score	df	Sig.
Step 0	Variables	TRI480	128.660	1	.000
		GAP_4	420.133	34	.000
		GAP_4(1)	13.127	1	.000
		GAP_4(2)	.006	1	.937
		GAP_4(3)	.692	1	.405
		GAP_4(4)	.750	1	.386
		GAP_4(5)	.682	1	.409

a. Residual Chi-Squares are not computed because of redundancies.

Variables not in the Equation[a]

			Score	df	Sig.
Step 0	Variables	GAP_4(6)	48.459	1	.000
		GAP_4(7)	5.535	1	.019
		GAP_4(8)	.105	1	.746
		GAP_4(9)	1.791	1	.181
		GAP_4(10)	16.685	1	.000
		GAP_4(11)	1.918	1	.166
		GAP_4(12)	2.218	1	.136
		GAP_4(13)	2.764	1	.096
		GAP_4(14)	1.791	1	.181
		GAP_4(15)	2.258	1	.133
		GAP_4(16)	18.086	1	.000
		GAP_4(17)	4.231	1	.040
		GAP_4(18)	2.764	1	.096
		GAP_4(19)	14.098	1	.000
		GAP_4(20)	20.948	1	.000
		GAP_4(21)	4.837	1	.028
		GAP_4(22)	2.764	1	.096
		GAP_4(23)	14.070	1	.000
		GAP_4(24)	18.579	1	.000
		GAP_4(25)	2.891	1	.089
		GAP_4(26)	7.107	1	.008
		GAP_4(27)	4.149	1	.042
		GAP_4(28)	99.670	1	.000
		GAP_4(29)	25.842	1	.000
		GAP_4(30)	.476	1	.490
		GAP_4(31)	6.709	1	.010
		GAP_4(32)	1.369	1	.242
		GAP_4(33)	110.270	1	.000
		GAP_4(34)	.054	1	.816

a. Residual Chi-Squares are not computed because of redundancies.

Block 1: Method = Forward Stepwise (Likelihood Ratio)

Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Step	455.614	34	.000
	Block	455.614	34	.000

Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Model	455.614	34	.000
Step 2	Step	26.096	1	.000
	Block	481.710	35	.000
	Model	481.710	35	.000

Model Summary

Step	-2 Log likelihood	Cox & Snell R Square	Nagelkerke R Square
1	1834.339[a]	.237	.319
2	1808.244[a]	.249	.335

a. Estimation terminated at iteration number 20 because maximum iterations has been reached. Final solution cannot be found.

Hosmer and Lemeshow Test

Step	Chi-square	df	Sig.
1	.000	8	1.000
2	20.939	8	.007

Contingency Table for Hosmer and Lemeshow Test

		Class = PH		Class = R		
		Observed	Expected	Observed	Expected	Total
Step 1	1	35	35.000	5	5.000	40
	2	228	228.000	38	38.000	266
	3	154	154.000	39	39.000	193
	4	33	33.000	11	11.000	44
	5	241	241.000	103	103.000	344
	6	119	119.000	82	82.000	201
	7	71	71.000	99	99.000	170
	8	42	42.000	90	90.000	132
	9	37	37.000	139	139.000	176
	10	16	16.000	101	101.000	117
Step 2	1	143	151.457	25	16.543	168
	2	143	142.709	27	27.291	170
	3	137	135.459	31	32.541	168
	4	137	123.632	31	44.368	168
	5	115	112.883	53	55.117	168
	6	111	103.671	57	64.329	168
	7	68	83.546	100	84.454	168
	8	62	56.473	106	111.527	168
	9	41	39.734	127	128.266	168
	10	19	26.437	150	142.563	169

Classification Table[c]

Observed			Predicted			
			Selected Cases [a]			Unselected Cases [b]
			Class			Class
			PH	R	Percentage Correct	PH
Step 1	Class	PH	816	160	83.6	350
		R	283	424	60.0	119
		Overall Percentage			73.7	
Step 2	Class	PH	829	147	84.9	358
		R	288	419	59.3	120
		Overall Percentage			74.2	

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. The cut value is .500

Classification Table[c]

Observed			Predicted	
			Unselected Cases [b]	
			Class	
			R	Percentage Correct
Step 1	Class	PH	69	83.5
		R	173	59.2
		Overall Percentage		73.6
Step 2	Class	PH	61	85.4
		R	172	58.9
		Overall Percentage		74.5

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 1[a]	GAP_4			311.527	34	.000	
	GAP_4(1)	21.899	28538.768	.000	1	.999	3.241E9
	GAP_4(2)	20.895	28538.768	.000	1	.999	1.187E9
	GAP_4(3)	21.206	28538.768	.000	1	.999	1.620E9
	GAP_4(4)	21.899	28538.768	.000	1	.999	3.241E9
	GAP_4(5)	21.429	28538.768	.000	1	.999	2.026E9

a. Variable(s) entered on step 1: GAP_4.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 1[a]	GAP_4(6)	22.577	28538.768	.000	1	.999	6.381E9
	GAP_4(7)	42.409	34904.585	.000	1	.999	2.618E18
	GAP_4(8)	21.206	28538.768	.000	1	.999	1.620E9
	GAP_4(9)	22.305	28538.768	.000	1	.999	4.861E9
	GAP_4(10)	42.409	30807.210	.000	1	.999	2.618E18
	GAP_4(11)	20.107	28538.768	.000	1	.999	5.402E8
	GAP_4(12)	19.414	28538.768	.000	1	.999	2.701E8
	GAP_4(13)	42.409	40276.528	.000	1	.999	2.618E18
	GAP_4(14)	22.305	28538.768	.000	1	.999	4.861E9
	GAP_4(15)	21.899	28538.768	.000	1	.999	3.241E9
	GAP_4(16)	42.409	30638.678	.000	1	.999	2.618E18
	GAP_4(17)	19.009	28538.768	.000	1	.999	1.801E8
	GAP_4(18)	42.409	40276.528	.000	1	.999	2.618E18
	GAP_4(19)	21.928	28538.768	.000	1	.999	3.336E9
	GAP_4(20)	21.962	28538.768	.000	1	.999	3.452E9
	GAP_4(21)	21.453	28538.768	.000	1	.999	2.074E9
	GAP_4(22)	42.409	40276.528	.000	1	.999	2.618E18
	GAP_4(23)	19.619	28538.768	.000	1	.999	3.315E8
	GAP_4(24)	19.935	28538.768	.000	1	.999	4.545E8
	GAP_4(25)	20.107	28538.768	.000	1	.999	5.402E8
	GAP_4(26)	19.820	28538.768	.000	1	.999	4.051E8
	GAP_4(27)	42.409	36782.508	.000	1	.999	2.618E18
	GAP_4(28)	19.414	28538.768	.000	1	.999	2.701E8
	GAP_4(29)	20.356	28538.768	.000	1	.999	6.926E8
	GAP_4(30)	20.107	28538.768	.000	1	.999	5.402E8
	GAP_4(31)	19.414	28538.768	.000	1	.999	2.701E8
	GAP_4(32)	20.395	28538.768	.000	1	.999	7.202E8
	GAP_4(33)	22.530	28538.768	.000	1	.999	6.088E9
	GAP_4(34)	21.024	28538.768	.000	1	.999	1.350E9
	Constant	-21.206	28538.768	.000	1	.999	.000

a. Variable(s) entered on step 1: GAP_4.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 2[b]	TRI480	.000	.000	20.419	1	.000	1.000
	GAP_4			213.861	34	.000	
	GAP_4(1)	21.844	28397.882	.000	1	.999	3.066E9
	GAP_4(2)	21.040	28397.882	.000	1	.999	1.373E9
	GAP_4(3)	21.127	28397.882	.000	1	.999	1.497E9
	GAP_4(4)	22.019	28397.882	.000	1	.999	3.653E9
	GAP_4(5)	21.616	28397.882	.000	1	.999	2.441E9
	GAP_4(6)	22.540	28397.882	.000	1	.999	6.153E9
	GAP_4(7)	42.332	34789.224	.000	1	.999	2.423E18
	GAP_4(8)	21.352	28397.882	.000	1	.999	1.875E9
	GAP_4(9)	22.277	28397.882	.000	1	.999	4.729E9
	GAP_4(10)	42.322	30676.744	.000	1	.999	2.400E18
	GAP_4(11)	20.547	28397.882	.000	1	.999	8.381E8
	GAP_4(12)	19.583	28397.882	.000	1	.999	3.196E8
	GAP_4(13)	42.399	40168.587	.000	1	.999	2.592E18
	GAP_4(14)	22.218	28397.882	.000	1	.999	4.460E9
	GAP_4(15)	21.857	28397.882	.000	1	.999	3.107E9
	GAP_4(16)	42.322	30507.491	.000	1	.999	2.400E18
	GAP_4(17)	19.088	28397.882	.000	1	.999	1.948E8
	GAP_4(18)	42.321	40176.823	.000	1	.999	2.399E18
	GAP_4(19)	21.907	28397.882	.000	1	.999	3.267E9
	GAP_4(20)	21.900	28397.882	.000	1	.999	3.245E9
	GAP_4(21)	21.538	28397.882	.000	1	.999	2.260E9
	GAP_4(22)	42.331	40176.788	.000	1	.999	2.423E18
	GAP_4(23)	19.900	28397.882	.000	1	.999	4.388E8
	GAP_4(24)	20.418	28397.882	.000	1	.999	7.372E8
	GAP_4(25)	20.261	28397.882	.000	1	.999	6.300E8
	GAP_4(26)	19.962	28397.882	.000	1	.999	4.669E8
	GAP_4(27)	42.336	36672.918	.000	1	.999	2.435E18
	GAP_4(28)	19.681	28397.882	.000	1	.999	3.528E8
	GAP_4(29)	20.528	28397.882	.000	1	.999	8.229E8
	GAP_4(30)	20.270	28397.882	.000	1	.999	6.353E8
	GAP_4(31)	19.486	28397.882	.000	1	.999	2.902E8
	GAP_4(32)	20.381	28397.882	.000	1	.999	7.101E8
	GAP_4(33)	22.459	28397.882	.000	1	.999	5.674E9
	GAP_4(34)	21.050	28397.882	.000	1	.999	1.387E9
	Constant	-21.118	28397.882	.000	1	.999	.000

a. Variable(s) entered on step 1: GAP_4.

b. Variable(s) entered on step 2: TRI480.

Model if Term Removed

Variable		Model Log Likelihood	Change in -2 Log Likelihood	df	Sig. of the Change
Step 1	GAP_4	-1144.977	455.614	34	.000
Step 2	TRI480	-917.170	26.096	1	.000
	GAP_4	-1055.070	301.897	34	.000

Variables not in the Equation

			Score	df	Sig.
Step 1	Variables	TRI480	21.763	1	.000
		Overall Statistics	21.763	1	.000

APPENDIX III

SPSS Collar Model Binary Logistic Regression Output

```
LOGISTIC REGRESSION VARIABLES Class
  /SELECT=validate EQ 1
  /METHOD=FSTEP(LR) TRI480 GAP_4
  /CONTRAST (GAP_4)=Indicator
  /SAVE=PRED COOK SRESID
  /PRINT=GOODFIT
  /CRITERIA=PIN(0.05) POUT(0.10) ITERATE(20) CUT(0.5).
```

Logistic Regression

Notes

	Output Created	02-Jun-2010 17:32:46
	Comments	
Input	Data	C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NMDGFhabitatmodel\Data2010\modeldata2b.sav
	Active Dataset	DataSet1
	Filter	Model_ID > 4000 & Class ne 'PH' & COO_1 < 2.0 (FILTER)
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data File	11076
Missing Value Handling	Definition of Missing	User-defined missing values are treated as missing
	Syntax	LOGISTIC REGRESSION VARIABLES Class /SELECT=validate EQ 1 /METHOD=FSTEP(LR) TRI480 GAP_4 /CONTRAST (GAP_4)=Indicator /SAVE=PRED COOK SRESID /PRINT=GOODFIT /CRITERIA=PIN(0.05) POUT(0.10) ITERATE(20) CUT(0.5).
Resources	Processor Time	0:00:01.578
	Elapsed Time	0:00:01.578
Variables Created or Modified	PRE_1	Predicted probability
	COO_1	Analog of Cook's influence statistics
	SRE_1	Standard residual

```
[DataSet1] C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NM
DGFhabitatmodel\Data2010\modeldata2b.sav
```

Case Processing Summary

Unweighted Cases [a]		N	Percent
Selected Cases	Included in Analysis	7684	69.4
	Missing Cases	0	.0
	Total	7684	69.4
	Unselected Cases	3392	30.6
	Total	11076	100.0

a. If weight is in effect, see classification table for the total number of cases.

Dependent Variable Encoding

Original Value	Internal Value
PC	0
R	1

Categorical Variables Codings

			Parameter coding					
		Frequency	(1)	(2)	(3)	(4)	(5)	(6)
GAP_4	1	274	1.000	.000	.000	.000	.000	.000
	2	2476	.000	1.000	.000	.000	.000	.000
	3	29	.000	.000	1.000	.000	.000	.000
	4	2	.000	.000	.000	1.000	.000	.000
	5	5	.000	.000	.000	.000	1.000	.000
	7	308	.000	.000	.000	.000	.000	1.000
	8	23	.000	.000	.000	.000	.000	.000
	9	2	.000	.000	.000	.000	.000	.000
	10	3	.000	.000	.000	.000	.000	.000
	11	16	.000	.000	.000	.000	.000	.000
	12	315	.000	.000	.000	.000	.000	.000
	13	206	.000	.000	.000	.000	.000	.000
	15	11	.000	.000	.000	.000	.000	.000
	17	8	.000	.000	.000	.000	.000	.000
	18	6	.000	.000	.000	.000	.000	.000
	19	13	.000	.000	.000	.000	.000	.000
	21	2	.000	.000	.000	.000	.000	.000
	22	191	.000	.000	.000	.000	.000	.000
	23	75	.000	.000	.000	.000	.000	.000
	25	31	.000	.000	.000	.000	.000	.000
	26	2	.000	.000	.000	.000	.000	.000
	29	67	.000	.000	.000	.000	.000	.000
	30	39	.000	.000	.000	.000	.000	.000
	32	5	.000	.000	.000	.000	.000	.000
	33	6	.000	.000	.000	.000	.000	.000
	35	3	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(7)	(8)	(9)	(10)	(11)	(12)	(13)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	1.000	.000	.000	.000	.000	.000	.000
	9	.000	1.000	.000	.000	.000	.000	.000
	10	.000	.000	1.000	.000	.000	.000	.000
	11	.000	.000	.000	1.000	.000	.000	.000
	12	.000	.000	.000	.000	1.000	.000	.000
	13	.000	.000	.000	.000	.000	1.000	.000
	15	.000	.000	.000	.000	.000	.000	1.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000
	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(14)	(15)	(16)	(17)	(18)	(19)	(20)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	1.000	.000	.000	.000	.000	.000	.000
	18	.000	1.000	.000	.000	.000	.000	.000
	19	.000	.000	1.000	.000	.000	.000	.000
	21	.000	.000	.000	1.000	.000	.000	.000
	22	.000	.000	.000	.000	1.000	.000	.000
	23	.000	.000	.000	.000	.000	1.000	.000
	25	.000	.000	.000	.000	.000	.000	1.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000
	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(21)	(22)	(23)	(24)	(25)	(26)	(27)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	1.000	.000	.000	.000	.000	.000	.000
	29	.000	1.000	.000	.000	.000	.000	.000
	30	.000	.000	1.000	.000	.000	.000	.000
	32	.000	.000	.000	1.000	.000	.000	.000
	33	.000	.000	.000	.000	1.000	.000	.000
	35	.000	.000	.000	.000	.000	1.000	.000

Categorical Variables Codings

		Parameter coding						
		(28)	(29)	(30)	(31)	(32)	(33)	(34)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000
	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

			Parameter coding					
		Frequency	(1)	(2)	(3)	(4)	(5)	(6)
GAP_4	36	231	.000	.000	.000	.000	.000	.000
	37	1562	.000	.000	.000	.000	.000	.000
	38	9	.000	.000	.000	.000	.000	.000
	39	11	.000	.000	.000	.000	.000	.000
	42	1591	.000	.000	.000	.000	.000	.000
	44	8	.000	.000	.000	.000	.000	.000
	45	139	.000	.000	.000	.000	.000	.000
	49	5	.000	.000	.000	.000	.000	.000
	50	10	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(7)	(8)	(9)	(10)	(11)	(12)	(13)
GAP_4	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	39	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(14)	(15)	(16)	(17)	(18)	(19)	(20)
GAP_4	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	39	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(21)	(22)	(23)	(24)	(25)	(26)	(27)
GAP_4	36	.000	.000	.000	.000	.000	.000	1.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	39	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(28)	(29)	(30)	(31)	(32)	(33)	(34)
GAP_4	36	.000	.000	.000	.000	.000	.000	.000
	37	1.000	.000	.000	.000	.000	.000	.000
	38	.000	1.000	.000	.000	.000	.000	.000
	39	.000	.000	1.000	.000	.000	.000	.000
	42	.000	.000	.000	1.000	.000	.000	.000
	44	.000	.000	.000	.000	1.000	.000	.000
	45	.000	.000	.000	.000	.000	1.000	.000
	49	.000	.000	.000	.000	.000	.000	1.000
	50	.000	.000	.000	.000	.000	.000	.000

Block 0: Beginning Block

Classification Table[d,e]

Observed			Predicted			
			Selected Cases[a]			Unselected Cases[b,,c]
			Class			Class
			PC	R	Percentage Correct	PC
Step 0	Class	PC	6983	0	100.0	3105
		R	701	0	.0	286
		Overall Percentage			90.9	

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. Constant is included in the model.

e. The cut value is .500

Classification Table[d,e]

			Predicted	
			Unselected Cases[b,,c]	
			Class	
Observed			R	Percentage Correct
Step 0	Class	PC	0	100.0
		R	0	.0
		Overall Percentage		91.6

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. Constant is included in the model.

e. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 0	Constant	-2.299	.040	3366.256	1	.000	.100

Variables not in the Equation[a]

			Score	df	Sig.
Step 0	Variables	TRI480	193.467	1	.000
		GAP_4	3249.293	34	.000
		GAP_4(1)	3.700	1	.054
		GAP_4(2)	165.803	1	.000
		GAP_4(3)	44.762	1	.000
		GAP_4(4)	19.928	1	.000
		GAP_4(5)	49.840	1	.000
		GAP_4(6)	49.696	1	.000
		GAP_4(7)	1.902	1	.168
		GAP_4(8)	19.928	1	.000
		GAP_4(9)	29.896	1	.000
		GAP_4(10)	83.928	1	.000
		GAP_4(11)	24.433	1	.000
		GAP_4(12)	19.048	1	.000
		GAP_4(13)	1.090	1	.296
		GAP_4(14)	7.778	1	.005
		GAP_4(15)	59.816	1	.000
		GAP_4(16)	129.719	1	.000
		GAP_4(17)	19.928	1	.000
		GAP_4(18)	20.004	1	.000

a. Residual Chi-Squares are not computed because of redundancies.

Variables not in the Equation[a]

			Score	df	Sig.
Step 0	Variables	GAP_4(19)	288.649	1	.000
		GAP_4(20)	310.057	1	.000
		GAP_4(21)	19.928	1	.000
		GAP_4(22)	.647	1	.421
		GAP_4(23)	105.726	1	.000
		GAP_4(24)	49.840	1	.000
		GAP_4(25)	59.816	1	.000
		GAP_4(26)	29.896	1	.000
		GAP_4(27)	15.423	1	.000
		GAP_4(28)	15.122	1	.000
		GAP_4(29)	.043	1	.836
		GAP_4(30)	1.106	1	.293
		GAP_4(31)	193.180	1	.000
		GAP_4(32)	79.775	1	.000
		GAP_4(33)	1410.155	1	.000
		GAP_4(34)	49.840	1	.000

a. Residual Chi-Squares are not computed because of redundancies.

Block 1: Method = Forward Stepwise (Likelihood Ratio)

Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Step	1957.578	34	.000
	Block	1957.578	34	.000
	Model	1957.578	34	.000
Step 2	Step	248.424	1	.000
	Block	2206.003	35	.000
	Model	2206.003	35	.000

Model Summary

Step	-2 Log likelihood	Cox & Snell R Square	Nagelkerke R Square
1	2735.363[a]	.225	.492
2	2486.939[a]	.250	.546

a. Estimation terminated at iteration number 20 because maximum iterations has been reached. Final solution cannot be found.

Hosmer and Lemeshow Test

Step	Chi-square	df	Sig.
1	.000	5	1.000
2	412.175	8	.000

Contingency Table for Hosmer and Lemeshow Test

		Class = PC		Class = R		
		Observed	Expected	Observed	Expected	Total
Step 1	1	21	21.000	0	.000	21
	2	1588	1588.000	3	3.000	1591
	3	516	516.000	5	5.000	521
	4	2402	2402.000	74	74.000	2476
	5	1459	1459.000	103	103.000	1562
	6	684	684.000	122	122.000	806
	7	313	313.000	394	394.000	707
Step 2	1	759	767.789	9	.211	768
	2	766	767.508	3	1.492	769
	3	766	766.038	2	1.962	768
	4	756	762.823	12	5.177	768
	5	760	753.635	7	13.365	767
	6	759	741.582	8	25.418	767
	7	753	729.472	15	38.528	768
	8	695	707.731	74	61.269	769
	9	637	646.101	131	121.899	768
	10	332	340.319	440	431.681	772

Classification Table[d]

			Predicted			
			Selected Cases[a]			Unselected Cases[b,,c]
			Class			Class
Observed			PC	R	Percentage Correct	PC
Step 1	Class	PC	6936	47	99.3	3091
		R	386	315	44.9	171
		Overall Percentage			94.4	
Step 2	Class	PC	6957	26	99.6	3098
		R	379	322	45.9	167
		Overall Percentage			94.7	

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. The cut value is .500

Classification Table[d]

			Predicted	
			Unselected Cases[b,,c]	
			Class	
Observed			R	Percentage Correct
Step 1	Class	PC	14	99.5
		R	115	40.2
		Overall Percentage		94.5
Step 2	Class	PC	7	99.8
		R	119	41.6
		Overall Percentage		94.9

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Some of the unselected cases are not classified due to either missing values in the independent variables or categorical variables with values out of the range of the selected cases.

d. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 1[a]	GAP_4			537.205	34	.000	
	GAP_4(1)	19.249	12716.568	.000	1	.999	2.290E8
	GAP_4(2)	17.724	12716.568	.000	1	.999	4.980E7
	GAP_4(3)	20.996	12716.568	.000	1	.999	1.313E9
	GAP_4(4)	42.406	31135.968	.000	1	.999	2.611E18
	GAP_4(5)	42.406	22018.312	.000	1	.998	2.611E18
	GAP_4(6)	19.845	12716.568	.000	1	.999	4.157E8
	GAP_4(7)	19.645	12716.568	.000	1	.999	3.403E8
	GAP_4(8)	42.406	31135.968	.000	1	.999	2.611E18
	GAP_4(9)	42.406	26461.344	.000	1	.999	2.611E18
	GAP_4(10)	22.302	12716.568	.000	1	.999	4.849E9
	GAP_4(11)	16.850	12716.568	.000	1	.999	2.079E7
	GAP_4(12)	15.881	12716.568	.000	1	.999	7885299.240
	GAP_4(13)	19.699	12716.568	.000	1	.999	3.592E8
	GAP_4(14)	20.693	12716.568	.000	1	.999	9.699E8
	GAP_4(15)	42.406	20759.502	.000	1	.998	2.611E18
	GAP_4(16)	42.406	16910.896	.000	1	.998	2.611E18
	GAP_4(17)	42.406	31135.968	.000	1	.999	2.611E18
	GAP_4(18)	19.709	12716.568	.000	1	.999	3.627E8
	GAP_4(19)	21.837	12716.568	.000	1	.999	3.046E9
	GAP_4(20)	42.406	14622.694	.000	1	.998	2.611E18

a. Variable(s) entered on step 1: GAP_4.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 1[a]	GAP_4(21)	42.406	31135.968	.000	1	.999	2.611E18
	GAP_4(22)	19.205	12716.568	.000	1	.999	2.192E8
	GAP_4(23)	21.461	12716.568	.000	1	.999	2.092E9
	GAP_4(24)	42.406	22018.312	.000	1	.998	2.611E18
	GAP_4(25)	42.406	20759.502	.000	1	.998	2.611E18
	GAP_4(26)	42.406	26461.344	.000	1	.999	2.611E18
	GAP_4(27)	19.578	12716.568	.000	1	.999	3.183E8
	GAP_4(28)	18.553	12716.568	.000	1	.999	1.141E8
	GAP_4(29)	19.124	12716.568	.000	1	.999	2.021E8
	GAP_4(30)	.001	17566.230	.000	1	1.000	1.001
	GAP_4(31)	14.932	12716.568	.000	1	.999	3053815.512
	GAP_4(32)	42.406	19069.490	.000	1	.998	2.611E18
	GAP_4(33)	42.406	13165.607	.000	1	.997	2.611E18
	GAP_4(34)	42.406	22018.312	.000	1	.998	2.611E18
	Constant	-21.204	12716.568	.000	1	.999	.000

a. Variable(s) entered on step 1: GAP_4.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 2[b]	TRI480	-.001	.000	132.154	1	.000	.999
	GAP_4			497.452	34	.000	
	GAP_4(1)	19.708	12711.790	.000	1	.999	3.622E8
	GAP_4(2)	18.739	12711.790	.000	1	.999	1.375E8
	GAP_4(3)	20.998	12711.790	.000	1	.999	1.317E9
	GAP_4(4)	43.049	30959.496	.000	1	.999	4.964E18
	GAP_4(5)	43.654	21297.512	.000	1	.998	9.094E18
	GAP_4(6)	20.002	12711.790	.000	1	.999	4.859E8
	GAP_4(7)	19.724	12711.790	.000	1	.999	3.681E8
	GAP_4(8)	46.082	28382.916	.000	1	.999	1.030E20
	GAP_4(9)	42.803	26413.176	.000	1	.999	3.883E18
	GAP_4(10)	22.311	12711.790	.000	1	.999	4.894E9
	GAP_4(11)	18.515	12711.790	.000	1	.999	1.099E8
	GAP_4(12)	17.559	12711.790	.000	1	.999	4.223E7
	GAP_4(13)	19.886	12711.790	.000	1	.999	4.327E8
	GAP_4(14)	20.735	12711.790	.000	1	.999	1.011E9
	GAP_4(15)	42.769	20689.731	.000	1	.998	3.754E18
	GAP_4(16)	42.412	16907.280	.000	1	.998	2.625E18
	GAP_4(17)	42.409	31134.003	.000	1	.999	2.618E18
	GAP_4(18)	20.603	12711.790	.000	1	.999	8.868E8
	GAP_4(19)	22.279	12711.790	.000	1	.999	4.741E9
	GAP_4(20)	46.184	13732.247	.000	1	.997	1.142E20
	GAP_4(21)	42.460	31133.154	.000	1	.999	2.756E18
	GAP_4(22)	21.677	12711.790	.000	1	.999	2.596E9
	GAP_4(23)	25.507	12711.790	.000	1	.998	1.195E11
	GAP_4(24)	43.691	20829.787	.000	1	.998	9.436E18
	GAP_4(25)	44.049	20211.892	.000	1	.998	1.349E19
	GAP_4(26)	42.489	26448.596	.000	1	.999	2.836E18
	GAP_4(27)	21.742	12711.790	.000	1	.999	2.770E9
	GAP_4(28)	19.870	12711.790	.000	1	.999	4.262E8
	GAP_4(29)	19.231	12711.790	.000	1	.999	2.248E8
	GAP_4(30)	1.215	16833.775	.000	1	1.000	3.369
	GAP_4(31)	15.223	12711.790	.000	1	.999	4084781.105
	GAP_4(32)	44.265	17393.544	.000	1	.998	1.675E19
	GAP_4(33)	42.479	13159.203	.000	1	.997	2.807E18
	GAP_4(34)	42.496	21998.765	.000	1	.998	2.856E18
	Constant	-21.202	12711.790	.000	1	.999	.000

a. Variable(s) entered on step 1: GAP_4.

b. Variable(s) entered on step 2: TRI480.

Model if Term Removed

Variable		Model Log Likelihood	Change in -2 Log Likelihood	df	Sig. of the Change
Step 1	GAP_4	-2346.471	1957.578	34	.000
Step 2	TRI480	-1367.682	248.424	1	.000
	GAP_4	-2179.597	1872.256	34	.000

Variables not in the Equation

			Score	df	Sig.
Step 1	Variables	TRI480	133.652	1	.000
		Overall Statistics	133.652	1	.000

```
COMPUTE chgdev=SRE_1 ** 2.
EXECUTE.
* Chart Builder.
GGRAPH
  /GRAPHDATASET NAME="graphdataset" VARIABLES=PRE_1 chgdev MISSING=LISTWISE R
EPORTMISSING=NO
  /GRAPHSPEC SOURCE=INLINE.
BEGIN GPL
  SOURCE: s=userSource(id("graphdataset"))
  DATA: PRE_1=col(source(s), name("PRE_1"))
  DATA: chgdev=col(source(s), name("chgdev"))
  GUIDE: axis(dim(1), label("Predicted probability"))
  GUIDE: axis(dim(2), label("chgdev"))
  ELEMENT: point(position(PRE_1*chgdev))
END GPL.
```

GGraph

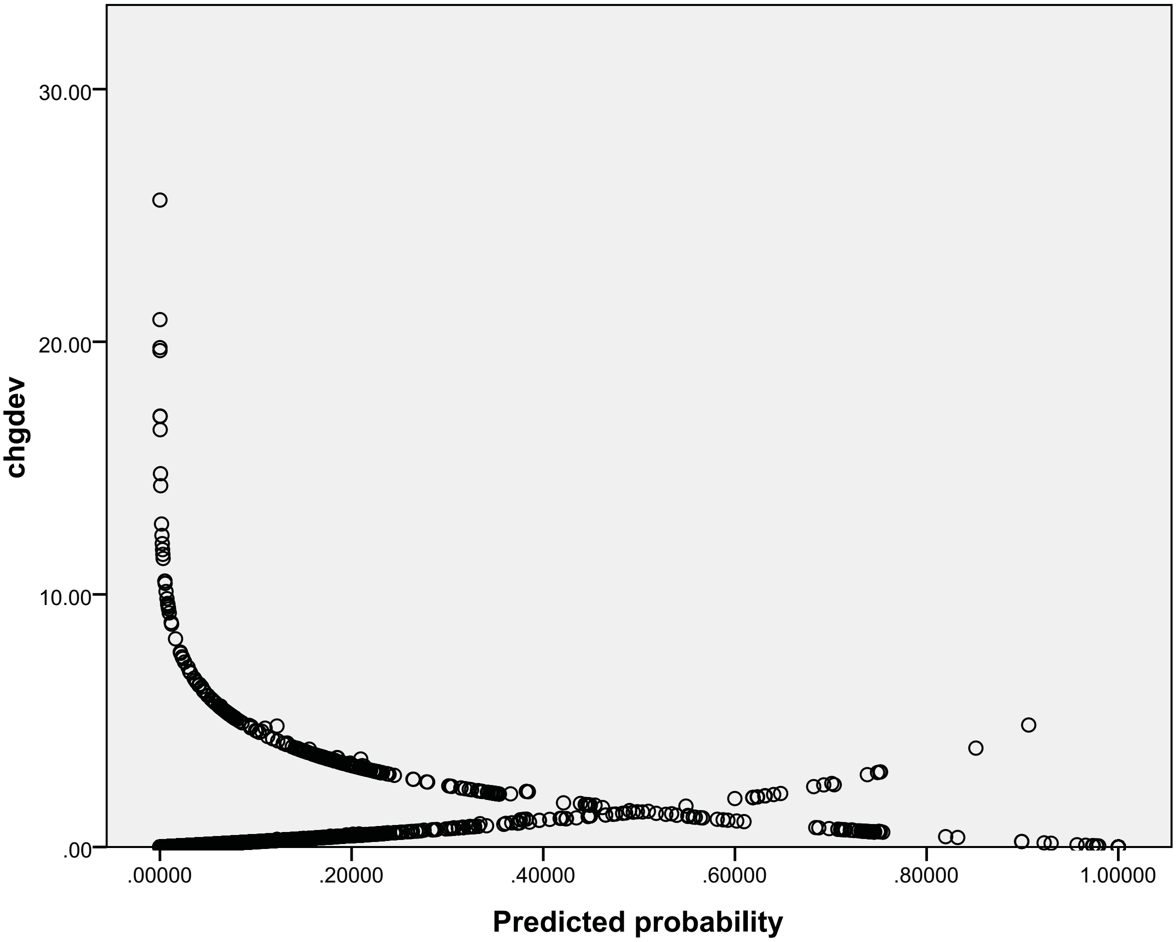
Notes

	Output Created	02-Jun-2010 17:35:29
	Comments	
Input	Data	C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NMDGFhabitatmodel\Data2010\modeldata2b.sav
	Active Dataset	DataSet1
	Filter	Model_ID > 4000 & Class ne 'PH' & COO_1 < 2.0 (FILTER)
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data File	11076

Notes

	Syntax	GGRAPH /GRAPHDATASET NAME="graphdataset" VARIABLES=PRE_1 chgdev MISSING=LISTWISE REPORTMISSING=NO /GRAPHSPEC SOURCE=INLINE. BEGIN GPL SOURCE: s=userSource(id("graphdataset")) DATA: PRE_1=col(source(s), name("PRE_1")) DATA: chgdev=col(source(s), name("chgdev")) GUIDE: axis(dim(1), label("Predicted probability")) GUIDE: axis(dim(2), label("chgdev")) ELEMENT: point(position(PRE_1*chgdev)) END GPL.
Resources	Processor Time	0:00:00.281
	Elapsed Time	0:00:00.296

```
[DataSet1] C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NM
DGFhabitatmodel\Data2010\modeldata2b.sav
```



```
* Chart Builder.
GGRAPH
  /GRAPHDATASET NAME="graphdataset" VARIABLES=PRE_1 COO_1 Class MISSING=LISTW
ISE REPORTMISSING=NO
  /GRAPHSPEC SOURCE=INLINE.
BEGIN GPL
  SOURCE: s=userSource(id("graphdataset"))
  DATA: PRE_1=col(source(s), name("PRE_1"))
  DATA: COO_1=col(source(s), name("COO_1"))
  DATA: Class=col(source(s), name("Class"), unit.category())
  GUIDE: axis(dim(1), label("Predicted probability"))
  GUIDE: axis(dim(2), label("Analog of Cook's influence statistics"))
  GUIDE: legend(aesthetic(aesthetic.color.exterior), label("Class"))
  ELEMENT: point(position(PRE_1*COO_1), color.exterior(Class))
END GPL.
```

GGraph

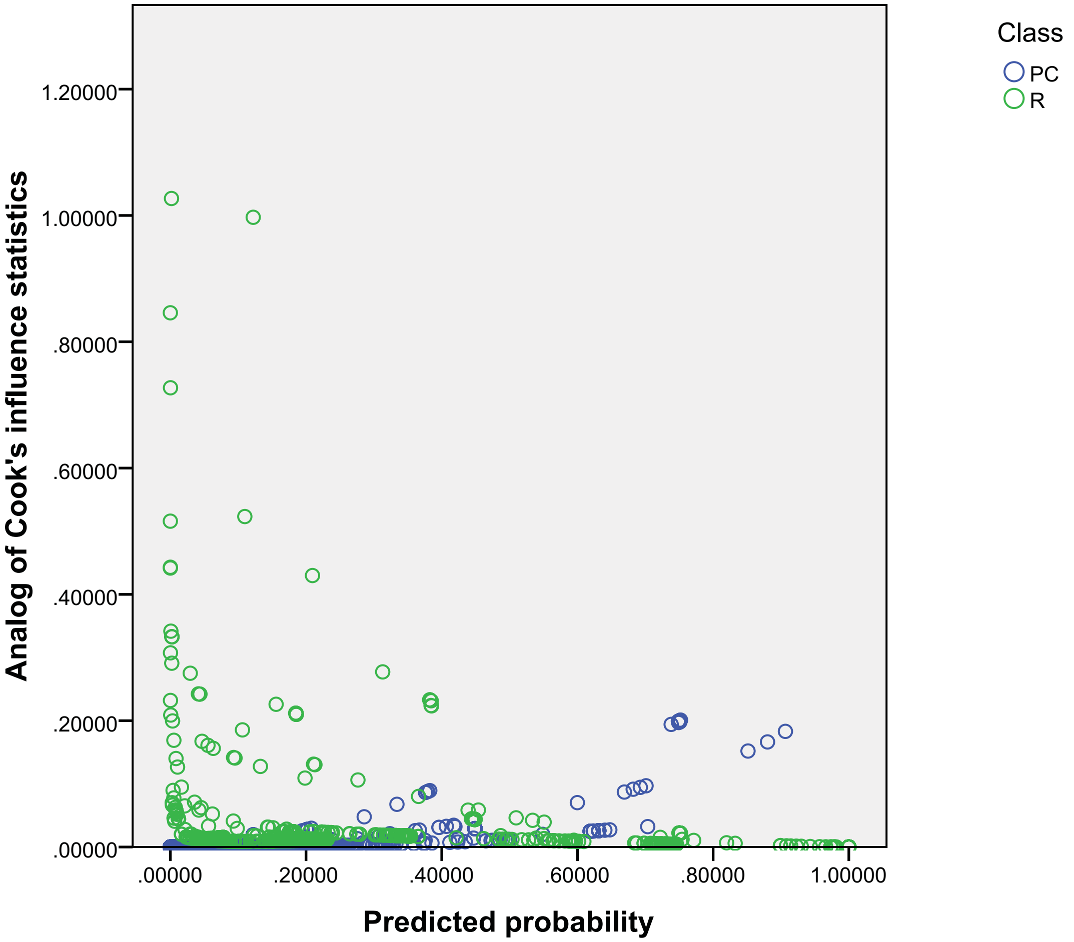
Notes

	Output Created	02-Jun-2010 17:36:13
	Comments	
Input	Data	C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NMDGFhabitatmodel\Data2010\modeldata2b.sav
	Active Dataset	DataSet1
	Filter	Model_ID > 4000 & Class ne 'PH' & COO_1 < 2.0 (FILTER)
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data File	11076
	Syntax	

```
GGRAPH
  /GRAPHDATASET NAME="
graphdataset" VARIABLES=PRE_1
COO_1 Class MISSING=LISTWISE
REPORTMISSING=NO
  /GRAPHSPEC SOURCE=INLINE.
BEGIN GPL
  SOURCE: s=userSource(id
("graphdataset"))
  DATA: PRE_1=col(source(s),
name("PRE_1"))
  DATA: COO_1=col(source(s),
name("COO_1"))
  DATA: Class=col(source(s), name
("Class"), unit.category())
  GUIDE: axis(dim(1), label
("Predicted probability"))
  GUIDE: axis(dim(2), label("Analog
of Cook's influence statistics"))
  GUIDE: legend(aesthetic
(aesthetic.color.exterior), label
("Class"))
  ELEMENT: point(position
(PRE_1*COO_1), color.exterior
(Class))
END GPL.
```

Resources	Processor Time	0:00:00.375
	Elapsed Time	0:00:00.390

```
[DataSet1] C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NM
DGFhabitatmodel\Data2010\modeldata2b.sav
```



```
USE ALL.
COMPUTE filter_$=(Model_ID > 4000 & Class ne 'PH'  & COO_1  <  2.0).
VARIABLE LABEL filter_$ "Model_ID > 4000 & Class ne 'PH'  & COO_1  <  2.0 (FI
LTER)".
VALUE LABELS filter_$ 0 'Not Selected' 1 'Selected'.
FORMAT filter_$ (f1.0).
FILTER BY filter_$.
EXECUTE.
LOGISTIC REGRESSION VARIABLES Class
  /SELECT=validate EQ 1
  /METHOD=FSTEP(LR) TRI480 GAP_4
  /CONTRAST (GAP_4)=Indicator
  /SAVE=PRED COOK SRESID
  /PRINT=GOODFIT
  /CRITERIA=PIN(0.05) POUT(0.10) ITERATE(20) CUT(0.5).
```

Logistic Regression

Notes

	Output Created	02-Jun-2010 17:37:37
	Comments	
Input	Data	C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NMDGFhabitatmodel\Data2010\modeldata2b.sav
	Active Dataset	DataSet1
	Filter	Model_ID > 4000 & Class ne 'PH' & COO_1 < 2.0 (FILTER)
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data File	11075
Missing Value Handling	Definition of Missing	User-defined missing values are treated as missing
	Syntax	

```
LOGISTIC REGRESSION
VARIABLES Class
  /SELECT=validate EQ 1
  /METHOD=FSTEP(LR) TRI480
GAP_4
  /CONTRAST (GAP_4)=Indicator
  /SAVE=PRED COOK SRESID
  /PRINT=GOODFIT
  /CRITERIA=PIN(0.05) POUT(0.10)
ITERATE(20) CUT(0.5).
```

Resources	Processor Time	0:00:01.547
	Elapsed Time	0:00:01.548
Variables Created or Modified	PRE_2	Predicted probability
	COO_2	Analog of Cook's influence statistics
	SRE_2	Standard residual

```
[DataSet1] C:\Documents and Settings\tperry\My Documents\My Dropbox\Cougar\NM
DGFhabitatmodel\Data2010\modeldata2b.sav
```

Case Processing Summary

Unweighted Cases [a]		N	Percent
Selected Cases	Included in Analysis	7684	69.4
	Missing Cases	0	.0
	Total	7684	69.4
	Unselected Cases	3391	30.6
	Total	11075	100.0

a. If weight is in effect, see classification table for the total number of cases.

Dependent Variable Encoding

Original Value	Internal Value
PC	0
R	1

Categorical Variables Codings

			Parameter coding					
		Frequency	(1)	(2)	(3)	(4)	(5)	(6)
GAP_4	1	274	1.000	.000	.000	.000	.000	.000
	2	2476	.000	1.000	.000	.000	.000	.000
	3	29	.000	.000	1.000	.000	.000	.000
	4	2	.000	.000	.000	1.000	.000	.000
	5	5	.000	.000	.000	.000	1.000	.000
	7	308	.000	.000	.000	.000	.000	1.000
	8	23	.000	.000	.000	.000	.000	.000
	9	2	.000	.000	.000	.000	.000	.000
	10	3	.000	.000	.000	.000	.000	.000
	11	16	.000	.000	.000	.000	.000	.000
	12	315	.000	.000	.000	.000	.000	.000
	13	206	.000	.000	.000	.000	.000	.000
	15	11	.000	.000	.000	.000	.000	.000
	17	8	.000	.000	.000	.000	.000	.000
	18	6	.000	.000	.000	.000	.000	.000
	19	13	.000	.000	.000	.000	.000	.000
	21	2	.000	.000	.000	.000	.000	.000
	22	191	.000	.000	.000	.000	.000	.000
	23	75	.000	.000	.000	.000	.000	.000
	25	31	.000	.000	.000	.000	.000	.000
	26	2	.000	.000	.000	.000	.000	.000
	29	67	.000	.000	.000	.000	.000	.000
	30	39	.000	.000	.000	.000	.000	.000
	32	5	.000	.000	.000	.000	.000	.000
	33	6	.000	.000	.000	.000	.000	.000
	35	3	.000	.000	.000	.000	.000	.000
	36	231	.000	.000	.000	.000	.000	.000
	37	1562	.000	.000	.000	.000	.000	.000
	38	9	.000	.000	.000	.000	.000	.000
	39	11	.000	.000	.000	.000	.000	.000
	42	1591	.000	.000	.000	.000	.000	.000
	44	8	.000	.000	.000	.000	.000	.000
	45	139	.000	.000	.000	.000	.000	.000
	49	5	.000	.000	.000	.000	.000	.000
	50	10	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(7)	(8)	(9)	(10)	(11)	(12)	(13)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	1.000	.000	.000	.000	.000	.000	.000
	9	.000	1.000	.000	.000	.000	.000	.000
	10	.000	.000	1.000	.000	.000	.000	.000
	11	.000	.000	.000	1.000	.000	.000	.000
	12	.000	.000	.000	.000	1.000	.000	.000
	13	.000	.000	.000	.000	.000	1.000	.000
	15	.000	.000	.000	.000	.000	.000	1.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000
	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000
	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	39	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(14)	(15)	(16)	(17)	(18)	(19)	(20)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	1.000	.000	.000	.000	.000	.000	.000
	18	.000	1.000	.000	.000	.000	.000	.000
	19	.000	.000	1.000	.000	.000	.000	.000
	21	.000	.000	.000	1.000	.000	.000	.000
	22	.000	.000	.000	.000	1.000	.000	.000
	23	.000	.000	.000	.000	.000	1.000	.000
	25	.000	.000	.000	.000	.000	.000	1.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000
	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000
	36	.000	.000	.000	.000	.000	.000	.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	39	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(21)	(22)	(23)	(24)	(25)	(26)	(27)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	1.000	.000	.000	.000	.000	.000	.000
	29	.000	1.000	.000	.000	.000	.000	.000
	30	.000	.000	1.000	.000	.000	.000	.000
	32	.000	.000	.000	1.000	.000	.000	.000
	33	.000	.000	.000	.000	1.000	.000	.000
	35	.000	.000	.000	.000	.000	1.000	.000
	36	.000	.000	.000	.000	.000	.000	1.000
	37	.000	.000	.000	.000	.000	.000	.000
	38	.000	.000	.000	.000	.000	.000	.000
	39	.000	.000	.000	.000	.000	.000	.000
	42	.000	.000	.000	.000	.000	.000	.000
	44	.000	.000	.000	.000	.000	.000	.000
	45	.000	.000	.000	.000	.000	.000	.000
	49	.000	.000	.000	.000	.000	.000	.000
	50	.000	.000	.000	.000	.000	.000	.000

Categorical Variables Codings

		Parameter coding						
		(28)	(29)	(30)	(31)	(32)	(33)	(34)
GAP_4	1	.000	.000	.000	.000	.000	.000	.000
	2	.000	.000	.000	.000	.000	.000	.000
	3	.000	.000	.000	.000	.000	.000	.000
	4	.000	.000	.000	.000	.000	.000	.000
	5	.000	.000	.000	.000	.000	.000	.000
	7	.000	.000	.000	.000	.000	.000	.000
	8	.000	.000	.000	.000	.000	.000	.000
	9	.000	.000	.000	.000	.000	.000	.000
	10	.000	.000	.000	.000	.000	.000	.000
	11	.000	.000	.000	.000	.000	.000	.000
	12	.000	.000	.000	.000	.000	.000	.000
	13	.000	.000	.000	.000	.000	.000	.000
	15	.000	.000	.000	.000	.000	.000	.000
	17	.000	.000	.000	.000	.000	.000	.000
	18	.000	.000	.000	.000	.000	.000	.000
	19	.000	.000	.000	.000	.000	.000	.000
	21	.000	.000	.000	.000	.000	.000	.000
	22	.000	.000	.000	.000	.000	.000	.000
	23	.000	.000	.000	.000	.000	.000	.000
	25	.000	.000	.000	.000	.000	.000	.000
	26	.000	.000	.000	.000	.000	.000	.000
	29	.000	.000	.000	.000	.000	.000	.000
	30	.000	.000	.000	.000	.000	.000	.000
	32	.000	.000	.000	.000	.000	.000	.000
	33	.000	.000	.000	.000	.000	.000	.000
	35	.000	.000	.000	.000	.000	.000	.000
	36	.000	.000	.000	.000	.000	.000	.000
	37	1.000	.000	.000	.000	.000	.000	.000
	38	.000	1.000	.000	.000	.000	.000	.000
	39	.000	.000	1.000	.000	.000	.000	.000
	42	.000	.000	.000	1.000	.000	.000	.000
	44	.000	.000	.000	.000	1.000	.000	.000
	45	.000	.000	.000	.000	.000	1.000	.000
	49	.000	.000	.000	.000	.000	.000	1.000
	50	.000	.000	.000	.000	.000	.000	.000

Block 0: Beginning Block

Classification Table[c,d]

			Predicted			
			Selected Cases [a]			Unselected Cases [b]
			Class			Class
		Observed	PC	R	Percentage Correct	PC
Step 0	Class	PC	6983	0	100.0	3105
		R	701	0	.0	286
		Overall Percentage			90.9	

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Constant is included in the model.

d. The cut value is .500

Classification Table[c,d]

			Predicted	
			Unselected Cases [b]	
			Class	
		Observed	R	Percentage Correct
Step 0	Class	PC	0	100.0
		R	0	.0
		Overall Percentage		91.6

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. Constant is included in the model.

d. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 0	Constant	-2.299	.040	3366.256	1	.000	.100

Variables not in the Equation[a]

			Score	df	Sig.
Step 0	Variables	TRI480	193.467	1	.000
		GAP_4	3249.293	34	.000
		GAP_4(1)	3.700	1	.054
		GAP_4(2)	165.803	1	.000
		GAP_4(3)	44.762	1	.000
		GAP_4(4)	19.928	1	.000
		GAP_4(5)	49.840	1	.000

a. Residual Chi-Squares are not computed because of redundancies.

Variables not in the Equation[a]

			Score	df	Sig.
Step 0	Variables	GAP_4(6)	49.696	1	.000
		GAP_4(7)	1.902	1	.168
		GAP_4(8)	19.928	1	.000
		GAP_4(9)	29.896	1	.000
		GAP_4(10)	83.928	1	.000
		GAP_4(11)	24.433	1	.000
		GAP_4(12)	19.048	1	.000
		GAP_4(13)	1.090	1	.296
		GAP_4(14)	7.778	1	.005
		GAP_4(15)	59.816	1	.000
		GAP_4(16)	129.719	1	.000
		GAP_4(17)	19.928	1	.000
		GAP_4(18)	20.004	1	.000
		GAP_4(19)	288.649	1	.000
		GAP_4(20)	310.057	1	.000
		GAP_4(21)	19.928	1	.000
		GAP_4(22)	.647	1	.421
		GAP_4(23)	105.726	1	.000
		GAP_4(24)	49.840	1	.000
		GAP_4(25)	59.816	1	.000
		GAP_4(26)	29.896	1	.000
		GAP_4(27)	15.423	1	.000
		GAP_4(28)	15.122	1	.000
		GAP_4(29)	.043	1	.836
		GAP_4(30)	1.106	1	.293
		GAP_4(31)	193.180	1	.000
		GAP_4(32)	79.775	1	.000
		GAP_4(33)	1410.155	1	.000
		GAP_4(34)	49.840	1	.000

a. Residual Chi-Squares are not computed because of redundancies.

Block 1: Method = Forward Stepwise (Likelihood Ratio)

Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Step	1957.578	34	.000
	Block	1957.578	34	.000

Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Model	1957.578	34	.000
Step 2	Step	248.424	1	.000
	Block	2206.003	35	.000
	Model	2206.003	35	.000

Model Summary

Step	-2 Log likelihood	Cox & Snell R Square	Nagelkerke R Square
1	2735.363[a]	.225	.492
2	2486.939[a]	.250	.546

a. Estimation terminated at iteration number 20 because maximum iterations has been reached. Final solution cannot be found.

Hosmer and Lemeshow Test

Step	Chi-square	df	Sig.
1	.000	5	1.000
2	412.175	8	.000

Contingency Table for Hosmer and Lemeshow Test

		Class = PC		Class = R		
		Observed	Expected	Observed	Expected	Total
Step 1	1	21	21.000	0	.000	21
	2	1588	1588.000	3	3.000	1591
	3	516	516.000	5	5.000	521
	4	2402	2402.000	74	74.000	2476
	5	1459	1459.000	103	103.000	1562
	6	684	684.000	122	122.000	806
	7	313	313.000	394	394.000	707
Step 2	1	759	767.789	9	.211	768
	2	766	767.508	3	1.492	769
	3	766	766.038	2	1.962	768
	4	756	762.823	12	5.177	768
	5	760	753.635	7	13.365	767
	6	759	741.582	8	25.418	767
	7	753	729.472	15	38.528	768
	8	695	707.731	74	61.269	769
	9	637	646.101	131	121.899	768
	10	332	340.319	440	431.681	772

Classification Table[c]

Observed			Predicted			
			Selected Cases[a]			Unselected Cases[b]
			Class			Class
			PC	R	Percentage Correct	PC
Step 1	Class	PC	6936	47	99.3	3091
		R	386	315	44.9	171
		Overall Percentage			94.4	
Step 2	Class	PC	6957	26	99.6	3098
		R	379	322	45.9	167
		Overall Percentage			94.7	

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. The cut value is .500

Classification Table[c]

Observed			Predicted	
			Unselected Cases[b]	
			Class	
			R	Percentage Correct
Step 1	Class	PC	14	99.5
		R	115	40.2
		Overall Percentage		94.5
Step 2	Class	PC	7	99.8
		R	119	41.6
		Overall Percentage		94.9

a. Selected cases validate EQ 1

b. Unselected cases validate NE 1

c. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 1[a]	GAP_4			537.205	34	.000	
	GAP_4(1)	19.249	12716.568	.000	1	.999	2.290E8
	GAP_4(2)	17.724	12716.568	.000	1	.999	4.980E7
	GAP_4(3)	20.996	12716.568	.000	1	.999	1.313E9
	GAP_4(4)	42.406	31135.968	.000	1	.999	2.611E18
	GAP_4(5)	42.406	22018.312	.000	1	.998	2.611E18

a. Variable(s) entered on step 1: GAP_4.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 1[a]	GAP_4(6)	19.845	12716.568	.000	1	.999	4.157E8
	GAP_4(7)	19.645	12716.568	.000	1	.999	3.403E8
	GAP_4(8)	42.406	31135.968	.000	1	.999	2.611E18
	GAP_4(9)	42.406	26461.344	.000	1	.999	2.611E18
	GAP_4(10)	22.302	12716.568	.000	1	.999	4.849E9
	GAP_4(11)	16.850	12716.568	.000	1	.999	2.079E7
	GAP_4(12)	15.881	12716.568	.000	1	.999	7885299.240
	GAP_4(13)	19.699	12716.568	.000	1	.999	3.592E8
	GAP_4(14)	20.693	12716.568	.000	1	.999	9.699E8
	GAP_4(15)	42.406	20759.502	.000	1	.998	2.611E18
	GAP_4(16)	42.406	16910.896	.000	1	.998	2.611E18
	GAP_4(17)	42.406	31135.968	.000	1	.999	2.611E18
	GAP_4(18)	19.709	12716.568	.000	1	.999	3.627E8
	GAP_4(19)	21.837	12716.568	.000	1	.999	3.046E9
	GAP_4(20)	42.406	14622.694	.000	1	.998	2.611E18
	GAP_4(21)	42.406	31135.968	.000	1	.999	2.611E18
	GAP_4(22)	19.205	12716.568	.000	1	.999	2.192E8
	GAP_4(23)	21.461	12716.568	.000	1	.999	2.092E9
	GAP_4(24)	42.406	22018.312	.000	1	.998	2.611E18
	GAP_4(25)	42.406	20759.502	.000	1	.998	2.611E18
	GAP_4(26)	42.406	26461.344	.000	1	.999	2.611E18
	GAP_4(27)	19.578	12716.568	.000	1	.999	3.183E8
	GAP_4(28)	18.553	12716.568	.000	1	.999	1.141E8
	GAP_4(29)	19.124	12716.568	.000	1	.999	2.021E8
	GAP_4(30)	.001	17566.230	.000	1	1.000	1.001
	GAP_4(31)	14.932	12716.568	.000	1	.999	3053815.512
	GAP_4(32)	42.406	19069.490	.000	1	.998	2.611E18
	GAP_4(33)	42.406	13165.607	.000	1	.997	2.611E18
	GAP_4(34)	42.406	22018.312	.000	1	.998	2.611E18
	Constant	-21.204	12716.568	.000	1	.999	.000

a. Variable(s) entered on step 1: GAP_4.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 2[b]	TRI480	-.001	.000	132.154	1	.000	.999
	GAP_4			497.452	34	.000	
	GAP_4(1)	19.708	12711.790	.000	1	.999	3.622E8
	GAP_4(2)	18.739	12711.790	.000	1	.999	1.375E8
	GAP_4(3)	20.998	12711.790	.000	1	.999	1.317E9
	GAP_4(4)	43.049	30959.496	.000	1	.999	4.964E18
	GAP_4(5)	43.654	21297.512	.000	1	.998	9.094E18
	GAP_4(6)	20.002	12711.790	.000	1	.999	4.859E8
	GAP_4(7)	19.724	12711.790	.000	1	.999	3.681E8
	GAP_4(8)	46.082	28382.916	.000	1	.999	1.030E20
	GAP_4(9)	42.803	26413.176	.000	1	.999	3.883E18
	GAP_4(10)	22.311	12711.790	.000	1	.999	4.894E9
	GAP_4(11)	18.515	12711.790	.000	1	.999	1.099E8
	GAP_4(12)	17.559	12711.790	.000	1	.999	4.223E7
	GAP_4(13)	19.886	12711.790	.000	1	.999	4.327E8
	GAP_4(14)	20.735	12711.790	.000	1	.999	1.011E9
	GAP_4(15)	42.769	20689.731	.000	1	.998	3.754E18
	GAP_4(16)	42.412	16907.280	.000	1	.998	2.625E18
	GAP_4(17)	42.409	31134.003	.000	1	.999	2.618E18
	GAP_4(18)	20.603	12711.790	.000	1	.999	8.868E8
	GAP_4(19)	22.279	12711.790	.000	1	.999	4.741E9
	GAP_4(20)	46.184	13732.247	.000	1	.997	1.142E20
	GAP_4(21)	42.460	31133.154	.000	1	.999	2.756E18
	GAP_4(22)	21.677	12711.790	.000	1	.999	2.596E9
	GAP_4(23)	25.507	12711.790	.000	1	.998	1.195E11
	GAP_4(24)	43.691	20829.787	.000	1	.998	9.436E18
	GAP_4(25)	44.049	20211.892	.000	1	.998	1.349E19
	GAP_4(26)	42.489	26448.596	.000	1	.999	2.836E18
	GAP_4(27)	21.742	12711.790	.000	1	.999	2.770E9
	GAP_4(28)	19.870	12711.790	.000	1	.999	4.262E8
	GAP_4(29)	19.231	12711.790	.000	1	.999	2.248E8
	GAP_4(30)	1.215	16833.775	.000	1	1.000	3.369
	GAP_4(31)	15.223	12711.790	.000	1	.999	4084781.105
	GAP_4(32)	44.265	17393.544	.000	1	.998	1.675E19
	GAP_4(33)	42.479	13159.203	.000	1	.997	2.807E18
	GAP_4(34)	42.496	21998.765	.000	1	.998	2.856E18
	Constant	-21.202	12711.790	.000	1	.999	.000

a. Variable(s) entered on step 1: GAP_4.

b. Variable(s) entered on step 2: TRI480.

Model if Term Removed

Variable		Model Log Likelihood	Change in -2 Log Likelihood	df	Sig. of the Change
Step 1	GAP_4	-2346.471	1957.578	34	.000
Step 2	TRI480	-1367.682	248.424	1	.000
	GAP_4	-2179.597	1872.256	34	.000

Variables not in the Equation

			Score	df	Sig.
Step 1	Variables	TRI480	133.652	1	.000
		Overall Statistics	133.652	1	.000

APPENDIX IV

Detailed calculations of mountain lion population size by GMU. H, C, and HC are abbreviations for harvest model, collar model, and harvest and collar models combined, respectively. Numbers in columns with “Excellent”, “Good”, “Moderate”, “Fair”, and “Poor” represent units of 100 sq Km area of that habitat quality category predicted by each model. These are then arranged by row for each GMU. For example, the harvest model predicts 960 sq Km of excellent mountain lion habitat in GMU 2C. The numbers in the columns with “hi” and “lo” represent the total of hi and lo density estimates for each habitat quality category multiplied by the area of that habitat quality category for each GMU. For example, the harvest model predicts between 24 and 36 resident adult mountain lions in GMU 2C.

GMU	Cougar_Zone	Havest lo	Harvest hi	Collar lo	Collar hi	Harvcol lo	Harvcol hi	H Excellent	H Good	H Moderate	H Fair	H Poor	C Excellent	C Good	C Moderate	C Fair	C Poor	HC Excellent	HC Good	HC Moderate	HC Fair	HC Poor
2C	A	24	36	20	29	28	41	9.607	2.106	6.770	0.952	1.476	5.671	7.019	6.623	0.012	1.587	11.366	3.286	5.590	0.335	0.334
7	A	56	83	58	83	75	109	11.874	7.915	62.350	0.946	5.436	5.431	35.608	39.720	0.014	7.747	15.859	31.554	38.711	0.309	2.088
2B	A	34	52	18	26	35	52	16.661	0.823	0.994	0.209	0.649	5.503	6.579	3.426	0.124	3.705	16.889	0.896	0.921	0.076	0.554
2A	A	25	37	20	28	31	46	11.101	1.237	3.531	0.204	4.240	5.013	9.339	3.086	0.014	2.860	14.076	1.931	2.837	0.021	1.447
5A	B	8	12	4	5	8	12	3.315	0.829	1.528	0.042	0.203	0.290	2.691	2.029	0.001	0.905	3.468	0.973	1.384	0.020	0.071
50	B	24	35	11	15	25	36	6.660	8.540	8.407	0.014	0.257	1.897	4.779	6.159	0.031	11.011	6.685	10.286	6.670	0.004	0.233
51	B	45	68	17	24	46	69	21.388	1.929	1.989	0.152	0.229	3.691	5.679	8.845	3.137	4.333	21.648	2.516	1.400	0.036	0.087
5B	B	18	27	7	11	19	28	8.675	0.488	1.101	0.207	0.237	1.762	1.847	5.542	0.579	0.979	8.867	0.947	0.633	0.063	0.198
48	C	8	12	2	3	8	12	3.845	0.187	0.149	0.193	5.421	0.417	0.151	2.321	0.664	6.240	3.847	0.200	0.136	0.193	5.419
49	C	21	32	4	7	21	32	10.516	0.259	0.113	0.005	0.073	0.840	0.423	3.303	5.300	1.099	10.544	0.262	0.110	0.003	0.047
53	C	29	42	6	8	29	43	12.337	3.748	1.441	0.000	0.191	1.031	1.224	3.464	6.072	5.928	12.423	3.780	1.409	0.000	0.105
43	C	30	44	16	22	31	45	10.961	4.299	9.395	0.268	24.340	2.539	10.612	2.462	0.075	33.575	11.023	6.158	7.543	0.245	24.295
46	C	36	54	11	17	36	54	17.714	0.443	1.003	0.268	13.309	2.531	2.024	10.408	2.045	15.729	17.717	0.465	0.982	0.268	13.306
45	C	70	104	19	27	70	105	33.792	1.017	2.805	0.058	1.741	3.546	5.569	8.899	15.020	6.379	33.851	2.017	1.805	0.050	1.690
42	D	33	48	13	18	36	53	8.167	10.252	17.804	3.117	71.809	3.532	4.432	3.739	0.995	98.451	8.531	12.884	17.748	2.748	69.237
47	D	9	14	3	4	9	14	2.190	3.861	3.689	0.558	20.919	0.940	0.465	1.089	0.336	28.387	2.201	3.873	3.689	0.547	20.907
41	D	4	6	4	6	6	8	0.538	0.124	7.189	0.035	39.591	0.550	1.460	4.017	0.005	41.444	0.622	1.566	7.189	0.031	38.068
59	D	5	7	2	3	5	8	0.831	2.113	3.746	0.468	41.564	0.390	0.354	1.718	0.106	46.155	0.845	2.156	3.746	0.455	41.521
9	E	80	119	69	99	96	139	27.819	6.890	45.505	0.271	5.773	12.808	38.553	22.983	0.817	11.096	29.629	32.448	19.315	0.024	4.842
10	E	88	131	50	72	91	136	39.478	4.999	11.485	0.290	1.528	9.136	27.463	18.802	0.601	1.777	40.699	6.582	9.900	0.008	0.590
6B	F	7	10	1	1	7	10	3.395	0.196	0.001	0.000	0.001	0.011	0.005	0.625	1.932	1.020	3.395	0.198	0.000	0.000	0.000
6A	F	47	70	22	31	50	74	20.854	1.989	8.910	0.127	0.619	4.982	7.359	10.153	4.930	5.074	21.447	5.239	5.367	0.056	0.390
6C	F	50	75	23	33	51	76	22.680	2.991	5.429	0.016	2.061	5.871	8.936	5.303	5.272	7.795	22.728	5.308	3.086	0.003	2.052
17	G	53	79	51	74	72	106	22.408	4.174	11.604	0.097	4.304	16.919	14.497	9.144	1.126	0.902	31.733	7.815	2.901	0.001	0.136
13	G	113	168	105	149	138	201	39.644	15.380	50.615	0.301	9.371	20.995	58.600	26.599	0.117	9.000	47.152	39.061	21.757	0.021	7.322
19	H	36	52	131	193	122	180	8.340	12.938	19.225	1.101	68.492	48.979	24.760	26.608	0.068	9.680	50.581	23.461	0.195	0.001	35.858
20	H	18	26	86	126	84	122	1.996	4.018	25.111	0.401	34.723	31.097	23.612	6.471	0.013	5.056	31.326	23.416	0.394	0.007	11.106
36	I	35	52	32	47	47	71	14.927	3.297	5.120	0.200	3.478	11.326	8.205	4.432	0.257	2.802	21.933	3.730	0.527	0.106	0.727
37	I	32	48	36	53	50	75	12.497	2.284	12.173	0.154	15.498	14.131	6.725	3.373	0.409	17.968	23.598	2.040	2.074	0.111	14.783
18	I	42	62	68	99	81	120	13.251	4.668	27.657	0.073	17.658	24.350	19.866	3.939	0.052	15.100	34.370	10.869	6.089	0.005	11.975
38	I	14	21	11	16	20	30	3.249	1.859	15.464	0.152	63.537	4.005	2.261	2.418	0.106	75.470	6.617	1.952	12.249	0.152	63.292
25	J	17	26	96	141	90	131	1.293	1.384	33.431	0.552	45.329	32.876	22.950	23.975	0.003	2.186	33.746	23.133	4.083	0.000	21.026
16B	J	48	72	17	25	48	72	23.816	0.272	0.126	0.133	0.085	4.228	2.051	14.512	3.313	0.328	23.985	0.354	0.009	0.000	0.084
21A	J	24	36	10	15	24	36	11.968	0.118	0.039	0.023	0.005	3.278	1.002	6.311	1.478	0.083	12.013	0.128	0.012	0.000	0.000
16C	J	22	33	8	12	22	33	10.463	0.417	1.438	0.001	0.113	1.029	3.943	7.097	0.201	0.162	10.483	1.381	0.470	0.000	0.098
16A	J	31	46	12	18	32	47	15.105	0.280	1.185	0.038	0.110	2.858	2.496	9.631	1.487	0.245	15.340	1.176	0.102	0.000	0.099
21B	J	42	62	93	137	101	148	12.532	7.517	24.864	0.875	20.286	34.422	25.354	5.143	0.011	1.142	40.239	21.652	2.409	0.008	1.766
16D	J	22	33	9	13	23	34	10.711	0.354	1.042	0.010	0.089	1.798	2.745	6.790	0.708	0.164	10.768	1.025	0.348	0.000	0.064
16E	J	25	37	20	28	28	41	8.690	1.568	14.571	0.003	0.045	2.583	12.014	9.928	0.118	0.233	8.736	8.402	7.737	0.000	0.001
15	J	67	100	28	41	68	102	30.413	3.169	8.741	0.005	0.063	3.560	13.351	22.879	0.807	1.794	30.507	5.494	6.353	0.000	0.037
24	K	56	84	50	74	74	110	25.699	1.265	8.549	0.234	3.432	18.949	9.429	9.490	0.891	0.421	35.324	3.214	0.161	0.000	0.481
22	K	17	26	12	17	20	30	7.955	0.667	1.449	0.072	0.049	4.117	2.651	1.887	1.299	0.239	9.730	0.427	0.015	0.000	0.021
23	K	78	116	115	171	139	208	30.343	4.817	31.500	0.441	8.817	48.887	14.008	11.830	0.249	0.944	66.770	5.877	0.278	0.000	2.994
26	L	29	42	93	138	98	146	5.579	4.642	32.698	0.763	16.059	39.670	12.307	7.175	0.012	0.577	43.637	12.255	0.336	0.000	3.514
27	L	15	22	44	65	47	70	3.165	2.897	14.289	0.530	6.019	19.128	4.742	2.723	0.046	0.261	21.385	4.612	0.179	0.000	0.725
33	M	11	17	57	85	57	85	0.188	0.034	26.963	0.064	31.527	26.727	3.397	1.575	0.000	27.076	26.745	3.402	1.299	0.057	27.273
31	M	35	53	163	241	164	242	0.625	0.030	85.266	0.000	130.064	65.378	27.178	20.060	0.000	103.369	65.400	27.207	21.819	0.000	101.559
32	M	31	46	126	186	129	191	2.785	2.627	56.787	0.164	94.919	53.761	17.500	6.401	0.020	79.600	55.516	17.186	7.047	0.130	77.404
39	M	8	12	7	11	11	17	1.229	1.547	9.900	0.297	55.290	2.274	1.233	3.965	0.041	60.750	3.228	1.708	8.209	0.273	54.845
40	M	13	19	9	14	15	22	1.195	1.757	21.569	0.917	72.265	1.106	0.912	16.025	0.320	79.338	1.897	2.510	21.001	0.826	71.468
52	N	19	28	2	4	19	28	8.759	0.679	1.377	0.000	0.080	0.218	0.185	2.972	3.077	4.444	8.838	0.735	1.321	0.000	0.001
4	N	32	48	6	8	33	49	15.685	0.824	0.660	0.022	0.771	0.958	1.684	3.119	4.889	7.313	15.965	1.162	0.322	0.015	0.498
12	O	70	103	51	71	75	109	21.888	17.099	27.574	0.072	0.573	3.606	41.735	16.589	0.033	5.244	22.465	24.140	20.533	0.000	0.069
56	P	8	12	5	7	8	12	3.524	0.568	1.267	0.609	40.100	1.449	1.686	0.966	0.159	41.809	3.526	0.571	1.267	0.609	40.095
57	P	13	19	4	6	13	19	6.059	0.570	0.482	0.408	3.468	1.658	0.682	0.830	0.174	7.644	6.060	0.570	0.481	0.408	3.467
58	P	12	17	4	5	12	17	2.645	4.746	5.218	0.900	26.116	1.118	1.022	0.977	0.244	36.264	2.708	4.861	5.218	0.794	26.044
29	Q	11	15	45	66	46	67	1.396	2.563	13.380	0.666	12.599	16.938	12.576	0.429	0.007	0.654	17.255	12.461	0.443	0.000	0.445
28	Q	8	12	37	54	34	51	0.674	2.600	10.864	0.163	13.449	13.960	6.878	6.783	0.000	0.130	14.214	6.699	0.058	0.003	6.778
30	Q	41	60	110	161	116	172	10.228	9.557	29.652	1.673	24.911	44.585	22.318	1.486	0.069	7.563	49.318	18.985	1.448	0.029	6.242
34	Q	55	83	44	65	71	106	24.861	4.362	4.485	0.399	9.035	15.100	9.667	13.221	0.776	4.378	33.324	5.003	0.524	0.085	4.205
55B	R	1	1	1	1	1	1	0.091	0.042	1.040	0.004	8.517	0.050	0.065	0.968	0.000	8.612	0.093	0.042	1.040	0.004	8.515
55A	R	74	111	19	28	75	112	36.608	0.545	0.287	0.147	2.968	4.155	1.694	18.081	7.645	8.980	37.036	0.552	0.280	0.139	2.546
54	R	13	19	3	5	13	19	6.363	0.157	0.126	0.160	2.093	0.712	0.194	2.386	2.507	3.100	6.364	0.161	0.122	0.160	2.092
8	S	22	33	12	17	23	34	8.861	1.208	7.501	0.011	6.286	2.142	6.816	3.093	0.878	10.937	8.888	4.025	4.662	0.010	6.281
14	S	35	53	25	36	41	61	14.219	1.619	13.184	0.003	13.857	4.392	13.089	10.557	1.062	13.784	15.676	9.327	4.363	0.002	13.515
35	T	34	51	13	19	35	52	16.503	0.720	0.361	0.011	0.160	3.353	2.589	8.850	0.303	2.661	17.190	0.361	0.047	0.002	0.156
11	T	23	35	15	21	24	35	9.457	3.564	3.525	0.007	0.105	2.472	10.088	2.085	0.000	2.014	9.517	3.650	3.437	0.000	0.054
1	T	78	116	89	128	116	170	25.311	3.463	58.335	2.528	11.884	19.826	36.313	41.011	0.939	3.433	38.349	29.025	32.766	0.108	1.273
3	T	54	80	20	29	55	82	24.253	2.669	6.476	0.168	0.614	2.137	11.930	13.708	0.341	6.064	24.618	3.840	5.300	0.108	0.314

* Habitat areas are given in 100sqKm increments

BLACK BEAR MANAGEMENT PLAN

1999-2010

Status and Objectives of Idaho's
Black Bear Resource

Idaho Department of Fish and Game
600 South Walnut Street
PO Box 25
Boise Idaho 83707

December 1998

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FOREWORD

Preserving Idaho's wildlife resources and hunting heritage will require cooperation from the citizens that are interested in black bears. This plan will provide the framework for the Department's management efforts for black bear and a solid foundation for ensuring the continued existence of viable black bear populations.

Many persons provided invaluable input to the Department during the development of this plan. A 9-member steering committee was formed early in 1998. Their charge was to propose a process for developing this plan that would involve a diversity of viewpoints regarding black bear management in Idaho. As a result of their efforts, a 20-member black bear planning team, composed of representatives from sporting interests and the general public, was convened on June 4, 1998. The planning team identified issues and strategies relevant to this plan and the decision criteria that would be used to evaluate the various management alternatives available to the Department.

The planning team identified several issues they believed the Department should address in this plan. Major issues included:

1. Methods of take
2. Management based on biological and/or sociological considerations
3. Management should be in the best interest of black bears
4. Provide for more flexibility to manage at the local or data analysis unit (DAU) level
5. Consider the impact of black bears on deer/elk populations
6. Develop criteria to indicate when black bears are abundant
7. Methods of gathering public input on black bear management program

General, recurring themes focused on customizing management to fit goals and objectives at the DAU level, using sound biology to establish those goals, improving public education and involvement, and evaluating biological and sociological implications of our management decisions. Decision criteria suggested by the planning team emphasized three general areas. They included:

1. Will the action have the desired effect?
2. Is the action feasible from a cost-effective and logistical standpoint?
3. What are the social implications?

Where appropriate, the Department has attempted to incorporate these suggestions into this plan.

1999-2010 BLACK BEAR MANAGEMENT

INTRODUCTION

Wildlife managers juggle many diverse issues in attempting to integrate the needs and desires of humans with the biological needs of black bears. The Idaho Department of Fish and Game periodically develops management plans that establish the Department's philosophy and management direction for black bears and serve as guidelines for setting black bear hunting seasons. This plan is the fourth plan written since 1980. Each plan represents a step forward in the development of a management program that will ensure the long-term viability of black bear populations and provide recreational opportunity for hunting and non-hunting resource users. Specific objectives are included in this plan to identify management direction for each DAU, which reflects the ecosystem management principle that predator and prey management should be linked to ensure a reasonable balance among species. The specifics regarding how the department will attempt to reach those objectives will be dealt with annually in the regular season setting process.

The Department is currently undergoing a transition in terms of responding to its constituency - the people of Idaho. As a result of current sociological trends, decisions about how the Department manages black bears have become very controversial. Many of Idaho's citizens disagree on issues such as spring black bear hunting seasons and using bait or hounds to hunt black bears. Although these issues have significant potential for influencing the general public's perception of the acceptability of hunting, in most cases they have only minimal biological impact on black bear populations. Habitat fragmentation and loss is far more important to the long-term survival of black bear populations and is, unfortunately, often lost in the debate over hunting methods.

The popularity of black bear as a big game animal to hunters using a variety of hunting techniques, and the concerns of some citizens about the use of those methods of take have combined to generate some controversy in the management of this species. This plan represents an attempt by the Department to consider the viewpoints of all Idahoans on how black bears should be managed in the state.

MANAGEMENT HISTORY

Although the black bear was classified as a game animal in 1943, with a bag limit of 1 per year, few protective laws were passed until 1973. Beginning in 1973, resident hunters were required to have a tag in their possession while hunting black bears in those Game Management Units (GMU) in northern Idaho that had summer hunting closures. Resident black bear hunters in much of southern Idaho, where seasons remained open to year-round hunting, did not need a tag. Non-resident black bear hunters were required to have a tag in all GMUs in the state.

In 1975, the Department allowed hunters to take 2 bears in 3 GMUs. The bag limit was increased to 2 bears in 21 additional GMUs in 1977. Females accompanied by cubs were protected during the spring season from 1973 through 1982. In 1983, females accompanied by cubs were protected during the spring and fall seasons. Year round hunting seasons and 2 bear bag limits were eliminated in 1986.

The Department has relied on two primary methods to collect black bear harvest data: 1) the mandatory check and report program implemented in 1983, and 2) the annual telephone harvest survey. The mandatory check-in report program requires the hunter to bring the skull and hide (1992) of their harvested black bear to an official check point within 10 days of the kill date and to fill out a harvest report form. In most cases a premolar tooth is extracted from the skull for aging. Pertinent data including kill date, location of kill, and method of take are recorded on the harvest form. Compliance with the mandatory report program is unknown.

The telephone survey of hunting license holders provided a second estimate of the black bear harvest. This survey contacted approximately three percent of the black bear tag holders and it provided information from successful and unsuccessful hunters. A statewide harvest estimate, recreation days, and hunter success rates were estimated. The black bear portion of the harvest survey was discontinued in 1996 due to funding cutbacks.

POPULATION BIOLOGY

In 1972 the Department initiated a black bear research project to collect biological data for a comprehensive management program. Six black bear populations were studied. These studies were designed to determine the status of each population, although data were also collected on food habits, physical condition, denning requirements, activity patterns, and habitat use patterns. Research information collected from black bear populations in lightly hunted and heavily hunted areas was used by Department biologists to develop harvest criteria and to interpret harvest data collected through the mandatory check program.

Detailed information about black bear biology in Idaho can be found in a book authored by John Beecham and Jeff Rohlman titled: “A Shadow in the Forest - Idaho’s Black Bear.” The University of Idaho Press published this book in 1994.

HABITAT MANAGEMENT

Black bear distribution in Idaho corresponds closely to the distribution of coniferous forests. North of the Snake River plain they are found throughout the forested mountains and foothills. Few black bears occur south of the Snake River, except in southeastern Idaho. About 75% of black bear habitat in Idaho is administered by the US Forest Service; 20% is controlled by private interests; and the rest is administered by other agencies, such as the Bureau of Land Management, Idaho Department of Lands, and Idaho Department of Fish and Game.

Idaho has approximately 30,000 square miles of black bear habitat. Although it is difficult to estimate the size of black bear populations, Department research has shown that black bear densities vary among areas in Idaho. The black bear social system limits density to 1.5 to 2 black bears per square mile in the best habitats. However, even in good quality habitats, many factors can influence the size of the black bear population in any given year. Several years of poor berry crops can result in reduced cub production and increased mortality of sub-adult black bears. Heavy hunting pressure can also reduce the population below the carrying capacity of the habitat.

Forest management practices, wildfires, and plant succession influence black bear habitat quality. The black bear's diet is primarily grasses and forbs during the spring and early summer. By mid-July, they begin adding fruits such as huckleberries, wild cherries, buffalo berries, hawthorn, and mountain ash to their diet. Approximately 10% of the black bear's annual diet is animal matter: insects comprise about 9% and vertebrates make up the remaining 1 percent. In many situations partial removal of the forest overstory helps black bear because it opens up the forest canopy and allows for increased plant production on the forest floor. However, increased human access into black bear habitats makes black bears more vulnerable to hunters. This factor partially offsets the benefits of logging activity.

Department-sponsored research on black bear habitat use patterns suggests that the following actions will maintain or enhance black bear habitat in areas where logging has been proposed.

Recommendations:

1. Minimize soil disturbance in areas where berry-producing shrubs are abundant by using rubber tired vehicles or logging over snow cover.
2. Use selection cuts to maintain black bear security cover. Retain 40-70% canopy coverage when huckleberry (<u>Vaccinium</u> sp.) is abundant in the understory.
3. Maintain relatively dense pole-sized timber stands in the overall vegetative mosaic on north and east aspects for use as bedding areas.
4. Retain some mature trees in logged areas to enhance their use by female black bears with cubs.
5. Maintain aspen stands in the overall vegetative mosaic.
6. Broadcast-burn slash or leave it untreated and minimize soil scarification to prevent damage to rhizomatous food plants.
7. Create leave patches or leave strips within cutting units for security cover. Clear-cuts should be small and have irregular borders to provide security cover.
8. Maintain a mix of different-aged cutting units to influence black bear density and distribution in an area.
9. Logging roads should be located out of creek/river bottoms where significant black bear foods occur.
10. Area closures to motorized vehicles should be implemented to reduce black bear mortality rates and increase habitat effectiveness.

Habitat loss and fragmentation due to human encroachment also has a subtle, yet permanent, impact on the long-term viability of black bear populations. Ultimately, the accelerating pace of habitat fragmentation and loss will dictate how long we can maintain black bear populations in some areas of the state. However, the prognosis for the future of black bears in much of the state remains positive because a majority of the land base is publicly owned. As long as we continue to consider the wellbeing of Idaho's wildlife resources when making habitat management decisions, those habitats will continue to support viable black bear populations.

POPULATION MANAGEMENT

The vulnerability of black bear to harvest varies greatly because of differences in habitat and access. Bears are less vulnerable where cover is dense and expansive. They are particularly vulnerable in highly roaded areas and habitats that provide only patches of security cover. This often results in populations with fewer adult black bears, especially males.

The sex and age of a black bear also affects its vulnerability to harvest. Adult males are typically most vulnerable because they are bold (often use open areas) and have larger home ranges. Consequently, the adult male segment of a population is the first to be reduced under hunter pressure. Sub-adult males are slightly less vulnerable. Females are least vulnerable, especially if accompanied by cubs. A low percentage of adult males (≥5 years old) in the harvest may be an indication of over-harvest.

Hunting pressure affects harvest rate, which affects age structure, sex ratios, and densities of black bear populations. As harvest rates increase, the proportion of sub-adult black bears (those less than 4 years old) in the harvest typically increases, whereas the proportion of adult males declines. At higher harvest levels, the proportion of females in the harvest increases, and harvest may result in a population decline if a large area is affected or if there are no reservoir areas nearby to produce dispersing sub-adult black bears. In reservoir areas, black bear populations are limited by the capacity of the habitat to support black bears and their social structure. Some species compensate for excessive adult mortality by producing more young. However, black bears do not respond in this manner. In fact, high adult mortality results in a younger age population and lower productivity (average number of young per litter). Young male black bears disperse from their mother's home range when they are 1.5 to 2.5 years old and often travel long distances to occupy vacant habitat. However, young female black bears rarely disperse far. As a result, black bear populations far from reservoir areas are slow to recover from over-harvest.

The ages of black bear captured during Department-sponsored research projects indicated that lightly hunted populations had a high ratio of adults to sub-adults (70:30), a high percentage of adult males (35%), and a median age of 7.5 years. Data collected from heavily hunted populations showed adult:sub-adult ratios favoring sub-adults (40:60), fewer adult males (21%), and a median age of 2.5-3.5 years. Studies of black bear populations in Alaska, Virginia, and Arizona showed similar relationships between lightly and heavily hunted populations.

Department research demonstrated that age and sex data derived from trapping was closely correlated with that from the harvest. It follows, therefore, that harvest criteria have potential for monitoring population status.

HARVEST CHARACTERISTICS

Black bears in Idaho are long-lived, they mature late (4-7 years old), and they have low reproductive rates. Short-term changes in the size of black bear populations are related to changes in birth rates associated with the availability of nutritious foods, especially late summer and fall berry production. Long-term trends are directly related to changes in habitat quantity and quality.

The reproductive characteristics of Idaho black bears suggest that harvest rates must remain low to ensure sustainable harvest goals. Unfortunately, no easy or inexpensive methods exist for assessing the status of black bear populations. Therefore, Department biologists must rely on indirect measurements (harvest data) to evaluate the effectiveness of management actions. These limitations re-emphasize the need to implement conservative management strategies for black bear.

During the past planning cycle, black bear tag sales have increased slightly for resident black bear hunters and decreased for non-resident hunters (Figure 1). At least part of the increase observed for resident hunters can be attributed to increased sales of Sportsmen Pak and Deer, Elk, Bear Pak licenses which include a black bear tag. The decrease in non-resident black bear tag sales (75% since 1987) is probably associated with increased costs for those black bear tags ($40.50 in 1987 and $226.50 in 1998). The sale of baiting permits ($1.50) was initiated in 1993. Sales of these permits increased from 1,195 in 1993 to 1,349 in 1995 and have since declined to about 1,200 in 1998. The sale of hound hunter permits has increased from 988 in 1993 to 1,257 in 1998 (Figure 2).

Black bear harvest during the last 12 years shows a cyclic pattern that is relatively stable or slightly increasing (Figures 3 and 4). During the 1986-1992 planning period, hunters took an average of 1,277 black bears. During 1993-1997, an average of 1,355 black bears was harvested. The Panhandle Region accounted for 34% of the harvest in the last planning period; 28% came from the Clearwater Region; 22% from the Southwest Region; 10% from the Salmon Region; and the remaining 7% came from the Magic Valley, Southeast, and Upper Snake Regions.

The emphasis of the 1992-2000 bear plan was to stabilize total harvest and reduce the harvest of female black bears. Management actions implemented by the Department resulted in a short-term reduction in total harvest and a shift in the seasonal harvest of bears, but did not influence the sex ratio in the harvest (Figures 5 and 6). Analysis of the harvest data suggests that shortening the spring hunting season did reduce the female harvest. However, eliminating hunting opportunity in early September (September 1-14) was ineffective in reducing total female harvest during September. Female black bears appear to be more vulnerable to harvest in the fall hunting season because many females are no longer accompanied by the previous years cubs and they have high energy demands.

The average number of days hunters used to successfully harvest a bear was less than 7 days for those using bait, hounds, incidental, or still hunting methods. Shortening long, 2-3 month spring and fall hunting seasons by 1-3 weeks would not affect the length of time that most hunters spend in the field pursuing bears. Analysis of harvest data suggest that shortening seasons results in short-term reductions in harvest, but hunters quickly learn to adapt and harvest levels increase.

Black bear tag holders use 4 primary methods for harvesting a black bear: spot and stalk (still hunting), hound hunting, hunting over bait, and incidental hunting (hunting black bears while primarily engaged in some other activity like deer or elk hunting, wood gathering, fishing, or camping). During the 1986-1991 planning cycle and the 1992-2000 cycle, still hunters took slightly more black bears than hunters using other methods (Figure 7) did. However, bait and hound hunters experienced the highest success rates. No differences were observed in the percentage of female bears taken by hunters using bait (28%), hounds (35%), incidental (36%), or still (35%) hunting methods.

1999-2010 GOALS AND OBJECTIVES

Goal: To ensure the long-term viability of black bear populations in Idaho and to provide recreational opportunity for the hunting and non-hunting public.

Objectives:

1. To establish harvest objectives and management approaches for each DAU that reflects the unique characteristics of that area.

2. To distribute recreational opportunity throughout black bear habitat in a manner that is consistent with population objectives for each DAU.

3. To improve harvest information by improving compliance with the mandatory check and report program and by implementing a telephone or mail survey to generate information on hunter numbers, hunter success rates, hunter effort. Improving compliance level with the mandatory check program will provide insight into the non-reporting bias.

4. To use an adaptive management approach in developing harvest goals and objectives in select DAUs as a means to further evaluate management descriptors. In some DAUs, harvest objectives will be set to significantly increase harvest. In other DAUs, harvest pressure will be significantly reduced to serve as a comparison of the sensitivity of the harvest descriptors.

5. To monitor the response to changes in the black bear harvest using our biological criteria and take steps to increase or reduce harvest when data indicate the opportunity or need.

6. To manage black bears to reduce conflicts among competing user groups.

7. To consider initiating research to:

    a. Develop a long-term population monitoring technique.

    b. Establish the link between harvest criteria and the characteristics of the standing population by determining age- and sex-specific vulnerability to different harvest techniques.

    c. Determine black bear mortality patterns and reproductive potential.

8. To work with the Outfitters and Guides Licensing Board to set outfitter quotas in DAUs where a harvest reduction is needed. This will include evaluating new license and renewal applications.

DECISION ELEMENTS

TELEPHONE SURVEY

Harvest data are the primary source of information used to make management decisions. Harvest trends derived from the mandatory check and report system are difficult to interpret without supporting data such as changes in hunter numbers or effort.

Therefore, the Department will develop an enhanced telephone survey that specifically targets black bear tag holders. Sampling effort will be focused on obtaining reliable harvest estimates at the DAU level, estimates of hunter numbers and effort expended by successful and non-successful hunters, and an estimate of compliance with the mandatory check and report requirement.

DAUs selected for intensive monitoring during this planning period will be sampled at a higher rate in an effort to evaluate the sensitivity of our harvest criteria.

MANDATORY CHECK AND REPORT

This program continues to provide most of the data that are collected on black bear in Idaho. Although compliance is unknown, we will continue to rely on this program to provide the data we need to evaluate harvest trends.

HARVEST CRITERIA

No economically feasible methods are available to monitor the abundance of black bears in Idaho. As a result, Department biologists have relied on a variety of indirect measures of harvest data to assess population trends. Management decisions are based upon harvest data collected through the mandatory check and report program. Although population trends are difficult to ascertain from harvest data, it is the only information available to biologists that can be collected in a systematic manner designed to minimize confounding variables such as hunter numbers, hunter effort, and season structure and length. When these variables are standardized or at least measured, harvest trends may have value in determining the effects of management actions.

During the last planning period (1992-2000), the Department used the percent females in the harvest, median age of harvested females and males, and, in limited areas, bait station survey results to monitor population trends. Specific criteria were established to indicate over-harvest and a desired level of harvest.

Further analysis of our harvest data suggest that median age is a useful tool to distinguish lightly hunted or unhunted populations from those that are hunted at moderate to heavy levels. However, median age does not appear to be very sensitive to population changes on a year-to-year basis. As a result, the Department is eliminating median age as a harvest criterion and will monitor the percent of males ≥ 5 years old in the harvest on a 3-year running average (Table 1).

This indicator appears to be a more sensitive measure of population harvest levels and is supported by data collected by the Department during 12 years of research on black bear ecology. The Department's bear team also recommended that the minimum threshold for adult males ≥5 years old in the harvest should not drop below 20% on a 3-year running average. However, the Department will try to evaluate the usefulness of this criterion in describing the status of a population, during this planning cycle, by attempting to push this threshold below 20% on an experimental basis in one or more DAUs. Harvest trends will be manipulated in other DAUs to further evaluate these population descriptors.

Table 1. Harvest statistics for black bears in Idaho, 1993-1997.

All DAUs	Total Harvest	Percent Female	Percent Males ≥5	3-Year Average Males ≥5
1993	1,126	35	39	
1994	1,304	34	34	
1995	1,331	34	34	35%
1996	1,522	33	32	33%
1997	1,552	34	29	32%
Total	6,835	34	33	

The Department will implement a 3-tiered set of criteria to evaluate population trend in various DAUs (Table 2). The Department will continue to monitor trends in percent females in the harvest, calculated on a 3-year running average.

Table 2. Harvest descriptors for black bear in Idaho.

Criteria	Light Harvest	Moderate Harvest	Heavy Harvest
Percent Females	<30%	30-40%	>40%
Percent Males ≥5	>35%	25-35%	<25%
Bait Station Survey	Increasing	Stable	Decreasing

We also recognize that certain areas in Idaho provide extensive secure habitat (reservoirs) for black bears. Unroaded and/or wilderness areas are prime examples. Hunting pressure is light in these core areas, resulting in relatively high percent males ≥5 years old and low percent females in the harvest. Because population turnover is low, there is little vacant habitat and young black bears, especially males, are forced to disperse into surrounding less secure habitats where harvest rates are often high. These young dispersing males will dominate the harvest statistics in the surrounding areas. Age criteria for the DAU may be violated in these areas, even though the core or reservoir population is secure and will continue to supply a surplus of dispersing black bears. Current harvest criteria may not apply in these situations. The key is to ensure that the harvest remains focused on the dispersing black bears and does not compromise the reservoir population. In such cases, management direction will be based on the Department's discretion and interpretation of a variety of factors including perceived black bear population status, social considerations, and other factors (i.e., weather patterns, changing road access, etc).

In some DAUs, black bear harvest is consistently low, resulting in small samples from which to monitor harvest parameters. This may lead to inaccurate conclusions. Hence, harvest criteria will be applied only to DAUs in which average annual harvest is at least 30 black bears. When harvest is <30 black bears, the criteria do not apply, and management decisions will be based on professional judgment.

SEASON FRAMEWORK

A variety of factors may influence black bear seasons locally. Increasing urbanization in black bear habitat, habitat characteristics, predation on deer and/or elk, and road densities are factors that will be considered on a local basis in the season setting process.

Black bear seasons will be structured to meet the management goals and objectives for each specific DAU. The Department recognizes that too much variation among DAUs in season length and timing, or in allowable methods of take, can create confusing, complex rules. It is the intent of the Department to minimize this complexity by standardizing seasons statewide in a manner consistent with the goals and objectives of the various DAUs.

BLACK BEAR - HUMAN CONFLICTS

The Department recognizes that black bears will occasionally damage private property, prey on domestic livestock, and jeopardize public safety. The improper storage of human foods and garbage is often the primary factor leading to bear-human conflicts. Other factors include inadequate supplies of natural foods, injuries, and, in the case of sub-adult bears, inexperience in locating natural foods. Human encroachment into black bear habitat is a major cause of many depredation problems. The Department has the responsibility for controlling black bears in nuisance and human safety situations. The U.S. Department of Agriculture's Wildlife Services program (Wildlife Services) may handle these complaints at the request of the Department, if mutually agreed upon by both parties. Wildlife Services has the responsibility for handling black bears involved in livestock depredation problems, including apiaries. The Department may handle these complaints at the request of Wildlife Services, if mutually agreed upon by both parties. Guidelines for handling bear-human conflicts can be found in Appendix I.

BLACK BEAR - DEER\ELK RELATIONSHIPS

Extensive studies of black bear food habits throughout their range clearly show that vertebrates (primarily deer and elk) make up a very small part of the bear's yearly diet (<2%). Black bears rarely prey on adult deer or elk. However, black bears do prey on deer and elk neonates (fawns and calves) in some localities where favorable conditions exist for taking these animals.

The *fact* of predation (black bears do kill and consume deer fawns and elk calves) has never been disputed in discussions about black bear predation on other big game species. The major area of debate has involved the ***effect*** of that predation on populations of deer and elk.

Predator-prey interactions are extremely complex and involve many factors such as weather conditions, status of the prey population, availability of alternate prey, presence and density of other predators, and habitat conditions. As a result, it is difficult to determine what the effect of predation may be in any specific situation. In situations where the prey population is at or near the carrying capacity of its habitat, predation on deer or elk neonates probably has very little effect on prey population size or growth rate, and efforts to regulate predator numbers will not result in a larger prey base. However, when adverse weather or habitat deterioration results in a prey population decline, predation may increase the rate of decline and even result in a lower population level than would occur in the absence of predation. If issues of scale, logistics, and economics allow, reducing predator numbers in this situation may decrease the rate of decline and provide some benefit to the prey population.

The Wildlife Manager must evaluate all of these factors and the prevailing social environment before determining a course of action that serves the best interests of both the predator and its prey.

CONFLICTS WITH GRIZZLY BEARS

The U.S. Fish and Wildlife Service classified the grizzly bear as a “threatened” species in 1975. The Department currently restricts use of dogs and bait to hunt black bears in grizzly bear recovery areas (Units 1, 62, 62A, and part of 61). This approach, in conjunction with intensive public relations work and selected road closures, seems to be effectively reducing grizzly bear mortality. This strategy will be continued and its effectiveness monitored. Additional steps that could be taken if deemed necessary include:

1. Separating black bear season from general big game seasons in grizzly bear recovery areas.
2. Require hunters hunting in grizzly bear recovery areas to view a bear identification video.
3. Implementing controlled black bear hunts in grizzly bear recovery areas to limit the number of black bear hunters.
4. Changing or eliminating black bear seasons to reduce grizzly bear mortalities in grizzly bear recovery areas.

At this point in time, we do not recommend incorporating these steps in our black bear management program because the current approach seems to be effective. If the current program proves inadequate, we will consider the actions listed above. Additionally, controlled hunts similar to the one implemented in DAU 1A will be considered in seasonally unoccupied areas currently designated as grizzly bear recovery areas.

HOUND HUNTING

Approximately 1,100 hunters in Idaho practice hound hunting and they harvested about 16% of the bears taken during 1993-1997.

Hound hunting permits will be required for every member of a hound hunting party during take seasons. This permit requirement applies to residents and non-residents, but does not apply to the clients of licensed outfitters or up to 4 immediate family members of a permit holder. Immediate family is defined exclusively as the parents, spouse, children, and grandchildren of the hound hunting permit holder.
A quota on non-resident hound hunters will be maintained during this planning period for the black bear take season. In those areas where the Department's management objective is to increase the harvest, the Department may consider liberalizing or removing the quota. The Department will also consider removing the quota during the dog-training season. The Department will continue to prohibit hound hunting in designated grizzly bear recovery areas.

HABITAT MANAGEMENT

Because black bears are an important wildlife resource, the Department desires to elevate their profile among wildlife biologists, land managers, and the public. Bears and their habitat will play a more significant role in land management decisions, and good black bear habitats will be managed as such. Biologists will use specific knowledge of black bear habitats to develop interim guidelines and will provide technical support to public land management agencies and private corporations to identify and manage important black bear habitats.

The Department recognizes that valuable black bear habitat has been inundated, and associated wildlife populations have been lost, because of hydroelectric projects in Idaho. The Department will seek funding for full compensation for the loss of this habitat and associated wildlife from the Bonneville Power Administration under the Columbia Basin Fish and Wildlife Program, and from Idaho Power Company and other hydropower developers and responsible project operators under other programs.

PUBLIC OPINION SURVEYS

Current information on the public's perception of our black bear management program can be obtained from periodic surveys of public attitudes. The Department will sponsor or conduct surveys, designed by professional social scientists, to gather pertinent information that will enhance the Department's ability to manage black bears.

LAW ENFORCEMENT

During the public review process, the Department documented a strong desire by the public for the aggressive prosecution of all fish and game violators and for stiffer penalties. The Department will continue to encourage the public to use the Citizens Against Poaching (CAP) program to report violations. We will continue to work with legislators, prosecutors, and judges to achieve significant penalties for those individuals convicted in the courts. The Department will also use undercover (covert) operations to address this problem.

PUBLIC EDUCATION

It is apparent that the public was eager to have more information about black bear biology and wildlife management principles in general. The Department will continue to provide information on the consumptive and non-consumptive values of black bears to the public. In 1994, the Department published a book based on Department-sponsored research on black bear ecology. That book, titled "A Shadow in the Forest - Idaho's Black Bear," is available at local bookstores. The Department also published a teacher's guide in 1995 that provides information on the biology of black bears and activities to help students learn important concepts about ecological factors affecting Idaho black bear populations.

WATCHABLE WILDLIFE

There is some public demand to view black bears in their natural environment. Therefore, the Department will provide opportunity in portions of some Units for viewing black bears. The Department may select areas for non-consumptive use where: 1) area closures on black bear hunting currently exist to protect threatened grizzly bear populations or to accommodate research; 2) road access exists into relatively open habitats where black bears can easily be seen; and, 3) where conflicts with other resource users in the area are minimal.

BAITING

About 1,250 hunters in Idaho used baiting as a method of take, and they were responsible for approximately 18% of the bears harvested during 1993-1997. Over 90% of the harvest by hunters using bait occurred during the spring season.

The Department will continue to allow hunters to use bait in those DAUs where the practice is consistent with the management objectives for that area. However, the Department will continue to prohibit baiting in designated grizzly bear recovery areas. The Department will also consider changes in the baiting rules that will reduce or alleviate conflicts between hunters using baits and campers and hikers, and in areas with nearby summer home developments. IDFG-recommended standards for baiting can be found in Appendix II.

STATEWIDE MANAGEMENT PROGRAM

Idaho is divided into 5 areas for purposes of managing black bear populations (Figure 8). Area 1 includes habitats that vary from dense, semi-coastal forests to patchy forest habitats along dry river breaks. Abundant road access and proximity to human population centers characterize Area 1 GMUs. Area 2 includes habitats similar to Area 1, but not as accessible by road and not as close to major population centers. Area 3 has limited access and much of it is officially designated as Wilderness. Area 4 includes a variety of habitats that are generally dry shrub and grass types with few berry-producing plants. The livestock industry is a major resource user of public lands in Area 4. Area 5 includes most of the irrigated lands in southern Idaho and the drier, desert portions of the state. Habitat quality in Area 5 is marginal for black bear and few black bears occur there. Based on similarities in habitat, road access, and proximity to urban population centers, 3 of the 5 black bear management areas (Area 1, 2, and 4) are divided into smaller groups, DAUs, to facilitate analysis of harvest information (Figure 1). The DAU concept was developed in 1985 to enhance the Department's ability to interpret harvest data and to simplify the rules regulating black bear harvest.

MANAGEMENT ACTIONS

The Department has two basic options available to influence harvest rates: adjusting 1) hunting opportunity (season length and timing), and 2) methods of take. Each approach has advantages and disadvantages and the preferred choice should be dictated by current conditions in the DAU and management objectives. First and foremost, management objectives must address the biological requirements of black bears. Once those are satisfied, harvest regulations are developed that reflects differences in vulnerability, hunting pressure, and road access among areas.

Season length and timing are ineffective approaches for regulating the total harvest of black bears. However, adjusting season length and timing can be an effective means of regulating harvest sex-ratios and in some cases, age structure. The vulnerability of black bears to hunting is influenced by extrinsic (weather, etc.) and intrinsic (seasonal behavior) factors. Adult males are the first bears to leave their winter dens, followed by sub-adult males and single females. Closing spring hunting seasons in early to mid-May focuses most hunting pressure on males and females unaccompanied by cubs or yearlings. It also provides additional protection for female bears accompanied by cubs-of-the-year because they are often the last bears to leave their winter dens. Adult males are the last bears to enter dens in the fall; females generally enter their dens in early to mid-October. As a result, late fall hunting seasons also focus hunting pressure on male black bears.

Regulating the methods of take that are used by hunters can be effective in adjusting total harvest, and potentially the sex and age composition of the harvest. Options available to the manager using this approach include: 1) unrestricted opportunity; 2) taking actions to reduce the efficiency of hunters using bait, hounds, or still hunting methods; and, 3) eliminating the activity as a legal method of take.

The Department will use one or more o(the following management options as needed for regulating black bear harvest.

To increase harvest in a DAU:

- Maximize hunting opportunity.
- Increase bag limit to two black bears per year.
- Increase bag limit to one black bear in spring season and one black bear in fall season.
- Increase/eliminate non-resident hound quota.
- Increase spring season length - maximum allowed 4/1 - 6/30.
- Increase fall season length - maximum allowed 9/1 - 11/15.
- Reduce tag cost.
- Contract with the U.S. Department of Agriculture, Wildlife Services Division to kill black bears in areas where sport hunting is not effective in reaching management goals.

To reduce harvest in a DAU:

- Eliminate baiting as a legal method of take.
- Eliminate hound hunting as a legal method of take.
- Eliminate black bear hunting during D/E seasons.
- Eliminate spring season.
- Eliminate fall season.
- Allow baiting in fall only.
- Allow hound hunting 4/1 - 5/15 and 9/1 - 9/30.
- Close spring season on 5/15.
- Implement controlled hunts.

Harvest management objectives for each of the 21 DAUs is summarized in Table 3.

Table 3. Harvest characteristics and management objectives for 21 DAUs in Idaho based on the percent males ≥5 years old in the harvest.

DAU	CURRENT STATUS	MANAGEMENT OBJECTIVE
1A	Light	Light
1B	Moderate	Heavy
1C	Heavy	Heavy
1D	Heavy	Heavy
1E	Heavy	Heavy
1F	Heavy	Heavy
1G	Light	Moderate
1H	Moderate	Light
1I	Light	Heavy
1J	Light	Moderate
1K	Moderate	Moderate
1L	Moderate	Light
2A	Light	Heavy
2B	Light	Moderate
3A	Light	Moderate
3B	Moderate	Moderate
4A	Heavy	Moderate
4B	Light	Moderate
4C	Light	Moderate
4D	Moderate	Moderate
4E	Light	Moderate

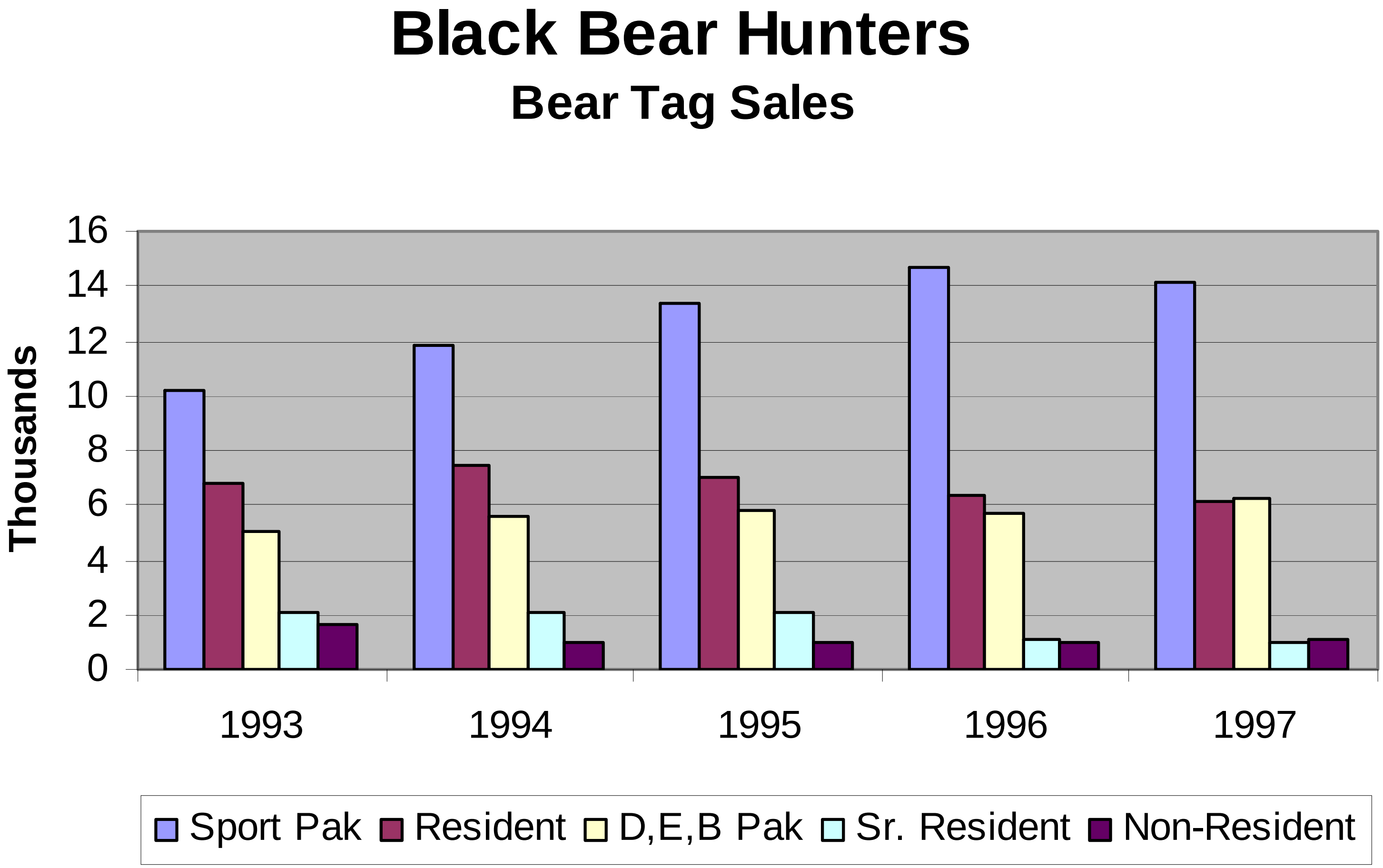

Figure 1. Black bear tag sales in Idaho, 1993-1997.

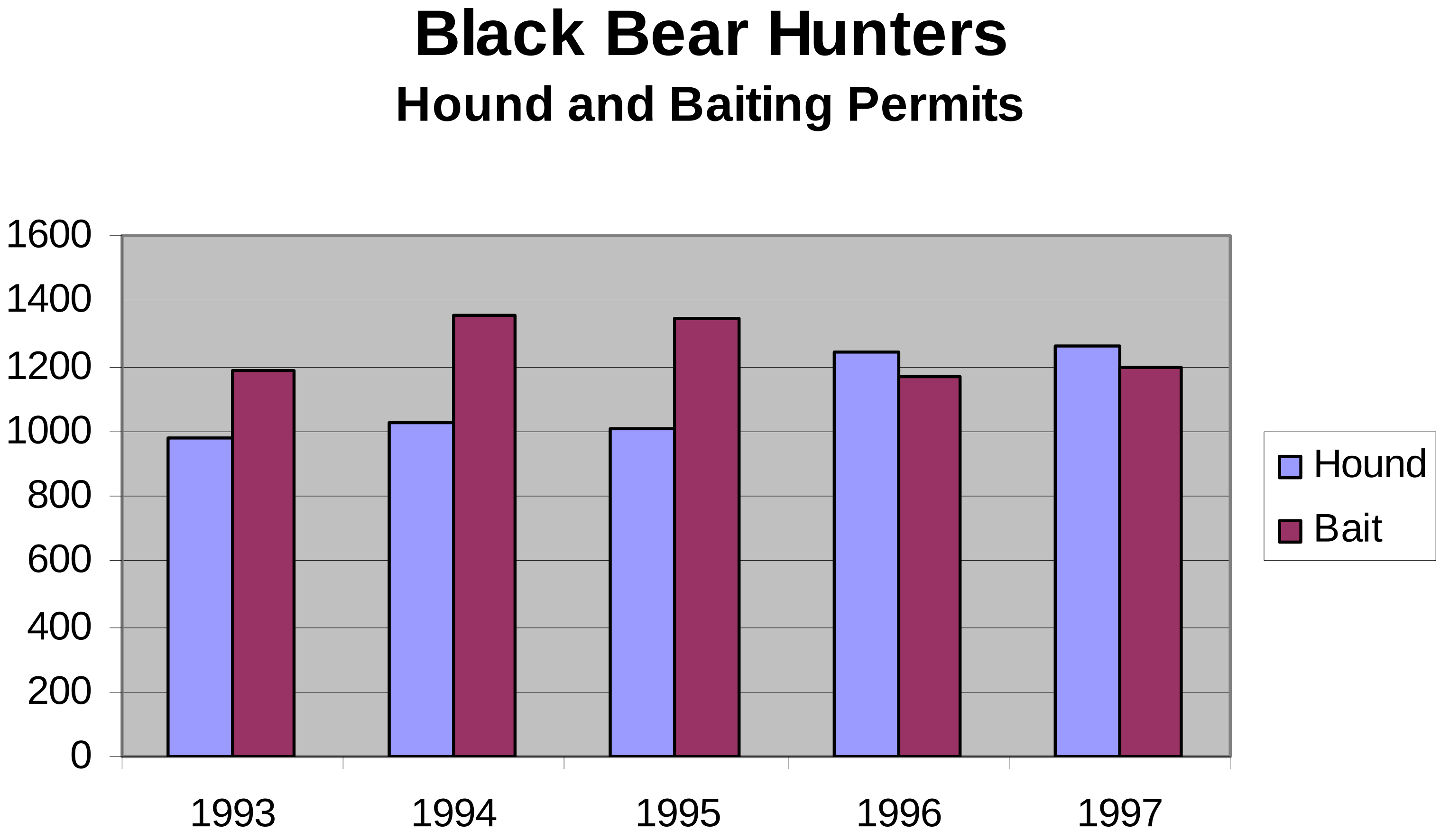

Figure 2. Hound hunter and baiting permits issued in Idaho, 1993-1997.

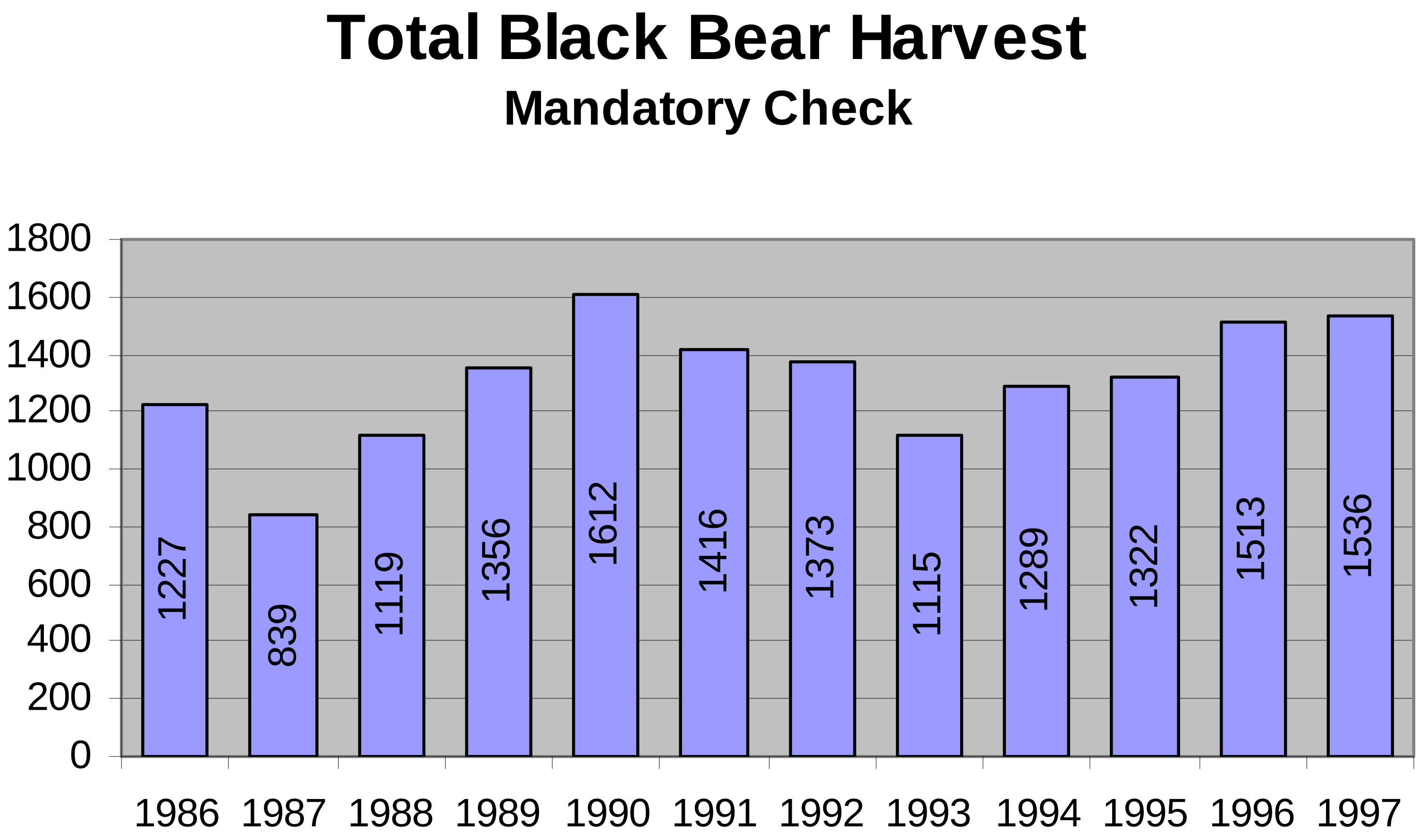

Figure 3. Number of black bears checked by hunters, 1986-1997.

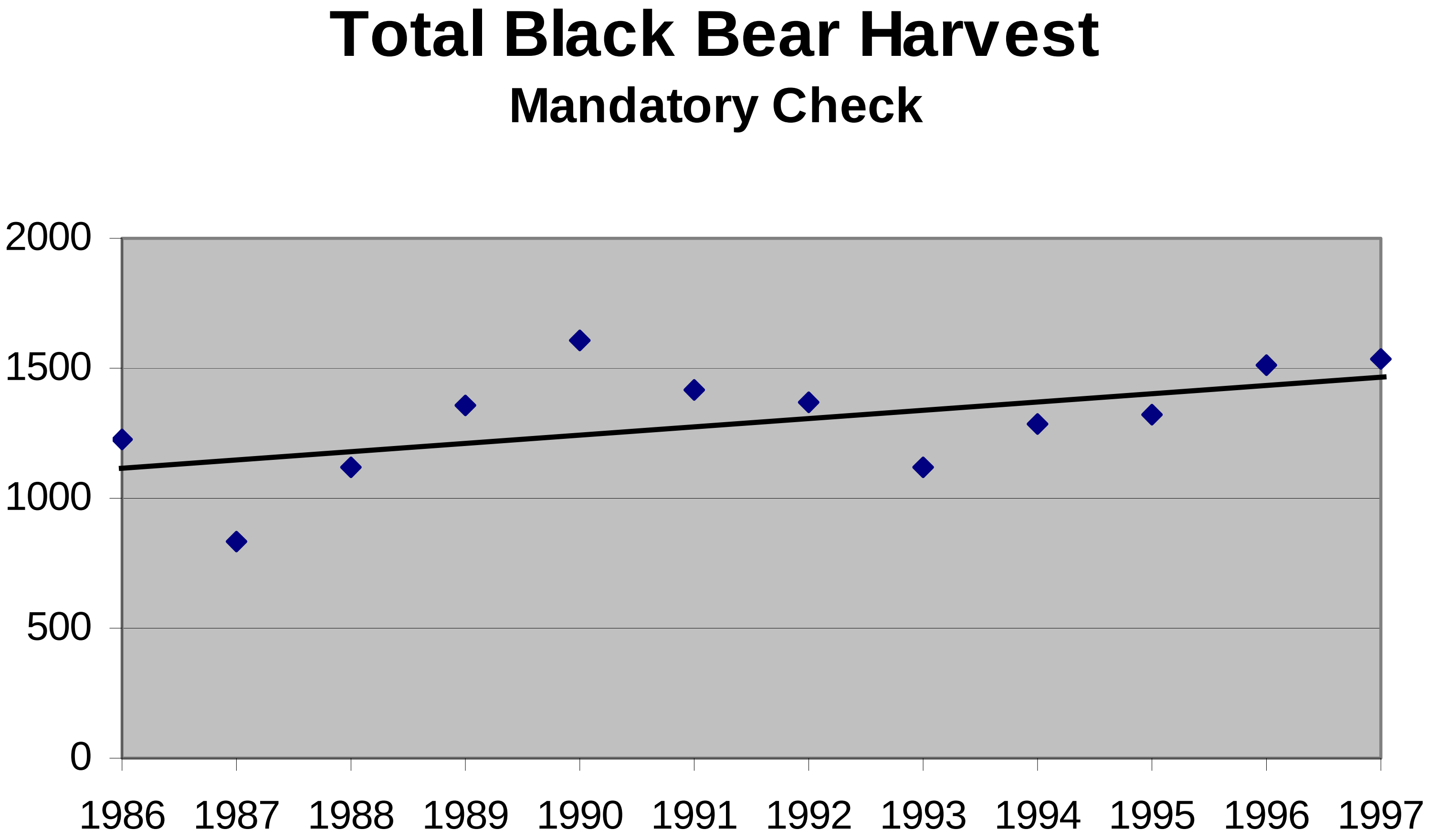

Figure 4. Trend in number of black bears checked by hunters, 1986-1997.