COUGARS OF THE SAN ANDRES MOUNTAINS, NEW MEXICO

by

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For 10 years we delved into the lives of cougars, sometimes getting close enough to hear them purr. Besides the observations we made to address our objectives, time and again we also observed cougars do things that we could attribute only to cognition and conscious thinking, characteristics that many of us humans normally reserve only for ourselves. To consider that we have some basic mental processes in common with cougars actually helped us be as objective in our observations and understanding of their life as was humanly possible. For those important lessons and for some of the most marvelous experiences of our lives, we are grateful to the cougars.

Finally, we acknowledge the San Andres Mountains ecosystem, where we conducted this research. The San Andres Mountains is unique in that it is the largest single block of primitive and ecologically intact Chihuahuan Desert mountains remaining in North America. Consequently, the mountain range has exceptional value for the conservation of wild life. The San Andres Mountains ecosystem deserves a coordinated effort by the responsible agencies (i.e., NMGF, WSMR, USFWS, JER, and NASA,WSTF) to apply the most reliable scientific information and methods available to natural resources management- a condition which does not presently exist.

-K.L., L.S., T.R., and M.H.

1. INTRODUCTION

by K. Logan, L. Sweanor and M. Hornocker

Across wild New Mexico today, the cougar (*Puma concolor*) is the last surviving large obligate carnivore. Wolves (*Canis lupus*) and jaguars (*Panthera onca*) that once roamed the land, competing with cougars, are now extinct in the wild, the victims of the heavy hunting and predator control efforts of the late 1800's and early 1900's that came with the new wave of human settlers. Predators were killed primarily to protect livestock and game and because of the fear that they were a direct threat to human life (Young 1946, Allen 1962, Nowak 1976).

Cougars did not escape the onslaught unaffected. In 1927, Ligon (cited in Young 1946) reported that federal and state control agents and cooperating hunters had practically eliminated cougars from the Upper Gila River drainage. Hibben (1937:6) emphasized that one impetus of his study of cougars in New Mexico in 1934 and 1935 was the growing alarm about the scarcity of cougars. "It was felt that the [cougar] was in danger of extinction in several areas of his former range. The number of [cougars] which the modern hunter encountered was alarmingly small compared to that reported two or three decades ago." Young (1946:28) suggested that the cougar in New Mexico "due to intensified hunting, is not as common as it was at the beginning of the present century. The animals may now be said to be confined mainly to the rougher mountainous sections west of the Rio Grande." Along with changes in the legal status of cougars in New Mexico in 1971, which curbed human-caused mortality, came the potential for cougar populations to rebound from low numbers and to recolonize historical habitat.

There have been no reliable estimates of the number of cougars in New Mexico. In 1917, Ligon guessed there were about 400 cougars (Bailey 1931). In 1967, Berghofer (1967) estimated that there were at least 350 cougars. These numbers likely are conservative and probably reflect the great difficulty of attaining accurate estimates of numbers of animals like cougars that are extremely cryptic and typically live at low population densities. From 1972 to 1974, an attempt by New Mexico Department of Game and Fish (NMGF) personnel to quantify cougar numbers by counting tracks produced an estimate of at least 493 cougars (of all ages) in the southwest region alone (Donaldson 1975). However, the methods used by Donaldson (1975) to estimate cougar numbers has never been tested in a known population.

1.1 COUGAR MANAGEMENT HISTORY IN NEW MEXICO

Cougars in New Mexico first received legal recognition in 1867 when the Territorial Legislature passed a predatory bounty law which provided for the payment of a $5.00 bounty (NMGF Operational Plan, 1987-1995]. The bounty was suspended in 1923 (Nowak 1976). In 1971, the cougar was placed on the list of New Mexico's protected wildlife species and the NMGF assumed management authority which included the establishment of hunting seasons, bag limits, and resolution of depredation on livestock (Evans 1983).

Cougar hunting regulations have varied since the cougar became a protected species (NMGF hunting proclamations, 1971-1995). In 1971, three-quarters of New Mexico was closed to cougar hunting. The southwestern quarter was open for 4 months with a bag limit of 1 cougar per hunter, and females followed by cubs and cubs <1 year old were protected thereafter. In subsequent years, more areas in New Mexico were progressively opened to cougar hunting, and the season length was extended to 11 months in duration. Between 1979 to 1983, almost all of New Mexico was opened to an 11-month- long cougar hunting season with an increased bag limit of 2 cougars per hunter. After 1979, hides of all cougars killed by hunters had to be tagged by the NMGF.

In 1983 the protected status of the cougar was challenged. Members of the agricultural industry concerned with depredation on livestock attempted to return the cougar to its former status as a "varmint" by introducing a bill to New Mexico's House of Representatives. The bill was tabled in committee, but the legislature requested more information from the State Game Commission and the NMGF. The NMGF responded by producing the first in depth report on cougars in the state titled, The Cougar In New Mexico- Biology, Status, Depredation Of Livestock, And Management Recommendations (Evans 1983). In the report, Evans concluded that cougar numbers probably had declined during the previous 11 years (1972-1983). His recommendations, bolstered by public sentiment, resulted in more conservative cougar hunting regulations.

In 1984 the cougar hunting season was 3 months long throughout almost all of New Mexico. However, there were 5 hunt units (2 in the southwest, 3 in the southeast) with harvest quotas of 10 to 17 cougars and where the season was extended 2 additional months. The objective in those units was to obtain a higher kill in specific areas where cougar depredation on livestock was problematic.

Between 1985 and 1995, cougar hunting regulations were uniform. Almost all areas of New Mexico were open to cougar hunting for 4 months (1 Dec. to 31 Mar.) with a bag limit of 1 cougar per hunter.

The new laws that protected the cougar in 1971 also put the responsibility on the NMGF to manage cougar depredation on livestock. The NMGF maintained 2 full-time predator control officers between 1971 to 1987 who pursued cougars in depredation incidents. Federal predator control personnel also were used when necessary. Once depredation incidents were verified, NMGF personnel were issued depredation permits authorizing the removal of the offending cougar(s). Either the cougar(s) was killed by predator control officers themselves, or the ranchers were given permission to kill the cougar(s). Sometimes exceptions to this process occurred when ranchers killed cougars that were directly threatening or in the process of killing livestock, or when depredating cougars were killed by licensed hunters during the sport-hunting season (Evans 1983). Today, federal predator control agents fill the void of the state-supported officers.

Because of unusually high cougar depredation on domestic sheep on ≤5 ranches in the Guadalupe Mountains in southeastern New Mexico, the NMGF responded with a special preventive control program starting in 1988. This program allows the killing of up to 14 cougars per year in an effort to prevent cougar predation on sheep. Moreover, other cougars that are involved in depredation incidents can be killed.

1.2 RESEARCH

There have been 4 research projects on cougars in New Mexico. The first was conducted in 1934 and 1935 by Hibben (1937). He investigated some basic life history of cougars in northern and western New Mexico and central and southeastern Arizona. The NMGF conducted cougar research in southwestern New Mexico during 1971 to 1978. Objectives focused on estimating cougar numbers from track counts, home range characteristics and movemements by radio-telemetry, and diet (Donaldson 1974, Donaldson 1975, Bavin 1976, Bavin 1978). The research ended because the objectives were not achieved (Welch 1979). Between 1982 and 1985, Smith et al. (1986), under contract with the National Park Service, conducted cougar research in southeastern New Mexico. Their research was "intended to provide better understanding of the [cougar] population dynamics within the Carlsbad Caverns and Guadalupe Mountains National Parks region. The need for this information arose from complaints by neighboring New Mexico sheep ranches of depredations by [cougars] believed to be coinhabiting Park lands and adjacent sheep ranches" (Smith et al. 1986:1).

The most recent study of cougars in New Mexico is described in this report. In 1985, the NMGF contracted the Hornocker Wildlife Institute (HWI) to study the ecology of cougars. The impetus for this study was the controversy that erupted in 1983 and 1984 regarding the status and management of cougars in New Mexico. In recognition of the lack of information that was available on cougars which could be used to address management issues, the State Game Commission and the NMGF decided to support this 10-year study (1985 to 1995).

1.3 MANAGEMENT NEEDS

Just as they did in 1983 and 1984, wildlife managers in New Mexico today need information on cougars to apply to management issues. Specific needs for managing cougars were identified by the 4 NMGF Area Supervisors during telephone interviews with K. Logan (HWI) in 1994. Those needs were prioritized on a state-wide basis as follows: 1) dealing with depredation on livestock; 2) education of the general public and NMGF personnel about cougars; 3) developing sport-hunting recommendations for the state cougar population; and 4) determining effects of cougar predation on game animals.

Depredation on livestock was an important concern, especially on domestic sheep in the southeast region. That region accounted for 67% (268 out of 400) of the depredation permits issued for cougars state-wide during the 16 year period from 1978 to 1993. An average of 25 permits per year were issued for depredating cougars in New Mexico (Haussamen 1994). Area Supervisors considered depredation to be of prime importance because of the political ramifications to cougar management and the economic costs to individual livestock producers. Supervisors wanted information on how cougars could be managed to minimize depredation in localized areas and how livestock could be managed to minimize depredation.

Because of the often controversial and emotional nature of issues regarding cougars, Area Supervisors thought that public education about cougars would contribute to informed public input on management activities. Besides an education on cougar biology and ecology, information was requested on how people should behave when they encounter cougars (to avoid attack) and how the increasing human population and attendant land development influence cougars. The education of NMGF personnel about cougar biology and ecology was considered important for the development and implementation of reliable cougar management activities and the ability of personnel to monitor the effectiveness of management activities.

To develop recommendations for sport-hunting, Supervisors requested information on cougar population dynamics and the effects of hunting on cougar populations. In addition, they also identified the need to improve the quality of data gathered on cougars killed by hunters to enable NMGF to reliably track trends in the cougar population. Uncertainty about cougar hunting management is warranted because from 1984 to 1995 the number of cougars harvested per year has increased from 79 to 150 and the number of licensed hunters per year has increased from 443 to 1,145. At the same time hunter success has declined from 0.18 to 0.13 (Weybright 1993, NMGF Cougar Harvest Surveys 1993-1995). Although the NMGF collects information on cougar harvest, including gender of animals killed, the effects of the present hunting management on cougars in New Mexico are unknown.

Finally, information on the effects of cougar predation on game animals, especially mule deer (*Odocoileus hemionus*), was requested because some sport-hunters were concerned that they might be competing with cougars for game. In addition, other wildife managers requested information about the effects of cougar predation on desert bighorn sheep (*Ovis canadensis mexicana*), a state-listed endangered species. The sheep population on the San Andres Mountains has been of particular concern because it is New Mexico's only remaining original population, which today numbers about 40 individuals.

1.4 STUDY GOAL AND OBJECTIVES

The goal and objectives of this research on cougars in New Mexico address many of the concerns voiced by wildlife managers. Our goal was to develop a foundation of knowledge on the ecology of cougars that managers could use to develop cougar management and conservation strategies.

We had 3 principal objectives:

(1) Describe the dynamics of a cougar population.

(2) Describe the social organization of cougars in the population.

(3) Quantify some of the relationships between cougars and desert mule deer (*O. h. crooki*) and desert bighorn sheep.

We were able to achieve the goal and objectives of our research, as well as, provide the most quantitative information of any cougar study to date. Thus, our findings give the New Mexico Department of Game and Fish a solid foundation on which to develop a state-wide cougar management plan that adresses vital issues, including: cougar predation on livestock, human safety, sport-hunting, and long-term cougar conservation.

Our work is reported in 7 chapters. Chapter 1 includes this introduction. Chapter 2 describes the San Andres Mountains study area. Cougar population dynamics are examined in Chapter 3. Chapter 4 describes the social organization of the cougar population. Chapters 5 and 6 quantify some of the relationships between cougars and desert mule deer and cougars and desert bighorn sheep, respectively. Chapter 7 presents information on an auxiliary project that resulted from the experimental removal of cougars as part of objective 1; cougars were moved from the San Andres Mountains to northern New Mexico in order to evaluate cougar translocation as a management tool. Chapters 3 through 7 present the methodology, results, discussion and management implications specific to each topic above. Because cougar population dynamics and social organization are so closely tied, management implications for those 2 topics are addressed jointly at the end of Chapter 3.

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CHAPTER 2. THE RESEARCH ENVIRONMENT

by L. Sweanor, K. Logan and M. Hornocker

The 2,059 km^2 study area was located in south-central New Mexico and encompassed the entire San Andres Mountains (SAM, Fig. 2.1). The range extended north from San Augustin Pass on U.S. Highway 70 in Dona Ana County to Mockingbird Gap in Socorro County. The area was almost completely within White Sands Missile Range (WSMR), which was under the jurisdiction of the U.S. Army. About 93 km^2 of the study area was outside the western boundary of WSMR and was comprised primarily of public domain administered by the Bureau Of Land Management (BLM). There, small private inholdings were owned by cattle ranchers that leased the BLM and State lands for grazing. Only about 13 people, including 4 cougar researchers, inhabited the SAM year-round (0.65 people per 100 km^2).

We designated 2 parts of the study area. The 703 km^2 Treatment Area (TA) comprised the southern one-third of the study area. We experimentally removed cougars from the TA. In addition, we studied survival rates and cause-specific mortality in radio-collared mule deer and bighorn sheep that lived on the TA. The Reference Area (RA) was 1,356 km^2 in size; no manipulations of the cougar population occurred there.

2.1 CHOICE OF STUDY AREA

We chose the San Andres Mountains as our study area for several reasons: (1) We preferred a desert area because intensive, long-term research on cougars in a desert environment had not been done. This gave us the greatest opportunity to contribute new knowledge about cougars. (2) The SAM was a large area of cougar habitat that was not contiguous with other large blocks of cougar-inhabited areas; thus, we could isolate a cougar population for intensive study. (3) The area was relatively undisturbed by man because access and activities were restricted by WSMR. (4) Through agreements with cooperating agencies, we could minimize the potential for man-caused confounding variables by prohibiting cougar hunting and fur-bearer trapping, and restricting mule deer hunting. In addition, because livestock was prohibited on all but 5% of the area, livestock were not an alternate source of food for cougars, nor could they compete with native ungulates. (5) A network of dirt roads and jeep trails enabled us to thoroughly explore the study area.

2.2 PHYSIOGRAPHY AND GEOLOGY

The San Andres Mountains are within the easternmost part of the Mexican Highland section of the Basin and Range physiographic province (Hawley et al. 1976). The mountain range is long and narrow, measuring over 127 km long and 9 to 30 km wide. It is part of a broken chain of mountains which extend into the Sierra Oscura to the north and terminate in the Organ and Franklin Mountains to the south. The range is flanked by 2 large desert basins: the Jornada del Muerto to the west, and the Tularosa to the east. The Tularosa Basin spans some 97 km east-west at its widest point, the Jornada del Muerto, about 55 km.

The San Andres Mountains are a westward tilted fault block of PreCambrian granite and Paleozoic-age limestone, dolomite, sandstone and shale (Eidenbach 1983, Kottlowski et al. 1956). A major fault zone borders the range to the east and separates the collapsed crest of the Tularosa Basin from the range's steep east face. The precipitous east escarpment rises up to 1,500 m above the basin floor and is characterized by cliff-forming limestones (Van Devender and Toolin 1983). In most places the east face has been eroded back from the original fault boundary. The resulting alluvial fans, formed from the weathering granite and limestone bedrock, are broken by a network of arroyos and outcrops of Precambrian granite and schist. Fault activity during the last 10 million years has disturbed some of the alluvial deposits and underlying bedrock, and fault scarps formed during the past 2 million years are present along most of the basin-range margin (Hawley 1983). There are numerous subsidiary tilted blocks, folds and canyons within the central portion of the mountain range. The west slope is relatively gentle; tilted sedimentary rocks dip 10 to 20 degrees westward into the younger rocks and valley fill of the Jornada del Muerto syncline (Kottlowski et al. 1956).

The south end of the San Andres Mountains are geologically similar to the adjacent Organ Mountains and consist of a coarse-grained phase of the Organ Mountains monzonite batholith. Mockingbird Gap, at the north end of the range, is a broad pass in a down-faulted anticlinal axis. The general north-south trend of the range continues northward into the Sierra Oscura; but there, the fault blocks dip eastward and are bounded on the west by a fault-line scarp (Kottlowski et al. 1956).

Elevations within the study area range from approximately 1,280 m along the east piedmont to 2,730 m at Salinas Peak. Fourteen major east-west canyons dissect the range and drain tributary canyons from the north and south. There are no permanent streams in the San Andres Mountains; however natural springs and seeps are scattered throughout the study area.

2.3 CLIMATE

The San Andres Mountains have a semi-arid climate. Most precipitation occurs during the late summer and early fall, when moist air circulating from the Gulf of Mexico causes intense, but brief and scattered rain showers (Breternitz and Doyel 1983). Winter moisture fluctuates depending on the relative latitude of the jet stream, and storms that do occur generally produce slow, drizzling rain or light snow. Precipitation also varies with elevation; Ares (1974) stated that annual precipitation is nearly 10.1 cm greater in the San Andres Mountains than the adjoining Jornada del Muerto plains. Weather is seasonal, with hot summers, warm springs and falls, and cold winters.

Specific precipitation data was obtained for the Ash Canyon gauge because it occurred at mid-elevation (1,731 m) in the central portion of TA and complete data has been collected there since 1937 by the U.S.D.A. Jornada Experimental Range. During the years 1985 to 1994, which included our research period, mean annual precipitation was 43.61 cm (SD = 11.40), which was 10.77 cm greater than the mean annual precipitation during the previous 48 years (1937-1984: $\overline{x}$ = 32.84 cm, SD = 10.24). Moreover, the first, third, and fifth highest annual precipitation occurred during our study (1991, 1992, 1986, respectively). The months of July through September constituted the rainy or growing season, when from 1985 through 1994, 45.4% of the precipitation fell. An average of 19.79 cm (SD = 5.89) of precipitation falls during the rainy season. Below average precipitation during the growing seasons of 1992 to 1994 contributed to severe drought, which continued through the end of the study.

Snow fell infrequently and primarily during December through February. Continuous snow cover did not persist for more than a few days except along the north-facing slopes at higher elevations. Individual storms generally brought less than 2.5 cm of snow to the lower elevations, whereas higher elevations occasionally received 12.7 cm or more. One severe storm in December, 1987 brought 46 cm of snow to elevations above 1,372 m.

Temperature records from the Jornada Experimental Station (elevation = 1,349 m, 15 km west of the SAM study area) for 1985 through 1994 produced a mean annual temperature of 14.5°C. July was the hottest month, with temperatures averaging 25.5°C. January was the coldest month; temperatures averaged 3.4°C. Extreme temperatures in summer reached 42.8°C and in winter dipped to -24°C.

March and April were typically the windiest months, with winds prevailing from the west and southwest. Constant high winds may persist for periods longer than 24 hours during early spring. Wind velocities as high as 187 km/hr have been recorded at Salinas Peak (WSMR records).

2.4 FLORA

Merriam's life zones represented in the San Andres Mountains include the Upper (primarily above 2,134 m) and Lower (below 1,981 m) Sonoran of the Chihuahuan Desert (Larson 1970). Two high peaks harbored some species indicative of the Transition Zone: small communities of Ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Quercus gambelli*) on Salinas Peak, and Gambel oak with an understory of snowberry (*Symphoricarpos rotundifolius*) on San Andres Peak.

Woodrat (*Neotoma* spp.) middens indicated that a mixed conifer forest was present at higher elevations during the late Wisconsin glacial age, approximately 15,000 years ago (Van Devender and Toolin 1983). During the early Holocene (about 9,000 years before present) the climate became warmer and dryer and desert-grassland began to develop. The vegetation and climate have been essentially modern for the last 4,400 years.

Seven general vegetation types were recognized in the study area. These included tall mixed desert shrub, low mixed desert shrub, grass, mixed mountain shrub, dry channel, moist riparian, and pinon (*Pinus edulis*) - juniper (*Juniperus* spp.). Vegetation was highly influenced by elevation, aspect, rock substrate and soil material. In some areas, 2 or more vegetation types occurred as codominants, and shrubs and grass were frequent subdominants in the pinon-juniper type.

Dominant plants in the tall mixed desert shrub type were generally over 1 m tall. Creosote (*Larrea divaricata*), mesquite (*Prosopis glandulosa*), mimosa (*Mimosa biuncifera*), and southwestern condalia (*Condalia lycioides*) typify this community and were generally found in the desert basins, on the alluvial fans, and on south and west facing slopes. Stony uplands supported ocotillo (*Fourquiera splendens*) and sotol (*Dasylirion wheeleri*). Drier slopes supported low mixed desert shrub vegetation such as mariola (*Parthenium incanum*), feathered dalea (*Dalea formosa*), prickly pear (*Opuntia* spp.), yucca (*Yucca baccata*) and agave (*Agave parryi*).

Common grasses included black, blue, and sideoats grama (*Bouteloua eriopoda*, *B. gracilis*, *B. curtipendula*), three-awn (*Aristida* spp.) and muhly (*Muhlenbergia* spp.). Black grama was often found in the limestone hills in association with ocotillo and mountain mahogany (*Cercocarpus montanus*). Muhly was typically found on the alluvial slopes. Localized stands of invader species such as burro grass (*Schleropogon brevifolius*) and snakeweed (*Gutierrezia* spp.) were indicative of past overgrazing; however, native grasses have recovered dramatically in most areas (Van Devender and Toolin 1983).

Protected slopes and higher elevations were covered with mountain shrubs, the most conspicuous being mountain mahogany (*Cercocarpus montanus*), skunkbush sumac (*Rhus trilobata*), Wright's silktassel (*Garrya wrightii*), oak (*Quercus* spp.) and pale hop tree (*Ptelea trifoliata*). Mountain shrub communities generally integrated with desert shrub communities where the soil became shallow and stony.

Pinon and juniper occurred in the coolest areas: generally north slopes and the highest elevations. Coverage varied from a few scattered trees to 100%. Trees were typically short and often did not exceed heights of 6 m. Of the junipers, one-seed (*J. monosperma*) was the most common. Alligator-bark junipers (*J. depeana*) were scarce and only found in the most protected areas.

Dry channel vegetation frequently occupied the major drainages. The wide canyon bottoms were typically gravelly and well-drained, and supported vegetation such as apache plume (*Fallugia paradoxa*), brickellbush (*Brickellia laciniata*), algerita (*Berberis trifoliolata*) and desert willow (*Chilopsis linearis*). Where springs and seeps occurred, ash (*Fraxinus velutina*), hackberry (*Celtis reticulata*), cottonwood (*Populus deltoides weslizeni*), and even cattails (*Typha angustifolia*) were found.

2.5 FAUNA

Three native ungulate species occurred on the study area: desert mule deer, desert bighorn sheep, and pronghorn (*Antilocapra americana*). Mule deer were the most abundant ungulate and occurred throughout the study area. Densities of mule deer on the SAM were not known, but we roughly estimated a range of 2 to 5 deer per km^2. Mule deer hunting was prohibited on the SAM between 1985 and 1989. Thereafter, sport-hunting for buck deer only was allowed in the northern one-quarter of the study area every other year including 1990, 1992, and 1994. During those 3 years the number of bucks killed was 44, 82, and 67, respectively.

About 200 desert bighorn sheep inhabited the San Andres Mountains in 1976 (Sandoval 1979), but a scabies outbreak in 1978 drastically reduced the population. During this study, about 40 sheep lived on the SAM; they ranged primarily on steep terrain along the east escarpment. Because of their low numbers and endangered species status, the SAM bighorn sheep population was protected from hunting.

Pronghorns infrequently ranged up into the foothills in the northern portion of the SAM in small bands of <20 animals; they were more common in the surrounding flats. About 30 to 40 buck only permits were issued to hunters each year (WSMR 1994).

Introduced species on the study area included the oryx (*Oryx gazella*) and javelina (*Tayassu tajacu*). Oryx were first introduced to WSMR in 1969 (Saiz 1975). Although oryx preferred the desert basins, the population continued to increase and expand its range during the course of the cougar study. Consequently, oryx began to utilize the large canyons that dissected the study area on a more frequent basis. By the close of the study in 1995, the oryx population numbered approximately 1,000 to 1,200 animals (WSMR 1994; p.50). Fifteen javelinas (*Tayassu tajacu*) were introduced into the San Andres Mountains during the 1970's (Anderson and

Taylor 1983). Although javelinas were rarely observed during the course of the study, 2 were snared and released during cougar capture operations.

Feral horses that resided in the Tularosa basin apparently increased in numbers from an estimated 500 to 600 in 1985 (WSMR 1994) to 1,700 to 1,800 in 1994 (Holderman et al. 1996); they were never observed within our study area. Although stray cattle often entered the study area from the west boundary fence, they numbered <100 head at any time.

The San Andres Mountains supported a variety of small mammals. The most visible include black-tailed jackrabbits (*Lepus californicus*) at lower elevations, and desert cottontails (*Sylvilagus audubonii*), rock squirrels (*Spermophilus variegatus*) and white-tailed antelope squirrels (*Ammospermophilus leucurus*) at higher elevations. Porcupines (*Erethizon dorsatum*) were rarely observed. Woodrat (*Neotoma mexicana*) sign was common in the canyons and around rocky outcrops.

About 183 species of birds and 35 species of reptiles and amphibians have been documented on the SAM (WSMR 1994). Ground-dwelling birds included 3 species of quail. Gambel's (*Callipepla gambelii*) and scaled (*Callipepla squamata*) quail were found in the dry channel and riparian communities; they were especially common during years of high precipitation. Montezuma quail (*Cytonx montezumae*) apparently occurred in small numbers with a very patchy distribution. Wild turkeys (*Meleagris gallopavo*) were extremely rare. Avian scavengers included turkey vultures (*Cathartes aura*), golden eagles (*Aquila chrysaetos*), red-tailed hawks (*Buteo jamaicensis*), and ravens (*Corvus* spp.), although all but the red-tailed hawks were relatively uncommon. Four species of rattlesnakes: rock (*Crotalus lepidus*), western diamondback (*C. atrox*), black-tailed (*C. molossus*) and prairie (*C. viridis*), occupied niches from the mountain tops to the basins.

Carnivores included the coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), badger (*Taxidea taxus*), ringtail (*Bassariscus astutus*), and striped skunk (*Mephitis mephitis*). Hog-nosed skunks (*Conepatus mesoleucus*) were present but probably less common. The cougar inhabiting the study area has been described as the subspecies *Felis concolor azteca* Merriam (Young 1946). No historical records have been found that indicate the presence of grizzly bears (*Ursus arctos*), Mexican wolves (Canis lupus baileyi), and jaguars (*Panthera onca*) on the SAM.

Black bears (*U. americanus*) probably occurred in very low numbers as late as the 1890's (Halloran 1946). One of the last bears was killed in about 1908 in Bear Den Canyon (J. P. Wood, Jr. pers. comm.). During the 10 years we studied cougars, we did not observe sign of black bears on the SAM. However, on 17 August 1990, Military Police found a black bear that had climbed a utility pole and was electrocuted at Seehorn Site about 3 km east of the mouth of San Andres Canyon (WSMR records). This bear may have dispersed from the Sacramento Mountains to the east, or the Oscura Mountains to the north. A wildlife biologist found bear feces and tracks at Cottonwood Spring in the southern portion of the Oscura Mountains on 10 May 1993 (WSMR records).

2.6 HISTORY OF LAND USE

Clovis points found near Mockingbird Gap and on the eastern edge of the San Andres Mountains indicated that early big game hunters occupied the Tularosa Basin area some 11,000 or more years ago (Beckett 1983, Breternitz and Doyel 1983). Subsequent climatic changes and possibly human predation (Owen-Smith 1990) caused the disappearance of many of the large mammalian species upon which these PaleoIndians depended. By the time modern climatic conditions prevailed (4,000 to 5,000 years ago), PaleoIndian adaptations had been replaced by subsistence hunting and gathering traditions known as Archaic. Evidence of this activity (baskets, grinding tools, projectile points) has been preserved in dry cave and shelter deposits on the SAM (Beckett 1983). Artifacts from periods after 200 A.D. (pithouses, pottery, and corn cobs) indicated a more sedentary lifestyle. The basin and range area was essentially abandoned after 1400 A.D., except for seasonal use (Breternitz and Doyel 1983).

When the Spanish arrived in southern New Mexico in 1540, most of the native peoples they encountered were settled in pueblos along the Rio Grande. The villages were subject to raids by nomadic Apaches, who had arrived in the area somewhat earlier. Raids on these villages and subsequent settlements continued into the 1880's when the last Apache bands were confined to reservations. Apache groups used the San Andres Mountains for seasonal harvesting, as a base from which to conduct their raiding activities, and later as a refugia from military persecution. In 1880 Chief Victorio fought the military in Hembrillo Canyon, a major east-west drainage in the center of the San Andres Mountains (Thrapp 1980, Sale and Laumbach 1989). Breastworks, pictographs and other artifacts are historical reminders of Apache occupation.

In the late 1800's, homesteaders established the first permanent ranches on the SAM (Eidenbach 1989). The 1880's brought an influx of Texas cattlemen to the area, but subsequent drought and overgrazing in the 1890's forced many ranchers to relocate, consolidate, or shift to sheep and goats. Settlement in the uplands continued through the late 1930's. Many ranches were run by smaller family outfits, raising angora goats, sheep, horses and cattle for their own use. Mining activity was also widespread but sporadic during this time (Eidenbach 1989). The principal ores mined were galena, copper, barite, and quartz (Sandoval 1979, Breternitz and Doyel 1983).

Government agencies began acquiring land in the area in 1912, when the Jornada Experimental Range, a branch of the U.S. Forest Service, was formed along the west flank of the mountains. In 1933, White Sands National Monument was established in the center of the Tularosa Basin. Eight years later, the San Andres National Wildlife Refuge (SANWR) was created near the southern end of the San Andres range. It encompassed about 230 km^2 of land, and was established primarily for the protection of desert bighorn sheep and other desert wildlife (Hoban 1986). The establishment of White Sands Proving Ground (later White Sands Missile Range) in 1945 had the largest impact on the San Andres Mountains. It effectively ended the historic period of mining and ranching in the area, and any other forms of public use. After only 50 to 60 years of settlement, the SAM were once again left essentially undisturbed by humans. Consequently, for the past 40 to 50 years, the mountains have been recovering naturally, making them, today, the largest single block of ecologically intact Chihuahuan Desert mountains remaining in southwestern North America.

2.7 HISTORY OF COUGAR EXPLOITATION

Ranchers and government trappers killed cougars on the SAM during the early 1900's to protect livestock (Eidenback and Morgan 1994). Mr. J. P. Wood, Jr.

(pers. comm.), who lived in Bear Den Canyon from 1935 to 1954 said that local ranchers kept cougars from becoming a significant problem by keeping them in "check" through trapping or hunting with hounds. U.S. Fish and Wildlife Service records (Munoz 1983) showed that 14 cougars were trapped on or near the SANWR for predator control purposes during 1940 to 1979. Another 5 cougars were killed on WSMR from 1966 to 1971 for the same purpose (Anderson and Taylor 1983). Sport hunters killed 8 cougars in the San Andres Mountains from December 1979 to February 1985, including 1 male (age not recorded), 4 females (ages not recorded), and 1 adult female and her 2 male cubs. During September 1980 to May 1984, the New Mexico Department of Game and Fish, the U.S. Fish and Wildlife Service Animal Damage Control (ADC) and the SANWR cooperated in cougar control to protect the remnant population of bighorn sheep (Sandoval 1979, Evans 1983). Trappers removed 42 cougars (approximately 34 were adults) during this period. Assuming a total of 40 adult cougars were killed during 43 months of exploitation on the SAM (December 1979 to February 1985), then the kill rate averaged 11.1 adult cougars per year. The kill rate for all 50 cougars (adults, subadults and cubs) averaged 13.9 cougars per year.

For the same purpose of predator control, an ADC trapper killed 13 other cougars on the Oscura Mountains during the 1 year period from October 1980 to October 1981. The Oscura Mountains are only 9 km northeast of the north end of the SAM and include about 673 km^2 of cougar habitat. No cougars were reported killed on the Oscura Mountains during our study. On the 272 km^2 Organ Mountains, which are connected to the south end of our study area, 5 cougars (3 males, 2 females) were reported killed from 1986 to early 1995 (NMGF records).

The original, rather crude records indicated that of the 40 cougars killed on the SAM for predator control purposes, 34 were adults (20 males, 14 females), 2 were yearlings (1 male, 1 female), and 6 were cubs (1 male, 5 females). Similar records for cougars taken on the Oscura Mountains indicated that 11 adults (6 males, 5 females) and 2 yearling females were killed. We inspected the skulls of 28 of the cougars (16 from the SAM, 12 from the Oscura Mountains) that were deposited at the Museum of Southwestern Biology (University of New Mexico, Albuquerque) to compare dental and suture characteristics with skulls of known-age and approximately known-age cougars we studied on the SAM. The estimated mean age for 9 adult males was 61.2 months (SD = 32.3), and the mean age of 11 adult females was 80.4 months (SD = 36). One male and 2 females were 13 to 18 months old. One male, 3 females, and 2 cougars of unknown sex were ≤12 months old.

Beginning in March 1985, and throughout this study, the SAM was closed to cougar hunting except for about 5% of the study area that lay outside of the west WSMR boundary. All tagged cougars on the entire SAM were protected . Furbearer trapping was also eliminated on the WSMR portion of the SAM for the duration of the study in order to minimize human-related deaths to cougars, especially cubs.

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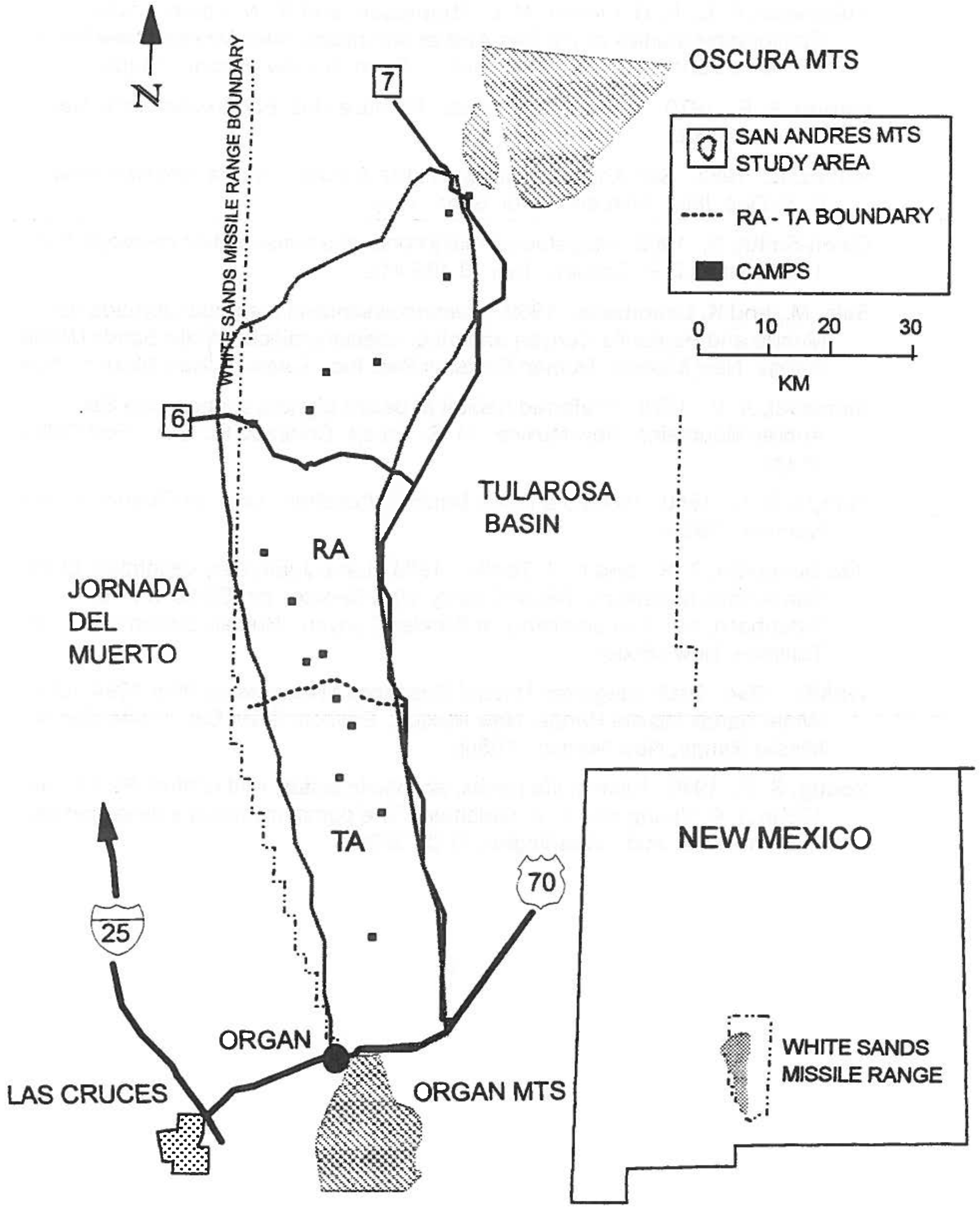

Fig. 2.1. The cougar study area (2,059 sq. km), San Andres Mountains, New Mexico, 1985-1995.

CHAPTER 3. COUGAR POPULATION DYNAMICS

by K. Logan, L. Sweanor, and M. Hornocker

Abstract: We studied cougar population dynamics on the 2,059 km^2 San Andres Mountains (SAM), New Mexico from August 1985 to March 1995. The study area was divided into a 703 km^2 treatment area (TA) and a 1,356 km^2 reference area (RA). We counted a total of 294 cougars, of which we captured and marked 241. Radio-collars were put on 126 cougars. We recorded a total of 13,947 cougar locations.

The cougar population was comprised of adults, subadults, and cubs; each age class comprised on average 0.58, 0.07, and 0.35 of the population. The oldest male and female cougars were about 152 months and 146 months, respectively. The sex structure of adults and subadults favored females; however, the ratios were not significantly different from 1:1 ($P > 0.10$). Cubs had a 1:1 sex ratio.

Cubs were born in every month, except February. A birth pulse occurred during July to September and coincided with the mule deer fawning season. Litters averaged 3.02 cubs for litters that were 9 to 49 days old. Gestation periods averaged 91.3 days. Birth intervals averaged 17.4 months when $\geq$1 cub survived to independence or to 12 months. Females associated with adult males for the first time at a mean age of 21.4 months old, and males associated with adult females for the first time at a mean age of 24.3 months old. Females conceived for the first time and bore their first litter at mean ages of 26.1 months and 29.1 months, respectively. Reproductive females bore 1 to 5 litters each. Twenty-six percent of the adult females produced 50% of the cubs and 71% of the recruits. Thirty-eight percent of breeding males were related to $\geq$45% of the progeny on the SAM, and $\geq$50% of the recruits.

Cubs had a maximum finite rate of survival of 0.68. Natural rates of survival were estimated by a maximum finite rate (cFRS) and the change in the mean number of cubs per litter (CN), which yielded rates of 0.71 and 0.73, respectively. Infanticide and cannibalism by male cougars was the greatest single cause of death in cubs (44%). Other causes included, starvation (37%), disease (11%), falls (4%), and coyote predation (4%). Subadult males and females had survival rates of 0.56 and 0.88, respectively. All subadults that died were killed by male cougars. Mean annual survival rates for adult males and adult females were 0.90 and 0.81, respectively. Intra-species strife was the single greatest cause of mortality in adult cougars (50% of male deaths and 53% of female deaths). Other causes were attributed to disease (17%), accidents (10%), old age (10%), snake bite (3%), and unknown (7%).

Offspring became independent from mothers at an average age of 13.4 months. Those that dispersed left their natal areas at an average age of 15.6 months. All males dispersed from their natal areas and most emigrated from the SAM altogether. Males dispersed an average distance of 101.3 km to their independent home ranges, and females

dispersed an average distance of 28.3 km to their independent home ranges. Dispersing cougars reached habitats in southern New Mexico within a 196 km radius of the SAM. Other females were philopatric.

Of the progeny that survived to adult age, about 83% of males emigrated and about 59% of females emigrated. The emigration rate from the SAM was about 3.8 males and 4.8 females per year.The rate of recruitment was about 3.6 males and 4.9 females per year.

On the TA, we experimentally reduced the adult cougars by 53% and independent cougars (adults + subadults) by 58% during December 1990 to June 1991. It took 31 months for the adult segment of the population to recover to the pre-treatment level. The replacement adults reoccupied the TA at the same sex ratio as before the treatment.

The cougar population on the SAM increased during the study as it recovered from effects of sport-hunting and control from 1979 to 1985. Density of adults estimated each January on the TA increased from 1.16 to 2.10 cougars/100 km^2 in the pre-treatment and treatment years (1988-1991) and from 0.84 to 1.99 cougars/100 km^2 in the post-treatment years (1992-1995). In the RA, January adult cougar densities increased from 0.94 to 2.01 cougars/100 km^2 during 1989 to 1995.

Observed exponential rates of increase (r) for adult cougars (using January estimates) in the TA during the pre-treatment and post-treatment years were 0.21 and 0.28, respectively. In the RA, the r was 0.11 for the years 1989 to 1995. When we calculated r for the RA in 4-year span similar to the TA, the r for 1989 to 1992 was 0.17 and the r for 1992 to 1995 was 0.05. This suggested a density dependent rate of increase. Gender-specific rates of increase indicated that adult females generally increased at higher rates than adult males. Observed exponential rates of increase calculated from annual adult density estimates produced similar patterns in r.

We thoroughly discuss our findings in relation to studies of other cougar populations in North America. Management implications are given.

3.1 OBJECTIVE

Our objective was to quantify the dynamics of the cougar population, including: sex and age structure, reproduction, survival rates, cause-specific mortality rates, dispersal, recruitment, density, and rates of increase. We experimentally removed adult and independent subadults from the TA to simulate a control action or extreme harvest so we could study the effects on the population. Cougars in the RA were not removed so we could study the dynamics of a portion of the SAM cougar population where human-induced changes were absent. This research design enabled us to gather basic information on cougar population dynamics which managers can use to develop management strategies for cougars to address a wide range of issues including: 1) control in areas where it may be absolutely necessary for the protection of livestock and humans; 2) setting harvest objectives for sport-hunting; and 3) long-term conservation.

3.2 FIELD METHODS

Cougar population dynamics were studied through year-round efforts to capture, mark, and radio-track cougars and document the presence of unmarked cougars. We attempted to capture and mark all of the adult cougars on the study area, and to capture and mark as many of the subadults and cubs as possible.

3.2.1 CAPTURING AND MARKING COUGARS

We established 16 base camps at strategic locations in the San Andres Mountains from which we searched for, captured and radio-tracked cougars (see Fig. 2.1). We systematically searched for cougar sign (i.e., tracks, scrapes, kills) along the primitive roads, in canyons and draws, and along ridgetops. Evidence of cougars was recorded in field journals and on 7.5 minute series (1:24,000 scale) U.S. Geological Survey topographic maps. We set snare lines to capture adults, subadults, and large cubs active on the area. Once we were satisfied we had captured and identified all of the cougars in an area served by a camp, we moved on the next camp to repeat the process in another part of the study area. We continued this process year-round and year after year for the duration of this study.

Adult and subadult cougars and large cubs were captured with foot-hold snares (Schimetz/Aldrich Spring Activated Animal Snare, Sekiu, Washington 98381). Snares were used as the main capture method instead of using trained dogs because trees where cougars could be safely bayed by dogs were scarce on the study area. We targeted unmarked or unknown cougars in the population and cougars that had radio-collars that were nonfunctional or had waning battery power. Cougars with well-functioning radio-collars were reliably identified in the field by radio-telemetry; therefore, we persistantly tried to avoid recapturing those cougars with foot-hold snares.

Snare assemblies were modified to minimize injuries to captured cougars and to avoid capturing non-target animals (e.g., mule deer, coyotes, gray foxes). We attached 2 to 4 heavy-duty rubber bungee cords to the drag line to absorb shock. A slide stop was attached to the foot loop by wrapping duct tape along 14 cm of the end of the foot loop adjacent to the angle-iron lock. This minimized the closure of the foot loop to 19 cm circumference; consequently, circulation to the cougar's foot was maximized and injuries were eliminated or minimized. In addition, small-footed non-target animals could pull free from the snares.

We tried to place snares at safe sites. Our site requirements included limber bushes with multiple basal stems for anchoring the double offset hook drag and a safety area of ≥5 m circumference around the anchor point. The safety area helped to minimize the probability that a struggling cougar might injure itself. It also minimized the chance that the snare cable would wrap around a stem or tree, and thus isolate the swivel to render it ineffective, and consequently, result in severe leg injury. In addition, snare sites were away from cliffs, trees, fences, cacti, yuccas, agaves, and water.

At the beginning of the study we tried using No. 4 1/2 steel traps (Woodstream Corp., Animal Trap Div., Lititz, Pennsylvania 17543) to capture cougars. However, we discontinued the use of traps after the first 5 months of the study because of the increased risk of injuries to cougars and especially non-target animals.

Snare sites were comprised of 1 to 6 snares that were set on paths used by cougars, at cougar scrape sites, or at cougar kill caches. Some snares were set in cougar activity areas and were baited with lures made of shiny pieces of tin dangling from string or wire. All snare sites were checked each day by 10:00 hours during spring and summer and by 12:00 hours during fall and winter to prevent excessive stress to captured cougars. In the hottest part of summer we sometimes checked snares twice per day. During particularly hot, cold, or snowy weather, we deactivated all snares.

Cougars captured in snares were immobilized with ketamine hydrochloride (100 mg/ml, Vetalar Parke-Davis, Div. of Warner-Lambert Co., Morris Plains, New Jersey 07950) dosed at about 12 mg/kg estimated body weight. The drug was injected remotely usually into the caudal thigh muscles by using a pole-syringe or by

3 to 5 ml capacity aluminum syringes fired from a CO_2-powered pistol. After induction, cougars were quickly removed from snares, their heads were covered, and their legs were tethered. If it was necessary to calm a cougar further, we injected xylazine hydrochloride (20 mg/ml, Rompun, Haver-Lockhart, Bay Vet Div., Cutter Laboratories, Inc., Shawnee, Kansas 66201) I.M. with a hand syringe; the dose was about 0.5 mg/kg body weight.

During hot ambient temperatures, we protected immobilized cougars from hyperthermia by placing them in shade and by cooling them with water. In cold temperatures, we protected them from hypothermia by placing them in sunlight and by wrapping them in a canvass or blanket.

Small cubs $\leq$72 days old were captured by hand or with a catch-pole; they were not given immobilizing drugs. In certain situtations, an unaggressive trained dog was used to help capture highly mobile cubs. In those cases, we used the dog only if there were nearby trees or boulders in which cubs could seek refuge.

Captured cougars were sexed, weighed, measured and thoroughly examined. Cougars captured early in the study were aged based on dental characteristics similar to approximately known age cougars described by Ashman et al. (1983:23-26). Photographs of cougars dentition, measurements of wear patterns on canines, and coloration were recorded. Later in the study we collected skulls, photographs, measurements, tooth wear descriptions and pelage descriptions of known age cougars in the population which were marked as cubs. We used those characteristics to age cougars with previously unknown life histories and, when necessary, to adjust the ages of cougars captured at the beginning of the study.

Captured cougars were marked by tatooing an identification number in 1 ear and by inserting a colored, numbered, plastic tag (Duflex Tags, Fearing Manufacturing Co., South St. Paul, Minnesota 55075) in the other ear. The tattoos marked the cougars for life. All adult and subadult cougars were fitted with a collar containing a 150 or 151 MHz transmitter with a mortality mode set to turn on after 6-13 hours of immobility (configuration MOD-500 transmitter with X-1 shock crystal and S6A mortality sensor, CLM collar, transmitter cast in polymer. Telonics, Inc., Mesa, Arizona 85204). Some of the cubs that were >31 days old also were radio-collared (configuration MOD-225 transmitter with S6A mortality sensor also by

Telonics, Inc.). We built cub collars ourselves out of expandable material that would break-away in ≤12 months.

3.2.2 RADIO-TRACKING COUGARS

Radio-collared cougars were relocated from the ground and from the air. Ground locations were obtained opportunistically by using portable radio receivers attached to hand-held directional antennas (TR-2 receiver with TS-1 scanner/programmer, RA-2A antenna, Telonics, Inc., Mesa, Arizona 85204). Ground telemetry locations were fixed by taking line-of-sight bearings on the strongest aural signal from the transmitter. Three or more bearings taken from different locations were mapped on 7.5 minute series topographic maps. Plotted bearings produced a triangle or polygon at the convergence. The approximate geometric center of the triangle or polygon was plotted to represent the location of the radio-collared cougar and was recorded as Universal Transverse Mercator Grid coordinates (U.T.M.s) to the nearest 0.01 km. Error around each location was estimated by using the distance (meters) from the center of the triangle or polygon to the most distant angle. This distance was used as the radius of a circle that contained the location of the cougar (see Saltz and Alkon 1985).

Telemetry flights were conducted once per week, unless poor weather or conflicts with WSMR activities precluded them. We attempted to locate all of the radio-collared cougars on the study area, as well as dispersing individuals, during each flight. Flights were made in fixed-wing aircraft (Cessna 182, 172 XP, or T337) with a directional antenna mounted on each wing strut. Antennas were connected via coaxial cables to the antenna switch box, receiver/scanner, and the aircraft intercom system. Aerial locations of radio-collared cougars were made at sites of peak aural signals which we determined by making at least 3 passes with the aircraft over peak signals. Because of variations in terrain at cougar locations and differences in flight altitude as influenced by terrain and air turbulence, we also estimated error at each location (radius of error circle). The center of the circle represented the cougar's location and was recorded as U.T.M. coordinates.

Accuracy of radio-telemetry locations was tested on an occasional basis throughout the study period, either by locating test collars, subsequently walking in on cougars to observe them visually, finding cougar sign at the locations, retrieving dropped collars, or finding dead cougars. During the first 3 years of the study, we tested acuracy during 8.1% of radio-telemetry locations; in all instances the radio-collars were within the error radii of the locations (Sweanor 1990).

At both radio-telemetry locations with small error and actual cougar locations, we recorded vegetation cover types and terrain features. We recorded elevation (20 foot intervals taken from 7.5 minute series topographic maps, converted to meters) aspect, and percent slope (measured with a USGS Topo Map Land Area and Slope Indicator, Reproduction Specialties, Inc., Denver, Colorado 80222).

Radio-collared cougars also were used to quantify survival and causes of mortality. When a dead cougar was found, the carcass and the site were examined carefully to help determine cause of death. In those cases where disease may have been present, we collected tissue samples which were later examined by a veterinary diagnostic laboratory.

3.2.3 EXPERIMENTAL REMOVAL OF COUGARS

We removed cougars from the 703 km^2 TA from 12 December 1990 to 21 June 1991 to reduce the adult and subadult cougar density. No cougars from the 1,356 km^2 RA were removed. Thus, we were able to determine the effects of removal on cougar population dynamics by studying the dynamics of 2 subpopulations: one that was exploited to simulate a severe control action (TA), and one that was allowed to continue functioning under natural conditions (RA).

The experimental removal also allowed us to address our other research objectives, including the effects of removal on cougar social structure (discussed in Chapter 4) and the relationship between cougars, desert mule deer and desert bighorn sheep (see Chapters 5 and 6). Because cougars were removed from the same area where all the radio-collared deer and all but 2 of the radio-collared sheep lived, we could quantify some of the effects of cougar reduction on survivorship and causes of mortality in the radio-collared samples of deer and sheep.

The cougars that were removed from the TA became the subjects of another study on the feasibility of using translocation as a cougar management tool. This research is presented in Chapter 7.

3.3 ANALYTICAL AND STATISTICAL METHODS

3.3.1 CLASSIFYING COUGARS

Cougars were classified as adults, subadults, and cubs. Adults were cougars that were capable of successful breeding. Subadults were independent of their mothers, but were not capable of successful breeding. Cubs were offspring that still were dependent on mothers. Residents showed site attachment (continuous use of an area over time). The area where a cougar restricted the majority of its movements was considered its home range. A cub that became a subadult and left the boundaries of its natal home range was considered a disperser, whereas progeny that did not disperse from their natal home ranges were philopatric. Any cub that established a home range post independence that overlapped >5 percent of its natal home range (based on the 90% Minimum Convex Polygon) was considered philopatric. Immigrants were new arrivals on the SAM who subsequently established residency. Recruits were either progeny born on the SAM or immigrants to the SAM that entered the resident adult segment of the SAM population. An emigrant was an individual that dispersed completely outside of the SAM.

3.3.2 CHARTING THE POPULATION

We used data on captures, radio-telemetry, tracks, and visual observations of cougars to chart the cougar population each year. Initially, all adult and subadult cougars captured for the first time were entered on the chart beginning with the day of capture. Cubs were entered on the chart at their estimated birth date.

We assumed that all independent cougars captured for the first time and that were <36 months old had just entered the population. However, cougars captured for the first time and $\geq$36 months old were assumed to have entered the population as adults at an earlier date. We defined entry dates for the latter group by using criteria based on empirical data gathered from the population, including: (1) ages of known-age and approximately known-age males and known-age females when they apparently reached adulthood; and (2) the mean ages of male and female cougars <36 months old captured for the first time. Four female cougars that were not captured were charted into the population because we were able to monitor their movements through a combination of tracks (all 4 females), associations with radio-collared offspring (2 females), associations with radio-collared males (1 female), and visual observations of a female and her cubs (1 female). Two other adult (24-30 mo. old) female cougars were never radio-collared because they were found as mortalities. It is possible the older female was marked, but because she was severely decomposed when found, we did not find an identifying eartag or tattoo. We charted the 2 females into the population at the dates they died.

We estimated the total number of adult cougars utilizing the TA and RA each year by counting all marked adults, adults observed indirectly (above), and adults back-logged onto the population chart because they were $\geq$36 months old when captured.

We developed a confidence rating (CR) from the chart to estimate the minimum proportion of adult cougars documented per year (January-December). The equation was:

$$CR = 1 - \frac{BL_{\text{year } i}}{BL_{\text{year } i} + C_{\text{year } i}}$$

where,

$BL_{\text{year } i}$ = the number of cougars back-logged into year_i;

$C_{\text{year } i}$ = the number of cougars actually detected (radio-collared or observed indirectly) during year_i.

Our intent was to document $\geq$90% of the adults present per year.

The chart of the cougar population facilitated estimates of the following parameters:

(1) Proportion of adult cougars radio-collared in the TA and RA each year. Applications:
   a. Quantification of the span of years where the mean proportion of adult cougars monitored in the TA and RA was $\geq$0.90.
   b. Quantification of adult cougars $\geq$36 months old that we probably "missed" during annual capture efforts.

c. Quantification of marked adult cougars monitored + adult cougars "missed" for estimates of adult cougars on the TA and RA that approached 100% of adult cougars that probably were present each year.

(2) Proportion of recruits comprised of SAM progeny and immigrants.

3.3.3 DENSITY

Charting the cougar population also facilitated population density estimates. Cougar density on the SAM was based on the known area utilized by resident cougars, primarily radio-collared individuals. We estimated cougar density in the TA and the RA using 2 methods: 1) cougar density each January; 2) annual cougar density.

Radio-collared cougars that lived along the TA-RA boundary, or moved in and out of the SAM at the north and south ends of the study area, were included in the TA and/or RA based on the proportion of their aerial locations recorded in each area during each 12 month period (January-December). For example, a cougar that was located 15 times in the TA and 28 times in the RA during a particular year would be assigned values of 0.39 in the TA and 0.61 in the RA for that year. Cubs were included in the TA and RA in identical proportions as their mothers. For the annual estimates we also determined the proportion of time per year that cougars were present on the SAM. For example, a cougar that apportioned its annual activities by 75% in the TA and 25% in the Organ Mountains, but was alive for 60% of the year was assigned a value of 0.45 in the TA for that year.

The equations for density estimates were as follows:

(1a) $$\text{Adult cougars each January}/100\ \text{km}^2 = \frac{\text{No. adults present during January of year}_i}{100\ \text{km}^2}$$

(1b) $$\text{Total cougars each January}/100\ \text{km}^2 = \frac{\text{No. adults + subadults + cubs present during January of year}_i}{100\ \text{km}^2}$$

Applications:

a. Population estimates for density and composition (i.e. cougars/100 km^2, proportions of adults, subadults and cubs in the population; sex ratios; age structure).
b. Regression analyses for the observed exponential rates of increase.
c. Quantification of the proportion of females raising cubs per year. Set in January to correspond with the New Mexico cougar hunting season (December-March).
d. Comparisons with published density estimates for other cougar populations.

(2) Adult cougars/100 km^2 in year$_i$ =

$$\frac{\text{Sum of proportions of each year each adult was present during year}_i}{100 \text{ km}^2}$$

Applications:

a. Adult density comparisons between years.
b. Adult density comparisons between the TA and RA.
c. Regression analyses for the observed exponential rates of increase.
d. Regression analyses with deer annual mortality rates and cougar predation rates.
e. Regression analyses with sheep annual mortality rates and cougar predation rates.

Obtaining an estimate of the density of adult cougars per year allowed us to examine relationships between cougars, deer and sheep. These analyses were important for meeting Objective 3 of our research and are discussed in detail in Chapters 5 and 6.

3.3.4 REPRODUCTION

We quantified the frequency of cougar births per month to identify potential birth pulses. Fecundity was quantified by the number of cubs per litter, the number of litters per female, and birth intervals. Gestation was determined by counting the number of days from the first day that female and male pairs were first observed in association to the birth date of resulting litters.

3.3.5 SURVIVAL AND MORTALITY

We estimated natural survival rates for cub, subadult and adult cougars (man-caused sources of mortality were excluded).

Cub survival rates were estimated using 2 methods. First, we calculated the maximum finite rate of survival (cFRS):

$$\text{cFRS} = \frac{\sum \text{cubs at Obs}_1 - \sum \text{cubs not present at Obs}_n}{\sum \text{cubs at Obs}_1}$$

where,

Obs_1 = first visual observation of cubs within a litter;

Obs_n = subsequent observation of a litter.

We assumed that cubs that disappeared from litters during subsequent observations had died.

Second, we calculated a maximum cub survival rate by calculating the change in the mean number of cubs per litter (CN):

$$\text{CN} = \frac{\text{Mean no. cubs in weaned litters}}{\text{Mean no. cubs in nursing litters}}$$

Weaned and nursing litters were discrete groups. We assumed that the smaller number of cubs in weaned litters was due to post-natal mortality.

We estimated the finite rate of survival (sFRS) for a sample of subadult cougars that were radio-collared during the study, where:

$$\text{sFRS} = \frac{\text{No. subadults that survived to adulthood}}{\text{No. radio-collared subadults monitored}}$$

A Chi-square 2X2 contingency table (Ott 1988) was used to test for significant differences between subadult male and female survival.

We estimated annual survival rates for radio-collared adult cougars using 2 methods. First, we estimated the adult finite rate of survival (aFRS):

$$\text{aFRS} = \frac{\text{No. adults that survived in year}_i}{\text{No. adults at the beginning of year}_i}$$

Second, we analyzed adult survival using the computer program MICROMORT (Heisey and Fuller 1985). This was our principal method because it was more quantitative, it allowed us to easily test for significant differences in rates, and results were comparable with survival information reported in other cougar studies.

Annual intervals began on January 1 each year. The program calculated annual survival rates from a daily survival rate (the probability of an animal surviving to 1 day). MICROMORT also calculated the survival rate over a span of intervals (years) by multiplying together the interval rates.

Radio-collared adult cougars were entered into the MICROMORT analyses on the days they were captured; subadults were entered into the analyses on the dates they reached adulthood. Mortality dates were based on radio-telemetry data and the state of decomposition of dead cougars. We reported a maximum rate of survival by assuming cougars with radio-transmitters that became non-functional were still alive. Only 1 out of 23 cougars could not be accounted for after transmitter failure. The other cougars either were recaptured and recollared, or, toward the end of the study, they were accounted for by tracks in their home ranges and their consistent ability to avoid the snares set for them. We estimated the survival rates of cougars with non-functional transmitters by counting to the last day we located the cougars before their collars quit. Cougars that died from human causes were included up to the day they died because the cougars were susceptible to other natural causes of mortality up to that day.

We tested for significant differences in adult survival rates between males and females (annual and span rates) and between same sexes in the TA and RA using Z-tests (Pollock et al. 1989):

$$Z = \frac{r_1 - r_2}{(V_1 + V_2)^{1/2}},$$

where r_1 and r_2 are the rates being compared and V_1 and V_2 are the variances of the rates. We estimated survival rates and made statistical comparisons only for those years where there were ≥7 radio-collared cougars in each sex.

We quantified all cougar mortalities which were documented during the entire study period. Cause-specific mortality rates were calculated as the proportion that each cause contributed to the total. We used the non-parametric S test for randomness (Noether 1976:193-195) to test the null hypothesis that intra-specific killing among subadult and adult cougars is random. The alternative hypothesis would be a monotone trend related to adult cougar density. Only data from the RA was used for this test to eliminate the potentially confounding effect of cougar removal on the TA.

3.3.6 DISPERSAL

Age at independence and dispersal was determined for a small sample of radio-collared cubs. A cub was reclassified as an independent subadult on the first date it was no longer located with its mother. Age at dispersal was the age at which a newly independent subadult made its first movement outside its natal home range without subsequently returning.

All dispersal distances and azimuth directions were calculated based on UTM grid coordinates (White and Garrott 1990). Dispersal distances of progeny born on the SAM were determined, when possible, by calculating the straight line distance from the arithmetic center of a progeny's natal home range (NAC) to the arithmetic center of its independent home range (IAC). All telemetry locations obtained on the cub or its mother during the 12 month period after the cub was born were used to determine its natal home range. The subsequent independent home range was determined by obtaining radio-locations on the cougar over a 12 month period after it showed site attachment to an area. When complete information was not available, we calculated dispersal distances based on one of the following combinations: NAC to mortality site; NAC to last telemetry location; capture site to IAC; capture site to mortality site; capture site to last telemetry location. We expected the dispersal distances calculated for animals with incomplete dispersal information would be shorter, because many of these cougars probably had not completed their dispersal movements, or they had been captured after they had already dispersed some distance.

Dispersal direction was determined by recording the angle of direction from a cougar's NAC or capture site to its IAC, mortality site or last location. Hypotheses concerning direction of movement were tested using circular distribution hypotheses tests (Zar 1984).

3.3.7 EMIGRATION

To estimate emigration, the emigration rate of tagged cubs was calculated, then applied to all detected cubs born during a 5.1 year period, 1 February 1990 to 23 February 1995. The equations were:

$$ER_t = \frac{\text{No. surviving tagged cubs x sFRS - SAM recruits}}{\text{Total No. tagged cubs}}$$

and,

$$E/yr = \frac{\text{No. cubs (tagged \& untagged) detected over 5.1 yr. period x } ER_t}{\text{5.1 year period}}$$

where:

5.1 yr. period = 1 February 1990 to 23 February 1995 (see recruitment below),
sFRS = subadult finite rate of survival for the SAM,
ER_t = emigration rate of tagged cubs,
E = total number of emigrants from the SAM.

Since the sFRS was used to calculate the emigration rate, these emigrants were considered successful (i.e. they survived to adulthood).

3.3.8 IMMIGRANT AND PROGENY RECRUITMENT

Recruitment was quantified based on a 5.1 year time span (1 February 1990 to 23 February 1995) and progeny born from 1 February 1988 to 19 November 1992. We chose these time frames because: 1) it gave sufficient time for untagged progeny born just prior to and at the beginning of the study to either die, emigrate or be recruited; 2) we had marked >90% of the adult population by February 1988 and consequently could detect the presence of all new litters or immigrants; and 3) cubs born between 1 February 1988 and 19 November 1992 became adults and potential recruits during the 5.1 year time period.

3.3.9 RATES OF INCREASE

Observed exponential rates of increase were calculated for the adult cougar populations in the TA and the RA using regression analyses. Density, expressed as numbers of adults in the TA and the RA and converted to the natural log (ln), was the dependent variable (y); time was the independent variable (x) scaled so the first year was equal to 1 (Caughley 1978, Van Ballenberghe 1983).

3.3.10 OTHER STATISTICAL TESTS

Chi-square analyses (Ott 1988) were used to test for differences in sex ratios. Parametric t-tests (Ott 1988) were used to test for differences between means when samples were large (i.e. when the samples approached the known population). A non-parametric equivalent of the t-statistic (Wilcoxon rank sum test, Zar 1984) was used for small samples because of the apparent non-normality of the data. Experimental errors were controlled at the 0.10 level of significance.

3.4 RESULTS

3.4.1 RESEARCH EFFORTS

Between 6 August 1985 and 31 March 1995 HWI personnel spent a total of 2,445 field days studying cougars, desert mule deer, and desert bighorn sheep on the SAM. On average, we spent 254 days per year in the field (range = 230-289). Normally, 4 people worked on the study full-time; we accumulated about 9,780 total person-days in the field. During 370 flights in light-fixed wing aircraft, we logged 1,852.1 hours while locating 126 radio-collared cougars (10-40 cougars per flight). We recorded a total of 13,947 daily locations of cougars; 9,614 (69%) were aerial locations and 4,333 (31%) were ground locations. We visually observed cougars at 337 ground locations (not including captures).

3.4.2 COUGAR CAPTURE RECORD

We captured and marked 241 individual cougars. Live cougars were handled a total of 396 times. Seventy-eight cougars (36 males, 42 females) were initially captured with foot-hold snares. Another 163 cougars (81 males, 82 females) were cubs when we initially captured them by hand.

We accumulated 40,533 snare days at 1,212 different snare sites to capture 108 individual cougars (48 males, 60 females) a total of 210 times with foot-hold snares (Table 3.1). Captures of marked cougars (132) out-numbered cougars captured for the first time with snares (78). On average, 212 snare days were needed to capture a cougar (range = 107-452).

Four adult cougars (1 male, 3 females) suffered severe injuries while they were caught in foot-hold snares and they had to be euthanized (3.7% of individuals captured by snares, 1.9% of all snare captures). A 14-month-old female cub suffered a broken leg while she was caught in a foot-hold snare. She was treated, rehabilitated, and released onto her natal area where she later established a home range and raised cubs.

The deaths of 9 cubs in 3 litters resulted from our research activities. One adult female that had to be euthanized as a result of capture injuries was apparently raising 4 newborn cubs (based on productive mammaries and placental scars). The cubs could not be located; they surely starved to death. A first time mother apparently abandoned all 4 of her 42 day old cubs after we marked them. One 6-month-old female cub died from septicemia after her expandable radio-collar slipped over her front leg and caused an open wound.

3.4.3 DEFINING THE ADULT POPULATION

Empirical data from known-age and approximately known- age radio-collared cougars were used as criteria to back-log those adult cougars into the population which were ≥36 months old at first capture. Thus, we adjusted the estimates of the adult cougar population to include those individuals that we had probably missed during previous years.

For female cougars, we used 21 months of age to define adulthood and the estimated age that females entered the adult population. Those criteria were based on: (1) the mean age of 7 known-age females when they first associated with adult males was 21.4 months (SD = 3.1); (2) the mean age of 18 approximately known-age female immigrants that were <36 months old when first captured was 21.4 months (SD = 2.6).

For male cougars, we used 24 months of age to define adulthood and the estimated age that males entered the adult population. Those criteria were based on: (1) the mean age of 1 known-age and 4 approximately known-age male cougars when they first associated with adult females was 24.3 months (SD = 2.5); (2) the mean age of 7 known-age males when they arrived on the area where they established their first territory was 23.9 months (SD = 6.3); (3) the mean age of 16 approximately known-age male immigrants that were <36 months old when first captured was 23.3 months (SD = 3.4).

The number of adult cougars (those $\geq$36 months old when first captured) back-logged into the population ranged from 0-1 per year in the TA and 0-4 per year in the RA (Table 3.2). Consequently, we chose to make appropriate comparisons in cougar population dynamics between the TA and the RA during the span 1988-1994 when the confidence rating (CR) for the TA averaged 0.97 and the CR for the RA averaged 0.93. All population tables and charts show the adjusted estimates for the adult cougar population. Consequently, between 1988 and 1994, annual estimates of the number of adult cougars on the TA and the RA probably approached 100% of the adult population actually present.

3.4.4 SEX STRUCTURE

Adults

The male:female (M:F) ratio of adult cougars counted per year in the TA (1988-1994) averaged 1:1.4 (Table 3.3). In the RA, the adult M:F ratio averaged 1:1.5. None of the annual comparisons of adult sex ratios either in the TA or the RA were significantly different from 1:1 ($X^2 < 2.71$, 1 d.f., $P > 0.10$).

Adult M:F sex ratios computed from January population estimates each year from 1989 to 1995 produced very similar results (Table 3.4). Mean sex ratios for the TA and the RA were 1:1.5 and 1:1.4, respectively. None of the annual comparisons of adult sex ratios in either the TA or the RA were significantly different from 1:1 ($X^2 < 2.71$, 1 d.f., $P > 0.10$).

Subadults

Because of the small number of subadults in each January population estimate, we quantified M:F ratios from the total number of subadults present during the January population estimates from 1988 to 1995 in the TA and from 1989 to 1995 in the RA. Subadult sex ratios for the TA (n = 5-6 males, 10-11 females) and the RA (n = 8 males, 10 females) were 1:1.7-1:2.2 and 1:1.2, respectively. None of the ratios were significantly different from 1:1 (TA: $X^2 = 1.0$ or 2.25, 1 d.f., $P > 0.10$); RA: $X^2 = 0.22$, 1 d.f., $P > 0.10$).

Progeny

We observed a total of 210 cubs in 76 litters. Three other litters with about 10 cubs died shortly after birth, before we were able to examine the cubs. We classified 182 cubs by their sex in nursing and weaned litters in which all the cubs were sexed. Of 148 nursling cubs from 50 different litters, 75 were males and 73 were females, the equivalent of a 1:1 sex ratio. Cubs in this group were observed at nurseries when they were 9-49 days old ($\bar{x} = 31.6$, SD=8.6). In another 15 weaned litters, in which cubs were 52-427 days old ($\bar{x} = 198.9$, SD=121.6), there were 14 males and 20 females; but the sex ratio was not significantly different from 1:1 ($X^2 = 1.06$, 1 d.f., $P > 0.10$).

3.4.5 AGE STRUCTURE

The Population

Three broad age classes, including adults, subadults, and cubs, were quantified for cougar population estimates made each January from 1989-1995 in the TA and the RA. In the TA (Table 3.5), adult males and females comprised a mean proportion of 0.23 (SD = 0.07) and 0.33 (SD = 0.08) of the population, respectively. Total adults comprised a mean of 0.56 (SD = 0.13), subadults a mean of 0.10 (SD = 0.09), and cubs a mean of 0.34 (SD = 0.10) of the population. Discounting the first January population estimate following the experimental removal of cougars in the TA (1992), the mean proportions of the major age classes in the population were: adult males = 0.25 (SD = 0.06), adult females = 0.36 (SD=0.05), total adults = 0.61 (SD=0.08), subadults = 0.07 (SD=0.07), and cubs = 0.32 (SD=0.10).

In the RA (Table 3.6), adult males and adult females comprised a mean proportion of 0.26 (SD = 0.03) and 0.35 (SD = 0.07) of the population, respectively. On average, adults comprised 0.61 (SD = 0.09) , subadults 0.06 (SD = 0.02), and cubs 0.33 (SD = 0.08) of the population.

The proportions of each age class in the TA and RA subpopulations each year are depicted in Fig. 3.1. Based on the 3 broad age classes, the average annual age structure in the TA and the RA were very similar (Fig. 3.2). Table 3.7 combines the TA and RA age composition data and summarizes the mean proportions of each age class for the entire cougar population on the SAM.

Adult Cougars

Ages (in months) of adult cougars in the TA and RA were estimated in January each year for the 7 year period 1989 to 1995 (Table 3.8). In the TA, adult males were generally older than adult females in the first 5 years, but not in the last 2 years. Male mean ages ranged from 46.7 to 97.7 months and female mean ages ranged from 50.4 to 80.5 months. The mean ages of adult males and females in the TA were not significantly different in 4 of the 7 annual comparisons ($P > 0.10$); however, male ages were significantly greater in 1989 and 1990, and female ages were significantly greater in 1995 ($P < 0.10$).

Ages of adult cougars in the RA had a similar profile to the TA, with males being generally older than females in the first 6 years but not in the last year (Table 3.8). Mean ages of adults ranged from 50.9 to 68.2 months for males and 43.9 to 65.9 months for females. Mean ages of adult males and females were not significantly different in 6 of the 7 annual comparisons ($P > 0.10$), but male ages were significantly greater in 1 year (1993; $P < 0.10$).

The mean ages of adults (males and females combined) in the TA were greater than the mean ages of adults in the RA in all years except 1995 (Table 8). However, the mean ages of adult cougars in the TA and the RA were not significantly different in 6 of the 7 annual comparisons ($P < 0.10$). The oldest estimated age for a male and a female cougar was 152 months and 146 months, respectively.

3.4.6 REPRODUCTION

Natality

We documented the birth of 220 cubs from 79 litters by 39 female cougars. Of those cubs, we captured and marked 174 (79%). Of the 46 cubs that were not marked, we know of about 10 cubs from 3 litters that died shortly after birth.

The mean litter size for 53 litters which we first observed 9 to 49 days post partum ($\overline{x}$ = 32.3, SD = 8.9) was 3.02 cubs (SD = 0.7, range = 2-4). All were nurslings. Twenty-six of the 53 litters were observed at birth nurseries (where the cubs were born); the other 28 litters were observed at secondary nurseries (nurseries used after mothers moved cubs away from birth nurseries).

Another 21 litters were first observed 52-427 days after birth ($\overline{x}$ = 175.7, SD = 112.0). Litter size for those weaned cubs averaged 2.19 (SD = 0.8, range = 1-3).

Timing Of Births

We were able to determine the month of birth for 78 litters (Fig. 3.3). Litters were born in every month except February. The greatest number of litters were born in August and September, each with 11. July had the second greatest number with 10 litters. Together, these 3 months contained 41% of the litters. The occurrence of cougar litters in those 3 months was significantly greater than expected ($X^2 = 16.02$, $P < 0.001$, 1 d.f.); the timing coincided with the birth period for mule deer fawns and the rainy season on the SAM, which occurred from July to September each year.

Mating, Gestation And Birth Intervals

Matings between radio-collared cougar pairs that resulted in cubs were documented on 35 occasions. Suspected mating associations were generally found using radio-telemetry, then often confirmed with further evidence such as tracks, shared kills, vocalizations, visual observations, and the subsequent birth of litters. Pairs that produced litters were together for 1 to 4 days. We documented 1 pair in an apparent breeding association for 6 days, but it did not result in cubs. Three females associated with 2 different males during the same estrus periods. One female associated with 1 male for 2 days and a different male during 3 subsequent days, suggesting a receptive period of 5 days. Associations between radio-collared adult males and 7 different females suggested estrus cycling at 13 to 33 day intervals ($\overline{x}$ = 21; see Maturity and First Litters in this Chapter and Male-Female Interactions in Chapter 4 for more information on cycling). The mean gestation period for 31 litters was 91.3 days (SD = 3.9, range = 83-103).

We quantified the length of 36 birth intervals. Birth intervals where at least 1 cub in the first litter survived to independence (n = 15) or to 12 months of age (n = 1) averaged 17.4 months (SD = 2.5, range = 12.6-22.1). For 15 other birth intervals where we did not know the fates of the first litter with certainty, the mean was 16.9 months (SD = 3.4, range = 12.2-22.5). For 5 females that lost their first litters, it took them an average of 101.0 days (SD = 116.9, range = 24-308) to successfully rebreed.

Maturity And First Litters

We used the timing of first male-female associations for known age and approximately known age female and male cougars to determine the ages of sexual maturity. Only females that eventually produced cubs were included in this analysis. Seven females with known birth dates associated with adult males for the first time when they were an average of 21.4 months old (SD = 3.1, range = 18-27). Of those 7 females, 2 produced litters that resulted from those associations. Three other females had 4 subsequent associations with adult males that were a mean of 22.8 days (SD = 8.7, range = 13-34) after the first association, which may indicate the females were in estrous. The mean and range of days between associations that we observed was similar to the mean and range of the length of estrous cycles for captive cougars compiled by Anderson (1983:31). Another 4 females with approximately known ages associated with adult males for the first time when they were an average of 22.3 months old (SD = 2.6, range = 20-25).

One known age male and 5 approximately known age males associated with adult females for the first time when they were an average of 24.3 months old (SD = 2.5, range = 21-27). At least 2 of those associations resulted in live litters 91 and 92 days later.

We compiled data on 12 known age female cougars to determine the ages of first successful reproduction. The females conceived apparently for the first time at a mean age of 26.1 months (SD = 6.0, range = 19-37). They bore their first live litters at a mean age of 29.1 months (SD = 6.0, range = 22-40 months). Another 8 females of approximately known ages conceived successfully at a mean age of 26.0 months (SD = 9.4, range = 15-42). They produced their first live litters at a mean age of 29.0 months (SD = 9.4, range = 18-45).

We captured and examined all of the cubs (nurslings 9-39 days old, $\bar{x}$ = 30.1, SD = 9.9) of 8 known age females that produced litters for the first time. The mean size of those first litters was 3.38 cubs (SD = 0.7, range = 2-4), which was not significantly different than the mean of 2.95 cubs for 22 subsequent litters born by 14 females (two-tailed t-test, t = 1.43, 28 d.f., *P* = 0.17). However, a one-tailed t-test indicated that first litters were significantly larger than subsequent litters (*P* = 0.08).

Reproductive Success

Out of 52 adult females, 39 (75%) produced live cubs. Of the 13 which did not, 7 died, 2 were translocated, and 4 were 26 to 42 months old ($\bar{x}$ = 35, SD = 8.2) at the end of the study. During each January from 1988 through 1994, an average of 73% (SD = 9.7, range = 63-86) of the adult females were raising cubs.

Reproducing females bore 1 to 5 litters each, and 10 females (26% of reproducing females) produced 50% (n = 110) of the cubs. The same 10 females produced 71% (17 of 24) of the recruits (cougars surviving to adulthood) comprised of the marked progeny born on the SAM. The productivity of 2 of the females was reduced because we translocated one and one died as a result of capture injuries.

Nine females produced 79 cubs in 27 litters, out of which 12 first filial generation (F_1) females produced 54 cubs in 17 litters (second filial generation or F_2). Consequently, the 9 parental generation (P_1) females were related to at least 63% (133 of 210) of the progeny we documented on the SAM.

Of the 34 adult male cougars we monitored during the study, 16 were documented in apparent productive breeding associations with females. Because cubs were born a gestation period later ($\bar{x}$ = 91.3 days), we assumed that the males first to associate with the females were the sires. Those matings resulted in 94 live cubs in 31 litters, comprising 43% of all the cubs and 39% of all the litters we documented. Five other cubs in two litters were not viable. Six adult males (38% of documented breeders) had 9 F_1 offspring (8 females, 1 male) that produced 45 F_2 progeny in 15 litters. Two adult males mated with their daughters on 3 occasions resulting in 10 cubs. The 6 P_1 males were related to at least 45% (100 of 220) of the progeny we documented on the SAM; they sired at least 50% (12 of 24) of the recruits comprised of marked progeny on the SAM.

3.4.7 MORTALITY AND SURVIVAL

Man-caused Mortality

The 4 adult cougars that died as a result of our research methods (see Cougar Capture Record above) included 3 females and 1 male. The 3 females represented 5% of the adult females we documented on the SAM during the study. The females ranged in age from about 60 to 69 months old. At the time of their deaths, one female was raising three 14-month-old cubs, and 1 female was raising about 4 newborn cubs. The adult male that died was about 38 months old. He represented 3% of adult males we documented on the SAM.

The 9 cubs that died as a result of our research activities represented 4% of the cubs we observed on the SAM. They ranged in age from newborn to 6 months old. One was a male, 2 were females; the remaining 6 were not handled to determine their sex.

Even though our study area was closed to hunting and trapping, cougars that lived along the western boundary were vulnerable to poachers. One unmarked female, about 24 months old, was killed by a cougar hunter. A 31 month old (known age) radio-collared female died as a result of severe injuries to her left fore foot caused by a steel leg-hold trap. A third radio-collared female was 26 month old (known age) when she was shot by a mule deer hunter. These three deaths caused by poachers represented 5% of the adult females we documented on the SAM.

Natural Mortality

Cubs

We documented 62 out of 211 cubs that died or disappeared from cougar families, resulting in a maximum finite rate of survival (cFRS) of 0.71 (149/211). The change in the mean number of cubs per litter (CN) method was calculated using 21 weaned litters with 46 cubs that were 52 to 427 days old and 53 nursing litters with 160 cubs that were 9 to 49 days old. The CN method produced a maximum cub survival rate of 0.73 (2.19/3.02), which was very similar to the cFRS. When research-related cub mortality was included, the cub survival rate on the SAM declined to 0.68 (149/220).

Of the 62 cubs that died or disappeared, we could identify the sexes of 38, including 20 males and 18 females. The other 24 cubs could not be clearly distinguished from living siblings.

Although 35 cubs disappeared from families, we were able to assign the cause of death to 27 other cubs (Fig. 3.4). Infanticide and cannibalism by male cougars caused 44% (12 cubs in 6 litters) of deaths. Ages of cougar-killed cubs ranged from 1.1 to 5 months ($\overline{x}$ = 2.1, SD = 1.1). Starvation resulted in 37% (n = 10) of cub deaths. Starvation of 5 cubs (all 5 mo. old) occurred because 2 mothers were killed by male cougars. Three 36 day old nurslings starved 8 days before their mother died of an undiagnosed disease. Two 5-month-old cubs probably starved not long after their mother died apparently while trying to kill a deer. Disease which caused diarrhea and dehydration resulted in 11% of deaths (3 cubs in 1 litter, 57 days old). A fall from a cliff killed 4% (n = 1, 59 days old) and coyotes killed 4% (n = 1, 6 mo. old) of the cubs.

Two female cubs that were orphaned at 7.5 and 9.8 months old survived. The former became a reproducing adult in an area overlapping her natal home range; the latter was killed by a male cougar when she was 18 months old.

Subadults

Survival rates and causes of mortality were determined for a relatively small sample of 25 radio-collared subadult cougars that we monitored while they were independent from mothers and until they became adults or died. Nine males were monitored for 1,797 days and 16 females were monitored for 2,590 days. Ages ranged from 8 to 27 months.

Subadult males had a survival rate of 0.56 which was significantly lower than the female survival rate of 0.88 ($X^2 = 3.35$, 1 d.f., $P<0.07$). Four males and 2 females died when they were 14.3 to 18.0 months old ($\overline{x}$ = 15.7, SD = 1.5). All were killed by male cougars (Fig. 3.4), but none were eaten. All subadults died as a result of bites that penetrated the braincase and/or the frontal region of the skull and cervical vertebrae.

Two of the male subadults were killed on their natal areas. One was killed by his sire at a mule deer cache; the other was killed by a new immigrant male at a mule deer cache (stomachs of both dead cougars were full of deer tissues).

The other 2 males were killed after they dispersed from their natal areas. One male was independent for only 19 days and had dispersed 42.2 km north of his natal area (distance = arithmetic center of natal area to death site) and was still on the SAM. His death probably was associated with a kill; the cougar had a stomach full with the remains of a newborn calf oryx. The other subadult male was independent for 82 days and had dispersed 133.8 km northeast of his natal area by crossing the Tularosa Basin and then onto El Capitan mountain. No evidence of a prey kill was found around his death site and his stomach was empty.

One of the subadult females was orphaned at 10 months of age when her mother was killed by an immigrant male cougar. She died at 18 month old, killed by the same male cougar on the SAM 16.3 km southwest of her natal area. No evidence of a prey kill was found and the female's stomach was empty. The other subadult female was independent for about 58 days when she was killed on her natal area by a male cougar. The death occurred at a cache of a mule deer that apparently was killed by the female. Her stomach was full of deer tissues.

In addition, we documented the mortalities of 1 marked (ear-tagged and ear tattooed) subadult male and 3 unmarked subadults (1 male, 2 females). The marked male was born in the TA, but died at about 24 months of age in the RA, probably during a dispersal move. Skull injuries suggested he had fought another cougar. The unmarked male had just immigrated to the south end of the SAM when, at 20 months old, he was chased up a utility pole by the resident, radio-collared male and electrocuted. One female died of undetermined causes at about 12 months old; we found only her skeleton. The second female died at about 8 to 9 months of age, also from undetermined causes. We suspect that this female may have been the untagged sibling of a radio-collared female that dispersed through the same area when she was about 9 months old.

Adults

We monitored 34 male and 51 female radio-collared cougars that were 18 to 152 months old to examine survival and mortality in adult cougars. Annual MICROMORT survival rates for each sex in the TA and the RA from 1987 to 1994 were tested for significant differences (Table 3.9). We found that annual survival rates between TA males and RA males differed ($P = 0.05$) in only 1 of the 8 years (1989) and the span rates were not significantly different ($P = 0.39$). The annual survival rates between TA females and RA females differed (*P*<0.06) in 2 of the 8 years (1991, 1993) and the span rates were not significantly different (*P* = 0.41). Because of the absence of consistent differences or trends in survival rates between adult males and females that lived in the TA and the RA, we combined all of the adult cougars in each sex on the SAM to examine survival rates.

Survival and mortality rates were calculated for adults during 1987 to 1994 when we monitored ≥7 radio-collared cougars for each sex per year (Table 3.10). Thirty-four male and 51 female radio-collared cougars were monitored for a total of 70,315 days (32,135 male days, 38,180 female days). Annual survival rates for adult males had a mean of 0.90 and a range of 0.79 to 1.0. Annual survival rates for adult females had a mean of 0.81 and a range of 0.52 to 1.0. The mean annual survival rates for males and females were not significantly different (*P* = 0.36). However, the 8-year span survival rate for males (0.45) was significantly greater (*P* = 0.04) than the span rate for females (0.19; Fig. 3.5).

For comparative purposes, we also calculated the finite rate of survival for adult cougars. Resulting mean annual survival rates for males and females were 0.90 and 0.82, respectively, which were practically identical to the MICROMORT results.

Causes of death were categorized for 29 adult cougars (10 males, 19 females) we found dead on the SAM from 1985 to 1995 (Table 3.11; Fig. 3.4). The mean age of adult males that died ($\overline{x}$ = 92.0, SD = 40.6) was significantly different (two-tailed t-test, t = 2.82, 27 d.f., *P*<0.10) than the mean age of adult females that died ($\overline{x}$ = 53.3, SD = 32.6).

Intraspecies strife was the greatest cause of mortality, comprising 50% of male deaths (n = 5) and 53% of female deaths (n = 10). Males killed 14 of the cougars; the sex associated with 1 female death was unknown. Four male deaths were due to neighboring resident males. Five adult females were killed by resident males, and 3 were killed apparently by new immigrant males. The identities of male cougars associated with the deaths of 1 male and 1 female were unknown. Intraspecies killing in adult cougars occurred at random and apparently was independent of adult cougar density (Z = 0.300, *P* = 0.76) in the RA where 9 of the deaths occurred from 1988 to 1994 (Fig. 3.6).

Disease was the second most important mortality factor in adult cougars. The pathogen could not be diagnosed in 4 of 5 deaths primarily because of tissue decomposition. However, septicemic plague (*Yersinia pestis*) was found in 1 female which we necropsied about 12 hours after death (New Mexico Dep. Agriculture Veterinary Services, Albuquerque).

All 3 accidental deaths to adult females occurred apparently while the cougars were trying to bring down mule deer. Three cougars that apparently died of old age were about 122 to 152 months old. The most unusual cause of death occurred when a female apparently was bitten by 1 of the 3 rattlesnake (*Crotalus*) species which were relatively common on the SAM. Causes of death in 2 females could not be determined.

3.4.8 Dispersal And Philopatry

We documented the ages at independence for 6 male and 9 female radio-collared offspring born to 9 mothers. Offspring became independent at a mean age of 14.0 months (SD = 1.6, range = 12.0-16.0) for males and 13.0 months (SD = 1.5, range = 11.1-15.1) for females. The mean age at independence for males and females combined was 13.4 months (n = 15, SD = 1.6). Siblings became independent within 0 to 1.5 months of each other.

The mean age at dispersal for independent subadults was 16.3 months for 6 males (SD = 2.1, range = 14.0-19.5) and 13.6 months for 2 females (SD = 0.9, range = 13.0-14.3). The mean age at dispersal for males and females combined was 15.6 months (n = 8, SD = 2.2).

Characteristics of dispersal and philopatry were documented for a total of 41 subadult cougars (Table 3.12). Eighteen males and 20 females were born on the SAM. One male and 2 females had unknown origins; they probably were born either on the Oscura Mountains to the north or the Organ Mountains to the south. As subadults, they moved through the SAM temporarily before traveling to other mountain ranges.

All but 2 male progeny dispersed. These 2 were killed by male cougars on natal areas 52 and 87 days after independence; we suspect they would have eventually dispersed if they had not been killed. Eight male progeny that were monitored from their natal areas to independent home ranges dispersed an average of 101.3 km (SD = 57.7, range 47.0-192.5). Five other males had moved an average of 114.7 km (SD = 65.2, range = 42.2-195.6) from their natal areas to the site where they died. Three male progeny with relatively incomplete information moved an average of 63.6 km (SD = 18.0) from either their natal area or capture site to a last location or mortality site. One male of unknown origin was captured on the SAM, but kept moving north to central New Mexico 175.7 km away.

Twelve female progeny were philopatric; they established independent home ranges as adults that overlapped their natal home ranges. Seven females that dispersed moved an average of 28.3 km (range = 5.6-78.5, SD = 26.0) from their natal areas to independent home ranges (NAC-IAC distance). Another female moved 76.6 km between her capture site and last location. Two females with unknown origins moved an average of 96.3 km (SD = 31.0) from their capture sites to their adult home range or last location.

Male progeny dispersed significantly farther from their NACs to IACs than female progeny (Wilcoxon rank sum, $n_1 = 7$, $n_2 = 8$, $T = 35$, $P < 0.025$). The directions of dispersal for 16 male and 8 female progeny were uniformly distributed about a 360° circle (males: $U^2 = 0.057$, $P>0.5$; females: $U^2 = 0.062$, $P>0.5$; See Fig. 4.12). Cougars that dispersed reached habitats in southern New Mexico within a 196 km radius of the SAM (Fig. 3.7).

3.4.9 Emigration

We estimated emigration rates for a 5.1 year time frame from 1 February 1990 to 23 February 1995 based on mortality and recruitment rates of 114 marked cubs (51 males, 63 females) out of 137 progeny born from 1 February 1988 to 19 November 1992. Of the 114 progeny, about 36 (16 males, 20 females) died and 21 (4 males, 17 females) were recruited onto the SAM.

We used our calculated subadult survival rates for males (0.56) and females (0.88) and assumed an even sex ratio for the 23 unmarked cubs to estimate sex-based emigration rates during the 5.1 year span. Of the 114 marked progeny, about 15.6 males (51 male cubs - 16 deaths x 0.56 subadult survival rate - 4 recruits) and 20.8 females (63 female cubs - 20 deaths x 0.88 subadult survival rate - 17 recruits) emigrated from the SAM. Males and females comprised 43% and

57% of the estimated successful emigrants, respectively. The estimated sex-based emigration rate based on 137 progeny was 3.8 males and 4.8 females per year.

Over the 5.1 year span, the estimated total successful emigrants included 19.4 males (3.8 males x 5.1 yr.) and 24.5 females (4.8 females x 5.1 yr.). Of the estimated 65 SAM progeny that survived to adult ages, about 83% of males emigrated (19.4 male emigrants / 19.4 male emigrants + 4 male recruits) and 59% of females emigrated (24.5 female emigrants / 24.5 female emigrants + 17 female recruits). Emigration rates are summarized in Table 3.13.

3.4.10 Recruitment and Immigration

During the 5.1 year time span from 1 February 1990 to 23 February 1995, we quantified 21 progeny (4 males, 17 females) that were recruited into the SAM adult population- a rate of 4.1 progeny recruited per year. For the same time span, we quantified 22 immigrants (14 males, 8 females) that were recruited into the adult population- a rate of 4.4 immigrants recruited per year. Consequently, the total recruitment rate was 8.5 cougars per year, including 3.6 males and 4.9 females. Progeny and immigrant recruitment rates for both males and females are presented in Table 3.14. Recruitment and emigration rates were approximately equal (Fig. 3.8).

3.4.11 Experimental Removal

We removed 13 cougars, including 5 males and 8 females from the 703 km^2 TA during 9 December 1990 to 22 June 1991 (Table 3.15). Cougars were removed alive and translocated to northern New Mexico where they were studied until 7 January 1993 to evaluate translocation in cougars (see Chapter 7). During the same removal period, 1 male and 1 female cub died of natural causes in the TA, and another female cub either died or dispersed from the TA.

Two adult male cougars returned to their original home ranges on the TA. One of the males returned on 21 July 1991, 166 days after removal. He remained in the TA population for the rest of the study. The other male returned to his original home range on 7 July 1992, 469 days after removal. However, he was present in his home range only for about 12 days; he died on about 1 July 1992 in the RA about 25 km north of the TA.

At the end of the experimental removal, the entire TA cougar population had been reduced by 47% (Table 3.16). Adult cougars had been reduced by 53%, and all independent cougars (adults and subadults combined) had been reduced by 58%.

By January 1994 (31 months post-treatment) the adult segment of the TA population had practically recovered to pre-removal levels, with a difference of -0.29 cougars (Table 3.17). Moreover, the sex ratios of the adult cougars in January 1991 and January 1994 were identical (1 male : 1.4 females).

Recruits into the TA originated from 3 sources: 3 females were progeny born to TA females that were not removed during the treatment; 3 cougars (2 males, 1 female) were progeny born to RA females; and 6 cougars (5 males, 1 female) immigrated to the TA from outside the SAM. The origin of 1 other recruited female was unknown.

3.4.12 Density

The cougar population on the San Andres Mountains increased during the study. Tables 3.17 and 3.18 show the cougar populations in the TA and the RA during January population estimates. The density of adult cougars in the TA increased from 1.16 to 2.10 per 100 km^2 during pre-treatment and treatment years (1988-1991) and from 0.84 to 1.99 per 100 km^2 in post-treatment years (1992-1995; Table 3.19). By January 1994, 31 months after the removal of 53% of the adults, the TA had almost recovered to its pre-treatment density (2.07 cougars/100 km^2 in January 1994 verses 2.10 cougars/100km^2 in January 1991). However, by January 1995, adult cougar density on the TA declined by 4% due to the death of 1 female. The density of all cougars (adults, subadults, and cubs) in the TA ranged from 2.01 to 3.91 per 100 km^2 in the pre-treatment and treatment years and from 2.78 to 4.12 per 100 km^2 in the post-treatment years.

January population estimates for the RA showed that the density of adult cougars increased from 0.94 to 2.01 per 100 km^2 between 1989 and 1995 (Table 3.20). The density of all cougars ranged from 1.72 to 3.90 per 100 km^2.

Table 3.21 summarizes the number of cougars that used the SAM each January from 1989 to 1995. The number of adult cougars each year ranged from 25 to 42, and the total number of cougars ranged from 42 to 82.

Estimates of adult cougar density based on cougars per year per 100 km^2 also increased over time. The annual density on the TA increased from 1.36 to 2.01 per 100 km^2 during pre-treatment years (1988-1990) and from 1.09 to 1.87 adults per year per 100 km^2 during treatment and post-treatment years (1991-1994; Table 3.22). The density of adult cougars per year per 100 km^2 in the RA increased from 0.72 to 1.79 during 1988 to 1994 (Table 3.23).

3.4.13 Rates Of Increase

The observed exponential rates of increase (*r*) for adult cougars in the TA and RA using both the January and annual density estimators are summarized in Table 3.24. Based on the TA January adult density estimates, *r* was 0.21 and 0.28 for the pre-treatment (1988-1991) and post-treatment years (1992-1995), respectively (Fig. 3.9). The January adult density estimates in the RA produced an *r* of 0.11 for the years 1989 to 1995 (Fig. 3.10). When we calculated *r* for the RA in 4-year spans comparable to the lengths of time analyzed in the TA, the *r* for 1989 to 1992 was 0.17 and the *r* for 1992 to 1995 was 0.05 (Fig. 3.11).

Overall, the January and annual density estimators produced similar patterns in *r* (Table 3.24). The annual adult density estimator produced identical pre-treatment (1987-1990) and post-treatment (1991-1994) *r* values in the TA of 0.19. The *r* for the number of adult cougars per year in the RA was 0.14 for the entire span from 1988 to 1994. When *r* was calculated for two 4-year spans in the RA, the *r* was 0.23 for 1988 to 1991 and 0.07 for 1991 to 1994.

Sex specific *r* in the TA and the RA are summarized in Table 3.25. Generally, the number of adult females increased at faster rates than did adult males regardless of the density estimator used. The rates of increase for adult males and females in the TA and the RA calculated by using the January density estimator are illustrated in Figs. 3.12, 3.13, and 3.14.

3.5 DISCUSSION

Cougars are one of the most difficult of the world's large mammals to study because they are cryptic and live at low densities on harsh landscapes. Thus, it is understandable that there have been only 7 relatively long-term studies of cougars enduring 8 years or more, including this one.

The first long-term, intensive study of cougar ecology was done in the central Idaho River Of No Return Wilderness during 1964 to 1972 (Hornocker 1969, Hornocker 1970, Seidensticker et al. 1973). Hornocker's first 5 years of research relied on intensive capture, marking, and recapture techniques to quantify the cougar population and ground and aerial surveys to assess the impact of cougar predation on mule deer and elk (*Cervus elaphus*). Not until the latter years of their research could Hornocker and Seidensticker employ the new technology of radio-telemetry to describe cougar social behavior. Thereafter, all other studies on cougar ecology have used capture-mark-recapture in conjunction with radio-telemetry to quantify population dynamics, and radio-telemetry to quantify movements, behavior, and habitat use.

In Nevada, cougars were studied at various intensities in 11 mountain ranges during 1972 to 1982 (Ashman et al. 1983). Numerous researchers studied cougars in the Escalante country of south-central Utah from 1978 to 1989 (Ackerman 1982, Hemker 1982, Van Dyke 1983, Barnhurst 1986, Laing 1988, Lindzey et al. 1989, Van Sickle 1990). The endangered Florida Panther has been studied in the wild since 1981 (Belden 1982, Maehr et al. 1989, Maehr 1990). On the Uncompahgre Plateau in southwestern Colorado, cougars were studied from 1981 to 1988 (Anderson et al. 1992). Cougars in Alberta, representing the northern extent of the distribution of the species, were studied from 1981 to 1989 (Ross and Jalkotzy 1992).

In the 6 studies (not including this one) the number of animals captured and marked for research purposes ranged from about 50 Florida panthers to about 100 cougars in Nevada and Utah. Sport-hunting for cougars was banned on the study areas in Colorado, Florida, and Utah. But cougars were experimentally removed from the Utah study area in 1987 (Lindzey et al. 1992). The degree of human exploitation on the other study areas ranged from light hunting pressure in central Idaho (Hornocker 1970) to heavy control and sport-hunting in Nevada (Ashman et al. 1983). Besides the long-term studies, numerous other shorter-term studies of cougars have been conducted in every western state that have cougar populations.

Investigations of cougar population characteristics and dynamics have employed a wide array of methods which have produced an equally wide range in reliability. For example, methods of estimating cougar numbers have included counting cougar tracks (Donaldson 1975), using cougar kill rates on radio-collared deer (Shaw 1980), and intensive capture-mark-recapture and radio-telemetry techniques (Ross and Jalkotzy 1992). When Anderson (1983:62) tabulated information from 23 studies, including methods used and resulting estimates of cougar density, he demonstrated the difficulty in making comparisons in cougar population characteristics or dynamics between study areas. Therefore, in this discussion, we made appropriate comparisons between the SAM cougar population and only those studies of populations where investigators used reasonably intensive capture-mark-recapture and radio-telemetry techniques and defined analytical techniques.

3.5.1 COUGAR POPULATION COMPOSITION

Sex Structure

The male to female sex ratio for cougars at birth approximates 1:1. Divergences away from an even sex ratio in older age classes in a population is probably influenced by sex-specific mortality rates and behavior.

We examined the largest number of nursing cubs (n = 148) indicating a 1:1 sex ratio (75:73). Robinette et al. 1961 reported an even sex ratio (12:12) on 24 cubs born at the National Zoological Park. Seidensticker et al. (1973) found 12 male and 12 female cubs that were various ages when they were first observed. Other studies also quantified the sex ratios of cubs representing a wide range of ages where post-natal mortality may have affected observed sex ratios. Even though there were more males than females in 2 studies (Ashman et al. 1983, Spreadbury 1989) and fewer males than females in 2 others (Logan et al. 1986, Ross and Jalkotzy 1992), none of ratios were significantly different from 1:1.

As cougars became independent subadults on the SAM, fewer males than females were present probably because males had greater rates of mortality and emigration (dispersal). Very rarely has the literature on cougars clearly quantified the sexes, ages, and behavior of independent subadults in a manner that allows us to make comparisons with SAM subadults. A notable exception was Ross and

Jalkotzy's (1992) Alberta study where they also found fewer male than female "independent juveniles and subadults" (9 males, 19 females).

In the SAM adult cougar population, as well as other populations studied, the tendency continues to be fewer males than females (Seidensticker et al. 1973, Shaw 1977, Logan et al. 1986, Hopkins 1989, Maehr et al. 1989, Spreadbury 1989, Ross and Jalkotzy 1992, Beier and Barrett 1993, Lindzey et al. 1994; also see Chapter 4.4.3). In adults, this characteristic is expected because males are territorial whereas females are not, and male home ranges generally are larger than those of females (Seidensticker et al. 1973, Logan et al. 1986, Hopkins 1989, Ross and Jalkotzy 1992, Spreadbury 1989, Maehr et al. 1989, Sweanor 1990, Beier and Barrett 1993). A probable result of territorialism and large home ranges is that fewer males are spaced out over larger areas in relation to females. (For a more detailed discussion of the influence of social behavior on the use of space by cougars, see Chapter 4: *Cougar Social Organization*).

Age Structure

The greatest proportion of the SAM population was comprised of adult cougars, followed in proportion by cubs then subadults. Similar relative proportions of those age classes were observed for cougars in Alberta (Ross and Jalkotzy 1992). From other literature on cougar age structure, it is impractical to make comparisons with the SAM population.

Ages of adult cougars on the SAM reflected their protection from sport-hunting during our research, inasmuch as, cougars could live to old ages. Morever, adult males generally were older and lived longer lives than adult females, reflecting the higher natural survival rates in adult males. The oldest ages for a male (152 months) and a female (146 months) that we recorded apparently are the oldest ages documented for wild cougars.

When Anderson (1983) compiled information for his critical review of literature on cougars, he stated, "Maximum longevity of wild puma is unknown but 3 captive males achieved ages of at least 12, 15, and 18 years and 1 female reached 10-12 years of age (Young 1946:59)." In Alberta, Ross et al. (1995) reported how a 132 month old male and a 108 month old female died while they were trying to kill a bighorn sheep and an elk, respectively. While studying a cougar population in

California that had not been hunted during the previous 12 to 17 years, Hopkins (1989) reported that a 101 month old male was killed by another cougar and a 128 month old female died of undetermined causes. In contrast, cougars subjected to moderate to heavy sport-hunting pressure in Wyoming very rarely reached 84 months of age (Logan et al. 1986).

3.5.2 REPRODUCTION

Natality

The mean litter size of 3.02 cubs that we documented for nurslings 9 to 49 days old was most comparable to the mean litter size of 3.14 found by Spreadbury (1989) in British Columbia when he inspected litters that were about 14 to 77 days old. In Alberta, Ross and Jalkotzy (1992) normally determined litter sizes from track observations when cubs were ≤4 months old and found 2.2 cubs per litter. Most other studies quantified litter sizes when cubs were older, after greater post-partum mortality probably occurred, as was likely the case with the older litters (52-427 days old) that we observed (2.19 cubs/litter). In Idaho where cubs were first observed at various ages, there were 2.6 cubs per litter (Hornocker 1970). In Wyoming litters <6 months old had 2.9 cubs per litter and litters >6 months old had 2.3 cubs per litter (Logan et al. 1986). In Utah, where 65% of the cubs were >3 months old when examined, there were 2.4 cubs per litter (Lindzey et al. 1994). Florida panthers exhibited the lowest documented mean litter sizes of 2.25 cubs in 4 litters ≤14 days old and 1.92 cubs in a total of 25 litters (Maehr and Caddick 1995). Prenatal litters were generally larger than post-partum litters reported in the literature. Litters from pregnant females in Nevada averaged 3.08 cubs (Ashman et al. 1983); in Utah and Nevada, prenatal litters averaged 3.39 cubs (Robinette et al. 1961).

Our observation of an average litter size of 3.38 for first litters in relation to 2.95 for subsequent litters raises questions that could be addressed in future research of cougar populations. An hypothesis that first litters are significantly larger than subsequent litters has implications in population dynamics if compensatory reproduction occurs in young-aged populations, such as those that are moderately to heavily exploited by sport-hunting or control. A potential consequence may be higher initial rates of increase for populations recovering from exploitation and lower rates of increase as populations age.

Timing Of Births

Although cougar cubs were born at every time of the year, there was a birth pulse. The birth pulse we documented during July through September on the SAM coincided with the mule deer fawning period when food was the most available and vulnerable to cougar mothers. In fact, on the SAM, deer fawns comprised the single most represented age class in cougar kills that we examined (see Chapter 5: *Cougars And Desert Mule Deer*). At the critical time when females must restrict their movements around nurseries and supply food to cubs with increasing energy demands, cougar births timed for periods when food is abundant and predictable is adaptive; females that produce litters at those times probably incur survival advantages and high net reproductive success.

The pattern of cougar births on the SAM conforms closely with the pattern observed in Nevada (Ashman et al. 1983), but there the birth peak occurred during June and July. In Wyoming, where 70% of cub births occurred from August to November, Logan (1983) suggested that mothers and weaned cubs could take advantage of high concentrations of mule deer and elk on winter ranges during November to March. Similarly, 78% of births occurred from June to November In British Columbia (Spreadbury 1989), 77% of births were from August to October in Utah (Lindzey et al. 1994), and 60% of births were during June to August in Alberta (Ross and Jalkotzy 1992). Anderson (1983:32) used data from Utah and Nevada cougars reported in Robinette et al. (1961) to show that pregnancy rates were significantly greater during June and July than during other months. He also compiled data on 53 wild litters from 14 sources showing that 66% of births occurred during June, July, September, October, and November.

Mating, Gestation, And Birth Intervals

Quantitative information on mating, gestation, and birth intervals in the published literature is sparse, especially for wild cougars. The mean gestation period of 91.3 days that we observed for 31 wild litters was practically identical to the mean of 91.9 days that Anderson (1983) calculated from data on 42 captive litters from 11 sources. Beier and Barrett (1993) estimated the mean gestation period for 4 litters at 93 days.

The close similarity between the mean (17.4 mo.) for 15 birth intervals where at least 1 cub survived to independence or to 12 months of age and the mean (16.9 mo.) of 15 other intervals where we did not know the fates of cubs in the first litter with certainty, suggest that in most cases in the latter group, at least 1 cub probably survived to independence.

In Utah, Lindzey et al. 1994 reported a mean birth interval length of 24.3 months for 7 intervals where $\geq$1 cub survived to $\geq$12 months. Ross and Jalkotzy (1992) calculated a mean birth interval of 19.7 months (n = 12), however, they cautioned that in 3 cases (25, 25, and 32 mo.) interceding litters could have been missed because of low monitoring frequency.

Maturity And First Litters

Male cougars on the SAM first exhibited reproductive behavior at an average age of 24.3 months. Although females first exhibited reproductive behavior at a younger age ($\bar{x}$ = 21.4 mo.), they conceived for the first time at an average age of 26.1 months and had their first litters at an average of 29.1 months old. The youngest known-age females became sexually active, conceived, and gave birth for the first time at 19, 19, and 22 months old, respectively. The youngest approximately known-age female to bear cubs conceived at about 15 months old and gave birth at about 18 months old; we considered her age to represent the extreme young age of maturity.

Similar to our findings, Ross and Jalkotzy (1992) reported on 6 known-age females in Alberta that had their first litters at an average age of 30.0 months. In Utah Lindzey et al. (1994) documented 6 known-age females that first gave birth at an average age of 26 months old. Maehr et al. (1989a) reported on 1 known-age Florida panther that conceived for the first time at about 18.5 months old and had her first litter at about 21.5 months old.

Reproductive Success

The large percentage of adult females raising cubs in January each year on the SAM (73%) also has been found in other populations. Logan (1983) found 55%

and 86% of adult females raising cubs during 2 consecutive winters in Wyoming. In Alberta, Ross and Jalkotzy (1992) found that during January 1981 to 1989, 42% of adult females were accompanied by cubs <6 months old. In Utah, cubs were born to about half of the resident female population each year (Hemker 1982).

Our study provides the only quantitative information presently available on reproductive success of adult cougars. Apparently, relatively small proportions of adult females and males (26% and 38% of documented breeding females and males, respectively) contributed the majority of net reproduction in our study population. If those adults represented genotypes favored by natural selection, then selection processes probably are changed by sport-hunting and control when cougars that otherwise would have survived and produced descendents are instead killed by humans.

3.5.3 MORTALITY AND SURVIVAL

Cubs

Actual cub survival rate on the SAM probably was lower than the maximum cub survival rates (cFRS with research mortalities = 0.68, cFRS excluding research mortalities = 0.71; CN = 0.73) that we calculated, because our data included cubs still dependent on mothers. We would expect additional mortality to occur up to independence. Cubs monitored from contact to dispersal in Utah had a 67% survival rate (Lindzey et al. 1989). Cubs living in fragmented habitat in southern California had an annual survival rate between 0.45 and 0.52 (Beier and Barrett 1993). In Alberta, 97.6% of cubs survived from first contact to independence (Ross and Jalkotzy 1992); however, investigators cautioned that mortality levels probably were underestimated because some animals were not detected until they were ≥0.6 years old, thus post-natal mortality could have occurred when cubs were younger.

On the SAM, male and female cubs died at approximately equal ratios (20:18). Information in the literature on the sexes of cubs that died is scarce. Hemker et al. (1982a) were the first to quantify cub mortality in the cougar population in Utah, but they did not report the sexes of cubs that died. Spreadbury (1989) reported 4 male and 2 female cub deaths in southern British Columbia. Beier and Barrett (1993) reported 9 male and 6 female cub deaths in California.

Subadults

Subadult males had a lower survival rate (0.56) than subadult females (0.88) probably because males faced higher risks as they dispersed at greater frequencies and traveled longer distances from natal areas. While dispersing, males must traverse more unfamiliar country with unknown hazards. Males also are at higher risk because they compete directly with other males for territory. On the other hand, if female subadults disperse at all, distances are significantly shorter, and they generally do not compete directly with other cougars for space. (For further discussion see 3.5.4: *Dispersal And Philopatry*)

Quantitative data on survival rates of independent subadults in other populations is practically non-existent in the literature primarily because most cougars in this age class dispersed from study areas and investigators lost contact with them. Anderson et al. (1992) calculated an annual survival rate of 0.64 for cougars (males and females combined) in the 12 to 24 month age class by using the product-limit procedure (Pollock et al. 1989). But, we caution a direct comparison with our results because Anderson's team did not indicate the status of those cougars (e.g., dependent or independent at younger ages, dispersers or resident adults at older ages), or how many cougars were in the analysis.

Adults

On the SAM, adult male cougars had higher survival rates ($\bar{x}$ = 0.90 annual rate, 0.45 span rate) and lived to older ages ($\bar{x}$ = 92.0 mo.) than adult females ($\bar{x}$ = 0.81 annual rate, 0.19 span rate; 53.3 mo.). Few other investigators have quantified adult cougar survival rates.

Lindzey et al. (1988) calculated survival rates using MICROMORT and the product-limit method (Kaplan and Meier 1958) for 3 to 8 resident adult cougars per year from 1980 to 1986 in Utah. They defined "resident adults" as "cougars $\geq$16 months of age that demonstrated continuous and predictable use of an area for $\geq$6 months". Annual survival rates for females were lower than the rates we calculated for SAM females; they ranged from 0.45 to 1.0 with means of 0.71 and 0.73 for MICROMORT and product-limit, respectively. Because only 1 male could be monitored in some years, they combined males and females together and calculated annual survival rates that ranged from 0.52 to 1.0 with means of 0.72 and 0.73 for MICROMORT and product-limit, respectively.

Beier and Barrett (1993) used the product-limit procedure (Pollock et al. 1989) for 20 adult cougars in southern California; males and females were combined due to small numbers. They calculated an adult annual survival rate of 0.75. Using the same method for adult cougars (males and females combined) in Colorado, Anderson et al. (1992) estimated annual survival rates at 0.69, 0.92, and 0.80 for cougars in age classes 24 to 36 months, 36 to 48 months, and 48 to 60 months, respectively. Again, sample sizes in each class were not given. In a cougar population in southeastern Arizona subjected to heavy predator control and sport-hunting, Cunningham et al. (1995) used MICOMORT to calculate survival rates for a small sample of 4 males and 2 to 5 females each year over a 3 year period. Annual survival rates ranged from 0.12 to 1.0 for males and 0 to 0.81 for females. Cunningham et al. (1995) iterated that female survival rates were higher than males except during 1 year when only 2 females were sampled. The higher male mortality rate was associated with a greater number of males involved in depredation control (16 males vs. 6 females killed).

Mortality Causes

In our study, cougars were the greatest single natural cause of mortality in other cougars, either from infanticide and cannibalism (44% of cub deaths) or intra-species strife (100% of subadult deaths, 52% of adult deaths). Males did all of the killing. Cannibalism of cubs also has been documented in Colorado, Idaho, Utah, British Columbia, Alberta, and California (Young 1946, Hornocker 1970, Hemker et al. 1982, Spreadbury 1989, Ross and Jalkotzy 1992, Beier and Barrett 1993, respectively). Intra-species strife has been documented across the geographic range for cougars in North America, including Texas, Florida, Wyoming, Alberta, British Columbia, Utah, and California (McBride 1976, Maehr 1990, Logan 1983, Ross and Jalkotzy 1992, Spreadbury 1989, Lindzey et al. 1989, Beier and Barrett 1993, respectively). Considering only natural causes of mortality, intra-species strife was the single greatest identifiable cause of death in Florida (Maehr 1990), and California (Beier and Barrett 1993), where cougars were protected from sport-hunting.

Clearly, cougars naturally impose strong selective pressures on themselves. Males are territorial, competing directly with other males for space and mates (for details see Chapter 4: *Cougar Social Organization*). An evolutionary result of direct competition between males may be the extreme sexual dimorphism in cougars. Anderson (1983:21) examined masses of cougars from 5 subspecies in North America and showed that male cougars weighed about 1.4 times more than, and were significantly heavier than females ($P < 0.005$). We expect that larger males are more capable of maintaining dominance over territory for long periods of time; thus, they are more reproductively successful than smaller males.

Females generally do not engage in fights with other cougars, except in some cases to protect cubs and food. Furthermore, because females raise cubs by themselves, they cannot afford to be seriously injured in aggressive encounters with conspecifics. This relatively tolerant behavior is adaptive because it probably increases the net reproductive success of females.

Humans were the major cause of death in hunted cougar populations in Idaho, Colorado, Nevada, Montana, Wyoming, Alberta, and Arizona (Hornocker 1970, Currier et al. 1977, Ashman et al. 1983, Murphy 1983, Logan et al. 1986, Ross and Jalkotzy 1992, Cunningham et al. 1995, respectively). Humans also were the major cause of death in cougar populations protected from hunting for research purposes in Arizona, British Columbia, and Colorado (Shaw 1977, Spreadbury 1989, Anderson et al. 1992, respectively). There, mortalities resulted from legal and illegal kill inside or outside of the study areas, predator control, and collisions with vehicles. In Florida panthers and California cougars that were protected by law, but where habitats were severely fragmented, humans caused most of the deaths by vehicle collisions and illegal shootings (Maehr 1990, Beier and Barrett 1993, respectively).

For cougars, which emerged as early as 2 million years ago (Anderson 1983), major human-caused mortality apparently is extremely recent. As far as we know, humans have hunted cougars in earnest for control and sport primarily since European immigrants settled the Western Hemisphere some 100 to 300 years ago. Human exploitation had the most dramatic effect in North America where by the late 1800's cougars were rare or absent in most of the eastern half of the continent. By the 1920's the cougar's range was restricted primarily to the mountainous areas of the West and swamps of Florida (Nowak 1976). Hunting continued; from 1910 to 1974 approximately 66,665 cougars were reported killed in 13 western states and provinces (compiled from Nowak 1976 by Anderson 1983). The effect of large scale human-caused mortality on natural selection in cougars is unknown.

Disease was an important cause of mortality in adult cougars on the SAM (17%). Anderson (1983) tabulated 20 diseases found in cougars and forwarded the opinion (p. 37) "that whatever parasites and diseases are endemic in wild puma none are apt to be population limiting." However, septicemic plague (*Yersinia pestis*) was not on his list of diseases. Besides the occurrence of the disease on the SAM, *Y. pestis* was diagnosed in 2 female cougars found dead within 50 to 100 m of one another in the Sandia Mountains in northern New Mexico in 1994 (New Mexico Dep. of Agriculture Veterinary Diagnostic Services, Albuquerque). It has also been found in cougars in California (W. Boyce, DVM, Univ. California, Davis, pers. comm.).

The effect of *Y. pestis* on cougar populations is presently unknown; however, there is a real probability significant morbidity may occur in localized areas, especially in New Mexico which has the highest incidence of the disease in North America. Moreover, the disease is not endemic to the Western Hemisphere; it was introduced in about 1895 via Chinese immigrants that came to San Francisco, California from Hong Kong. *Y. pestis* is especially pathogenic in felids. The disease may become increasingly infectious in cougars particularly during periods of severe declines in major ungulate prey, such as during drought, when cougars may have to rely more on smaller prey items. Cougars can become infected from bites from disease carrying fleas on rodents and rabbits which they eat, or by consuming infected tissue. Occurrence of the disease in deer apparently is rare. The disease also is transmittable to humans through the bite of an infected flea or direct contact with an infected carcass (B. Chomel, DVM, Zoonotic Disease Expert, U.C. Davis pers. comm.; Thorne et al. 1982).

Accidents to cougars on the SAM involved females that were primarily (3 of 4) trying to bring down large prey. Such incidents also have been described for cougars in Utah, Idaho, and Alberta (Gashwiler and Robinette 1957, and Lindzey et al. 1988; Hornocker 1970; Ross and Jalkotzy 1992, respectively). Females may be more vulnerable to such sources of mortality than males because of their smaller size in relation to ungulate prey. In Alberta (Ross et al. 1995), 3 of 4 cougars that died from prey capture attempts were females. Cougars also have drowned while attempting to cross rivers at flood stage in Arizona (Cunningham et al. 1995). Incidences of fatal snakebite, like we apparently observed in 1 female, probably are very rare.

3.5.4 DISPERSAL AND PHILOPATRY

Dispersal of cougar offspring from natal areas and even origin populations has been described in cougar studies across North America (Seidensticker et al. 1973, Logan et al. 1986, Ross and Jalkotzy 1992, Anderson et al. 1992, Beier and Barrett 1993, Lindzey et al. 1994). Progeny on the SAM became independent ($\bar{x}$ = 13.4 mo.) and dispersed from natal areas ($\bar{x}$ = 15.6 mo.) at somewhat similar ages to cougars in Alberta ($\bar{x}$ = 15.2 mo., 16.0 mo. at independence and dispersal, respectively; Ross and Jalkotzy 1992), Florida (dispersal age $\bar{x}$ = 17.3 mo.; Maehr 1990), California (dispersal age $\bar{x}$ = 18.0 mo.; Beier and Barrett 1993), and Utah (dispersal age = 16-19 mo.; Hemker et al. 1984). Based on our observations of ages at reproductive activity in cougars, it appears that in general, dispersal events occurred in cougars that were not yet mature.

Dispersal distances reported in other cougar studies were similar to our observations. Anderson et al. (1992) summarized the dispersal distances for 65 North American cougars; the means of means and extremes were 85.0 km (29-274) for 33 males and 31.4 km (9-140) for 32 females. Comparatively, males from the SAM tended to disperse longer ($\bar{x}$ = 101.3 km), but females shorter ($\bar{x}$ = 28.3 km) distances. Overall, SAM males dispersed 3.6 times as far as dispersing SAM females. If philopatric females on the SAM also are considered, then SAM males dispersed 9.7 times as far. The longest dispersal movement appears to be that of male tagged as a cub in northern Wyoming and killed west of Denver, Colorado at 30 months old- a distance of 483 km (Logan, unpubl. data).

Although cougars did not show a significant preference in dispersal direction, the majority of dispersing cougars (54%) moved in relation to the north-to-south orientation of the SAM (345°-9° north or 166°-191° south). Dispersers were not always confined to cougar habitat; many of them that left the SAM crossed expanses of non-habitat from 45 to 65 km wide (the Jornada del Muerto and

Tularosa Basin, respectively). However, dispersal movements across those areas were completed in short periods of time (generally <7 days). When available, cougars used patches of habitat to link their dispersal movements. Because much of southern New Mexico is relatively undeveloped, dispersers were generally unimpeded by any large scale human activities, such as those found in southern California (Beier and Barrett 1993).

Dispersal was independent of cougar density for male progeny on the SAM. Most males not only dispersed from their natal areas, but the entire SAM study area. However, some females dispersed while others were philopatric; both behaviors appeared to be independent of density. Similar behavior of independent progeny was described in cougars in Alberta and Utah (Ross and Jalkotzy 1992, Lindzey et al. 1994). For a discussion on the adaptive significance of dispersal, see Chapter 4.5.4.

3.5.5 EMIGRATION

Dispersers leaving the SAM were emigrants from the population. Male progeny emigrated at a higher rate (83%) than female progeny (59%). Similarly, more male progeny than female progeny emigrated from study areas in Alberta and Utah (Ross and Jalkotzy 1992, Lindzey et al. 1994). Patterns of emigration-dispersal distances, directions, rates- exhibited by cougars on the SAM demonstrated the importance of this behavior to metapopulation dynamics. Cougars dispersing from the SAM entered the major patches of cougar habitat in the southern one-half of New Mexico, thus contributing to other populations in those patches in numbers and genotypes at a rate of about 4 male and 5 female cougars per year. While cougars were leaving the SAM population and going to other populations, other cougars were leaving other populations in southern New Mexico and making their way to the SAM (Immigrants).

3.5.6 RECRUITMENT AND IMMIGRATION

Recruits on the SAM were comprised of approximately equal proportions of progeny and immigrants (4.1 progeny: 4.4 immigrants per year). The estimated 8.5 recruits per year, which included about 3.6 males and 4.9 females, replaced adults that died and were translocated and enabled the population to increase. Most female recruits were progeny; most male recruits were immigrants.

Other investigators also have emphasized the importance of immigration to the maintenance of local populations (Seidensticker et al. 1973, Hemker 1984, Logan et al. 1986, Beier and Barrett 1993). But no other studies have estimated rates of recruitment and the contributions from progeny or immigrants.

3.5.7 EFFECTS OF REMOVAL

It took the TA cougar population about 31 months to recover after we removed 53% of the adults. Recovery was achieved through both immigration and progeny recruitment. Furthermore, recovery was facilitated by cougars in the adjacent protected RA and the incomplete removal of resident adult females in the TA; 3 of the recruits (2 males, 1 female) were born in the RA, and 3 females were progeny of 2 TA females that were not removed during the treatment. About 50% of the recruitment in the TA after treatment was by progeny born on the SAM.

Lindzey et al. (1992) conducted the only other experimental removal in a cougar population in Utah. Removals and natural deaths of 5 resident adults from a 1,900 km^2 core area within a 4,500 km^2 study area resulted in a 42% reduction in 1 year. The adult segment of the population recovered in 9 months. The rapid recovery probably was facilitated by the adjacent protected area (hunting was banned) which was 1.4 times larger than the treated area. Similar to our findings, recruitment was comprised of progeny and immigrants.

3.5.8 DENSITY

The density of adult cougars on the SAM increased during the study. January population estimates showed that adult cougars per 100 km^2 in the TA increased from 1.16 to 2.10 (pre-treatment:1988-1991) and from 0.84 to 1.99 (post-treatment 1992-1995); in the RA density increased from 0.94 to 2.01 per 100 km^2 (1989-1995). Adult cougar density in the TA (pre-treatment and post-treatment) and the RA measured as the number of adult cougars per year per 100 km^2 also increased over time.

From the time we began our research in 1985 the cougar population on the SAM was recovering from the effects of control in conjunction with sport-hunting that occurred from 1979 to 1985. About 40 of the 50 cougars that were killed were adults: 17 in the TA (14 for control, 3 by hunters) and 23 in the RA (20 for control, 3 by hunters). The estimated kill rate of 11.1 adults per year exceeded the recruitment rate of 8.5 cougars per year (Feb. 1990-Feb.1995) that we estimated.

Moreover, the lower density of adult cougars on the RA in relation to the TA probably was affected by the killing of 13 cougars in 1 year (Oct. 1980-Oct. 1981) for control purposes on the Oscura Mountains (north of the RA). The kill included 11 adults removed at an estimated rate of 1.6 adults per 100 km^2 per year (11 adults killed on 673 km^2/yr.). This control probably severely reduced the Oscura Mountains cougar population; consequently, dispersal of subadults from the Oscura Mountains and the attendant immigration of cougars into the RA would have been reduced.

The range of January adult cougar densities (adults/100 km^2) on the TA and the RA were similar to ranges of adult densities reported in Idaho (1.2-2.1, revision by Hornocker in Anderson 1983:61), Wyoming (1.3-1.6, Logan et al. 1986), California (0.9-2.0, Hopkins 1989), and Alberta (1.7-2.1, Ross and Jalkotzy 1992). Adult cougar densities in British Columbia (0.93-1.1, Spreadbury 1989) were at the low end of the density range on the SAM. However, adult densities in Utah (0.32-0.63, Lindzey et al. 1994) were much lower than we observed.

Annual January density estimates for all classes of cougars combined (adults, subadults, and cubs/100 km^2) were more variable, increasing in some years, but decreasing in others. The dynamics was affected primarily by the numbers of cubs produced each year. Ranges of cougar densities in the TA (2.01-3.91 pre-treatment, 2.93-4.25 post-treatment) and the RA (1.72-3.90) were similar to ranges of cougar densities in Idaho (3.2-4.2, Seidensticker et al. 1973), Wyoming (3.5-4.6, Logan et al. 1986), Alberta (2.7-4.7, Ross and Jalkotzy 1992), and British Columbia (3.5-3.7, Spreadbury 1989). Again, Utah had the lowest reported densities of cougars (0.77-1.37, Lindzey et al. 1994).

Similarities in cougar densities were apparent even though the environments where cougars were studied were different. The cougar population on the SAM was not influenced by climatic factors that caused seasonal population concentrations or dramatic shifts in habitat use (Sweanor 1990). However, cougar populations in Idaho, Wyoming, Alberta, British Columbia, and Utah were concentrated on low elevation winter ranges because cougars and the primary ungulate prey were constricted by deep snow at higher elevations. As snow receded in summer, cougars followed ungulate prey to higher elevations (Seidensticker et al. 1973; Logan and Irwin 1985). As a result, cougar home ranges either enlarged (Seidensticker et al. 1973, Hemker 1982, Ross and Jalkotzy 1992) or cougars occupied summer home ranges distinct from winter home ranges (Seidensticker et al. 1973, Hemker 1982, Ross and Jalkotzy 1992, Pierce 1996). Population densities have not been estimated for cougars on summer ranges in those environments; however, intuitively, densities of cougars would be expected to be lower than on winter ranges.

Other than in our study, there are no other reliable estimates of population density or dynamics for cougars in desert environments. McBride (1976) studied cougars for 4 years in a 100 mile wide strip along the entire Texas-Mexico border; but he could only guess at how many cougars there were. A 2 year study of cougar ecology in Big Bend National Park, Texas by Pence et al. (1986) did not yield adequate information for estimates of population density or dynamics. Smith et al. (1986) studied cougars for 3 years in the vicinity of Carlsbad Caverns National Park, New Mexico and Guadalupe Mountains National Park, Texas where cougars were subjected to heavy control efforts in an attempt to protect domestic sheep. During the study, 65 cougars, including 13 out of 22 radio-collared individuals, were killed on or near ranches bordering the National Parks. On the subject of cougar density estimates on the study area, Smith et al. (1986:105) stated, "Because of the large area encompassed by this study, the rapid turnover of the population, and funding limitations, this was difficult to achieve, even for the smaller areas within the study area."

Density of breeding adult cougars in a population probably is determined ultimately by habitat quality. Seidensticker et al. (1973) hypothesized that a "vegetation-topography/prey numbers-vulnerability complex" was important in determining the amount of terrain used by resident cougars, the degree of home range overlap, and hence, the density of the breeding population. Logan and Irwin (1985), Belden et al. (1988), and Laing and Lindzey (1991) quantified how cougars use habitat selectively. Logan (1983) explained how specific habitat features conferred advantages to cougars in hunting prey and in intra-species communication. Quigley et al. (1989) studied the cougar population on the same area where Hornocker (1970) and Seidensticker et al. (1973) studied the cougars 11 years earlier and found that the area supported more females than before. They hypothesized that the increase in cougars was a numerical response to an approximate one-third increase in the elk population. In addition, movements of cougars in relation to migrating prey suggest that prey density is an important regulating factor in cougars (Pierce 1996).

Following this logic, the carrying capacity for the cougar population on the SAM probably is ultimately defined by the quantity and quality of the habitat, particularly the food resource (see Chapter 5: *Cougars and Desert Mule Deer*). Because we studied cougars on the SAM during periods marked by unusually high precipitation (which likely resulted in high primary and secondary production) and drought (which resulted in severe declines in primary and secondary production and surface water), we hypothesize that we observed the cougar population within the natural ranges of carrying capacity for this desert environment. (See Chapter 2: *The Research Environment*).

3.5.9 Rates Of Increase

The observed exponential rates of increase for the SAM population indicated that depressed cougar populations can increase at relatively high rates (0.17 - 0.28 for January estimates) after protection. Furthermore, the rate of increase appears to be density dependent, because the rate in the RA slowed from 0.17 to 0.05. The absence of growth in the TA in 1995 may also reflect this. We hypothesize that as density approached carrying capacity, the rate of population increase declined.

Adult females generally increased at a faster rate than adult males because female recruitment was comprised primarily of progeny, whereas male recruitment was dependent primarily upon immigrants. Most surviving male progeny left the SAM population and were not available for local recruitment.

Quantitative data on rates of increase for cougar populations is practically nonexistent in other literature. Ashman and Molini (1976:123-124) were the first to indirectly address rates of increase by roughly examining cougar harvest rates in the Ruby Mountains, Nevada. They suggested that harvest rates of >25% caused population declines.

Ross and Jalkotzy (1992) and Lindzey et al. (1994) presented data on increasing cougar populations in Alberta and Utah, respectively; but they only reported that the populations increased. We used their data for regression analyses to calculate observed exponential rates of increase (*r*) for adults in each population. For the Alberta population, *r* ranged from 0.04 to 0.08 for the range of densities given in 3 consecutive estimates. In Utah, the adult population was relatively stable during the first 5 years; but during the last 4 years, the *r* was 0.24. The differences in *r* between these 2 populations probably were influenced in part by hunting and the starting population densities. The Alberta population was hunted at a rate of 0 to 21% of independent cougars each year and adult density started at 1.7-1.8/100 km^2 (Ross and Jalkotzy 1992). On the other hand, the Utah population was protected from hunting and adult density started at 0.32/100 km^2. The rates of increase in the Alberta and Utah populations were consistant with those in the SAM cougar population.

Some populations may be stable over periods of time. Examples include the Utah cougar population (above) during the first 5 years of study, and the lightly hunted cougar population in Idaho which was relatively stable for 8 years (Seidensticker et al. 1973). However, both of these populations increased during subsequent years (Lindzey et al. 1994, Quigley et al. 1989).

3.6 MANAGEMENT IMPLICATIONS OF COUGAR POPULATION DYNAMICS AND COUGAR SOCIAL ORGANIZATION

1. **Finding:** To reliably quantify cougar population dynamics in our 2,059 km^2 study area, year-round efforts by a highly trained research team were required to capture, mark, release, and radio-track cougars.

   Implications: Except for the methods we used , no other methods have proven reliable for determining cougar population dynamics. But our methods are too expensive and time consuming to apply to larger regions for the purpose of monitoring cougar populations. Having very cryptic, solitary behavior, and occurring at low population densities in rugged and/or densely vegetated habitat, cougars cannot be observed quantitatively from the ground or aircraft like many other big game animals. Thus, managers cannot rely on direct observational data to monitor population trends or to gauge the effects of management actions. In addition, track counts have not been tested for their accuracy or precision on cougar populations with known characteristics anywhere in the Southwest. Furthermore, track surveys would still require a large amount of resources (i.e., people, time, money) to detect even 30% changes in track densities (Beier and Cunningham 1996).

Given the limitations humans have in determining the numbers and/or trends in cougars, there will probably always be important uncertainties regarding cougar populations especially at the landscape or state-wide levels, including the effects of: management actions, illegal killing, habitat fragmentation and loss, prey fluctuations, and disease outbreaks. A management strategy that recognizes those uncertainties, is anchored in cougar biology and ecology, and considers specific objectives for cougar populations, is one that will be the most effective in dealing with people-related cougar management problems that may require actions ranging from control to complete protection.

A state-wide cougar management plan for New Mexico could include actions to meet specific objectives for cougar populations or areas. For example, chronic hot spots where cougars prey on livestock or threaten human safety could be managed for control while using sport-hunting as the mechanism for cougar reduction. Other cougar populations could be managed for sustained harvest to provide sport-hunting opportunity. Still other areas could be managed as refuges to protect cougars. Our research findings present the New Mexico Department of Game and Fish with the best opportunity it has ever had to develop a state-wide cougar management plan that is based on reliable scientific information and can effectively address the people's concerns about cougar management and long-term cougar conservation. Working components for such a plan are in the following Findings & Implications.

2. **Findings:** We documented January adult cougar densities on the TA as low as 1.16 cougars/100 km^2 after 3 years of protection following control, and 0.84 cougars/100 km^2 after experimental removal. On the RA, the low adult cougar

density was 0.94 cougars/100 km^2 after 4 years of protection following control. The high adult cougar densities in the TA were 2.10 cougars/100 km^2 after 6 years of protection following control and 1.99 cougars/100 km^2 4 years after experimental removal. In the RA, the high adult cougar density was 2.01 cougars/100 km^2 after 10 years of protection following control. The high densities we observed were as high as cougar densities have been estimated in North America.

Implications: The range of adult cougar densities that we quantified on the SAM could be considered as reference densities for other cougar populations in New Mexico. Cougar populations subjected to prolonged control or heavy sport-hunting pressure may support densities similar to the low densities found on the SAM, whereas populations subjected to years of protection may support the high densities found on the SAM. Our January population estimates correspond to the present New Mexico cougar hunting season (Dec.-Mar.); thus, reference densities could be used to set initial harvest objectives, which could later be modified if reliable data on local cougar populations are gathered, such as by monitoring track routes and mortality.

3. **Findings:** The maximum rates of increase (based on January population estimates) for adult cougars on the SAM ranged from 0.17 (on the RA) to 0.28 (on the TA). The RA exhibited a low rate of increase of 0.05 during the last 4 years of the study and as carrying capacity declined. In the TA, the adult cougar density actually declined slightly between 1994 and 1995. Gender- specific rates of increase for adult cougars in the RA ranged from 0.07 to 0.08 for males and 0.04 to 0.26 for females.

Implications: The maximum rates of increase that we calculated for adult cougars may be the maximum rates at which protected cougar populations can increase following severe declines. Cougar populations that approach carrying capacity may have rates of increase that are ≤ 0.05. Rates of population increase appear to be density dependent.

The rates of increase of adult cougars on the SAM may be considered as reference rates of increase in other cougar populations in New Mexico; however, those numbers should be used with caution. Almost all other cougar populations in New Mexico are hunted and/or probably have higher rates of other human-caused mortality (e.g., predator control, illegal killing, road mortalities) than the SAM population; therefore, actual rates of increase in those populations are probably lower, zero, or negative.

If the objective is sustained harvest, we recommend using the observed exponential rates of increase that we calculated for the RA as initial maximum harvest rates. Annual harvest should not exceed 8% of the adult males and the harvest of females should be strictly controlled (see Findings & Implications 4). Harvest quotas could be set for hunt areas to manage gender-specific harvest. (Genders can be distinguished while cougars are bayed).

For cougar populations managed for control, the annual kill rates for adult cougars may have to exceed the maximum rate of increase we observed in the TA (0.28). Severe population decline (>50%) could be achieved in as few as 3 years. But if extreme kill rates persist, the cougar population will go extinct.

For cougar populations managed for increase, then rates of increase may be similar to those we observed on the SAM once the population is protected. The rate of increase probably will be affected by the density of the population in relation to the carrying capacity (i.e., the rate would be expected to decline to zero as the population approached carrying capacity). The TA and RA cougar populations demonstrated that it may take 3 to 10 years for a cougar population to recover to a relatively high density.

Unfortunately, cougar numbers and effects of present cougar management in New Mexico are not known; thus, important uncertainties exist. If cougar conservation in New Mexico is a long-term goal, then uncertainties of cougar management can be countered by large refuges (≥2,590 km^2 or 1,000 mi.^{2}) where cougars are protected (see Findings & Implications 5 & 6 for more justifications).

4. **Findings:** On the SAM an average of 73% of the adult females were raising cubs in January of each year. Similarly, large proportions of adult females raise cubs each year in other cougar populations in North America. On the SAM, a small proportion of adult females were the most reproductively successful.

Generally, females raising cubs had smaller home ranges than females without cubs.

Cougar populations are maintained by recruitment of locally born progeny and immigration, each of which contributed about 50% of the recruits on the SAM.

Implications: Cougar families are vulnerable to mortality during the current New Mexico cougar hunting season (Dec.-Mar.). By December, most of the cub-rearing females have weaned cubs, thus their mammaries are non-productive and not distended. Consequently, unless cubs are at the female's side, a hunter cannot tell from conditions of the mammaries whether or not a female has cubs.

The behavior of mothers to leave cubs behind at kills or rendezvous sites while they go hunting creates the opportunity for hunters to kill mothers and leave cubs to starve to death. While using hounds to tree and bay cougars for research in Wyoming, Logan (1983) found that mothers were away from their kittens during 50% of encounters. Even finding tracks of cubs with females is not reliable, Barnhurst (1986) found that tracks of cubs 0-6 months old were found with their mother's tracks only 19% of the time, and tracks of cubs 7 to 12 months old were found with their mother's tracks 43% of the time. Because mothers generally use relatively smaller home ranges than lone females, they tend to leave many tracks in local areas as they travel, hunt, and return to waiting cubs. These behaviors may enhance the vulnerability of mothers to cougar hunters.

The killing of cub-rearing females not only removes productive adult females from the population, but it also indirectly contributes to deaths of cubs, the potential recruits into the local and other cougar populations within dispersal distances. For cougar populations having the management objective of sustained yield, the harvest of females can be strictly controlled with quotas.

5. **Findings:** Dispersing progeny emigrated from the SAM at high rates (83% and 59% of surviving male and female progeny, respectively). Emigrants reached cougar habitats throughout southern New Mexico. Moreover, about 50% of the recruits to the SAM population came from other cougar populations in

New Mexico. Cougars used habitat patches as they moved between populations.

Implications: The cougar population in New Mexico may be described as a metapopulation- a population distributed in subpopulations. Subpopulations are linked via movements of dispersing cougars. Emigration and the subsequent immigration and recruitment of cougars into other subpopulations and habitats have vital adaptive consequences, including: numerical and genetic maintenance and/or enhancement, and colonization of unoccupied habitat.

When cougars are managed for control and sport-hunting or where other high human-caused mortality occurs, considerations should be given to the potential impacts on other cougar subpopulations in the region. Areas subjected to high mortality due to control, heavy harvest, or killing of nuisance animals would function as sinks where immigrating cougars have high rates of mortality. Consequently, high mortality of dispersing cougars, the potential recruits of subpopulations, may lower resilience of a metapopulation.

Refuges- areas containing cougar subpopulations that are protected from human-caused mortality- would be important components of a flexible state-wide management strategy. Refuges would function as robust biological "savings accounts" that contribute to population resilience (Weaver et al. 1996) by countering management-related uncertainties or mistakes in other exploited subpopulations or where fragmentation increases mortality (McCullough 1996). At least 2 refuges >2,590 km^2 or 1,000 mi.^{2} may be adequate in New Mexico (i.e., 1 each in the north and south). For example, our data indicate that an obvious refuge in the south would be the San Andres Mountains and Oscura Mountains chain on WSMR, which is a very primitive area about 2,733 km^2 (1,055 mi.^{2}) in size, and where people do not live, livestock are prohibited, and cougars very rarely kill livestock on adjacent ranches. Individual cougars from refuges involved in livestock predation could still be killed within the current regulations pertaining to cougars that kill livestock.

Conservation of wild landscape linkages between cougar subpopulations is essential to maintaining the metapopulation. Consequences of accelerating human developments (e.g., urbanization, highways) and attendant fragmentation of wildlands include increasing incidences of cougar-human encounters, killing of nuisance cougars, cougar deaths from vehicle collisions, and disruption of natural dispersal patterns.

6. **Findings:** The social organization and other behaviors of cougars are strong forces influencing natural selection. Adult male cougars are territorial, exhibit direct competition that often results in fighting, and sometimes cannibalize other cougars. Intra-species killing was the most important cause of death for both genders and all age classes in the unhunted cougar population we studied. Territoriality in males and mutual avoidance in females probably helps to maximize reproductive success. Dispersal and philopatry of offspring are each adaptive strategies that may maximize fitness at the individual level.
   Implications: These behavioral characteristics may have evolved principally during the past 2 million years and prior to the large-scale human exploitation of cougars that has occurred during the past 100 to 300 years. Thus, the very recent events of human exploitation of cougars may have occurred only during the last 0.005 to 0.015% of the evolutionary history of the species. Human exploitation through sport-hunting, control, and extinctions probably disrupts the traditional patterns of natural selection in cougars, the long-term effects of which are unknown. Refuges for cougars would enable subpopulations to continue to evolve relatively naturally, and thus provide diversity of genotypes in todays world of mostly human-determined selection. Dispersal of cougars from refuges will also ensure that those genotypes will be carried to human impacted subpopulations.

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Table 3.1. Summary of cougar snare capture efforts on the San Andres Mountains, New Mexico, 1985-1995.

Year	No. marked cougars 1st captured[a]	Total cougars recaptured[b]	No. snare captures	No. snare sites	No. snare days[c]	No. snare days/ capture
1985 (Aug.-Dec)	3	1	4	16	426	107
1986	7	0	7	129	1,446	207
1987	6	9	15	211	2,149	143
1988	14	13	27	227	5,072	188
1989	7	15	22	215	3,987	181
1990	7	18	25	244	4,675	187
1991	5	34	39	287	7,689	197
1992	15	16	31	258	4,066	131
1993	6	16	22	282	5,793	263
1994	7	10	17	268	4,778	281
1995 (Jan.-Feb.)	1	0	1	69	452	452

[a] Cougars 1st captured included 36 males, 42 females.

[b] Marked cougars recaptured included 35 males recaptured 77 times and 34 females recaptured 55 times.

[c] Steel leg-hold traps were used in 114 trap days. Only 1 female was caught. We ceased using traps 22 January 1986.

Table 3.2. Number of cougars ≥36 months old that were back-logged into the population each year, San Andres Mountains, New Mexico, 1986-1994.[a]

	YEAR								
AREA	1986	1987	1988	1989	1990	1991	1992	1993	1994
TA[b]									
No. M:F	0:3	1:2	0:1	0:0	0:0	0:0	0:1	0:1	0:0
CR[c]	0.70	0.77	0.93	1.0	1.0	1.0	0.93	0.94	1.0
			TA 1988-1994 $\bar{x}$=0.97[d]						
RA[b]									
No. M:F	5:3	2:2	0:0	1:2	1:2	2:2[e]	1:1	1:1	0:0
CR[c]	0.33	0.66	1.0	0.87	0.88	0.90	0.93	0.94	1.0
			RA 1988-1994 $\bar{x}$=0.93[e]						

[a] We assumed that all cougars that were ≥36 months old when first captured had entered the adult population at an earlier date. We back-logged those cougars on a population chart to the month that females were 21 months old and males were 24 months old (see text for empirical criteria).

[b] TA=Treatment Area; RA=Reference Area.

[c] CR=Confidence Rating = 1-No. cougars back-logged/No. adult cougars counted and back-logged per yr. CR estimates the minimum proportion of the adult population counted per year.

[d] Comparisons between TA and RA population dynamics were made for the span 1988-1994 when the mean CR was 0.97 and 0.93, respectively. By back-logging adult cougars we probably missed, population estimates probably approach 100% of adults actually present.

[e] A relatively high number of adult cougars were missed in the RA in 1991 because of the greater effort we spent in the TA during the experimental removal.

Table 3.3. Sex ratios of adult cougars counted on the TA and RA each year, 1988-1994, San Andres Mountains, New Mexico.[a]

	TA[b]			RA[b]		
	No. adults			No. adults		
Year	Males	Females	M:F Ratio[c]	Males	Females	M:F Ratio[c]
1988	7	8	1:1.4	9	9	1:1
1989	8	10	1:1.3	9	14	1:1.6
1990	7	12	1:1.4	9	15	1:1.7
1991	7	10	1:1.4	11	17	1:1.6
1992	5	9	1:1.8	11	18	1:1.6
1993	7	10	1:1.4	13	20	1:1.5
1994	9	10	1:1.1	14	18	1:1.3

[a] Sex ratios were determined for the number in each sex counted during an entire 12 month period.

[b] TA=Treatment Area (703 km^2). RA=Reference Area (1,356 km^2). Individuals that overlapped the TA-RA boundary were counted in both areas.

[c] None of the sex ratios were significantly different from 1:1 ($X^2<2.71$, 1 d.f., $P>0.10$).

Table 3.4. Sex ratios of adult cougars on the TA and RA during January population estimates each year, 1989-1995, San Andres Mountains, New Mexico.

	TA[a]			RA[a]		
	No. adults[b]			No. adults[b]		
Year	Males	Females	M:F Ratio[c]	Males	Females	M:F Ratio[c]
1989	7	7	1:1	8	7	1:0.9
1990	5	10	1:2	8	13	1:1.6
1991	7	10	1:1.4	9	12	1:1.6
1992	3	4	1:1.3	9	15	1:1.7
1993	5	9	1:1.8	11	15	1:1.4
1994	7	10	1:1.4	11	15	1:1.4
1995	7	9	1:1.3	12	17	1:1.4

[a] TA = Treatment Area (703 km^2); RA = Reference Area (1,356 km^2).

[b] Adult cougars that overlapped the TA-RA boundary were counted in each area.

[c] None of the sex ratios were significantly different from a 1:1 ratio ($X^2<2.71$, 1 d.f., $P>0.10$).

Table 3.5. Proportion of cougars in 3 broad age classes in the TA population each January, 1989-1995, San Andres Mountains, New Mexico.

	Adults[a]				
Year	Males	Females	Total	Subadults[a]	Cubs[a,b]
1989	.32	.32	.64	.18	.18
1990	.20	.41	.61	.12	.27
1991[c]	.25	.36	.61	.04	.36
1992[c]	.14	.18	.32	.23	.45
1993	.17	.31	.48	.10	.41
1994	.30	.42	.72	0	.28
1995	.25	.32	.57	0	.43
Mean	.23	.33	.56	.10	.34
SD	.07	.08	.13	.09	.10

[a] Age classes: Adults= cougars capable of successful breeding (females ≥21 months old, males ≥24 months old); Subadults= cougars independent from mothers but not capable of successful breeding; Cubs= offspring dependent on mothers.

[b] Proportion of cubs was calculated using the mean of the range of the number of cubs present.

[c] Between 9 December 1990 and 21 June 1991, 13 cougars (11 adults and 2 subadults) were removed from the TA.

Table 3.6. Proportions of cougars in 3 broad age classes in the RA population, each January, 1989-1995, San Andres Mountains, New Mexico.

	Adults[a]				
Year	Males	Females	Total	Subadults[a]	Cubs[a,b]
1989	.27	.24	.51	.07	.42
1990	.24	.38	.62	.06	.32
1991	.25	.34	.59	.03	.38
1992	.23	.38	.61	.05	.33
1993	.22	.30	.52	.10	.38
1994	.26	.35	.61	.09	.30
1995	.32	.46	.78	.05	.16
Mean	.26	.35	.61	.06	.33
SD	.03	.07	.09	.02	.08

[a] Age classes: Adults= cougars capable of successful breeding (females ≥21 months old, males ≥24 months old); Subadults= cougars independent of mothers but not capable of successful breeding; Cubs= offspring dependent on mothers.

[b] Proportion of cubs was calculated using the mean of the range of the number of cubs present.

Table 3.7. Age structure of the cougar population (TA and RA combined) during January estimates, 1989-1995, San Andres Mountains, New Mexico.

	Adults[a]				
Year	Males	Females	Total	Subadults[a]	Cubs[a,b]
1989	.29	.27	.56	.11	.33
1990	.22	.37	.59	.09	.32
1991	.26	.32	.58	.03	.38
1992	.19	.30	.49	.11	.40
1993	.19	.32	.51	.09	.40
1994	.24	.38	.62	.06	.31
1995	.27	.40	.68	.03	.29
Mean	.24	.34	.58	.07	.35
SD	.04	.05	.06	.03	.05

[a] Age classes: Adults= cougars capable of successful breeding (females ≥21 months old, males ≥24 months old); Subadults= cougars independent of mothers but not capable of successful breeding; Cubs= offspring dependent on mothers.

[b] Proportion of cubs was calculated using the mean of the range of the number of cubs present.

Table 3.8. Mean ages (in months) of adult cougars on the TA and RA each January, 1989-1995, San Andres Mountains, New Mexico.

AREA	Males			Females			All adults	
Year	n	mean age	SD[a]	n	mean age	SD[a]	mean age	SD[a]
TA								
1989	7	76.3[b]	31.0	7	50.4[b]	22.3	63.4	30.0
1990	5	83.0[b]	19.6	10	52.2[b]	24.4	62.5	27.1
1991	7	76.4	33.7	10	58.9	29.5	66.1	32.5
1992	3	97.7	40.1	4	80.5	23.1	87.9[c]	32.7
1993	5	78.0	49.7	8	60.1	36.3	67.0	42.9
1994	7	55.3	36.4	9	66.9	37.3	61.8	37.4
1995	7	46.7[b]	16.4	8	72.5[b]	34.0	60.5	30.1
RA								
1989	8	50.9	24.2	7	50.1	19.7	50.5	22.2
1990	8	56.6	26.1	13	43.9	24.1	48.8	25.6
1991	9	64.3	27.5	12	53.6	24.8	58.2	26.5
1992	9	64.9	32.2	15	47.1	21.5	53.8[c]	27.4
1993	11	68.2[b]	34.5	15	47.5[b]	18.1	56.3	28.2
1994	11	62.8	30.0	15	52.4	20.5	56.8	25.5
1995	12	64.8	35.2	14	65.9	20.5	65.3	28.3

[a] SD = population standard deviation.

[b] Mean ages of adult males and females were significantly different, two-tailed t-test, *P*<0.10.

[c] Mean ages of adult cougars in the TA and the RA were significantly different, two-tailed t-test, *P*<0.10.

Table 3.9. MICROMORT survival rates of adult cougars in the Treatment Area (TA)[a] and Reference Area (RA)[a], 1987-1994, San Andres Mountains, New Mexico.

	Males		Females	
Year	TA	RA	TA	RA
1987	1.0	0.763	0.500	0.562
1988	1.0	1.0	0.758	0.814
1989	0.708	1.0[b]	1.0	1.0
1990	1.0	1.0	0.813	0.823
1991	1.0	0.865	1.0	0.827[b]
1992	1.0	1.0	1.0	0.919
1993	0.840	0.720	1.0	0.765[b]
1994	0.829	0.904	0.790	0.905
Span Rates	0.493	0.430	0.244	0.198

[a] TA = 703 km^2; RA = 1,356 km^2.

[b] TA and RA survival rate comparisons were significantly different (Z-test, $P<0.10$).

Table 3.10. MICROMORT annual survival rates for adult cougars, 1987-1994, San Andres Mountains, New Mexico.[a]

	Males			Females		
Year	n	Survival rate	s^2	n	Survival rate	s^2
1987[b]	9	0.873	0.014	7	0.523	0.038
1988[b]	14	1.0	0.0	13	0.765	0.021
1989[b]	14	0.844	0.010	19	1.0	0.0
1990[b]	13	1.0	0.0	22	0.789	0.009
1991	15	0.896	0.010	22	0.871	0.007
1992	13	1.0	0.0	24	0.944	0.003
1993	16	0.790	0.012	24	0.834	0.008
1994	20	0.862	0.008	19	0.869	0.007
Mean		0.905	0.043		0.811	0.031
Span Rate[b]		0.450	0.015		0.188	0.008

[a] MICROMORT survival rates were computed with data from 34 radio-collared adult males (32,135 days) and 51 radio-collared adult females (38,180 days).

[b] Survival rates were significantly different ($Z=2.184$, $P=0.01$).

Table 3.11. Number and ages of adult cougars found dead and natural causes of mortality on the San Andres Mountains, New Mexico, 1985-1995.[a]

	Males			Females		
Cause of death	no.	%	Age in mos. ($\bar{x}$, SD)	no.	%	Age in mos. ($\bar{x}$, SD)
STRIFE	5	50	80.2, 41.5	10	53	50.5, 33.6
DISEASE	3	30	74.7, 9.3	2	11	78.0, 15.6
ACCIDENTS	0	0		3	16	45.0, 22.5
OLD AGE	2	20	147.5, 6.4	1	5	122.0
UNKNOWN	0	0		2	11	30.0, 5.7
SNAKE BITE	0	0		1	5	34.0
Subtotals	10		92.0, 40.6[b]	19		53.3, 32.6[b]

[a] This table includes all adult cougars found dead of natural causes during the study.

[b] Mean ages of adult males and females that died were significantly different (two-tailed t-test, t = 2.82, 27 d.f., $P<0.10$).

Table 3.12. Dispersal distances and philopatry for subadult cougars, San Andres Mountains, New Mexico, 1985-1995.[a]

	Male dispersal distance (km)				Female dispersal distance (km)			
Subadult origin, Distance estimator[b]	n	$\bar{x}$	SD	range	n	$\bar{x}$	SD	range
SAM progeny, NAC - IAC	8	101.3[c]	57.7	47.0-192.5	7	28.3[c]	26.1	5.6-78.5
SAM progeny,[d] NAC - MS	5	114.7	65.2	42.2-195.6				
SAM progeny, NAC - LL	1	53.4						
SAM progeny, CS - LL	1	53.1			1	76.6		
SAM progeny CS - MS	1	84.4						
Unknown, CS - IAC					1	74.4		
Unknown, CS - LL	1	175.7			1	118.2		
Philopatric progeny, NAC - IAC	0[d]				12			

[a] Cougars dispersed if the independent home range overlapped <5% of the natal home range (using the 90% Minimum Convex Polygon estimator) or the last location or mortality site was outside of the natal home range.

[b] Origins and endpoints of Distance Estimators: NAC (Natal home range Arithmetic Center), IAC (Independent home range Arithmetic Center), MS (Mortality Site), CS (Capture Site), LL (Last Location).

[c] Mean male dispersal distances were significantly greater than mean female dispersal distances (one-tailed Wilcoxon rank sum test, $n_1=7$, $n_2=8$, $T=35$, $P<0.025$).

[d] Two male subadults that were killed by male cougars on their natal areas are not included in this table.

Table 3.13. Emigration of cougar progeny from the San Andres Mountains, New Mexico, 1 February 1990 to 23 February 1995.

Succesful Emigrants	Emigration Rates[a]	
	no./yr.[b]	no./100 km^2/yr.[b]
Males	3.8	0.18
Females	4.8	0.23
Totals	8.6	0.41

[a]Emigration rates estimated from mortality and recruitment rates of 114 marked cubs (51 male, 63 females) out of 137 progeny born from 1 Feb. 1988 - 19 Nov. 1992. We used subadult survival rates (sFRS) for males (0.56) and females (0.88) and assumed an even sex ratio for the 23 unmarked progeny.

[b]Equations:

1. (51 male cubs - 16 male deaths) x 0.56 sFRS - 4 male recruits = 15.6 male emigrants.
2. 15.6 male emigrants ÷ 51 male cubs = 0.31 male emigration rate.
3. [51 marked male cubs + (0.5 males x 23 unmarked cubs)] x 0.31 male emigration rate ÷ 5.1 yr. = 3.8 male emigrants per yr.
4. (63 female cubs - 20 female deaths) x 0.88 sFRS - 17 female recruits = 20.8 female emigrants.
5. 20.8 female emigrants ÷ 63 female cubs = 0.33 female emigration rate.
6. [63 marked female cubs + (0.5 females x 23 unmarked cubs)] x 0.33 female emigration rate ÷ 5.1 yr. = 4.8 female emigrants per yr.
7. 3.8 male emigrants per yr. x 100 km^2 ÷ 2,059 km^2 = 0.18 male emigrants per 100 km^2 per yr.
8. 4.8 female emigrants per yr. x 100 km^2 ÷ 2,059 km^2 = 0.23 female emigrants per 100 km^2 per yr.

Table 3.14. Recruitment rates of progeny and immigrants into the adult cougar population, 1 February 1990 to 23 February 1995, San Andres Mountains, New Mexico.[a]

	Progeny Recruitment		Immigration Recruitment		Total Recruitment	
	no./yr	no./100 km^2/yr	no./yr	no./100 km^2/yr	no./yr	no./100 km^2/yr
Males	0.8	0.04	2.8	0.14	3.6	0.17
Females	3.3	0.16	1.6	0.08	4.9	0.24
Totals	4.1	0.20	4.4	0.22	8.5	0.41

[a] SAM study area = 2,059 km^2.

[b] Recruitment of progeny based on 18 marked progeny (3 males, 15 females) and 3 probable progeny (1 male, 2 females) recruited during the 5.1 year span.

[c] Recruitment of immigrants based on 22 cougars (14 males, 8 females) recruited during the 5.1 year span.

Table 3.15. Cougars removed from the 703 km^2 TA, 9 December 1990 to 22 June 1991, San Andres Mountains, New Mexico.

Age & Sex Category	No. removed	Age (mo.)		
		$\bar{x}$	SD	range
Adult males	5[a]	64.0	32.8	30-102
Adult females	6	46.0	28.9	22-102
Subadult females	2	16.5	0.7	16-17

[a] One adult male returned to his original home range on the TA 166 days after removal; he lived there for the duration of the study. A second adult male returned to his original home range on the TA 469 days after removal, but he was there only for about 12 days before he moved north onto the RA and died.

Table 3.16. Cougar population, number of cougars removed, and post-removal cougar population on the TA, San Andres Mountains, New Mexico, December 1990 to July 1991.

Population description	Adults		Subadults		Cubs			Total
	Males	Females	Males	Females	Males	Females	Unkown	
PRE-TREATMENT (Dec. 1990)								
Cougars present	7	10	0	2	4	5	2	30
TREATMENT (Dec. 1990-June 1991)								
Cougars removed[a]	5[b]	6	0	2	1[c]	2[c]	0	16
Removal rate	0.71	0.60		1.0	0.25	0.40	0	.53
POST-TREATMENT (July 1991)								
Cougars present	3b	5	0	0	3	3	2	16
Removal rate[d]	0.57	0.50		1.0	0.25[d]	0.40[d]	0	.47

[a] Cougars were removed alive and translocated to northern New Mexico between 9 Dec. 1990 - 22 June 1991. See Chapter 7 for the study of the translocated cougars.

[b] One adult male that was removed returned to his original home range 166 days later on 21 July 1991, after the removal period. He remained as a member of the TA population until the end of the study.

[c] During the removal period, one male cub and 1 female cub from 1 litter died, and 1 female cub from another litter either dispersed or died.

[d] Post removal reduction rate = proportion of cougars removed from each category. Reduction rate for all adults = 0.53. Reduction rate for all independent cougars (adults + subadults) = 0.58. Reduction rate for the total population = 0.47.

Table 3.17. Estimated cougar population[a] on the 703 km^2 TA each January, 1988-1995, San Andres Mountains, New Mexico.

	Adult		Subadult			
Year	Males	Females	Males	Females	Cubs	Total
1988	5.14	3.02	0	0	6	14.16
1989	5.94	6.04	1	2.59	2.89-4.67	18.46-20.24
1990	4.47	8.82	1	2	4.19-9.01	20.48-25.30
1991[b]	6.34	8.47[b]	0	1[b]	7-11.68	22.81-27.49
1992	2.67	3.22	0.68	4	10	20.57
1993	4.08	8.20	2-3[c]	0-1[c]	6.20-14.60	21.48-29.88
1994	5.32	9.20	0	0	5-8	19.52-22.52
1995	5.78	8.20	0	0	9-15	22.98-28.98

[a] Radio-collared cougars that lived along either the TA-RA or study area boundaries were included in the TA and/or RA based on the proportion of their aerial locations in each area during each 12-month period. Cubs were included in the TA and RA in identical proportions as their mothers.

[b] Cougars were experimentally removed from the TA from 9 Dec. 1990 to 22 June 1991. The Jan. 1991 estimate reflects the absence of 1 adult female and 1 subadult female that were removed Dec. 1990.

[c] Subadults present in Jan. 1993 consisted of either 3 males or 2 males and 1 female.

Table 3.18. Estimated cougar population[a] on the 1,356 km^2 RA each January, 1989 - 1995, San Andres Mountains, New Mexico.

	Adult		Subadult			
Year	Males	Females	Males	Females	Cubs	Total
1989	6.81	5.96	1	0.41	9.11-12.33	23.29-26.51
1990	7.04	11.18	1	1	10-14	30.22-32.22
1991	7.84	10.53	0	1	9-17.32	28.37-36.69
1992	8.33	14.28	0.32	1	8.5-14.5	32.43-38.43
1993	9.66	14.80	2	3	13.8-23.40	43.26-52.86
1994	8.97	14.54	2	2	9-16.48	36.51-43.99
1995	11.16	16.10	1	1	6	35.26

[a] Radio-collared cougars that lived along either the TA-RA or study area boundaries were included in the TA and/or RA based on the proportion of their aerial locations in each area during each 12-month period. Cubs were included in the TA and RA in identical proportions as their mothers.

Table 3.19. Estimated density of cougars on the 703 km^2 TA each January, 1988 - 1994, San Andres Mountains, New Mexico.

	Cougars / 100 km^2			
Year	Adult Males	Adult Females	Total Adults	Total Cougars[a]
1988	0.73	0.43	1.16	2.01
1989	0.84	0.86	1.70	2.63-2.88
1990	0.64	1.25	1.89	2.91-3.60
1991	0.90	1.20[b]	2.10	3.24-3.91
1992[c]	0.38	0.46	0.84	2.93
1993	0.58	1.17	1.75	3.06-4.25
1994	0.76	1.31	2.07	2.78-3.20
1995	0.82	1.17	1.99	3.27-4.12

[a] Total Cougars includes adults, subadults, and cubs.

[b] The Jan. 1991 estimate reflects the absence of 1 adult female that was removed in December 1990.

[c] Cougars were experimentally removed from the TA from 9 Dec. 1990 - 22 June 1991.

Table 3.20. Estimated cougar density on the 1,356 km^2 RA each January, 1989 - 1995, San Andres Mountains, New Mexico.

	Cougars / 100 km^2			
Year	Adult Males	Adult Females	Total Adults	Total Cougars[a]
1989	0.50	0.44	0.94	1.72-1.96
1990	0.52	0.82	1.34	2.23-2.38
1991	0.58	0.78	1.36	2.09-2.71
1992	0.61	1.05	1.66	2.39-2.83
1993	0.71	1.09	1.80	3.19-3.90
1994	0.66	1.07	1.73	2.69-3.24
1995	0.82	1.19	2.01	2.60

[a] Total Cougars includes adults, subadults, and cubs.

Table 3.21. The estimated number of cougars using the San Andres Mountains (2,059 km^2), New Mexico, each January 1989-1995.

	Adult[a]				
Year	Males	Females	Subadults	Cubs	Total[b]
1989	13	12	5	12-17	42-47
1990	12	20	5	14-21	51-58
1991	15	19	2	16-29	52-65
1992	11	17	6	20-26	54-60
1993	14	23	7	20-38	64-82
1994	15	24	4	14-25	57-68
1995	17	25	2	15-21	59-65

[a] Range of no. adult cougars = 25-42.

[b] Range of total no. cougars = 42-82.

Table 3.22. Density of adult cougars (cougars / yr. / 100 km^2) on the TA (703 km^2), 1986-1994, San Andres Mountains, New Mexico.

	Cougars / yr.[a]			Cougars / yr. / 100 km^2		
Year	Males	Females	Total	Males	Females	Total
1986	3.44	5.02	8.46	0.49	0.71	1.20
1987	4.02	4.20	8.22	0.57	0.60	1.17
1988	5.14	4.46	9.60	0.73	0.63	1.36
1989	4.91	7.48	12.39	0.70	1.06	1.76
1990	5.55	8.57[b]	14.12[b]	0.79	1.22	2.01
1991	2.67	4.96	7.63	0.38	0.71	1.09
1992	3.66	6.96	10.62	0.52	0.99	1.51
1993	4.45	8.62	13.07	0.63	1.23	1.86
1994	4.82	8.33	13.15	0.69	1.18	1.87

[a] Cougars / yr. = sum of proportions of each year that each adult cougar was present on the TA.

[b] Assuming that the 1 adult female that we removed on 9 Dec. 1990 would have been present to 31 Dec., females / yr. would equal 8.63, and the total would equal 14.18. In rates of increase calculations, we used 14.18 cougars / yr.

Table 3.23. Density of adult cougars (cougars / yr. / 100 km^2) on the RA (1,356 km^2), 1988-1994, San Andres Mountains, New Mexico.

	Cougars / yr.[a]			Cougars / yr./ 100 km^2		
Year	Males	Females	Total	Males	Females	Total
1988	4.70	5.01	9.71	0.35	0.37	0.72
1989	7.14	8.10	15.24	0.53	0.60	1.13
1990	7.62	10.49	18.11	0.56	0.77	1.33
1991	8.41	11.25	19.66	0.62	0.83	1.45
1992	8.77	13.35	22.12	0.65	0.98	1.63
1993	9.28	14.67	23.95	0.68	1.08	1.76
1994	9.10	15.20	24.30	0.67	1.12	1.79

[a] Cougars / yr. = sum of proportions of each year that each adult cougar was present on the RA.

Table 3.24. Observed exponential rate of increase (*r*) in adult cougars on the San Andres Mountains, New Mexico, 1988-1995.

Population Estimator Area, Years	Regression Equation	r^2	*r*
No. Adult Cougars each Jan.			
TA,			
1988-1991[a] (Pre-treatment)	y = 1.960 + 0.209x	0.93	0.21
1992-1995 (Post-treatment)	y = 0.593 + 0.278x	0.71	0.28
RA,			
1989-1992	y = 2.440 + 0.172x	0.88	0.17
1992-1995	y = 2.906 + 0.053x	0.70	0.05
1989-1995	y = 2.580 = 0.110x	0.87	0.11
No. Adults Cougars Each Year			
TA,			
1987-1990[a] (Pre-treatment)	y = 1.915 + 0.188x	0.98	0.19
1991-1994 (Post-treatment)	y = 1.176 + 0.186x	0.87	0.19
RA,			
1988-1991	y = 2.140 + 0.231x	0.88	0.23
1991-1994	y = 2.935 + 0.071x	0.89	0.07
1988-1994	y = 2.351 + 0.138x	0.84	0.14

[a] Observed exponential rates of increase for the TA were calculated by including the adult female that was removed in Dec. 1990 in both the Jan. 1991 population estimate and the 1990 annual population estimate.

Table 3.25. Observed exponential rates of increase (*r*) for adult male and female cougars, San Andres Mountains, New Mexico, 1988-1995.

Population Estimator:	Males			Females		
Area, Years,	Regression Equation	r^2	*r*	Regression Equation	r^2	*r*
No. Adult Cougar each Jan.						
TA,						
1988-1991[a] (Pre-treatment)	$y = 1.605 + 0.035x$	0.09	0.04	$y = 0.885 + 0.380x$	0.88	0.38
1992-1995 (Post-treatment)	$y = -0.218 + 0.257x$	0.92	0.26	$y = 0.006 + 0.291x$	0.59	0.29
RA,						
1989-1992	$y = 1.835 + 0.071x$	0.96	0.07	$y = 1.665 + 0.255x$	0.80	0.26
1992-1995	$y = 1.813 + 0.079x$	0.67	0.08	$y = 2.510 + 0.035x$	0.72	0.04
1989-1995	$y = 1.823 + 0.077x$	0.91	0.08	$y = 1.930 + 0.138x$	0.75	0.14
No. Adult Cougars each Year						
TA,						
1987-1990[a] (Pre-treatment)	$y = 1.355 + 0.091x$	0.73	0.09	$y = 1.110 + 0.267x$	0.91	0.27
1991-1994 (Post-treatment)	$y = 0.061 + 0.196x$	0.93	0.20	$y = 0.802 + 0.177x$	0.82	0.18
RA,						
1988-1991	$y = 1.470 + 0.180x$	0.83	0.18	$y = 1.445 + 0.269x$	0.90	0.27
1991-1994	$y = 2.110 + 0.030x$	0.76	0.03	$y = 2.360 + 0.100x$	0.91	0.10
1988-1994	$y = 1.664 + 0.094x$	0.74	0.09	$y = 1.671 + 0.170x$	0.87	0.17

[a] Observed exponential rates of increase for the TA were calculated by including the adult female cougar that was removed in Dec. 1990 in both the Jan. 1991 population estimate and 1990 annual population estimate.

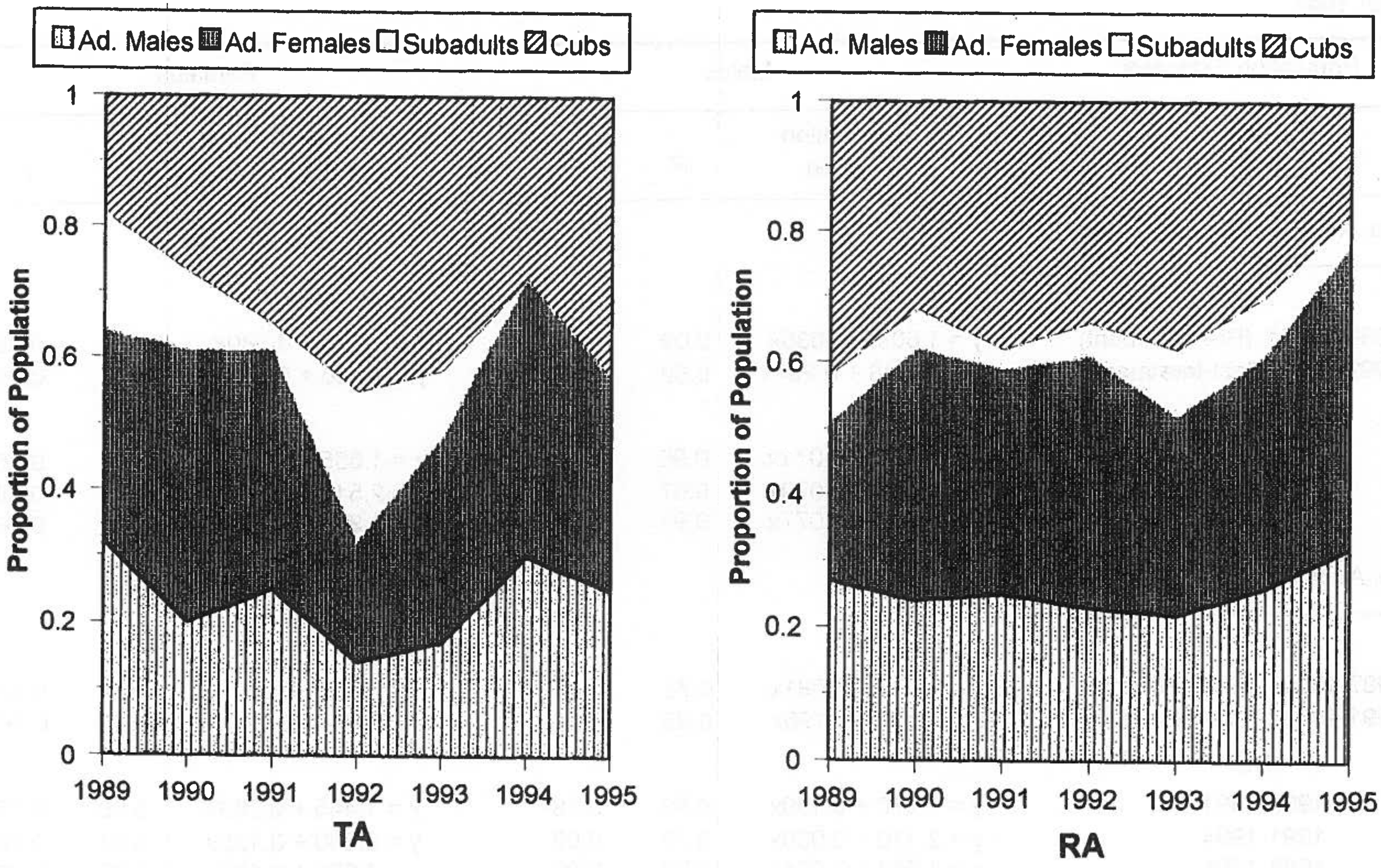

Fig. 3.1. Age structure of the cougar population in the TA and RA each January, San Andres Mountains, New Mexico, 1989-1995.

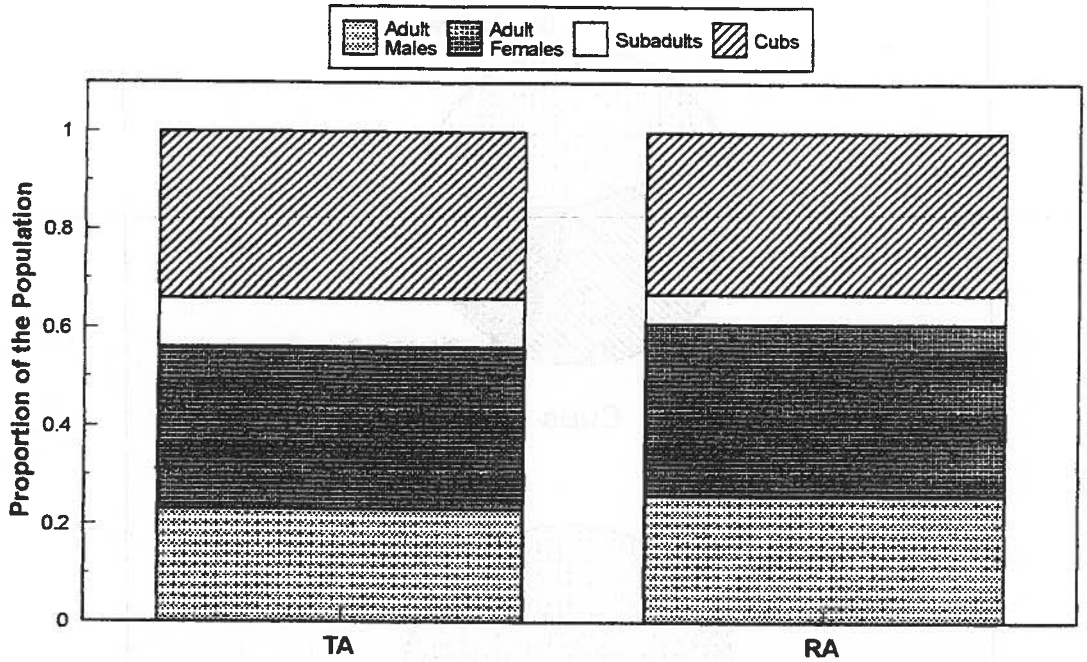

Fig. 3.2. The average proportions of adults, subadults and cubs in the cougar populations in the TA and the RA, San Andres Mountains, New Mexico, 1989-1995.

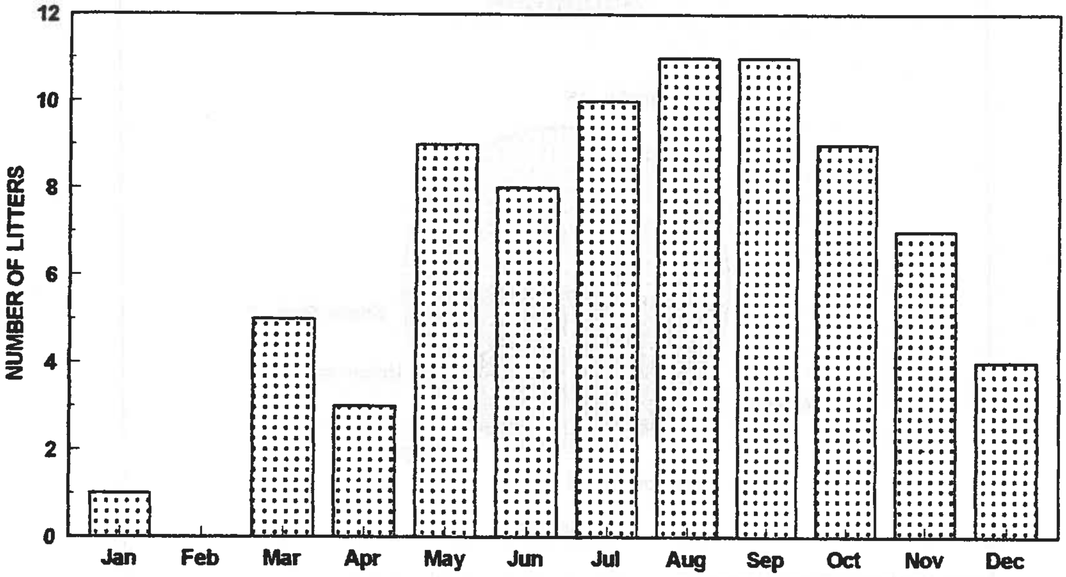

Fig. 3.3. Month of birth for 78 cougar litters born on the San Andres Mountains, New Mexico, from 1986 through 1994.

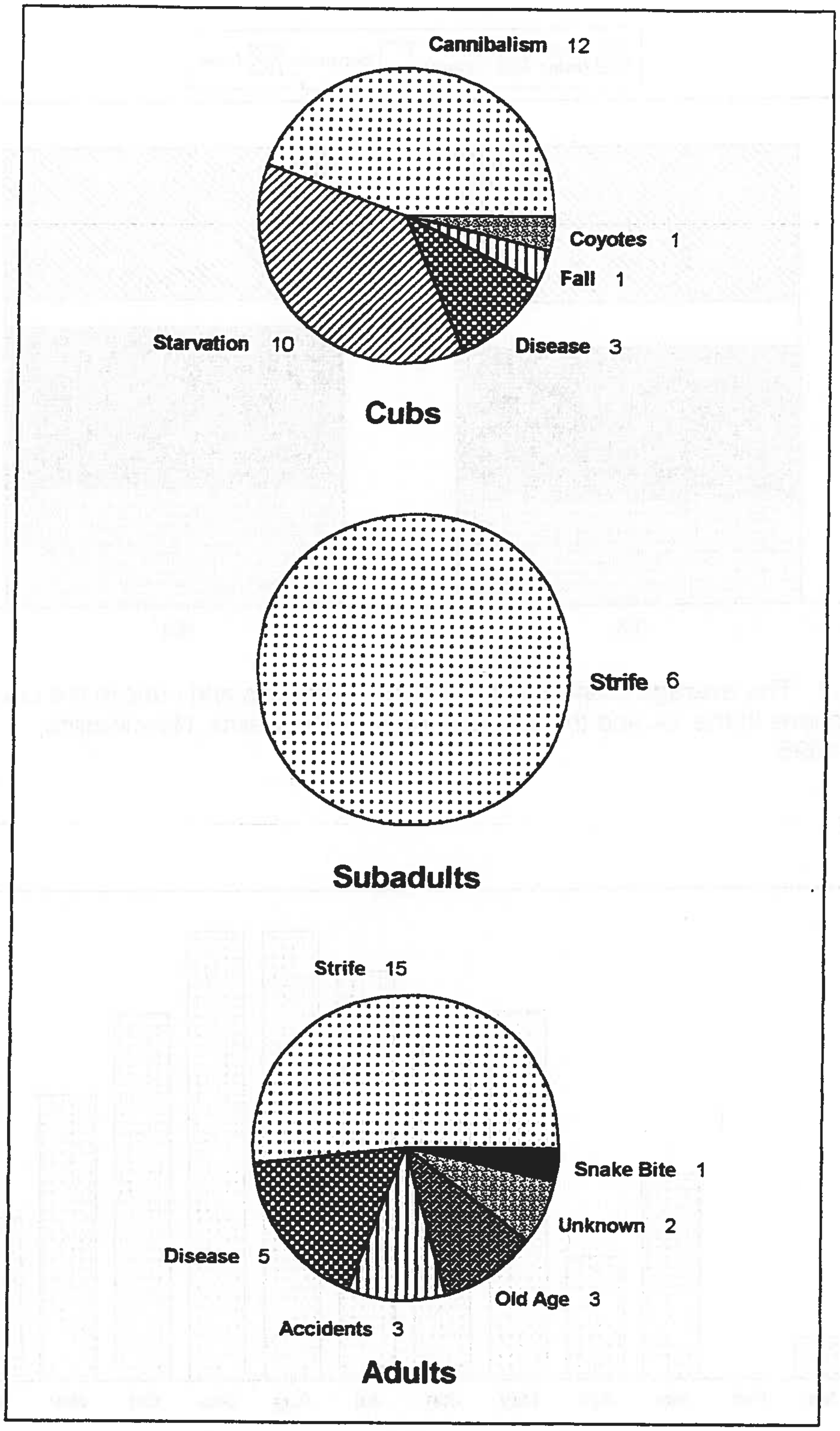

Fig. 3.4. Causes of mortality for cub (n=27), subadult (n=6) and adult (n=29) cougars on the San Andres Mountains, New Mexico from 1986 - 1994.

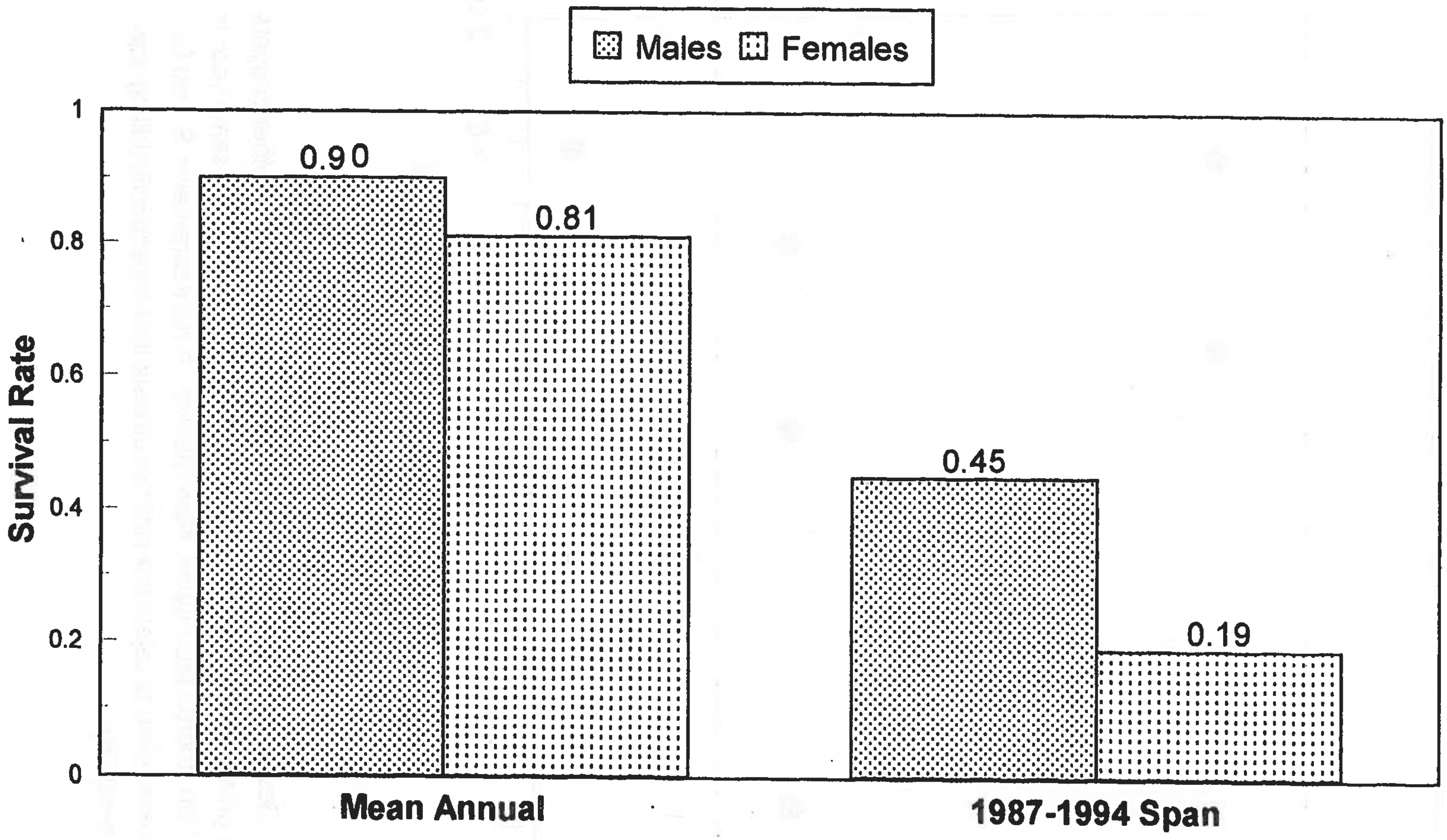

Fig. 3.5. Mean annual and span survival rates for adult radio-collared cougars, 1987-1994, San Andres Mountains, New Mexico.

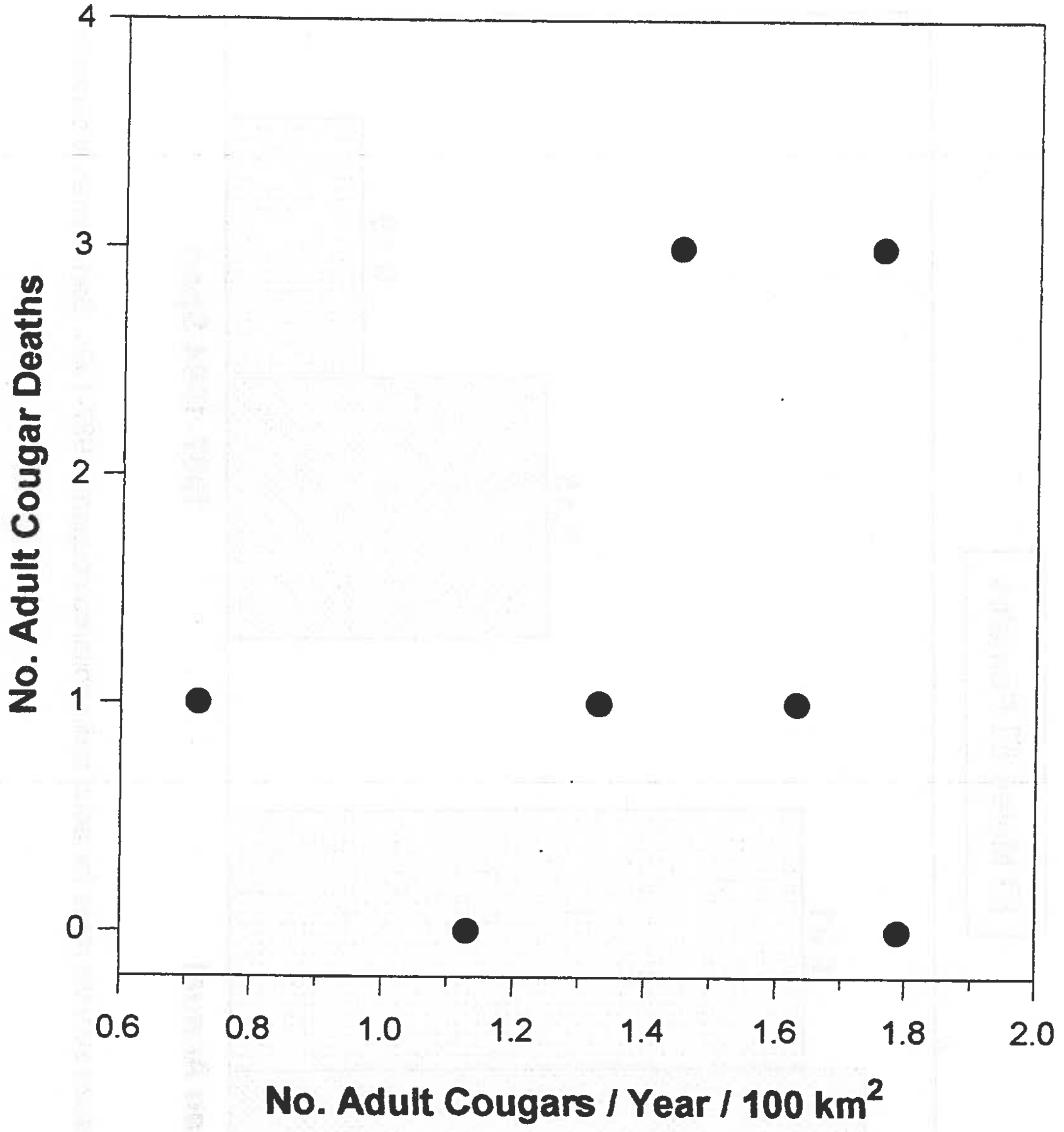

Fig. 3.6. Scatter plot of the number of adult cougars killed by other cougars during a given year versus the adult cougar density during the same year in the RA, San Andres Mountains, New Mexico. A non-parametric S Test for randomness failed to reject the null hypothesis that intraspecific killing was random (*P*=0.76).

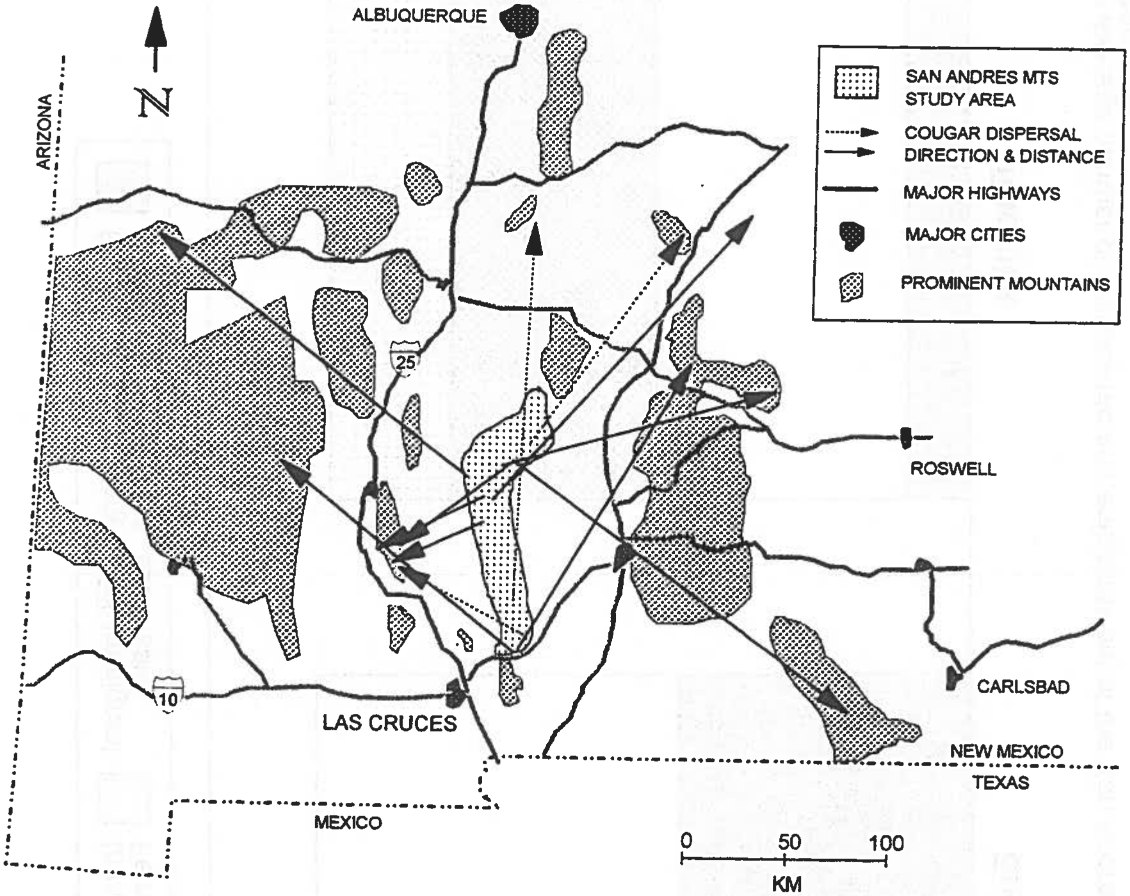

Fig. 3.7. Dispersal directions, distances and endpoints for 12 cougars from the San Andres Mountains study area (SAM) to areas outside the SAM. Nine of the cougars were born on the SAM (solid dispersal lines); the other 3 had unknown origins (dotted dispersal lines). Endpoints were either the arithmetic center of a cougar's independent home range, its mortality site, or its last location.

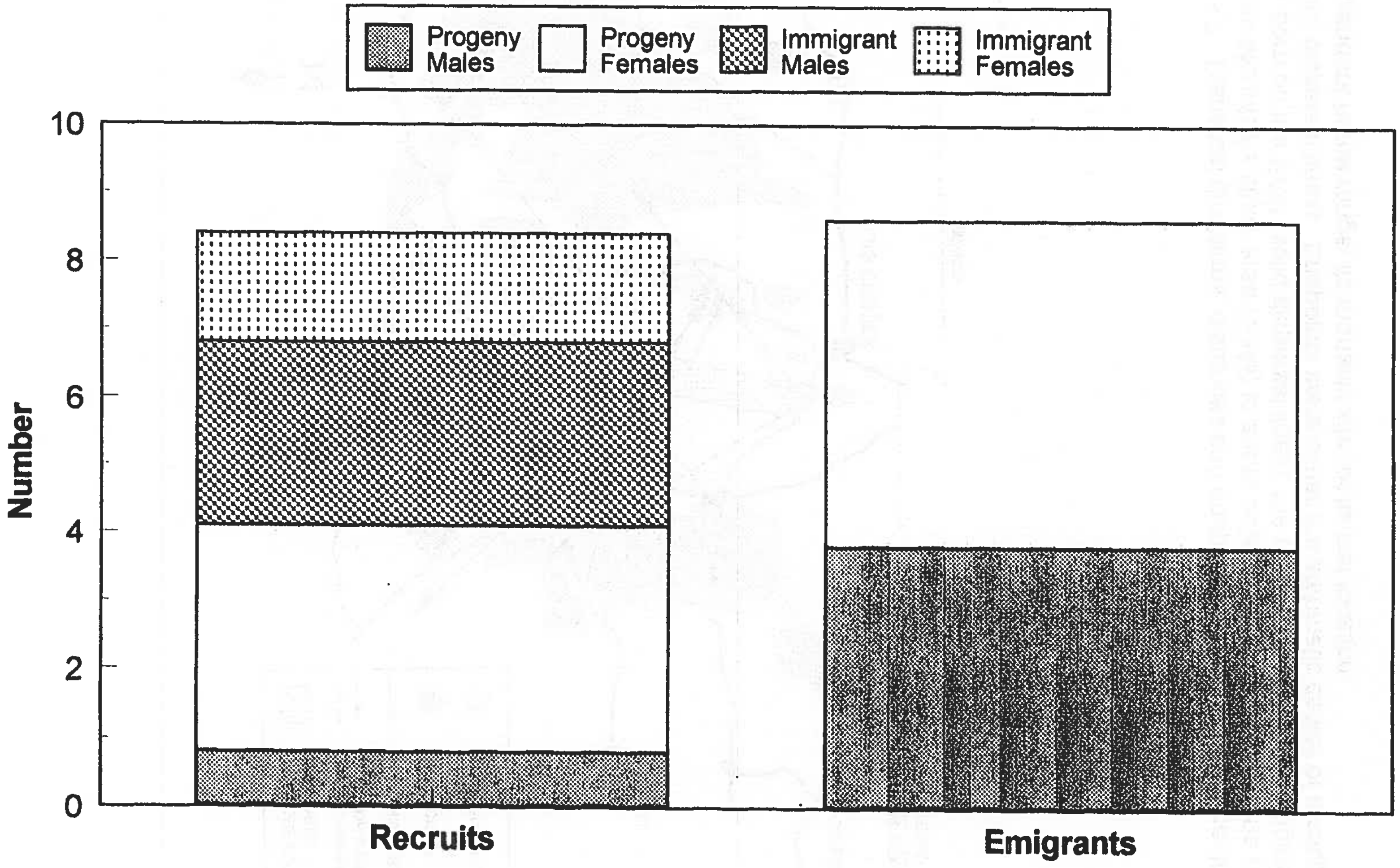

Fig. 3.8. The average number of recruits into and emigrants out of the San Andres Mountains cougar population each year, 1990-1995.

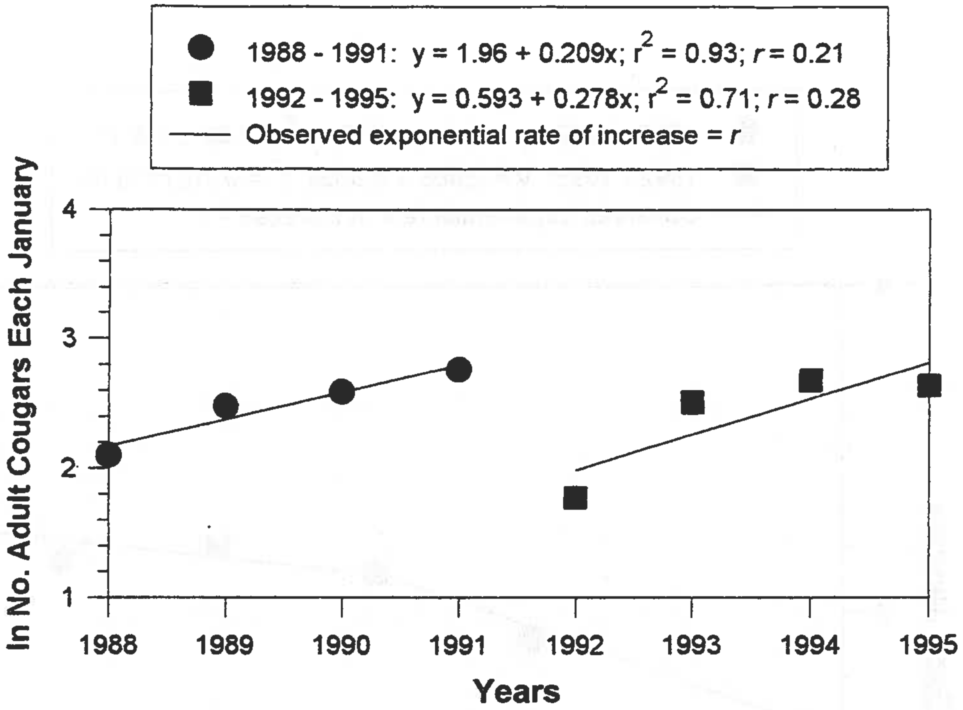

Fig. 3.9. Observed exponential rate of increase in adult cougars in the TA using January population estimates, 1988-1991 and 1992-1995, San Andres Mountains, New Mexico.

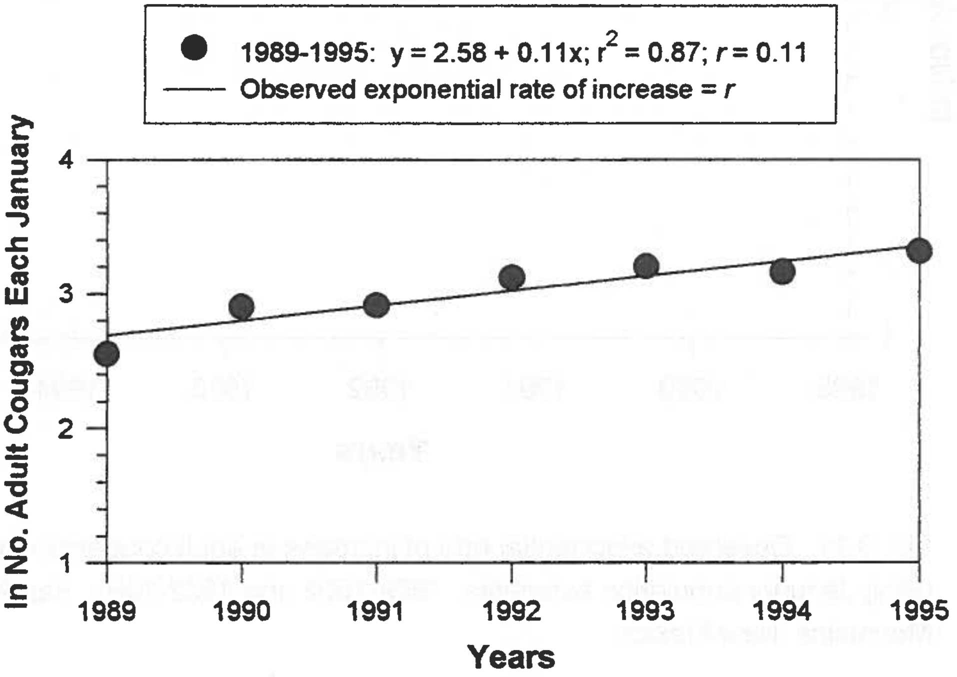

Fig. 3.10. Observed exponential rate of increase in adult cougars in the RA using January population estimates, 1989-1995, San Andres Mountains, New Mexico.

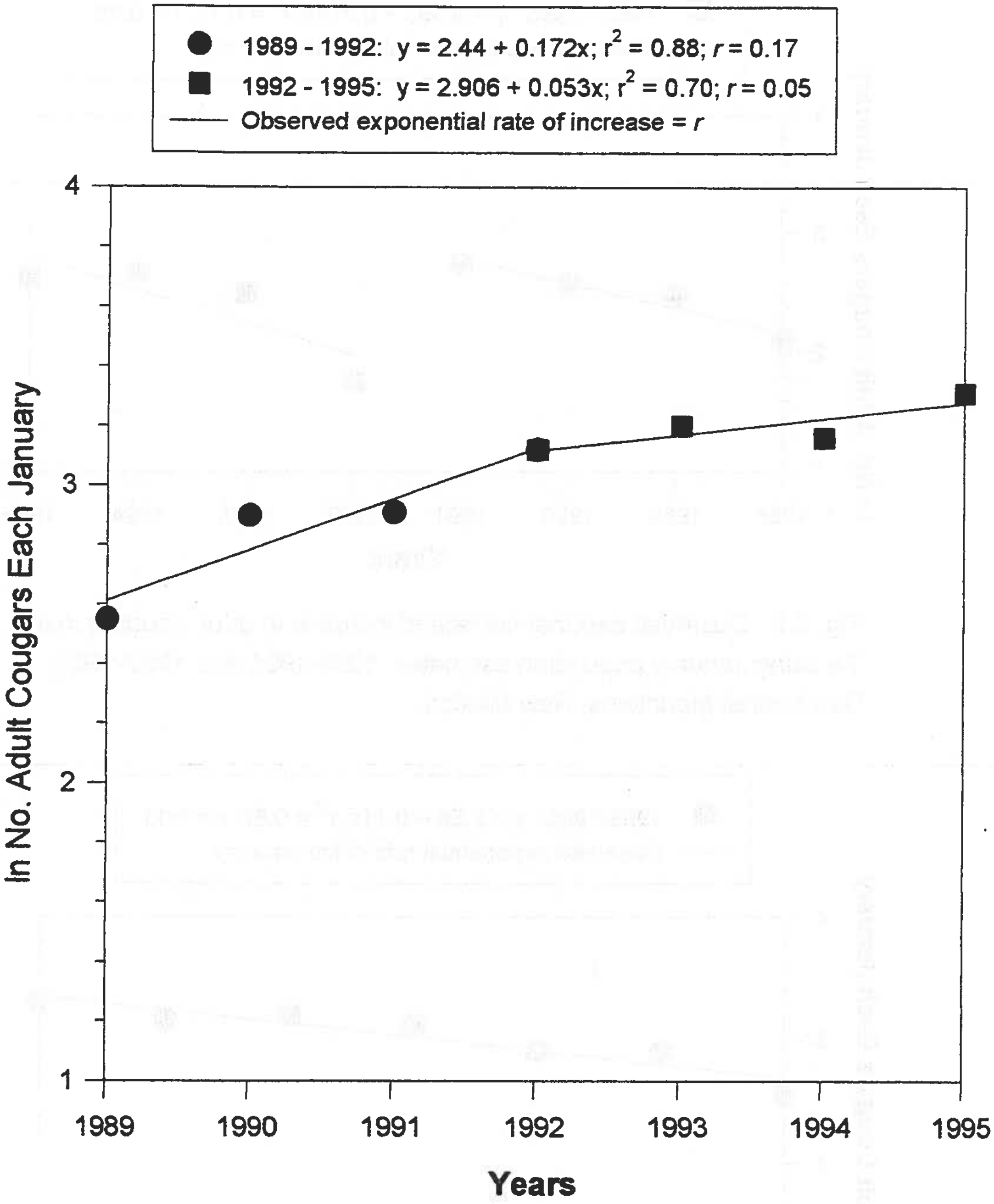

Fig. 3.11. Observed exponential rate of increase in adult cougars in the RA using January population estimates, 1989-1992 and 1992-1995, San Andres Mountains, New Mexico.

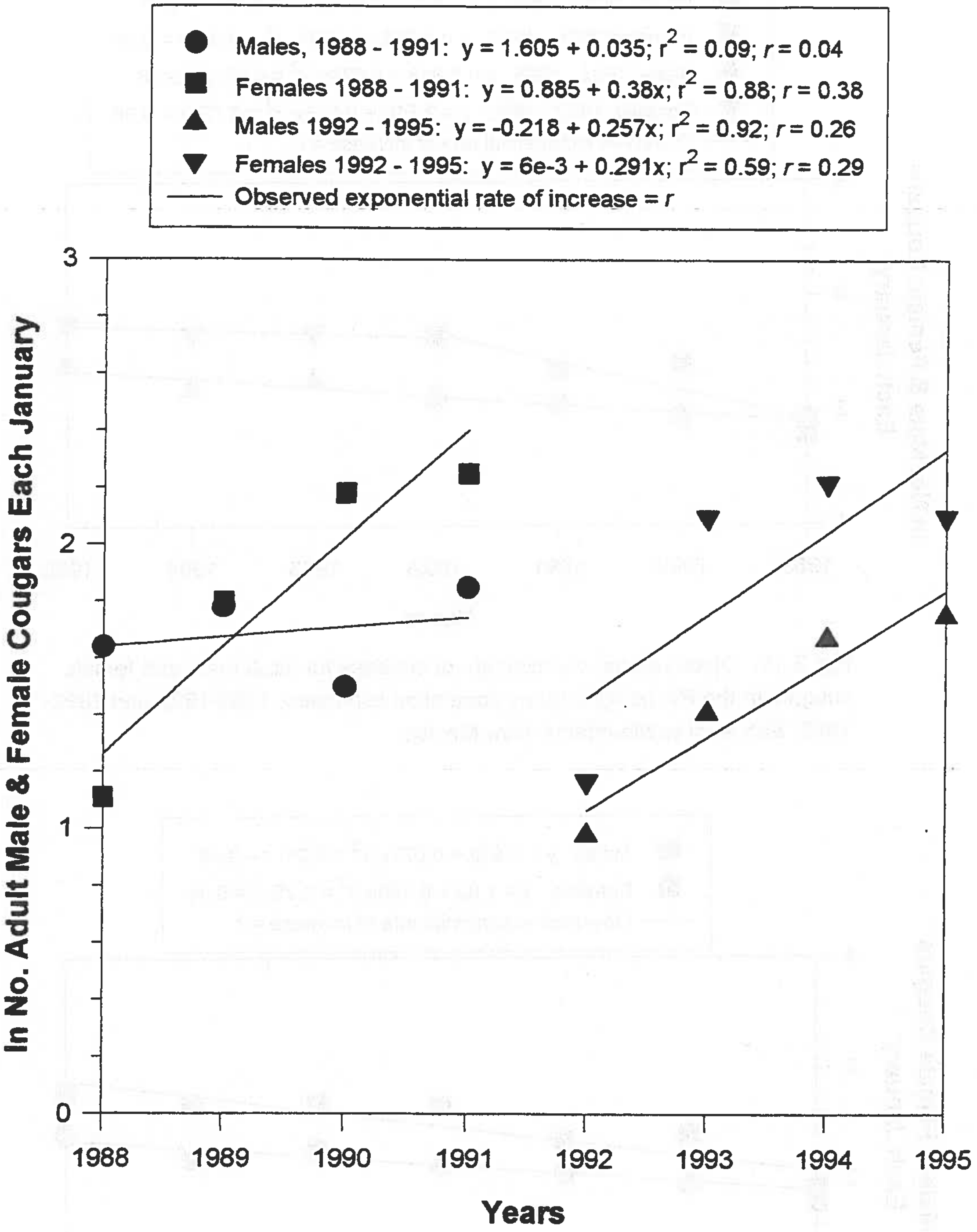

Fig. 3.12. Observed exponential rate of increase for adult male and female cougars in the TA using January population estimates, 1988-1991 and 1992-1995, San Andres Mountains, New Mexico.

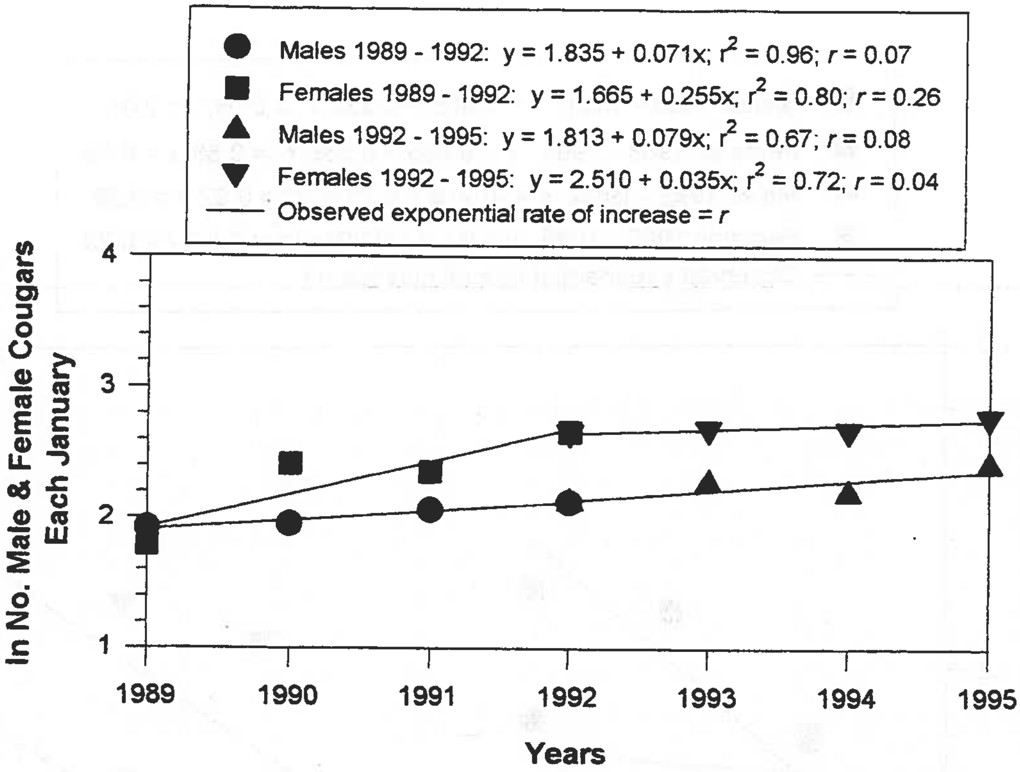

Fig. 3.13. Observed exponential rate of increase for adult male and female cougars in the RA using January population estimates, 1989-1992 and 1992-1995, San Andres Mountains, New Mexico.

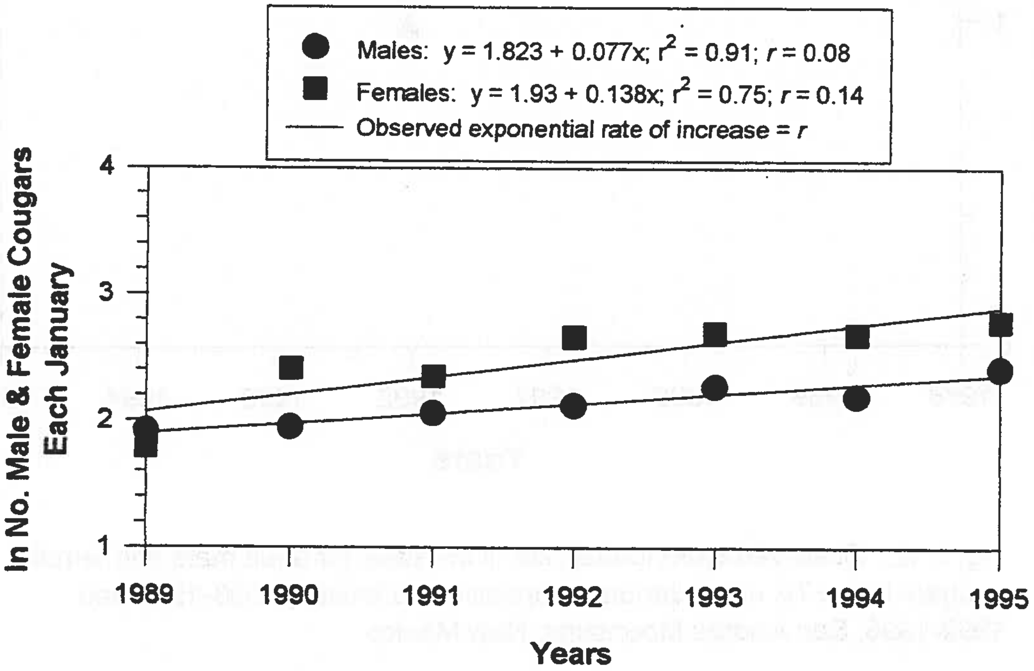

Fig. 3.14. Observed exponential rate of increase for adult male and female cougars in the RA using January population estimates, 1989-1995, San Andres Mountains, New Mexico.

CHAPTER 4. COUGAR SOCIAL ORGANIZATION

by L. Sweanor, K. Logan and M. Hornocker

Abstract: We conducted cougar research on on the 2,059 km^2 San Andres Mountains (SAM), New Mexico from August 1985 through March 1995. The SAM was divided into a 703 km^2 treatment area (TA) and a 1,356 km^2 reference area (RA). Cougars were protected from human exploitation in the SAM except for a 6.5- month period (Dec. 1990 to June 1991) when 58% of the independent cougars were removed from the TA. Population characteristics and social organization were determined using capture-recapture, ground-tracking, and radio-location data. We counted a total of 294 cougars, of which we captured and marked 241. Radio-collars were put on 126 cougars (49 males, 77 females). We recorded a total of 13,947 cougar locations. The population was comprised of, on average, 58% adults, 7% subadults, and 35% cubs. The male:female sex ratio of adult, subadult and cub cougars did not differ significantly from 1:1 ($P > 0.10$), however the adult and subadult classes favored females. Except for a short period during and after cougar removal in the TA, January population density estimates generally increased over time; they ranged from 1.2 to 2.0 adults/ 100 km2 from 1989 to 1995.

Home ranges were estimated using both the adaptive kernal (ADK) and minimum convex polygon (MCP) home range estimators. Annual home ranges based on the 90% ADK averaged 192.2 km^2 for adult males and 71.9 km^2 for adult females. Female annual home ranges were significantly smaller than male annual home ranges ($P < 0.0001$). Male home range size generally increased with increasing cougar density, whereas female home range size decreased. Female home range size during an entire reproductive cycle (birth of 1 litter to birth of subsequent litter) averaged 64.9 km^2. Cyclic and annual home range sizes for the same group of females were not significantly different ($P > 0.1$). Female home range size increased as the age of dependent cubs increased, and was largest when a female was solitary. Home range sizes of females with young cubs (≤ 6 months) were significantly smaller than those of females that were solitary ($P < 0.05$).

On average, adult females exhibited stronger annual home range fidelity than males. The percent of an adult male's home range that was utilized by that same male from year to year averaged 51.6% and 57.5% based on the 90% MCP and 90% ADK, respectively. For adult females, the amount of overlap averaged 60.3% and 62.2% based on the 2 methods, respectively. Males had significantly less annual home range overlap (90% MCP, $P = 0.09$) than females. Distances between mean annual locations for adult males and adult females averaged 5.7 km and 2.6 km, respectively. The distances between means of annual locations were significantly greater for males than for females ($P < 0.001$). Distances

between means of locations when females were raising young cubs (≤6 mo.), raising older cubs (7-12 mo.), and solitary averaged 3.1, 2.0, and 2.9 km, respectively, and they were not significantly different ($P > 0.10$).

Cubs became independent and dispersed at, on average, 13.4 and 15.6 months of age, respectively. All males dispersed from their natal home ranges; in contrast, some females were philopatric. Dispersal distances for males and females from their natal to independent home ranges averaged 101.3 and 28.3 km, respectively. Males dispersed significantly farther than females ($P < 0.025$). The directions of dispersal were uniformly distributed around a 360^0 circle ($P > 0.05$). Dispersal duration ranged from 0.2 to 7.8 months.

Annual home range overlap between adult males was generally greater than that found for adult females. The mean of means in annual home range (90% ADK) overlap was 62.8% between adult males and 49.2% between adult females. The amount of within-gender overlap increased with increasing cougar density. Adult males shared their annual home ranges (90% ADK) with, on average, 2.9 to 4.3 other adult males. Each adult female shared part of her annual home range with, on average 2.1 to 3.9 other adult females. The percent area adult females shared with adult males was greater than the percent area each male shared with adult females, as well as greater than the percent area shared between cougars of the same sex. Adult females shared an average of 89.1 to 96.6% of their home ranges (90% ADK) with 3.0 to 3.5 adult males each year. Analysis of the movements of cougars over 6- to 12-month periods indicated that cougar home ranges (particularly those of males) were dynamic and cougars of the same gender did not generally utilize shared areas at the same time.

Social interactions outside the mother-offspring family unit were rare. Independent cougars were located in association during only 4.9% of locations. The majority of associations (76.0%) were between males and females, of which 73.5% were for apparent breeding purposes. Of all the associations, 20 (7.6%) resulted in mortalities; mortalities included 5 adult males, 4 subadult males, 9 adult females, 2 subadult females, and 1 dependent cub. All mortalities were caused by adult immigrant or adult resident male cougars. Ten cubs from 5 litters were also killed by males, apparently while their mothers were not with them. Scars found on all captured adult males indicated fighting was fairly common.

Cougars communicated through visual, tactual, auditory, and olfactory mechanisms. Vocalizations included apparent distress calls (mews and chirps by nursling cubs), contact calls between family members (purrs, whistles), advertisement calls (ouch calls and caterwauls), and threat calls (hisses, spits and growls). Cougars, almost exclusively males, left visual and olefactory markers (scrapes) throughout their home ranges. Individual scrape sites could be utilized by more than 1 resident male, and were visited by females.

Land tenure in this study population was primarily based on prior rights; however, in males, prior rights were often contested. Cougars spaced themselves through territorial behavior in males and mutual avoidance behavior in females. The territorial and avoidance components of the land tenure system may be mechanisms which regulate the rate at which the cougar population increases toward carrying capacity.

4.1 OBJECTIVES

Prior to this research, there was no comprehensive study of cougar social organization in a desert environment. Studies on cougar social organization have been conducted in more northern temperate environments (most notably Hornocker 1969 and Seidensticker et al. 1973). These studies have provided a foundation of information; however, there is a potential for variability in social and home range structuring depending on geology, prey, climate and other variables (Seidensticker et al. 1973). Because social organization affects cougar population density and the way in which individuals use their environment, this information is essential for effectively managing and conserving the species. Humans manipulate cougar populations, either through hunting or for control purposes; thus, we also need to understand what effect those manipulations have on cougar population structure, and ultimately survival. We specifically wanted to address the following:

1. Determine the spatial and temporal distribution of cougars within the San Andres Mountains study area (SAM);
2. Describe cougar behavioral interactions based on sex, age and social status;
3. Determine the effects of an experimental removal (simulated control effort) on the social structure of the population.

4.2 FIELD METHODS

Field methods are described in detail in Chapter 3: *Cougar Population Dynamics*, and will be briefly summarized here. Information on cougar social organization, including individual use of space and relationships between cougars in space and time, was quantified primarily through intensive year-round efforts to capture, mark, release and radio-locate cougars on the study area. Our intent was to radio-collar all adults, tag all cubs with identifying markers, and radio-collar as many subadults as possible. Field work began in August 1985 and continued through March 1995.

Physical information was collected on each captured cougar, including sex, weight, condition, and age. Ages were initially estimated by using dental characteristics described in Ashman et al. (1983:23-26); then, as we collected information on tooth wear and pelage characteristics from known-age cougars in the population, we confirmed or adjusted the ages of cougars with unknown life histories.

All captured cougars were marked with an eartag and ear tattoo. Adult and subadult cougars were fitted with radio-collars that were equipped with mortality sensors. Radio-collars equipped with mortality sensors were also placed on 38 cubs that were from 1-14 months of age. Small cubs were fitted with transmitters on expandable, break-away collars.

Radio-collared cougars were relocated by triangulation from known locations on the ground, and from fixed-wing aircraft. Flights were conducted approximately once per week, in an attempt to locate each radio-collared cougar. Specific cougars were located more frequently to obtain detailed information on associations and movements. Locations were recorded as Universal Transverse Mercator Grid coordinates (U.T.M.) to the nearest 0.01 km, then entered in a database. All locations used in analyses had estimated error radii of $\leq$500 m, and 91.5% of the locations had error radii of $\leq$300m.

4.3 ANALYTICAL AND STATISTICAL METHODS

4.3.1 TERMINOLOGY

Terminology used to describe cougar age class and social status is modified from that found in Seidensticker et al. (1973), Hemker et al. (1984) and Sweanor (1990). We identified 3 age classes in the population: cubs (or kittens), subadults, and adults. Cubs were offspring still dependent on their mothers. Subadults were independent of their mothers, but were not capable of successful breeding. Adults were capable of successful breeding. For each radio-collared, known-age cougar on the SAM that was radio-monitored during the transition phase between subadulthood and adulthood, adulthood was based on the first documented association (when ≥18 months of age) with a cougar of the opposite sex. For cougars that were radio-collared at older ages, we considered age at adulthood to be 21 months for females and 24 months for males (see Chapter 3.4.3).

We used several terms to describe a cougar's social status. A resident was an adult or subadult that showed site attachment (continuous use of an area over time). A cub that became a subadult and left the boundaries of its natal home range (HR) was considered a disperser. A transient was largely nomadic; it did not restrict its activities to any one area. Any progeny that established a home range post independence that overlapped >5 percent of its natal HR (based on the 90% Minimum Convex Polygon) was considered a non-disperser, or philopatric. Immigrants were new arrivals on the SAM who subsequently established residency, whereas emigrants completely dispersed outside of the SAM population.

4.3.2 POPULATION CHARACTERISTICS

Because our aim was to describe cougar social organization and consequently the relationships between individual cougars, it was imperative that we knew as many individuals in the population as possible. We estimated the proportion of adult cougars we were aware of (collared and uncollared) during any given year based on our capture-recapture record, each cougar's age at first capture, movements of the radio-collared cougars, and the presence of sign that indicated the presence of uncollared individuals. We assumed that all cougars captured for the first time when they were <36 months old had just entered the SAM population. However, cougars captured for the first time when they were ≥36 months old were assumed to have entered the population on the date we considered them to have become adults: 24 months for males; 21 months for females. We adjusted our estimates of the adult cougar population by back-logging those older individuals (cougars that we probably failed to capture during previous years) into the population. During each year from 1988 through 1994, we had to back-log from 0-4 adult cougars into the population; these animals comprised less than 10% of the population during any given year (see Table 3.2). Consequently, from 1988 through 1994, the number of adult cougars on the SAM that we were aware of probably approached 100% of the adult population actually present. Most of the social organization analyses are based on the 1988-1994 time interval because we knew we were monitoring (via radio-telemetry or sign) over 90% of the adult population.

Methods for determining cougar density on the SAM are described in detail in Chapter 3.3.3 We determined densities for the Treatment Area (TA) and Reference Area (RA) separately because we experimently reduced the number of independent cougars in the TA by 58% during December 1990 through June 1991 (see Table 3.16). Density estimates are presented in Tables 3.17-3.23.

4.3.3 HOME RANGE SIZE

We defined home range as the area where an animal restricted the majority of its movements; it was the "area traversed by an individual in its normal activities of food gathering, mating and caring for young" (Burt 1943:351). Home range was estimated for individual resident cougars using the minimum convex polygon (MCP; Hayne 1949) and the adaptive kernal (ADK; Worton 1989) methods. Program CALHOME (Kie et al. 1994) was utilized to perform these calculations. The MCP was used because of its graphic simplicity, wide historical use, ease of calculation (Jennrich and Turner 1969, White and Garrott 1990), and its comparitive value to the many other studies which have used this method to describe cougar home range size. Because home range size calculated using the MCP is greatly influenced by outliers (Ackerman et al. 1989, White and Garrott 1990), both a 100% and 90% MCP were calculated.

The ADK, a non-parametric method for estimating an animal's probabilistic utilization distribution (UD; Worton, 1989, Kie et al. 1994), was also used to calculate home range size because it was a flexible model that was considered to provide the most realistic representation of a home range (Worton 1989). The harmonic mean, a home range estimator used by Sweanor (1990) to describe home range size for cougars on the SAM from 1985-1988, was not utilized because it was shown to be an inappropriate application of kernal methods (Worton 1987, 1989). Both the 90% and 60% ADK utilization distributions were calculated; the 60% UD was considered the core area. When running the program, grid cell size was set at 50x50. We let CALHOME calculate the optimum bandwidth (or smoothing parameter) for each data set, then re-ran each data set using an 80% bandwidth.

This was done because a smaller bandwidth may result in a better fit of the data (lowest least-squares cross-validation or LSCV score) when an animal uses 2 or more separate core areas (Kie et al. 1994). The bandwidth that produced the lowest LSCV score was used to determine home range size unless the 90% UD was broken into a greater number of polygons.

In order to make reliable comparisons between individuals and ensure that successive locations were spatially independent, home ranges were calculated using locations from the weekly flights (during which all radio-collared individuals were generally located) augmented with ground locations, as long as all locations were >3 days apart. Thus, during the weeks we were unable to fly, our samples could be bolstered with ground locations. The majority of locations were taken during diurnal and crepuscular periods.

We calculated an annual home range for each cougar that was present for at least 10 months of any particular 12 month period (January 1-December 31). The number of locations utilized to calculate each annual home range ranged from 32 to 52. Sweanor (1990) found that when using the harmonic mean estimator, a minimum of 35 locations and a 10 month sampling period were adequate to describe cougar annual home range size. Only 3 of our annual home range estimates involved less than 35 relocations. To obtain a better understanding of the adequacy of our sample size, we randomly chose an annual period from 1 of our study animals (M19), then randomly deleted locations and graphed the area of each 90% ADK home range. The asymptote of the locations-area curve was 24, indicating our sample of 32 was sufficient (see Bekoff and Mech 1984). We tested for differences between adult male and female annual home range sizes using the Wilcoxon rank sum test (Ott 1988).

For females, home range size was also calculated based on reproductive status. We calculated home range size for those females we were able to radio-monitor during an entire reproductive cycle (birth of 1 litter to the birth of the subsequent litter). The cycle was then divided into 3 consecutive 6-month periods: female raising cubs ≤6 months old; female raising cubs 7-12 months old; and female raising cubs >12 months old or no cubs (cubs became independent at, on average, 13.4 months of age; see Chapter 3.4.8). We tested for differences between annual and reproductive cycle home range sizes using the Wilcoxon rank sign test. In addition, we used analysis of variance (Kruskal-Wallis test and multiple comparisons) to test for differences in a female's home range size during periods when she was raising small cubs, large cubs, and no cubs.

Seasonal home ranges were not calculated because home range size and location did not change in any predictable pattern based on seasons. Sweanor (1990) found that cougars used portions of the same home ranges during the 2 seasons she delineated.

4.3.4 DISTRIBUTION AND MOVEMENTS

Fidelity

Individual home range fidelity was assessed by examining home range use in time and space. Annual home range fidelity, defined as the degree to which a cougar used the same area year after year, was examined for all adult cougars for which we had at least 2 annual home range estimates. We measured annual fidelity using 2 methods. First, using both the 90 % ADK and 90% MCP home range estimators, we determined the average percent annual home range overlap for each individual. For example, if we obtained 3 annual home range estimates on a cougar that was monitored during 1987 through 1989, the percent of home range overlap between the 3 pairs of years (1987 and 1988; 1988 and 1989; 1987 and 1989) would have been calculated, then averaged. Overlap was measured by combining annual home range output files on Freelance for Windows (Release 2.1), overlaying a 1 km grid on the video image from within the program, and counting the number of overlapping 1 km squares. We tested for differences in the percent overlap (and hence, fidelity) between males and females using the Wilcoxan rank sum test.

As a second method of determining fidelity, we used the locational data to measure the distance between each cougar's mean x and y coordinates during successive years. This method eliminated the biases associated with home range estimators (White and Garrott.1990). A Wilcoxon rank sum test was used to test for differences in the median distance between the mean annual locations of male and female cougars (similar to Garrott et al. 1987).

We also measured a female's fidelity during an entire reproductive cycle (birth of one litter to birth of the next litter) by using the second method described above. The distances between each female's mean x and y coordinates during 3 six-month periods (cubs <6 months; cubs 7-12 months; and no cubs) were measured; then, analysis of variance (Kruskal-Wallis and multiple comparisons) was used to test for differences in the distances between mean locations.

Dispersal and Philopatry —

Based on telemetry locations, we described the movements of newly independent progeny. Methods for determining philopatry and measuring dispersal distances of progeny born on the SAM were discussed in Chapter 3.3.6.

Spatial and Temporal Relationships

Cougar interrelationships were primarily assessed by measuring home range overlap between individuals. Overlap between all individual adult cougar home ranges in the SAM during 2 years prior to (1989, 1990) and 1 year after (1993) the removal of cougars from the TA was determined using the ADK measure of home range. These years were chosen because: 1) the greatest proportion of resident cougars had functional radio-collars; and 2) by the end of 1993, the TA had 2.5 years to recover from the experimental removal; thus we could compare the social organization of the overall population before the experimental removal of cougars and after it had had time to recover from removal. For each year, areas shared by 2 cougars were determined, then expressed as a percent of each cougar's home range. We then calculated the total percent of a cougar's home range overlapped by all other cougars of the same, and opposite, sex. Home range overlap was determined for both the 90% and 60% UD.

Home ranges were calculated, and overlap measured, for all adult cougars that were present for >3 months during the year in question. This allowed inclusion of cougars that, during the year, either arrived as adults on the SAM, attained adult status, or died. If a cougar's radio-collar became nonfunctional during the year, but sign or subsequent recapture indicated the animal was still alive, we estimated the individual's home range and overlap utilizing the locations from a 12-month interval closest to the time period being analyzed. For example, if a cougar's radio-collar became nonfunctional 1 June 1993, yet we knew it was present through December 1993, we would estimate its 1993 home range by utilizing locations from 1 July

1992 through 31 May 1993. Fortunately, the majority of cougars retained functional collars during the years overlap was measured. Using the sample of 3 years (1989, 1990 and 1993), we compared the differences in annual home range overlap based on gender.

Because the number of cougars inhabiting the SAM through the course of a year varied (some cougars died and others established residency), and because home range estimators can be biased, thus including areas an animal may not normally utilize (White and Garrott 1990), we also produced graphics using only the weekly locational data. We examined the weekly movements of neighboring cougars during shorter time intervals (≤12 months). We specifically examined movements of: 1) cougars present in the TA before, during and after the removal of 58% of the independent cougar population in the TA; 2) males before and after the arrival of immigrant males; 3) female cougars and their adult female progeny; and 4) female philopatry and fidelity over time. We did this to determine: 1) whether those cougars that overlapped in space also overlapped temporally; 2) why some individuals showed weak home range fidelity over time.

4.3.5 INTERACTIONS AND COMMUNICATION

Intraspecific interactions were primarily determined indirectly from radio-telemetry. Cougars which were located within the same radius error circle were considered in association. When possible, we attempted to confirm the association and determine its purpose. Breeding pairs were confirmed by the subsequent birth of cubs. Breeding activity was highly suspected given the following conditions: 1) a male was documented in association with an adult female that was not known to be pregnant, and either without cubs or caring for cubs that were ≥9 months old; and 2) either we obtained visual observations of a pair, heard vocalizations that indicated the female was in estrus, located a pair together for consecutive days with no resulting female mortality, found tracks of the pair traveling together, and/or documented reproductive cycling behavior in the female. Locating a male and female pair together as in Condition 1 above without corroborating evidence from Condition 2 was considered as possible breeding activity. Aggressive encounters were confirmed by finding mortalities or fresh wounds on captured individuals. Behavior between females and their cubs was documented by visually observing the family groups, finding their tracks, and by radio-tracking 38 radio-collared cubs. Sweanor (1990) also analyzed scraping behavior in resident males.

Experimental errors for all statistical tests were set at the 0.10 level of significance.

4.4 RESULTS

4.4.1 CAPTURES AND RADIO-TELEMETRY

We captured and marked 241 individual cougars between 6 August 1985 and 31 March 1995,. The majority (73%) of cougars were first captured as cubs. Of the total, 126 cougars (49 males, 77 females) were fitted with radio-collars. The other 115 individuals (all small cubs) were only marked with eartags and tattoos. Cougars were radio-collared for the first time as adults (n=62), subadults (n=26) and cubs (n=38). Twenty-two of the cougars first marked as cubs on the SAM were radio-monitored as adults on the SAM.

In addition to the marked individuals, we documented the presence of 5-6 adults, all females, that were never radio-collared during the course of the study. Two of the uncollared females were young (24-30 mo. old) adults found as mortalities and 2 were not present on the SAM until 1994. One female (the Goat Mountain female or GMF) was present from March 1992 through the end of the study. Her presence and movements were documented through sign, the capture and radio-collaring of a suspected offspring from her first litter, and the visual observations of her 3 cubs from a second litter. We also documented the mortalities of 3 other unmarked cougars (1 subadult male, 2 subadult females).

We obtained 13,947 cougar locations during the study; they were comprised of 69% aerial locations and 31% ground locations. Radio-collared cougars were located from 1-569 times each ($\bar{x}$=110).

4.4.2 POPULATION STRUCTURE AND DENSITY

The male:female sex ratios of adult, subadult and cub cougars on the SAM did not differ significantly from 1:1 (Chapter 3.4.4). During the study, the adult sex ratio averaged approximately 1 male per 1.4 to 1.5 females; whereas the subadult sex ratio averaged approximately 1 male per 1.7 to 2.2 females. The sex ratio for young cubs (still suckling), was 1:1.

Three broad age classes were delineated in the SAM cougar population: adults, subadults, and cubs. The greatest proportion of the population was comprised of adults (49-68% annually), followed by cubs (29-40% annually), then subadults (3-11% annually). When analyzed separately, the age structure of the TA and RA were very similar (see Fig. 3.2).

Except for a short period during and after cougar removal on the TA, the overall adult cougar density on the SAM increased (see Table 3.21). January estimates of adult cougar density ranged from a low of 1.2 adults per 100 km^2 in 1989 to a high of 2.0 adults per 100 km^2 in 1995. The January density estimates for 1990 through 1994 were 1.6, 1.6, 1.4, 1.8 and 1.9 adults per 100 km^2, respectively. Cougar density in the TA exceeded the RA density during the years prior to cougar removal and again within 2 years post-removal (see Tables 3.19-3.23); however, it required about 31 months for the TA to recover to its pre-removal density. During the years in which home range overlap between individual adults was measured (1989, 1990, 1993), the January adult density in the TA was 1.70, 1.89, and 1.75 adults / 100 km^2, respectively, while the RA density was 0.94, 1.34, and 1.80 adults / 100 km^2, respectively.

4.4.3 HOME RANGE SIZE

Annual Home Range

The mean annual home range sizes for resident adult male and female cougars are depicted in Tables 4.1 and 4.2, respectively. Some individuals utilized home ranges of widely different sizes over the years they were monitored, as indicated by the high standard deviations. Average annual home range size also varied widely among individual cougars. Mean annual home range size (90% ADK) ranged from 59.3 to 336.4 km^2 for adult males (n = 23, $\bar{x}$ = 192.2 km^2, SD = 70.8) and 30.1 to 209.2 km^2 (n = 29, $\bar{x}$ = 71.9 km^2, SD = 37.4) for adult females. Female home ranges averaged between 35.4 to 39.3% the size of male home ranges, depending on the home range estimator used (Fig. 4.1). Adult male home range size was significantly greater than female home range size using both the ADK

(90% and 60%) and MCP (100% and 90%) home range estimators (Wilcoxon rank sum, $Z \geq 5.44$, $P < 0.0001$).

The average home range sizes for male and female cougars during 1989, 1990 and 1993, respectively, are presented in Table 4.3. Male home range size generally increased with increasing adult cougar density, whereas female home range size decreased. Male home range size increased by an average of 40.3% from 1989 to 1993, based on the 90% ADK home range estimator. Conversely, female home range size decreased by, on average, 40.2%. However, female core area sizes remained relatively constant. During that same period, the adult population increased from 1.2 cougars per 100 km^2 to 1.8 cougars per 100 km^2.

Female Cyclic Home Range

The home range utilized by a female during an entire reproductive cycle, beginning with the birth of one litter and ending with the birth of the next litter (termed cyclic home range hereafter), was determined for 9 females over 11 cycles (Table 4.4). In all 11 cycles, at least 1 cub from each of the first litters survived to independence. The mean number of months per cycle was 17.6 months. Similar to annual home range size, there was variation in individual cyclic home range size. Cyclic home range size (90% ADK) ranged from 17.7 to 131.2 km^2 ($\bar{x} = 64.9$, SD = 37.8). Based on information from 2 females (F37, F47), the same female could also utilize a different size home range depending on which litter she was raising. F37's cyclic home range from 1989 to 1991 was 80% the size of her home range during her previous cycle, and F47's cyclic home range during 1990 to 1991 was 42.6% the size of her home range during a subsequent cycle in 1993 to 1994. A female's cyclic home range size was not significantly larger than the same female's mean annual home range size based on the ADK (both 90% and 60% UDs) and the 90% MCP home range estimators (one-tailed Wilcoxon rank sign test; n = 11, $T_- \geq 23$, $P > 0.1$), but it was significantly greater than mean annual home range size when the 100% MCP home range estimator was used ($T_- = 8$, $P = 0.01$).

Table 4.5 presents home range sizes for female cougars during 3 consecutive 6-month periods when they were raising young cubs ($\leq$6 months old; Period I), raising older cubs (7-12 months old; Period II) and when they were primarily solitary (their cubs were independent and they had not yet produced another litter; Period III). We were able to determine home range sizes for 7 different females during all 3 periods on 8 occasions. We also determined home range sizes for 6 different females during 2 consecutive periods (Periods I and II) on 7 other occasions. Two females utilized larger home ranges (90% ADK) during Period II than during Period III, and another female's core use area (60% ADK) was larger during Period I than during either Period II or Period III. Overall, however, home range size increased as the age of the cubs increased, and was largest when the female was solitary (Fig. 4.2). The average home range sizes (90% ADK) for females during the 3 consecutive periods were 26.4, 47.0, and 67.0 km^2, respectively. Home range sizes of females during Period I were significantly smaller than during Period III, based on both the ADK and MCP home range estimators (Kruskal-Wallis and Multiple Comparisons, $P < 0.05$). However, home range sizes of females during Period II were only found to be significantly larger than during Period I using the 100% MCP home range estimator ($0.05 < P < 0.1$).

4.4.4 DISTRIBUTION AND MOVEMENTS

Fidelity

Tables 4.6 and 4.7 present the average home range overlap between years for individual adult male and female cougars on the SAM. Both males and females exhibited variation in annual home range overlap, and consequently, fidelity. Adult male home range overlap was determined for 16 males that were monitored from 2 to 7 years each. Using the 90% MCP and 90% ADK home range estimators, the percent of a male's home range that was utilized by that same male from year to year averaged 51.6% (range = 20.6-78.2%) and 57.5% (range = 27.3-81.8%), respectively. Adult female home range overlap was determined for 21 females that were monitored from 2 to 6 years each. The percent of a female's home range that was utilized by that same female from year to year averaged 60.3% (range = 32.6-85.6%) and 62.2% (range = 41.3-81.6%) based on the 90% MCP and 90% ADK, respectively.

Overall, males exhibited less home range fidelity than females. Based on the 90% MCP home range estimator (but not the 90% ADK), males had significantly less annual home range overlap (Wilcoxon rank sum, $Z = -1.38$, $P = 0.09$) than females (Fig. 4.3).

Figs. 4.4 and 4.5 depict the annual home range overlap (90% ADK and 90% MCP, respectively) for 4 different males that exhibited relatively strong home range fidelity. Average annual home range overlap ranged from 71.3 to 81.8% for the 4 males. In contrast, Figs. 4.6 and 4.7 depict the annual home range overlap for 4 different males that showed weak home range fidelity (20.6-37.5% overlap). M36 and M53 both exhibited directional home range shifting (Fig. 4.6). Within 3 years after capture, M53 had shifted far enough north that he was utilizing an area completely outside of his first estimated annual home range (90% MCP). By the fourth year after capture, M53 had shifted completely outside the SAM. M36 shifted north more slowly than M53; nevertheless, within 4 years he was also utilizing an area completely outside of his first estimated annual home range. Home range shifting by M38 and M46 (Fig. 4.7) was more complex. Both males initially shifted their activities toward the south, then back toward the north. All 8 males, regardless of degree of fidelity, were documented in breeding associations with females during the periods their annual home ranges were calculated, and 7 of the 8 males sired cubs.

Fig. 4.8 depicts the annual home range overlap (90% ADK and 90% MCP) for 2 adult females, F15 and F21. F15 exhibited moderate fidelity; her mean annual home range overlap (54.3-58.9%) approached the average found for all females. F15 did shift her activities somewhat over time, first toward the northeast, then back south and west. Between 1987 and 1991 F15 also raised 3 litters. In contrast to F15, F21 exhibited relatively weak home range fidelity; her mean annual home range overlap (32.6-41.3%) was lower than that found for any other female. Over a 3 year period, F21 shifted her activities north, then back south. F21 shifted north during 1992, the year she was raising her fourth litter of cubs and the year after the experimental removal of cougars in the TA where she was a resident.

As a second method of determining annual fidelity, we measured the distance between a cougar's mean locations during successive years. A total of 88 distances between mean annual locations were calculated for 35 individual cougars (n=15 males, 20 females). Distances between mean annual locations ranged from 0.2 to 23.9 km ($\bar{x} = 5.7$, SD = 5.2) for adult males and 0.3 to 10.0 ($\bar{x} = 2.6$, SD = 2.1) for adult females (Fig. 4.9). The distances between means of annual locations were significantly greater for males than females (Wilcoxon rank sum, Z = 3.38, P <

0.001). Thus, although females such as F15 showed shifting tendancies in both home range overlap and mean annual locations (Fig. 4.8), the magnitude of the shift was significantly smaller.

When we examined a female's home range use during an entire reproductive cycle, we found that, in general, they showed strong fidelity. Figure 4.10 depicts the home ranges of 2 typical adult females during 3 consecutive 6-month periods of their reproductive cycles. The home ranges (90% ADK) of both females became larger and more connected as their cubs grew, but their mean locations during each of the 3 periods were almost identical. We measured the distance between mean locations during each of the 3 periods for 7 different females during 8 cycles (Table 4.8) and found that overall, females did not show any greater shifting tendancies in their mean locations based on their reproductive status (Kruskal-Wallis, $H = 0.75$, df = 2, $P > 0.1$). The distances between mean locations averaged 3.1, 2.0, and 2.9 km for Period I - Period II, Period II - Period III and Period I - Period III, respectively.

Dispersal and Philopatry

Cubs born on the SAM became independent from their mothers at, on average, 13.4 months of age (n = 15, range = 11.1-16.0). Females generally became independent about 1 month earlier than males. Cougars that dispersed from their natal areas began their dispersal moves at, on average, 15.6 months of age (n=8, range = 13.0-19.5). The majority of surviving cubs dispersed from their natal areas and the much larger study area. Of the surviving progeny, we estimated that about 83% of males and 59% of females emigrated from the SAM (see Chapter 3.5.4).

Characteristics of dispersal and philopatry were documented for 41 subadult cougars (19 males, 22 females) over the 10 year study (see Table 3.12). Of these subadults, 38 were born on the SAM; the origins of the other 3 (M221, F148, F159) were unknown. All but 2 male progeny (M64, M108) dispersed from their natal areas. We suspect both M64 and M108 would also have dispersed if they had not been killed by the same male cougar (M88) 52 and 87 days after independence, respectively. M64 and M108 died when they were 14.3 and 14.6 months old, respectively, which is younger than the mean age we documented for the onset of dispersal behavior. Additionally, M108 had already made 1 short-term (< 1 week duration) exploratory move of 18 km to the north of his natal area just 17 days before he was killed by M88.

In contrast to the males, only 8 of the sample of 20 females born on the SAM dispersed after independence. We documented philopatry in 12 female cubs born to 5 different females (pairs of siblings were involved in 5 cases) over the course of the study. In addition, 4 other females established home ranges adjacent to their mothers (2 of the mothers were also the mothers of philopatric females). Therefore, we documented close genetic relationships between 7 mothers and 16 female progeny. Six of the 12 philopatric females produced litters of their own, at least 2 of which were sired by the philopatric females' own fathers. Philopatry by 2 littermates (F89 and F90) is depicted in Fig. 4.11.

We documented dispersal distances for 17 males and 10 females (Table 3.12). The most complete dispersal information was obtained on 15 dispersers (8 males, 7 females), all of which were monitored from their natal home ranges to their independent home ranges (see Chapter 3.3.6 for explanation of terms). Dispersal distances (natal home range arithmetic center to independent home range arithmetic center, NAC-IAC) averaged 101.3 km (range = 47.0-192.5, SD = 57.7) for the 8 males and 28.3 km (range = 5.6-78.5, SD = 26.0) for the 7 females. Males dispersed significantly greater distances from their NACs to IACs than females (Wilcoxon rank sum, $T = 35$, $P < 0.025$).

Incomplete dispersal information was obtained on 9 other cougars (8 males, 1 female) which had been born on the SAM. Either we could not estimate the cougar's NAC, the cougar died before it had established an independent home range, or we lost radio-contact with the individual before it established an independent home range. Dispersal distances for these cougars ranged from 42.2 to 195.6 km. The farthest dispersal distance recorded was for M214, who was tagged with his 2 siblings when he was 39 days old. M214 was killed by a hunter 195.6 km northwest of his NAC when he was 29 months old.

The 3 cougars of unknown origin dispersed between 74.4 and 175.7 km from their capture sites to either their last location or IAC. One of these cougars, F159, dispersed the farthest documented distance of any female (118.2 km).

Cougars dispersed in all directions (Fig. 4.12). The directions of dispersal for 16 male and 8 female progeny were uniformly distributed about a 360° circle (males: $U^2 = 0.057$, $P>0.5$; females: $U^2 = 0.062$, $P>0.5$); however, 52% of the cougars dispersed in directions that followed the generally north-south orientation of the SAM.

Because only 9 subadults (6 males, 3 females) wore functional radio-collars at the time they initiated dispersal behavior, and 3 of the 9 (all males) died or dropped their collars prior to establishing an independent home range, we were unable to obtain much information on dispersal duration. Our small sample indicated that dispersal duration was quite variable. Disperal duration ranged from about 0.2 to 1.7 months for the 3 females, and 1.5 to 7.8 months for the 3 males.

Fig. 4.13 depicts the natal home ranges, dispersal movements and subsequent independent home ranges for 2 cougars (M82, F9) with different dispersal behaviors. M82 made an exploratory dispersal movement when he was 15.6 months old (Fig. 4.13A). He traveled 57.1 km south in the SAM over a 7 day period, but returned to his natal home range within 28 days of initiating this exploratory dispersal movement. About 3 months later, at the age of 19.5 months, M82 began his successful dispersal movement. He dispersed 90.1 km to the south end of the SAM within a 1.4 month period. He then spent the following 3 months in the Organ Mountains, which are connected to the south end of the SAM. At 24 months of age M82 made an eastward movement, across the Tularosa Basin toward the Sacramento and Guadalupe Mountains. Over the next 3 months, M82 moved 158.3 km east, to the place where, at 27 months of age, he began to establish an independent home range. His successful dispersal move took him 7.8 months.

In contrast to M82, F9's dispersal duration was only 1.7 months long (Fig. 4.13B). She dispersed immediately after independence at 14.3 months of age. Within 1.7 months she had dispersed 78.5 km northwest, to the area where she began to establish an independent home range. F9 was documented in breeding associations within this home range at 22 months of age.

Spatial and Temporal Relationships

Spatial Overlap

We determined the amount of annual home range overlap between adult cougars of the same and opposite genders during 3 annual periods (1989, 1990 and 1993; Table 4.9). Mean annual home range overlap between adult males ranged from 48.7 to 75.0 percent (90% ADK) and increased as the overall density of adult males in the population increased. Core overlap (60% ADK) also increased with increased cougar density, from a low average of 18.7% in 1989 to a high of 47.1% in 1993. Although we did not calculate home range overlap for 1994, we suspect it would have been even higher, given the fact that the number of adult males in the population continued to increase slightly (see Table 3.21). Some portion of an individual male's home range (90% ADK) was shared by, on average, 2.9 to 4.3 other adult males during each of the 3 years. Males even shared parts of their core areas with, on average, 1.7 to 2.5 other adult males. As an example, Fig. 4.14 depicts the spatial overlap between adult male cougars during 1990. The 1990 male home range overlap using the 90% MCP is presented in Fig. 4.15A for visual comparison.

Home range overlap between adult females averaged about 80% of that found for adult males. Home range overlap between individual females ranged from 39.2 to 60.5% (90% ADK) and, similar to the males, increased with increasing adult female cougar density. Core overlap ranged from 12.7 to 26.2%. Each female shared some part of her home range (90% ADK) with, on average, 2.1 to 3.9 other adult females, and shared her core area with from 1.2 to 1.7 females. Figures 4.15B and 4.16 depict the spatial overlap of adult females during 1990 using the MCP and ADK home range estimators, respectively.

Each adult male shared, on average, 49.7 to 63.2% of his annual home range (90% ADK) with from 3.8 to 4.7 adult females. In contrast to within-gender overlap, the amount of area that the average adult male shared with adult females declined with increasing density.

The percent area each female shared with adult males was greater than the percent area each male shared with adult females, as well as greater than the area shared between cougars of the same sex. Adult females shared, on average, 87.8 to 96.6% of their home ranges (90% ADK) with from 3.0 to 3.5 adult male cougars.

There was no apparent relationship betweeen adult density and the amount of area the average adult female shared with adult males.

Movements

Males

We examined the movements and relationships between adult male cougars on the TA during the periods prior to, during, and after the removal of 5 of the adult males (Fig. 4.18). Although extensive home range overlap was recorded between adult males during 1990 (90% ADK; 64.8%; Table 4.9), movements of individual TA males during the second half of 1990 (Fig. 4.17A) indicated relatively exclusive use areas. The greatest overlap in use occurred between M7, M49 and M114. Unlike all the other males at that time, M114 was a new arrival to the SAM (September 1990). During the period that 5 males were removed from the TA (January-March 1991; Fig. 4.17B), M3, who was 1 of only 2 remaining adults males in the TA, expanded his area of use. M3 traveled up to 21 km north of the area he had been utilizing during the 6 months prior to cougar removal; he visited areas that had been used by 4 of the removed males, and apparently bred with 3 females that had not yet been translocated (2 of the females occupied home ranges that had not formerly overlapped his home range). In July 1991 (Fig. 4.17C.), M88 returned to his former home range from his translocation site in northern New Mexico, and for the next 12 months utilized some of the same areas as M3. M3 and M88 may have fought sometime between July 1991 and January 1992, because when M88 was recaptured in January 1992, we found canine punctures had damaged his collar's radio-transmitter. By July 1992, M3 had abandoned the area he shared with M88 and completely shifted his home range to the north. As 2 immigrant males arrived on the TA, (M173 in August 1992 and M193 in May 1993; Fig. 4.17E-F), M3 continued to shift his activities north. By June 1993 (Fig. 4.17F), the structure of the adult males on the TA was approaching the situation found in 1990 prior to cougar removal. The males were again using relatively exclusive areas, with 2 exceptions: M88 shared area with new immigrant M193, and M3 shared area with an old male (M5) who died of old-age related problems in May 1993. At this point M3 was utilizing an area that was 10 to 30 km north of the northernmost area he had utilized just prior to cougar removal. He successfully bred with F149 in this home range in 1994.

To further examine the relationships between resident and immigrant males, we plotted the movements of M88 and M193 after M193's arrival on the SAM in May 1993 (Fig. 4.18). During the 1 year period after M193's arrival, he associated with M88 on 2 known occasions (Fig. 4.18a). After the first association, M193 left the SAM, spent 8 weeks in the Dona Ana Mountains (an isolated mountain range ~18 km west of the SAM and ~60 km^2 in size), then returned to the SAM. Within 3 weeks of returning to the SAM, he associated with M88 again. M193 spent the next 21 days within 1 km of the site where the association took place, suggesting he was recovering from fighting injuries. M193 recovered from the apparent injuries, then continued to use a shared area with M88. However, within 6 months of the second association (Fig. 4.18B), M88 had abandoned the shared area and shifted north. His southernmost movements during the period from 12 to 18 months after M193's arrival were 6 km north of any movements he had made in the year prior to that time, and none of his movements overlapped M193's. Thus, it took the 2 adult males about 12 months to establish exclusive home ranges after M193's arrival on the SAM.

The movements of neighboring resident adult males during consecutive 12 month periods also indicated the relatively exclusive, but dynamic nature of individual home ranges (Fig. 4.19). One of the reasons male home ranges may have been so dynamic may have been due to the arrival of new immigrant males. As immigrant males successfully established home ranges as adults (for example M46, Fig. 4.19, 1989), neighboring males (most notably M36) could respond by shifting away from them.

Females

Although the annual home range overlap between females averaged 47.8% in 1990, when we examined the movements of adult females on the TA over a shorter, 6 month interval before the removal of 6 adult females (Fig. 4.20A), we found some of the same exclusive home range use as found in the adult males. Only 2 females (F44 and F58) showed extensive overlap. Three females were progeny of other resident females: F30 and F31 were F21's daughters, and F44 was F37's daughter. Because F21's collar was non-functional at the time, we could not determine the degree of overlap between her and her daughter's movements; however, F37 and F44 showed almost no overlap in movements. Only 3 adult females were left in the TA after the removal: F6, F21 and F47 (Fig. 4.20C). The response of the 3 females to the removal of their neighbors could not be fully examined because F21's radio-transmitter was non-functional until March 1991 and F6's transmitter became non-functional in April 1992. Nevertheless, movements and sign indicated that 2 of the females (F6, F47) continued to use the same areas over time regardless of the loss of their neighbors. F21 showed a slight northward shift and expansion of her movements primarily after the arrival of F103 from the RA and the establishment of her daughter, F149, to the north of her. By December 1992, 5 new females had been recruited into the adult TA population; 3 were born to resident TA females, 1 immigrated from the RA, and 1 apparently immigrated from outside of the SAM. As the female population recovered from the removal, female home ranges remained relatively exclusive (Fig. 4.20C-F). The females that showed the greatest shared areas were related (F47 and her 2 daughters, F107 and F109).

Fig. 4.21 depicts another example of the relationship between a mother and her adult daughters (F41 and 4 daughters from 3 litters). F54 established a home range adjacent to her natal area after independence. Movements of F41 and F54 over the 12-month period after F54 reached adulthood indicated that the 2 females utilized relatively exclusive areas (Fig 4.21A). In contrast, F41's daughter from her sequential litter (F91) was philopatric (Fig. 4.21B). During the 12-month period after F91 reached adulthood, the movements of F41 and F91 overlapped extensively. An examination of the movements of F41 and her 4 adult daughters (F54, F91 and 2 daughters from a third litter, F130 and F132) demonstrated the variability of spatial relationships from exclusivity to extensive overlap between family members (Fig. 4.21C).

Some females, such as F21, showed shifting behavior in their movements over time. In F21's case, we were able to document shifting after the arrival of new adult females. However, that may not always be the reason for a shift. We documented a shift in F107's home range even though no new females had begun to establish residency near her. When we examined F107's movements after independence (Fig. 4.22A) we found that, until her third year as an adult, F107 was philopatric. F107 produced 2 litters within her natal area, the second of which was cannibalized by her own father, M88, when the cubs were 2 months old. By the time F107 produced her third litter (5.5 months later), she had shifted her activities and was utilizing a home range completely outside her natal area (Fig. 4.22B).

4.4.5 INTERACTIONS

Associations Between Independent Cougars

Independent cougars were documented in association during 4.9% of all radio-telemetry locations. We documented a total of 263 separate associations, the majority of which were between males and females (76.0%). The percent of associations between males (12.6%) was only slightly higher than the percent of associations that occurred between females (11.4%). Cougars associated in the combinations listed in Table 4.10. The majority of associations were for breeding purposes (58.9%; Fig. 4.23); however, we documented associations unrelated to breeding activities during 26.6% of all associations. Twenty associations resulted in mortalities; they occurred during 1.3% of breeding associations (n=2) and 25.7% of non-breeding associations (n=18). Specific associations are described below.

Male-Male

Associations between males were documented on 33 occasions: 8 were between adult males and an estrus female, 11 were apparently disputes over food or territory and unrelated to an estrus female, and 14 were for undocumented reasons. Nine of the associations (27.3%) resulted in mortalities.

Adult males associated with subadults on 8 occasions; of those, 4 resulted in subadult mortalities. M88 killed 2 subadult males (M64, M108) prior to the dispersal of those males from their natal areas. Both of the subadults were feeding on deer kills when they were killed. M88 was a new immigrant to the SAM when he killed M64, but he was an established resident when he killed his son, M108. Another subadult, Male 300, was chased up a power pole by resident adult M1 and electrocuted (see Sweanor 1990). A fourth subadult (M140) was killed by an unknown male (probably adult M46 or M192) as he dispersed north in the SAM from his natal area. His stomach was full of oryx meat, so it is probable the males were competing for food. Two other subadults (M26, M221) initiated long-distance dispersal movements immediately after associations with resident males.

Adult males associated with other adult males on 25 occasions, 5 (20%) of which resulted in mortalities of 1 of the males. Two of the mortalities involved competition between resident males for estrus females. The other 3 mortalities were unrelated to breeding activities, and were probably due to competition for territory. In one case, resident M14 was killed by immigrant M19, who subsequently usurped much of M14's former home range (see Sweanor 1990, pp. 116-117). In a second case, M3 killed his neighbor M1. M1 and M3 had neighboring home ranges for about 3 years, until immigrant M22 arrived on the SAM. After M22's arrival, M1 shifted his home range activities south and M22 established a home range adjacent to M3 (see Sweanor 1990 for further details). After M3 killed M22 during a breeding dispute, M1 returned to his former home range. He was killed within 4 months of his return. In the third case, resident M73 was killed by an unknown male, possibly immigrant M219 who subsequently utilized much of M73's former home range.

One documented male mortality (M198) was not included in the association analysis (Table 4.10) because we could not categorize his association. M198 was a tagged progeny from the TA. He died in the RA when he was 23 to 25 months old, apparently from head injuries inflicted by another male cougar. We do not know whether M198 was still dispersing when he died.

Scarring found on captured males indicated fighting was fairly common. Most captured males had visible scars on their heads, shoulders, and/or forearms. Although some cougars did not show any visible signs of fighting, past fighting behavior may sometimes go undetected. During one recapture, we found that the protective coating and the metal casing on M88's radio-transmitter had been punctured by canines from another male cougar, yet excluding healed ear notches, M88 had no visible scars. Healed skull injuries found on cougars after their deaths also indicated prior fighting behavior. Over the 10 year study period, we examined the skulls of 18 male cougars (14 adults, 4 subadults) that either died on the SAM, died after they dispersed from the SAM, or died after translocation from the SAM. Ten (71%) of the adult males and 1 (25%) of the subadult males sustained skull injuries that they survived (i.e. bone tissues had mended). Injuries found on 4 of the cougar skulls (3 adults, 1 subadult) may have been sustained while trying to kill prey. However, 7 other cougars (50% of adults) had healed skull injuries consistent with canine penetrations from other cougars. One such injury is described by Sweanor (1990).

Male - Female

Breeding Associations

Of the 200 documented associations between males and females, 147 (73.5%) were apparently for breeding purposes. Cougars were known to be breeding during 33 (17%) of these associations, because all the females involved became pregnant from the associations. At least 3 of the successful breeding associations involved females with dependent cubs that were between 10 and 14 months old. Breeding behavior was highly suspected on 57 other occasions, and possible breeding activity occurred on 57 occasions.

Because most cougars were not located on a daily basis, the number of days breeding pairs remained together was infrequently documented. Pairs were known to associate for from 1 to 6 days, and females sometimes associated with more than 1 male during an estrus cycle (see Sweanor 1990 for specific examples). Apparent estrus cycling by 7 different females indicated cycles ranged from 13 to 33 days ($\overline{x}=21$); however, it is possible we missed associations for those females with longer cycles. As an example, F109 associated with M88 on 23 February 1992, re-associated with him during a 3 day period 20 days later, then associated with him again for a 7-day period 14 days after that. She did not produce cubs from the associations. In another example, F103 associated with M173 on 4 and 5 January, 6 February, and 27 February 1994, indicating estrus cycles of 33 and 21 days, respectively. She became pregnant during the 27 February association. Each female was documented associating with up to 5 different males during the course of the study. Two females also successfully produced litters sired by their own fathers (F107 and M88, F91 and M46). The youngest known-age females to successfully breed with a male were 19 months old. See Chapter 3.4.6 for more detailed information on female maturity.

Non-breeding Associations

Males and females were documented in non-breeding associations on 53 occasions (26.5% of all male-female associations). During 39 (73.6%) of the non-breeding associations, adult males were associating with females that were either pregnant (n=13) or raising cubs <9 months old (n=26). On 8 other occasions adult males associated with adult females that were not either pregnant or raising cubs, and in 1 case a male associated with his 12.5 month old daughter. Subadult males were documented in association with adult females on 5 occasions. Eleven (20.8%) of the non-breeding associations resulted in mortalities.

We were unable to determine the reason for the majority of associations between males and pregnant females, but at least 1 of them involved a deer kill. None of the associations between males and pregnant females resulted in mortalities.

Four of the 26 associations (15.4%) between males and females with cubs resulted in female mortalities. In 2 cases the females were killed near deer kills they had cached. F15 was suckling young cubs and F86 was raising 5-month-old cubs when they were each killed. Because F15's cubs were still nursing, they probably died from starvation. Tracks found in the area around F86's cache after her death suggested her cubs were also orphaned. F86 was cannibalized, so the male apparently regarded her as prey. In 2 other cases, no evidence of a kill cache was found. F61 was apparently traveling with her 2 five-month-old male cubs when she and at least 1 cub were killed by a male. The cub, but not F61, was cannibalized. F61 may have been trying to protect her cubs from the predatory male when she was killed. F2 was killed, but not cannibalized, when her cubs were 9.5 months old. We could not determine whether her cubs were traveling with her when she died; however, at least 1 cub (F10) survived to 18 months of age. We suspect that M29 was responsible for 3 of the 4 female mortalities. There was no indication that the males that killed the females were the fathers of the respective females' cubs. At least 2 of the killings were apparently done by newly immigrant males.

Seven of 8 non-breeding associations between males and females that were neither raising cubs or apparently pregnant resulted in mortalities. Two of the females, an older resident (F60) and a subadult (F96), were killed by a new immigrant male (M88) near deer caches. Deer kills were not involved in 5 other female mortalities. Two females (F40, F185) were 24 and 29 months of age, respectively, when they were killed and cannibalized by resident adult males (M19 and M29, respectively). F57's cubs had apparently just become independent prior to her being killed and cannibalized by a male, probably adult M46 or M38. We highly suspect M46, because he had just begun to shift his home range south into the area overlapping F57's home range when she was killed. Another female (F10) was 18 months old when she was killed by resident male M22 (the same male had probably killed her mother 8.5 months earlier). Because she had associated with M1 on a previous occasion (at 17 months of age), it is possible F10 was becoming reproductively mature. However, she was not pregnant when she died. Another female (F39) was chased off a cliff by M22 when she was just 22 months old. We had documented her in what we had suspected was a 2-day breeding association with M22 just 1 month earlier.

Of the 5 separate associations documented between adult females and subadult males, 1 involved a deer cache and another involved both food and an estrus female. We did not know the reasons for the other 3 associations, but none resulted in mortalities.

Forty-two of the non-breeding associations (79.2%) between males and females did not result in a mortality. Although it was impossible in most cases to determine the reason for the association, some of them appeared to be non-aggressive encounters. Four of the pregnant females involved in associations with males were pregnant with the corresponding male's cubs at the time of the associations. In three other instances, males that were the known fathers of nursing litters associated with their lactating mates. These males traveled with their mates over 1-3 day periods, at times within 1 km of the nurseries. In one case the pair traveled away from the nursery, spent 1-2 days about 6 km from the nursery, then separated when the female returned to her cubs. We suspect the female purposefully led the male from the site of her nursery. In a separate case, a male allowed a lactating female to feed on a deer kill he had made. The cubs were not brought to the cache, and we did not know whether he was their father. In 1 other instance, a resident adult male (M38) usurped a deer kill from an immigrant female (F240) without harming her. F240 was caught in a snare set at her deer kill when M38 came to the site. He carried the deer carcass to a site 215 m away before feeding on it.

One documented female mortality was not included in the association analysis (Table 4.10) because we could not categorize her association. Skeletal remains of a 30-month-old female (F304) indicated she was killed by another cougar (canine punctures were evident in her braincase). Because the carcass was so decomposed, we could not determine if she was tagged. Re-examinations of tagged cougar carcasses indicated that identifying markers (including eartags) were often lost over time.

Injuries on female cougar skulls were also indicative of prior, dangerous encounters with other cougars. Of 29 female cougar skulls (24 adults, 5 subadults) collected from cougars that either died on the SAM or died after translocation, we found that 5 (21%) of the adults and 1 (20%) of the subadults had survived prior skull injuries. Only 2 (8%) of the adult females had sustained injuries consistent with bites from other cougars. The low percentage of females with prior skull injuries may signify a relatively low incidence of fighting between males and females, and/or the low probability that females survived fights with males. All females that were captured on the SAM during the study showed no overt scars from fighting; however, of the 11 females that died during associations with males on the SAM, 9 had sustained mortal bites to the skull.

Female-Female

Females were located together during 11.4% (n=30) of all documented associations, none of which resulted in mortalities or known injuries. Three of the associations were apparently not related to breeding activities (neither female was in estrus), because both females were either pregnant or raising young cubs. We also assumed 3 other associations were not related to breeding activities because the cougars were sharing a deer kill. We did not know the reason for the other 24 associations, but we suspected some of them may have involved an estrus female looking for a mate. We suspected this for 3 reasons: 1) In all 24 associations, at least 1 of the females was either without cubs, or her cubs had reached the age of independence; 2) some of the females were documented associating with adult male cougars within 3 to 9 days (n=4) or 14 to 28 days (n=2) of the female-female association, suggesting they were in estrus; and 3) one female became pregnant within 1 week of the female-female association.

Associations Between Independent Males and Cubs

We documented 5 associations between independent male cougars and cubs where we suspected the mother of the cubs was not present (n=4), or we knew the mother was not present (n=1). All 5 associations resulted in cub mortalities. In 2 of these cases entire litters were cannibalized. In the first case, resident adult M52 entered F45's nursery, killed, then ate all 4 of F45's 1 month-old cubs while F45 was feeding on a deer kill about 1 km from the nursery. In the second case adult M88 apparently killed and cannibalized all 3 of F107's cubs when they were 2 months old. M88 was F107's father and, and based on breeding associations, also the apparent father of the litter he cannibalized. Individual radio-collared cubs from 3 other litters were killed (2 of which were cannibalized) when they were 1.5, 2.8 and 3.0 months old, respectively. All 3 cubs were killed by males resident to the area.

Families

Each year an average of 73% of the adult females on the SAM were raising cubs (see Chapter 3.4.6). Radio-telemetry data and visual observations indicated that female cougars remained close to their nurseries when cubs were <8 weeks old. Capture information on 148 cubs from 50 nursing litters indicated cubs were not capable of independent travel when they were less than 5 weeks old. Observations of cubs first captured at 6.5 to 8.5 weeks of age indicated they could quickly manuever over steep, rocky terrain and travel moderate distances. However, cubs apparently were not capable of following their mothers long distances until they were about 9 weeks old. Cubs making their first long-distance movements (range = 2.8-7.0 km) from the vicinity of their birth sites ranged in age from 9.0 to 10.5 weeks. By this age, most cubs were probably weaned and dependent on meat. Females were documented nursing cubs up to 7 weeks old, whereas the youngest cub documented eating meat was 9 weeks old.

On average, females were located with their young (≤6 months old), radio-collared cubs during 81% of their telemetry locations (n=246), and with their older (>6 months old) radio-collared cubs during 82% of their telemetry locations (n=208). The majority of these locations were at apparent day beds.

Cubs remained dependent on their mothers for, on average, 13.4 months. Age at independence for 15 radio-collared cubs (6 males, 9 females) born to 9 females averaged 14.0 months for males and 13.0 months for females. Siblings became independent within 0 to 1.5 months of each other. A mother's breeding activities may have prompted independence in some cubs, but not always. We documented 3 females that were pregnant while they were still caring for dependent young. Two female cubs (F68, F10) that were orphaned at 7.5 and 9.8 months of age, respectively, survived, but we do not know the fates of their male littermates. F68 remained philopatric and produced a litter of her own, whereas F10 was killed as an 18-month-old subadult by a male cougar southeast of her natal area.

4.4.6 COMMUNICATION

Cougars communicated through visual, tactual, auditory, and olfactory mechanisms. Although we were unable to directly observe the postures, gestures and tactile responses exhibited by associating cougars, we occasionally were able to discern the results of the communication (e.g. scarring, mortal injuries, dispersal, pregnancies).

Auditory communications were documented on several occasions. Sweanor (1990) describes some vocalizations heard between male - female pairs that included low gargling growls, throaty yowls, squeaks and whistles. Young cubs (<6 weeks old) often emitted high pitched chirps and mews while at dens with their mothers. We documented these vocalizations when we were approaching or watching families at nurseries, and after the mothers were apparently aware of our presence. In most situations the mother stopped nursing, so we suspect the vocalizations were neonatal distress calls (Peters and Wozencraft 1989). Purring (by both cubs and mothers) was also occasionally documented while cubs were nursing. Whistles, which were occasionally heard while we were radio-tracking the members of a family group, were considered contact calls (Peters and Wozencraft 1989, Padley 1996). Sweanor (1990) describes a unique combination whistle that was emitted by a female cub 9 days after she was orphaned. We also documented vocalizations termed “ouch” calls by Padley (1996). In the SAM, ouch calls were made by both males and females. Most ouch calls were heard during crepuscular hours when a lone cougar was traveling within 400m of the researcher. Generally a cougar would emit 1 or 2 ouch calls, move some distance, then call again. In one case, telemetry indicated adult M88 was emitting ouch calls while traveling toward F103. F103, who was raising 1-month-old cubs, apparently also moved toward M88. Although Padley (1996) suggested ouch calls signified frustration, ouch calls on the SAM may also have been a method of advertisement. Ouch calls were sometimes intermixed with caterwauls (longer, loud vocalizations of varied pitch and intensity; probably identified as screams and yowls by Padley). Caterwauls were documented by lone cougars, and also during male -female associations. During 3 visual observations (all suspected breeding associations), the cougars were within 10 m of each other when one cougar caterwauled. Apparent defensive and offensive threat calls included hisses, spits and growls. These vocalizations were often emitted by cougars when they were captured in snares. Females also occasionally growled when we approached to within 25 m of nurseries.

Indirect methods of communication included olfactory signals (tracks, urine, feces or scats, probable scent from anal or other glands) and visual signals (scrapes, scratches on trees, scat mounds, kill caches). Scrapes (small mounds of soil, and/or dried vegetation scraped into a pile with the hind feet, were made by every resident male on the SAM. Males token-urinated on most scrapes, and some scrapes were marked with scats. Males generally scraped in prominant locations and along travelways (e.g. ridgelines, channel bottoms, under large trees and ledges, at kill sites). Sweanor (1990) found that some scrape sites were reused on an irregular basis by up to 3 different resident males. When Sweanor (1990) analyzed scrapes made by 4 adult males with overlapping home ranges, she found that from 23 to 40% of the scrape sites utililzed by an individual male were shared with other males.

Adult females rarely scraped. Tracks and radio-telemetry indicated that females visited scrape sites, and solitary females occasionally marked them with urine. Some females visited scrape sites and vocalized in the vicinity while they were apparently in estrus. Females generally did not leave any visual markers when they defecated, or they made scat mounds. Scat mounds consisted of 1 or more scats buried in a pile of soil or other debris. Toilets were often found near kill-cache sites and were sometimes used by more than 1 member of a family group.

Cougars sometimes scratched the bark of cottonwood (*Populus* spp.) and willow (*Salix* spp.) trees. Lamellae from cougar claws could be found in the scratches indicating that the principal purpose was probably claw grooming; however, scent from the feet probably remained. Scratch sites were generally associated with scrape sites.

4.5 DISCUSSION

We studied the social organization of a cougar population that was protected and was recovering from the effects of heavy exploitation (sport hunting and control) which occurred during 1979 to 1985 (see Chapter 2: *The Research Environment*). Sweanor (1990) reported on the social organization of cougars on the SAM during the first 3 years of our research (1985 to 1988), which heretofore, was the most quantitative examination of the subject in the literature. Those findings were corroborated with the additional research that we conducted from 1989 to 1995. The social organization of the cougar population on the SAM was very similar to other cougar populations studied in North America.

4.5.1 SEX STRUCTURE AND DENSITY

The SAM cougar population was very similar in structure and density when compared to other cougar populations. The sex ratio of adult cougars in the SAM favored females, a characteristic also found in other populations in Idaho, Wyoming, California, Florida, Utah, Alberta (Hornocker 1970, Seidensticker et al. 1973, Logan et al. 1986, Hopkins 1989, Beier and Barrett 1993, Maehr et al. 1989, Lindzey et al. 1994, Ross and Jalkotzy 1992, respectively). Although Sweanor (1990) reported a sex ratio in the SAM that slightly favored males, the bias was not significant and was probably due to the heavy control efforts prior to the study's initiation. The SAM cougar population also reached densities similar to those reported for northern temperate areas (see Chapter 3: *Cougar Population Dynamics*).

4.5.2 HOME RANGE SIZE

Cougar home range size in the SAM varied widely within and among individuals. The variations in each individual's home range size from year to year was probably related to a variety of factors, including changes in food availability, energy demands (primarily for females raising cubs), the arrival of new immigrant cougars, and the deaths of neighboring resident cougars. Home range size on the SAM did not vary in any predictable pattern based on seasonal changes (Sweanor 1990), probably because the major prey source (mule deer) did not migrate, and females did not have a specific breeding season (see Chapter 3.4.6). The increasing size of a female's home range as her cubs aged was probably related both to increasing energy demands (Ackerman 1982) and the improved traveling capabilities of older cubs.

Within-gender differences in individual home range sizes were probably amplified by variations in the quality of the cougar habitat throughout the SAM. Seidensticker et al. (1973) stated that home range size may be dependent on stalking cover, topography, numbers of ungulates, ungulate carrying capacity and vulnerability of prey. Logan and Irwin (1985), Belden et al. (1988), and Laing and Lindzey (1991) showed cougars used features of the habitat selectively. Logan (1983) explained how specific habitat features conferred advantages to cougars in hunting prey and in intra-species communication. Home range size tended to increase in the northern end of the SAM, where mountainous areas were broken by large expanses of desert flats. In areas with fragmented habitat patches, larger home ranges probably are essential to provide adequate food and prospects for mates.

Female home range size declined with increasing density; conversely, male home range size increased. The negative relationship we observed between adult cougar density and female home range size may have been a result of females attempting to avoid other females (this avoidance behavior is further discussed in section 4.5.3). Quigley et al. (1988) also documented a reduction in female home range size with increasing cougar density. The tendancy of female core use areas to remain relatively constant suggested that there may be a minimal area requirement for survival and rearing young. Female home range size is probably dictated by the availability of food resources (Ross and Jalkotzy 1992) and energetics (Ackerman 1982). The reason for the increase in male home range size with increasing density is unclear, but may have been a way of minimizing competition and potentially increasing mating opportunities. There was a noticable expansion of adult male cougar home ranges into the flats adjacent to the SAM during 1993 and 1994 when the mule deer population declined dramatically (see Chapter 5: *Cougars and Desert Mule Deer*). Additionally, there was only 1 female resident present at the north end of the SAM in 1993, where some of the largest male home ranges occurred (Fig. 4.24).

Cougar studies have consistantly reported larger home ranges for males than females (Seidensticker et al. 1973, Murphy 1983, Hemker et al. 1984, Logan et al. 1986, Hopkins 1989, Anderson et al. 1992, Ross and Jalkotzy 1992). Because cougars have a polygynous or promiscuous mating system (Seidensticker et al. 1973, Anderson 1983) and males take no part in raising the young, it is probably adaptive for males to traverse larger areas in attempts to encounter and breed with as many receptive females as possible. Males that do so likely increase their reproductive success. The larger home range size is probably not related to the male's larger body size (Hopkins 1989) or to greater energy demands (Ackerman et al. 1986; Sandell 1989).

Cougar home range sizes reported in the literature vary widely. This may result in part from the differing techniques used to measure home range size, but also from the differing ecological conditions each population encounters. Annual home ranges for male and female cougars in the SAM were intermediate to small in size compared to those recorded elsewhere. The smaller size of home ranges may have been affected by at least 2 factors. First, the prey source in the SAM did not migrate. Second, the San Andres Mountains are a long, narrow sliver of cougar habitat (where stalking, nursery and resting cover, and adequate numbers of a large prey species are available) surrounded on 2 sides by inhospitable, wide desert basins. The isolated nature of the SAM may generally force individuals to use smaller areas in an effort to both utilize the best habitat and avoid one another. Only when habitat conditions became poor (during the drought and subsequent deer decline in 1993 and 1994) did some cougars (generally males) expand their home ranges further into the adjacent desert flats (see Fig. 4.24).

Cougars in Utah had some of the largest home ranges of any study; annual male and female home ranges averaged 685 km^2 and 826 km^2, respectively (Hemker et al. 1984). Moreover, the density of cougars in the Utah population was the lowest documented in North America (Lindzey et al. 1994). Home range sizes comparable to those found in the SAM have been reported in California (Hopkins 1989), British Columbia (Spreadbury 1989) and in the Guadalupe Mountains of New Mexico (Smith et al. 1986). The Guadalupe Mountains study area was located within a Chihuahuan desert environment similar to the SAM.

4.5.3 DISTRIBUTION AND MOVEMENTS

Overall, resident adult females maintained relatively stable home ranges. This behavior may be adaptive, since familiarity with the home range is advantageous in the exploitation of food resources, especially for females raising cubs (Seidensticker et al. 1973). However, female home range shifts were occasionally documented. Shifts may have been the result of females jockeying for available space, such as exhibited by F21 after the arrival of F103 on the TA (also see Sweanor 1990 for other examples). They may also be caused by the loss of security in the present home range. For example, the traumatic experience of losing her cubs may have prompted F107 to shift her home range outside the area where the loss took place (Fig. 4.22). Because she had also been residing in an area where 2 adult males (M88 and M193) were competing for territory, she may have been looking for a more stable environment. Males may be in a state of heightened aggression during periods when they are competing with other males for territory; consequently a female may be at greater risk. M88 cannibalized F107's cubs just 3 days after he was apparently in a fight with a relatively new immigrant, M193.

In contrast to the females, most males showed greater variation in home range fidelity and shifting. Shifting was probably in response to the removal of other resident males (either through death or translocation), the arrival of new males, pressure exerted by more aggressive neighboring males, or the reduction in available mates within a male's territory. M3 expanded his home range after his neighboring competitors and the majority of his potential mates were translocated from the TA. Within 3 months after his male neighbors were removed M3 was utilizing areas formerly used by 4 of his male neighbors, and he had apparent breeding associations with 3 females (2 of which he had not had previous contact with). M1 returned to his former home range after a neighboring competitor had been killed by another resident male. Other males that apparently usurped area from males they apparently killed included M19 (see Sweanor 1990) and M219. Males that apparently shifted because of aggressive neighboring males (some of which were new immigrants) included M1 (see Sweanor 1990), M3, M36, and M88. Because all adult males exhibited scars from fighting at one time or another during the course of the study, we suspect all males occasionally tested one another and directly competed for territory and mates.

Spatial overlap of annual home ranges was documented between both adult male cougars and adult female cougars; however, the overlap between male home ranges was more extensive. Most studies (Seidensticker et al. 1973, Shaw, 1980, Ashman et al. 1983, Logan et al. 1986, Hopkins 1989, Ross and Jalkotzy 1992) documented overlap of neighboring cougar home ranges, but in general, it was the female home ranges that overlapped more extensively. The lower degree of overlap between female home ranges in the SAM, even at high densities and especially in the core areas, suggested females were practicing mutual avoidance (see Hornocker 1969).

Because male home ranges were more dynamic, the high degree of spatial overlap found between male home ranges may have, in part, been an artifact of the time frame used to delineate the home range boundaries. Leyhausen (1965) stated that the common use of an area does not necessarily mean simultaneous use. Close examination of the movements of individual cougars of the same gender over shorter time periods indicated that areas that overlapped spatially were usually avoided temporally (see Figs. 4.17-4.20). Additionally, it apparently took long periods of time for some adult males to resolve territorial disputes. For example, M88 and M193 shared portions of their home ranges and apparently fought at least twice during the 12-month period after M193 arrived on the SAM; after that point, their home ranges were exclusive.

The greatest amount of overlap occurred between females and males, where the amount of area individual females shared with males approached 100%. Documented associations between cougars indicated that cougars were more tolerant of individuals of the opposite sex, or that they sought out members of the opposite sex more frequently. Although associations were infrequent (only 4.9% of the total number of locations involved associating cougars), the majority (76%) involved males and females. This is similar to the findings of Seidensticker et al. (1973) in Idaho.

Of the 200 male-female associations documented in this study, 147 likely involved breeding pairs. However, only 33 (22.4%) of these associations resulted in litters. This suggests that females may have a low rate of conception or that they suffer a high rate of abortion. Several species of felids, including cougars, have high copulation rates and low conception rates (Eaton 1976, Anderson 1983). Such increased breeding associations may be beneficial. Eaton (1976) speculated that high copulation rates in cougars evolved to evaluate male vigor, and thus increase female reproductive success. We speculate that increased breeding associations may also increase female survival. A female that has several estrus cycles prior to becoming pregnant has more opportunities to associate with larger, potentially dangerous males in a positive way. Such positive associations may increase recognition and reduce aggression when the pair meets again under other circumstances. In this study males killed females on 10 occasions, demonstrating the potential for aggressive associations.

In concurrance with Hornocker (1969), it was apparent that cougars were essentially solitary and tended to avoid one another. Direct associations were rare (only 5% of locations on the SAM), and involved high risks. Twenty-six percent of male-male and 6% of male-female associations on the SAM resulted in mortalities. Associations that occurred were of brief duration. Visual, vocal and olfactory signals probably allowed cougars to communicate without direct contact, and thus reduced the chances for serious encounters. Although cougar vocalizations did not carry the long distances typical of the the roaring cats, vocalizations were probably important in advertising presence, maintaining cohesion of the family unit, and in bringing breeding pairs together. Scent marks such as scrapes were probably used as “bulletin boards” that both male and female cougars visited to determine the temporal presence of conspecifics. Scent marking is central to the advertisement of land tenure (Gorman and Trowbridge 1989). Seidensticker et al. (1973) reported that scrapes appeared to delineate home range boundaries. Although Sweanor (1990) found that males scraped throughout their home ranges, she was unable to ascertain the frequency at which boundary and interior scrape sites were revisited. However, because overlap between male home ranges was fairly extensive, and males often shared scrape sites, it would probably be advantageous for males to continually advertise their presence throughout their home ranges. Scat mounds and scent left at kills, in tracks, at scratch sites, and at day beds probably also informed other cougars of the presence of conspecifics.

4.5.4 DISPERSAL AND PHILOPATRY

Patterns of dispersal and philopatry on the SAM were similar to those reported elsewhere. Dispersal appeared to be independent of density (see Chapter 3.5.4). Anderson et al. (1992) compiled dispersal information on 65 North American cougars and found that males dispersed, on average, 2.7 times as far as females. Philopatry has only been documented in female cougars (Anderson et al. 1992, Ross and Jalcotzy 1992, Lindzey et al. 1994), however, non-dispersal of progeny was recorded more often on the SAM than in other studies.

Sweanor (1990) discussed several reasons why dispersal is adaptive in cougars: 1) extreme inbreeding is avoided; 2) outcrossing is enhanced; 3) competition for food and space between siblings and parents is minimized; 4) unoccupied habitat will have a greater likelihood of colonization; and 5) small, isolated populations can be rescued from extinction risks (Greenwood 1980, Dobson 1982, Moore and Ali 1984, Hornocker and Bailey 1986).

Males may be more likely to disperse than females because they may be more successful at obtaining territory and mates without encountering direct competition from larger, more experienced fathers. Costs of dispersal would probably be offset by greater reproductive opportunities (Greenwood 1980). Conversely, females may enhance their reproductive success by remaining philopatric when conditions (habitat and prey) are favorable. Females that are philopatric already are in habitat where they are familiar with sources of food and potential nurseries. Furthermore, females that are philopatric may already be familiar with adult males (future mates) in the area, and thus minimize the chances of encountering potentially aggressive, unfamiliar males. Although philopatric females run the risk of breeding with fathers (we documented 3 occasions), such incestuous inbreeding probably occurs too infrequently in cougars to produce deleterious genetic effects in the population. Recruits on the SAM were comprised of approximately equal proportions of progeny and immigrants, but the majority of recruited females were progeny (see Chapter 3.5.4). Philopatry resulted in 7 female enclaves, which we defined as groups of genetically related females in the population.

The dispersal duration documented for M82 (7.8 mo.) after independence on the SAM indicates that subadult dispersers may be considered transients for long periods. Subadult dispersers were the only cougars to exhibit transient behavior on the SAM. Most of the transient behavior alluded to in the literature (Hornocker 1970, Seidensticker et al. 1973, Logan et al. 1986, Spreadbury 1989) may in fact be dispersal behavior exhibited by subadults (see Sweanor 1990 for a more thorough discussion of dispersal and transient behavior).

4.5.5 LAND TENURE

Cougars on the SAM demonstrated a similar land tenure system as described for cougars in Idaho (Hornocker 1970, Seidensticker et al. 1973). Land tenure was primarily based on prior rights; new cougars established long-term residency when sufficient space and resources were made available. Recruits (progeny and immigrants) established residency in areas made vacant by cougar deaths or translocations, and generally avoided other cougars temporally if not spatially. Females practiced mutual avoidance behavior, and were never documented in physical confrontations with other females.

But contrary to Seidensticker et al. (1973), male cougars in the SAM often contested each others prior rights to an area. Males were territorial; they advertised their presence, patrolled, and directly competed with other males for rights to area and mates. However, territories were not rigid; males were always responding to the presence or absence of neighboring males, and home range shifts were not uncommon. For example, the relatively weak home range fidelity reported for M3 (Table 4.6, Fig. 4.17A-F) was probably a result of his home range expansion after the removal of neighboring males, followed by his attempt to avoid other males as they immigrated to the TA and began to establish their own territories. Avoidance behavior is probably reinforced through fighting. Scarring found on captured male cougars, as well as the deaths of both subadult and adult males during associations, indicated fighting was not uncommon. In fact, intra-species fighting has been documented across the geographic range for cougars in North America (McBride 1976, Logan 1983, Spreadbury 1989, Lindzey et al. 1989, Maehr 1990, Ross and Jalkotzy 1992, Beier and Barrett 1993). Fights between adult males generally resulted in either 1) subsequent home range shifts by one of the combatants in an attempt to avoid future aggressive encounters (as shown with

M88 after his confrontations with M193), or 2) the death of a combatant and either retention or subsequent usurpation of the area by the victor.

Male cougars were responsible for all of the intra-species killing that we documented. Deaths were a result of territorial disputes between males, competition between males for breeding opportunities, apparent competition for food (between males and between males and females), and predation (killing of females and cubs by males). Since solitary carnivores such as the cougar generally only encounter conspecifics for mating, they may have dispensed with most of the behavioral mechanisms that prevent damage to conspecifics (Lorenz 1971). Risks of such serious confrontations probably reinforce mutual avoidance behavior in cougars.

On the SAM cougars spaced themselves through territorial behavior in males and mutual avoidance behavior in females. This behavior may be adaptive because it helps maximize reproductive success, as well as, mediate how cougars partition space and food resources in environments where food resources fluctuate. We hypothesize that cougar populations are ultimately limited by habitat quality and quantity (particularly food); however, their social organization may influence how cougars respond to food availability. In the SAM, the cougar population increased rapidly after control and experimental removal (maximum rates of increase were 0.17-0.28; see Chapter 3.4.13). As the SAM population rebuilt, the land tenure system mediated how space was reoccupied; cougars generally occupied open areas first. As vacated spaces were filled, the rate of increase slowed considerably in the RA (to 0.05 during the last 4 years) and the density of adults actually declined slightly in the TA during the last year (1994 to 1995). Concurrent with these lower rates of increase, drought conditions in late 1992 through 1994 contributed to a decline in the mule deer population. These factors suggested that the cougar population was approaching carrying capacity and that rates of population increase were density dependent. The territorial and avoidance components of the land tenure system may be mechanisms which regulate the rate at which the cougar population increases toward carrying capacity; this may contribute to the relative stability of the system.

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Table 4.1. Average annual home range size for 23 adult male cougars on the San Andres Mountains, New Mexico, 1986-1994.

Male No.	n[a]	$\bar{x}$ No. Locations[b]	HOME RANGE ESTIMATOR[c] Adaptive Kemal (km^2)			
			Adaptive Kemal (km^2)		Minimum Convex Polygon (km^2)	
			90%	60%	100%	90%
3	7	46.3	187.0 (61.5)	75.1 (42.3)	180.3 (51.3)	122.5 (43.8)
5	6	42.7	186.4 (63.3)	53.2 (20.1)	162.7 (48.1)	118.5 (40.4)
7	4	45.8	183.3 (75.9)	63.9 (40.2)	170.4 (94.7)	121.2 (72.4)
18	4	43.8	336.4 (225.9)	144.3 (126.4)	367.8 (247.3)	209.0 (125.7)
19	3	44.7	192.4 (20.6)	68.0 (2.6)	185.1 (11.7)	125.1 (5.3)
20[d]	1	32.0	305.5	117.8	320.6	272.9
22	1	46.0	153.4	40.0	142.1	92.0
29	1	42.0	126.1	54.7	108.9	83.3
36	6	43.0	222.6 (74.0)	70.6 (11.5)	245.5 (144.6)	133.1 (32.6)
38	6	43.5	248.8 (71.7)	104.9 (17.3)	242.9 (51.9)	163.4 (36.0)
46	4	46.2	229.6 (97.2)	72.8 (39.7)	213.5 (40.6)	155.8 (38.3)
49	2	46.5	113.2 (5.4)	43.0 (5.3)	96.1 (5.2)	61.0 (4.7)
52	6	40.0	104.4 (19.5)	43.6 (16.8)	104.7 (25.6)	68.5 (17.7)
53[d]	3	39.3	245.8 (115.1)	59.2 (19.3)	232.3 (52.3)	171.7 (48.6)
73	1	39.0	177.8	74.2	139.2	124.2
88	3	47.0	174.1 (40.6)	67.8 (13.7)	171.4 (25.2)	123.1 (23.4)
124	1	44.0	81.4	24.8	85.0	66.1
138	2	46.5	249.6 (93.4)	79.6 (17.3)	268.9 (23.5)	163.2 (39.2)
151	2	41.5	271.2 (77.4)	71.3 (26.0)	271.4 (66.3)	168.8 (14.8)
161	1	41.0	259.7	42.7	202.0	150.8
173	2	46.0	132.8 (8.2)	61.2 (7.4)	122.4 (3.5)	90.2 (6.3)
193	1	46.0	59.3	16.8	75.2	53.0
210	1	43.0	180.0	70.7	194.6	128.4
$\bar{x}$ of $\bar{x}$		43.3	192.2 (70.8)	66.1 (28.2)	187.1 (76.2)	128.9 (51.1)

[a] n=the number of years (1 January through 31 December) for which annual home range size was calculated. Annual home ranges were only calculated for cougars that were radio-monitored for ≥10 months of a given 12 month period.

[b] The average number of locations obtained each year. Only aerial locations augmented with ground locations which were >3 days apart were utilized.

[c] Mean (standard deviation).

[d] Both M20 and M53 shifted their home range activities to the north and outside the study area over time. Only those years when they spent time within the study area are reported here.

Table 4.2. Average annual home range size for 29 adult female cougars on the San Andres Mountains, New Mexico, 1986-1994.

Female No.	n[a]	$\bar{x}$ No. Locations[b]	HOME RANGE ESTIMATOR[c]			
			Adaptive Kernal (km^2)		Minimum Convex Polygon (km^2)	
			90%	60%	100%	90%
2	1	35.0	139.8	43.9	121.5	73.6
4	2	40.5	37.2 (2.1)	10.4 (1.2)	39.2 (3.0)	22.2 (7.1)
6	2	40.0	116.0 (11.4)	40.4 (5.0)	96.8 (0.1)	60.4 (9.3)
15	5	44.6	58.9 (14.2)	19.0 (8.5)	58.9 (14.8)	37.5 (11.8)
21	3	45.0	63.6 (23.1)	23.3 (9.1)	73.7 (9.6)	46.7 (19.8)
27	2	43.5	60.1 (13.7)	14.6 (1.6)	79.9 (1.3)	33.1 (3.4)
28	3	45.7	89.9 (46.5)	30.0 (8.9)	89.8 (47.2)	59.1 (24.7)
31	1	46.0	72.8	21.6	71.3	49.3
37	3	44.0	113.8 (15.2)	40.6 (18.1)	90.9 (2.0)	59.9 (8.2)
41	3	45.0	48.5 (16.0)	23.0 (4.0)	55.3 (17.7)	38.0 (9.8)
45	6	43.8	37.8 (11.4)	11.4 (2.9)	38.0 (8.5)	27.1 (6.8)
47	6	47.8	33.9 (11.0)	11.4 (5.7)	42.1 (13.1)	24.2 (9.0)
54	3	44.3	63.9 (36.5)	20.1 (11.6)	62.7 (32.1)	40.2 (18.2)
57	3	44.3	46.7 (11.2)	17.9 (5.3)	50.7 (4.0)	33.4 (9.7)
58	2	48.0	67.8 (32.6)	14.0 (2.0)	92.2 (32.0)	41.6 (21.6)
65	3	41.7	61.4 (26.4)	18.1 (3.3)	58.8 (21.3)	36.2 (11.5)
68	1	47.0	30.1	8.8	25.7	16.1
86	1	44.0	92.8	28.0	117.7	57.8
87	2	41.5	107.8 (30.4)	34.9 (19.1)	106.8 (39.1)	71.0 (19.4)
89	1	43.0	45.7	16.4	43.0	28.4
90	2	44.0	64.0 (5.6)	26.9 (1.1)	65.6 (0.5)	42.4 (2.5)
91	3	44.7	45.5 (14.4)	19.5 (6.8)	55.4 (10.7)	34.2 (8.2)
103	2	49.5	54.3 (0.7)	28.2 (5.0)	66.6 (20.2)	40.4 (2.1)
107	1	47.0	67.6	19.4	72.2	52.3
126	2	41.0	80.7 (2.1)	26.4 (12.7)	74.2 (10.0)	43.2 (12.2)
128	1	44.0	47.0	21.3	46.8	33.6
130	1	44.0	66.2	21.2	78.2	43.0
147	2	39.0	209.2 (110.6)	54.1 (16.4)	210.0 (122.4)	148.2 (89.2)
149	2	43.5	61.4 (20.9)	21.0 (13.4)	48.0 (19.0)	33.0 (18.7)
$\bar{x}$ of $\bar{x}$		43.8	71.9 (37.4)	23.6 (10.7)	73.5 (35.5)	45.7 (24.1)

[a] n=the number of years (1 January through 31 December) for which annual home range size was calculated. Annual home ranges were only calculated for cougars that were radio-monitored for ≥10 months of a given 12 month period.

[b] Average number of locations obtained each year. Only aerial locations augmented with ground locations which were >3 days apart were utilized.

[c] Mean (standard deviation).

Table 4.3. Mean home range size[a] for male and female cougars on the San Andres Mountains, New Mexico, each year, 1989, 1990 and 1993.

Year[b]	n	Male HR Size (km^2)[c]		n	Female HR Size (km^2)[c]	
		90% ADK	60% ADK		90% ADK	60% ADK
A[d]						
1989	11	159.1 (53.6)	55.0 (28.0)	9	75.4 (43.5)	23.7 (13.9)
1990	10	193.1 (96.6)	69.1 (25.7)	12	59.6 (26.2)	18.6 (6.1)
1993	10	223.2 (89.5)	73.8 (27.0)	10	45.1 (24.0)	19.6 (11.4)
B[d]						
1989	12	156.7 (51.8)	52.7 (30.3)	17	73.6 (34.9)	23.3 (11.3)
1990	14	169.6 (87.1)	62.1 (25.4)	20	57.5 (24.6)	18.7 (7.6)
1993	17	198.9 (102.3)	69.3 (34.5)	24	50.5 (26.5)	19.3 (10.9)

[a] Home range size was calculated using the Adaptive Kernal (ADK) home range estimator.

[b] Corresponding January adult cougar densities for 1989, 1990, and 1993 were 1.2, 1.6, and 1.8 adults/100 km^2, respectively.

[c] Mean (standard deviation).

[d] In **A**, mean home range size was determined for each sex each year based on the individual adult cougars that were radio-monitored for at least 10 months of that particular 12 month period. In **B**, mean home range size was determined for each sex each year based on all the individual adult cougars that were present as adults on the SAM for >3 months of that particular 12 month period. For example, an adult cougar that died 1July 1989 would have a 1989 home range size based on its locations from 1 January through 1 July.

Table 4.4. Female cougar home range size during an entire reproductive cycle (birth of 1 litter to the birth of subsequent litter, n=11), San Andres Mountains, New Mexico. At least 1 cub in each first litter survived to independence.

Cougar No.	Dates[a]	No. Months[b]	No. Locations[c]	HOME RANGE ESTIMATOR (KM^2)[c] ADK		MCP	
				90% (-)	60% (-)	100% (+)	90% (-)
4	06/04/86-11/01/87	16.9	66	30.8	11.0	50.8	27.5
15	05/15/87-11/24/88	18.3	68	56.0	17.6	74.2	38.1
21	10/04/91-05/05/93	19.0	75	115.6	45.4	116.1	88.0
37	05/07/88-09/18/89	16.0	61	131.2	62.8	116.5	84.8
37	09/18/89-03/19/91	18.3	69	105.0	33.2	105.0	33.2
41	09/14/88-03/14/90	18.0	71	63.6	25.5	75.1	47.2
45	05/25/91-11/19/92	17.8	66	26.0	6.7	35.6	20.0
47	08/24/90-10/25/91	14.0	57	17.7	5.1	22.7	14.7
47	05/26/93-10/22/94	16.8	69	40.4	13.8	47.2	31.7
65	03/09/90-08/14/91	17.1	60	70.9	24.0	79.6	24.0
91	08/16/92-06/05/94	21.6	81	57.0	24.4	66.2	41.1
Mean		17.6 (1.9)		64.9 (37.8)	24.5 (17.4)	71.7 (31.5)	40.9 (24.3)

[a] First date = birth date of first litter; second date = birth date of second litter.

[a] Number of months from the birth of 1 litter to the birth of the next litter.

[b] All aerial locations augmented with ground locations that were >3 days apart.

[c] ADK=Adaptive Kernal; MCP=Minimum Convex Polygon. A (+) indicated the cyclic home range size was significantly larger than the annual home range size (*P* = 0.01) and a (-) indicated that there was no significant difference in cyclic and annual home range sizes (*P* > 0.1; Wilcoxon signed-rank test).

Table 4.5. Home range (HR) sizes (means and standard deviations) for female cougars during 3 consecutive 6-month periods of their reproductive cycles, San Andres Mountains, New Mexico, 1986-1994.

n	I. HR Size, Cubs ≤6 mo. old[a]					II. HR Size, Cubs 7-12 mo. old					III. HR Size, No Cubs[b]				
	$\bar{x}$ No. Locations	ADK		MCP		$\bar{x}$ No. Locations	ADK		MCP		$\bar{x}$ No. Locations	ADK		MCP	
		90%	60%	100%	90%		90%	60%	100%	90%		90%	60%	100%	90%
8[c]	23.1	26.4^{+} (8.3)	9.7^{+} (5.9)	23.0^{++} (5.9)	16.6^{+} (4.6)	23.2	47.0 (21.5)	15.4 (6.1)	40.6 (15.9)	25.9 (11.4)	23.4	67.0 (21.1)	23.4 (12.2)	56.0 (14.5)	37.6 (10.6)
7[d]	24.4	24.3* (21.8)	9.9* (11.0)	20.6* (18.9)	15.8* (16.6)	24.1	57.9 (46.0)	18.0 (13.4)	41.7 (20.2)	28.7 (15.3)					

[a] A $^{++}$ indicates HR size I was significantly smaller than the corresponding HR size II and III. A $^{+}$ indicates HR Size I was significantly smaller than the corresponding HR Size III only (Kruskal-Wallis and Multiple Comparisons, $P<0.05$). A* indicates HR Size I was significantly smaller than the corresponding HR size II (Wilcoxon rank sum test, $P<0.025$). HR sizes II and III were not significantly different.

[b] During this 6 month period, females were either raising cubs of dispersal age (>12 months old) or they were without cubs (cubs had become independent). The average age at independence for cubs in the San Andres Mountains was 13.8 months.

[c] HR sizes determined for 7 different females during 3 consecutive 6-month periods on 8 occasions. At least 1 cub in each litter was known to have survived to 12 months of age.

[d] HR sizes determined for 6 different females during 2 consecutive 6-month periods on 7 occasions. At least 1 cub in each litter was known to have survived to 12 months of age. This sample of 7 is discrete from the sample of 8 above.

Table 4.6. Average home range overlap between years for individual adult male cougars (n=16) on the San Andres Mountains, New Mexico, 1986-1994.

			HOME RANGE ESTIMATOR			
			90% MCP		90% ADK	
Male No.	No Years Monitored[a]	$\bar{x}$ No. Locations	$\bar{x}$ overlap (%)	SD	$\bar{x}$ overlap (%)	SD
3[b]	7	46.3	33.9	29.4	43.2	29.6
5	6	42.7	71.7	19.8	69.5	21.4
7	4	45.8	41.4	29.1	50.8	21.9
18	4	43.8	33.4	34.6	37.6	38.4
19	3	44.7	78.2	5.3	78.5	10.9
20	3	34.3	57.2	15.3	64.3	19.7
36	6	43.0	23.2	25.4	31.2	25.7
38	6	43.5	37.5	24.5	42.8	23.3
46	4	46.2	31.9	24.2	27.3	21.3
49	2	46.5	65.8	5.0	81.8	3.9
52	6	40.0	67.1	17.6	66.5	20.2
53	4	38.0	20.6	23.1	42.1	31.0
88	3	47.0	71.7	13.0	75.8	15.2
138	2	46.5	48.0	11.5	63.0	6.9
151	2	41.5	74.4	6.5	71.3	20.4
173	2	46.0	70.0	4.9	74.7	4.7
Mean			51.6	19.9	57.5	18.0

[a] Each year began 1 January and ended 31 December. Home range overlap was only calculated between years where the cougar was monitored for ≥10 months.

[b] M3 was residing on the TA before, during and after the experimental removal of 11 adult cougars (5 males, 6 females) from the TA.

Table 4.7. Average home range overlap between years for individual adult female cougars (n=21) on the San Andres Mountains, New Mexico, 1986-1994.

			HOME RANGE ESTIMATOR			
			90% MCP		90% ADK	
Female No.	No Years Monitored[a]	$\bar{x}$ No. Locations	$\bar{x}$ overlap (%)	SD	$\bar{x}$ overlap (%)	SD
4	2	64.5	57.8	18.5	64.5	3.5
6	2	40.0	73.4	11.2	63.2	6.2
15	5	44.6	54.3	21.7	58.9	17.6
21[b]	3	45.0	32.6	19.9	41.3	25.5
27	2	43.5	85.6	8.8	71.8	16.3
28	3	45.8	47.4	33.7	45.2	21.5
37	3	44.0	66.3	13.1	71.2	9.5
41	3	45.0	50.5	26.6	44.8	20.8
45	6	43.8	53.6	22.9	57.7	20.5
47[b]	6	47.8	49.8	22.4	56.8	18.8
54	3	44.3	40.7	24.9	54.9	31.0
57	3	44.3	74.7	17.8	69.0	13.9
58	2	48.0	72.1	37.3	74.5	35.8
65	3	41.7	58.1	19.7	66.4	24.5
87	2	41.5	72.8	19.9	69.4	19.6
90	2	44.0	72.4	4.2	81.6	7.1
91	3	44.7	61.0	20.7	57.8	20.2
103	2	49.5	54.1	2.7	72.8	0.9
126	2	41.0	78.5	22.2	70.6	1.9
147	2	39.0	52.0	67.9	52.3	67.5
149	2	43.5	58.4	33.0	61.6	21.0
Mean			60.3	13.3	62.2	10.6

[a] Each year began 1 January and ended 31 December. Home range overlap was only calculated between years where the cougar was monitored for ≥10 months.

[b] F21 and F47 were residing on the TA before, during and after the experimental removal of 11 adult cougars (5 males, 6 females) from the TA.

Table 4.8. Distances between mean locations for females during 3 six-month periods of their reproductive cycles[a], San Andres Mountains, New Mexico, 1987-1992.

Female No.	DISTANCE (km^2) Period I - Period II	Period II - Period III	Period I - Period III
15	0.50	0.80	1.06
21	9.51	4.03	6.07
37	5.57	0.59	5.10
41	2.22	2.30	1.61
41	1.62	0.38	1.90
45	0.36	2.50	2.67
65	1.90	3.92	2.73
91	3.14	1.74	2.07
Mean (SD)	3.10 (3.07)	2.03 (1.43)	2.90 (1.76)

[a] Female locations were obtained during 3 consecutive 6-month periods. Period I = female raising cubs ≤6 months old; Period II = female raising cubs 7-12 months old; Period III = female either solitary or raising cubs >12 months old.

Table 4.9. Mean percent annual home range overlap[a] between individual adult cougars of the same and opposite gender[b], San Andres Mountains, New Mexico.

Year		MALE - MALE			FEMALE - FEMALE			MALE - FEMALE			FEMALE - MALE	
		% Overlap			% Overlap			% Overlap			% Overlap	
	n[c]	90%	60%	n	90%	60%	n	90%	60%	n	90%	60%
1989	12	48.7 (15.0)	18.7 (14.9)	17	39.2 (27.3)	12.7 (14.7)	12	63.2 (24.0)	37.2 (23.9)	17	89.1 (19.4)	62.3 (27.5)
1990	14	64.8 (21.6)	45.1 (26.7)	20	47.8 (34.8)	25.0 (32.9)	14	62.6 (21.1)	43.2 (26.3)	20	87.8 (15.2)	59.3 (34.0)
1993	17	75.0 (17.7)	47.1 (24.5)	24	60.5 (31.2)	26.2 (22.8)	17	49.7 (29.4)	32.1 (24.0)	24	96.6 (6.4)	75.7 (29.8)
$\bar{x}$ of $\bar{x}$	14.3	62.8 (13.3)	37.0 (15.9)	20.3	49.2 (10.7)	21.3 (7.5)	14.3	58.5 (7.6)	37.5 (5.6)	20.3	91.2 (4.8)	65.8 (8.7)

[a] Home range overlap was measured using the 90% and 60% Adaptive Kernal (ADK) home range estimator. Means and standard deviations reported.

[b] There were 4 comparisons: Male-Male = the average percent of an individual male's home range that was shared with other males; Female-Female = the average percent of an individual female's home range that was shared with other females; Male-Female = the average percent of an individual male's home range that was shared with females; and Female-Male = the average percent of an individual female's home range that was shared with males.

[c] Home range overlap was calculated for all adults that resided on the San Andres Mountains study area for >3 months of a 12 month period. Home ranges were determined utilizing aerial locations augmented with ground locations that were >3 days apart.

Table 4.10. Associations (n=263) between independent radio-collared cougars[a] on the San Andres Mountains, New Mexico, 1985-1995.

Association Type[b]	Number of Associations[c]	Number of Mortalities
AM - AF0	149 (182)	6
AM - AFC	39 (41)[d]	5[e]
AM - AM	25 (25)	5
AF0 - AF0	13 (13)	
AF0 - AFC	9 (11)	
AM - SM	8 (10)	4
AM - SF	7 (8)	1
AFC - AFC	4 (4)	
AF0 - SM	3 (5)	
AFC - SM	2 (2)	
SF - SF	2 (2)	
AF0 - SF	1 (1)	
AFC - SF	1 (1)	

[a] Seven associations that resulted in mortalities are not included here because we could not categorize the association. M198 was apparently killed by a male cougar when he was 23-25 months old and F304 was killed by an unknown cougar when she was about 2.5 years old. Neither cougar was radio-collared and we did not know the status of either cougar in the population. Additionally, 2 entire litters and 1 cub from each of 3 litters were killed by males. We did not categorize these associations because either the mother was not present when the cubs were killed (n=1), or we did not know if the mother was present when the cubs were killed (n=4).

[b] A=Adult; S=Subadult; M=Male; F=Female; 0=Female without cubs or cubs $\geq$9 months old; C=Female had cubs <9 months old or she was known to be pregnant.

[c] Associations are listed in descending order of frequency. The first number represents the number of separate associations; the number of location days are in parenthesis.

[d] Includes 4 adult females and 1 dependent cub; it is probable other cubs were also killed but not found.

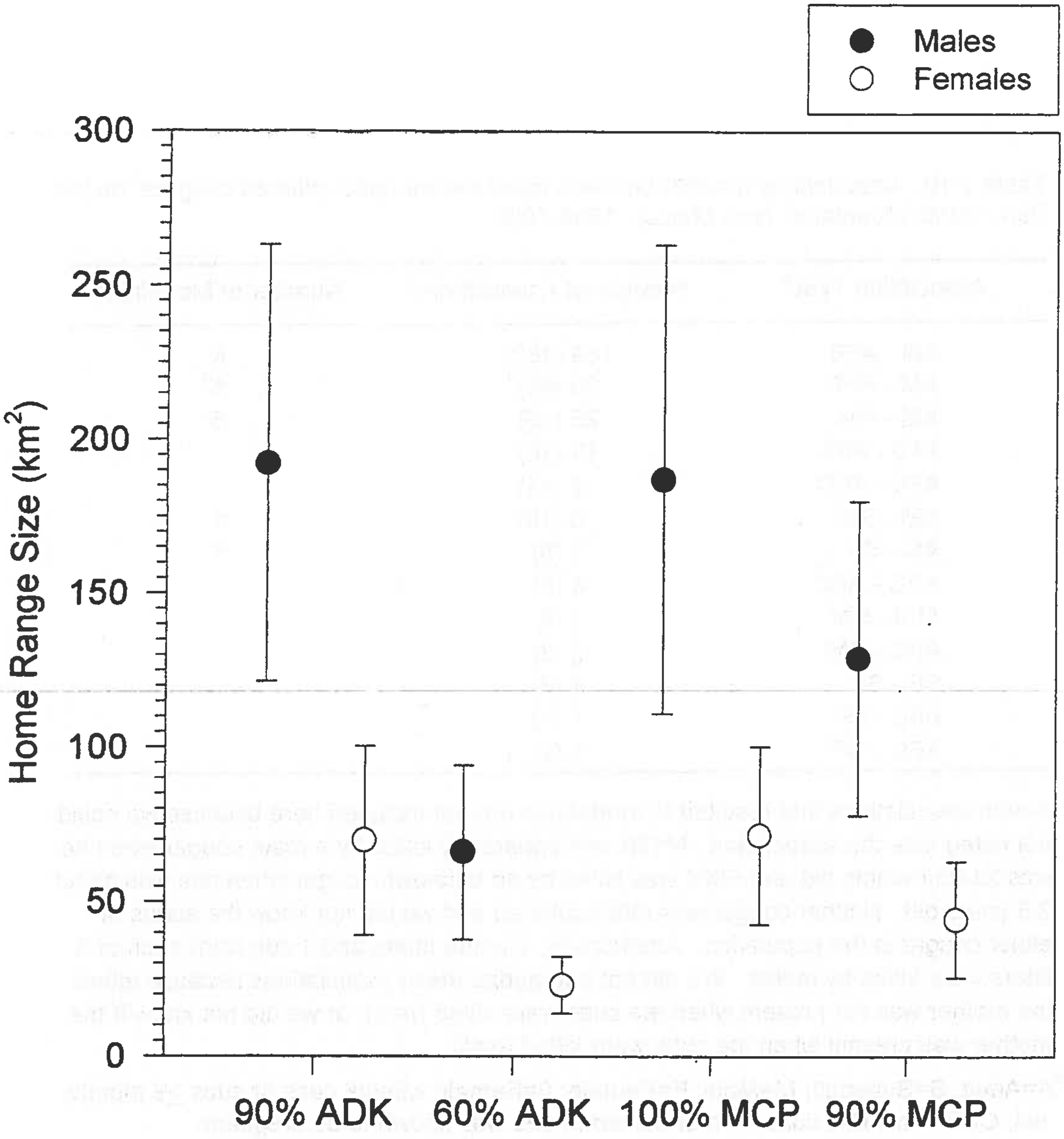


Fig. 4.1. The means of the means and standard deviations of the annual home range size for adult male (n=23) and female (n=29) cougars on the San Andres Mountains, New Mexico, 1986-1994. Male home range size was signficantly greater than female home range size using both the ADK and MCP home range estimators (Wilcoxan rank sum, *P*<0.0001).

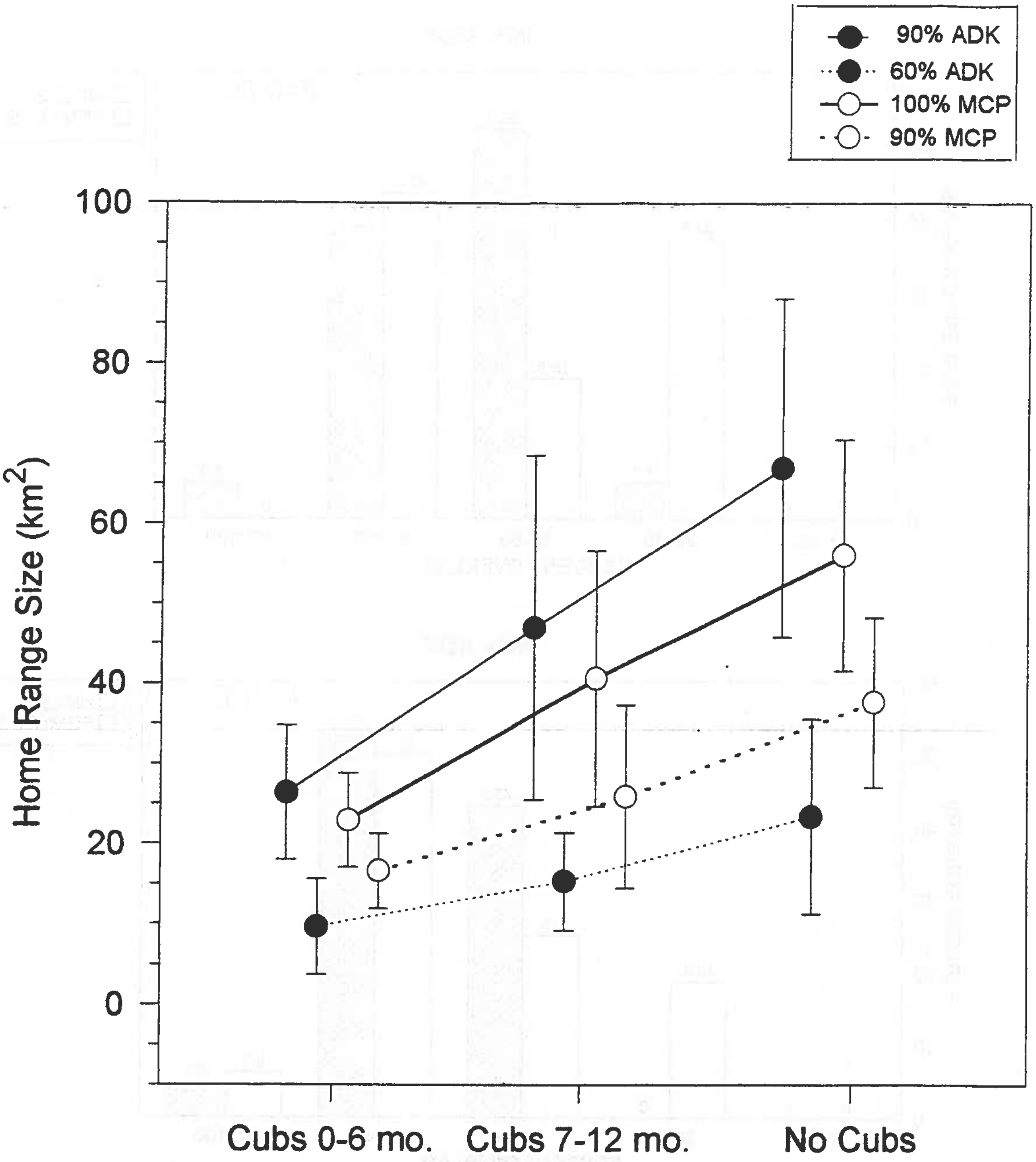


Fig. 4.2. Home range size (mean and standard deviation) for female cougars (n=8) during 3 consecutive 6-month periods in the San Andres Mountains, New Mexico, 1986-1994. Home range sizes were calculated for the same females when they were raising young cubs ($\leq$6 mo.); raising older cubs (7-12 mo.); and when they were either without cubs or raising cubs of dispersal age (>12 mo).

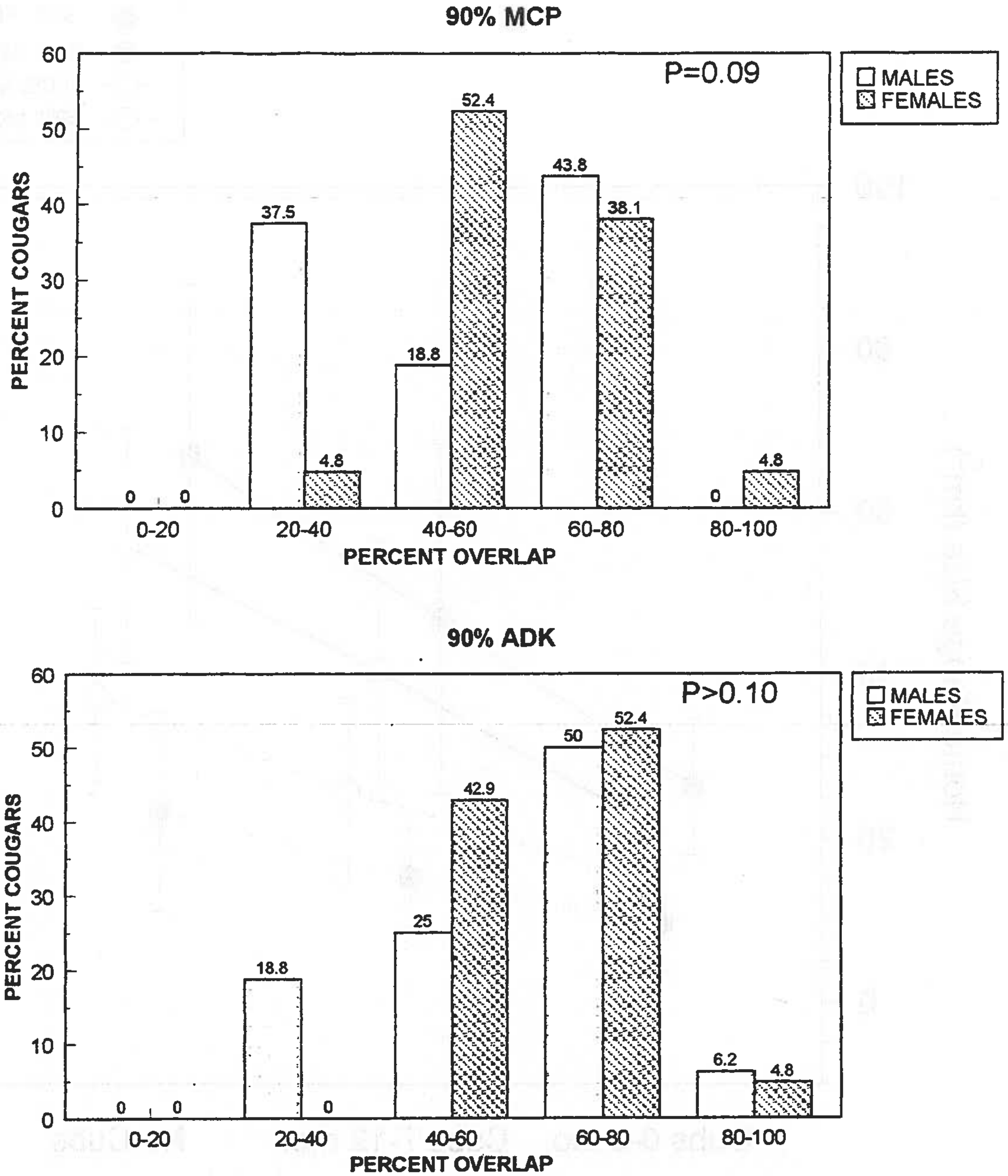


Fig. 4.3. The average percent of home range overlap between years for individual adult male (n=16) and female (n=21) cougars using 2 different home range estimators, San Andres Mountains, New Mexico. Each cougar was monitored for 2-7 years, 1986-1994. Both males and females exhibited variation in home range overlap and consequently , fidelity. Overall, males exhibited less home range fidelity. Based on the 90% MCP home range estimator, males had significantly less annual home range overlap than females (Wilcoxon rank sum, Z=-1.38, p=0.09).

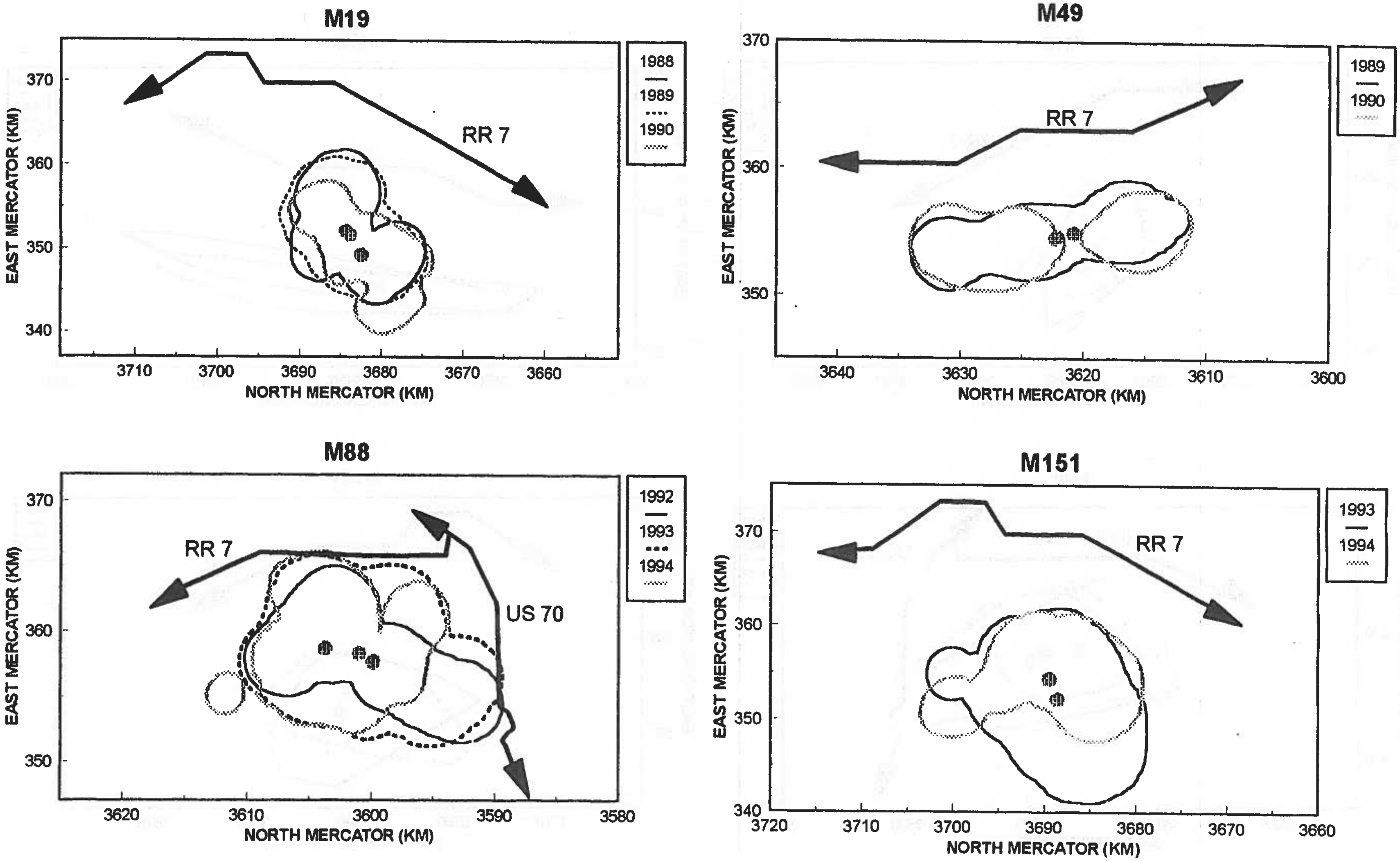


Fig. 4.4. Annual home range overlap (90% ADK) for 4 adult male cougars on the San Andres Mountains, New Mexico. Mean annual overlap ranged from 71.3-81.8% for the 4 males, indicating strong home range fidelity. The grey dots indicate the mean locations for each year.

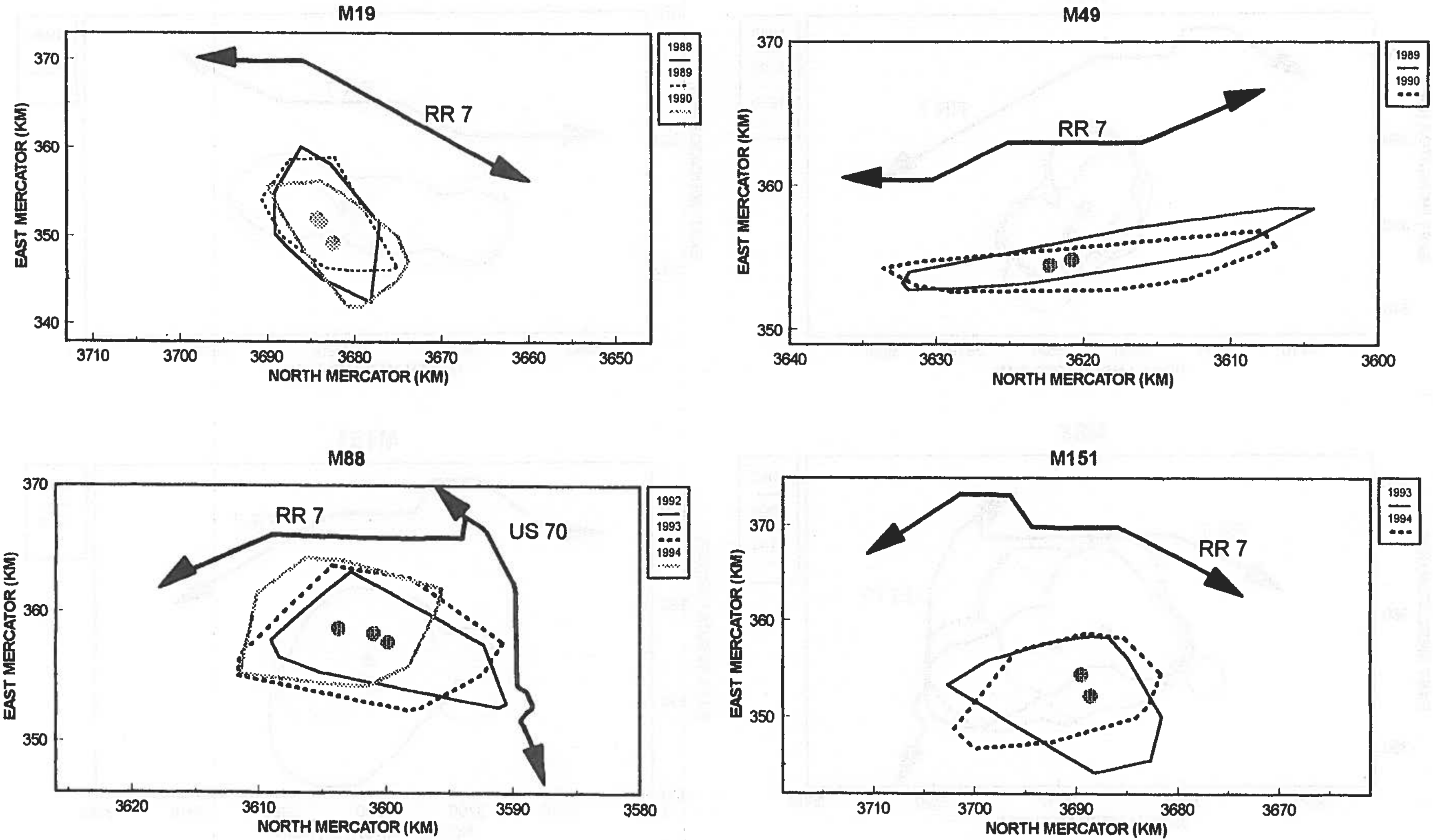


Fig. 4.5. Annual home range overlap (90% MCP) for 4 male cougars on the San Andres Mountains, New Mexico. The mean annual overlap ranged from 65.8-78.2% for each of the 4 males, indicating strong home range fidelity. The grey dots indicate the mean locations for each year.

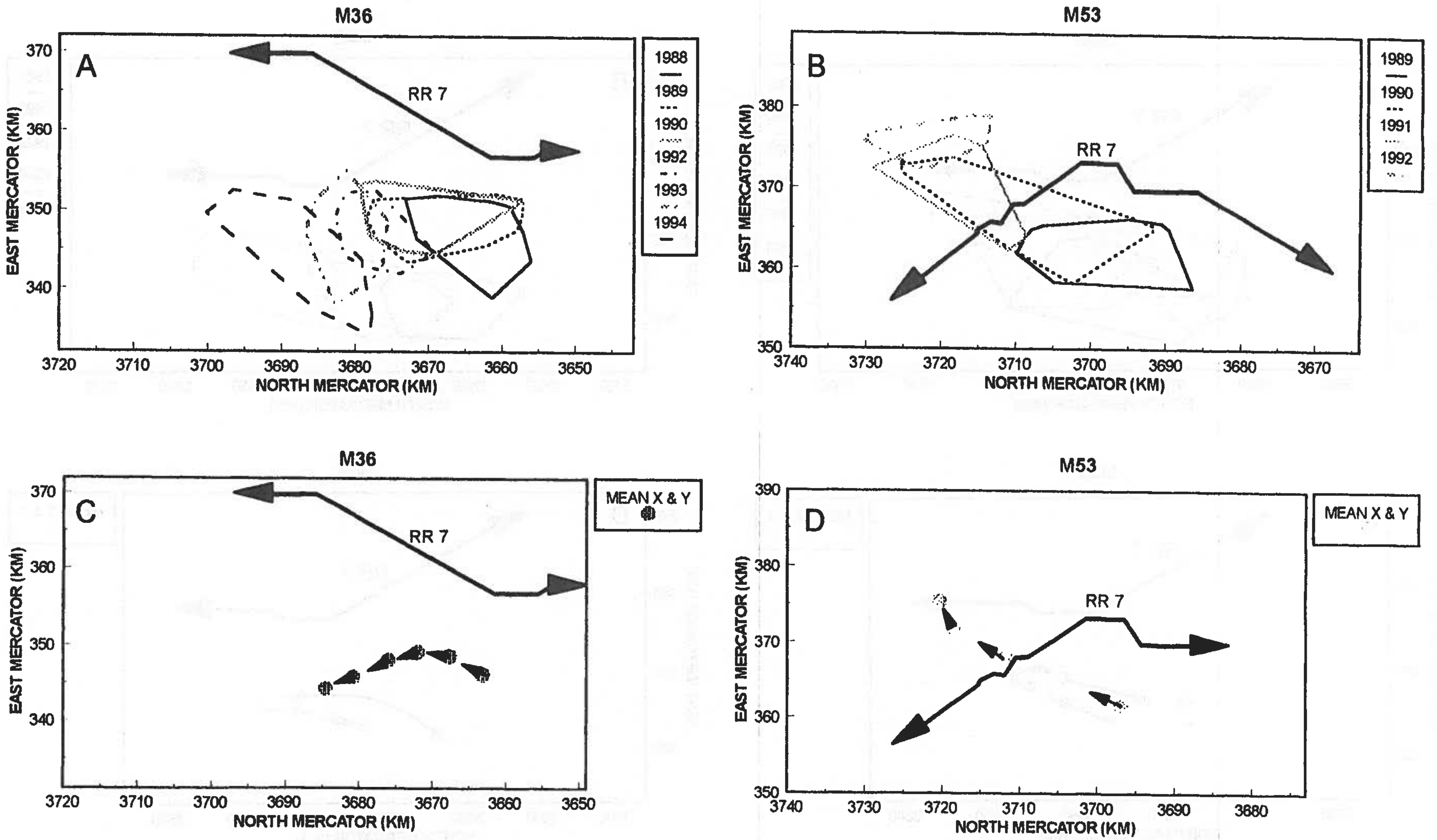


Fig. 4.6. Annual home range overlap and directional home range shifting depicted for 2 adult male cougars on the San Andres Mountains, New Mexico. A and B show the annual home ranges (90% MCP) for M36 and M53; C and D show the corresponding mean east and north UTMs for each year. Annual home range overlap averaged 23.2% and 20.6% for M36 and M53, respectively. M53 eventually shifted completely outside the SAM.

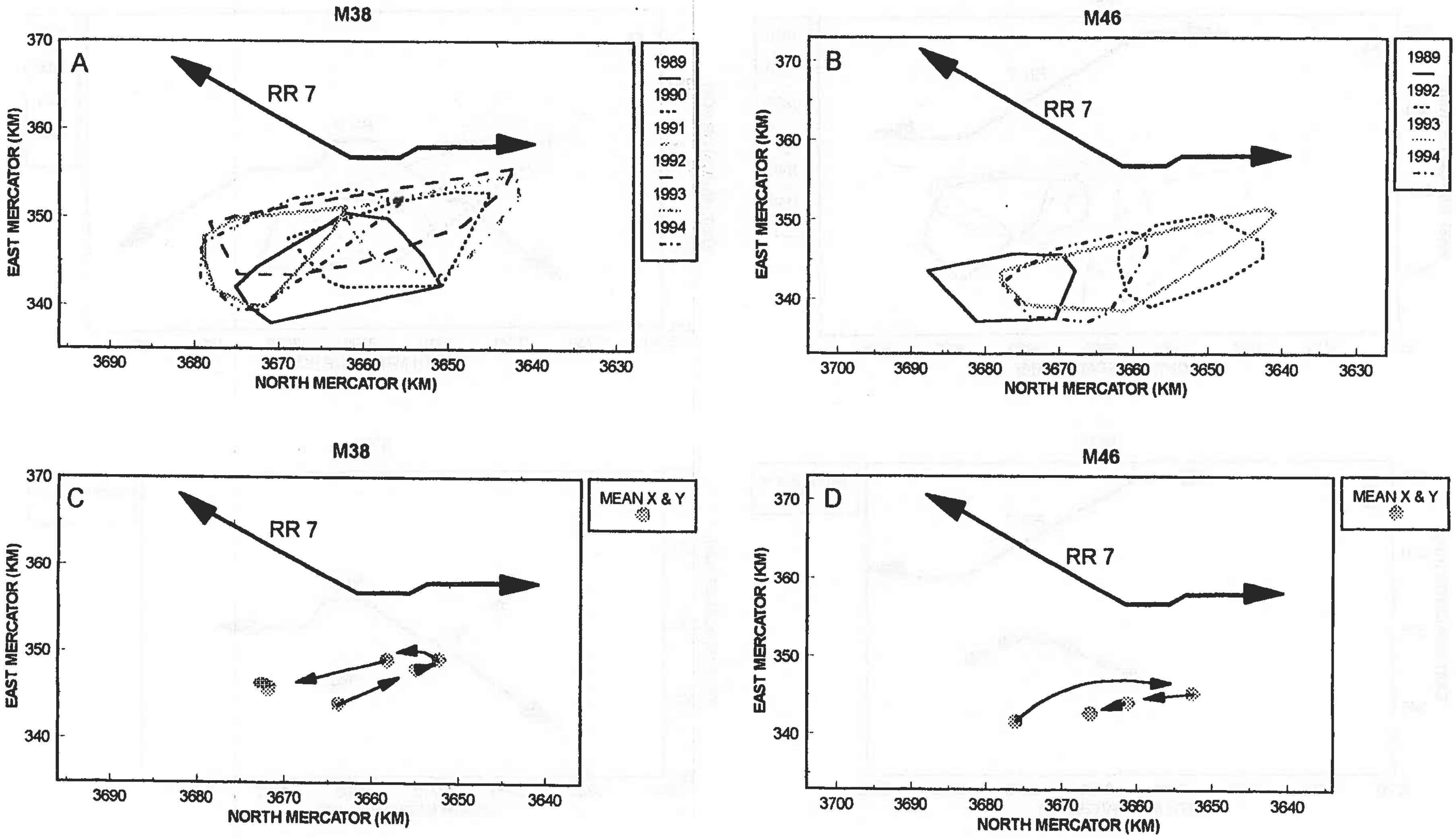


Fig. 4. 7. Annual home range overlap and shifting depicted for 2 adult male cougars on the San Andres Mountains, New Mexico. A and B show the annual home ranges (90% MCP) for M38 and M46; C and D show the corresponding mean east and north UTMs for each year. Both males shift south, then back north over time. Annual home range overlap averaged 37.5% and 31.9% for M38 and M46, respectively.

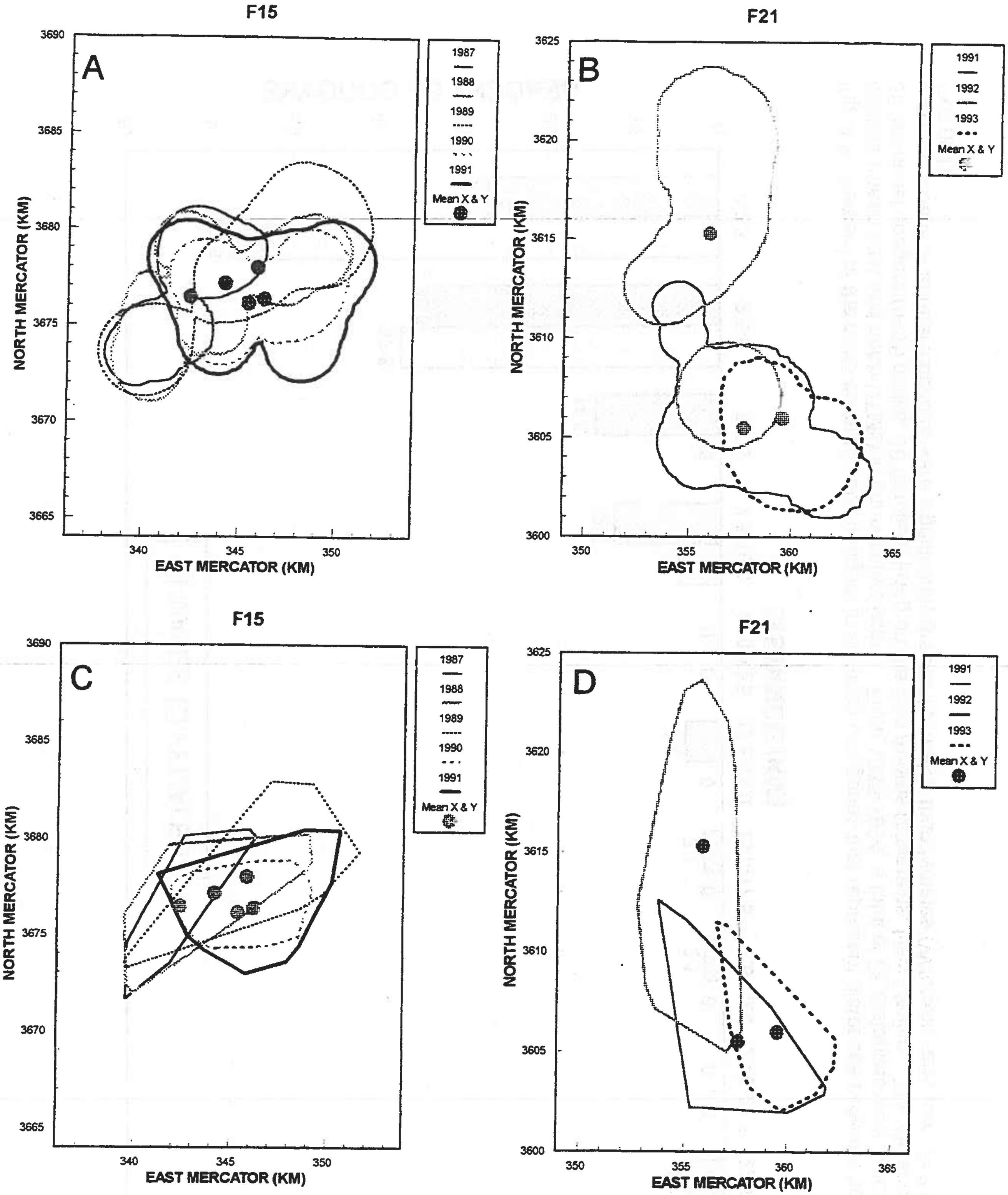


Fig. 4.8 . Annual home range overlap for 2 adult female cougars, F15 and F21, on the San Andres Mountains, New Mexico. Annual overlap was determined based on the 90% Adaptive Kernal (A and B) and the 90% Minimum Convex Polygon (C and D). Mean east and north UTM coordinates for each year are depicted by the gray dots. F15's annual home range overlap averaged 58.9% and 54.3% using the ADK and MCP methods, respectively. F21 showed less home range fidelity than F15; F21's average annual overlap was 41.3% and 32.6% using the ADK and MCP methods, respectively.

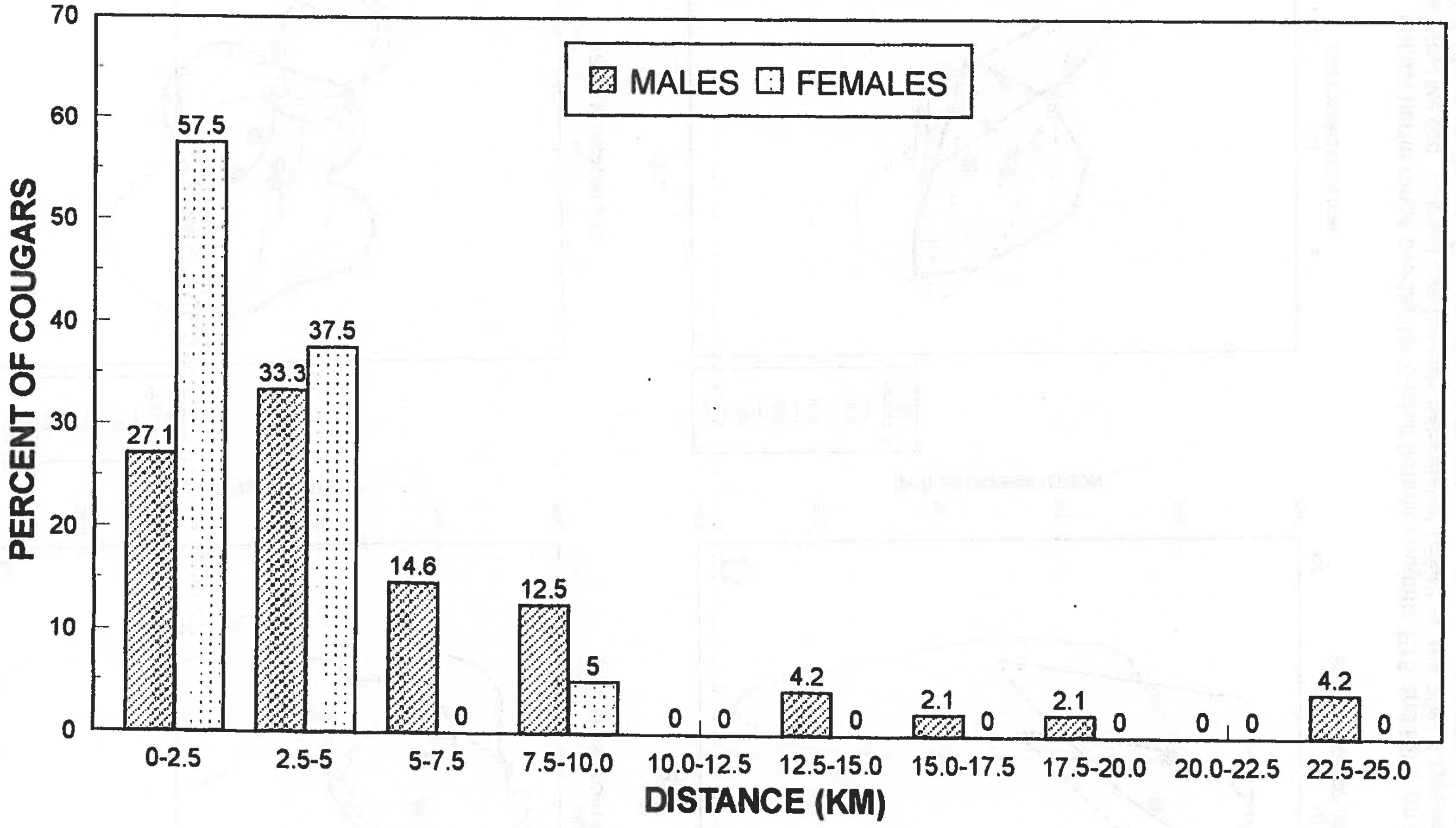
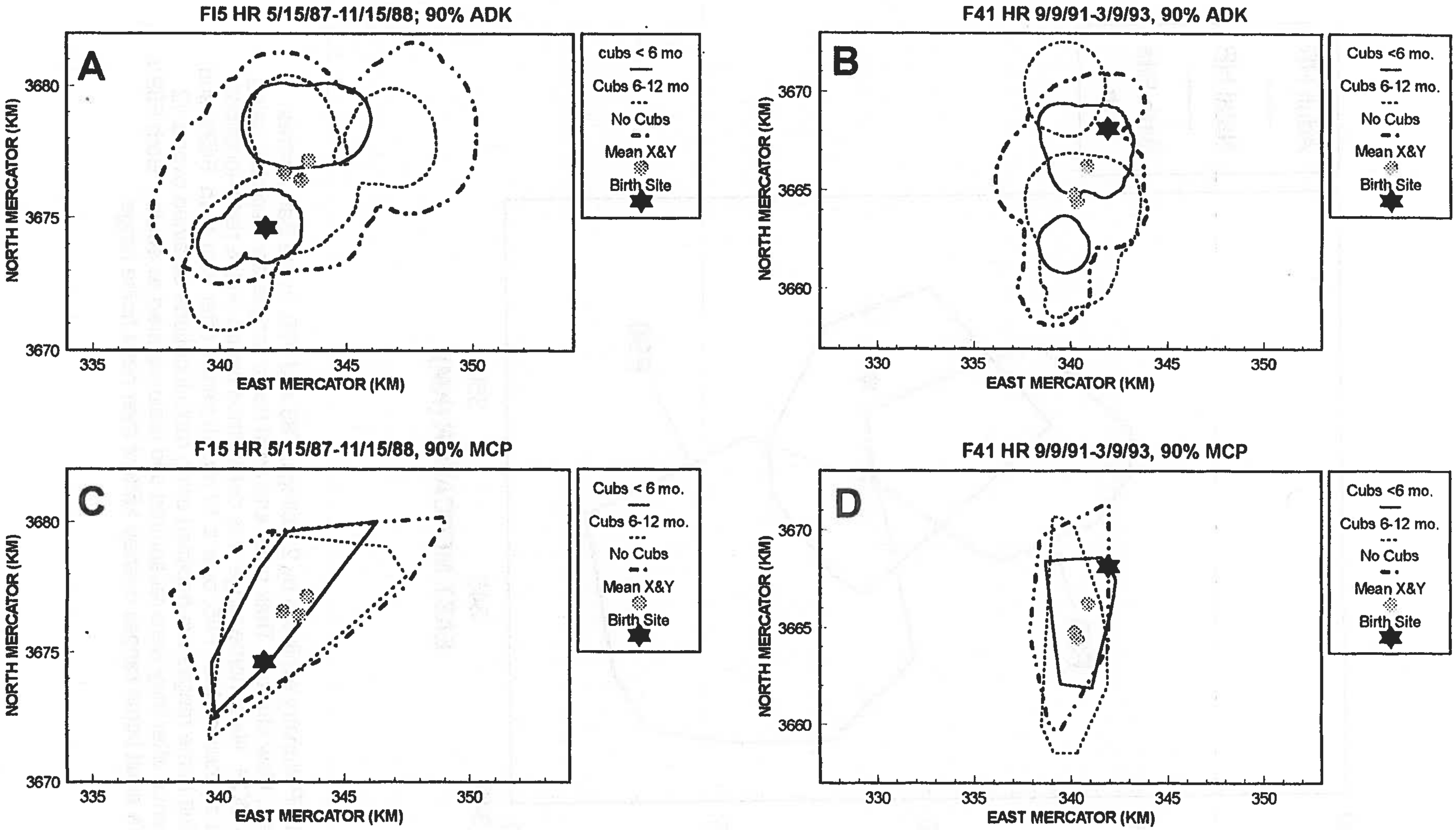


Fig. 4.9. Percent of the radio-collared adult cougars in distance categories that represent distances between home range centers (mean east and north UTMs) in consecutive years. From 1986-1994, a total of 88 distances were calculated for 35 individual cougars (n=15 males, 20 females) living on the San Andres Mountains, New Mexico. The distances between means of annual locations were significantly greater for males than females (Wilcoxon rank sum, Z=3.38, *P*<0.001).


FI5 HR 5/15/87-11/15/88; 90% ADK

F41 HR 9/9/91-3/9/93, 90% ADK

F15 HR 5/15/87-11/15/88, 90% MCP

F41 HR 9/9/91-3/9/93, 90% MCP

Fig. 4.10 . Home ranges (HR) for 2 resident adult female cougars during 3 consecutive 6 month periods of their reproductive cycles, San Andres Mountains, New Mexico. F15 bore consecutive litters of cubs on 5/15/87 (Nursery 1) and 11/24/88; F41 bore a litter on 9/9/91 (Nursery 1) and a suspected consecutive litter in May-June 1993. During the 6 month period "No Cubs," both F15 & F41 were either accompanied by cubs >12 months old, or they were solitary (cubs had become independent). HRs are depicted using both the 90% Adaptive Kernal (ADK; A & B) and 90% Minimum Convex Polygon (MCP; C & D).

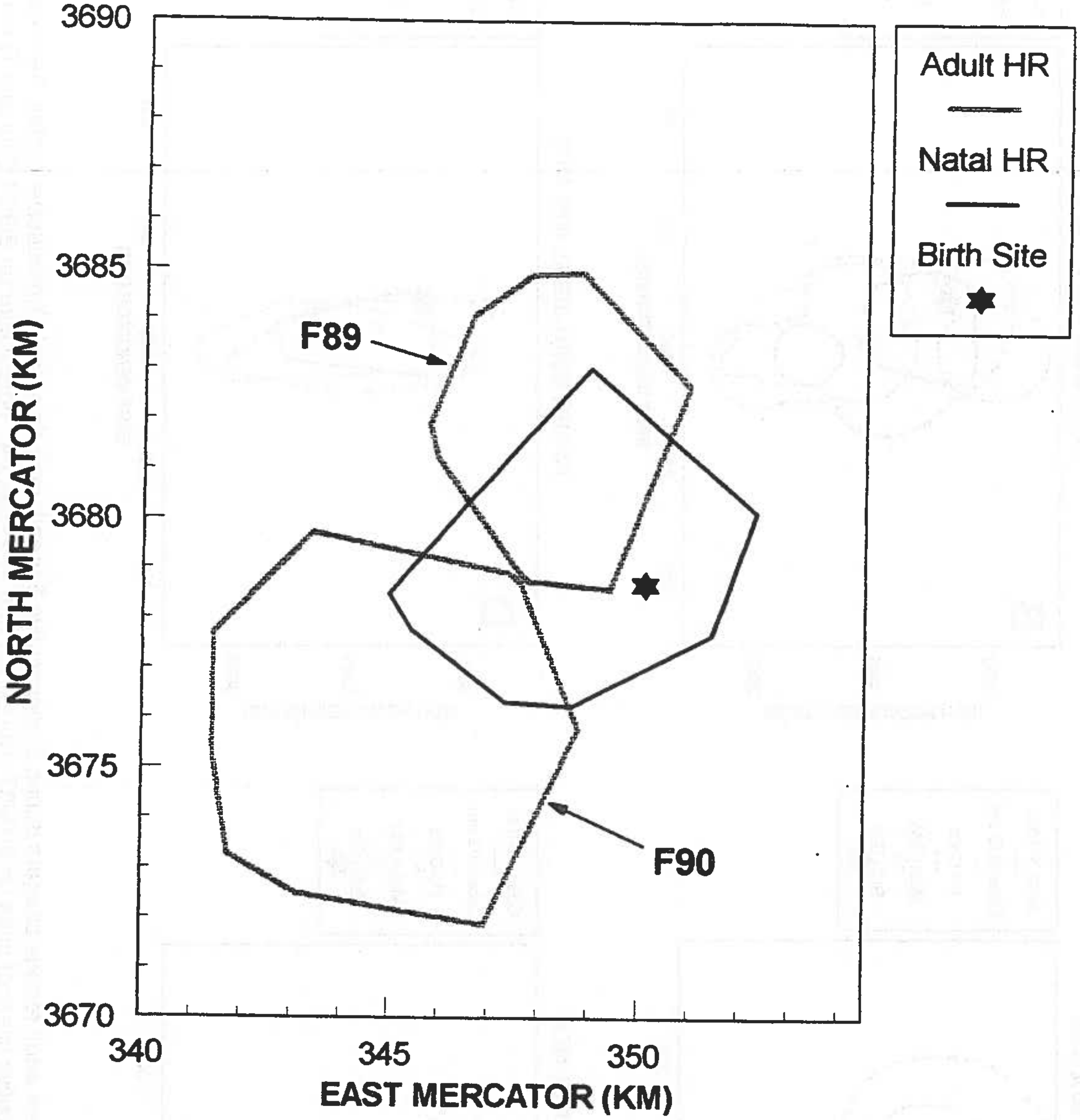


Fig. 4.11. Philopatry exhibited by 2 siblings, F89 and F90, in the San Andres Mountains, New Mexico. Their natal and adult home ranges are depicted using the 90% MCP. Natal home range was determined based on the radio-locations obtained on their mother, F65, over a 12 month period after their birth. F89's and F90's adult home ranges are depicted using radio-locations obtained over a 12 month period after they were recaptured and radio-collared as adults. Both F89"s and F90's adult home ranges overlap >5% of their natal home range.

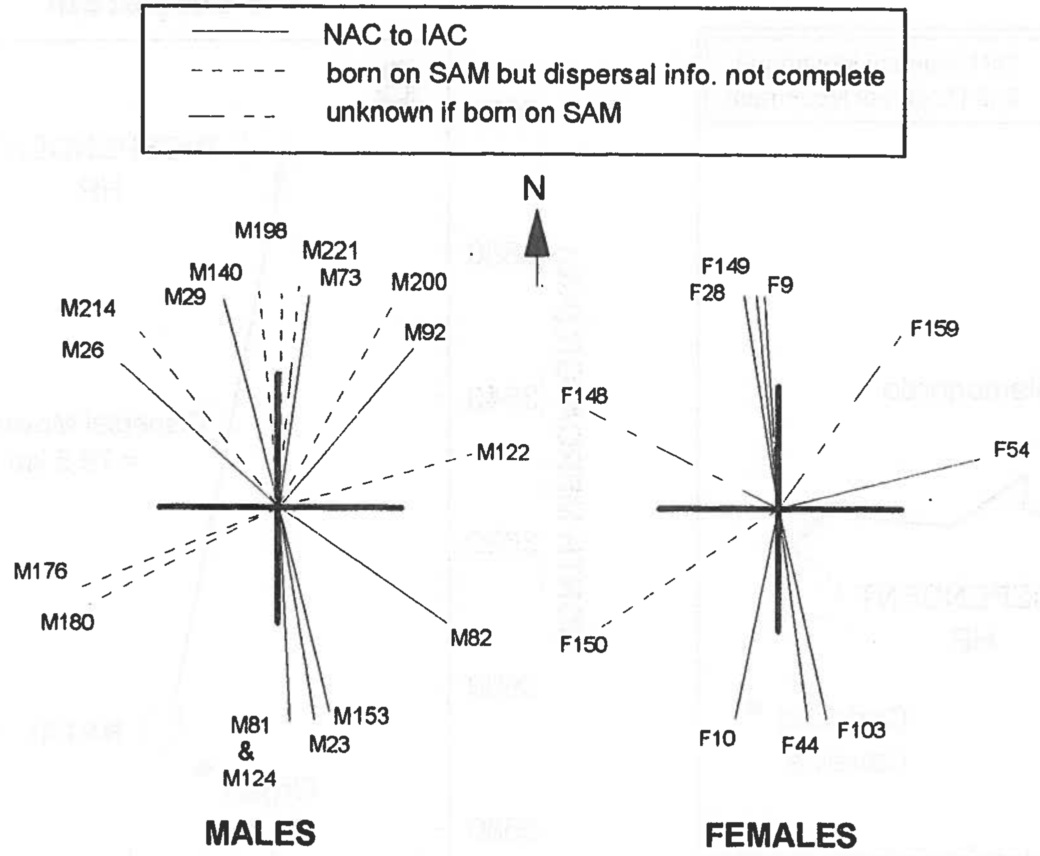


Fig. 4.12. Dispersal direction for 24 cougar progeny and 3 cougars of unknown origin, San Andres Mountains, New Mexico. Dispersal directions were based on the Natal Arithmetic Center (NAC) to Independent Arithmetic Center (IAC) for 15 progeny, the NAC or Capture Site (CS) to Mortality Site or Last Location (LL) for 8 progeny, and from CS to IAC or LL for 3 cougars of unknown origin.

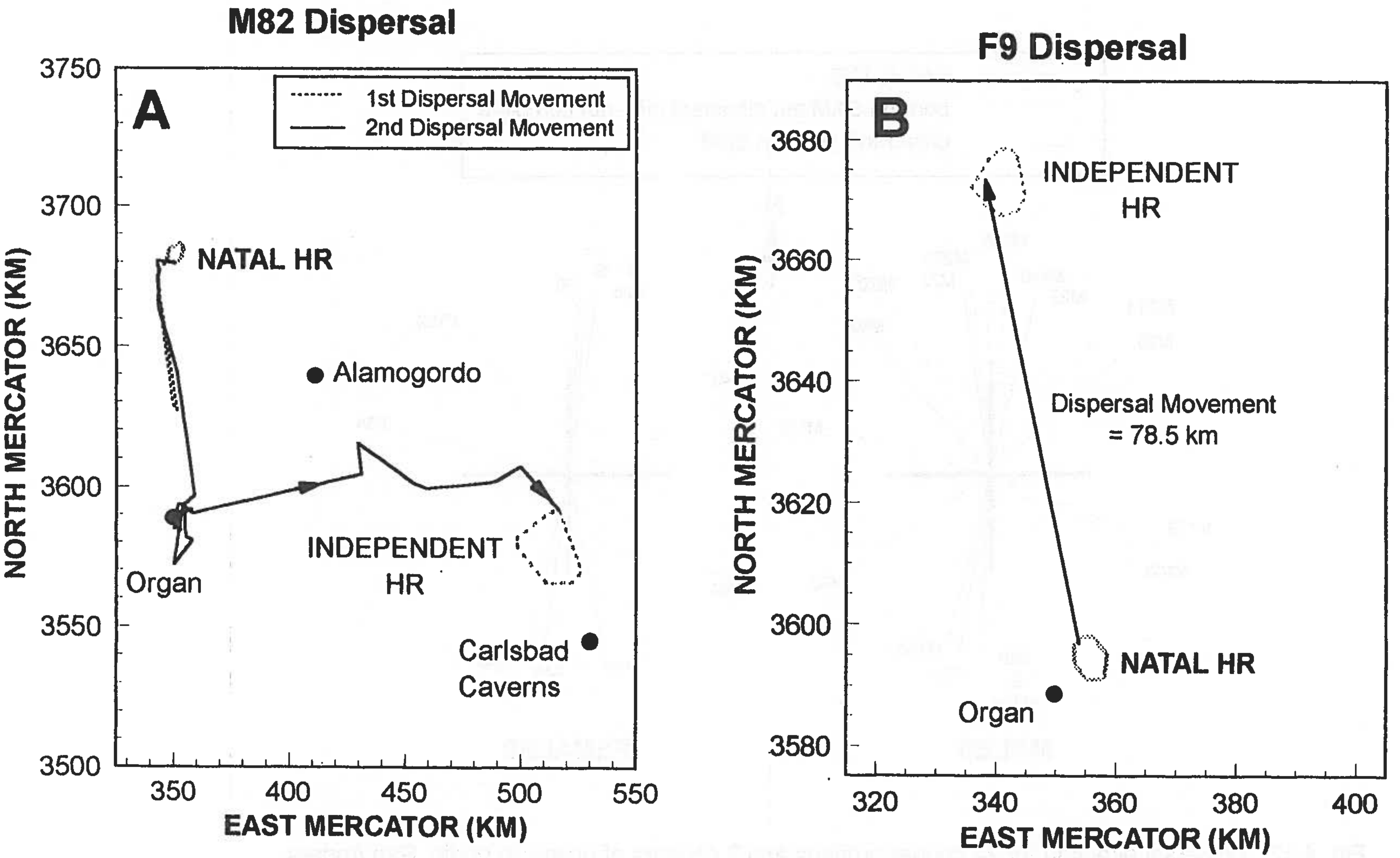


Fig. 4.13. Dispersal movements of 2 cougars from their natal home ranges in the San Andres Mountains (SAM), New Mexico to their independent home ranges. After a successful dispersal move that lasted 7.8 months, M82 established a home range in the Guadalupe Mountains, New Mexico, 192.5 km southeast of his natal area. F9 dispersed 78.5 km north-northwest of her natal home range in a 1.7 month period before establishing an independent home range in the the northern part of the SAM.

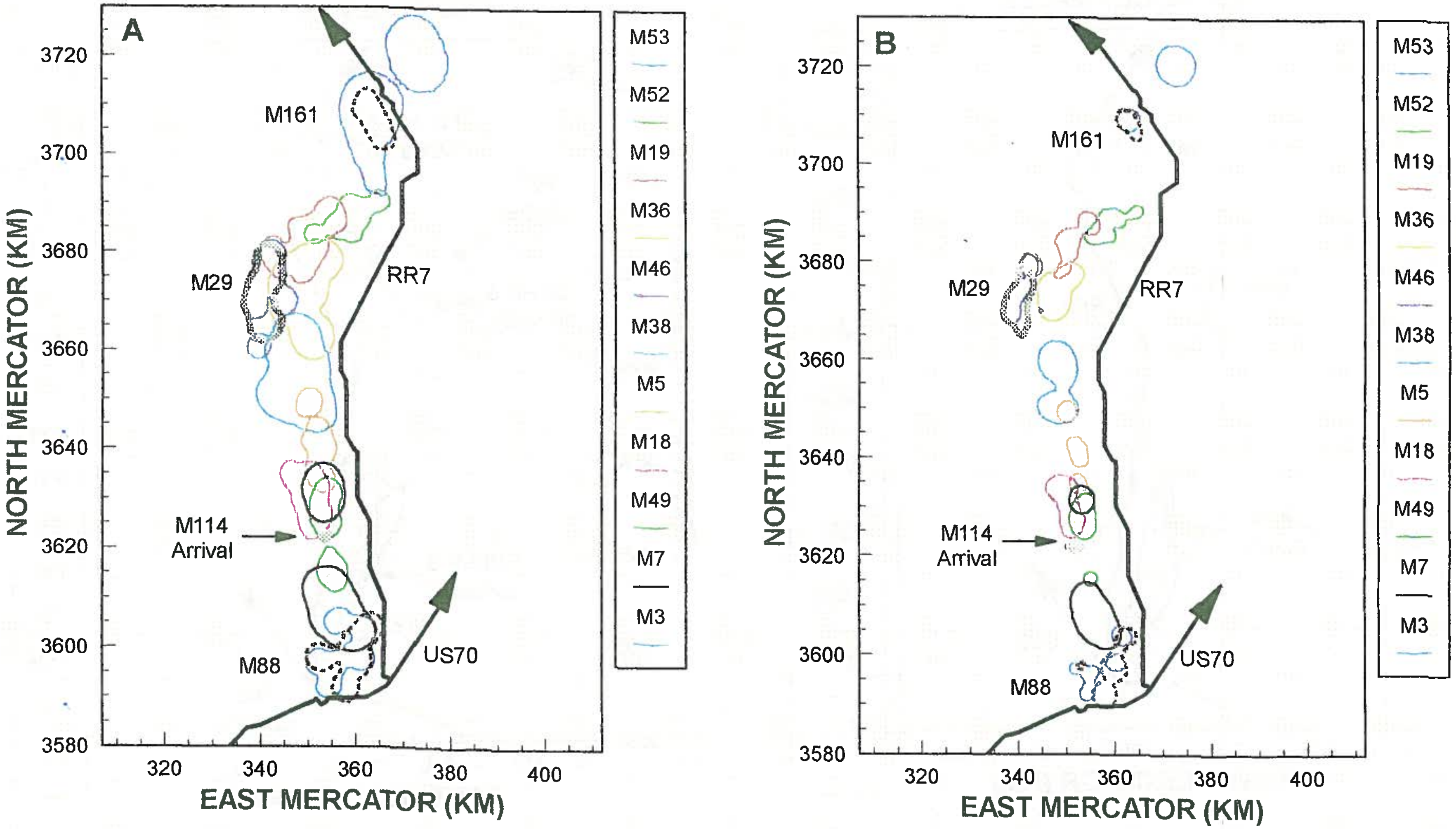


Fig. 4.14. Home range (HR) overlap for resident adult male cougars on the San Andres Mountains (SAM), New Mexico during 1990. Annual HRs are depicted using the 90% (A) and 60% (B) Adaptive Kernal. HRs for males that were new arrivals on the SAM and present as adults for only part of the year (M161 for 6 months, M88 for 9 months) are depicted by gray dotted lines. One adult male (M29) was not radio-collared during 1990 but was known to be present. His home range is depicted (thick gray line) using locations over a 12-month period after he was radio-collared in April 1991. M114 arrived on the SAM in October 1990; his HR is not depicted. No other adult male cougars were known to have been present on the SAM during 1990.

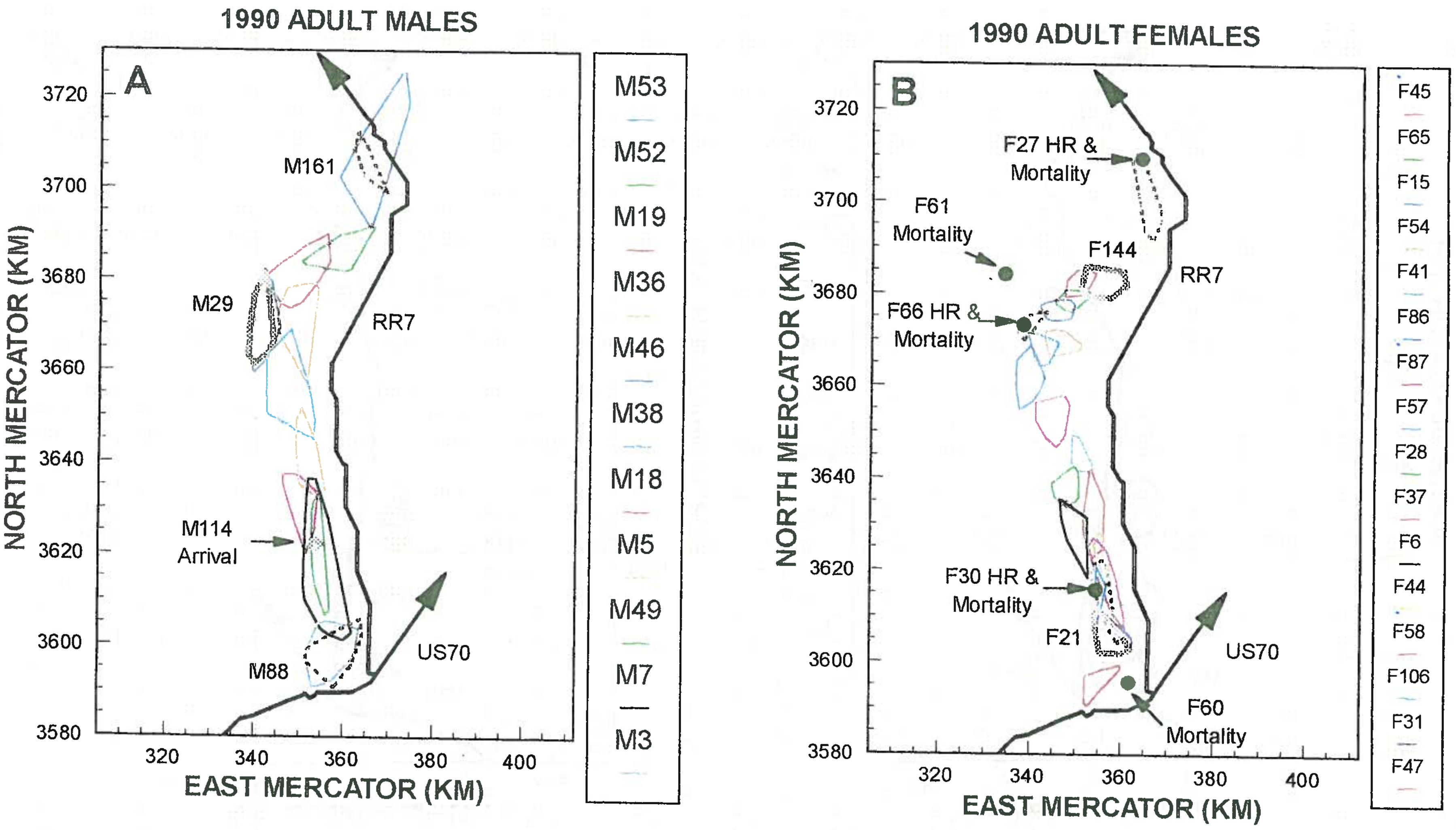


Fig. 4.15. Home range (HR) overlap for resident adult male (A) and female (B) cougars on the San Andres Mountains (SAM), New Mexico, 1990. Annual HRs are depicted using the 90% Minimum Convex Polygon. HRs for cougars that were present on the SAM as adults for only part of the year (n=5) are depicted by gray dotted lines. M88 and M161 arrived on the SAM in March and June, respectively; whereas F27, F66 and F30 died in April, May and July, respectively. Three cougars were known to be present but either wore non-functional collars (F21, F144) or had not yet been radio-collared (M29). Their HRs are depicted (thick gray lines) using radio-locations from 12 month periods in 1991 (M29, F21) or by estimating the HR based on cougar sign (F144). F60 and F61 died in February, and M114 arrived on the SAM in October; their HRs are not depicted. No other adult cougars were known to be present on the SAM during 1990.

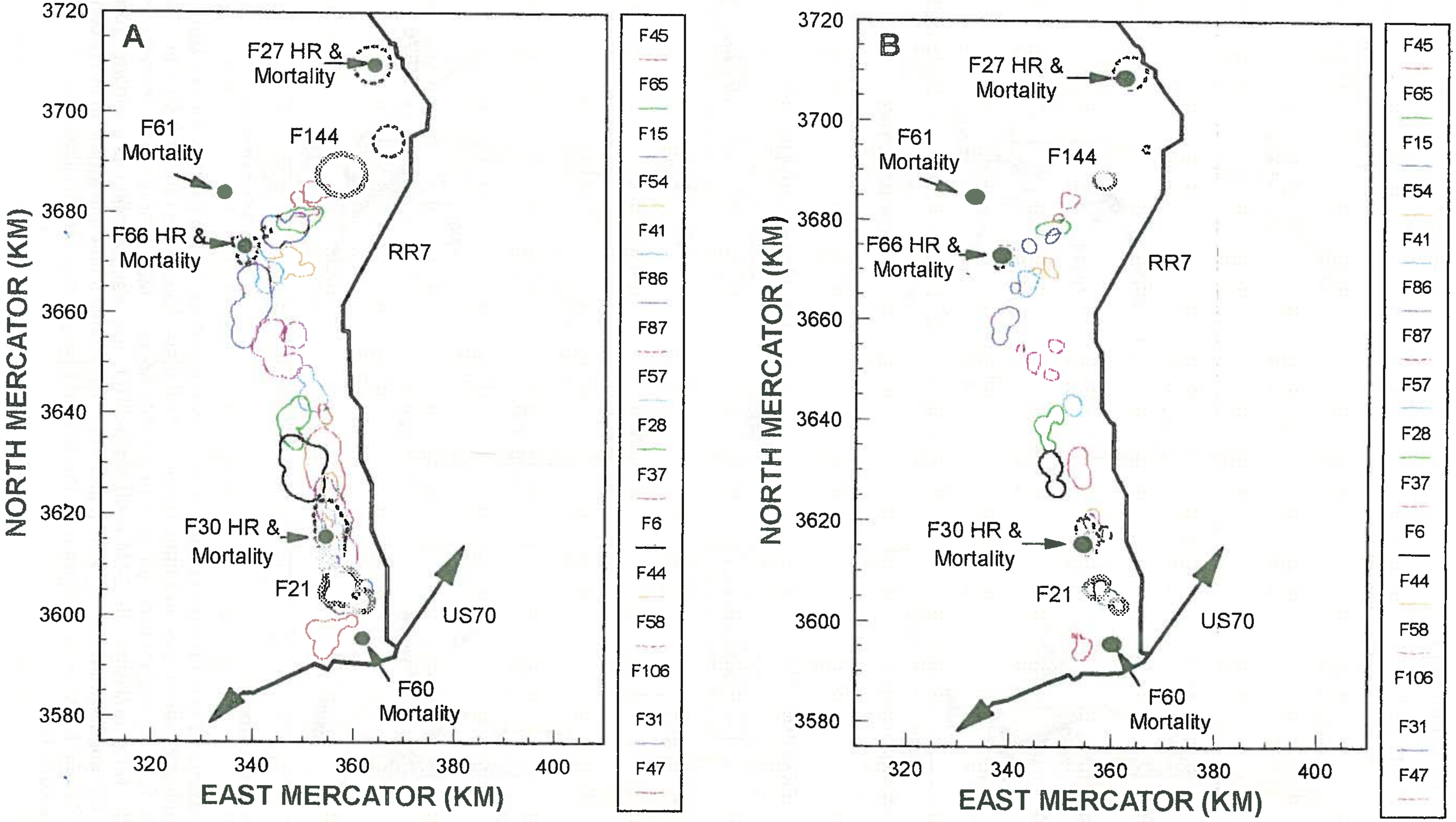


Fig. 4.16. Home range (HR) overlap for resident adult female cougars on the SAM, New Mexico, during 1990. Annual HRs are depicted using the 90% (A) and 60% (B) Adaptive Kernal. HRs for females that were only present as adults for part of the year (F27, F30, F66) are depicted by gray, dotted lines. F27, F66 and F30 died in April, May and July, respectively. HRs for 2 females (F21, F144) that were present in 1990 but whose radio-collars were non-functional are depicted (thick, gray-lined polygons) by using F21's 1991 HR and by estimating F144's HR from tracks and other sign. Because F60 and F61 died early in the year (February); their HRs are not depicted. No other adult female cougars were known to have been present on the SAM during 1990.

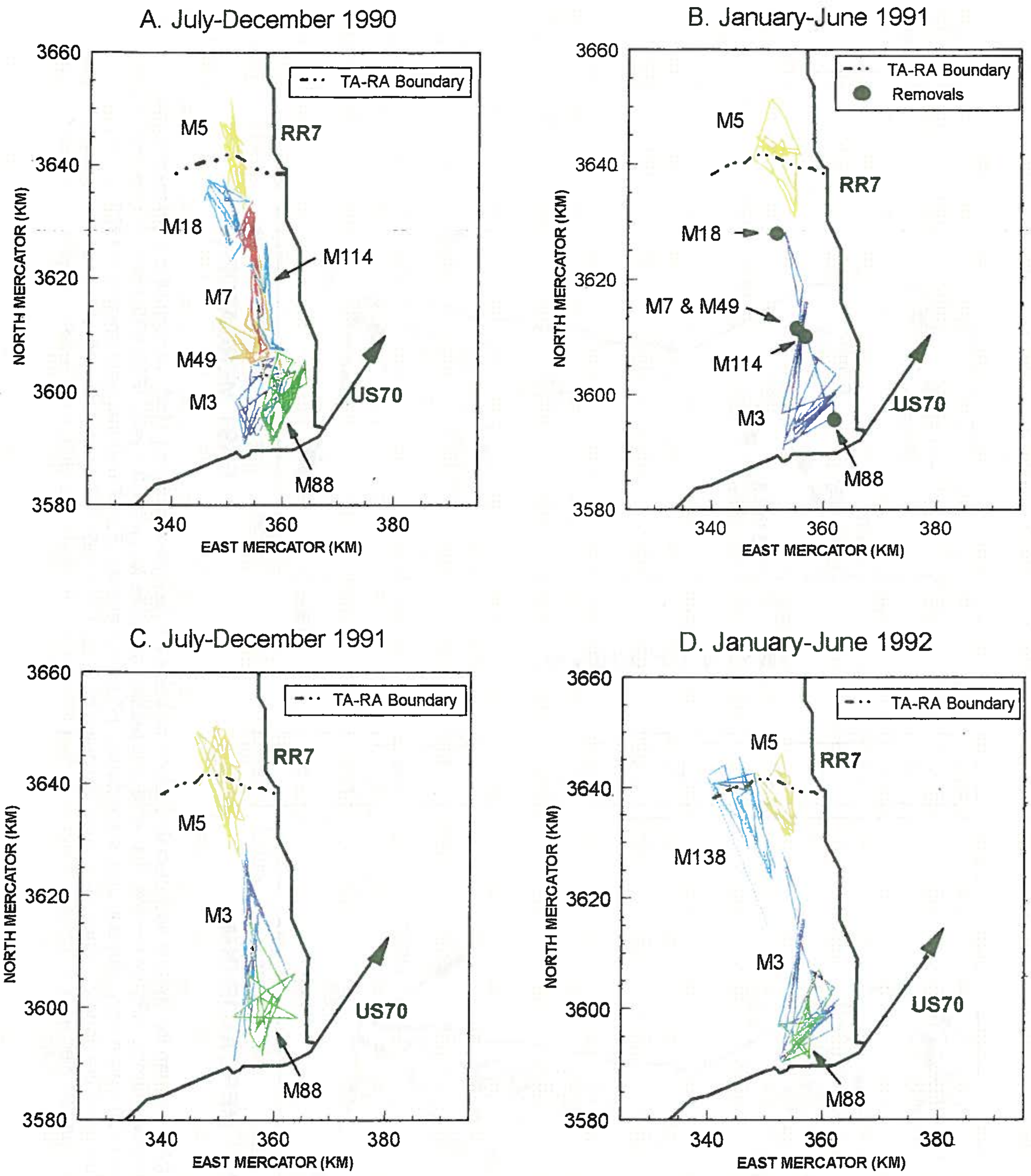
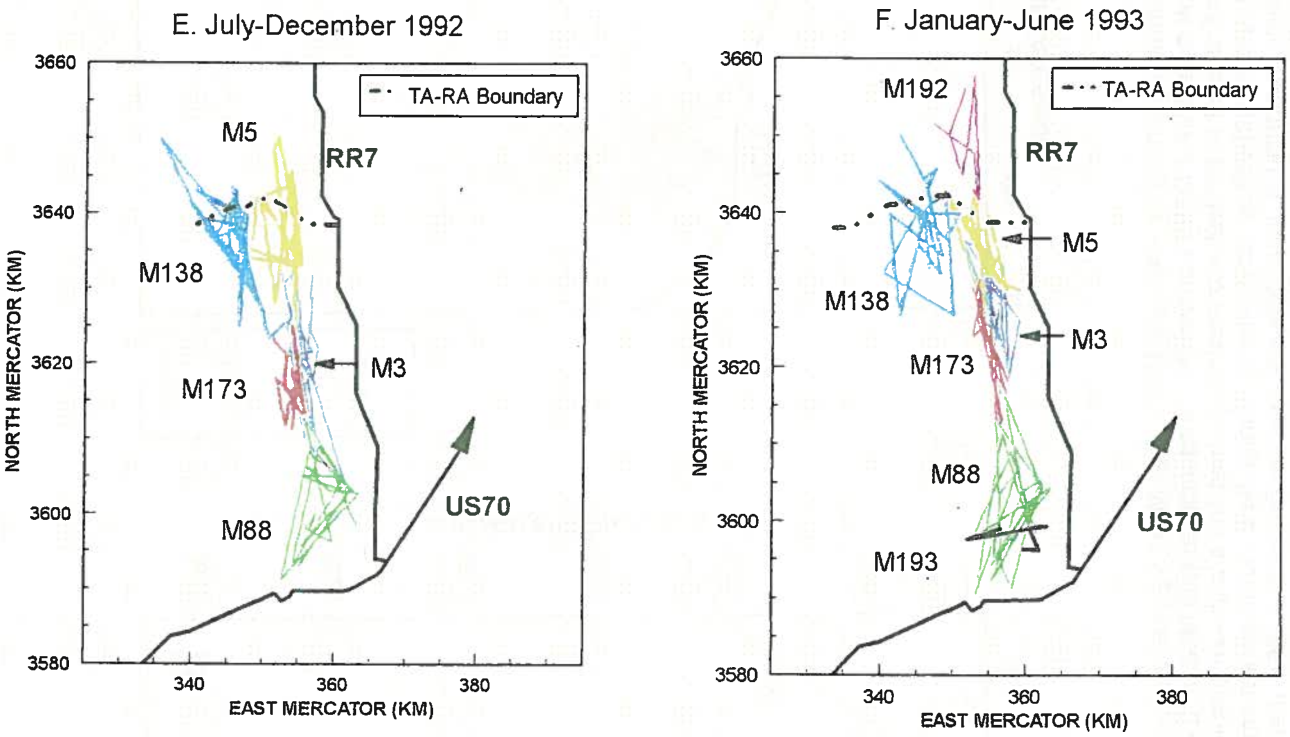


Fig. 4.17. Weekly movements of adult male cougars in the Treatment Area (TA) of the San Andres Mountains (SAM), New Mexico during 6 consecutive six-month periods. Five adult males were removed from the SAM during January-March 1991 (B) and translocated to northern New Mexico. M88 returned to his former home range in July 1991 (C). M138 arrived on the SAM in November 1991 and was classified as a subadult (dotted line, D) until March 1992 when he became an adult (solid line). M173 was a new immigrant to the SAM in August 1992 (E). M192 and M193 were immigrants to the SAM in April and May 1993, respectively (F). M5 died of old age in late May, 1993.



E. July-December 1992

F. January-June 1993

Fig. 4.17, cont. Movements of adult male cougars in the TA of the SAM, New Mexico during 6 consecutive six-month periods.

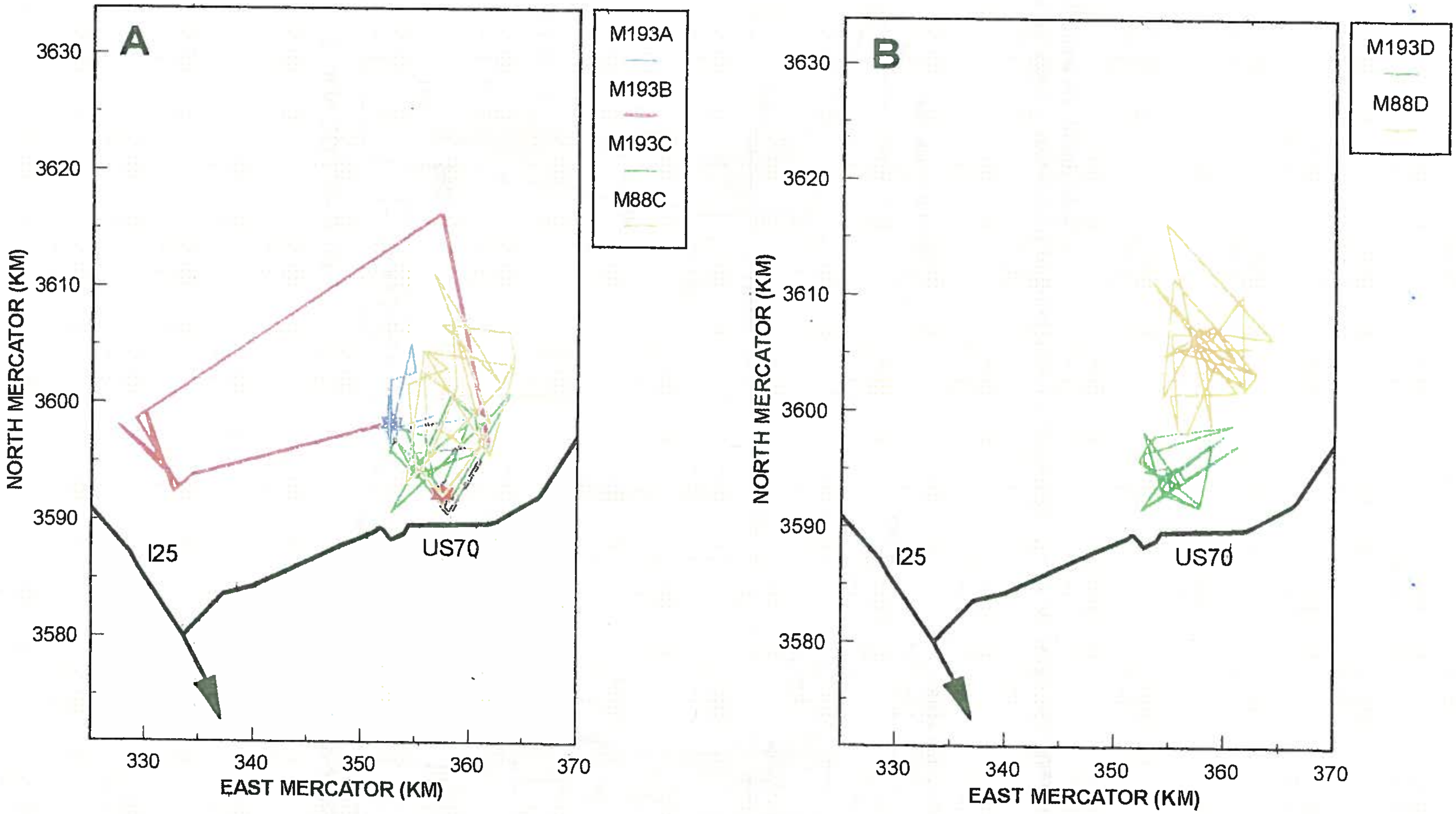


Fig. 4.18. Movements of 2 adult male cougars, M88 and M193, after M193's arrival on the San Andres Mountains, New Mexico in late May 1993. During the 1 year period after M193's arrival (A), he associated with M88 on 2 known occasions (stars): 13 September and 2 December. M193's movements prior to the first and second associations are shown by the blue and red lines, respectively. M193's and M88's movements (shown in green and yellow, respectively) during the 6 month period after the second association still indicate overlap in their home ranges. However, beginning in June 1994 and through December 1994, there was no overlap in the movements of the 2 males (B). Thus, it took about 12 months after M193's arrival for the 2 males to establish exclusive home ranges.

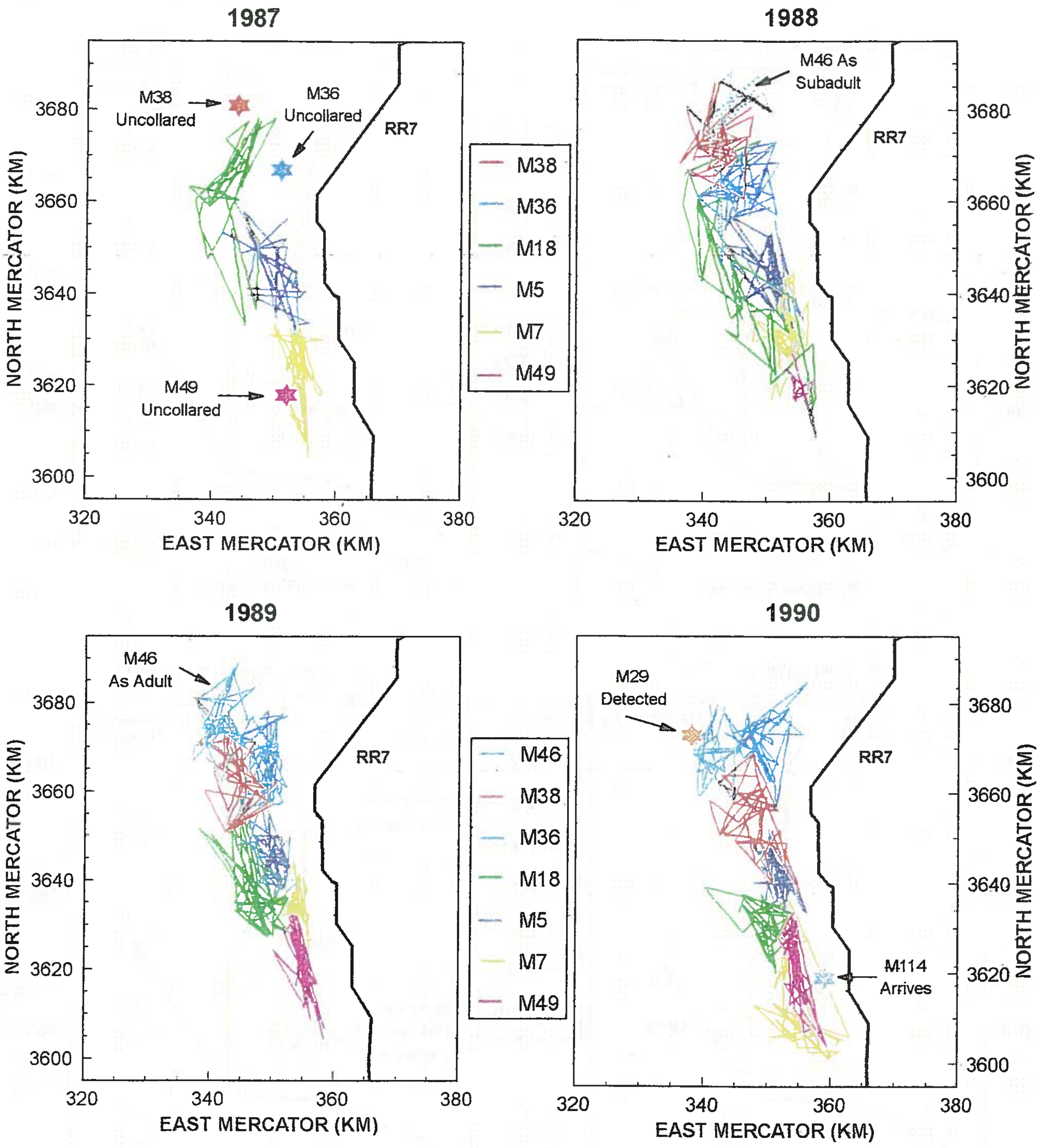


Fig. 4.19. Weekly movements of neighboring resident adult male cougars during 4 consecutive 12 month intervals on the San Andres Mountains (SAM), New Mexico, indicating the dynamic nature of individual home ranges and territorial behavior. M36, M38 and M49 were probably present during 1987, but they were not captured and radio-collared until January 1988, February 1988 and September 1988, respectively. M46 was captured as a subadult (~18 mo. old) in June 1988, and became an adult in January 1989. M29 immigrated from the south end of the SAM (where he was born to F21) and was detected in the RA in 1990 but was not radio-collared until 1991. M114 was a new immigrant adult (27 mo. old) to the SAM in October 1990.

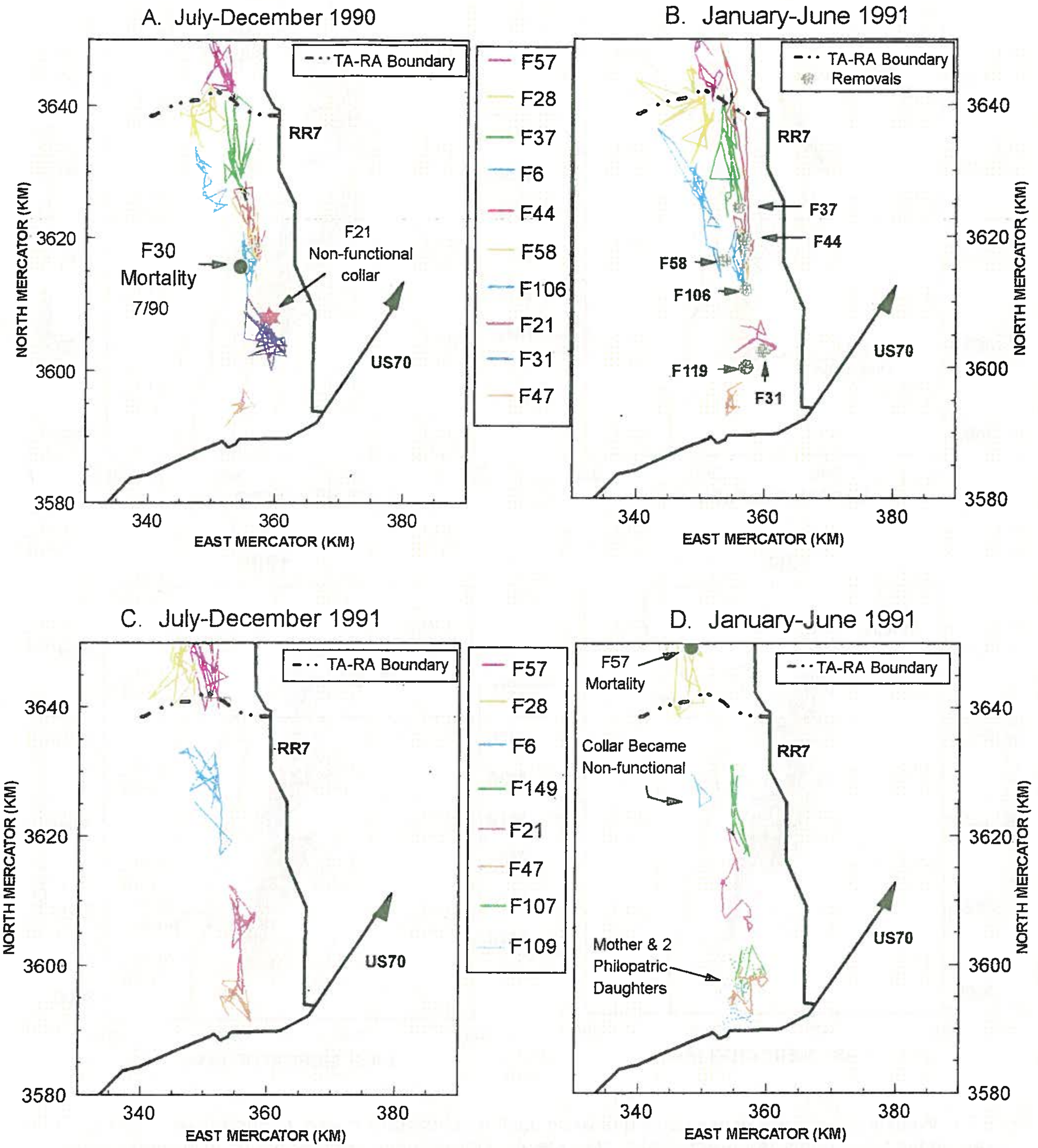


Fig. 4.20. Weekly movements of adult female cougars in the Treatment Area (TA) of the San Andres Mountains, New Mexico during 6 consecutive 6-month periods. F30 died in July 1990 (A). Six adult females were removed from the TA during December 1990 through June 1991 (B). Five of the 6 females were resident adults in the TA: the sixth (F119) was a new immigrant. No new adult females were documented during time C; however, during March-April 1991 (D), 3 females (F107, F109 and F149) who were born on the TA, began establishing residency within part of their natal home ranges (F107 and F109, daughters of F47) or adjacent to her natal home range (F149; daughter of F21). F6's collar became non-functional in March 1992 (D); however, sign indicated her continued presence. The Goat Mountain female (GMF) arrived on the TA in March 1992 and produced her first litter in June 1992. F103 immigrated from the RA in June 1992 (D) and produced her first litter in September 1992 (E).

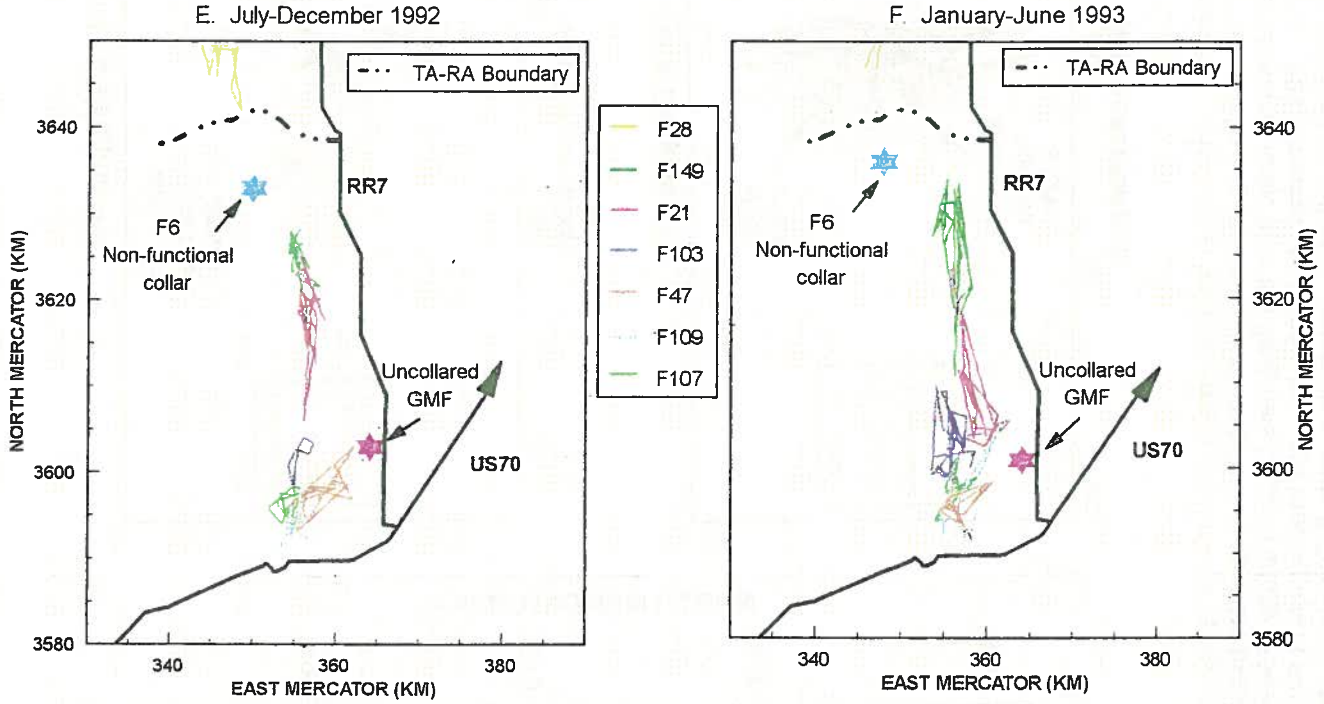


Fig. 4.20, cont. Weekly movements of adult female cougars in the TA of the SAM, New Mexico during 6 consecutive six-month periods.

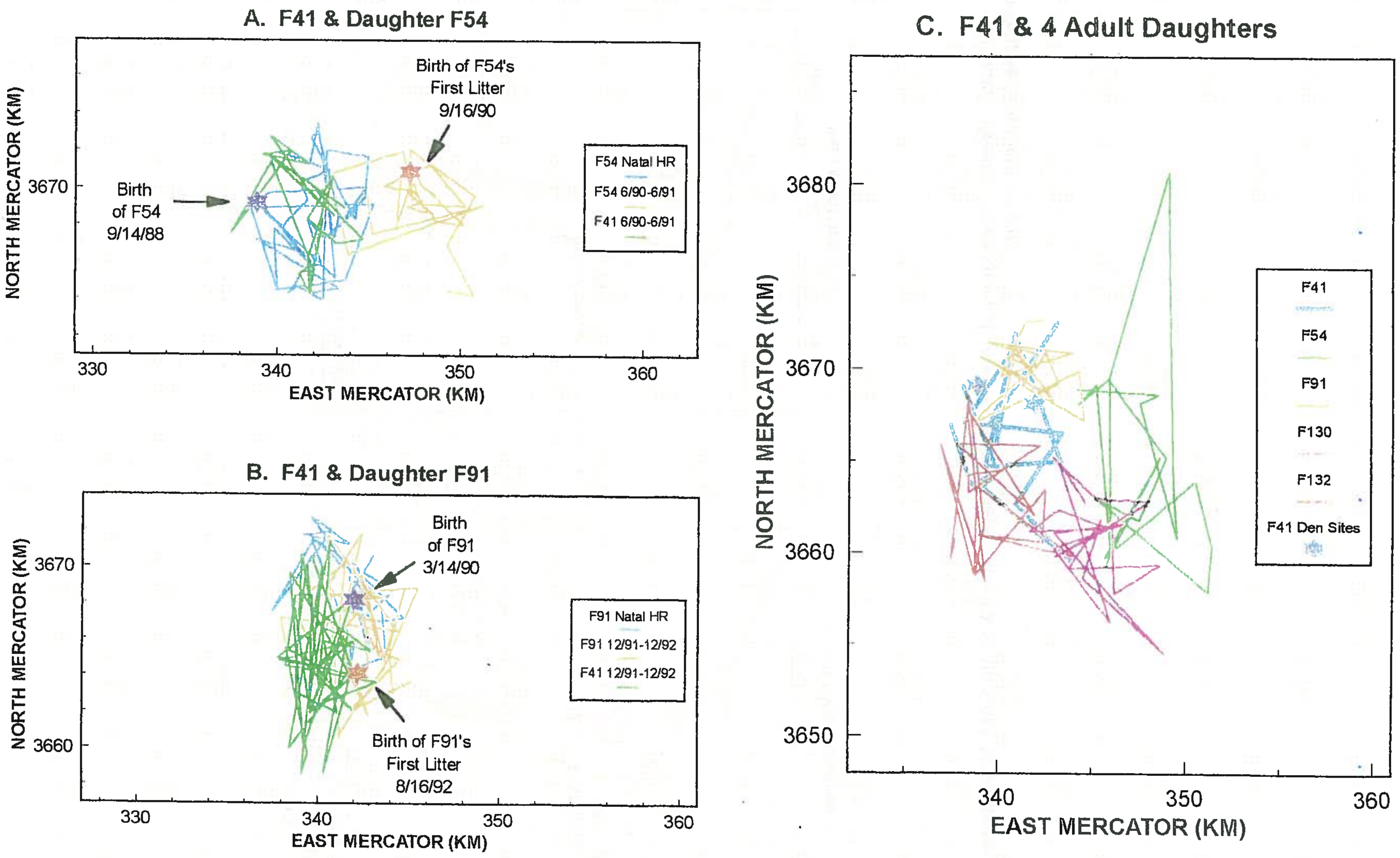
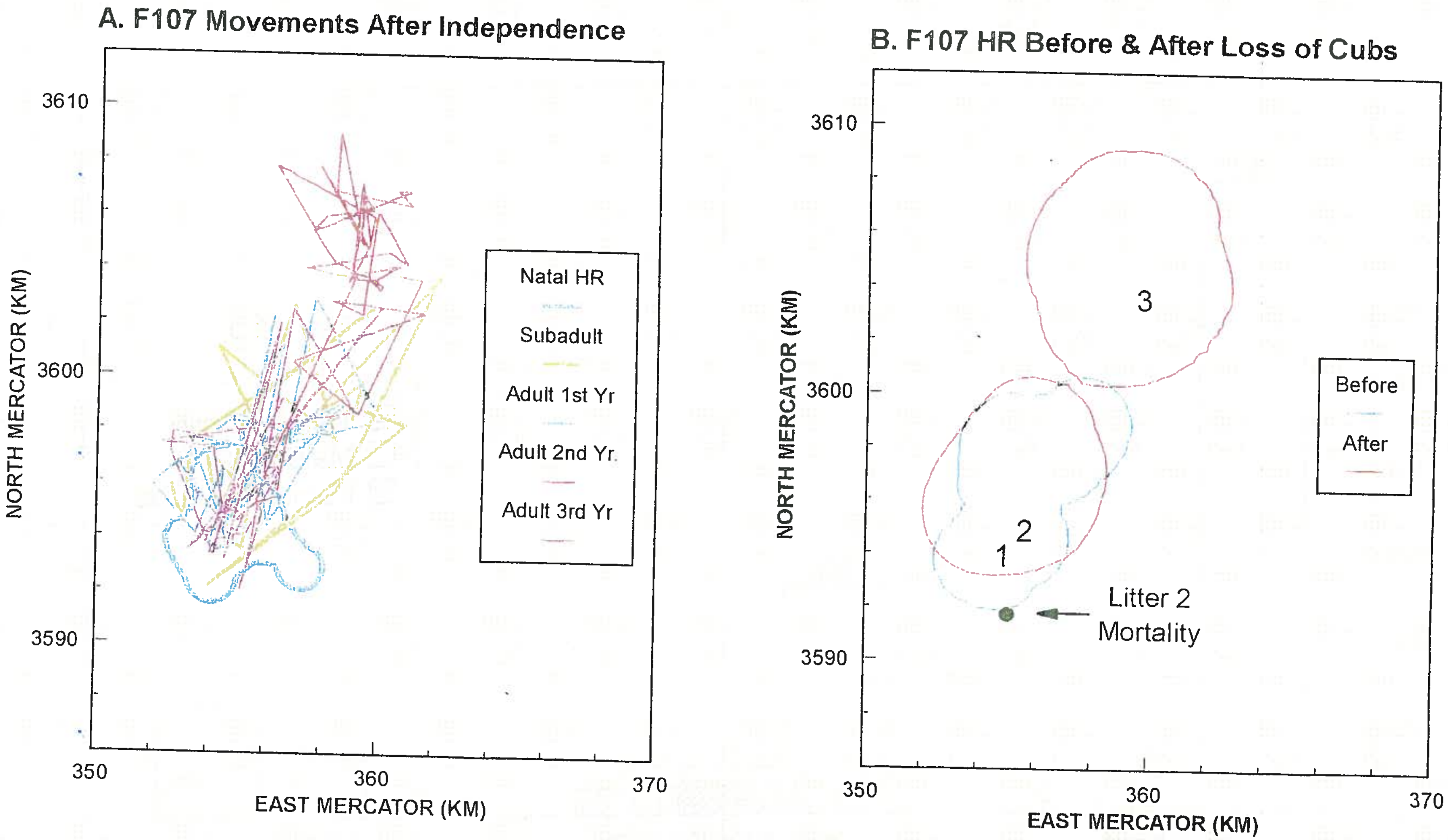


Fig. 4.21. Weekly movements of F41 and 4 of her adult daughters (F54, F91, F130 and F132) from 3 consecutive litters. In A and B, F41's movements over a 12-month period following the birth of F54 and F91 are depicted by the blue lines. Superimposed are movements of F41 and her daughters over the same 12-month period after the daughters became adults. F54 established a home range (HR) adjacent to her natal HR and was considered a disperser. F91 remained philopatric. In C, the movements of F41 and her 4 adult daughters are depicted for a 6-month period, October 1994 - March 1995. F130 and F132 were siblings born 9 September 1991 at the same den as F91



A. F107 Movements After Independence

B. F107 HR Before & After Loss of Cubs

Fig. 4.22. Cougar F107 movements (A) and home range (HR; 90% Adaptive Kernal; B) after independence, San Andres Mountains, New Mexico. F107 became independent at 11.1 months of age and was classified as a subadult until she associated with an adult male cougar at 18 months of age. As a subadult and for 2 years as an adult, she utilized a similar area , then during the third year as an adult, she shifted her activities north. She gave birth to 3 litters (Numbers in B) over a 22-month period. The second litter was killed by adult cougar M88 when the cubs were 2 months old. F107 subequently began to shift her activities north. Once her third litter was born, she exclusively utilized an area outside her former HR (upper red polygon in B).

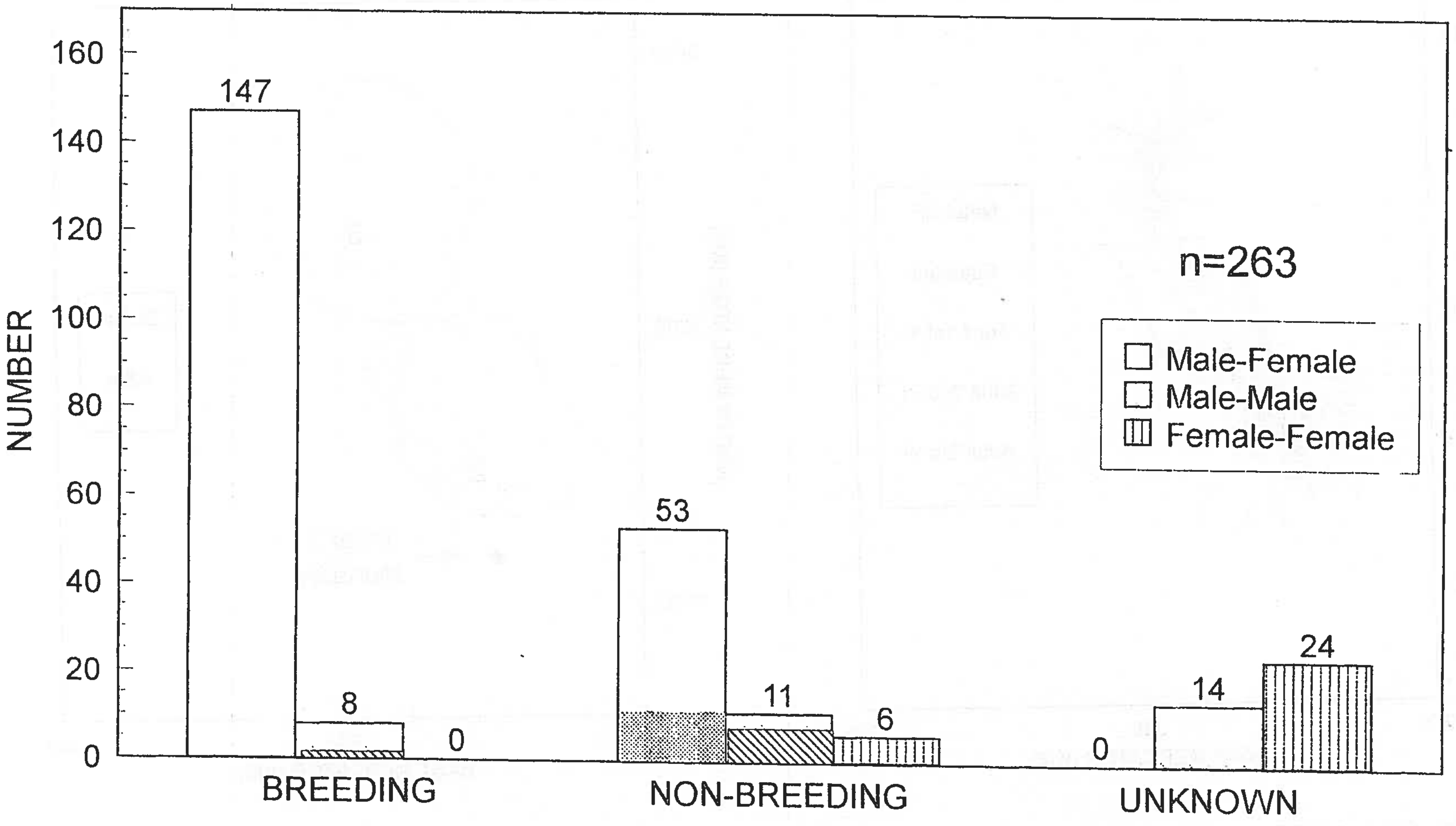


Fig. 4.23. Number of associations (n=263) between independent cougars that were related to breeding activities, non-breeding activities, or unknown activities on the San Andres Mountains, New Mexico, 1985-1995. Associations resulting in mortalities (n=20) are shown by the darker portions of the bars. Mortalities resulted during 1.3% of breeding associations and 25.7% of non-breeding associations. Cougars were located in association during 4.9% of all radio-locations.

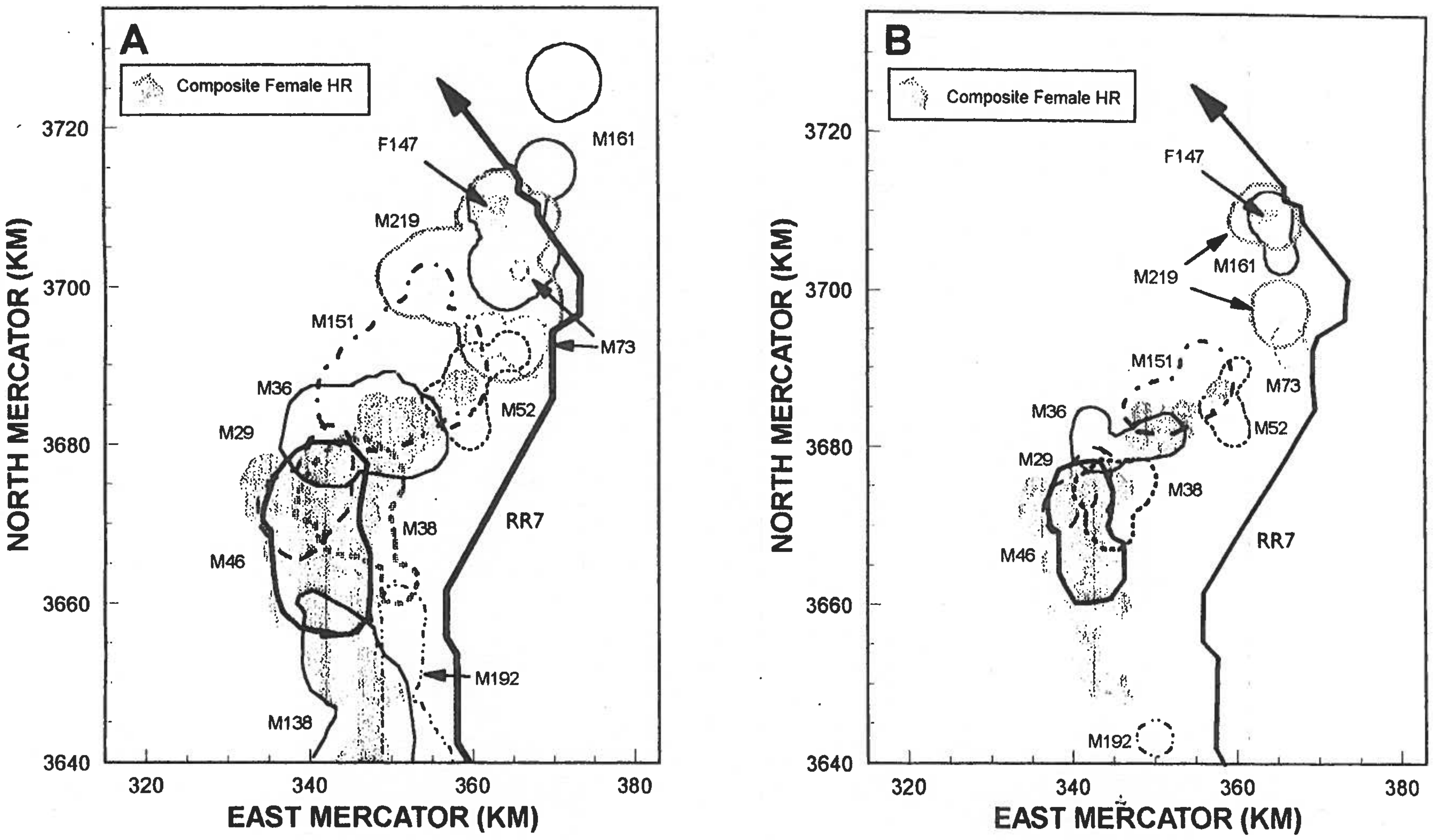


Fig. 4.24. Home range overlap between adult male and female cougars in the north half of the San Andres Mountains, New Mexico, 1993. Home ranges were measured using the 90% ADK (A) and 60% ADK (B) home range estimator. All areas utilized by females are shaded in gray. The percent of a male's home range overlapped by female home ranges in 1993 averaged 49.7%and 32.1% based on the 90% and 60% ADK, respectively. Females, on average, shared 96.6% and 65.8% of their home ranges with males, based on the 90% and 60% ADK, respectively.

CHAPTER 5. COUGARS AND DESERT MULE DEER

by K. Logan, L. Sweanor and M. Homocker

Abstract: We studied the relationships between cougars, desert mule deer, and precipitation on the San Andres Mountains (SAM), New Mexico from 1985-1995. Experimental removal of cougars from a 703 km^2 treatment area (TA) within the SAM allowed us to examine the effects of cougar predation on deer over a range of cougar densities. Density of adult cougars on the TA during the pre-treatment span (1987-1990) increased from 1.17 to 2.01 cougars/yr./100 km^2. After reducing the number of adult cougars by 53% and the number of independent cougars by 58%, the density of adult cougars increased during the post-treatment span (1991-1994) from 1.09 to 1.87 cougars/yr./100 km^2. Mule deer comprised 84% average annual frequency of occurrence in cougar feces and 91% of animals we found killed by cougars. Cougars apparently did not select for either gender. Fawns comprised about 27% of the cougar-killed deer we found by chance. We documented 15 cases of scavenging by cougars. Deer population composition surveys showed declining trends in fawn:doe ratios during the pre-treatment (52-36 fawns:100 does) and post-treatment (41-7 fawns:100 does) spans. We calculated survival rates and cause-specific mortality rates for 175 radio-collared mule deer. During the pre-treatment span, survival rates for radio-collared deer were generally stable. Average annual survival rates for bucks (0.876) and does (0.883) were practically equivalent, and span survival rates did not differ significantly (0.583 and 0.606 for bucks and does, respectively). However, survival rates for radio-collared deer during the post-treatment span declined and were significantly lower than in the pre-treatment span ($P<0.02$). The average annual survival rate for bucks (0.662) was lower than for does (0.787), and span survival rates were significantly different (0.172 and 0.370 for bucks and does, respectively; $P=0.01$). Cougar predation rates on radio-collared deer during the pre-treatment span were generally stable, averaging 0.066 per year; and mortality rates from other causes of mortality were not significantly different, averaging 0.056 per year. But cougar predation rates on radio-collared deer increased significantly ($P<0.001$) during the post-treatment span, averaging 0.226 per year. Mortality rates from other causes of mortality were essentially the same as before, averaging 0.054 per year. Precipitation accumulations during the growing season (July-Sep.) and habitat conditions that we observed indicated that severe drought conditions struck the SAM during 1992-1995. Linear regression analyses using deer survival rates, deer mortality rates, cougar predation rates, and fawn:doe ratios as the dependent variables; and adult cougar density, growing season precipitation, and annual precipitation as the independent variables, helped to explain relationships between cougars, deer, and habitat

conditions (as indexed by precipitation). We concluded that the deer population was either stable or increasing when the deer population was below ecological carrying capacity (during 1987-1990). But, when the deer population exceeded carrying capacity because of the drought, fawn production declined drastically and deer were more vulnerable to cougars. During the drought, cougar predation was the major proximate source of mortality which helped to drive the deer population downward. But habitat condition (quantity and quality) was the ultimate limiting factor. Management implications are given.

5.1 OBJECTIVE

Our objective was to quantify some of the relationships between cougars and desert mule deer on the SAM for these reasons: 1) Deer are the major prey of cougars in North America (Anderson 1983), therefore, a basic understanding of the food requirements of cougars are needed to develop long-term conservation strategies. Furthermore, it is necessary to understand how changes in cougar numbers and other environmental factors may effect prey populations. 2) An understanding of the dynamics of cougar predation on mule deer may be incorporated into the management of deer and cougars where sport-hunting also is a mortality factor on deer populations. 3) In areas where cougars are dependent on deer and where endangered species are vulnerable to cougar predation (e.g., desert bighorn sheep on the SAM), an understanding of cougar-deer relationships may be useful in devising management strategies that may minimize predation risks to endangered species.

5.2 FIELD METHODS

We studied the relationships between cougars and desert mule deer in a TA on the SAM by 1) quantifying cougar prey selection; 2) quantifying the survival and causes of mortality of a radio-collared sample of deer; and 3) evaluating the relationship between deer mortality rates and cougar predation rates on deer in respect to adult cougar density. We relied on the radio-collared deer to quantify effects of cougar predation on deer ≥1 year old because no quantitative data existed on the deer population size or dynamics for our study area. Nor were there any tested, reliable methods we could use to estimate population dynamics short of conducting an intensive, long-term study on the deer population concurrent with the cougar study. For example, New Mexico's mule deer population / environment / hunt computer model (Humphreys and Elenowitz 1988) has not been adequately tested (Bednarz 1989; Dr. E. O. Garton, Prof.of Statistics, Univ. Idaho, pers. comm.). In addition, because a drought struck the SAM beginning in late 1992 and strong relationships exist between precipitation in arid environments and mule deer, including: forage availability, quality, and selection; body condition; the reproductive cycle; and fawn production and survival (Urness 1981, Haywood et al. 1987, Humphreys and Elenowitz 1988), we examined the relationship between precipitation and cougar-mule deer interactions.

5.2.1 COUGAR PREDATION

Animals found dead on the study area that were potential cougar prey were examined to determine the probable proximate cause of death, species, sex, age, and general physical condition prior to death. Mule deer that were born during the most recent birth season were easily distinguished from animals ≥1 year old. Ages of mule deer ≥1 year old were estimated from tooth eruption and wear patterns (Robinette et al. 1957). Dentaries of dead deer were collected and the eruption and wear patterns were compared to a reference collection of deer dentaries so that assigned ages were as reliable as field determinations would allow.

Specific criteria was used to categorize dead animals as cougar prey, probable cougar prey, and animals that died of other causes. Animals that died of other causes were not associated with evidence that implicated cougars as the cause of death.

Cougar prey were those animals associated with the following: cougar canine punctures to the back of the neck, the throat, or the head; cougar feeding patterns (plucking or shaving of hair, opening the carcass first at the abdomen or thorax, expulsion of the stomachs, consumption of bones); cougar tracks (in the attack sequence and/or at the cache), feces or scrapes and prey carcass drag marks; and coverage of the prey with ground debris (soil, leaves, sticks).

Probable cougar prey were animals with tissues consumed or decomposed to the degree that cougar canine punctures could not be found and where ground conditions could not record an attack sequence. However, there was evidence of cougar feeding patterns (plucking or shaving of hair, expulsion of the stomachs, consumption of bones); cougar tracks, feces, or scrapes; prey carcass drag marks; and coverage of the prey with ground debris.

In addition, we also collected cougar feces on the SAM which were analyzed for content by M. Elmer, M.S. student, University of Idaho, Moscow. His preliminary findings are reported here for over 800 feces collected from 1985 to 1994.

5.2.2 DEER POPULATION CHARACTERISTICS

Mule deer population composition was determined by ground-based observers during 4 years and by helicopter-based observers in 6 years. Aerial and ground survey sampling techniques met or exceeded recommendations by Humphreys and Elenowitz (1988) so that precision could be maximized, i.e., a minimum of 25 groups and 100 does were counted in all surveys, regardless of the method. Counts were made in winter in 9 years and in fall in 1 year.

Ground-based observations were made with 7-10 power binoculars or 15-45 power spotting scopes. Mule deer were classified as bucks and does ≥1 year old and fawns. When possible, we distinguished between yearling (1 year old) and adult (≥2 year old) deer. Recounts of deer were eliminated by not counting deer whenever there was a possibility of reobservation.

Helicopter-based observations were made by 2 experienced NMGF personnel in a Bell 206 Ranger or Hughes 500D. Classification counts were made during low-level flights between 07:05 and 10:45 in a 1 day period. Deer were classified as bucks, does, and fawns.

Survivorship and causes of mortality were determined for 175 radio-collared deer (91 bucks, 84 does) that were ≥1 year old and lived on the TA during 1987-1994. Mule deer were captured during 9 capture operations from October 1986 to October 1993. Deer were captured by NMGF, HWI, USFWS, and WSMR personnel by using the drive net technique (Beasom et al. 1980; 2 operations) and by NMGF personnel using a net gun fired from a helicopter (Hughes 500D, Bell 206 Ranger; 7 operations). Three deer that were accidentally captured in foot-hold snares (set for cougars) were radio-collared and became part of the sample we monitored.

Deer requiring immobilization were injected I.V. with xylazine hydrochloride (Rompun, 20 mg/ml) dosed at 1 mg/kg estimated body weight. After processing the deer, xylazine hydrochloride was reversed with an I.V. injection of yohimbine hydrochloride (Antagonil, 5 mg/ml, Wildlife Laboratories, Fort Collins, Colorado 80524) dosed at 0.2 mg/kg body weight. Otherwise, deer were physically restrained. Captured deer were examined to record sex, rough estimates of age (by dental characteristics described in Robinette et al. 1957), and apparent general physical condition. Deer ≥1 year old were each fitted with a collar containing a 148 or 149 MHz transmitter with a mortality mode set to turn on after 2 hours of constant immobility (configuration MOD-500 transmitter with S6A mortality sensor by Telonics Inc.).

We monitored radio-collared deer weekly from the ground in order to detect mortalities. In addition, monthly flights in fixed wing aircraft were made to check for survival and mortalities of all of the radio-collared deer, particularly those deer that were missed during ground-based monitoring. When a dead deer was found, the carcass and the site were examined carefully to determine cause of death.

5.2.3 PRECIPITATION

Monthly and annual precipitation accumulation was obtained for the Ash Canyon gauge because it occurs at mid-elevation (1,731 m) in the central portion of the TA and complete data has been collected there since 1937 by the U.S.D.A. Jornada Experimental Range.

5.3 ANALYTICAL AND STATISTICAL METHODS

5.3.1 COUGAR POPULATION

Our study of cougar population dynamics is described in detail in Chapter 3: *Cougar Population Dynamics*. We quantified adult cougar density on the TA as the number of adults/yr./100 km^2. After studying the dynamics of the population during a pre-treatment span (1987-1990), we experimentally reduced the cougar population (the treatment) by 53% of the adults and 58% of the independent cougars (adults+subadults) during December 1990 to June 1991. Subsequently, we studied the dynamics of the cougar population during a post-treatment span (1991-1994).

5.3.2 COUGAR PREDATION

Animals we found dead were quantified in the 3 categories- cougar kills, probable cougar kills, and animals that died of other causes. For statistical analyses, we combined the cougar kills and probable cougar kills categories because of the very high probability that cougars actually killed animals in the latter group as prey.

M. Elmer quantified prey items in the cougar diet by frequency of occurrence of food items in feces. We present his preliminary findings as average annual frequencies for individual items or groups of items.

5.3.3 DEER POPULATION CHARACTERISTICS

Mule deer composition counts were converted to ratios of bucks and fawns per 100 does. Ratios were tabulated for each year and used in regression analyses (Ott 1988) with annual adult cougar density, annual radio-collared mule deer survival and mortality rates, and annual and growing season (July to September) precipitation on the TA.

We estimated mule deer survival and cause-specific mortality rates for radio-collared deer during 1987 through 1994 by using program MICROMORT (Heisey and Fuller 1985). Radio-collared deer were entered for analyses 14 days after the date of capture to eliminate those deer where capture related injuries caused mortality or contributed to the vulnerability of deer to predation. Deer that died during the 14 day period post capture were eliminated from analyses. Annual survival rates were estimated beginning on 1 January of each year. Because we occasionally visually observed deer that wore non-functional radio-collars, we calculated maximum survival rates by including deer with malfunctioned transmitters up to the last day that our records showed that transmitters were working.

Survival rates and cause-specific mortality rates were tested for significant differences by using Z-tests (Pollock et al. 1989, expressed in Chapter 3.3.5).

5.3.4 DEER-COUGAR RELATIONSHIPS

We examined deer-cougar relationships by quantifying the proportion of cougar kills comprised of mule deer. The number of mule deer killed by cougars and deer that died of other causes in each sex and age class were quantified. Chi-square analyses (Ott 1988) were used to test for gender selection in mule deer. In addition, we used linear regression analyses to examine deer-cougar relationships on the TA during the pre-treatment (1987-1990), post-treatment spans (1991-1994), and the 8-year (1987-1994) spans including:

(1) the relationship between annual radio-collared deer mortality rates and annual adult cougar density (cougars/yr./100 km^2, see Chapter 3.3.3);

(2) the relationship between annual cougar predation rates on radio-collared deer and annual adult cougar density; and

(3) the relationship between the annual ratio of fawns per 100 does and annual adult cougar density. We used the t statistic to test for a functional relationship between the dependent and independent variables.

5.3.5 PRECIPITATION-DEER RELATIONSHIPS

Annual and growing season (July-Sep.) precipitation totals were plotted over time and mean accumulations for the pre-treatment and post-treatment spans were tested for significant differences using the Wilcoxon rank sum test (Ott 1988). Annual and growing season accumulations during 1987-1994 were compared to the 58 year means (1937-1994) recorded at the Ash Canyon gauge.

We used linear regression analyses to examine deer-precipitation relationships during the pre-treatment, post-treatment, and 8-year spans including:

(1) the relationship between radio-collared deer survival rates and annual precipitation;

(2) the relationship between radio-collared deer survival rates and growing season precipitation;

(3) the relationship between the ratio of fawns:100 does and annual precipitation;

(4) the relationship between the ratio of fawns:100 does and growing season precipitation. The t statistic was used to test for a functional relationship between the dependent and independent variables.

Experimental errors for all statistical tests were controlled at the 0.10 level of significance.

5.4 RESULTS

5.4.1 COUGAR POPULATION

In the pre-treatment span, the density of adult cougars increased by 72%, from 1.17 cougars/yr./100 km^2 in 1987 to 2.01 cougars/yr./100 km^2 in 1990. In the post-treatment span, adult cougar density also increased by 72%, from 1.09 cougars/yr./100 km^2 in 1991 to 1.87 cougars/yr./100 km^2 in 1994 (Fig. 5.1).

5.4.2 COUGAR PREY

We recorded 525 animals that were killed or probably killed by cougars for food during 1985 to 1995 (Table 5.1). Desert mule deer comprised 91% of the prey animals and included 77 radio-collared deer. Cougars eaten by other cougars comprised 2% of the sample and the second greatest percentage. Desert bighorn sheep ranked third at 1.9%; all of the sheep (n = 10) were radio-collared. Pronghorn, oryx calves, coyotes, skunks, badgers, ringtails, leporids, porcupines, and golden eagles each contributed ≤1% of the animals we found used by cougars. In addition to those animals, cougars also killed but did not eat 14 other cougars, 4 gray foxes, 1 coyote, and 1 long-eared owl (*Asio otus*).

Preliminary results from the cougar fecal analysis showed that mule deer was the most important food item, comprising an average annual frequency of 84%, while pronghorn, javelina, desert bighorn sheep, and oryx comprised 1%, 1%, 0.8%, and 0.2%, respectively. Cougar hair or other remains were found in 4% of feces annually. Leporids represented small prey with the largest average annual frequency at 4%. Other small prey, including coyotes, mustelids, rodents, birds, and reptiles, comprised an average annual frequency of 8%.

Although small numbers of cattle (including newborn calves) often were in cougar home ranges along the western edge of our study area, we did not find any cattle killed by cougars during the 10 years of research; nor did the ranchers report any cougar-killed livestock. Furthermore, no remains of livestock were found in cougar feces.

5.4.3 CHARACTERISTICS OF DEAD DEER

We found 540 dead mule deer during 1985 to 1995. Cougars killed 89% (n=479) of those deer and 11% (n=61) died of other causes. Age and gender of the deer that died are in Table 5.2. Fawns comprised 22% (n=107) of the total number of deer killed by cougars, and 71% of those were ≤6 months old. When we excluded the radio-collared deer from the total (n=77 during 1986-1995) and included only those deer killed by cougars that we found by chance (n=402), then fawns comprised 26.6% of the sample of deer killed by cougars. Buck and doe fawns were killed in proportions approximately equal to a hypothetical 1:1 sex ratio ($X^2 = 2.50$, 1 d.f., $P > 0.10$). Data on deer that died of other causes was too limiting to attempt meaningful comparisons with deer killed by cougars. Deer on the TA were not hunted and access was restricted to the area by WSMR; therefore, legal and illegal hunting were not sources of mortality.

5.4.4 SCAVENGING

We documented 15 cases where cougars scavenged on mule deer (n = 12) and desert bighorn sheep (n = 1) that died of non-predator causes. Two deer were each used by 2 cougars. Scavenging was done by 12 male and 3 female cougars from 1 to 29 days after the death of the animal. Consumption of animals ranged from as little as 1 to 2 kg to almost complete consumption of edible portions. Scavenged animals were sometimes handled just like killed prey; carcasses were dragged to concealing vegetation, vital organs were the first eaten, stomachs were rejected, carcasses were covered with ground debris between meals, and cougars made scrapes in and around feeding sites.

5.4.5 DEER POPULATION CHARACTERISTICS

Composition

Results of mule deer population composition surveys conducted from 1988 to 1994 are summarized in Table 5.3. Fawn:doe ratios plotted to corresponding birth years (Fig. 5.2) ranged from highs of 51 and 52 fawns:100 does in 1987 and 1988, respectively, to a low of 36 fawns:100 does in 1990. Fawn:doe ratios increased again in 1991 to 41 fawns:100 does, but then declined to 7 fawns:100 does in 1994.

Mortality and Survival of Radio-collared Deer

Of 175 radio-collared mule deer (91 bucks, 84 does) that we used in MICROMORT analyses during 1987 through 1994, cougars killed 73 (41.7%, 40 bucks, 33 does). Radio-collared cougars were implicated in 49 (67%) of the cougar-caused deaths. Male and female deer were killed by cougars in proportions relative to their occurrence in the radio-collared population ($X^2 = 0.229$, 1 d.f., $P > 0.10$). Twenty-nine other radio-collared deer (18 bucks, 11 does) died of other causes, most of which could not be determined. Males and females died from other causes in proportion to their occurrence in the radio-collared population ($X^2 = 1.170$, 1 d.f., $P > 0.10$). Four deer (3.9% of deaths) possibly were killed by coyotes.

Survival rates of radio-collared bucks, does and combined sexes indicated a bimodal pattern that fit the pre-treatment and post-treatment phases of the study (Table 5.4, Fig. 5.3). Mean annual deer survival rates in the pre-treatment years were 0.876 for bucks and 0.883 for does. Respective span survival rates (0.583, 0.606) for bucks and does were not significantly different ($P = 0.42$).

Survival rates during the post-treatment years averaged 0.662 for bucks and 0.787 for does. Span survival rates for bucks (0.172) and does (0.370) were significantly different ($P = 0.013$). Span survival rates during the post-treatment years for each gender and all radio-collared deer combined were significantly lower than in the pre-treatment years. For the entire 8-year span, bucks had a significantly lower survival rate than does (0.100 and 0.224, respectively; $P = 0.02$).

Cougar predation rates on radio-collared deer reflected the same bimodal pattern we saw in survival rates (Table 5.5, Fig. 5.3). During the pre-treatment years, annual cougar predation rates averaged 0.058, 0.074, and 0.066 for bucks, does, and combined sexes, respectively. The pre-treatment span cougar predation rates for bucks (0.196) and does (0.250) were not significantly different ($P = 0.31$).

In the post-treatment years, mean annual cougar predation rates were 0.265 for bucks, 0.179 for does, and 0.226 for bucks and does combined. Bucks had a significantly higher span cougar predation rate (0.637) than does (0.508, $P = 0.10$). Post-treatment span cougar predation rates on bucks, does, and combined sexes were significantly higher than those respective rates for the pre-treatment years ($P < 0.007$).

Mortality rates of radio-collared deer from other causes of mortality did not have the bimodal pattern exhibited in survival and cougar predation rates (Table 5.6, Fig. 5.3). During pre-treatment years, bucks, does, and all radio-collared deer combined had mortality rates from other causes that averaged 0.066, 0.044, and 0.056, respectively. Span mortality rates for bucks (0.221) and does (0.144) were not significantly different ($P = 0.19$).

The post-treatment span mortality rates from other causes for bucks, does, and all radio-collared deer combined were not significantly different from the respective rates in the pre-treatment years ($P \geq 0.35$). Mean annual rates of mortality from other causes was 0.073 for bucks and 0.034 for does. Span mortality rates for bucks (0.191) and does (0.122) were not significantly different ($P = 0.19$).

When we compared cause-specific mortality rates in the pre-treatment span, we found that mortality rates in bucks and does from cougar predation (0.196 and 0.250, respectively) were not significantly different ($P = 0.41$, $P = 0.12$, respectively) from rates of other causes (0.221 and 0.144, respectively). Likewise, when bucks and does were combined, the rate of cougar predation (0.223) was not significantly different from the rate of mortality from other causes (0.184, $P = 0.29$).

However, when we made the same comparisons for the post-treatment span, we found that cougar predation rates on bucks (0.637), does (0.508), and all radio-collared deer combined (0.585) were significantly greater (all $P < 0.001$) than rates from other causes of mortality (0.191, 0.122, and 0.163, respectively).

5.4.6 DEER-COUGAR RELATIONSHIPS

Table 5.7 summarizes linear regression analyses of mule deer and cougar relationships. During the 8-year span there was a weak positive relationship between radio-collared mule deer mortality rates and the density of adult cougars on the TA ($r^2 = 0.25$, $0.025 < P < 0.05$, Fig. 5.4). However, cougar predation rates on radio-collared deer was independent of adult cougar density ($P > 0.10$, Fig 5.5). Fawn:doe ratios had a weak negative relationship with adult cougar density ($r^2 = 0.40$, $0.025 < P < 0.05$, Fig. 5.6).

Regression analyses emphasized the bimodal pattern in deer mortality rates exhibited in the pre-treatment and post-treatment spans (Table 5.7). Cougar density increased in importance as a factor affecting deer mortality rates and cougar predation rates during the post-treatment span. Fawn:doe ratios and adult cougar density had a strong negative relationship during the pre-treatment span ($r^2 = 0.94$, $0.01 < P < 0.025$), but during the post-treatment span the slope of the regression line was not significantly less than 0 ($P > 0.10$).

5.4.7 DEER-PRECIPITATION RELATIONSHIPS

Precipitation

Precipitation totals for the research period 1985 to 1994 are presented in Fig. 5.7. Annual precipitation totals during the pre-treatment span was generally lower ($\bar{x} = 36.04$ cm, SD = 9.11) than in the post-treatment span ($\bar{x} = 48.35$ cm, SD = 12.45). However, means were not significantly different (Wilcoxon rank sum, $n_1 = 4$, $n_2 = 4$, T = 13, $P > 0.10$). In the pre-treatment span, 2 years with precipitation below the 58-year average interposed years with above average precipitation. During the post-treatment span, annual precipitation totals declined each year, with only 1994 having below average precipitation.

Growing season precipitation totals during the pre-treatment span were generally higher ($\bar{x} = 20.65$, SD = 4.87) than in the post-treatment span ($\bar{x} = 18.66$, SD = 8.62), but means were not significantly different (Wilcoxon rank sum, $n_1 = 4$, $n_2 = 4$, T = 19, $P > 0.10$). In the pre-treatment span, 2 years with growing season precipitation below the 58-year average interposed years with above average precipitation. In contrast, the last 3 years of the post-treatment span had below average growing season precipitation.

Table 5.7 summarizes results of linear regression analyses of deer-precipitation relationships. During the 8-year span, growing season (July-Sep.) precipitation accumulation had weak positive relationships with annual deer survival rates ($r^2 = 0.45$, $0.025 < P < 0.05$, Fig. 5.8) and fawn:doe ratios ($r^2 = 0.41$, $0.025 < P < 0.05$, Fig. 5.9). Annual precipitation totals were not correlated with either annual deer survival rates ($r^2 = 0.002$, $P > 0.10$) or fawn:doe ratios ($r^2 = 0.012$, $P > 0.10$).

The importance of precipitation to deer survival rates and fawn:doe ratios also exhibited a bimodal pattern between the pre-treatment and post-treatment spans. In the pre-treatment span, deer survival rates and fawn:doe ratios apparently were independent of growing season and annual precipitation accumulation (r^2 ranged from 0.0008-0.08, all $P > 0.10$). However, in the post-treatment span, growing season precipitation was highly correlated with annual deer survival rates ($r^2 = 0.93$, $0.01 < P < 0.025$) and moderately correlated with fawn:doe ratios ($r^2 = 0.78$, $0.05 < P < 0.10$). Annual precipitation totals were strongly correlated with annual deer survival rates ($r^2 = 0.86$, $0.025 < P < 0.05$) and fawn:doe ratios ($r^2 = 0.96$, $0.025 < P < 0.05$).

5.5 DISCUSSION

5.5.1 COUGAR PREDATION

Cougars depended on desert mule deer as their primary food on the SAM. Consequently, cougars were the chief predator and the single-most important cause of mortality in deer. Cougar predatory behavior probably is defined by local prey availability and vulnerability (Iriarte et al. 1990); thus, we suspect that other prey animals on the SAM occurred in numbers too small (javelina, pronghorns, desert bighorn sheep) and/or biomass too low (e.g., leporids, rodents) to be important sustaining sources of food for cougars. As the oryx population in the Tularosa Basin increased during this study, greater numbers of oryx ranged onto the SAM. Although the large mass of adult oryx probably minimized their vulnerability to cougars, calves were vulnerable. Cougars probably killed calves opportunistically, particularly when they were not closely guarded by adult oryx.

Other studies of cougar diet and predation in the desert southwest also found that mule deer were the most important food for cougars (Hibben 1937, Donaldson 1975, Shaw 1977, Smith et al. 1986, Cashman et al. 1992). In Big Bend National Park, Texas javelina were common and occurred in the cougar diet about as frequently as deer (Leopold and Krausman 1986, Waid 1990). For temperate North America in general, deer were the major prey of cougars (Anderson 1983). But where elk (*Cervus elaphus*) and bighorn sheep were locally abundant, those ungulates were more important than mule deer as food (Spreadbury 1989, Harrison 1990, respectively). In southwestern Alberta, moose (*Alces alces*) were the most important prey for male cougars, while mule deer and white-tailed deer (*O. virginianus*) were the most important prey for female cougars (Jalkotzy et al. 1992).

Although we intensively studied the cougars along the western boundary of the SAM, we observed an absence of cougar predation on cattle from adjacent ranches. This is a common occurrence in most areas of the west where cougars and cattle are sympatric. However, in some localized parts of the southwest, livestock is used as food by cougars. For example, in the Guadalupe Mountains of New Mexico and Texas, sheep, cattle, and goats together comprised 9% of the diet of cougars (frequency of occurrence in feces, Smith et al. 1986). In 2 areas in Arizona, cattle (primarily calves) comprised 26% to 34% of the diet of cougars (frequency of occurrence in feces, Shaw 1977, Cunningham et al. 1995).

5.5.2 SCAVENGING

Reports of scavenging cougars in the literature were exceptional (Anderson 1983), thus contributing to the general notion that cougars almost exclusively eat prey they have killed. We may have reported a higher incidence of cougar scavengers than any other study, but we can not reliably claim that the behavior occurred more often in our study area than in other environments. Our field policy of periodically checking on the status of carcasses may have simply enabled us to observe scavenging by cougars more frequently.

Because scavenging cougars treated carcasses much like killed prey, there was the potential that some of the animals classified as probable cougar kills actually died of other causes and were then scavenged by cougars. Consequently, rates of cougar predation on radio-collared deer probably are positively biased. This bias may be especially real during the severe drought conditions of 1994 when deer were more vulnerable to mortality.

5.5.3 DEER, COUGARS, AND PRECIPITATION

We addressed some of the relationships between cougars and desert mule deer by quantifying: 1) cougar predation; 2) the relationships between cougar density and fawn production; and 3) the relationship between cougar density and survival and mortality rates of radio-collared deer ≥1 year old. Effects of cougar predation changed over time and were probably related to changes in the ecological carrying capacity (Caughley 1975, cited in Bartmann et al. 1992) of habitat as it was affected by drought conditions during growing seasons in 3 consecutive years (1992-1994). However, we could not quantify the numerical impact of cougar predation on the deer population because we did not quantify changes in mule deer density for the duration of the study.

Fawns comprised a large proportion (about 27%) of the number of deer we found by chance that were killed by cougars. Because cougars almost completely consumed fawns (especially small ones), there probably was a negative bias in detecting fawns as cougar prey. Consequently, we suspect our record on cougar-killed deer actually underrepresented fawns used by cougars.

We believe that the importance of fawns to cougars changed as a declining ecological carrying capacity during the drought years resulted in poor fawn production on the SAM. (See Short 1981, Connolly 1981, and Bartmann et al. 1992 for extensive discussions on how climate and habitat conditions affect deer productivity and survival). Consequently, cougar predation pressure probably shifted away from fawns and toward older deer.

Fawns also appear to be closely associated with reproduction of cougars on the SAM. We found that the cougar birth pulse coincides with the fawning season (July-Sep., see Chapter 3.4.6). This periodic abundance of vulnerable prey (fawns) probably confers survival advantages to cougar mothers and their offspring to the extent that the birth pulse may be defined by natural selection.

Other studies have quantified the use of mule deer fawns by cougars. Hornocker's (1970) classic study of cougar-prey interactions in Idaho showed that cougars killed fawns in greater numbers relative to their numerical availability in the population. On the other hand, Hopkins (1989) found that cougars in California killed fawns in proportion to their occurrence in the population. In a study of mule deer mortality rates on the Kaibab Plateau, Arizona, McCulloch and Brown (1986) found that cougars killed radio-collared fawns (6-9 mo. old) at a significantly higher rate than radio-collared does >30 months old.

On the SAM, cougars killed bucks and does $\geq$1 year old in relation to their availability in the radio-collared population. Predation rates on bucks and does during the pre-treatment span did not differ significantly. But cougar predation rates on bucks in the post-treatment span were significanty higher than predation rates on does, suggesting there was a shift in the vulnerability of bucks relative to does during those years. We could not address potential causes for changes in vulnerability because we did not intensively investigate deer population dynamics, behavior, habitat use, or health during the study.

In studies that have relied on estimates of deer population composition, cougar selection differed. Cougars killed bucks more than expected and does less than expected in Utah (Robinette et al. 1959, Ackerman 1982), Idaho (Hornocker 1970), and California (Hopkins 1989). The difference between those findings and ours may be real or they may have to do with inherent biases in the way deer populations and cougar kills were sampled. Researchers have opined that bucks were more vulnerable than does because they usually were alone, used higher elevations, and were in weakened physical condition especially after the rut (Hornocker 1970) or that bucks were less wary during the rut and they preferred the same habitats that cougars used (Robinette et al. 1959).

Deer survival rates we calculated agreed with our general field observations that the SAM mule deer population either increased or was stable during the pre-treatment span, but declined during the post-treatment span. The decline was becoming evident to us in 1993. In anticipation of further decline after 1993, we modified our deer population composition count by conducting it in the fall of 1994 (instead of the following winter) so that we could reliably distinguish between yearling deer and adult does. Our 1994 count of 35 yearlings per 100 adult does versus the 1993 fawn:doe ratio of 27:100 suggested that the adult doe segment of the population had declined, and corroborated the low annual survival rate for does in 1994 (0.655). However, the composition count did not reflect the severity of the decline in the buck segment of the population that was indicated by the low buck annual survival rate (0.435). Obviously, compostion counts should be interpreted with caution because the reference class (in this case does), which ideally should be stable, instead varied over time (McCullough 1994).

Our observations improved our understanding of how cougars and environmental conditions may interact to influence effects of cougar predation on mule deer over time. Deer mortality caused by cougars or other causes was relatively equal and stable during the pre-treatment span even though the cougar population increased. Furthermore, although cougars were the major cause of mortality in deer, the deer population appeared to be stable or increasing. We hypothesize that precipitation and attendant habitat conditions sufficiently contributed to deer productivity and survival to the extent that the deer population escaped potentially negative effects of cougar predation during the pre-treatment span (i.e., deer were below the ecological carrying capacity).

Conditions were different in the post-treatment span. Cougar predation rates on deer ≥1 year old increased significantly as cougar density increased and as declining growing season precipitation resulted in a reduction in the ecological carrying capacity and lower fawn production. Cougars contributed directly to the deer population decline as the major proximate cause of mortality; but habitat condition (quantity and quality) probably was the ultimate cause for the decline of the deer population by enhancing the vulnerability of deer to mortality factors (i.e., predation, malnutrition, disease).

As mentioned previously, because of lower fawn production, cougar predation pressure that might have been absorbed by fawns probably shifted toward older deer. Moreover, 3 consecutive years with growing season drought conditions probably enhanced the vulnerability of deer through negative effects on physical condition and by causing deer to alter movement patterns into unfamiliar areas to seek out more nutritious foods and surface water. Does especially seek out habitats with better forage characteristics and they have high water requirements particularly during the hot, dry parts of the year and during late pregnancy and lactation (Short 1981, Hervert and Krausman 1986, Ordway and Krausman 1986). Does will even abandon home ranges where traditional water sources have dried up in order to seek out other water sources (Hervert and Krausman 1986).

On the SAM, deer normally concentrated in areas around water sources during the hot, dry portion of the year (April to June). This especially occurred in 1994 when the rainy season did not materialize (July to Sep.) and many water sources went dry. Even some springs once thought to be perennial went completely dry. We hypothesize that deer which concentrated around limited water sources had increased vulnerability to cougar predation. Our observations of cougars and radio-collared deer during the hot, dry period of 1994 supported the hypothesis. Out of 18 radio-collared deer killed by cougars in 1994, 6 (33%) were killed by cougars at water sources; 5 of those (28%) were killed in June.

The most important consequence of drought conditions during the post-treatment span was the reduction in the ecological carrying capacity of the habitat for deer and cougars. Deer survival rates and fawn productivity probably would have declined even without cougar predation. Consequently, even though cougar predation apparently expedited the decline of the deer population, it is likely that cougar predation had greater compensatory effects in these conditions (Bartmann et al. 1992).

In the absence of cougar predation, we suspect that the deer population might have increased at a faster rate during the pre-treatment years, thus achieving a higher population number and density prior to the drought. Then, during the drought, the deer population would exceed the ecological carrying capacity and contribute to severe habitat degredation, resulting in poor productivity and greater mortality from malnutrition and disease. Thus, the deer population would decline. Moreover, because of the degraded habitat, the deer population would have a lower potential for growth after the drought ended.

Cougar predation, on the other hand, by acting as a year-round mortality factor on the deer population, probably helps to dampen and protract severe population oscillations, and thus may reduce habitat damage. In the long run, cougar predation may contribute to relative ecological stability in wild environments (Hornocker 1970).

Although our study was 10 years in duration, it still was too short for us to document how the cougar population responded to a diminished prey base. We expect that after a lag time following drastic prey decline, cougars would have lower survival. Cubs would be especially vulnerable because mothers would have to hunt for longer periods, thus leaving cubs more exposed to predation, especially by other cougars (see Chapter 3.4.7). In addition, cubs probably would be more prone to malnutrition and disease. Changes in the use of space might occur as cougars range over broader areas to hunt for dwindling prey. Greater overlap in the use of space by cougars may result, and consequently increase the chances of encounters, intra-species fighting, and death. Direct competition for killed prey or carrion might occur more frequently between subadult and adult cougars, and also result in increased fighting and mortality (see Chapter 3.4.7). Cougars might shift their diet more to smaller animals which may be potential carriers of lethal diseases such as plague, thus resulting in greater mortality. Some cougars probably would starve to death (Shaw 1980). The consequence of lower survival rates over time would be a lower cougar density.

Other investigators generally have concluded that although cougars may be the major source of mortality, it is the habitat that ultimately limits prey populations. Hornocker (1970:37) concluded that elk and deer populations in central Idaho "were limited by the winter food supply, and that predation by [cougars] was inconsequential in determining ultimate numbers of elk and deer." The elk and deer populations on his study area increased even though they were prey for a lightly hunted cougar population similar in density to the cougar population we studied on the SAM (see Chapter 3.5). Hopkins (1989) gathered data on cougar:prey ratios in the Diablo Range, California that supported his hypothesis that cougars were not exhibiting a strong limiting force on the deer herd. There the cougar population was not hunted and the density was similar to that on the SAM. During the period Lindzey et al.(1994) studied a protected low density cougar population in south-central Utah, the mule deer population increased.

On the other hand, Shaw (1977) concluded from his study of hunted cougars in central Arizona that cougars were contributing to the low deer populations, but that cougar predation rates at the level he observed would not prevent the deer herd from increasing if other sources of mortality were significantly reduced. Also in Arizona, Ockenfels (1994) found that cougar predation on female pronghorn was high enough to stabilize or decrease the pronghorn population in an area where rugged, brushy terrain made the normally open plains dwelling pronghorns vulnerable to cougars. He suggested (p.6) that cougar predation on pronghorns "is probably inconsequential in rolling grassland habitat where little cover exists".

Seidensticker et al. (1973) hypothesized that the land tenure system of cougars maintains the density of breeding adults below the level set by food supply alone. Lindzey et al. (1994) concluded that their study apparently supported the hypothesis. But those investigators did not experience a dramatically reduced carrying capacity like we did resulting in significantly higher cougar predation rates. We concluded from our study of cougar social organization on the SAM that the cougar population is ultimately limited by the food resource (see Chapter 4.5).

Long-term research on cougar-prey-habitat relationships during normal conditions and drastic environmental variations should illuminate further the range of effects of cougar predation on ungulate populations, attendant cougar population dynamics, and the contributing ecological conditions.

5.6 MANAGEMENT IMPLICATIONS

1. **Finding:** Cougars on the SAM were dependent on large, deer-sized prey, just like other cougars in North America.

   Implication: Long-term wildlife conservation strategies in New Mexico need to consider the dependency of cougars on large prey, primarily mule deer, white-tailed deer, and elk. Where locally abundant, javelina may be an important food.

2. **Finding:** On the SAM, cougars killed an average of 7% of mule deer ≥1 year old annually when the deer population was stable or increasing, and an average of 23% of deer ≥1 year old annually when the deer population exceeded the ecological carrying capacity.

   Implication: Because sport-hunting is a mortality factor external to the wild system, management objectives for mule deer populations that support cougar populations should consider potential additive and compensatory effects of sport-hunting.

3. **Findings:** Over a relatively long period (8 yrs. in this case), the density of adult cougars (within the ranges we observed) had only a minor relationship to deer survival rates and no apparent relationship to cougar predation rates on deer ≥1 year old. In a shorter 4-year period, when deer were apparently below ecological carrying capacity, adult cougar density had no relationship to cougar predation rates on deer, and the deer population was either stable or increasing. However, during a subsequent 4-year period, when climate (in this case drought) reduced the carrying capacity of the habitat, and consequently increased the vulnerability of deer, cougar predation rates on deer ≥1 year old increased significantly. Thus, cougars became the major proximate cause of mortality contributing to the deer population decline. Poor habitat condition was the ultimate limiting factor.

Implications: Short-term reduction of cougar numbers, through either control or heavy sport-hunting pressure, and during periods when deer are below carrying capacity, probably will not cause a significant increase in deer numbers. Reductions in cougar numbers probably would have to exceed >50% of the adult cougars over a sustained period of time to have an effect. If the control effort is successful, then sport-hunting may have to maintain the deer population within the carrying capacity to avert severe habitat deterioration and pronounced oscillations in the deer population. Under those conditions, more intensive efforts than are generally practiced by managers today would be necessary to monitor the deer population and its effects on the habitat.

Cougar control should not be expected to reverse deer population declines that are ultimately being caused by habitat deterioration (i.e., the deer population has exceeded the carrying capacity).

Given the uncertainties of how cougar and deer population dynamics are affected by interacting environmental factors in any particular area, if cougar control is attempted with the objective of increasing deer numbers, then it should be approached as an experiment. This would entail concurrent monitoring of cougar and deer population dynamics, as well as environmental factors, for the purpose of measuring the actual effects of cougar removal on the deer and cougar populations.

Similarly, cougar control aimed at minimizing predation on livestock and threats to human safety also should be executed as experiments. In this way, managers can determine the effects of the control action.

5. **Finding:** On the SAM, cougars depended primarily on desert mule deer for food and only occasionally preyed on the state endangered desert bighorn sheep (see Chapter 6: *Cougars And Desert Bighorn Sheep*).

Implication: In areas where endangered desert bighorn sheep exist, sport-hunting of mule deer should be managed so that deer removal does not contribute to increased cougar predation on sheep. This concept may be extended to localized areas where cougars prey on livestock.

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Table 5.1. Prey killed by cougars on the San Andres Mountains, New Mexico, 1985 - 1995.[a,b]

Species	No. recorded	Percent
Desert mule deer	479	91.2
Desert bighorn sheep	10	1.9
Pronghorn	5	1.0
Oryx calf	3	0.6
Cougar	13	2.0
Coyote	3	0.6
Striped skunk	3	0.6
Badger	1	0.2
Ringtail	1	0.2
Leporids	1	0.2
Porcupine	5	1.0
Golden Eagle	1	0.2
TOTAL =	525	

[a] Cougar prey included cougar kills and probable cougar kills.

[b] In addition to those animals tabulated above, cougars killed but did not eat 14 cougars, 4 gray foxes, 1 coyote, and 1 long-eared owl.

Table 5.2. Age and gender of mule deer that died on the San Andres Mountains, New Mexico, 1985-1995.

Cause of Death	Age (yr.)											
Sex	<1	1	2	3	4	5	6	7	8	9	10+	Sub- totals
Cougar Kills[a]												
Bucks	15	12	27	15	16	24	23	23	21	5	22	203
Does	25	9	28	23	22	8	24	17	10	2	16	194
Unk. sex	67	3	6	3	0	2	0	0	1	0	0	82
Subtotals	107	24	61	41	38	44	47	40	32	7	38	479
Other causes[b]												
Bucks	1	1	0	4	6	1	6	2	6	2	6	35
Does	1	0	1	3	3	5	3	1	3	1	1	22
Unk. sex	4											4
Subtotals	6	1	1	7	9	6	9	3	9	3	7	61

[a] Cougar kills include deer that were killed and probably killed by cougars.

[b] Other causes were not related to cougar predation.

Table 5.3. Mule deer population composition, San Andres Mountains, New Mexico, 1988-1994.

Dates (method)	No. deer counted	No. groups	Mean group size	Actual Count Bucks	Actual Count Does	Actual Count Fawns	Bucks / Fawns[a] per 100 Does
1-10-88 (helicopter)	242	47	5.2	85	104	53	82/51
1-15-89 (helicopter)	244	51	4.8	53	126	65	42/52
1-14-90 (helicopter)	192	41	4.7	51	100	41	51/41
1-1 to 31-91 (ground)	277	60	4.6	81	144	52	56/36
2-8-92 (helicopter)	216	49	4.4	61	110	45	56/41
1-23-93 (helicopter)	187	43	4.4	46	103	38	45/37
12-1-93 to 1-24-94 (ground)	312	68	4.6	60	199	53	30/27
10-1 to 11-30-94 (ground)	318	85	3.7	83	219	16	38/7

[a] Ratios of fawns per 100 does were used in regression analysis to correspond to the year of birth.

Table 5.4. Survival rates of radio-collared mule deer on the TA, San Andres Mountains, New Mexico, 1987-1994.[a]

Span	Bucks			Does			B&D combined	
Year	n	Rate	s^2	n	Rate	s^2	Rate	s^2
Pre-treatment								
1987	15	0.933	0.004	26	0.921	0.003	0.925	0.002
1988	36	0.883	0.004	40	0.864	0.004	0.873	0.002
1989	41	0.784	0.005	48	0.889	0.003	0.839	0.002
1990	54	0.902	0.003	47	0.856	0.003	0.876	0.002
Mean =		0.876			0.883		0.878	
Span rate =		0.583[b,c]	0.007		0.606[b,c]	0.006	0.594[c]	0.003
Post-treatment								
1991	53	0.803	0.003	42	0.945	0.001	0.865	0.001
1992	47	0.763	0.004	44	0.732	0.005	0.748	0.002
1993	40	0.648	0.007	36	0.817	0.005	0.726	0.003
1994	25	0.435	0.010	23	0.655	0.011	0.537	0.006
Mean =		0.662			0.787		0.719	
Span rate =		0.172[c]	0.002		0.370[c]	0.006	0.252[c]	0.002
8-year								
Span rate =		0.100[c]	0.001		0.224[c]	0.003	0.150	0.0009

[a] Survival rates were computed using MICROMORT and data from 91 radio-collared bucks (78,686 days) and 84 radio-collared does (86,172 days), 1987-1994.

[b] Span survival rates of pre-treatment bucks and does were not significantly different ($P = 0.42$).

[c] Span survival rates of post-treatment bucks and does, pre- and post-treatment bucks, pre- and post-treatment does, pre- and post-treatment bucks and does combined, and 8-year span rates for bucks and does were significantly different ($P < 0.02$).

Table 5.5. Cougar predation rates on radio-collared mule deer on the TA, San Andres Mountains, New Mexico, 1987-1994.[a]

Span	Bucks			Does			B&D combined	
Year	n	Rate	s^2	n	Rate	s^2	Rate	s^2
Pre-treatment								
1987	15	0.067	0.004	26	0.040	0.002	0.050	0.001
1988	36	0.039	0.001	40	0.102	0.003	0.073	0.002
1989	41	0.062	0.002	48	0.083	0.002	0.073	0.001
1990	54	0.065	0.002	47	0.072	0.002	0.069	0.001
Mean =			0.058		0.074		0.066	
Span rate =		0.196^{b,c}	0.006		0.250^{b,c}	0.005	0.223^{c}	0.003
Post-treatment								
1991	53	0.175	0.003	42	0.028	0.001	0.110	0.001
1992	47	0.118	0.002	44	0.195	0.004	0.156	0.002
1993	40	0.288	0.006	36	0.147	0.005	0.222	0.003
1994	25	0.478	0.010	23	0.345	0.011	0.417	0.005
Mean =		0.265				0.179		0.226
Span rate =		0.637^{c}	0.004		0.508^{c}	0.006	0.585^{c}	0.003

[a] Cougar predation rates were computed using MICROMORT and data from 91 radio-collared bucks (78,686 days) and 84 radio-collared does (86,172 days), 1987-1994.

[b] Span cougar predation rates of pre-treatment bucks and does were not significantly different ($P = 0.31$).

[c] Significant differences were found for the following span rate comparisons: pre- and post-treatment bucks ($P<0.001$); pre- and post-treatment does ($P=0.007$); post-treatment bucks and post-treatment does ($P=0.10$); and pre- and post-treatment bucks and does combined ($P<0.001$).

Table 5.6. Rates of other causes of mortality (unrelated to cougar predation) in radio-collared mule deer on the TA, San Andres Mountains, New Mexico, 1987-1994.[a]

Span	Bucks			Does			B&D combined	
Year	n	Rate	s^2	n	Rate	s^2	Rate	s^2
Pre-treatment								
1987	15	0.000	0.000	26	0.040	0.002	0.025	0.001
1988	36	0.078	0.003	40	0.034	0.001	0.055	0.001
1989	41	0.155	0.004	48	0.028	0.001	0.088	0.001
1990	54	0.033	0.001	47	0.072	0.002	0.055	0.001
Mean =		0.066			0.044		0.056	
Span rate =		0.221[b]	0.005		0.144[b]	0.003	0.184[b]	0.002
Post-treatment								
1991	53	0.022	0.001	42	0.028	0.001	0.024	0.000
1992	47	0.118	0.002	44	0.073	0.002	0.096	0.001
1993	40	0.064	0.002	36	0.037	0.001	0.051	0.001
1994	25	0.087	0.003	23	0.000	0.000	0.046	0.001
Mean =		0.073			0.034		0.054	
Span rate =		0.191[b]	0.003		0.122[b]	0.003	0.163[b]	0.001

[a] Rates of other causes of mortality were computed using MICROMORT and data from 91 radio-collared bucks (78,686 days) and 84 radio-collared does (86,172 days), 1987-1994.

[b] Span rates of other causes of mortality for pre-treatment bucks and does, post-treatment bucks and does, pre- and post-treatment bucks, pre- and post- treatment does, pre- and post-treatment bucks and does combined were not significantly different (*P*>0.10).

Table 5.7. Regression analyses of relationships involving radio-collared mule deer (bucks & does combined) survival and mortality rates, fawn:doe ratios, adult cougar density, and precipitation on the TA, San Andres Mountains, New Mexico, 1987-1994.

Span Analyzed Relationship (y/x)	Slope	r^2	t-test result
1987 - 1994			
Deer mortality rate / cougar density	0.181	0.25	$0.025 < P < 0.05$
Cougar predation rate on deer / cougar density	0.150	0.18	$P > 0.10$
Fawn:doe ratio / cougar density	-26.406	0.40	$0.025 < P < 0.05$
Deer survival rate / July-Sep. precipitation	0.013	0.45	$0.025 < P < 0.05$
Deer survival rate / annual precipitation	0.000	0.00	$P > 0.10$
Fawn:doe ratio / July-Sep. precipitation	1.398	0.41	$0.025 < P < 0.05$
Fawn:doe ratio / annual precipitation	0.129	0.01	$P > 0.10$
Pre-treatment: 1987 - 1990			
Deer mortality rate / cougar density	0.060	0.42	$0.05 < P < 0.10$
Cougar predation rate on deer / cougar density	0.017	0.36	$P > 0.10$
Fawn:doe ratio / cougar density	-19.806	0.94	$0.01 < P < 0.025$
Deer survival rate / July-Sep. precipitation	-0.002	0.08	$P > 0.10$
Deer survival rate / annual precipitation	0.001	0.08	$P > 0.10$
Fawn:doe ratio / July-Sep. precipitation	0.121	0.00	$P > 0.10$
Fawn:doe ratio / annual precipitation	-0.025	0.00	$P > 0.10$
Post-treatment: 1991 - 1994			
Deer mortality rate / cougar density	0.305	0.70	$0.05 < P < 0.10$
Cougar predation rate on deer / cougar density	0.285	0.60	$0.05 < P < 0.10$
Fawn:doe ratio / cougar density	-32.857	0.64	$P > 0.10$
Deer survival rate / July-Sep. precipitation	0.015	0.93	$0.01 < P < 0.025$
Deer survival rate / annual precipitation	0.010	0.86	$0.025 < P < 0.05$
Fawn:doe ratio / July-Sep. precipitation	1.552	0.78	$0.05 < P < 0.10$
Fawn:doe ratio / annual precipitation	1.196	0.96	$0.025 < P < 0.05$

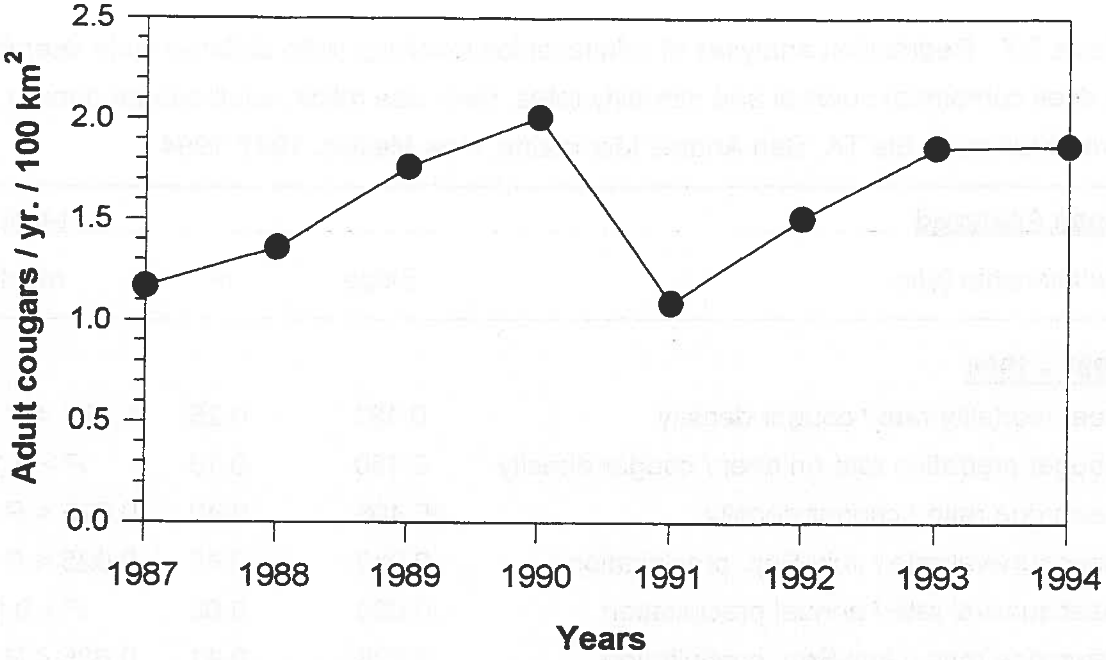

Fig. 5.1. Changes in the density of adult cougars on the TA, 1987 - 1994, San Andres Mountains, New Mexico.

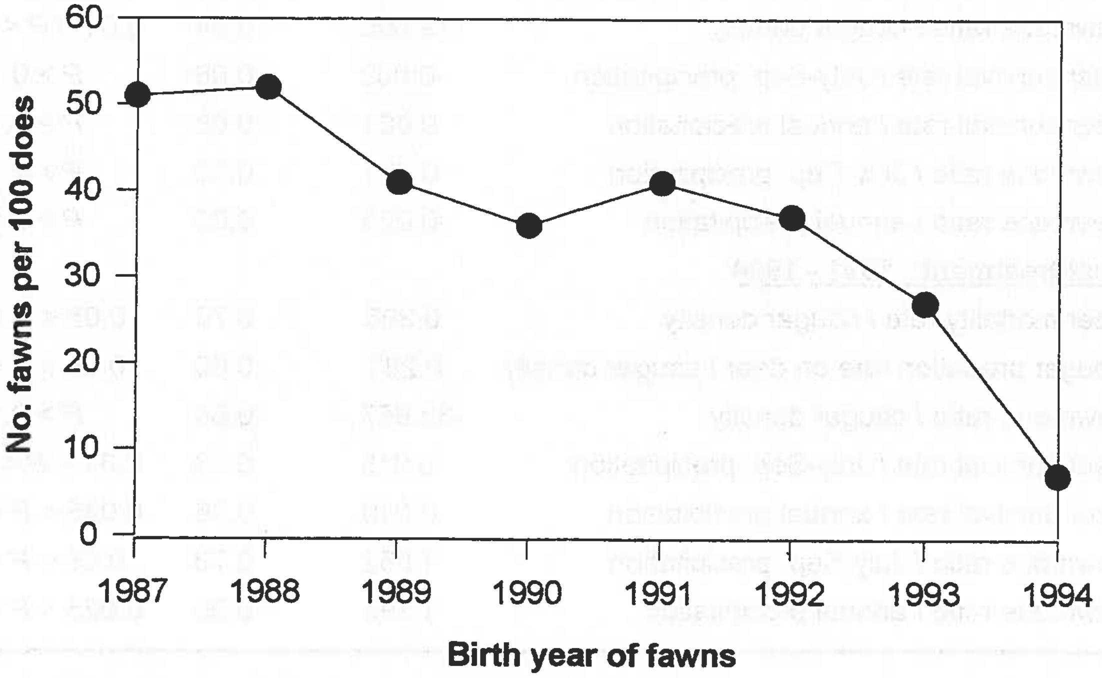

Fig. 5.2. Mule deer fawn:doe ratios on the San Andres Mountains, New Mexico, 1987 - 1994.

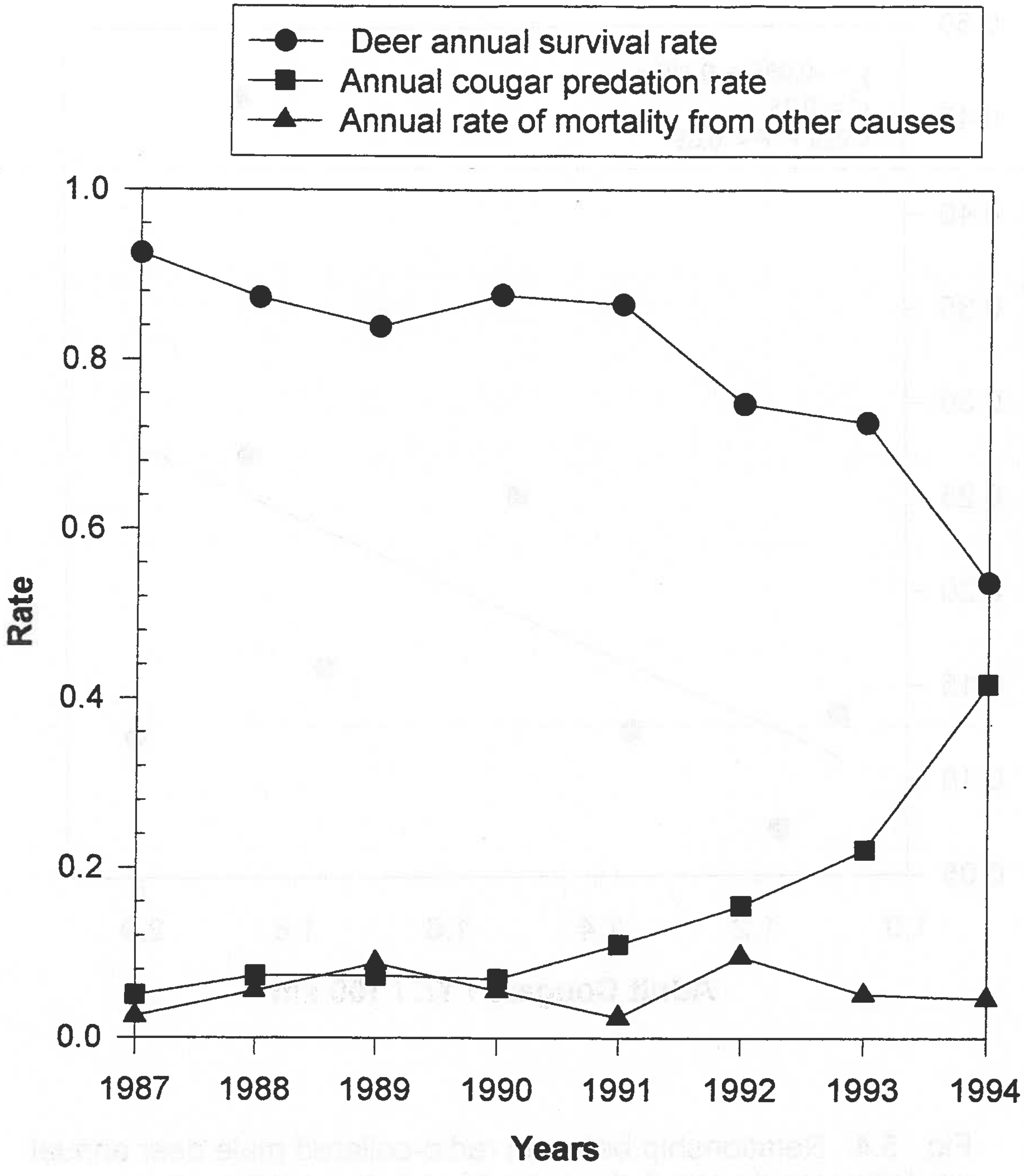

Fig. 5.3. Annual rates of survival, cougar predation, and mortality from other causes for radio-collared mule deer on the TA, 1987 - 1994, San Andres Mountains, New Mexico.

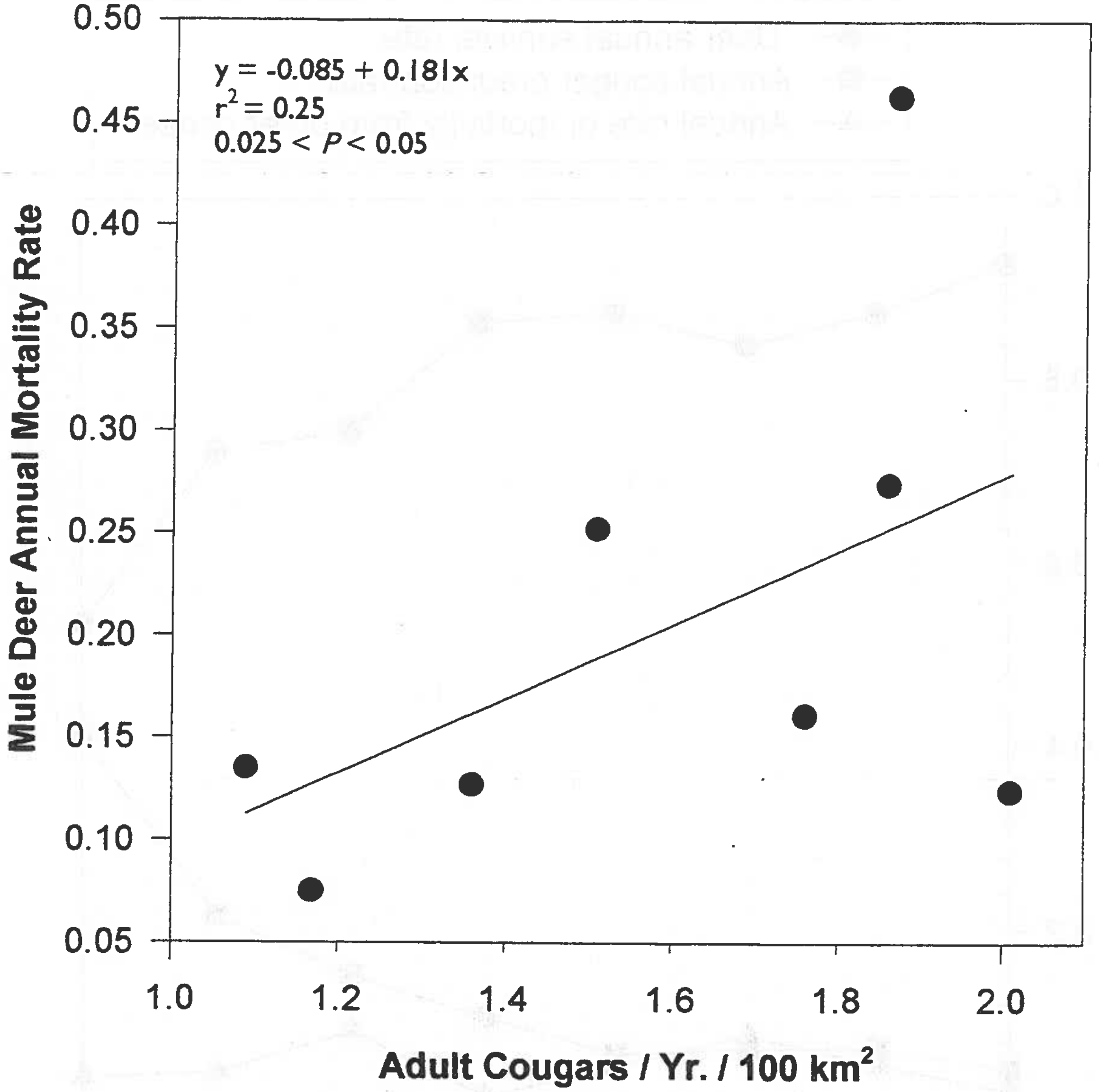

Fig. 5.4. Relationship between radio-collared mule deer annual mortality rate (bucks & does combined) and adult cougar density on the TA, 1987 - 1994, San Andres Mountains, New Mexico.

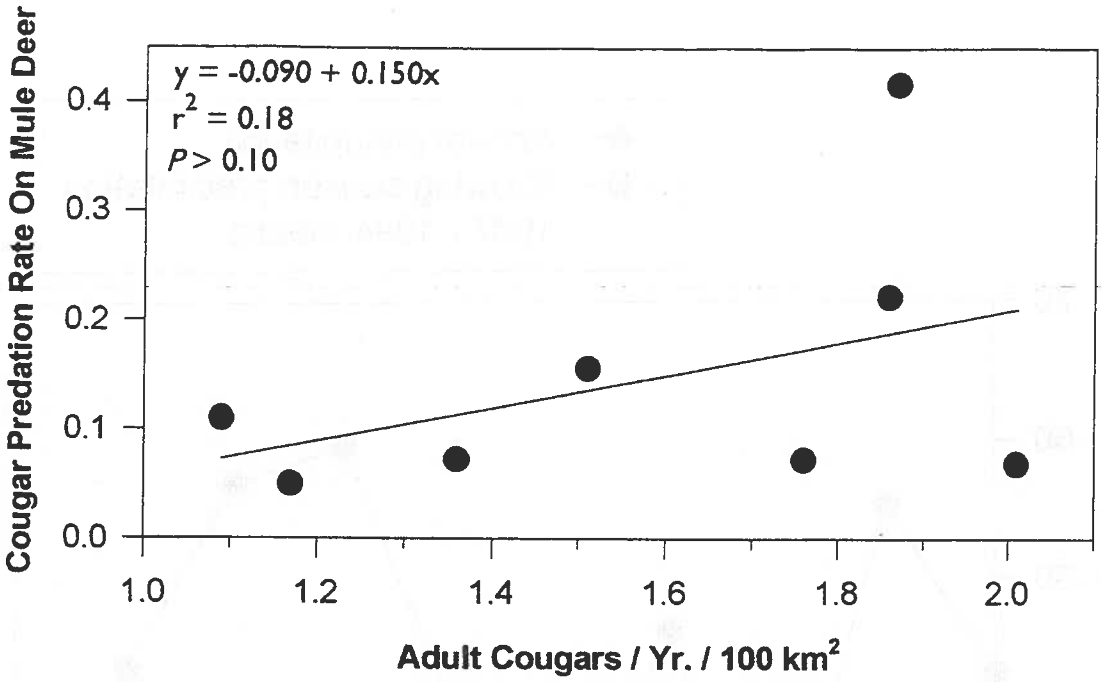

Fig. 5.5. Relationship between annual cougar predation rates on radio-collared mule deer (bucks & does combined) and adult cougar density on the TA, 1987 - 1994, San Andres Mountains, New Mexico.

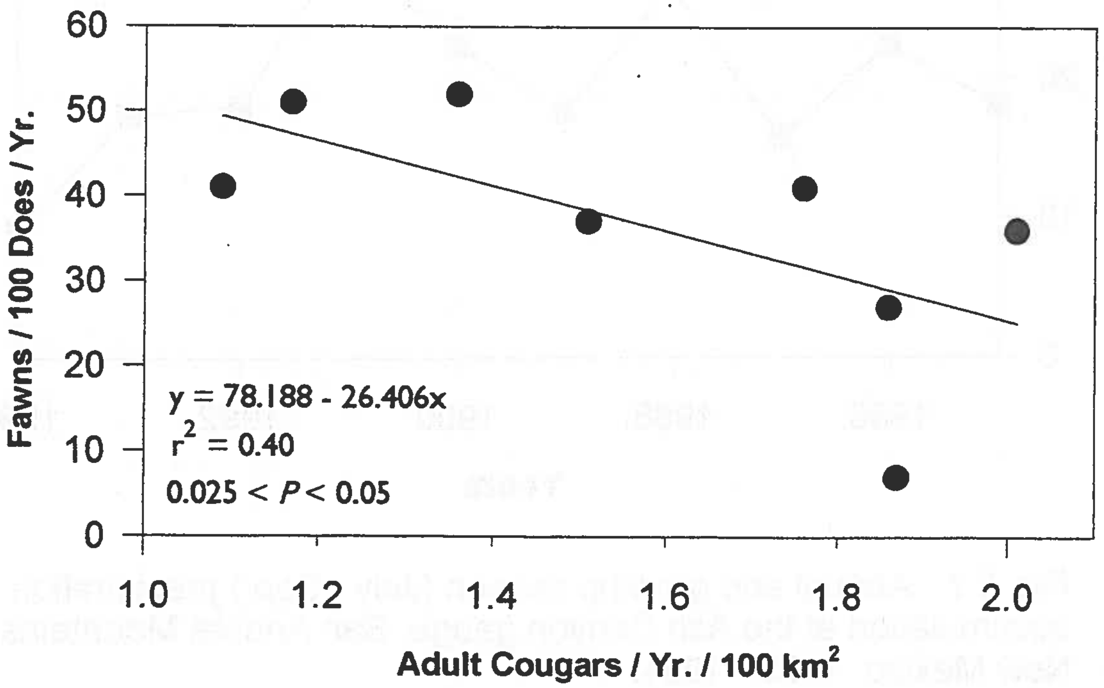

Fig. 5.6. Relationship between mule deer fawn to doe ratio and density of adult cougars on the TA, 1987 - 1994, San Andres Mountains, New Mexico.

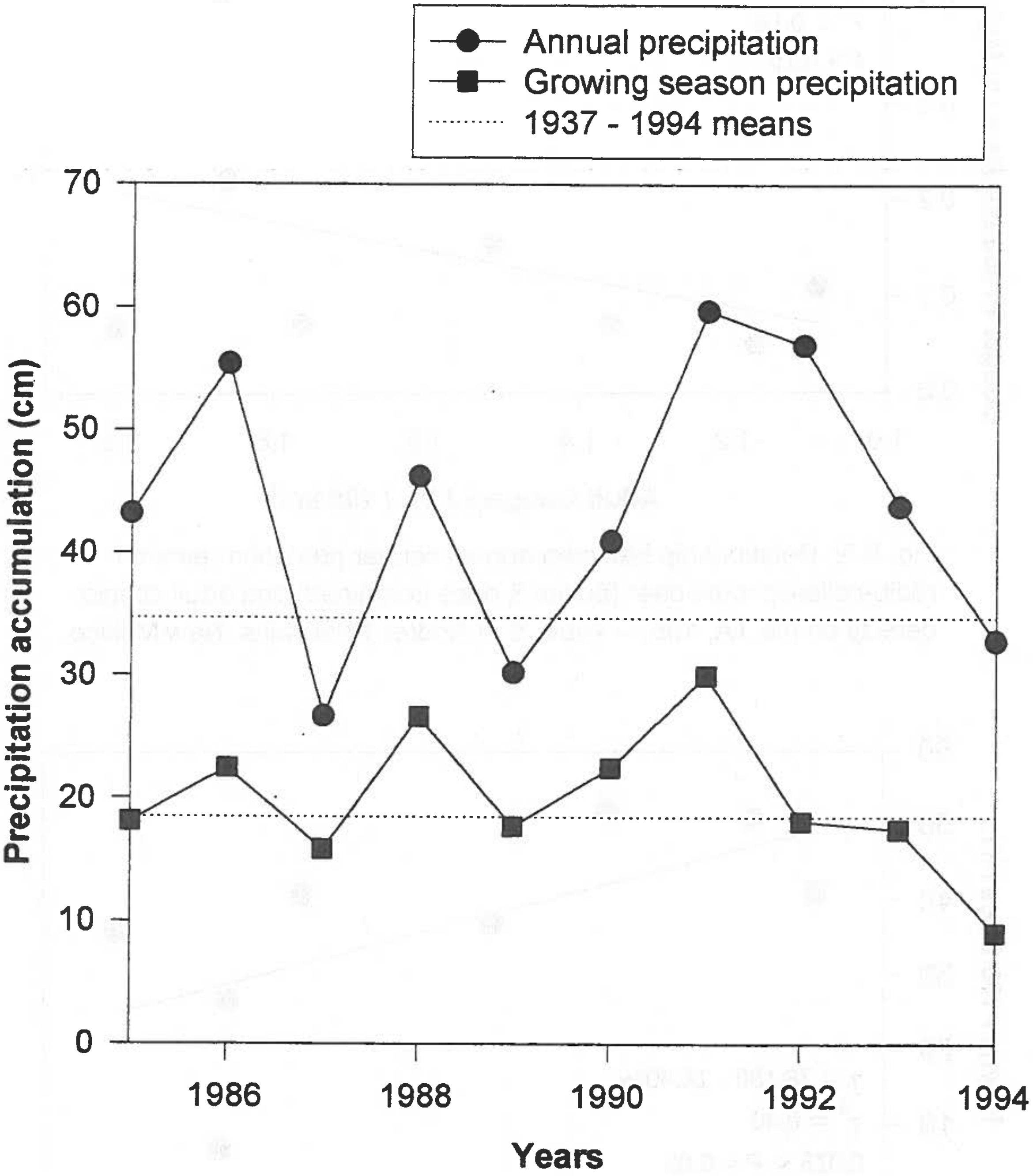

Fig. 5.7. Annual and growing season (July - Sep.) precipitation accumulation at the Ash Canyon gauge, San Andres Mountains, New Mexico, 1985 - 1994.

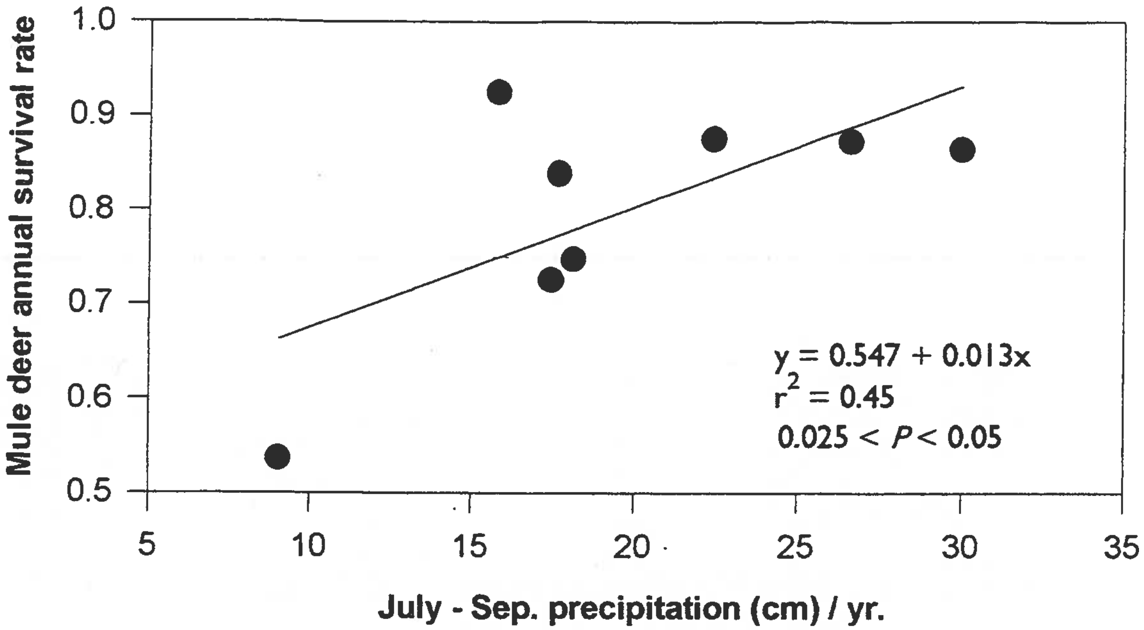

Fig. 5.8. Relationship between radio-collared mule deer annual survival rate (bucks & does combined) and July to September precipitation each year, 1987 - 1994, San Andres Mountains, New Mexico.

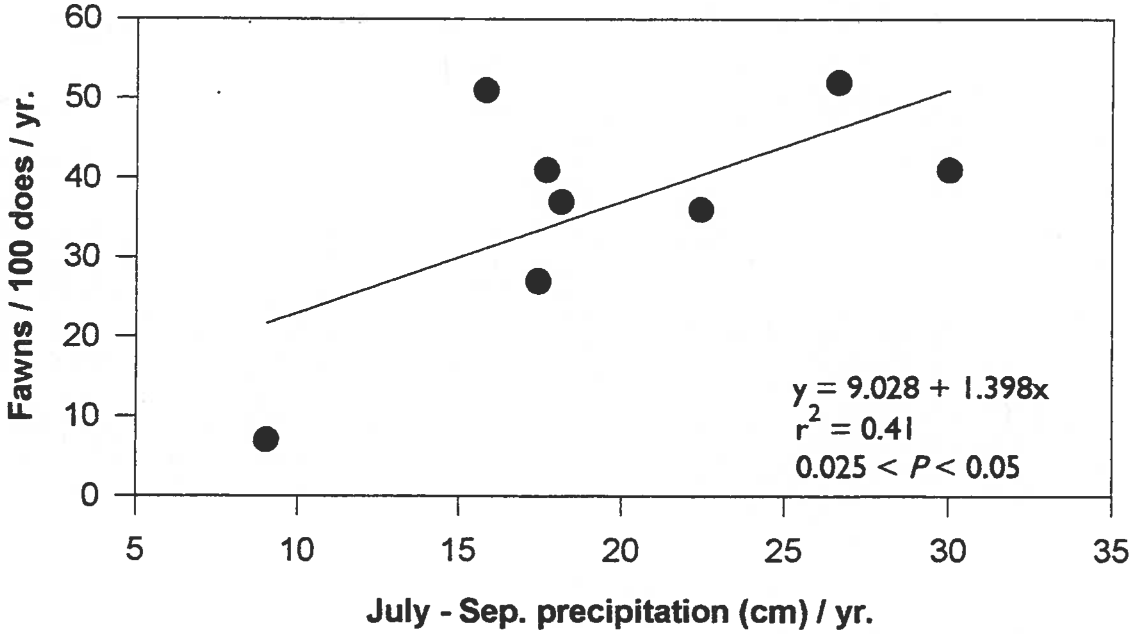

Fig. 5.9. Relationship between mule deer fawn to doe ratio and July to September precipitation each year, 1987 - 1994, San Andres Mountains, New Mexico.

CHAPTER 6. COUGARS AND DESERT BIGHORN SHEEP

by K. Logan, L. Sweanor and M. Hornocker

Abstract: We studied the relationships between cougars and desert bighorn sheep on the San Andres Mountains (SAM), New Mexico. Experimental removal of cougars from a 703 km^2 treatment area (TA) enabled us examine effects of cougar predation over a range of cougar densities. In the pre-treatment span (1986-1990), adult cougar density increased from 1.17 to 2.01 cougars/yr./100 km^2. In the post-treatment span (1991-1994), adult cougar density increased from 1.09 to 1.87 cougars/yr./100 km^2. Radio-collared desert bighorn sheep comprised 1.9% (n=10) of the animals we found killed by cougars and 0.80% average annual frequency of occurrence in cougar feces. Another 16 radio-collared sheep died of other causes, which included falls from cliffs (n=5), old age (n=3), scabies (n=2), disease (n=2), undetermined causes (n=2), breached birth (n=1), and capture accident (n=1). Scabies (*Psoroptes ovis*) infested 53% of the radio-collared sheep that died. Survival rates for lambs and yearlings were 0.771 and 0.778, respectively. The average annual survival rates for radio-collared adult sheep and for radio-collared yearling and adult sheep combined were 0.818 and 0.814, respectively. The estimated mortality rates for each age class was applied to data from annual sheep population surveys and yielded results that suggested that the sheep population was relatively stable during the study; we estimated that the population numbered about 40 sheep. Linear regression analyses indicated there were no significant functional relationships between either sheep mortality rates and adult cougar density or cougar predation rates on sheep and adult cougar density. We concluded that the density of adult cougars was inconsequential to sheep mortality rates and cougar predation rates. Management implications are given.

6.1 OBJECTIVE

Our objective was to quantify some of the relationships between cougars and desert bighorn sheep on the SAM. This was important because desert bighorn sheep are a state-listed endangered species; only about 280 individuals are free-ranging in New Mexico today (Pederson 1996). The SAM supports the largest naturally established population of desert bighorn sheep in the state, numbering about 40 individuals; but there is potential for the population to increase (Dunn 1994). By studying how cougars affect desert bighorn sheep, we aimed to provide information that may contribute to the recovery of the sheep population in New Mexico and particularly on the SAM.

6.2 FIELD METHODS

We studied relationships between cougars and desert bighorn sheep using a similar approach to our our study of cougars and mule deer. We quantified cougar prey selection on the SAM and the survival and causes of mortality of radio-collared sheep on the 703 km^2 TA. In addition, we examined relationships between sheep mortality rates and cougar predation rates on sheep in respect to adult cougar density. However, the small population of sheep, the small number of radio-collared sheep during the study, and varied methods used by management agencies to survey the sheep population presented limitations to methods we could use to quantify relationships between cougars and sheep.

6.2.1 COUGAR PREDATION

Cougar predation and diet on the SAM was documented following the methods described in Chapter 5: *Cougars And Desert Mule Deer.* Desert bighorn sheep found dead were examined and then placed into 1 of 3 categories: cougar prey, probable cougar prey, and animals that died of other causes. (See Chapter 5.2.1 for criteria). Cougar diet was quantified for about 800 cougar feces that we collected from 1985 to 1994.

6.2.2 SHEEP POPULATION CHARACTERISTICS

The desert bighorn sheep population was monitored annually by ground- and helicopter-based surveys conducted by personnel of the USFWS and the NMGF. Observed sheep were classified as adult rams and ewes, yearling rams and ewes, and lambs (distinguished by sex when possible). Ground-based surveys were done in 9 years by using binoculars and spotting scopes. During 1986 through 1989 and 1994, ground-based counts were year-long. The ground-based counts in 1990, 1991, and 1992 were done during December, August 31 to September 10, and from May through December, respectively. A helicopter survey was conducted in 1993 by two observers in a Hughes 500D. All surveys were conducted by observers that primarily homed on radio-collared sheep and counted and classified all sheep observed.

Survival and cause-specific mortality was monitored for 43 radio-collared sheep (16 rams, 27 ewes) from August 1985 through 1994. The sheep we monitored were captured by NMGF personnel using a netgun fired from a helicopter (Hughes 500D or Bell 206 Ranger) during 10 capture operations conducted from October 1980 to October 1993. All sheep were physically restrained and hobbled, then examined to record sex, age, and general physical condition. Radio-collars placed on sheep carried 148, 149, or 150 MHz transmitters with a mortality mode set to turn on after 2 or 6 hours of immobility (configuration MOD-500 with S6A mortality sensor by Telonics Inc.). Attempts were made by agency personnel to maintain a relatively high proportion of radio-collared sheep in the population (>50%) by capturing sheep annually from 1980 through 1985, and again in 1988, and 1989. However, from November 1989 to October 1993 the number of radio-collared sheep available for monitoring waned due to a temporary hands-off policy adopted by cooperating management agencies (USFWS, NMGF, WSMR; P. Hoban, SANWR manager, pers. comm.).

We monitored radio-collared sheep from the ground on a weekly basis to document mortalities. We also checked the fates of all of the radio-collared sheep during the same monthly flights that we checked all of the radio-collared mule deer (see Chapter 5.2.2). Sheep with functional transmitters that we missed during ground checks were found during flights.

6.3 ANALYTICAL AND STATISTICAL METHODS

6.3.1 COUGAR POPULATION

Details of our study of cougar population dynamics are described in Chapter 3: *Cougar Population Dynamics*. We quantified adult cougar density on the TA as the number of adults/yr./100 km^2. After studying the dynamics of the population during a pre-treatment span (1986-1990), we experimentally reduced the cougar population (the treatment) by 53% of the adults and 58% of the independent cougars (adults+subadults) during December 1990 to June 1991. Afterwards, we studied the dynamics of the cougar population during a post-treatment span (1991-1994).

6.3.2 SHEEP POPULATION CHARACTERISTICS

Sheep population counts and composition were tabulated each year. We used those data to determine minimum numbers of sheep and to obtain the following variables useful for estimating population trend.

The annual lamb survival rate (proportion of lambs that survived to 1 year old) was estimated by calculating the Finite Rate of Survival (lFRS):

$$\text{lFRS} = \frac{\text{No. yearlings observed 1987-1994}}{\text{No. lambs observed in previous years 1986-1993}}$$

We estimated the annual yearling survival rate (proportion of yearlings that survived to 2 years old) by calculating the Finite Rate of Survival (yFRS) for the small sample of 9 radio-collared yearling sheep monitored during the study:

$$\text{yFRS} = \frac{\text{No. radio-collared yearlings that survived}}{\text{No. of radio-collared yearlings monitored}}$$

Adult sheep annual survival rates were estimated with program MICROMORT (Heisey and Fuller 1985) for 34 radio-collared adults (13 rams, 21 ewes, $\geq$2 years old) which occupied the TA from 1986-1994. Sexes were combined to maximize the sample size. One ram that ranged on the TA and the reference area (RA) was included in the analysis only during the period he was present on the TA. Two other ewes that lived exclusively in the RA were excluded from MICROMORT analyses. Sheep were entered into the analysis 14 days after the date of capture to eliminate those sheep where capture related injuries may have caused mortality or capture-related activities may have contributed to vulnerability of predation. Annual survival rates were estimated beginning on 1 January of each year. We calculated maximum rates of survival because all sheep whose radio-collars became non-functional were visually observed alive even after their transmitters quit. Therefore, we included sheep with non-functional collars up to the last day we received live signals on them.

We multiplied annual mortality rates (1-survival rate) for each age class (lambs, yearlings, adults) by the number of sheep that were counted in each class during annual surveys. The total number of estimated annual mortalities (mortalities of all classes summed) was then subtracted from the number of annual births observed. The differences for all years were then summed to obtain a general trend in the sheep population during the study.

6.3.3 SHEEP-COUGAR RELATIONSHIPS

A total of 36 radio-collared sheep were used for analyses of sheep-cougar relationships during 1986-1994. The sheep included 28 adults (11 rams, 17 ewes) and 8 yearlings (4 rams, 4 ewes) that occupied the TA. Six of the yearlings survived to enter the adult age class (i.e., 34 adults: 13 rams, 21 ewes). Maximum survival rates and cause-specific mortality rates were calculated with program MICROMORT. Cause-specific mortality rates were tested for significant differences by using the Z-test (Pollock et al. 1989, expressed in Chapter 3.3.5). Because of the small number of radio-collared sheep in each gender, we did not test for significant differences in survival rates or cause-specific mortality rates for each gender.

Linear regression analyses (Ott 1988) were used to examine the relationship between: (1) radio-collared sheep mortality rates and adult cougar density (cougars/yr./100 km^2), and (2) cougar predation rates on radio-collared sheep and adult cougar density. We used the t statistic to test for a functional relationship between the dependent and independent variables.

Experimental errors for all statistical tests were controlled at the 0.10 level of significance.

6.4 RESULTS

6.4.1 COUGAR POPULATION

In the pre-treatment span (1986-1990), the density of adult cougars increased by 72% from a low of 1.17 cougars/yr./100 km^2 to 2.01 cougars/yr./100 km^2. In the post-treatment span, adult cougar density also increased by 72%, from 1.09 cougars/yr./100 km^2 in 1991 to 1.87 cougars/yr./100 km^2 in 1994.

One other cougar was removed from the TA besides those removed during the treatment. A 23-month-old known-age male cougar that immigrated from the RA was removed on 6 April 1989 because he killed 3 sheep (1 yearling ram, 2 ewes- 12 and 16 years old) between January and March 1989. HWI personnel removed the cougar to comply with the policy of the cooperating management agencies (USFWS, NMGF, WSMR) that required us to remove any cougar known to kill more than 1 sheep on the SAM.

6.4.2 SHEEP MORTALITIES

Cougar Prey

Out of the 525 animals that were killed or probably killed by cougars for food on the SAM during 1985 to 1995 (see Table 5.1) desert bighorn sheep comprised 1.9% (n = 10). Cougar fecal analysis showed that sheep averaged 0.8% frequency of occurrence annually. All of the cougar-killed sheep that were found, which included 4 rams and 6 ewes, were radio-collared. Ages ranged from 0.80 to 16 years old ($\bar{x}$ = 5.48 yr., SD = 4.99).

Five of the sheep that were cougar prey had clinical scabies. Infestations ranged in severity from lesions on the flanks to both ear canals completely plugged with scabs. Another 6-year old ewe apparently was in poor physical condition prior to being killed by a cougar; femur marrow was pink and gelatinous in consistency.

Other Sheep Deaths

Sixteen other radio-collared sheep, including 8 rams and 8 ewes, died from causes not related to cougar predation from 1985 to 1995. Probable causes of death included falls from cliffs (3 rams, 2 ewes), old age (2 rams, 1 ewe), scabies (2 rams), undetermined disease (2 ewes), undetermined causes (2 ewes), breached birth (1 ewe), and a capture accident (1 ram). Ages ranged from 1 to 14 years old ($\bar{x}$ = 6.44, SD = 3.67). One radio-collared ram that apparently died from scabies was scavenged by a radio-collared male cougar. An uncollared yearling ewe died from undetermined causes not related to predation. When it was found, a coyote was scavenging the carcass as it lay partially submerged in a spring-fed pool.

Ten of the 16 radio-collared sheep that died of other causes had clinical scabies. The least severe case consisted of lesions on one leg, but the most severe infestations may have caused death. One ram had hemorrhaging and suppurative lesions over 40% of its body, while another ram had lesions over 75% of its body.

6.4.3 SHEEP POPULATION CHARACTERISTICS

The total number of sheep observed during annual surveys on the SAM ranged from 22 to 37 and appeared to reflect the duration and method of the survey (Table 6.1). Both longer search time and the use of a helicopter resulted in a greater number of sheep observations. Consequently, totals in Table 6.1 probably represent the minimum number of sheep present each year. There were probably lone uncollared sheep or small bands of sheep not associated with radio-collared sheep that were not observed during surveys.

The ratio of adult rams to adult ewes ranged from 0.30:1 to 1:1 and averaged 0.67:1. The ratio of lambs to adult ewes ranged from 0.33:1 to 0.69:1 and averaged 0.51:1.

The estimated survival rate for lambs (lFRS) was 0.771 (37 yearlings observed 1987-1994 / 48 lambs observed 1986-1993). The estimated survival rate for yearlings (yFRS) was 0.778 (7 radio-collared yearlings survived / 9 radio-collared yearlings monitored).

Radio-collared sheep monitored each year comprised 36% to 83% of the number of adults and yearlings observed during annual surveys (Fig. 6.1). The annual survival rates for radio-collared adult sheep (rams and ewes combined) ranged from 0.639 to 1.0 and averaged 0.818. Survival rates of all radio-collared sheep (adults and yearlings combined) are presented in Table 6.2. For rams and ewes combined, annual survival rates ranged from 0.639 to 1.0 and averaged 0.814.

When we applied the estimated mortality rates to the numbers of lambs, yearlings, and adults observed each year and subtracted the estimated number of deaths from the number of observed births per year, we found that births were approximately equal to deaths (summation = 0.24) during 1986 to 1994 (Fig. 6.2). We interpreted this as evidence that the sheep population was relatively stable during the 9 year period. We estimated that the total sheep population actually numbered about 40 individuals.

6.4.4 SHEEP-COUGAR RELATIONSHIPS

Cougar predation rates on radio-collared sheep were significantly lower ($P = 0.04$) than rates of mortality from other causes (Table 6.3). A plot of radio-collared sheep mortality rates, cougar predation rates, and adult cougar density on the TA did not suggest any relationships (Fig. 6.3). Moreover, linear regression analyses indicated there were no significant relationships between: 1) radio-collared sheep annual mortality rates and adult cougar density ($r^2 = 0.075$, $P > 0.10$, Fig. 6.4), and 2) cougar predation rates on radio-collared sheep and adult cougar density ($r^2 = 0.023$, $P > 0.10$, Fig. 6.5).

6.5 DISCUSSION

Cougars occasionally killed desert bighorn sheep on the SAM during 1985 to 1994. Although cougar predation was the single most identifiable cause of death in sheep, sheep had a greater risk of dying from non-predator causes. We found that the density of adult cougars on the TA was inconsequential to sheep mortality rates and the rate of cougar predation on sheep. Furthermore, the fates of 3 radio-collared sheep that lived partially (1 ram) or exclusively (2 ewes) on the RA agreed with our findings on sheep on the TA. The 3 sheep survived to the end of the study on the RA where the adult cougar density increased at a rate of 0.14 per year (see Chapter 3.4.12).

Given the small population of sheep, we suspect that the rate of cougar predation on sheep was influenced primarily by chance encounters while cougars were hunting deer. After all, mule deer comprised the bulk of the cougar's diet (see Chapter 5.4). On the SAM, mule deer ranged from the desert basins to the same rugged, high elevation terrain preferred by sheep. We also documented cougars killing deer in sheep habitat. As long as wildlife distribution on the SAM has been recorded (Halloran 1944, Halloran 1946), sheep, mule deer, and cougars have used the mountainous habitats; apparently, the sheep have evolved with cougars.

We documented only 1 cougar that killed more than 1 sheep during the study. The removal of the cougar to comply with agencies' policy may have affected the results somewhat because the cougar may have killed more sheep if it had remained. In a remnant sheep population, an individual cougar with a predilection for sheep may have a great impact on overall sheep survival. Nevertheless, we believe that the removal of the cougar did not bias our examination of sheep mortality rates and cougar predation rates in relation to adult cougar density.

Our findings of an absence of a relationship between sheep mortality rates and cougar predation rates on sheep in respect to adult cougar density corroborates the finding by Evans (1983). He studied the relationship between survival rates of radio-collared sheep and the control of cougars on the SAM. "Test results indicated depredation control and the removal of 40 cougars from the San Andres Mountains was not related to the increase in bighorn survival... The index of association, r^2, between survival rates and cougar removals were near $r^2 = 0$..." (Evans 1983:13).

The SAM sheep population continues to harbor a very high prevalence of scabies (53% of radio-collared sheep that died), the disease believed to be responsible for the sheep die off that occurred during 1978 and 1979 (Lange et al. 1980). Prior to the decline, the sheep population had stabilized at approximately 200 individuals (Sandoval 1979). But the November 1979 population estimate was 80 sheep (Sandoval 1980). Even after cooperating agencies attempted to salvage the sheep, which included removal, treatment, and reintroduction of surviving original sheep, the population declined to 40 sheep in 1981 (Hoban 1990). This marked the third time since 1941 that the sheep population had declined to $\leq$53 individuals (Hoban 1990).

Scabies may influence the vulnerability of sheep to a host of mortality factors. Otoscopic examination of ears of infected sheep on the SAM in 1988 and 1989 by Clark (1990) revealed severe secondary infections which probably rendered the ears "incompatible with normal function" (p.34). He stated that many sheep may be deaf or nearly so, a suspicion upheld in experiments by Norrix et al. (1995) that showed hearing in desert bighorn sheep was compromised when the ear canal was altered. They concluded that, "Bighorn sheep with psoroptic scabies may become susceptible to [cougars] and other predators due to decreased hearing sensitivity or changes in the spectral patterns of environmental sounds" (p.226). Clark (1990) also suggested that scabies may have a negative influence due to protein exudation, hypothermia, increased energy loss, debilitation, inflammation, and immunosuppression. Furthermore, we suggest that if scabies does cause severe malfunction of the ears, which apparently are organs vital for equilibrium, then scabies may also contribute to deaths from accidental falls (19% of all deaths; 31% of deaths due to non-predator causes).

In addition, we observed that sheep with scabies were distracted and inattentive. Irritation of scabies infected areas apparently provoked the sheep to often scratch themselves by rubbing against rocks and bushes. Sheep also lick or bite infected areas (deVos 1989). Deafness and inattentiveness probably at least make affected sheep less capable of detecting potential predators or of noticing the warning signals or flight of other herd members that may detect predators. Infested sheep may also draw the attention of stalking predators like cougars that may be attracted to sheep that are the least attentive and exhibit abnormal behavior. Thus sheep with scabies probably are more vulnerable to predation than healthy sheep.

The SAM sheep population exhibited a relatively high reproductive and recruitment rate sufficient for population growth. Remington (1989) suggested that a sheep population required a fall lamb:ewe ratio of 26.5 lambs:100 ewes to maintain a stable or slightly increasing population. Using the number of lambs and ewes (adults plus yearlings) in the SAM sheep surveys (Table 6.1), we calculated a mean ratio of 39 lambs:100 ewes (range = 25-55:100) for the 1990, 1991, and 1993 fall counts. By applying the estimated 0.77 survival rate to lambs in the year-long surveys (1986-1989 and 1994), we calculated a mean lamb:ewe ratio of 36:100 (range = 18-53:100). Yearling to ewe ratios averaged 37:100 (range = 0-73:100) from 1986 to 1994. Lamb:ewe ratios were even higher when our calculations included only adult ewes; mean ratios were 46 lambs:100 ewes for 1990, 1991 and 1993, and 39 lambs:100 ewes for 1986-1989 and 1994.

Still the SAM sheep population was relatively stable and was probably limited by mortality primarily in the adult segment of the population. We hypothesize that the high incidence of disease, in this case scabies, in the sheep population enhances the vulnerability of sheep to all causes of mortality, and as long as the high prevalence remains, the sheep population will probably not increase without augmentation. Moreover, HWI personnel found scabies in some mule deer killed by cougars (4 specimens with mites and clinical symptoms). Consequently, mule deer can be a host that may transmit mites to sheep.

The relationships between sheep and cougars that we quantified may change if the current drought and depressed mule deer population persists (see Chapter 5). Cougars may have to hunt longer, cover greater portions of their home ranges, or even expand their home ranges to successfully kill ungulate prey. In the process, the probability of cougars encountering sheep may increase, thus resulting in greater predation on sheep.

Two other studies have quantified information on cougar-bighorn sheep relationships. Hornocker (1970) studied cougar population dynamics and relationships with ungulate prey in the central Idaho wilderness. There, a cougar population with a similar density to that found on the SAM (see Chapter 3), had an insignificant effect on a Rocky Mountain bighorn sheep (*O. c. canadensis*) population that numbered about 125 animals. Over a 4 year period, Hornocker recorded only 2 cougar kills of bighorn sheep and zero occurrences of sheep remains in 235 food items found in 198 cougar feces. Mule deer and elk, which comprised the primary food for cougars, increased in numbers during the study.

The second study involved cougars, coyotes, and California bighorn sheep (*O. c. californiana*) on the Junction Wildlife Management Area in central British Columbia. Harrison (1990) found that sheep and mule deer were the primary and secondary foods, respectively, for 2 cougar family groups that he studied intensively. Rams were selected as prey; but, ewes and lambs were not important prey for cougars. No lamb deaths were attributed to cougar predation. Harrison concluded that poor post-rut body condition and restricted rear and peripheral vision were factors that increased the rams' vulnerabiltiy to cougar predation. Furthermore, Harrison found that cougar kill rates were influenced by coyotes; "Coyotes increased cougar predation rates by scavenging cougar kills and, importantly, by displacing the cougars from kills" (p.85).

Other investigators have documented cougar predation on desert bighorn sheep, however, quantifiable data on sheep populations, cougar predation rates, and cougar populations are nonexistent except for our study. Out of 93 literature citations in the "Disease and Mortality" section of the Annotated Bibliography of Desert Bighorn Sheep Literature, 1897-1983 (Krausman et al. 1984), there were only 2 titles that specifically dealt with cougars and sheep. One described an account of a cougar killing a sheep (Cronemiller 1948) and the other (Blaisdell

1961) gave a few quoted anecdotal accounts of cougar predation on sheep and the observers' opinions on impacts of cougar predation on sheep. In his review of relationships between desert bighorn sheep and predators, including: wolves, coyotes, gray foxes, bobcats, cougars, and eagles, Kelly (1980) concluded (p.194), "There is little evidence that the total pressure from all of the predators (excepting man) has any impact on the total bighorn population. This may be due to the low population density of these predators in bighorn ranges". However, Kelly did not present any supporting data.

Studies in other parts of New Mexico have documented cougar predation on desert bighorn sheep. Evans (1983) reported that 10 of 32 sheep that were reintroduced to the Big Hatchet Mountains were killed by cougars. Elenowitz (1983) found that a cougar killed 1 out of 34 radio-collared sheep reintroduced into the Peloncillo Mountains. The death comprised 5% of the total mortalities (n = 22). Bronchopneumonia was the principal cause of mortality, comprising 79% of adult deaths and about 75% of lamb deaths. Knadle and Thompson (1993) found that a cougar killed 1 out of 23 radio-collared sheep reintroduced into the Ladron Mountains. There, cougar predation comprised 20% of documented deaths.

The most recent reports from California and Nevada, albeit preliminary, indicate that cougars may limit desert bighorn sheep in certain situations. Rubin et al. (1996) studied cause-specific mortality in 91 radio-collared sheep in the Peninsular Ranges of California and found that cougar predation caused 63% (27 of 43) of all mortalities. They concluded that "It appears that [cougar] predation has been a significant limiting factor during the past 3 years, and sustained high levels of predation by [cougars] may adversely affect the long-term viability of this threatened metapopulation of bighorn sheep." Wehausen (1996) reported that cougars in the eastern Mojave Desert caused a 37.5% annual mortality rate in radio-collared ewes which drove the population down.

Unfortunately, none of the above reports enhanced our understanding of the dynamics of those situations by providing data on the the cougar populations, the cougar prey base, or habitat conditions as they related to desert bighorn sheep and cougars. Long-term research that addresses sheep and cougar population dynamics and habitat conditions in a range of ecological carrying capacities would be enlightening.

6.6 MANAGEMENT IMPLICATIONS

1. **Finding:** In the environmental conditions in which we studied cougar-desert bighorn sheep relationships, the density of adult cougars was inconsequential to desert bighorn sheep mortality rates and the rate of cougar predation on sheep.

   Implication: Given these conditions, controlling cougars in an attempt to increase sheep survival rates and to increase the sheep population would probably be ineffective.

2. **Finding:** After removing a single cougar that was known to have killed 3 sheep within a 3-month span in 1989, cougar predation on sheep declined considerably.

   Implication: By removing an individual cougar with a demonstrated predilection for killing sheep, the survival of sheep may be improved.

3. **Finding:** Sheep on the SAM had a high prevalence of psoroptic scabies (53% of sheep that died during this study) which probably made them vulnerable to a variety of mortality factors, including predation. Scabies was also documented in the desert mule deer.

   Implication: The sheep population probably will not increase (without augmentation) as long as this level of disease prevalence persists. Studies of the interrelationships between desert bighorn sheep and scabies and other hosts, as well as, development of practical treatments for free-ranging sheep are needed.

4. **Finding:** Desert mule deer comprised the prinicipal food for cougars on the SAM (see Chapter 5.4.2).

   Implication: Management objectives that include sport-hunting deer in areas where endangered desert bighorn sheep live should consider potential indirect negative effects on sheep. Sport-hunting mortality in mule deer, whether additive or compensatory, may contribute to greater cougar predation pressure on sheep (see Chapter 5.6).

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Table 6.1. Observed desert bighorn sheep on the San Andres Mountains, New Mexico, 1986-1994.

	Adults		Yearlings			Lambs			
Year	Rams	Ewes	Rams	Ewes	Un.[a]	Rams	Ewes	Un.	Total
1986[b]	9	15	3	2		4	3		36
1987[b]	9	13	3	3		3	5	1	37
1988[b]	10	11	3	5		3	2		34
1989[b]	10	15	3	2			3	1	34
1990[c]	7	9		3		2	1		22
1991[d]	3	10	2	1				6	22
1992[e]	6	13			3	5	2	2	31
1993[f]	7	11	5	2				5	30
1994[b]	12	12			2			8	34

[a] Un. = Undetermined gender.

[b] Numbers for 1986 - 1989 and 1994 were from ground-based observational and radio-telemetry data that was gathered year-long (SANWR unpubl. data).

[c] The 1990 numbers were from ground-based observational and radio-telemetry data gathered during December and known mortalities that occurred during the rest of the year (SANWR unpubl. data).

[d] The 1991 numbers were from ground-based observational and radio-telemetry data gathered during Aug. 31 - Sep. 10 (NMGF unpubl. data).

[e] The 1992 numbers were from ground-based observational and radio-telemetry data gathered during May - Dec. (SANWR unpubl. data).

[f] The 1993 numbers were from a helicopter survey conducted on Nov. 20 and 21 (NMGF unpubl. data).

Table 6.2. Survival rates of radio-collared desert bighorn sheep on the TA, San Andres Mounains, New Mexico, 1986 - 1994.[a]

	Rams			Ewes			R&E Combined	
Year	n	Rate	s^2	n	Rate	s^2	Rate	s^2
1986	9	0.792	0.017	15	0.743	0.012	0.762	0.007
1987	7	0.645	0.040	11	0.795	0.017	0.740	0.012
1988	7	0.584	0.049	9	0.827	0.025	0.716	0.019
1989	6	0.745	0.048	9	0.730	0.027	0.735	0.017
1990	5	0.805	0.030	6	1.000	0.000	0.910	0.007
1991	4	1.000	0.000	6	1.000	0.000	1.000	0.000
1992	2	0.445	0.130	6	0.694	0.032	0.639	0.027
1993	3	1.000	0.000	7	1.000	0.000	1.000	0.000
1994	3	0.700	0.062	7	1.000	0.000	0.903	0.009
Mean =		0.726			0.857		0.814	
Span rate =		0.056	0.004		0.248	0.012	0.156	0.005

[a] Survival rates were computed using MICROMORT and data from 36 radio-collared adults and yearlings, including 15 rams (11,954 days) and 21 ewes (22,935 days), 1986-1994.

Table 6.3. Rates of mortality in radio-collared desert bighorn sheep (rams and ewes combined) from cougar predation and other causes of mortality, San Andres Mountains, New Mexico, 1986 - 1994.[a]

	Cougar Predation		Other Causes	
Year	Rate	s^2	Rate	s^2
1986	0.119	0.004	0.119	0.004
1987	0.065	0.004	0.195	0.010
1988	0.000	0.000	0.284	0.019
1989	0.265	0.017	0.000	0.000
1990	0.090	0.007	0.000	0.000
1991	0.000	0.000	0.000	0.000
1992	0.000	0.000	0.361	0.027
1993	0.000	0.000	0.000	0.000
1994	0.000	0.000	0.097	0.008
Span rate =	0.302[b]	0.008	0.542[b]	0.010

[a] Cause-specific mortality rates were computed using MICROMORT with data from 36 radio-collared sheep, including 15 rams (11,954 days) and 21 ewes (22,935 days).

[b] Span rates of cougar predation and of other causes of mortality were significantly different ($P = 0.04$).

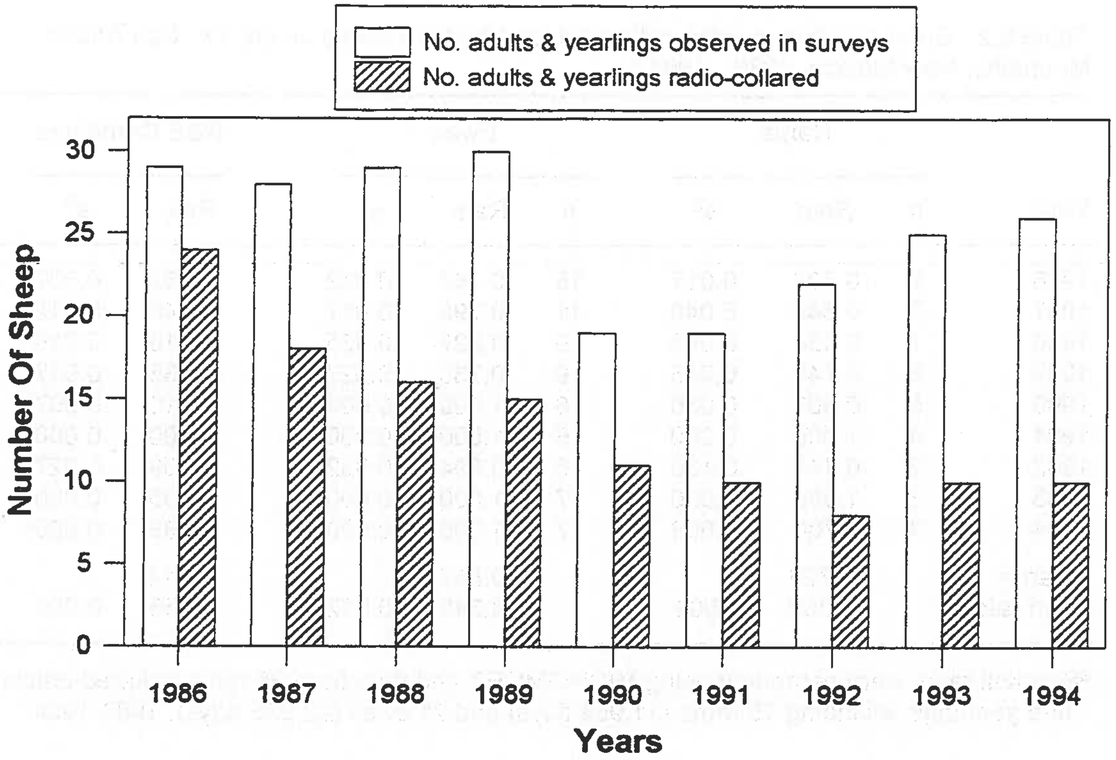

Fig. 6.1. Number of adult and yearling desert bighorn sheep observed in annual surveys and radio-collared during each year, 1986-1994, San Andres Mountains, New Mexico.

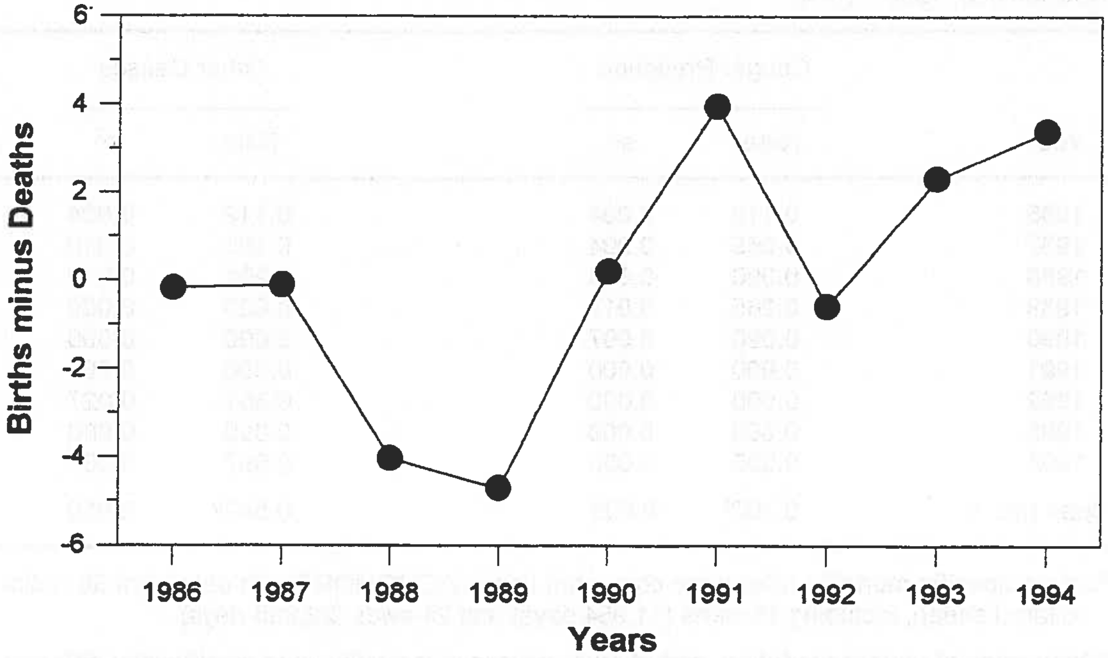

Fig. 6.2. The difference of births minus deaths in desert bighorn sheep each year, 1986-1994, San Andres Mountains, New Mexico. Nine-year summation = 0.24.

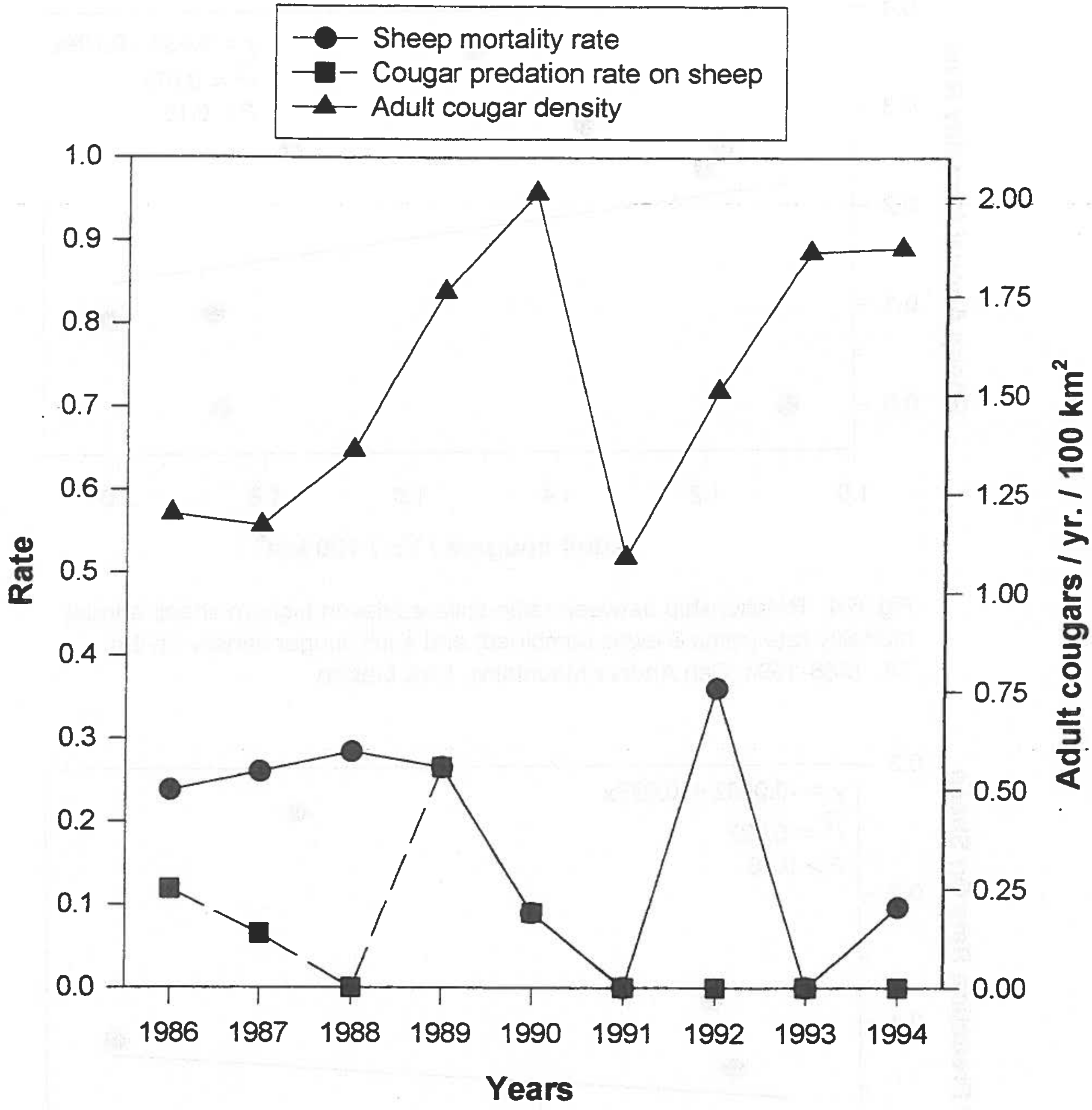

Fig. 6.3. Rates of mortality and cougar predation on radio-collared desert bighorn sheep and adult cougar density on the TA, 1986-1994, San Andres Mountains, New Mexico.

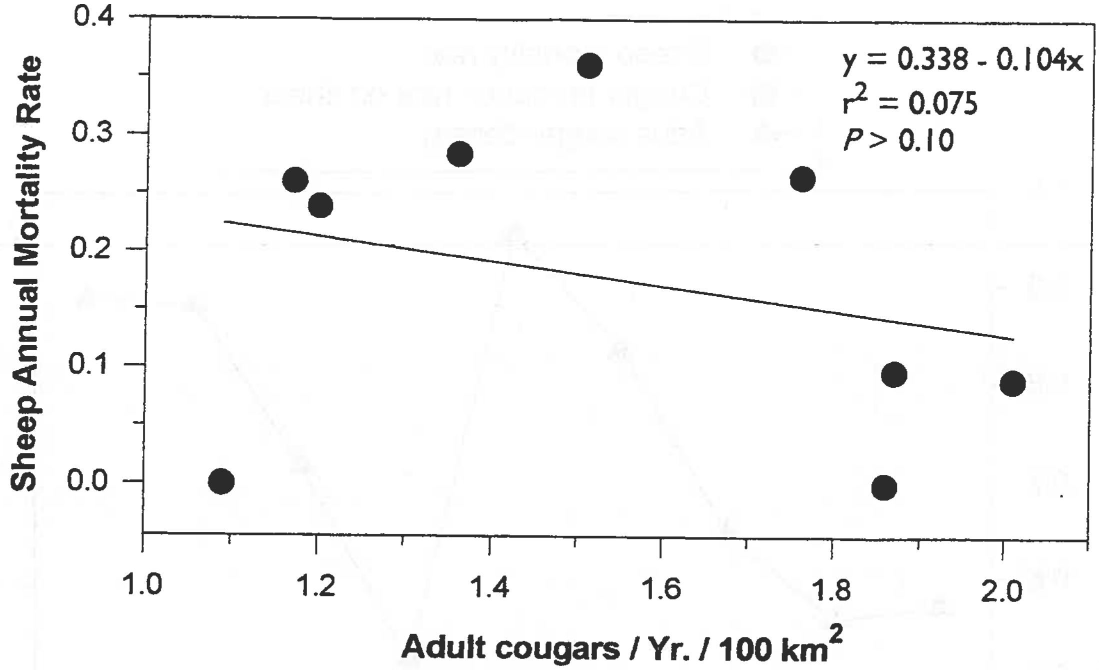

Fig. 6.4. Relationship between radio-collared desert bighorn sheep annual mortality rate (rams & ewes combined) and adult cougar density on the TA, 1986-1994, San Andres Mountains, New Mexico.

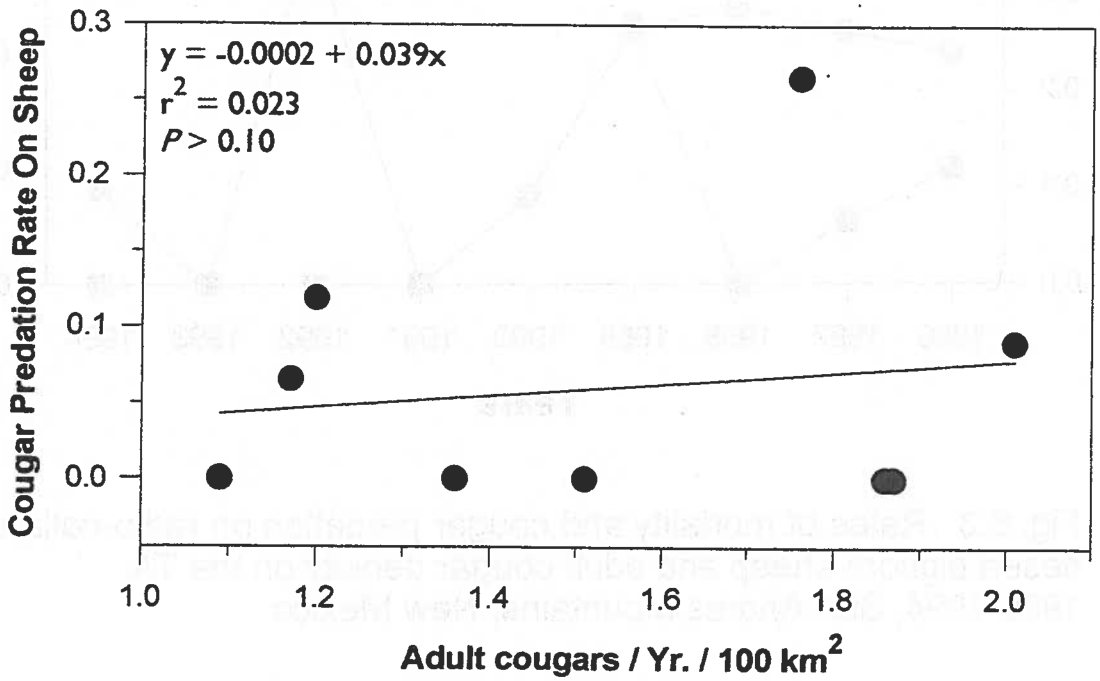

Fig. 6.5. Relationship between cougar predation rates on radio-collared desert bighorn sheep (rams & ewes combined)and adult cougar density on the TA, 1986-1994, San Andres Mountains, New Mexico.

CHAPTER 7. EVALUATING COUGAR TRANSLOCATION IN NEW MEXICO

by T. Ruth, K. Logan, L. Sweanor and M. Hornocker

Abstract: We translocated wild cougars with known social and behavioral histories to evaluate the feasibility of translocation as a management tool to re-establish cougar populations in historic ranges, relieve the threat of inbreeding in isolated populations, and to manage nuisance cougars. Thirteen cougars were translocated an average of 477 km from the San Andres Mountains (SAM) study area in south-central New Mexico to 9 release sites in northeastern New Mexico.

The cougars were translocated over a 7 month period (9 Dec. 1990 through 22 June 1991) and radio-monitored through 7 January 1993. A fourteenth cougar was translocated 338 km from the SAM to northwestern New Mexico on 8 April 1989 and monitored to 29 May 1990. Initial movement directions away from release sites (n = 13) ranged from 22°-313° and were uniformly distributed about a 360° circle ($P > 0.50$). Eight (4F:4M) of 14 cougars had endpoints >80 km from their release sites and endpoint directions that were almost exclusively south, southwest, or southeast ($\bar{x} = 181°$, range = 116°-237°), suggesting the cougars homed toward the source population. Two males returned to their original home ranges in the SAM. Distances moved from release sites to endpoints ranged from 3-285 km for 8 females and 11-494 km for 6 males. Nine of 14 translocated cougars died during the study. Annual survival rates for translocated cougars averaged 0.55 for females and 0.44 for males and were lower for both sexes during the second year of the study. Movement directions and distances, as well as survival rates, were compared between the translocated cougars and a reference population in the SAM. Translocation was most successful with cougars that were in age class II (12-27 months of age). For management or conservation programs, we suggest that age class II cougars are the best candidates for translocation.

7.1 OBJECTIVES

We conducted a 2-year study of wild-caught translocated cougars to evaluate translocation as a management tool to: 1) re-establish cougar populations in historic ranges, 2) relieve the threat of inbreeding in isolated populations, and 3) manage nuisance cougars. Because of changing cultural attitudes and increasing habitat fragmentation, translocation of cougars may become an increasingly important management and conservation technique (Hornocker 1991).

Few data currently exist on which to base management or conservation decisions involving translocations of cougars. In general, studies have described movements of 1 to 2 translocated cougars (Ruth 1991, Anderson et al. 1992, Williams 1992). Belden and Hagedorn (1993) evaluated the feasibility of translocating 7 cougars from Texas into northern Florida. Early removal of study animals resulted after cougars moved into urban areas and livestock operations and the authors recommended a need for additional research on cougar translocations.

Based on current knowledge, we felt that information on translocating wild cougars could assist the present effort to augment the genetics of endangered Florida panthers (*Puma concolor coryi*) which number about 30 to 50 individuals (Maehr 1990, Belden and Hagedorn 1993), and it could be used by agencies in the 6 western states and 2 Canadian provinces which currently translocate cougars to protect humans and livestock (Tully 1991). Furthermore, studies of translocated cougars may provide information needed to weigh risks involved in translocations of other rare felids that are biologically similar, such as the Amur leopard (*Panthera pardus*) and the snow leopard (*P. uncia*), where it may be necessary to augment small populations or to re-establish populations on historic range (H. Quigley, pers. comm., Wemmer and Sunquist 1988).

Our objectives were to document orientation, movement, establishment, and survival of translocated cougars and to make comparisons with similar parameters for cougars in a reference population. The cougars we studied had been subjects of intensive research carried out on the ecology of cougars in southern New Mexico during 1985-1995 (Logan et al. 1990, Sweanor 1990). Therefore, a detailed data base existed on the social status of the cougars we translocated, as well as on cougars in the reference population. To date, this is the only study which compares the biology of individual cougars before and after translocation and compares parameters with a reference population of cougars.

7.2 STUDY AREAS

7.2.1 SOURCE AREA

Translocated cougars were obtained from the San Andres Mountains study area (SAM, 2,059 km^2), which lies within the WSMR in south-central New Mexico (Fig. 7.1). Cougars were captured and translocated from a 703 km^2 treatment area within the southern portion of the SAM. Cougars were not removed from within a northern reference area (1,356 km^2).

Terrain on the SAM was rugged and characterized by steep-walled canyonlands. Elevations ranged from 1,300 to 2,733 m. A semi-arid climate and vegetation typical of the Chihuahuan Desert predominated (Larson 1970, Logan et al. 1990, Sweanor 1990). Hot summers and mild winters were typical (Sweanor 1990). Annual precipitation averaged 41.9 cm at the Ash Canyon rain gauge (elevation = 1,731 m) during 1982-1991 (U.S.D.I. Fish and Wildlife Serv., unpubl. data). Forty to 50% of the precipitation fell during the months of July through September (Sweanor 1990). Desert mule deer (*Odoecoileus hemionus crooki*) were the primary prey of cougars on the SAM (Logan et al. 1990).

Since the establishment of WSMR in 1945, the SAM became a relatively undisturbed ecosystem where human access was highly restricted and domestic livestock use was prohibited. Five small cattle ranches abutted the SAM, but no cattle were reported killed by cougars during this study. From 1940 to 1985, cougars were killed for sport hunting and predator control. However, in March 1985, the SAM was closed to all cougar hunting to accommodate our research. Mule deer hunting did not occur from 1983 to August 1990. Thereafter, limited entry, buck-only deer hunts were held every other fall season, during which an average of 65 bucks were killed. The year-long human density on the SAM was approximately 0.63 people/100 km^2.

7.2.2 RELEASE AREA

The release area for 13 cougars was in Colfax County in northeastern New Mexico (NENM) and was situated in the easterly foothill extension of the Sangre de Christo Mountains (Fig. 7.1). The area was approximately 2,280 km^2 in size, was comprised of state and private owned lands, and consisted primarily of temperate mountain forest vegetation. Elevations ranged from 1,990 to 3,792 m. The terrain was rugged and convoluted by numerous canyons and drainages. Mild summers and winters were typical. Average annual precipitation ranged from about 36 cm at elevations <1,829 m to 51-76 cm at elevations $\geq$2,743 m. Annual snowfall averaged 152-229 cm at elevations >2,286 m and 51-64 at lower elevations (Anderson et al. 1982). Ungulate species native to the NENM area were mule deer (*O. hemionus*), Rocky Mountain elk (*Cervus elaphus*), and pronghorn (*Antilocapra americana*).

Domestic cattle, horses, and mules were common throughout the area. Other wild prey available to cougars included wild Merriam's turkey (*Meleagris gallopavo*), raccoon *(Procyon lotor*), and porcupine *(Erethizon dorsatum)*. Generally, prey availability was highest on the release area and lowest on the source area. Black bears (*Ursus americanus*) were possible competitors for prey and scavengers of cougar kills. Black bears were not present in the source area.

The release area was adjacent to several small towns (Raton, Cimarron, Ute Park). Human access to public lands was unlimited and open to hunters that were drawn for the state game hunts. Human access to private lands was limited to owners, employees, and guests. The density of resident humans in the release area during the study was approximately 1.05 people/100 km^2.

The NENM area was chosen based on characteristics that were considered to enhance the translocation effort, including: 1) the greatest distance from the source population while still within the state of New Mexico; 2) differences in habitat components such as moderated climate, greater primary production and attendant greater types and availability of prey; 3) a hunted cougar population where territory and home range vacancies were present so that translocated cougars might assimilate into the existing population; and 4) cooperation from the state wildlife agency, the local public, private land owners, and local guides and outfitters.

A fourteenth cougar (M23) was translocated to Sandoval County in northwestern New Mexico and released on Mesa Chivato on the Cibola National Forest. The physical environment there was very similar to the NENM release area.

7.3 METHODS

Cougars were translocated from a 703 km^2 treatment area on the SAM. One cougar was translocated on 8 April 1989 and 13 cougars were translocated during 7 December 1990 to 21 June 1991. All translocated cougars were independent of their mothers and ranged in age from 16 months to 108 months. Ages were based on characteristics of known-aged cougars from the SAM population and aging techniques developed by Ashman et al. (1983).

Cougars were captured with modified spring-activated leg-hold snares and chemically immobilized (Logan et al. 1990). Each cougar was fitted with a new color-coded radio-collar with a 6-hour inactivity sensor to indicate mortality (Telonics, Inc., Mesa, AZ 85204). Twelve cougars received a bleached and/or freeze branded symbol on a shoulder or hip to enhance field identification. Cougars were loaded into individual wooden crates and transported to release sites by vehicle. Each cougar was provided water and offered 0.45-2.7 kg of beef heart, liver, kidney and/or chicken livers.

Releases were considered "hard" because the cougars were liberated from confinement in a fully ambulatory state within 48 hours of capture. No supplemental food source, such as a deer carcass, was provided at the release site (RS). Translocated individuals were set free at 9 separate RSs at different times. None of the cougars were translocated a second time.

Translocated cougars, except M23, were monitored from 9 December 1990, when the first cougar was released, until 7 January 1993. During 1991, we attempted to locate each translocated cougar twice per week from small fixed-wing aircraft (Cessna 175 and 182) using a directional antenna mounted to each wing strut (Sweanor 1990). Later, cougars were monitored once per week from aircraft. More detailed movement data was obtained via ground radio-telemetry on focal individuals. Frequency of ground locations was dependent upon access to private lands due to the wide ranging movements of the cougars away from RSs. Aerial and ground locations were plotted on 7.5 minute (1:24,000 scale) U.S.G.S. topographic maps. Each location was recorded as Universal Transverse Mercator grid coordinates (0.01 km).

We continued to capture, mark, release, and monitor cougars within the entire SAM study area during the course of the translocation experiment. No cougars from the 1,356 km^2 reference area on the SAM were translocated. These animals served as the reference population. We utilized survival data from the reference population for the same 2-year period (1991-1992) as baseline information to make comparisons with survival rates of the translocated cougars. We also compared dispersal behavior of cougars born on the SAM with the movement behavior of translocated cougars.

An initial movement (IM) was determined by a movement >7 km away from the RS that was followed by continued directional movement (Fritts et al. 1984). Endpoints (EP) for cougars were defined as the last location due to death, return to the original home range, or the last location at the end of the study (Fritts et al. 1984). Prior to translocation most of the cougars had established residency on home ranges (HR). A resident cougar used a predictable area for ≥6 months (Lindzey et al. 1988), and its HR was the area where it obtained food, mates, and raised young (Burt 1943:351). Some post-translocation cougars also showed predictable use of an area for ≥6 months; however, some of these areas were quite large and in some cases it was unknown whether the cougar would continue to remain in the area to breed and produce young. We designated these large, predictable use areas as utilization areas (UAs). In this paper, individual cougars are identified by a number preceded by an F for females and an M for males.

We defined 4 age classes of cougars for comparisons of translocated and reference area cougars. No cougars from age class I (animals < 12 months old and typically dependent on maternal care for survival) were translocated. Age class II cougars included animals 12-27 months of age. This covered the period when cougars were subadults (independent but not breeding), dispersers, or recently established adults. Empirical data from the SAM study area indicated females and males entered the adult age class at, on average, 21 months (range = 19 -27 months) and 24 months (range = 21-27 months) of age, respectively (K. Logan, unpub. data). Additionally, published information on cougars indicates natal dispersal is initiated at 12-24 months of age (Anderson 1983, Beier and Barrett 1993). Age class III cougars included prime adults (28-96 months old) which typically had resident status. Age class IV, cougars >96 months old, was also delimited in order to examine whether there were movement and survival differences in older-aged animals.

All kilometer distances and azimuth directions were calculated from UTM grid coordinates from locations (White and Garrott 1990). Circular distribution descriptive statistics (Zar 1984, White and Garrott 1990) were used to calculate mean angles of direction from release sites to initial movement points, capture sites, endpoints, and arithmetic centers of HRs or UAs. Dispersal directions and distances traveled by cougars that were born on the SAM were calculated from the arithmetic center of their natal HRs (12 month period) to the arithmetic center of the UA or HR where they established for ≥6 months post-dispersal. Hypotheses concerning direction of movement were tested using circular distribution hypotheses tests (Zar 1984).

Telemetry data were analyzed using program HOMERANGE (Ackerman et al. 1989) to calculate 100% and 90% minimum convex polygons (MCP, Hayne 1949). Because MCP size is greatly influenced by outliers (Ackerman et al. 1989), we used the 90% MCP to make comparisons between HRs and UAs pre- and post-translocation.

Annual survival rates for translocated cougars were calculated (MICROMORT, Heisey and Fuller 1985) and compared to annual survival rates of independent cougars in the SAM reference area during the same 2 year period. We did not compare survival between subadults and adults because of the low sample size in radio-days for subadults in both the translocated and reference populations. Daily survival rates for monthly intervals were not significantly different for translocated or reference area cougars (Heisey and Fuller 1985, Fuller 1990); therefore, we pooled months into 1991 and 1992 intervals and calculated survival on an annual basis. There were 387 days in the 1991 interval (including 22 days from December 1990 when 2 cougars were released) and 373 days in the 1992 interval (including 7 days in January 1993 when the study ended). We assumed significance at $P < 0.05$.

7.4 RESULTS

Fourteen cougars of independent status were radio-monitored for 1-1734 days ($\bar{x}$ = 608 days) prior to translocation from the SAM (Table 7.1). Thirteen of these cougars (8F:5M) were translocated an average of 477 km (range = 450-510 km) over a 7 month period (9 Dec 1990 through 22 Jun 1991) to NENM. The fourteenth cougar (M23) was translocated 338 km from the SAM to the Cibola National Forest, NM on 6 April 1989 after he killed 3 desert bighorn sheep (a state endangered species) during the period of January-March 1989 (Logan et al. 1990). The 8 female and 6 male cougars were monitored for 11-713 days ($\bar{x}$ = 451 days) and 109-702 days ($\bar{x}$ = 437 days), respectively, after translocation. We lost radio contact with 6 translocated cougars for periods of 1-3.5 months during our tracking efforts.

Four (3F:1M) translocated cougars were in age class II, 8 (4F:4M) were in age class III, and 2 (1F:1M) were in age class IV at the time they were translocated. The mean weight for females and males was 32.5 kg and 59.8 kg, respectively. All cougars were captured, transported, and released without injury.

7.4.1 DIRECTIONAL ORIENTATION AND DISTANCE TRAVELED

Translocated cougars were located within a 7.0 km radius of their RSs for 2-24 days ($\bar{x}$ = 8 days for females; $\bar{x}$ = 4 days for males) after release. Initial movements occurred at 4-30 days ($\bar{x}$ = 11 days) after release (Table 7.1). Initial movement directions ranged from 22°-313° (Table 7.2, Fig. 7.2a) and were uniformly distributed about a 360° circle (Watson One-Sample U^2 Goodness of Fit Test [Zar

1984:441], $P > 0.50$).

Endpoint directions for 14 translocated cougars ranged from 24°-225° (Table 7.2). However, cougars (4F:4M) who had an EP >80 km from their RS (Fig. 7.2b) had EP directions that were almost exclusively south, southwest, or southeast of their RS and ranged from 116°-237° ($\bar{x} = 181°$). The EP directions for these eight cougars (F44, F58, F106, F119, M18, M49, M88, M114) were not uniformly distributed about a 360° circle (Watson One-Sample U^2 Goodness of Fit Test [Zar 1984:441], $0.002 < P < 0.005$). The mean direction home for the cougars who had an EP >80 km from their RS was 198° (n = 8). The 95% confidence interval for the direction to home for these individuals was 181° ± 32° (One-Sample Test for the Mean Angle [Zar 1984:445]) and did contain the specified direction home value of 198° suggesting that the cougars exhibited directional orientation to the source population (Zar 1984, White and Garrott 1990).

Six cougars (43%) did not show homing tendencies and included the 2 class IV cougars and 1 class II cougar (F97) who died within 3.6 months of translocation. These animals may have attempted to home if they had lived longer. Additionally, 2 class II cougars (F95, M23) and 1 class III cougar (F31) did not home; they established HRs close to their release sites (within 39 km).

Males moved, on average, 1.9 times as far as females from RSs to EPs. The mean straight-line distance traveled from RSs to EPs was 117.9 km for females (n = 7, range = 3-285 km, F97 not included due to her death 11 days after release), and 218.2 km (n = 6, range = 11-494 km) for males. Class III cougars moved farther on average than either class II or class IV cougars. Endpoint distances averaged 40.0 km (n = 3, F97 not included) for cougars in age class II, 247.6 km (n = 8) for cougars in age class III, and 16.5 km (n = 2) for cougars in age class IV.

Two of the 14 cougars (both age class III) returned to the source area (Fig. 7.3a). Cougars M88 and M49 returned to their original HRs in 166 and 469 days, respectively, after release. They were not translocated again.

As a comparison, we documented the dispersal distances and directions traveled for 15 cougars (7F:8M; all age class II) that were born on the SAM, dispersed from their natal HRs and subsequently established independent HRs elsewhere, either within or outside the SAM (Sweanor et al., in prep.). Another 12 females established independent HRs within their natal HRs and were not included in the analysis. Both females (Watson One Sample U^2 Goodness of Fit Test, $P = 0.48$) and males (Watson One Sample U^2 Goodness of Fit Test, $P > 0.5$) established HRs in directions that were uniformly distributed around a 360° circle (i.e. there was no significant dispersal direction). Distances moved by dispersers averaged 28.3 km for females (range = 5.6-78.5 km) and 101.3 km for males (range = 48.7-192.5 km).

Translocated females moved significantly farther than females that naturally dispersed from their SAM natal areas ($t = 2.00$, 12 df, $P = 0.036$). Translocated male cougars moved on average 2.2 times as far as males that naturally dispersed from their SAM natal areas; however, the difference was not significant ($t = 1.62$, 12 df, $P = 0.07$).

7.4.2 UTILIZATION AREAS AND ESTABLISHMENT

Overall, translocated cougars used an area of approximately 76,837 km^2 (100% MCP) or one-quarter (24.5%) of the size of New Mexico (314,260 km^2) during their movements after release. However, 9 of the 14 (64.3%) translocated cougars eventually restricted their movements to predictable UAs for >6 months (Table 7.3, Figs. 7.3b, 7.4 and 7.5). Cougars initially arrived at UAs between 31 and 392 days ($\bar{x}$ = 156 days) post-release.

Three class II cougars (F95, F119, M23) and 1 class III cougar (F31) established UAs within 5-84 km ($\bar{x}$ = 34.3 km) of release sites. Three of the 4 cougars were progeny of the SAM population and were a subadult (F95) and recently established adults (F31, M23) at the time they were translocated. The fourth cougar, F119, was a new immigrant to the SAM and may have been attempting to establish residency at the time she was captured and translocated. Cougars F95, F119, and F31 settled into UAs soon after release ($\bar{x}$ = 53 days, range = 31 to 80 days; Fig. 7.4a,b).

Pre-translocation HRs and post-translocation UAs (90% MCP) of cougars ($n = 5$, all age class III) for which paired comparisons could be made (F31, F44, F58, F106, M18; Table 7.3) were significantly different ($t = -2.33$, 4 df, $0.025 < P < 0.05$). Mean post-translocation UAs were larger for females ($\bar{x} = 439.8$ km^2, $n = 4$) and males ($\bar{x} = 989.9$ km^2, $n = 1$) than mean HRs for females ($\bar{x} = 38.0$ km^2, $n = 4$) and males ($\bar{x} = 73.6$ km^2, $n = 1$) prior to translocation. However, 3 females (F31, F95, F106) had post-translocation UAs which were comparable (only 1.0-1.8 times as large, 90% MCP) to their HRs prior to translocation. The mean HR size (90% MCP) for cougars for a 12-month period prior to translocation was 50.3 km^2 ($n = 4$) for females (F31, F37, F44, F58) and 142.7 km^2 (n = 4) for males (M7, M18, M49, M88).

Movements and establishment in UAs may have been influenced by several factors. Cougar M18's movements (Fig. 7.4b) and apparent settlement into a UA may have been associated with injuries he received from a strike with a vehicle prior to his death. His movements prior to settlement indicated he crossed Interstate 25 and U.S. highways 104 and 129 six separate times. Investigation of M18's death site and the subsequent necropsy revealed a break to his right femur. His right leg, foot and toes were atrophied from disuse. The degree of ossification of the bone at the fracture indicated that the break had occurred approximately 3-4 months before M18 died (Dr. T. Smith, DVM, pers. comm.) and probably influenced his movements prior to his death. However, M18 had been utilizing a fairly predictable area for approximately 5-6 months before sustaining the injuries.

Three of the translocated cougars (F58, F106, M49) localized in an area or areas for 3-6 months before making another substantial movement and establishing a UA (F58, F106; Fig. 7.3b and 7.4a) or returning to the source area (M49; Fig. 7.3a). In these cases, major highways (Interstates 25 and 40; U.S. highways 56, 60, 64, 84, 380) and urban areas appeared to pose temporary barriers to continued movements of the cougars. Translocated cougars came close to urban and suburban areas during their movements, possibly because natural travel corridors often funneled into towns or cities. Cougar M49 was located in the center of Taos, NM for 1 day (Fig. 3a) and within 100 m of houses after traveling NE to SW down the Rio Pueblo drainage. He bedded in dense willow (*Salix* spp.) and Russian olive (*Elaeagnus angustifolia*) within the riparian area during the day. On the following day, M49 had returned NE up the Rio Pueblo and into the Taos Mountains where he was located 8 km from Taos. Although M49 and other translocated cougars came close to urban areas, no sightings of translocated cougars were reported during the study.

Two translocated females (F31, F95) produced offspring. These females were 2 of 3 cougars that had similar HR sizes pre- and post-translocation. Cougar F31 established a HR within 19 km of her RS and approximately 80 days after release (Fig. 7.5). She bred with a local uncollared male cougar in early to mid-May 1991 and subsequently had a litter of 5 kittens (1F:3M; 1 unknown). On 20 April 1992, F31 died from bacterial septicemia, orphaning a single surviving female kitten of 8 months of age. Cougar F95 established a HR near her RS and 46 days after release (Fig. 7.5). She had a litter of 3 kittens (2F:1M) around 9 May 1992. The kittens and F95 were alive at the end of the study.

7.4.3 MORTALITY CAUSES AND SURVIVAL RATES

Nine of 14 translocated cougars died during the study. The survival status of a tenth cougar (M23) was unknown due to the loss of his radio signal; therefore he was not included in the mortality category or survival analysis. The 5 females and 4 males died after surviving an average of 262.8 days and 375.5 days, respectively. Three translocated cougars died during 1991 after surviving an average of 52.3 days (range = 11-109 days) post-release. The other 6 cougars died over a 139 day period (Feb. to Jul.) in 1992 after surviving an average of 443.2 days post-release.

Cause-specific mortalities (Table 7.4) of translocated female and male cougars for the 1991 interval were attributed to intraspecific aggression (n = 2, age class IV) and death associated with prey capture (n = 1). During the 1992 interval, cause-specific mortalities were attributed to prey capture (n = 1), human causes (n =1), bacterial infection (n = 1), and unknown causes (n = 3). We suspected cause of death to be disease and/or stress related for at least 2 of the 3 cougars (M114, M49) that died of unknown causes. All mortalities during 1991 (n = 2) and 1992 (n = 3) in the SAM reference population were due to intraspecific aggression.

Annual survival rates averaged 0.55 for translocated females and 0.44 for translocated males. Survival rates for translocated females were higher during 1991 than 1992 (Table 4), but the difference was not significant (Z = 0.72, *P* =0.24). Survival rates for translocated males were significantly higher in 1991 than 1992 (Z = 1.69, *P* = 0.05).

During the same 2 year period, 16 independent female and 12 independent male cougars were monitored in the SAM reference area for 68-760 days ($\bar{x}$ = 494 days) and 82-760 days ($\bar{x}$ = 440 days), respectively. Annual survival rates averaged 0.86 for both females and males. There was no significant difference in survival rates between 1991 and 1992 for both reference area females (Z = 0.72, *P* = 0.22) and males (Z = 0.20, *P* = 0.42).

During 1991, the survival rates (Table 7.4) for translocated females and males were not significantly different than the survival rates for reference area females (Z = 0.66, *P* = 0.25) and males (Z = 0.36, *P* = 0.36). However, survival rates for 1992 were significantly lower for translocated than reference area females (Z = 2.10, *P* = 0.02) and males (Z = 2.70, *P* = 0.004).

Small sample sizes precluded calculation of survival rates for age classes. However, 2 of 4 (0.50) age class II cougars, 2 of 8 (0.25) age class III cougars, and no age class IV cougars (n = 2) survived to the end of the study.

7.5 DISCUSSION

The effect of translocation on cougars appeared to be influenced by the sex, age, and social status of the individual prior to translocation. Translocation was the most effective for cougars in age class II. Surviving cougars in age class II moved the shortest distances from RSs and quickly established HRs or UAs (F95, F119, M23). The 2 females in this group included an independent subadult (F95) and a new immigrant (F119) on the SAM that may have been attempting to establish residency. Therefore, neither female had established residency or social dominance prior to translocation. The only male (M23) in this age class had only recently established residency as an adult on the SAM prior to translocation.

The 2 cougars in age class IV also did not move far away from RSs. They lived only 37 and 109 days post-release and may have moved farther had they survived. Their fates demonstrate high immediate mortality risks associated with translocating old-age cougars. The female (F37) and male (M7) in this age class were long-established resident adults in the source population and had produced or sired 3 litters of offspring each during the 4 years prior to translocation.

Translocation was not very effective for cougars in age class III, which generally represented cougars that were residents in the source population. Those cougars demonstrated the greatest movements away from RSs and homing tendencies towards the SAM. The only cougar (F31) in class III that established a HR near the RS had not produced cubs on the SAM, although she had been a resident adult for 21 months. Another female (F106) in this group which had not produced cubs and was a resident adult on the SAM for approximately 7 months, established a HR about 285 km away from the RS. All other cougars in class III were reproducing females (F44, F58), established territorial males (M18, M49, M88), or a male establishing residency (M114).

Translocated cougars exhibited initial movement directions similar to the random directions taken by natal dispersers; this may indicate that they behave similarly when initially investigating unfamiliar landscapes. In contrast, translocated cougars in Florida (Belden and Hagedorn 1993) and wolves in Minnesota (Fritts et al.

1984) initially oriented towards home. Initial movements of translocated cougars in our study may have been influenced by the presence of resident cougars, human activity, searches for prey, or attempts to orient to sights and smells that were familiar. There were no apparent physiographic barriers that might have influenced initial movements. Subsequent movements of translocated cougars and establishment of UAs probably were influenced by factors associated with natural dispersal mechanisms, homing abilities, presence of resident cougars, resource learning, and physiographic and human associated barriers.

Translocated age class II cougars moved shorter distances and translocated age class III cougars moved greater distances than natal dispersers (all age class II) from the SAM. However, translocated cougars exhibited similar behavior to natal dispersers in that female cougars moved shorter distances than males. Means of means and extremes of dispersal distances for 65 North American cougars were 85.0 km (29-274 km) for 33 males and 31.4 km (9-140 km) for 32 females (Anderson et al. 1992:66). Male cougars tend to disperse from maternal home ranges more often and move greater distances than females (this study, Pall et al. 1988, Lindzey et al. 1994). Approximately 68% of cougars that survived to age class II in the SAM naturally disperse to habitat away from the population of origin (Sweanor et al., in prep.). Therefore, age class II cougars may adapt quickly in or near release sites because innate dispersal mechanisms predispose them to settle in areas different from natal HRs.

The 2 translocated male cougars (M49, M88) that returned to the source area were originally immigrants to the SAM. The ability of these cougars to maintain an appropriate orientation to home suggests that they may have utilized cognitive maps (Griffin 1981) and encountered familiar landscapes and reference points during their travels post-translocation (Fritts et al. 1984). Olfactory stimulus has also been implicated as a possible factor affecting orientation (Griffin 1981, Rogers 1984).

Utilization areas of translocated cougars were much larger than their pre-translocation HRs and generally were larger than HRs reported for resident cougars in other populations (range of means = 81 to 826 km^2 for both sexes, n = 1 to 8, MCP; Anderson 1992:44-45). Post translocation UAs for cougars in New Mexico were generally larger ($\bar{x}$ = 1314.0 km^2, n = 9, 100% MCP; Table 7.3) than HRs reported for translocated cougars in Florida ($\bar{x}$ = 471.0 km^2, n = 4, 100% MCP; Belden and Hagedorn 1993).

In New Mexico, large movements and large UAs of translocated cougars may have resulted from interactions with resident cougars. Cougar social structure has generally been described as a land tenure system based on prior rights where individuals exhibit mutual avoidance (Hornocker 1969). Although prior rights to HRs may be contested (Sweanor 1990), we suspect that translocated age class III cougars probably were seeking to return to the source population. Within the source population, class III cougars had relatively secure residency because they had established social dominance and most had produced offspring. An alternative hypothesis is that translocated cougars may have continued to move through some areas because of very low densities or absence of resident cougars, particularly of the opposite sex, which could have induced translocated cougars to settle in those areas.

In addition, UAs of translocated cougars may have been large due to their unfamiliarity with habitat resources, especially food type and location. Knowledge of habitat resources (i.e., food, water, cover, mates) within a HR are natural requisites to survival, mating, and the successful rearing of offspring (Seidensticker et al. 1973:32). Some translocated cougars may have avoided attempting to capture and handle unfamiliar prey such as elk and continued to search for prey items of a more familiar size. However, one female (F31) who established a home range near the RS successfully killed and consumed at least one bull elk.

Finally, movements and establishment of translocated cougars may have been influenced by human activities. Surviving translocated cougars in north Florida were removed prior to the end of the study because during deer hunting seasons cougars either were killed or they abandoned their home ranges and subsequently moved into urban areas and livestock operations (Belden and Hagedorn 1993). In our study, 9 translocated cougars were released during the New Mexico cougar hunting season during December-March, 1990-1991. We were unable to determine if hunting and dog activity influenced movements of the cougars. However, after an initial movement north away from the RS, 2 females returned and subsequently established HRs during the hunting season. Although the females were treed by hounds 1-3 times during the 1991-1992 hunting season, they remained in their HRs. Cougar F95's HR partially overlapped the target shooting ranges on the NRA Whittington

Center; she produced offspring and remained on her HR through the end of the study.

In some instances movements of translocated cougars were temporarily blocked by towns and highways, causing the cougars to either change directions or localize their activities on one side of the obstacle for up to 6 months before continuing to move. Effects of those man-made obstacles may indicate that naturally dispersing cougars in the region also are negatively impacted.

Other researchers have documented effects of human activities and developments on wild cougars. A busy highway was a barrier to movement by radio-collared adult female Florida panthers (Maehr et al. 1991). In a cougar population almost surrounded by urbanization in California, dispersing male cougars occupied as many as 4 transient home ranges sequentially for up to 8 months at a time (Beier 1995). Thirteen of 18 transient cougar home ranges in that population abutted the urban-wildland interface.

The significantly higher mortality rates for translocated cougars compared to cougars in the SAM reference population demonstrated that translocation projects bear high risks of death for cougars. These mortality risks may be long term, since the majority of deaths in the translocated cougars occurred during the second year after release. Chronic stress may be a factor, especially in translocated cougars in age class III and IV, resulting in increased susceptibility to some types of mortality such as disease and intraspecific aggression.

Causes of mortality of cougars we translocated were similar to natural mortality causes for resident cougars, including intraspecific aggression and injuries related to prey capture in the SAM population (Sweanor 1990) and populations in Idaho, Utah, and Alberta (Hornocker 1970, Lindzey et al. 1988, Pall et al. 1988, respectively). Disease also was a natural mortality factor for cougars in Alberta (Ross and Jalkotzy 1992) and California (Beier and Barrett 1993).

Human-caused mortality was much lower than we anticipated. Even though cougar hunters on the release area complied with our request to not kill translocated cougars, the cougars that left the release area were at risk of being killed by non-informed hunters. Sport hunting typically is the largest cause of mortality in hunted cougar populations (Hornocker 1970, Currier et al. 1977, Shaw 1980, Logan et al. 1986, Ross and Jalkotzy 1992).

Vehicle collisions resulted in only 1 cougar death even though most of the translocated cougars eventually crossed several major highways and paved secondary roads. Similarly, in Florida, 7 translocated cougars crossed roads frequently (2.7 crossings/cougar day), but only 1 cougar was reported grazed by a vehicle (Belden and Hagedorn 1993). In states with higher human densities than New Mexico, humans were the main cause of mortality for wild and translocated far-ranging carnivores. Vehicle collisions were the single greatest cause of mortality for resident cougars in fragmented habitat in southern California (Beier 1995) and Florida (Roelke 1987). Trapping, shooting, and automobile-caused mortality were the greatest threats to translocated wolves in Michigan (Weise et al. 1975) and Minnesota (Fritts et al. 1985).

7.6 MANAGEMENT IMPLICATIONS

Decisions to translocate cougars ultimately depends upon management policies, goals, and actions that may address a broad range of issues including: (1) attacks on humans, (2) predation on livestock or pets, (3) overlap with human development, (4) augmentation or reintroduction projects; and (5) species survival tool for existing, self-sustaining populations.

(1) Attacks on humans-- Euthanasia of cougars that commit unprovoked attacks on humans is the only method that maximizes public safety. Translocation is not a reliable alternative because of the unpredictable movements demonstrated by translocated cougars.

(2) Predation on livestock or pets-- Independent young cougars (≤27 months old) that prey on livestock or pets may successfully be translocated to remote cougar habitat that does not contain livestock or residential areas with pets. Release areas should be large enough to accommodate initial exploratory movements up to 84 km away from release sites and home ranges up to 1,314 km^2. Such areas should additionally have low highway and town densities and adequate prey resources. Managers should identify such locations on a regional or state-wide basis and develop a protocol to facilitate decisions, actions, and record-keeping on cougar translocations. Further, we recommend that managers should attach a visible marker (ear-tag, neck

band) with an appropriate return address to each translocated cougar so that the effectiveness of translocations from reobservations of tagged cougars can be assessed.

Cougars that are >27 months old would generally be expected to move longer distances away from release sites and are more likely to leave remote areas altogether. Thus, they may prey on livestock or pets again. Consequently, euthanasia of those offending cougars is an effective alternative. Cougars that show clinical signs of disease should not be translocated.

(3) Overlap with human development-- Cougars that overlap or encounter human developments pose complex management problems that should be dealt with on a case-by-case basis. Occasionally, females with maturing kittens may increase their use of rural residential areas because of access to wild and domestic prey and the physiological demands associated with providing for maturing kittens (Ruth 1991). However, those same females may infrequently overlap with residential areas when without kittens. Additionally, young cougars dispersing from natal areas occasionally encounter residential areas as they search for habitat where they may establish home ranges. Although most of those cougars probably leave developed areas on their own, some become trapped by civilization and must be removed for safety reasons. Young cougars on the verge of dispersing, or those that have recently dispersed, may be ideal candidates for translocation to remote cougar habitats.

(4) Augmentation and reintroduction projects-- Translocating cougars to augment a population or re-establish a population in vacant historical habitat involves much more complex biological, social, and economic considerations than the 3 situations mentioned above. This is primarily because the areas targeted for release sites would be cougar populations (e.g., Florida panthers) that are isolated from the nearest self-sustaining population by large expanses of severely fragmented habitats, and habitats where cougars have been extirpated by humans (i.e., eastern United States). Important basic considerations in reintroductions of other felids (Wemmer and Sunquist 1988), red wolves (Phillips 1990), and other mammals (Kleiman 1990) should be applied to reintroductions of cougars. Belden and Hagedorn (1993) identified the primary considerations for panther reintroductions to be habitat area

size, prey density, and human population density and secondary considerations to include public education and resolution of depredation complaints.

We recommend that additional considerations include the type of cougars that will be selected for augmentations or reintroductions. Independent cougars ≤27 months old that are health-screened and inoculated and with no prior history of threatening humans or preying on livestock or pets are the best candidates. Female and male cougars within this age group are capable of breeding as early as 19-21 months of age (K. Logan, unpubl. data). Self-sustaining cougar populations in western North America are potential sources for wild cougars. Removal of some independent cougars ≤27 months old from self-sustaining populations probably would not jeopardize the breeding segment of source populations.

The establishment of just a few cougars per generation in an isolated population in need of genetic augmentation may be enough to reduce the rate of genetic erosion (Frankel and Soule 1981). Augmentation projects probably would benefit the most from translocated female cougars because females had higher survival rates than males and did not move as far away from release sites as males.

Optimal sex ratios may enhance the rate of establishment of founder cougars in reintroduction projects. Reintroduced groups of cougars may be optimally comprised of independent animals ≤27 months old and with female:male sex ratios of 2:1 because that ratio mimics the natural adult sex ratio in 5 self-sustaining western populations that were studied for 8 to 10 years (mean sex ratio = 2.18:1 for females:males; Seidensticker et al. 1973, Anderson et al. 1992, Ross and Jalkotzy 1992, Lindzey et al. 1994, this study reference population). Because survival rates of reintroduced cougars are expected to be relatively low, multiple translocations of cougars over several years probably would be necessary to achieve a breeding population that produces progeny that survive to adulthood.

(5) Species survival tool-- Without high habitat quality, translocations have low chances of success regardless of how many animals are released or how well they are prepared for release (Griffith et al. 1989). In addition, because translocated cougars have low survival rates and relatively unpredictable movement patterns, the use of translocation as a long-term survival tool for existing, self-sustaining cougar populations may be unreliable and very costly. Therefore, for self-sustaining cougar

populations, we recommend a pro-active approach to conservation aimed at maintaining large expanses of cougar habitat with adequate connectivity to other habitat to accommodate natural dispersal mechanisms.

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Table 7.1. Background information for 14 cougars translocated from the San Andres Mountains, New Mexico, 6 April 1989 and 7 December 1990 through 22 June 1991, and monitored through 7 January 1993.

Sex and no.	Capture date	Age[a]	Age class and status[b]	Origin[c]	Time period 1[d]	No. radio fixes	Release date	Time period 2[e]	No. radio fixes	Days to IM[f]
F97	12/07/90	16	II; no	born	166	37	12/09/90	11	8	
F95	01/16/91	17	II; no	born	220	52	01/18/91	713	176	7
F119	01/03/91	20-24	II; no	immigrant	1	1	01/05/91	405	87	6
F106	04/12/91	28	III; yes	unknown	218	43	04/13/91	635	85	4
F44	06/21/91	37	III; yes	born	344	69	06/22/91	361	34	30
F31	12/07/90	39	III; yes	born	651	166	12/09/90	500	130	21
F58	03/23/91	48	III; yes	unknown	833	143	03/25/91	654	84	6
F37	06/14/91	96-108	IV; yes	unknown	1221	213	06/15/91	37	8	8
M23	04/06/89	23	II; yes	born	253	73	04/08/89	416	10	
M114	01/14/91	30	III; no	immigrant	85	13	01/16/91	438	56	9
M88	02/03/91	32	III; yes	immigrant	331	78	02/05/91	702	44	7
M49	03/24/91	66	III; yes	immigrant	933	173	03/25/91	469	56	11
M18	03/02/91	84-96	III; yes	unknown	1518	210	03/03/91	486	69	14
M7	03/10/91	96-108	IV; yes	unknown	1734	316	03/11/91	109	31	9

[a] Known or estimated age in months (Ashman et al. 1983, Logan et al. 1990, Sweanor 1990).

[b] Age class II = cougars 12-27 months old, III = cougars 28-96 months old, IV = cougars >96 months old; no = cougar was not a resident adult on the San Andres Mountains or the cougars status was unknown at the time of translocation, yes = the cougar was a known resident adult prior to translocation.

[c] Origin indicates whether the cougar was born on or immigrated to the San Andres Mountains.

[d] Time period (days) in which cougar was monitored prior to translocation.

[e] Time period (days) in which cougar was monitored from release to death or end of study.

[f] Number of days until first documented initial movement (IM) away from the release site.

Table 7.2. Distances and directions moved for 14 cougars after translocation from the San Andres Mountains, New Mexico, 8 April 1989 and 9 Dec 1990 through 22 June 1993, and monitored through 7 January 1993.

Cougar sex and no.	Distance (km)/direction $(^0)$ moved by cougars		
	RS to CS	RS to IM	RS to EP
age class II			
F97	469/196°	3/32°	3/32°
F95	510/201°	12/301°	3/225°
F119	501/196°	10/73°	78/116°
M23	342/170°		39/201°
age class III			
F106	461/197°	14/275°	285/208°
F44	457/197°	60/22°	235/237°
F31	472/196°	30/75°	18/109°
F58	477/201°	19/227°	184/180°
M114	472/199°	32/246°	176/153°
M88	490/199°	13/217°	494/199°
M49	465/197°	11/313°	412/199°
M18	450/198°	21/170°	177/150°
age class IV			
F37	480/201°	7/184°	22/24°
M7	492/201°	8/110°	11/106°

[a] RS = release site, CS = capture site, IM = initial movement, EP = end point.

Table 7.3. Minimum convex polygon (MCP) areas for cougars prior to and after translocation from the San Andres Mountains, New Mexico during 1989 to 1993.

Sex and no.	Time period (mo.) pre/post translocation	Pre-translocation			Post-translocation		
			MCP (km^2)			MCP (km^2)	
		n[a]	100%	90%	n	100%	90%
Home range or utilization area							
F31	14.0/14.0	92	84.4	57.6	106	131.4	56.6
F44	7.0/7.0	41	88.5	54.3	24	3023.8	1079.0
F58	8.5/8.5	46	40.5	17.6	37	2731.4	582.3
F95[b]	7.1/22.0	51	81.0	45.8	154	87.0	59.4
F106	7.1/9.0	43	26.6	22.4	52	53.1	41.1
F119[c]	/12.0	1			74	2796.5	1215.4
M23[d]	8.3/13.6	69	175.1	115.0	10	1160.5	894.8
M18	9.0/9.0	34	82.9	73.6	37	1240.5	989.9
M114[e]	2.7/9.5	13	81.1	32.0	36	601.9	318.4
Temporary localization area[f]							
F58	/3.0				13	379.4	117.1
F106	/3.0				13	1807.9	729.3
M49	/3.0				10	242.7	167.3
M49[g]	/6.0				27	3208.6	2025.4

[a] Number of radio-location fixes.

[b] Home range pre-translocation was based on period during which F95 was newly independent from her mother.

[c] F119 was a new immigrant to the San Andres Mountains at the time of her capture for translocation.

[d] M23 was monitored infrequently on an opportunistic basis after translocation, thus his post-translocation utilization area may be inadequately represented.

[e] M114 was a new immigrant to the San Andres Mountains and was monitored for 2.7 months prior to translocation.

[f] Three cougar temporarily localized in an area or areas for approximately 3 to 6 months before making continued directional movements of substantial distance and subsequently establishing a utilization area.

[g] M49's location data covered a period one day short of 6 months, after which time he was located back in the San Andres Mountains source area.

Table 7.4. Survival and mortality rates of translocated cougars and San Andres Mountains reference area cougars during 1991 and 1992[a].

			Mortality rates[d]					
	n[b]	s[c]	m_1	m_2	m_3	m_4	m_5	v[e]
1991								
Females	8/14	0.66/0.81	0.17/0.19	0.18/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.037/0.015
Males	5/8	0.75/0.85	0.25/0.15	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.045/0.020
1992								
Females	6/14	0.46/0.92	0.00/0.08	0.17/0.00	0.00/0.00	0.18/0.00	0.18/0.00	0.042/0.006
Males	4/11	0.26/0.88	0.00/0.12	0.00/0.00	0.25/0.00	0.00/0.00	0.49/0.00	0.041/0.012
$\bar{x}$ annual								
Females	8/16	0.55/0.86						0.115/0.087
Males	5/12	0.44/0.86						0.115/0.110

[a] Information listed with translocated cougars first, San Andres Mountains reference area cougars second.

[b] Number cougars monitored during given year.

[c] Survival rates.

[d] Mortality rates due to intraspecific killing (m_1); prey capture (m_2); human causes (m_3); bacterial infection (m_4); unknown causes (m_5).

[e] Variance.

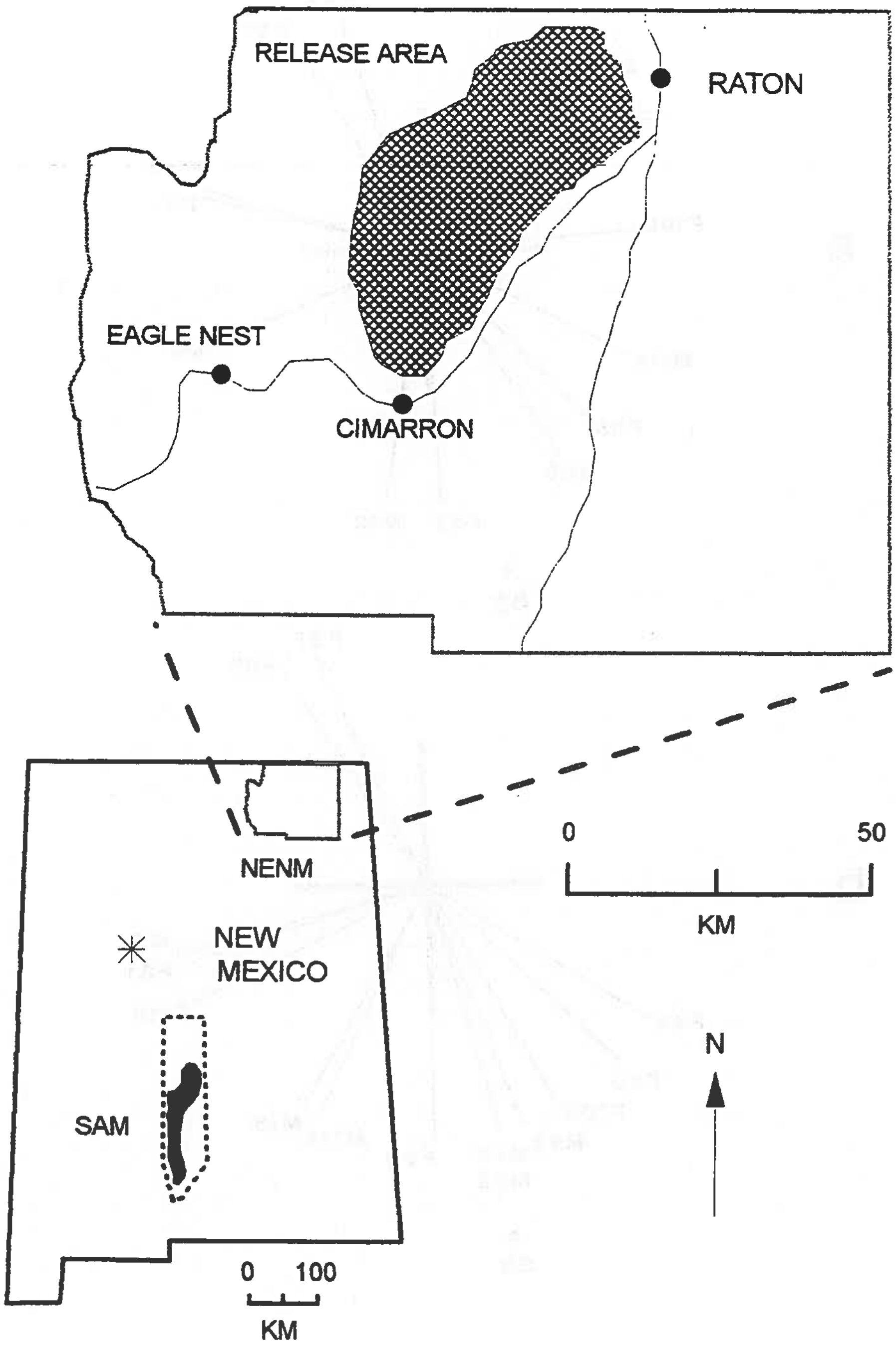

Fig. 7.1. Release area in northeastern New Mexico (NENM) for 13 cougars translocated from the San Andres Mountains (SAM), New Mexico, 7 December 1990 through 15 June 1991, and monitored through 7 January 1993. A fourteenth cougar (M23) was translocated from the SAM to the Cibola National Forest (*) on 6 April 1989.

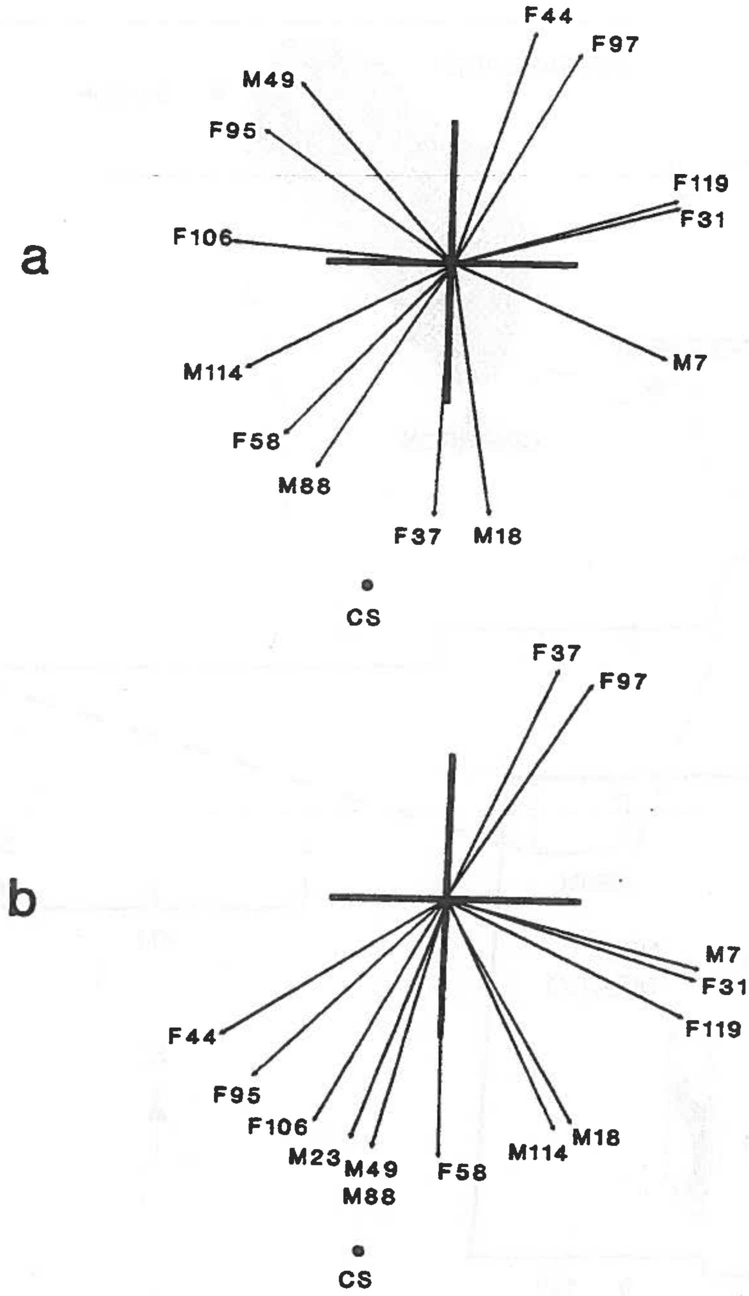

Fig. 7.2. (a) Initial movement directions away from release sites for 13 cougars translocated to northeastern New Mexico, 1990 to 1991; and (b) endpoint directions from release sites for 14 translocated cougars. Cougar M23 (translocated 6 April 1989) does not appear in (a) because monitoring was sporadic and initial movement data was unavailable. Actual direction home (198°) is indicated by CS (capture site).

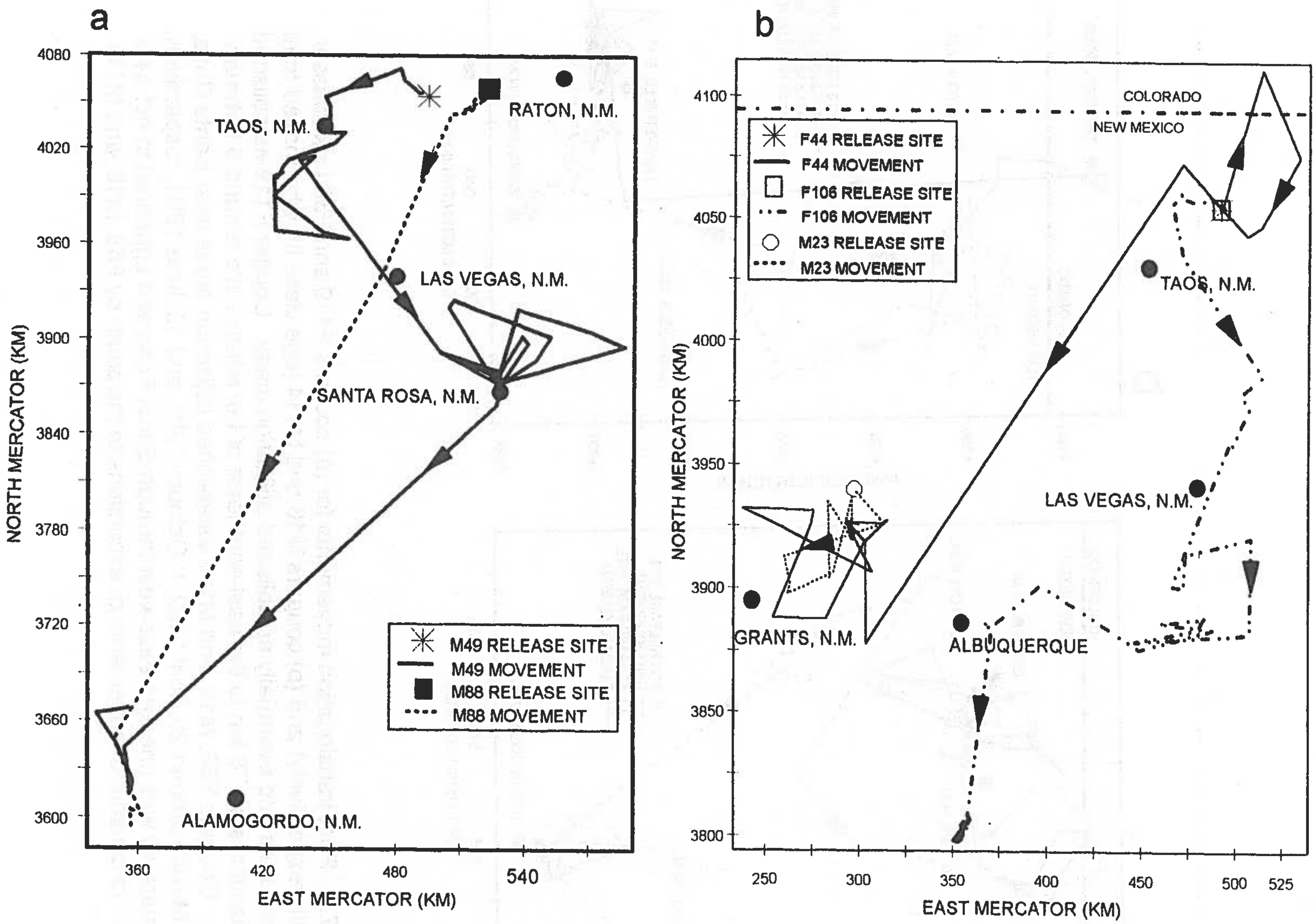

Fig. 7.3. Post-translocation movements for (a) cougars M88 and M49 (age class III) who returned an average of 477 km to the source area in the San Andres Mountains (SAM); and (b) cougars F44 and F106 (age class III) who moved from reslease sites, oriented towards home, and subsequently established utilization areas. Cougar M23 (age class II) established a home range near his release site after translocation from the SAM.

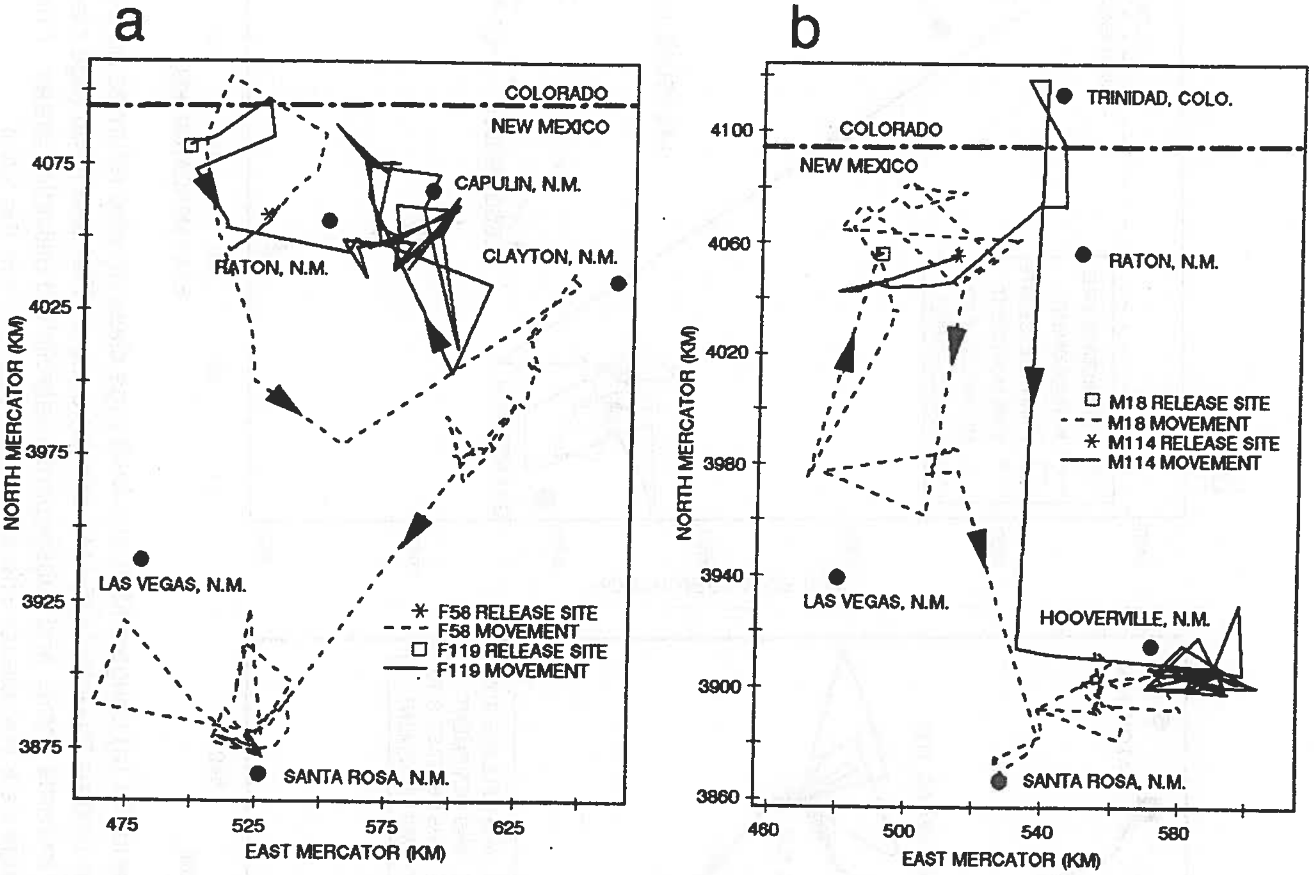

Fig. 7.4. Post-translocation movements for (a) cougars F119 and F58 (age class II and III, respectively) and (b) cougars M18 and M114 (age class III) who moved from release sites and eventually established utilization areas. Cougar F119 established a utilization area 78 km to the east-southeast of her release site around 5 February 1991. Cougars F58, M18, and M114 established utilization areas near Santa Rosa, New Mexico around 20 April 1992, 6 October 1991, and 13 June 1991, respectively. Interstate 40 was oriented east-west through Santa Rosa and appeared to act as a barrier to continued movements or excursions to the south by F58, M18, and M114.

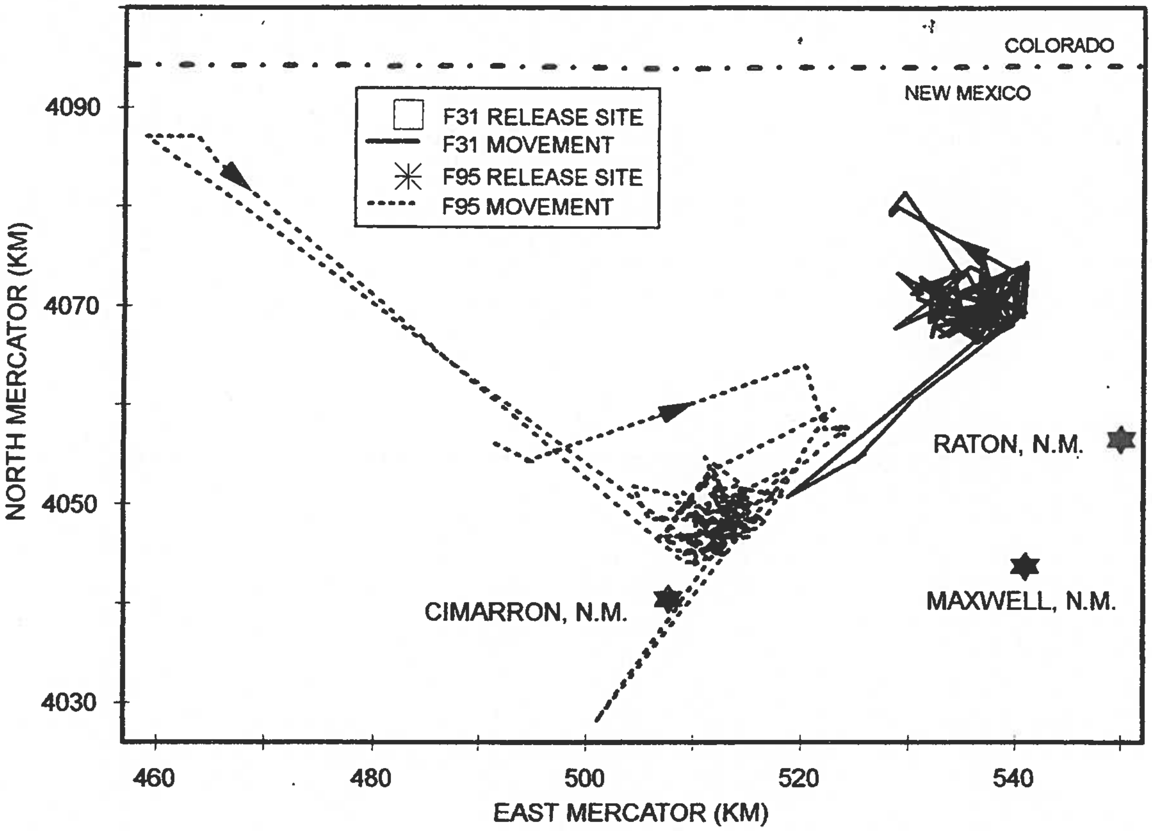

Fig. 7.5. Post-translocation movements for cougars F31 and F95 who established near their release sites in northeastern New Mexico and produced offspring on 10 August 1991 (F31) and 9 May 1992 (F95).