FULL-SEASON PRODUCTIVITY OF GRAY VIREOS AT SEVILLETA NATIONAL WILDLIFE REFUGE, NEW MEXICO: 2019-2021 FINAL REPORT

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Cooperators: New Mexico Department of Game and Fish (Share with Wildlife), U.S. Fish and Wildlife Service (Sevilleta National Wildlife Refuge), New Mexico Ornithological Society, University of Toledo, NSF Sevilleta Long-Term Ecological Research (LTER) Program, Cleveland Museum of Natural History, University of New Mexico

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Abstract. With funding from the New Mexico Department of Game and Fish's (NMDGF) Share with Wildlife program, during 2019-2021, we studied Gray Vireo (*Vireo vicinior*) demography and habitat associations at the Sevilleta National Wildlife Refuge (NWR) in central New Mexico as part of an ongoing project that began in 2017. We assessed and implemented successful capture, banding, tissue sampling, and harness attachment methods and monitored nests and juveniles post-fledging. We systematically located and monitored 140 nests (*n* = 38 in 2019, *n* = 45 in 2020, *n* = 57 in 2021 as of 6 July 2021), all of which were in oneseed juniper (*Juniperus monosperma*) trees, with 58% lateral vegetation cover (i.e., a measure of concealment) and 14% tree cover (i.e., cover within 25-m radius buffers around nest locations) on average. Model-averaged nest success was 0.37 in 2019 and 0.32 in 2020; nests are still being monitored in 2021. Nests were located in areas of greater percent tree cover (trees/ha) relative to the surrounding landscape. Nest success in 2019-2020 was lowest at higher elevations, which may be related to differences in predator communities as forests transition from juniper to piñon pine (*Pinus edulis*). Nest parasitism rate by Brown-headed Cowbirds (*Molothrus ater*) was 24% in 2019, 9% in 2020, and ~40% in 2021 (as of 6 July 2021). The demographic impact of nest parasitism is likely small because Gray Vireo pairs typically abandoned parasitized nests and repeatedly re-nested after failure from parasitism or predation (i.e., most pairs eventually succeeded). Accounting for re-nesting, we estimate that 87% of females successfully nested in 2019 and 2020 and produced a mean fledged brood size of 3.3 (± 0.6). Interestingly, but as yet unexplained, genetic results indicated that fledged young were 56% male and 44% female in 2019-2020. We used radio telemetry to track 90 Gray Vireo juveniles (*n* = 41 in 2019, *n* = 49 in 2020) during the post-fledging period (i.e., after nest departure) and monitored survival, space use, and habitat associations; tracking is ongoing in 2021. We specifically focused survival analysis on days 1-12 days post-fledging because we did not observe mortality after day 11. Model-averaged daily juvenile survival rate from days 1-12 post-fledging was 0.57 in 2019 and 0.50 in 2020; survival was best predicted by age, with a rapid increase in survival over the first week outside the nest. All mortalities were attributed to predation and environmental exposure. Over the entire monitoring period, fledglings occupied oneseed junipers during 94% of observations. During the first 12 days post-fledging, within 25-m radius buffers at daily locations, fledglings used areas with similar percent tree cover to that of nesting sites and greater than that of random locations. Similarly, fledglings occupied individual trees and shrubs with lateral vegetation cover similar to that of nest locations. Minimum daily distance traveled, distance from nests, and variance associated with these measures, all increased with age. Except for the use of a larger area, habitat associations of Gray Vireos during the post-fledging period were similar to that used for nesting, indicating that maintenance of large patches of moderately dense juniper is desirable for this species. Specifically, areas used for nesting and post-fledging habitat in our study were characterized by 90 ± 25 juniper trees/ha. We radio-tracked only 5 adults during 2019-2021, but including previous years, we have observed no evidence of adult mortality (n = 23 adults tracked), suggesting that adult survival during the breeding season is high. We used our demographic parameter estimates to inform a female-based stochastic population growth model and found that the study population was numerically stable in 2019-2020 (λ =1.00, 95% CI = 0.93 – 1.04). However, we note that 2019 and 2020 were years of relatively moderate environmental conditions and that fledgling survival was considerably lower during the 2018 drought, indicating that long-term population growth may be negative. No habitat variable improved models of nest or fledgling daily survival. This could reflect that demographic parameters vary with different habitat characteristics than those that we measured or that there is little variability in habitat quality across our study area, or both. Study is needed from populations in more heterogeneous and human-impacted landscapes to allow comparison with our results. We are continuing with more detailed analyses of nest survival, juvenile survival, climatic factors, arroyo associations, habitat associations, and population growth to include in manuscripts for publication, and we predict these manuscripts to be completed in 2021-2022. Our 2021 field season is ongoing, which was partially funded by NMDGF. Notably, historically severe drought conditions have persisted from late 2020 through mid-2021 in New Mexico. Interestingly, Gray Vireos initiated nesting >3 weeks later in 2021 compared to previous years, likely in response to drought. We are currently conducting an experimental study of the impacts of drought on juvenile condition and survival in this population, with results expected after the field season.

Introduction

Traditionally, due to lack of appropriate technology, many studies that quantify reproductive success of songbirds include only the nesting stage, thereby excluding the post-fledging period. However, these two components of full-season productivity can be interdependent, and either measure alone can be misleading (Anders and Marshall 2005, Streby and Andersen 2011, Streby et al. 2014). Importantly, annual population growth (ƛ) in birds may be particularly sensitive to juvenile (hereafter, fledgling) survival, in addition to nonbreeding period (including migration) survival, but these two portions of the annual cycle are studied least often (Anders and Marshall 2005, Streby and Andersen 2011, Cox et al. 2014).

The post-fledging period, or the stage after fledglings leave the nest and prior to migration, is critical to assessing avian productivity and population growth (Wightman 2009, Streby 2010, Cox et al. 2014); however, this stage has not been studied in Gray Vireos (Barlow et al. 1999). The survival of fledglings is important for population growth, and annual variation in fledgling survival can cause population fluctuations (Sullivan 1989, Robinson et al. 2004, Anders and Marshall 2005, Streby and Andersen 2011, Cox et al. 2014). Fledglings of relatively large songbirds (e.g., Wood Thrush [*Hylocichla mustelina*]; 40-50 g) were first tracked with radio telemetry > 25 years ago (Anders et al. 1997, 1998), and the technology is now sufficiently small with adequate battery life to track tiny songbirds (e.g., Golden-winged Warbler [*Vermivora chrysoptera*]; 7-10 g). However, because this technology is new compared to the ability to find and monitor nests (Bendire 1889), and because of the expense and difficulty in collecting data on individual fledglings, the post-fledging period remains one of the most poorly understood portions of the full annual cycle in birds, along with migration (Baker 1993, Cox et al. 2014). In the Northern Hemisphere, many post-fledging studies have been conducted in temperate forests (e.g., Anders et al. 1997, Anders et al. 1998, Streby and Andersen 2011, Vitz and Rodewald 2011, Chandler et al. 2012, McKim-Louder et al. 2013, Streby and Andersen 2013, Jenkins et al. 2017, Vernasco et al. 2017, Delancey and Islam 2019, Raybuck et al. 2020), grasslands (e.g., Yackel Adams 2006, Fisher and Davis 2011), and riparian areas and wetlands (e.g., Vormwald et al. 2011). Southwestern desert and arid land systems are under-represented in the literature of fledgling movements and survival (see Cox et al. 2014).

One such desert-dwelling species, the Gray Vireo (*Vireo vicinior*), is a small (~11-14 g), under-studied, migratory songbird that breeds primarily in piñon (*Pinus* spp.)-juniper (*Juniperus* spp.) savannas and structurally similar arid landscapes in the southwestern USA and northwestern Mexico (Barlow et al. 1999; but see Hargrove and Unitt 2017 for chaparral habitat associations of the likely-disjunct California population). Across their breeding range, Gray Vireos are listed as Species of Concern by the US Fish and Wildlife Service, listed on the Partners in Flight Watch List, listed as state Threatened and a Species of Greatest Conservation Concern (SGCN) in New Mexico (NMDGF 2016), listed as a Priority Species by Utah Partners in Flight (Parrish et al. 2002), considered to be of conservation concern in Arizona (AZGFD 2012) and Colorado (CPWD 2015), described as rare and locally uncommon in Texas (Lockwood and Freeman 2004), and have declined substantially in California in recent decades but are not state-listed there primarily due to deficient data (AZGFD 2012, Hargrove and Unitt 2014).

Causes for concern with Gray Vireo population trends include habitat loss, climate change, brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), and impacts of drought (Barlow et al. 1999, Walker and Doster 2009, Hargrove and Unitt 2017). The piñon-juniper habitat that most Gray Vireos, and some other species of conservation concern (e.g., Pinyon Jays [*Gymnorhinus cyanocephalus*]), depend on during the breeding season is being continually altered for livestock and by extensive juniper chaining, pine mortality (e.g., driven by drought), tree cutting for firewood, and fire suppression, among other processes (DeLong and Williams 2006, Schlossberg 2006, Walker and Doster 2009, Crow and van Riper 2010, Johnson et al. 2018). Additionally, Gray Vireos occupy a restricted distribution and have a relatively small global population (estimated at ~560,000 individuals; Rosenberg et al. 2016). Range-wide population trends for Gray Vireos are unclear because this species occupies remote breeding areas that are often away from roads and are therefore not well surveyed by Breeding Bird Survey (US Geological Survey; see Sauer et al. 2017) routes or birdwatchers (Barlow et al. 1999, Schlossberg 2006, Hargrove and Unitt 2017). Because of the lack of knowledge of Gray Vireos, empirical estimates of demographic rates, such as post-fledging survival, are necessary for informing science-based conservation decisions (Schlossberg 2006, NMDGF 2007, Fischer 2020).

Our objective was to study full-season (i.e., from spring arrival to fall departure) productivity and habitat associations, including adult survival and habitat selection, nesting habitat associations, and fledgling survival and habitat selection of Gray Vireos at the Sevilleta National Wildlife Refuge (NWR) in New Mexico. This study fills critical information gaps about a SGCN and can inform habitat conservation and management plans.

Methods

This report covers the period of 2019-2020 and a portion of the 2021 field season, during which our work was supported by funding from the New Mexico Department of Game and Fish's Share with Wildlife Program. We indicate throughout when samples or results are included from previous years of the same study. This work was conducted under the University of Toledo IACUC protocol #108708. All sampling and marking methods in 2019-2020 were identical to those implemented in 2017-2018 (see Fischer 2020).

Study Area

We continued our Gray Vireo demography study on the Sevilleta NWR in Socorro County, New Mexico within the Central Management Unit (outlined in the Gray Vireo Recovery Plan [NMDGF 2007]). Breeding Gray Vireos have been studied annually at the NWR since 2011 through the NSF REU Program hosted by the University of New Mexico. Sevilleta NWR is a 93,000-ha refuge that protects a massive arid land ecosystem at the northern limit of the Chihuahuan Desert and is managed by the US Fish and Wildlife Service (USFWS 2012). We conducted this study on the eastern side of the Sevilleta NWR, within the foothills of Los Pinos Mountains (mean elevation ~1785 m; 34.22041°N, 106.69314°W), where Gray Vireos are known to breed (Figure 1).

Vegetation in the study area was predominantly juniper savanna comprised mainly of juniper (*Juniperus monosperma*), creosote bush (*Larrea tridentata*), and other shrubs (e.g., oak [*Quercus* spp]., sumac [*Rhus* spp.], and alder-leaf mountain mahogany [*Cercocarpus montanus*]), grasses (e.g., *Bouteloua* spp.), and succulents (e.g., yucca [*Yucca* spp.], cholla [*Cylindropuntia* spp.], and prickly pear cactus [*Opuntia*] spp.), with piñon pines (*Pinus edulis*) at higher elevations (see Stevens and Fischer 2018, Fischer 2020).

Annual precipitation in the study region averages ~250 mm, is seasonal, and generally bimodal, with most rain falling during the monsoon in July – September and additional precipitation (rain and snow) occurring in winter months (Notaro et al. 2010, Baez et al. 2013, Muldavin et al. 2014, Petrie et al. 2014, Kwiecinski et al. 2020). Temperatures in May to August range from ~15-38 °C.

Capturing, Banding, and Tissue Sampling

To catch adult Gray Vireos, we used 12-m mist-nets and conspecific song and call playback to elicit aggression and territorial responses. All adults were marked with unique combinations of 3 color bands and one metal USGS band. Juveniles were captured by hand from nests prior to fledging and marked with one color band representing a year cohort (blue in 2019, yellow in 2020, and green in 2021) and one metal USGS metal band. We recorded standard morphometric data, including mass, age, wing length, and tail length. Adult sex was determined by both breeding condition (cloacal protuberances and brood patches) and behavior, and molecular sex of juveniles was determined via DNA analysis at no additional cost by collaborators at the Cleveland Museum of Natural History.

We took small hallux (i.e., hind claw) clippings and removed 3-5 crown feathers from adults for future analysis of spectral reflectance (which may correspond to body condition at the time of growing the feathers) and diet in the lab. We also sampled blood (<1% of body mass) in adults and juveniles from a vein in the wing using sterile 27-gauge needles and heparinized capillary tubes. Samples were spun in the field using a centrifuge to separate red blood cells from plasma. Red blood cells were mixed with cryoprotectant buffer (90% fetal calf serum, 10% DMSO) and flash-frozen in the field.

Plasma samples were flash frozen in the field and were used to examine relative hydration using osmometry. All samples are being stored at -80C pending lab analysis. We made peripheral blood smear slides and stored remaining red blood cells in lysis buffer for avian blood parasite screening (e.g., haemosporidian parasites) in collaboration with the University of New Mexico. The plasma samples will also be used to assess body condition and immune capacity using multiple immune response assays. Following sampling and marking (see below), all birds were released at the capture location.

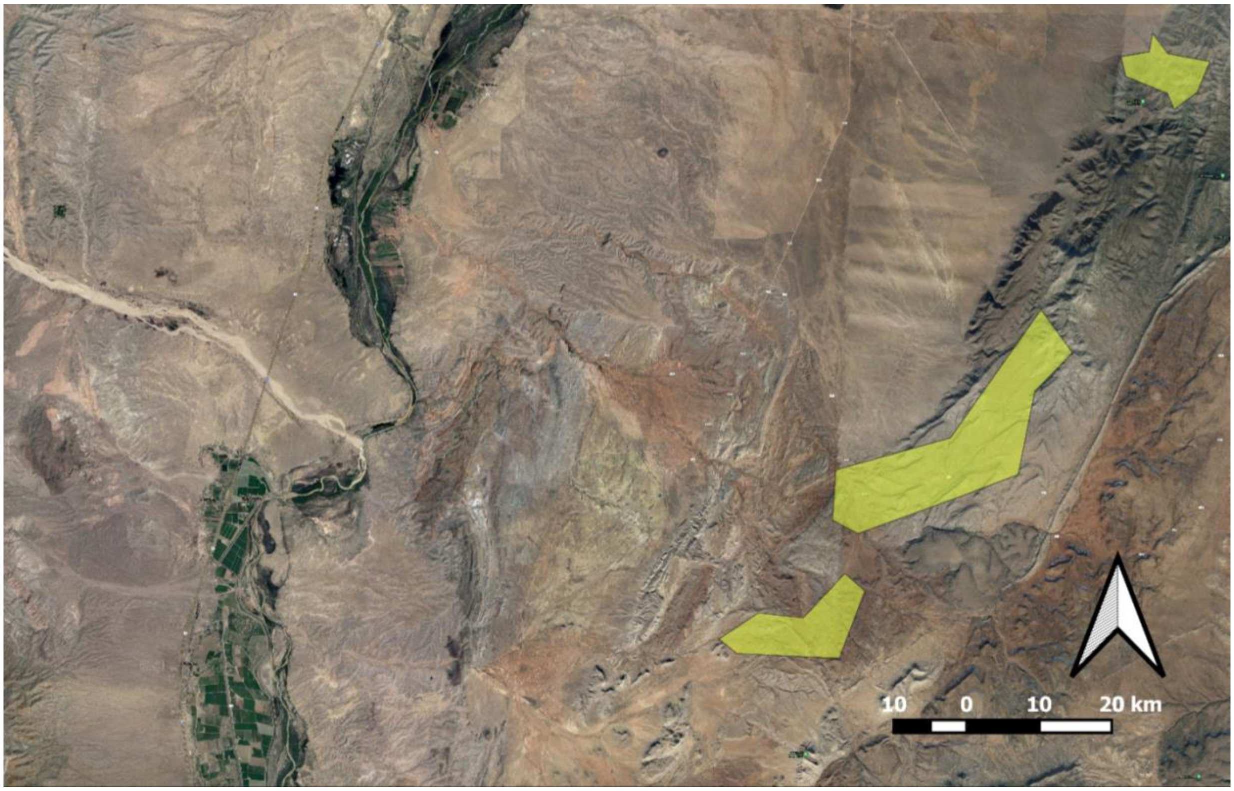

Figure 1. Study areas (gold polygons) for Gray Vireo full-season productivity and habitat associations research in Los Pinos Mountains within the Sevilleta National Wildlife Refuge, Socorro County, New Mexico (2017-2021). The three sites from North to South are Pinon Canyon, Sepultura Flats, and Tomasino.

Nest Searching, Monitoring, and Vegetation Data

We searched for nests by following singing males and by radio tracking incubating or brooding females to their nests both during the day and at night. Nest locations were recorded using handheld GPS devices. After locating nests, we monitored them every 3-4 days to record adult activity, nest contents (i.e., presence of Brown-headed Cowbird eggs/young, Gray Vireo eggs/young), and nest condition. We determined nest fates by visiting until the expected fledging date. Nests were considered successful if ≥1 young fledged, but final analysis differentiated numbers of young fledged. Nests were considered parasitized if they contained ≥ 1 Brown-headed Cowbird eggs; we never observed a Gray Vireo fledging from a parasitized nest in 2019-2020 and thus all parasitized nests in these years were considered failures. All other failed nests were considered depredated (e.g., nests shredded, vireo eggshell fragments on ground, etc.) or destroyed due to weather (e.g., nests that fell due to strong winds).

Once nests were inactive (i.e., failed or fledged), we collected associated vegetation data, including: substrate, diameter and foliage cover of nest tree, lateral vegetation cover, nest height, nest tree height, and the orientation (compass bearing) of the direction that the nest was facing out from the tree (nests in the center of the tree were measured as ‘center’ and the mean bearing from the overall nest sample was substituted). We measured overall nest tree foliage cover using a 1-m × 1-m profile board divided into 100 squares, which one observer held as another observer estimated percent cover on the opposite side of the tree. Observers then rotated 90° to get a second estimate; both numbers were averaged to obtain one overall estimate of nest tree foliage cover. We measured lateral vegetation cover, which is a measure of the concealment of nests or fledglings (see below) in vegetation, using a 2-m tall × 0.25-m wide profile board divided into eight squares, which we hung from a collapsible stand at each nest position (see Streby et al. 2013a, 2016; Figure 2). We visually estimated percent cover in each of the eight squares from 10 meters North and 10 meters East of the profile board. All 16 values were then averaged to obtain one estimate of lateral vegetation cover for each nest (see Streby et al. 2013a, 2016).

Figure 2. Profile board used to estimate lateral vegetation cover, a measure of concealment, at nest locations and daily fledgling locations. Profile boards were 2-m tall × 0.25-m wide and were divided into eight squares. We visually estimated percent cover in each of the eight squares from 10 meters North and 10 meters East of the profile board. All 16 values were then averaged to obtain one estimate of lateral vegetation cover at each nest and fledgling location.

We took photographs facing directly above and below each nest for future analysis of canopy cover and ground cover. In addition to 2019-2020 nest data, we included nest vegetation data from previous years (2017-2018; *n* = 73) to increase our sample size for summarizing habitat associations. Nest monitoring and nest vegetation data collection are ongoing in 2021 and thus are not included in analyses reported here.

Radio Transmitter Harness Design and Attachment

In 2017-2020, we used 0.6-g radio transmitters (~3.5% of body mass; Blackburn Transmitters, Nacogdoches, TX) with a modified figure-eight leg-loop harness (Rappole and Tipton 1991, Streby et al. 2015) that has been successfully implemented in other studies of small songbirds (e.g., Peterson et al. 2016). Nestlings were removed from nests 2-3 days prior to expected fledging and marked with one color band and one metal U.S. Geological Survey numbered band. We randomly selected between one and four nestlings from each nest and fitted them with radio transmitters (Figure 3). We recorded mass and took blood samples from all nestlings (see methods above).

Radio Tracking Fledglings

We used standard, ground-based telemetry methods to monitor survival, space use, and habitat associations of Gray Vireo fledglings from 2017-2020; fledgling tracking is ongoing in 2021. We used VHF handheld receivers (Model R410, Advanced Telemetry Systems, Isanti, MN, USA) and directional antennas (Model RA-23K flexible “H”-type, 148-154 MHz, Telonics Inc., Mesa, Arizona, USA) for all radio telemetry.

Figure 3. Gray Vireo fledgling with VHF radio transmitter attached using a figure-eight leg-loop harness.

Fledglings were tracked daily during the first 12 days post-fledging, after which we reduced tracking frequency to once every 3 days. Inclement weather sometimes prohibited daily tracking (e.g., when roads were washed out), but the logistic exposure survival analysis we used incorporates variable interval lengths (Shaffer 2004). We tracked all fledglings until confirming or suspecting mortality, transmitter failure, or signal loss (i.e., a fledgling either left the study area or was carried away by a predator). In cases of signal loss, we made ≥ 3 attempts to locate fledglings. Upon successfully locating each fledgling using radio telemetry, we recorded their location using a GPS unit with waypoint averaging for accuracy of < 5 m. In addition, we recorded fate (i.e., alive or dead), other fledglings and/or adults observed nearby, activity of adults and fledglings (e.g., foraging, feeding), vocalizations (e.g., begging), fledgling height from ground, and vegetation data (i.e., substrate and lateral vegetation cover). We measured lateral vegetation cover of daily fledgling locations (i.e., where the fledgling was initially observed when tracking) using the same methods as for nests (see above; Figure 2). We took photographs facing directly above and below each fledgling location for future analysis of canopy cover and ground cover.

We followed similar methods to Streby et al. (2016) and Yackel Adams et al. (2006) to identify potential predator types (i.e., small mammals, avian predators, etc.) of Gray Vireo fledglings that were being radio-tracked if we were unable to confirm the predator species. We attributed predation to small mammals if transmitter signals emanated from underground burrows or if we recovered transmitters along with appendages (i.e., legs and feet) or leg bands that had been removed (see Streby and Andersen 2011). We acknowledge that when fledglings were located underground, we were unable to rule out predation by snakes, which often use small mammal burrows (Kinlaw 1999) and are known to depredate birds. We assumed avian predators if we recovered transmitters that were kinked and/or located in a pile of plucked feathers. We assumed non-predation (i.e., apparent exposure) when we observed intact carcasses (see Yackel Adams et al. 2006) with no sign of carnage or feather loss or when otherwise undamaged carcasses were covered by ants, which we assumed occurred following death by exposure.

Nest Success and Logistic Exposure Modeling

We used logistic exposure models (i.e., modified generalized linear models; Shaffer 2004) to estimate nest success and to allow for covariates and hypothesis testing following Mayfield's exposure methods (1961, 1975). Covariates for nest survival models included year, ordinal date, nest age from initiation (i.e., date of first laid egg), nest height from ground, nest tree height, nest tree diameter, elevation (meters above sea level), lateral vegetation cover (i.e., concealment), tree foliage cover, percent tree cover within a 25-m radius (see below), and site (i.e., Piñon Canyon, Sepultura Flats, and Tomasino; see Figure 1). We considered $\alpha \leq 0.05$ to be statistically significant and models were ranked and chosen using Akaike's Information Criterion adjusted for small sample sizes (ΔAICc; Burnham and Anderson 2002). We considered a parameter to be uninformative if a model including that parameter was otherwise identical to the highest-ranking model and was within 2 AICc (Arnold 2010).

GIS Methods and Analysis of Fledgling Movements

We obtained 1-m-resolution digital orthophotography (National Agricultural Imagery Program [NAIP] available through New Mexico Resource Geographic Information System [RGIS]) to visualize our study areas. Because some radio-marked females selected nest sites outside of where we searched, and because we could not predict where fledglings would travel, we established the boundaries of our study sites post hoc such that the area included all nest and fledgling locations with a buffer of ~100 m. We used supervised classification in ArcMap (v10.7.1) to differentiate shrubs and trees (e.g., juniper, piñon pine, oaks, creosote) from bare ground, rock, and smaller vegetation (e.g., forbs) to create a measure of tree cover (including both trees and shrubs). Grasses and other plants not mentioned previously were excluded from image classification because fledglings were not observed using those substrates and so we draw no inference about the contribution of these plants to Gray Vireo habitat.

We imported the classified raster for use in QGIS, an open-source mapping software (QGIS Development Team 2020). We classified the tree layer raster in QGIS as binomial (i.e., tree or not tree), such that percent area covered by tree could be calculated for any area to estimate tree cover. We created 25-m radius buffers around each fledgling location (during the first 12 days post-fledging because we did not observe mortality after day 11) and nest location. We selected the 25-m radius (~1,964 m^2) buffer by consulting literature for home range sizes of small mammals in the Southwestern USA, the assumed predominant predators of Gray Vireo fledglings at Sevilleta NWR. We assumed this 25-m buffer size was biologically relevant based on potential predators (because predation is typically the primary source of songbird fledgling mortality; Cox et al. 2014) and small enough to describe potential variation in survival among areas used by fledglings. Small mammals in this ecosystem occupy home ranges from ~200-2000 m^2 (e.g., 486 m^2 in white-throated woodrats [*Neotoma albigula*], Macêdo and Mares 1988; 220 m^2 in females and 1900 m^2 in males in Southern Plains woodrats [*N. micropus*]*,* Conditt and Ribble 1997).

We generated 600 random points and associated 25-m buffers within study site polygons (see Figure 1) to compare post-fledging and nest habitat associations with available areas. Within each 25-m buffer, we used the classified tree layer raster and extracted the percentage of tree cover using zonal statistics by dividing the number of tree pixels by the total number of pixels and multiplying by 100. Tree cover percentages from buffers were then added as covariates in nest and fledgling survival models (see above and below, respectively).

Fledgling Survival and Logistic Exposure Modeling

Prior to running survival models, we used Winterstein's Chi-squared test of independence to assess interdependence among fledglings within broods in which we monitored >1 fledgling (Winterstein 1992). Winterstein *P*-values < 0.05 would indicate that survival among broodmates is non-independent and individuals should not be treated as independent samples (Winterstein 1992), which would warrant inclusion of brood as a random effect in our models.

We used logistic exposure models to estimate fledgling survival and to allow covariates and hypothesis testing following Mayfield's exposure methods (1961, 1975). Covariates for fledgling survival models included year, ordinal date, age from hatch, fledgling height from ground, elevation, substrate, lateral vegetation density, and tree cover within a 25-m radius of fledgling locations. In these models, we included only the first 12 days post-fledging because we did not observe any mortalities after day 11 in any year. We censored non-predation mortalities (i.e., apparent exposure) from analysis of habitat associations with survival because those mortalities were clearly associated with annual climatic conditions and not with vegetation variables (S.E. Fischer, unpublished data). Those fledglings that died on day-1 post-fledging due to exposure were therefore excluded from habitat-associated models altogether. Other than those birds, regardless of mortality type, fledgling fates (i.e., alive or dead) were paired with the previous day's habitat data for analysis. This is standard procedure when modeling habitat effects on survival data collected daily, because 1) we are testing whether current habitat use is associated with survival through the following 24-hours, and 2) the location of a recovered carcass is not reliably associated with habitat use (i.e., when a predator carries a fledgling to a burrow, nest, or caching site, that site is irrelevant to fledgling habitat use). We included a random effect of brood in our fledgling survival models to account for interdependence among individuals from the same nest following the results of the Winterstein's Chi-squared test of independence ($P = 0.003$; see above). We considered $\alpha \leq 0.05$ to be statistically significant and models were ranked and chosen using Akaike's Information Criterion adjusted for small sample sizes (ΔAICc; Burnham and Anderson 2002). We considered a parameter to be uninformative if a model including that parameter was otherwise identical to the highest-ranking model and was within 2 AICc (Arnold 2010).

Fledgling Movements and Brood Division Behavior

We used data from 2017-2019 to calculate minimum daily distance traveled and daily distance from the nest using the Haversine (i.e., shortest distance between daily points on the sphere) method using the geosphere package in R (v.1.5-10; Hijmans 2019). We included only distances between consecutive daily locations (in 2017-2018 this included most days throughout the entire tracking period and in 2019-2020 included primarily data from the first 12 days post-fledging due to logistical constraints; see above) because it is inappropriate to interpolate minimum distance moved during a period shorter than that observed (e.g., minimum distance over two days cannot be divided by two to estimate daily distance unless the individual moves constantly in one direction). To avoid pseudoreplication in all movement analyses, we averaged all daily movement values for broods in which broodmates fledged at the same age from hatching. If daily data were not available for all broodmates, we used data from single broodmates. To account for variation in ages from hatching in all other broods, we randomly selected one fledgling for analyses, unless we had more observation data for one broodmate, in which case we chose that fledgling to include in analyses. We acknowledge the possibility that broodmates with more observation data were more likely to be observed and may have moved shorter distances; however, broodmates generally tended to move similar distances. In broods that exhibited clear brood division, we considered movement data from female-reared fledglings to be independent from those of male-reared fledglings and were therefore considered separately in movement analyses. We defined brood division conservatively as clear spatial segregation between adult males and females and their associated fledglings. Therefore, we accounted for the minimum percentage of brood division and acknowledge that this phenomenon may be more prevalent than was detectable (e.g., inconspicuous or smaller differences between adult males and females in terms of space use, especially for broods in which we tracked fewer fledglings).

Population Growth Modeling

We used our estimates and associated variance for nest success, re-nesting rates, fledged brood size, adult breeding survival, fledgling survival, and fledgling sex ratio, along with generalized estimates of non-breeding survival for adults and juveniles, to parameterize female-based birth-pulse stochastic population growth models for 2019-2020 (as in Streby and Andersen 2011). In this model, fledgling survival included mortalities from all causes. This model is preliminary and is subject to minor changes as more detailed modeling of some parameters is completed. We used the mean of the 2019 and 2020 values for each parameter and ran 5000 iterations of a population growth model, during each of which values were randomly selected for each parameter from a distribution of possible values informed by the mean and standard deviation of our parameter estimates. We then calculated the mean and 95% CI of λ (annual population growth) from the 5000 iterations, whereby a value >1.0 indicates positive growth, <1.0 indicates negative growth, and a 95% CI overlapping 1.0 indicates no annual numerical change in population size.

Results

Nest Monitoring, Banding, and Radio Tracking Sample Size Summary

Table 1. Samples sizes of Gray Vireo nests monitored and adults and juveniles banded (and sampled) and radio-tracked during 2017-2021 at the Sevilleta National Wildlife Refuge, New Mexico, USA. Bolded rows indicate data from 2019-2021 funded by New Mexico Department of Game and Fish Share with Wildlife grants.

	Nests monitored	Adults banded	Adults tracked	Nestlings banded	Fledglings tracked
2017	49	74	11	45	30
2018	36	63	7	19	19
2019*	**38**	**33**	**2**	**70**	**41**
2020*	**45**	**34**	**2**	**62**	**49**
2021*+	**57+**	**50+**	**1+**	**30+**	**2+**
Total 19-21*	**140**	**117**	**5**	**162**	**92**
Project Total	225	254	23	226	141

+ Our 2021 field season is ongoing; here we report sample sizes as of 6 July 2021.

Nest Success and Nesting Habitat Associations

We located and monitored 140 nests (*n* = 38 in 2019, *n* = 45 in 2020, *n* = 57 in 2021) from 2019-2021. Nest initiation dates (i.e., date of first egg laid) ranged from 11 May to 30 June in 2019-2020. Mean nest initiation date was 3 June ± 11 in 2019 and 26 May ± 13 in 2020. Of nests that fledged ≥ 1 young, mean clutch size was 3.7 ± 0.5 SD in 2019 and 3.4 ± 0.5 SD in 2020; mean fledged brood size was 3.3 ± 0.6 SD in 2019 and 3.2 ± 0.7 SD in 2020. All nests were in oneseed juniper trees (*n* = 225, 2017-2021). The average nest tree was 3.4 m ± 1.0 SD tall (range: 1.7-7.8 m) and 4.8 m ± 1.8 SD (range 1.6-10.2 m) wide. Nests were 2.1 m ± 0.7 SD (range: 0.9-4.3 m) from the ground. Mean nest tree foliage cover was 76 ± 17% (*n* = 156 nests) and mean nest orientation (the compass bearing the nest was facing out from the tree center) was 181° ± 97° SD but ranged from 0-359°. Nests were more obscured at 10m from the side (mean 58 ± 26% SD) compared to 10m from the front (mean 32 ± 29% SD; $t = -8.368$, $df = 306.960$, $p < 0.001$). Many nests were located in or near arroyos (i.e., ephemeral, intermittently dry drainage channels [Waters and Haynes 2001] often associated with larger and more numerous shrubs compared to surrounding areas presumably due to increased soil moisture [Balding and Cunningham 1974]; S.E. Fischer, personal observation; Figure 7).

Daily nest survival was negatively correlated with elevation, the only variable in the best-supported model (m above sea level; Figure 4). Of the 83 nests from 2019-2020, 39 failed, 67% of which were depredated (44% or *n* = 7/16 of failures in 2019; 83% or *n* = 19/23 of failures in 2020). Nest parasitism rate by Brown-headed Cowbirds was 24% (*n* = 9/38) in 2019 and 9% in 2020 (*n* = 4/45). Woodhouse's Scrub-Jay (*Aphelocoma* *woodhouseii*) is the only predator we identified actively depredating a nest. We identified Pinyon Jay as a probable nest predator after observing Gray Vireos intensely scolding jay flocks adjacent to active nests. Model-averaged nest success (proportion of nesting attempts that were successful) was 0.37 in 2019 and 0.32 in 2020. Pairs often re-nested after nest failure whether due to brood parasitism or nest predation. This propensity for pairs to re-nest (e.g., we observed up to 7 nesting attempts per pair) after failure meant that the impact of brood parasitism on seasonal productivity was not strong. The energetic investment of repeatedly re-nesting could have carryover effects into migration, the non-breeding period, and subsequent breeding seasons; our dataset is not adequate to address those potential effects. Accounting for re-nesting, we estimated that 90% and 85% of pairs produced a successful nest in 2019 and 2020, respectively. In 2020, we observed double brooding for the first time in our study population. This pair initiated a nest on 19 May, which fledged on 16 June; one of four fledglings survived, which we tracked. While the one surviving fledgling was still dependent on adult care, the pair initiated a second nest on ~27 June, which fledged on 25 July, though all 3 fledglings died. During incubation and brooding of the second nest, the surviving fledgling from the first nest remained near the natal territory to be fed by the parents.

Of the 131 nestlings from 2019 and 2020 for which we obtained genetic sex data, 56% were male and 44% were female. This was not statistically different from a 50:50 sex ratio, but it did reduce our population growth rate estimates, in which fecundity is calculated as females fledged per breeding female.

Post-Fledging Survival and Habitat Associations

We monitored 90 Gray Vireo fledglings (*n* = 41 in 2019, *n* = 49 in 2020) from 40 nests (*n* = 21 in 2019, *n* = 19 in 2020); fledgling tracking is ongoing in 2021. Model-averaged daily juvenile survival rate from days 1-12 post-fledging was 0.57 in 2019 and 0.50 in 2020. All mortalities occurred during the first 12 days post-fledging and were attributed to predation and environmental exposure. Fledging dates in 2019-2020 ranged from 6 June to 24 July (mean = 29 June ± 8 days SD) and mean nestling stage length (i.e., the age from hatch at which a fledgling departed the nest) was 12 ± 1 days SD but ranged from 9-15 days. Of the 46 mortalities in 2019-2020, 43% (*n* = 20) were due to predation and 57% (*n* = 26) due to exposure. Of the 20 predation mortalities, 50% (*n* = 10 of 20) were attributed to small mammals or snakes, 35% were attributed to avian predators (*n* = 7 of 20), and 15% (*n* = 3 of 20) were due to unknown predators.

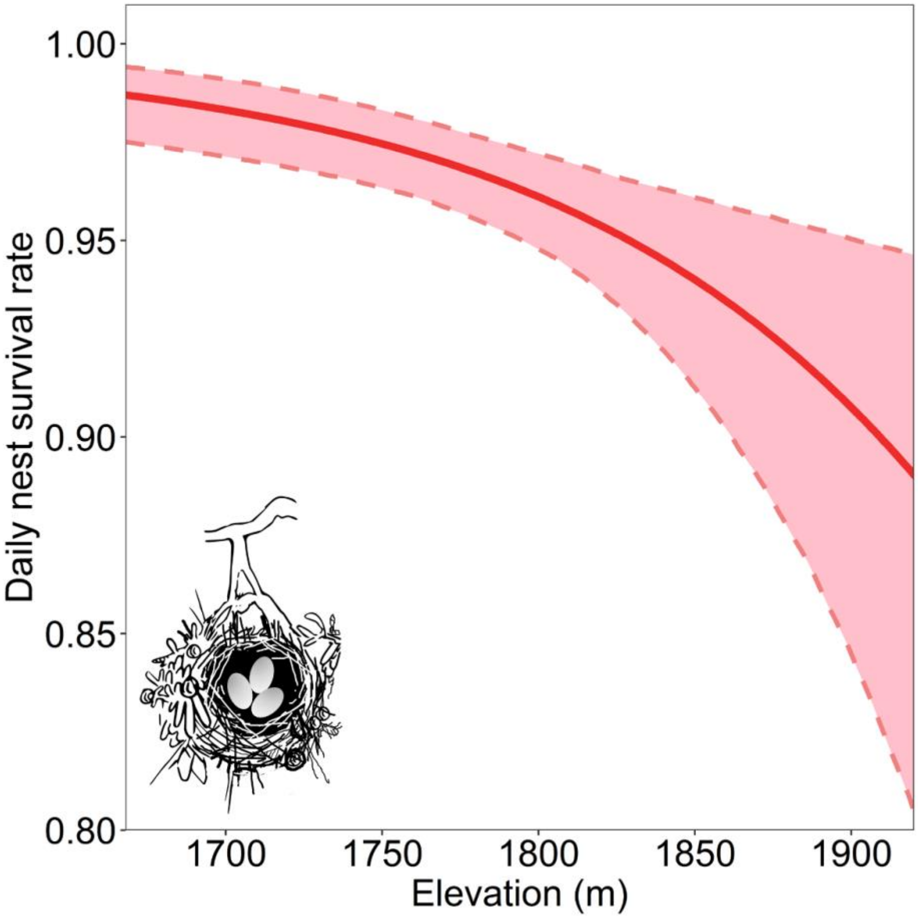

Figure 4. Daily survival rate of Gray Vireo nests as a function of elevation at the Sevilleta National Wildlife Refuge, New Mexico 2019-2020. Estimates were produced from the best-supported logistic exposure model.

Focusing on predation, daily survival of fledglings was positively associated with age (Figure 5). Two models slightly outperformed the age-only model, one including age and hatch date and one including age and ordinal date. These models suggested a tendency toward lower survival for young that fledged later in the season. However, 95% confidence intervals around the effects of hatch date and ordinal date included zero, suggesting weak or non-meaningful effects. Other apparently competitive models (i.e., ordinal date, hatch date, and age from fledging, all of which were likely correlated) did not appear to contain additional informative parameters because those models included only one addition parameter and ΔAICc was < 2 for each (Arnold 2010). Fledgling survival was lowest during the first 2 days post-fledging (i.e., between ages 10-13 days from hatching) with no observed mortality after day 11 from fledge (i.e., ~21-24 days from hatching) in any year (2017-2020). We were unable to determine the date upon which fledglings became independent of adult care due to logistical constraints, as many were still observed with parents as late as 45 days post-fledging (i.e., ~58 days after hatching) and some transmitter batteries began expiring around ~28-36 days of use. We observed wing fluttering behavior and confirmed adults feeding fledglings as late as 43 days post-fledging (54 days after hatching).

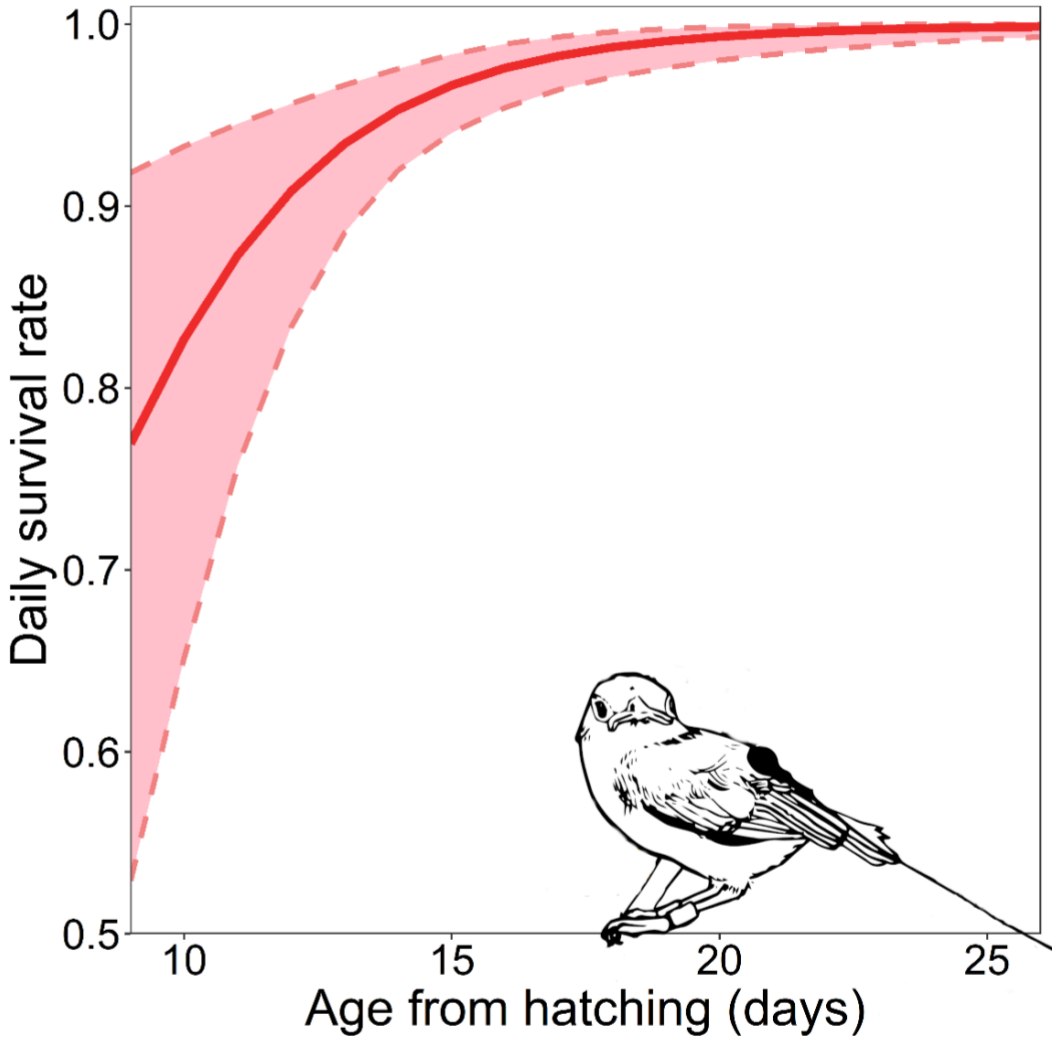

Figure 5. Daily survival rate of Gray Vireo fledglings at the Sevilleta National Wildlife Refuge, New Mexico, from 2017-2020. Estimates were produced from the best-supported logistic exposure model using only fledglings that died due to predation (i.e., excluding fledglings that died due to exposure), with a random effect of brood, and age from hatching as the sole covariate.

During the first 12 days post-fledging at the 25-m-radius scale, Gray Vireo fledglings used areas of greater percent tree cover (mean 13 ± 9%) compared to random points (mean 9 ± 9%; $t = -10.6$, $df = 1206.5$, $P < 0.001$; Figure 6). At the same spatial scale, fledglings and nests (mean 14 ± 10%) were in areas of similar percent tree cover ($t = -0.5$, $df = 194$, $P = 0.2$; Figure 6). Including data from the entire monitoring period, fledglings occupied oneseed juniper during 94% of observations (n = 739/790 observations). For the remaining 6% of observations (51 of 790 observations), fledglings were found most often in oaks, alder-leaf mountain mahogany, and creosote bush. Less than 10 observations were made in each of sumac (*Rhus microphylla*, *R. trilobata*, etc.), piñon pine, cholla, red barberry (*Mahonia haematocarpa*), fourwing saltbush (*Atriplex canescens*), and dead vegetation. Over the entire monitoring period, fledglings used locations with a mean of 61 ± 23% lateral vegetation cover, which did not differ from nest locations (mean 58 ± 26%, t = -1.2, df = 187.5, P = 0.2). Fledglings occupied a range of elevation from 1648-1924 m and were often associated with arroyos (Figure 7).

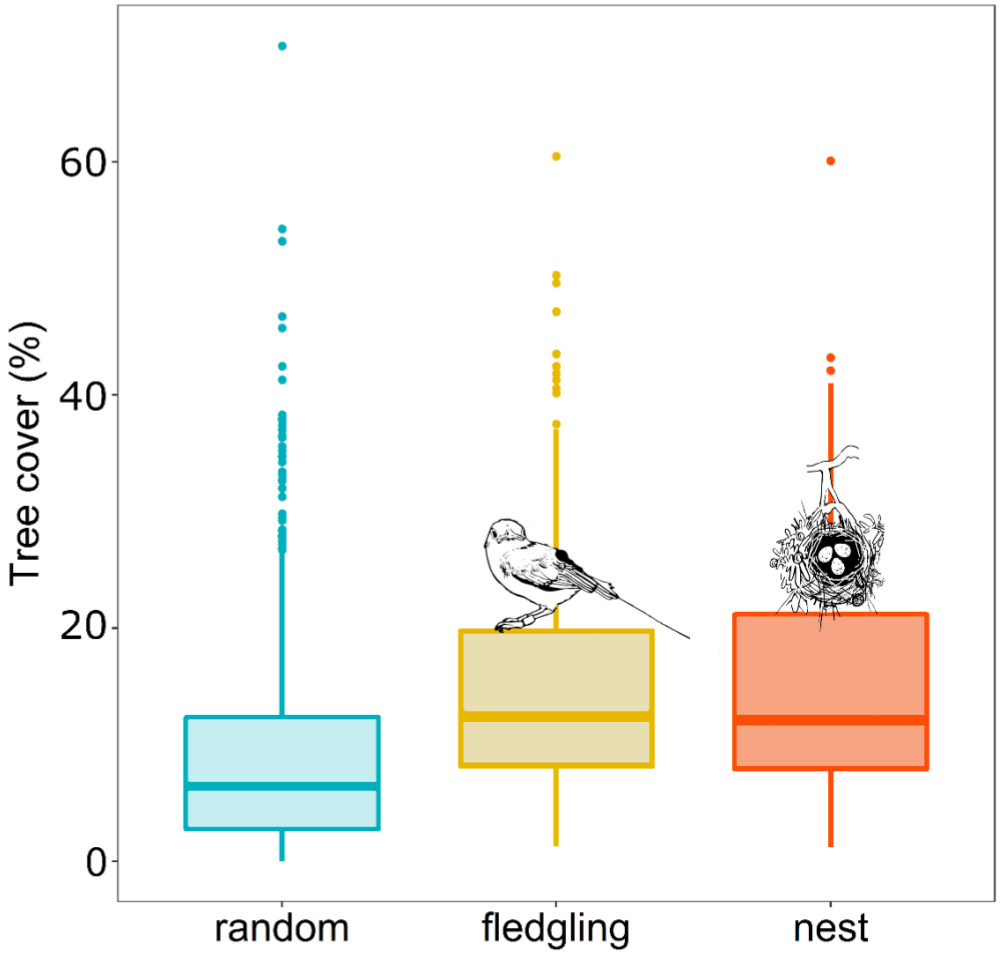

Figure 6. Mean percent tree cover (i.e., cover within 25-m radius buffers) at random, fledgling, and nest locations of Gray Vireos at the Sevilleta National Wildlife Refuge, New Mexico (2017-2020).

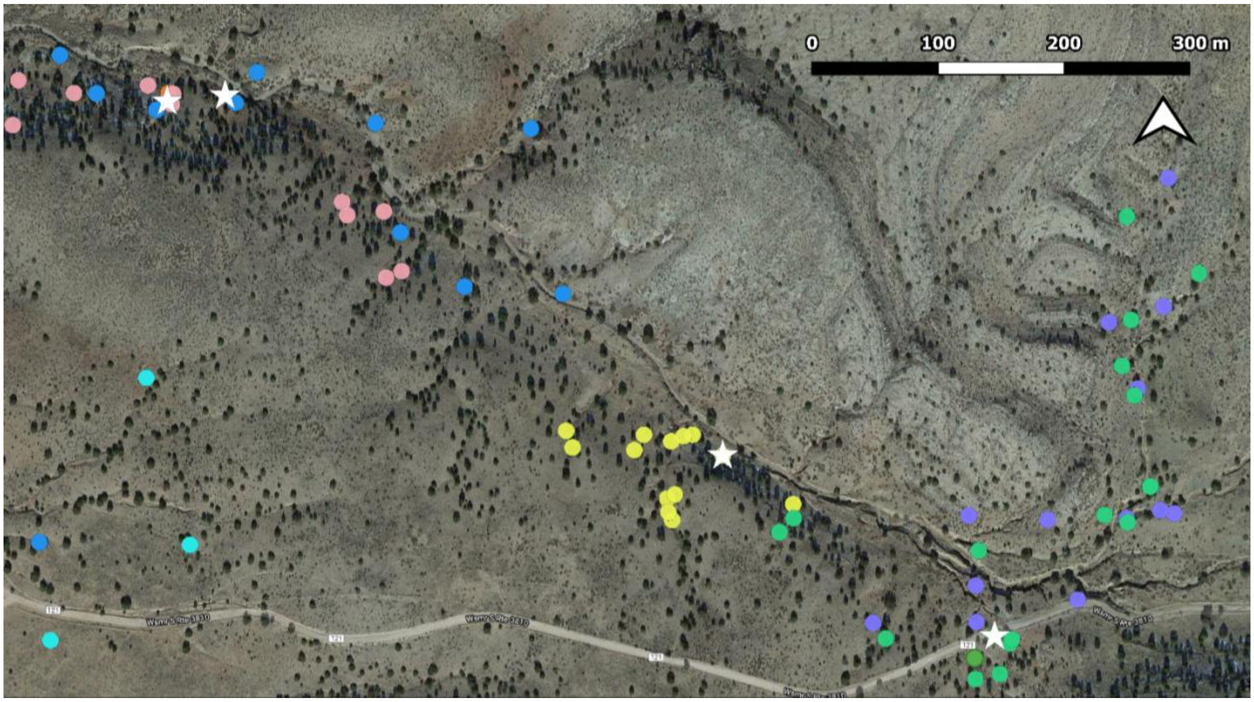

Figure 7. Examples of Gray Vireos using arroyos and areas of relatively dense tree cover within juniper savannas during the nesting and post-fledging stages in 2017-2020 at the Sevilleta National Wildlife Refuge, New Mexico. White stars indicate nest sites and different color circles depict locations where different individual fledglings were observed.

Fledgling Movements and Brood Division Behavior

The minimum daily distance traveled, distance from nests, and variance associated with these measures increased with age in Gray Vireo fledglings (see Fischer 2020). There was a pronounced increase in the variance around minimum daily distance and distance from nest at ~40 days after hatching, attributable to a combination of some birds making relatively large movements at that time and our relatively small sample size of older fledglings. We confirmed brood splitting (i.e., clear spatial separation of male- and female-reared fledglings) in 3 broods from 2017-2020. We do not know what percentage of broods were split because, for most broods, we did not mark all fledglings. We also did not account for broods that may have been split regarding parental sex but did not segregate spatially or for broods in which a fledgling attended to by only one parent may have been the only fledgling that survived the early post-fledging period. In the three broods that were clearly divided (Figure 8), females and their associated fledglings traveled away from the nesting territory, while males and their associated fledglings remained near the nest. Spatial separation in split broods occurred ~9 days after fledging. In 2017, we observed one case of brood division in which an adult female and one fledgling moved west and separated from the male and one associated fledgling between days 8-9 post-fledging (Figure 8-a). In 2018 and

2020, we observed one pair dividing their brood (see 2018 locations in Figure 8-b). The adult female and the associated fledgling moved away from the natal area around day 9, after which they gradually traveled > 2.5 km from the nest and maintained a small area; the adult male and the associated fledgling maintained a larger area around the nest. In 2019, we did not observe any apparent cases of brood division.

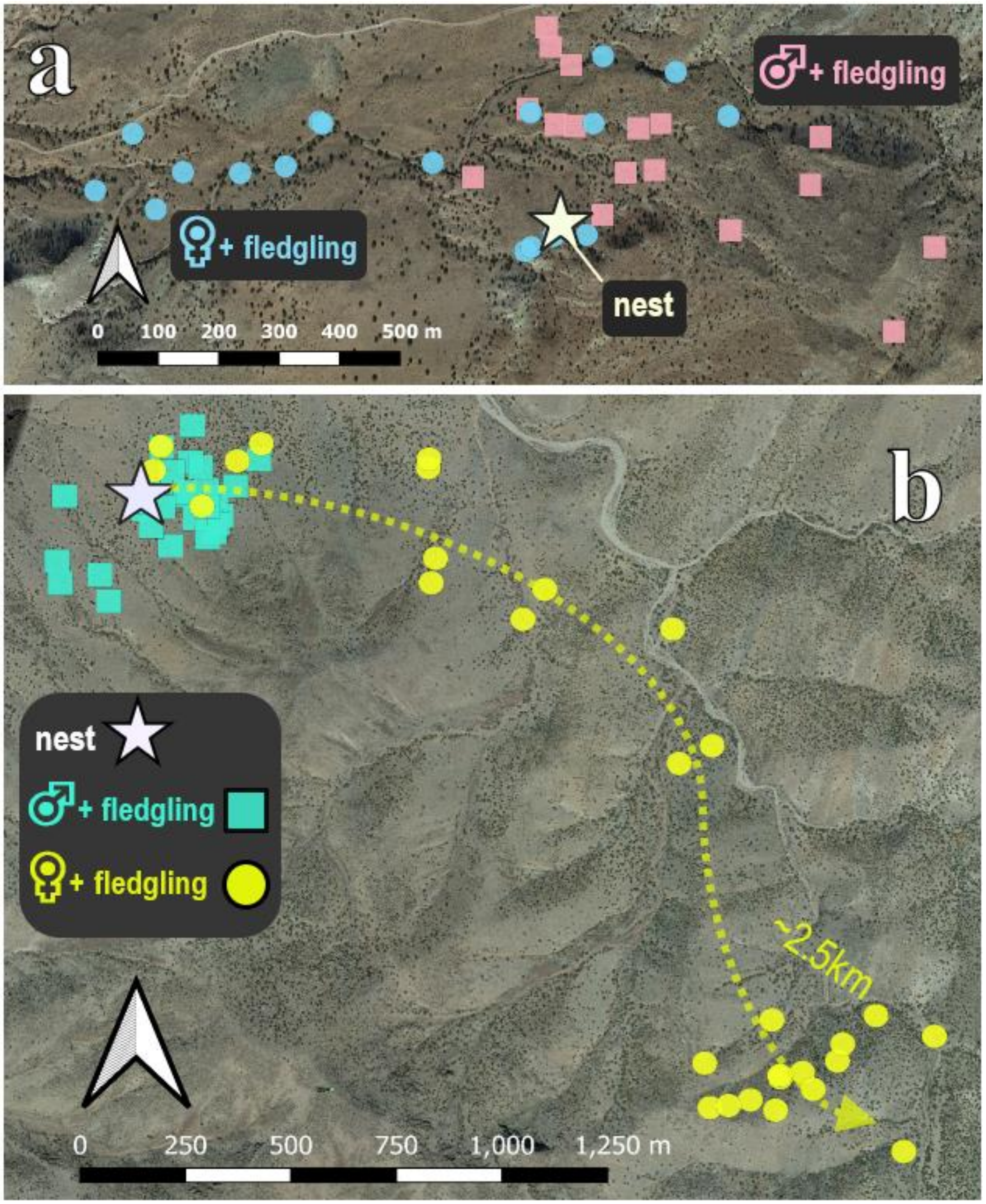

Figure 8. Examples of brood division behavior in Gray Vireo pairs during the post-fledging period in 2017 (a) and 2018 (b) at the Sevilleta National Wildlife Refuge, New Mexico. Stars indicate the nest site and colored circles represent daily observations of fledglings.

Population Growth Modeling

Our female-based birth-pulse stochastic population growth model resulted in an estimated annual growth rate (λ) of 1.00 (95% CI = 0.93 – 1.04), indicating that the population was likely numerically stable in 2019 and 2020.

Discussion

Nest Success and Nesting Habitat Associations

Our model-averaged nest success estimates of 0.32 and 0.37 fall within the range reported elsewhere in New Mexico for Gray Vireos (0.20-0.43; Hargrove et al. 2017). Other accounts of nest success in the state only report apparent success (25-100%), making it more difficult to compare to model-averaged estimates (DeLong and Williams 2006). Nest success at the Sevilleta is much higher than the estimate of 0.08 in a locally declining California population (Hargrove and Unitt 2017). Analyses of nest success, nesting habitat associations and habitat selection are ongoing. Our sample size will increase after including 2017-2018 data in our survival models.

We found that Gray Vireo daily nest survival, but not fledgling survival, was negatively correlated with elevation. It may be that too many trees, or the transition to a piñon pine community at higher elevations, provides more cover for potential nest predators, such as Woodhouse's Scrub-Jays. Woodhouse's Scrub-Jays are strongly tied to pine trees, are opportunistic feeders known to consume eggs, and are increasing in abundance (Koenig et al. 2009, Curry et al. 2020); this species is likely more common at our higher elevation study sites where piñon pines are more abundant. Schlossberg (2006) found that Gray Vireos in Arizona and Utah preferred lower elevations independent of vegetation, and our observations of lower nest survival at higher elevations may be the explanatory mechanism. As suggested by DeLong and Williams (2006) and Harris et al. (2020), Gray Vireos may avoid areas with too low or too high densities of junipers; however, Schlossberg (2006) only found weak support for effects of juniper density on the species' abundance. Within the juniper savannas, nest and fledgling locations were in areas with relatively greater percent juniper cover than the mean for the site as a whole. This suggests that there is an optimal, intermediate range of percent juniper cover, and possibly other tree species, for Gray Vireos in the region. Combined, our findings indicate that large areas of 90 ± 25 junipers per hectare, at relatively low elevations within the range used for nesting, is beneficial to Gray Vireos throughout the breeding season. These conditions are most common along arroyos, and in areas where arroyos are relatively abundant, indicating that preserving vegetative communities within and near arroyos in breeding areas is desirable for Gray Vireo conservation.

Woodhouse's Scrub-Jays are the only nest predator we confirmed. We suspect that these corvids are the most common nest predator, similar to Hargrove and Unitt (2017) finding that California Scrub-Jays (*Aphelocoma californica*) were the most common predators of Gray Vireo nests in California using data from cameras. Hargrove and Unitt (2017) also described gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), and Bewick's Wren (*Thryomanes bewickii*) as nest predators, all of which are present at our study site. Other potential nest predators, some of which are also predators of Gray Vireo fledglings, may include Common Raven (*Corvus corax*), Pinyon Jay, snakes, and other mammals.

We observed considerably lower parasitism rates of 24% and 9% in 2019 and 2020, respectively, compared to other years in our study (~47% in 2017, ~50% in 2018, ~40% in 2021; S.E. Fischer unpublished data). Statewide, parasitism rates are usually >50% (range 0-71%; DeLong and Williams 2006), so it is likely that the Sevilleta is at the lower end of the spectrum. Further study is needed to assess factors explaining parasitism variation among years and sites, such as those that are more heterogeneous or grazed. All such comparisons should take into consideration the Gray Vireo's consistent response to brood parasitism of nest abandonment and re-nesting. Even in areas or years of moderately high parasitism rates, immediate abandonment and several re-nesting attempts (generally between 1-3 but up to 7) can result in high rates of eventual nest productivity. It is possible that the energetic investment in repeated nesting attempts results in carryover effects that manifest in ways we could not measure. However, 1-3 renesting attempts after failure is common in songbirds in the presence or absence of brood parasitism, and abandonment and renesting as an immediate response to parasitism is likely an adaptive behavioral trait because that energetic cost is small compared to the relatively high energetic and fitness cost of spending an entire breeding season raising a cowbird. We observed only one instance of Gray Vireos raising a cowbird nestling/fledgling (S.E. Fischer, unpublished data), suggesting that Gray Vireos are not a beneficial host for cowbirds and are simply parasitized indiscriminately (i.e., not selectively) by cowbirds.

Post-Fledging Survival and Habitat Associations

The post-fledging period in Gray Vireos was similar in many ways to that of other songbirds. The fledgling period survival rate (~0.50-0.57) in Gray Vireos was within the range of survival rates reported in a recent meta-analysis (range 0.23-0.87; Cox et al. 2014). Compared to other small songbirds, post-fledging survival was lower than that of Willow Flycatchers (*Empidonax traillii*, 0.74) and Dusky Flycatchers (*E. oberholseri*, 0.72; Vormwald et al. 2011), Western Bluebirds (*Sialia mexicana*, 0.64; Wightman 2009), Spotted Towhees (*Pipilo maculatus*, 0.69; Shipley et al. 2013), and Golden-cheeked Warblers (*Setophaga chrysoparia*, 0.73; Trumbo 2019), but was higher than Henslow's Sparrows (*Centronyx henslowii*, 0.35; Young et al. 2019) and Sprague's Pipits (*Anthus spragueii*, 0.29; Fisher and Davis 2011). Survival was similar to Golden-winged Warblers (*Vermivora chrysoptera*, 0.52; Streby et al. 2016) and Cerulean Warblers (*Setophaga cerulea*, 0.48; Raybuck et al. 2020).

We observed the highest fledgling mortality during the first few days post-fledging, which is consistent with other altricial songbirds (Anders et al. 1997, Cox et al. 2014). We observed no fledgling mortality after 11 days post-fledging and the modeled daily survival rate reached ~1.0 at ~17 days after hatching, or ~5 days post-fledging. The rate at which fledgling survival approached and stabilized near 1.0 was considerably faster in Gray Vireos than what has been observed in most altricial songbirds (~2 weeks post-fledging for survival to stabilize; Cox et al. 2014). Age was the only significant predictor of the survival rate among the covariates we considered, consistent with many other post-fledging studies (Cox et al. 2014). Hatching date and ordinal date each tended towards lower survival later in the breeding season, but confidence intervals around their effects included zero. In our study system, a fledgling's age from hatching is a more biologically relevant measure of development than the number of days since it fledged, and we suspect this may be the case in other systems in which age at fledging varies among and within broods.

Small mammals or snakes accounted for the majority of Gray Vireo fledgling predation at the Sevilleta NWR, though in 2019-2020 we did not confirm exact predator species. In 2017-2018, we were able to identify 2 predators and one probable predator; we tracked one transmitter to a Swainson's Hawk (*Buteo swainsoni*) nest, one to a desert striped whipsnake (*Masticophis taeniatus taeniatus*), and one to a pile of feathers under a tree on which we observed a Loggerhead Shrike (*Lanius ludovicianus*) on the same day (Fischer 2020). Potential, but unconfirmed predators of Gray Vireo fledglings included small mammals, such as white-throated woodrats, Southern Plains woodrats, rock squirrels (*Ostospermophilus variegatus*), and Texas antelope squirrels (*Ammospermophilus interpres*); and mesocarnivores such as coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus scottii*; Hanna 1944, Barlow et al. 1999). Other potential predators included Northern Mockingbird (*Mimus polyglottos*), Scott's Oriole (*Icterus parisorum*), and several snake species.

Lateral vegetation cover at fledgling locations and percent tree cover within 25-m radius buffers around fledgling locations were not associated with fledgling survival, suggesting that predation on Gray Vireo fledglings is either independent of micro- and meso-scale vegetation characteristics or varies with habitat characteristics we did not consider. Given the high availability at our study area of vegetation consistent with that used by Gray Vireos and the use by Gray Vireos of areas similar in habitat structure throughout the nesting and post-fledging periods, it is possible that predation rates within our study area are relatively consistent but may vary at larger geographic scales (i.e., source-sink dynamics among isolated habitat patches, sites, or regions). Additional analyses, such as those using different buffer sizes and/or configurations, may add further context to our results. Nests and fledglings were located in areas with significantly denser tree cover compared to random points in our study area, consistent with previous studies (Johnson et al. 2014, Harris et al. 2020, Wickersham et al. 2020). However, Gray Vireos tend not to nest in areas with > 30% juniper cover (50-m radius scale; Harris et al. 2020), suggesting again that there is an optimal juniper density for this species. Based on the areas used for nesting and by fledglings in our study, ~90 ± 25 juniper trees per hectare over as large of an area as practicable, is desirable. We did not statistically assess the dispersion of trees within the 25-m buffer areas we used to assess tree density. However, anecdotally, we observed no apparent pattern of fledglings selecting for or against trees growing in relative isolation or clumps.

Fledgling Movements

Despite considerable movements, fledgling Gray Vireos occupied juniper-dominated areas that were nearly identical in structure to their nest locations. A suite of other species that do not shift habitat use from the nesting to the post-fledging stage and can be considered habitat specialists like Gray Vireos include: Willow Flycatchers (a riparian-obligate; Vormwald et al. 2011), Sprague's Pipits (a grassland-obligate; Fisher and Davis 2011), Dickcissels (*Spiza americana*, a grassland-obligate; Jones et al. 2017), and Black-capped Vireos (*Vireo atricapilla*, juniper-oak shrubland species; Martinez et al. 2019). This congruity between nesting and post-fledging habitat may indicate that adult Gray Vireos select nest sites that are already adjacent to, or within, high quality post-fledging habitat, as previously suggested for grassland songbirds (Jones et al. 2017). Given the large post-fledging areas used by Gray Vireos in our study, it is possible that Gray Vireos use non-nesting cover types or maintain smaller post-fledging home ranges in other, more heterogeneous landscapes. We were unable to investigate whether habitat associations of fledgling Gray Vireos change after independence from adult care, as they do in some songbirds, including the Black-capped Vireo (Dittmar et al. 2014, 2016), because even 45 days outside the nest was not long enough to observe fledglings moving independently from adults. However, in our study area, there are few options of other cover types with trees or shrubs taller than creosote or juniper within 10 km of our sites, so changes in cover type associations would require large movements or considerable elevational shifts upon independence.

Conclusion

We intended to identify habitat characteristics associated with variation in nest and fledgling survival to inform management to benefit Gray Vireos. Aside from elevation being negatively correlated with nest survival, we found that nest and fledgling survival rates did not significantly vary with measured habitat variables. Gray Vireos almost exclusively used juniper throughout the entirety of the breeding season, including the nesting and post-fledging stages, indicating the importance of this habitat type in the Central Management Unit identified in the Gray Vireo Recovery Plan (NMDGF 2007). Including all causes of mortality, we estimated 50-57% period survival for fledglings from 2019-2020 and 32-37% success for nests from 2019-2020. Population growth rates derived from female-based stochastic birth-pulse models suggest that Gray Vireos at Sevilleta NWR were numerically stable in 2019-2020. However, interannual variation in fledgling survival may cause fluctuations in ƛ, especially during droughts. Analyses incorporating data from previous years (2017-2018) are ongoing and additional data collection is ongoing. Additional full-breeding-season research, including post-fledging ecology of both dependent and independent fledglings, will be needed in more disturbed and heterogeneous landscapes to identify potential habitat factors limiting population productivity and to determine if habitat conditions at Sevilleta NWR may simply be a benchmark to be replicated elsewhere. Because of the ongoing habitat alterations (e.g., juniper chaining, prescribed fire, herbicide treatments, natural gas development, and cattle grazing; see Johnson et al. 2014, Hartsell et al. 2020) across the Gray Vireo's relatively limited and patchy breeding distribution, controlled experimental research with pre- and post-treatment data collection will be beneficial to determine management treatment impacts on this SGCN. Additional empirical estimates of Gray Vireo fledgling survival and nest success, as well as habitat variables that impact these parameters, are needed across the vireo's breeding range, especially in locally declining populations, and where habitat associations differ from those at the Sevilleta NWR (e.g., California; Hargrove and Unitt 2017). More broadly, given the importance of fledgling survival to avian population growth, full-season productivity (including the post-fledging period) studies are an urgent need in deserts, arid lands, and semi-arid lands, where avian communities are collapsing (Sauer et al. 2017, Iknayan and Beissinger 2018).

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