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Research Paper

Post-fledging survival, movements, and habitat associations of Gray Vireos in New Mexico

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ABSTRACT. Annual population growth in songbirds can be particularly sensitive to post-fledging survival, but research and management are frequently biased toward the nesting stage. Post-fledging information is particularly scarce for species breeding in desert bird communities, many of which have collapsed in recent decades. During 2017–2019 at Sevilleta National Wildlife Refuge, New Mexico, USA, we used radio telemetry to monitor survival, movements, and habitat associations of 90 fledgling Gray Vireos (*Vireo vicinior*), a desert-dwelling species of conservation concern. We used logistic exposure models to investigate the relationship between fledgling survival and habitat features at two spatial scales. Overall, we estimated that 51 ± 8% of fledglings survived the monitoring period. All mortalities occurred during the first 12 days post-fledging and were attributed to predation and environmental exposure. In daily survival models focused on predation mortalities, age was the strongest predictor of survival. Daily survival rate was not related to any habitat variables we measured. Percent tree cover used by birds during the first 12 days post-fledging was similar 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, habitats used by Gray Vireos during the post-fledging period were similar to those used for nesting in our study population, indicating that maintenance of large patches of moderately dense juniper is desirable for this species. More study is needed from populations in less pristine and more heterogeneous landscapes. More broadly, given the importance of first-year survival in demographic models and the declines of dryland birds, information is needed on the post-fledging period of many desert songbirds.

Survie après l'envol, déplacements et associations avec l'habitat de Viréos gris au Nouveau-Mexique

RESUME_. La croissance annuelle des populations de passereaux peut être particulièrement sensible à la survie après l'envol, mais la recherche et la gestion sont souvent orientées vers le stade de la nidification. Les données suivant l'envol sont particulièrement rares pour les espèces nichant au sein de communautés d'oiseaux de désert, dont beaucoup se sont effondrées au cours des dernières décennies. En 2017-2019, au Sevilleta National Wildlife Refuge au Nouveau-Mexique (États-Unis), nous avons utilisé la radiotélémétrie pour suivre la survie, les déplacements et les associations avec l'habitat de 90 Viréos gris (*Vireo vicinior*) prêts à l'envol, une espèce désertique dont la conservation est préoccupante. Nous avons utilisé des modèles logistiques d'exposition pour étudier la relation entre la survie des oisillons et les caractéristiques de l'habitat à deux échelles spatiales. Dans l'ensemble, nous avons calculé que 51 ± 8 % des oisillons ont survécu durant la période suivie. Toutes les mortalités sont advenues au cours des 12 premiers jours après l'envol et ont été imputées à la prédation et à l'exposition à l'environnement. Dans les modèles de survie quotidienne axés sur les mortalités imputables à la prédation, l'âge était le facteur prédictif de la survie le plus fort. Le taux de survie quotidien n'était lié à aucune des variables de l'habitat que nous avons mesurées. Le couvert forestier utilisé par les oiseaux pendant les 12 premiers jours suivant l'envol avait un pourcentage similaire à celui des sites de nidification, mais était supérieur à celui de sites choisis aléatoirement. De même, les oisillons ont utilisé des arbres et des arbustes ayant une couverture végétale latérale similaire à celle des sites de nidification. La distance quotidienne minimale parcourue, la distance par rapport aux nids et la variance associée à ces mesures ont toutes augmenté avec l'âge. À l'exception de l'utilisation d'une plus grande aire, les Viréos gris ayant récemment pris leur envol ont utilisé des milieux qui étaient semblables à ceux utilisés pour la nidification dans la population à l'étude, ce qui indique que le maintien de grandes parcelles de genévriers modérément denses est souhaitable pour cette espèce. D'autres études sont nécessaires et devraient cibler des populations vivant dans des paysages moins vierges et plus hétérogènes. De façon générale, étant donné l'importance de la survie au cours de la première année dans les modèles démographiques et le déclin des oiseaux de zones sèches, les futures recherches devraient se concentrer sur la période suivant l'envol de nombreux passereaux de désert.

Key Words: *desert ecology; fledgling songbird; full annual cycle; juniper savanna; juvenile survival; radio telemetry; Vireonidae; Vireo vicinior*

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INTRODUCTION

Understanding population dynamics and demography within the context of a species' life cycle stages is a critical step toward effectively implementing conservation and management strategies (Anders and Marshall 2005, Streby and Andersen 2011, Kramer et al. 2018). In migratory songbirds, this means considering the full annual cycle, including periods that may be difficult to study, such as migration (Webster et al. 2002, Marra et al. 2015), the nonbreeding season (Sillet and Holmes 2002, Ritterson et al. 2021), and the post-fledging period (Anders and Marshall 2005, Cox et al. 2014). Traditionally, due in part to technological limitations, many studies that quantify habitat associations of breeding songbirds only consider the nesting period, thereby neglecting the post-fledging period (Streby et al. 2014). However, habitat associations and relationships with survival can differ between the nesting and post-fledging periods (e.g., Anders et al. 1998, Marshall et al. 2003, Streby et al. 2011, Delancey and Islam 2019; but see also Fisher and Davis 2011, Vormwald et al. 2011, Jones et al. 2017, Goguen 2019), and annual population growth (λ) in songbirds can be particularly sensitive to fledgling survival (Anders and Marshall 2005, Streby and Andersen 2011, Cox et al. 2014).

Fledgling survival in most altricial songbirds is generally lowest during the first week after departing from the nest, likely because young fledglings are usually incapable of coordinated, sustained flight and lack fully developed feathers, increasing their vulnerability to predation and exposure to other environmental factors (Sullivan 1989, Anders et al. 1997, Tarwater et al. 2011, Lloyd and Martin 2016). The post-fledging period in altricial songbirds can be divided into two stages: (1) the dependent stage, during which fledglings are attended by parents, and (2) the independent stage, after independence from adult care and prior to migration or dispersal (Dybala et al. 2013, Cox et al. 2014, Goguen 2019). The length of these stages varies among, and sometimes within species (Tarwater and Brawn 2010, Cox et al. 2014). As fledglings age, their minimum daily distance traveled and distance from the nest typically increase (Cohen and Lindell 2004, Vitz and Rodewald 2010, Fisher and Davis 2011, Vormwald et al. 2011), and many factors can influence movements and survival, such as food availability (Vitz and Rodewald 2011, Jenkins et al. 2017, Ruhl et al. 2020). In North America, most post-fledging studies have been conducted in temperate forests, grasslands, and riparian areas (Cox et al. 2014). Knowledge of full annual cycle ecology, including the post-fledging period, is especially limited for arid land songbirds and other western USA Nearctic-Neotropical migrants (McKinnon and Love 2018, Hedley 2019). This dearth of knowledge is especially concerning given the ongoing community-wide declines in desert birds that have been documented over the past century (Iknayan and Beissinger 2018, Riddell et al. 2019, Riddell et al. 2021).

One such desert-dwelling species, the Gray Vireo (*Vireo vicinior*), is a small (~11–14 g) migratory songbird that breeds primarily in piñon-juniper 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). Gray Vireos are listed as threatened in New Mexico (NMDGF 2016), as a species of conservation concern by U.S. Fish and Wildlife Service (USFWS 2008), and as a Watch List Species by Partners in Flight (Rosenberg et al. 2016). These designations are primarily because of a lack of demographic information, a restricted distribution, a relatively small global population (estimated at ~560,000 individuals; Rosenberg et al. 2016), and ongoing habitat alterations (Schlossberg 2006, NMDGF 2007, Johnson et al. 2014). Range-wide population trends for Gray Vireos are unclear because this species occupies remote breeding areas that are often away from roads where large-scale surveys generally occur (Barlow et al. 1999, Schlossberg 2006, Hargrove and Unitt 2014, 2017). For example, the Breeding Bird Survey (BBS; U.S. Geological Survey) does not report Gray Vireos from California where remote off-road studies have described precipitous declines of ~75–95% since the 1940s (Hargrove and Unitt 2014, Hargrove and Unitt 2017). With the caveat of potentially poor coverage of breeding areas, BBS data suggest that Gray Vireo populations are increasing range-wide (see Pardieck et al. 2019). Demographic data other than nest success are not available for this species; nest success is typically between 25% and 50% in New Mexico (DeLong and Williams 2006, Fischer 2020; S. E. Fischer, *unpublished data*) but is as low as 8% in some populations, such as in California (Hargrove and Unitt 2017). Empirical estimates of other demographic rates, such as post-fledging survival, are necessary for informing science-based conservation decisions, especially given the lack of knowledge on Gray Vireos compared to many North American songbirds (Schlossberg 2006, NMDGF 2007, Fischer 2020).

We used radio telemetry to quantify post-fledging movements, survival, and habitat associations of dependent fledgling Gray Vireos. We hypothesized that fledgling survival and movements would be lowest in the first few days outside the nest, as in other altricial songbirds (Cohen and Lindell 2004, Fisher and Davis 2011, Vormwald et al. 2011, Cox et al. 2014). We expected fledglings to be independent of adult care within approximately four weeks of fledging, consistent with many other songbirds (Cox et al. 2014). We hypothesized that fledglings in areas of sparser tree cover (i.e., low abundance of trees and shrubs) would experience greater rates of predation compared to those in areas with denser tree cover, because predators might have greater search efficiency and greater opportunity to detect fledglings in less structurally complex areas. Lastly, we expected fledglings to use areas with greater percent tree cover compared to that around nests based on differentiation in habitat associations between nesting and post-fledging stages in many songbirds (Anders et al. 1998, Marshall et al. 2003, Vitz and Rodewald 2006, Streby et al. 2011, Raybuck et al. 2020).

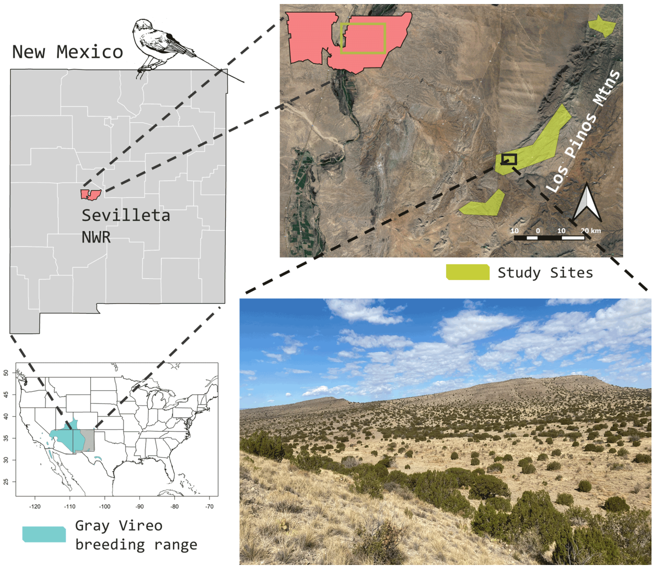
METHODS

This research was conducted in compliance with University of Toledo IACUC protocol #108708, Sevilleta NWR Special Use permit #19-09R, NMDGF permit #3673, and federal Bird Banding Lab permit #24072.

Study area

We conducted this study at Sevilleta National Wildlife Refuge (NWR), a 93,000-ha refuge in Socorro County, New Mexico, USA, that encompasses a variety of arid land biomes at the northern limit of the Chihuahuan Desert (Fig. 1). The Sevilleta NWR is managed by the United States Fish and Wildlife Service (USFWS) and was relatively undisturbed during and prior to our study; cattle have not grazed on Sevilleta NWR since 1973, and habitat alteration is minimal. Our study areas were on the eastern edge of Sevilleta NWR within the foothills of Los Pinos Mountains (mean elevation ~1785 m; 34°13′13″ N, 106°41′35″ W; Fig. 1), where breeding populations of Gray Vireos have been previously monitored (see Vizzachero 2016, Stevens and Fischer 2018). Vegetation in the study area was predominantly juniper (*Juniperus monosperma*) savanna comprised mainly of juniper trees ranging from ~1 to 8 m (typically 2 to 4 m) tall, creosote bush (*Larrea tridentata*), and other shrubs (e.g., *Quercus* spp., *Rhus* spp., and *Cercocarpus montanus*), grasses (e.g., *Bouteloua* spp.), and succulents (e.g., *Yucca* spp., *Cylindropuntia* spp., and *Opuntia* spp.), with piñon pines (*Pinus edulis*) at higher elevations.

Fig. 1. Study area within Los Pinos Mountains on the eastern side of Sevilleta National Wildlife Refuge (NWR), New Mexico, USA, where we studied post-fledging ecology of Gray Vireos (*Vireo vicinior*).



Field methods

Nest searching and monitoring

We searched for nests from May to July in the years 2017–2019 by following Gray Vireos exhibiting nesting behavior, e.g., singing or carrying nesting material, and by attaching radio transmitters to and tracking adult females to their nests during the day and night. Radio telemetry is a cost-effective tool for finding nests and can reduce potential confirmation bias in traditional searching methods (Powell et al. 2005, Peterson et al. 2015). We recorded nest locations using handheld Global Positioning System (GPS) devices with waypoint averaging to improve accuracy. We monitored nests every 3 to 4 days to record adult activity, nest contents (i.e., presence and number of eggs or nestlings of Gray Vireos and Brown-headed Cowbirds [*Molothrus ater*]), and nest fate, i.e., active or failed. We minimized time spent at nests and minimized contact with nest contents or substrates to reduce potential cues for nest predators. Gray Vireo nests are often parasitized by Brown-headed Cowbirds (~50% parasitism in New Mexico; DeLong and Williams 2006), usually resulting in nest abandonment; Brown-headed Cowbird young fledge from < 1% of Gray Vireo nests (S. E. Fischer, *personal observation*). During the late nestling stage, we observed nests daily to determine fledge date and to begin tracking fledglings.

Nestling banding and radio transmitter attachment

We used 0.6-g radio transmitters (~5% of body mass; Blackburn Transmitters, Nacogdoches, Texas, USA), with a modified figure-eight leg-loop harness (Rappole and Tipton 1991, Streby et al. 2015) identical to methods used in other studies of small migratory songbirds with no apparent negative effects (e.g., Streby et al. 2013, Peterson et al. 2016). We expected transmitter harnesses to degrade and fall off approximately two months after deployment; no marked nestlings observed breeding in subsequent years have retained transmitters (S. E. Fischer, *personal observation*). Nestlings were removed from nests ~2 to 3 days prior to expected fledging and marked with one plastic color band and a metal U.S. Geological Survey numbered band. We randomly selected and attached radio transmitters to one to four, but usually two or three, nestlings per nest. Following sampling and tagging, all nestlings were returned to their nest.

Tracking fledglings and sampling vegetation

We used ground-based radio telemetry methods to track each fledgling daily in 2017 and 2018, and to monitor survival, space use, and habitat associations. In 2019, on account of logistical constraints induced by an unexpectedly large sample size, we reduced tracking frequency to once every 3 days after fledglings reached 12 days post-fledging. Inclement weather sometimes prohibited daily tracking, such as when access roads were washed out in monsoon rain events, but the logistic exposure survival models we used are robust to variable interval lengths (Shaffer 2004). We tracked each fledgling until encountering one of the following: (1) fledgling mortality, (2) expiration of the radio transmitter battery at ~50 days, which occurred at different fledgling ages because we sometimes reused transmitters, or (3) radio signal loss. If radio signals were lost < 7 days post-fledging, we assumed predation mortality because all radio transmitters were deployed with > 14 days of remaining expected battery life and because no living fledgling we tracked moved outside of signal detection range during this period (see also Bernath-Plaisted et al. 2021).

Upon relocating each radio-marked fledgling, we recorded GPS location, fate (i.e., alive or dead), presence or absence of other Gray Vireo fledglings (radio-marked or not) or adults nearby, presence or absence of fledgling or adult behaviors (e.g., foraging, feeding, begging), fledgling height from ground, and characteristics of the vegetation the fledgling was using (i.e., substrate and lateral vegetation cover). We estimated lateral vegetation cover, a measure of the concealment of nests and fledglings in individual trees and shrubs, 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 and fledgling location, i.e., where the fledgling was initially observed when tracking (see Streby and Andersen 2013a). We visually estimated percent cover in each of the eight squares while standing 10 m North and 10 m East of the profile board. All 16 values were then averaged to obtain one estimate of lateral vegetation cover at nest and fledgling locations (Streby and Andersen 2013a).

When we relocated a fledgling that had been depredated, we followed similar methods to Streby et al. (2016) and Yackel Adams et al. (2006) to determine whether the fledgling was depredated by a mammalian or an avian predator. We attributed predation to small mammals if radio transmitter signals emanated from underground burrows, or if we recovered transmitters with legs, feet, or leg bands (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 that predation was caused by avian predators when we recovered radio transmitters with kinked antennas or if we found transmitters in or near a pile of plucked feathers. We classified mortality as caused by 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 to occur following death by exposure.

Data analysis

Fledgling movements and habitat associations

We obtained 1-m spatial-resolution digital orthophotography (National Agricultural Imagery Program [NAIP]) available through New Mexico Resource Geographic Information System (RGIS; http://rgis.unm.edu/) to visualize our study areas. We established the boundaries of our study sites post-hoc such that the study area included all nest and fledgling locations with a buffer of 100 m because some radio-marked females selected nest sites outside of our search area and because we could not predict where fledglings would travel. We used supervised classification in ArcMap (10.7.1) to differentiate shrubs and trees (e.g., juniper, piñon pine, oaks, creosote; hereafter, “tree”) from bare ground, rock, and smaller vegetation (e.g., forbs) to create a measure of percent tree cover. Grasses and other low ground vegetation were excluded from tree cover classification because fledglings were not observed using those substrates. We imported the classified tree cover raster for further analysis in QGIS, an open-source mapping software (QGIS Development Team 2020). We classified each cell of the raster as binomial (i.e., each cell is tree or not tree), such that the percent of an area covered by trees and shrubs could be calculated at any scale across our study site.

We created 25-m radius buffers around each fledgling location during the first 12 days post-fledging and around each nest location to explore potential relationships between survival and habitat features conducive to the most likely predators, such as small mammals and snakes. We selected a 25-m radius (~1964 m^2) buffer by consulting literature for home range sizes of small mammals in the southwest USA (Macêdo and Mares 1988, Conditt and Ribble 1997) because small mammals accounted for 62% of predation mortalities. We assumed this 25-m radius buffer was biologically relevant based on potential predators and was small enough to capture potential variation in survival among areas used by fledglings; Harris et al. (2020) included the same buffer size to describe nesting habitat associations in Gray Vireos. We generated 600 random points across our study area and calculated tree cover within 25-m radius buffers around those points to determine if tree cover at nesting and fledgling locations differs from what is generally available. Within each buffer, we calculated the percent tree cover using zonal statistics by dividing the sum (number of tree pixels) by the count (total number of pixels) and multiplying by 100. Percent tree cover from buffers was then used as a covariate in survival models. We counted the number of juniper trees within 100 randomly selected fledgling location buffers to estimate relative juniper density in areas used by fledglings for applications in conservation and management. We then multiplied each juniper count by five to estimate number of juniper trees per hectare.

We calculated minimum daily distance traveled and daily distance from the nest using the Haversine (i.e., the shortest distance between daily points on the sphere) method in the geosphere package in R (1.5–10; Hijmans 2019). We included only distances between consecutive daily locations because it is inappropriate to interpolate minimum distance moved over multiple days (e.g., minimum distance over 2 days cannot be divided by 2 to estimate daily distance unless the individual moves constantly in one direction). We averaged daily movement values for broods in which individuals fledged at the same age from hatching to avoid pseudoreplication in all movement analyses. However, some Gray Vireos clutches hatched and fledged asynchronously in our study. To account for broods in which individuals fledged asynchronously, we randomly selected one individual per brood for analyses, unless we had more observation data for one individual, in which case we chose that individual for movement analyses. Therefore, we included 45 individuals ($n = 591$ locations) in analysis of minimum daily distance traveled and 34 individuals ($n = 697$ locations) to analyze daily distance from nest. We acknowledge the possibility that broodmates with more observation data were more likely to be observed and may have moved shorter distances; however, broodmates tended to move similar distances to one another. 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 included both in movement analyses. We defined brood division as clear spatial segregation between adult male- and female-reared fledglings (see Fischer 2020). We present movement results as medians instead of means because movement data were not normally distributed.

Fledgling survival and logistic exposure modeling

Prior to running survival models, we used Winterstein’s third chi-square test of independence to assess interdependence among fledglings within broods in which we monitored more than one fledgling (Winterstein 1992). Winterstein P-values < 0.05 indicate that survival among broodmates is non-independent and that broodmates should not be treated as independent biological units (Winterstein 1992). Survival of broodmates was interdependent (Winterstein’s third chi-square test, $P < 0.001$) and therefore we included a random brood effect in all survival models. In R (v3.6.1; R Core Team 2018), we used the logistic exposure method (Shaffer 2004) to estimate fledgling survival and to model associations between covariates and survival. Covariates included age from hatching, hatch date, fledgling height from ground, elevation, substrate lateral vegetation cover, site, and percent tree cover within a 25-m radius. We used hatch date as the covariate to test for temporal variation in survival because all date-related covariates (i.e., ordinal date, fledge date, and hatch date) were highly correlated (Pearson’s correlation coefficient, $r > 0.85$ for all comparisons). In our models, we included only the first 12 days post-fledging because we did not observe any mortalities more than 11 days after fledging. We censored non-predation exposure mortalities from analysis of habitat associations with survival because those mortalities were apparently associated with annual climatic conditions and not with vegetation variables (Fischer 2020, see also Streby et al. 2016). However, we included in our predation-related analysis the survival of these fledglings prior to exposure-related mortality, unless they died in the first day after fledging, to avoid biasing survival estimates downward by censoring these birds altogether and excluding survival days. Predation rates did not differ among years in preliminary models (Fischer 2020), so we included data from all years in each model here. In preliminary analysis, we compared all single-variable models and found that age far outperformed all other variables, as expected. We then compared seven two-variable models including age plus each other variable, including one model with a quadratic term for age, for a total of nine models including the null constant survival and age-only models. Models were ranked and chosen using Akaike's Information Criterion adjusted for small sample sizes (ΔAICc; Anderson and Burnham 2002).

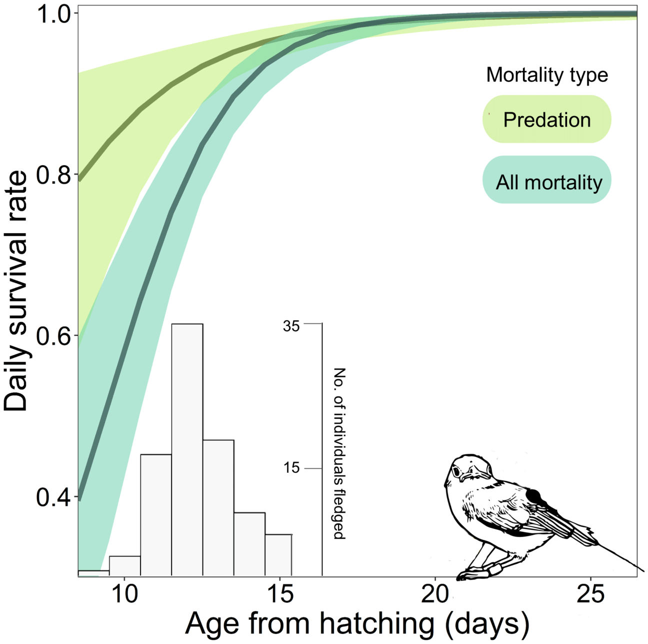
Most fledgling songbird studies have defined fledgling age as the number of days since an individual left the nest (but see Cohen and Lindell 2004). However, Gray Vireos fledged from their nests 9–15 days after hatching, and this variation was not attributable to variation in growth rates, i.e., 14 days after hatching, birds were developmentally indistinguishable regardless of whether they had fledged. We therefore used age from hatching in our movement analyses and survival models to account for the wide range of development at the time of fledging. We used a two-sample *t*-test to compare lateral vegetation (microhabitat) cover between fledgling and nest points and a one-way ANOVA test to compare tree (macrohabitat) cover among fledgling, nest, and random points. We present means ± SE unless noted otherwise.

We used R (v3.6.1; R Core Team 2018) to derive overall Gray Vireo fledgling daily survival estimates, including data from 2017-2019 and all types of mortality for demographic applications and comparisons with other populations and species. When estimating period survival, we applied a correction to the daily survival estimates to account for the proportion of fledglings in the sample each day because fledglings departed the nest at different ages from hatch (range: 9–15 days; median and $\bar{x}$ = 12 days). This correction was necessary because, for example, an individual that fledged at 12 days was not in the sample for ages 9–11 days.

RESULTS

We monitored 90 Gray Vireo fledglings (*n* = 30 in 2017, *n* = 19 in 2018, and *n* = 41 in 2019) from 42 nests (*n* = 13 in 2017, *n* = 8 in 2018, *n* = 21 in 2019). The mean length of the monitoring period was 28 ± 9 days (maximum = 45 days). Gray Vireos fledged from nests from 14 June to 19 July ($\bar{x}$ = 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 to 15 days (Fig. 2). Model-averaged fledgling period survival pooled across years, and corrected for variable ages from hatching, was 0.51 ± 0.08 and the mean daily survival rate was 0.95 ± 0.01 (*n* = 46/90 survived the monitoring period). Of the 44 mortalities, 21 (48%) were attributed to predation and 23 (52%) were attributed to exposure. Of the 21 predation mortalities, 13 (62%) were attributed to small mammals or snakes, six (29%) to avian predators, and two (9%) to unknown predators. We identified two individual predators and one probable predator. We tracked one radio transmitter to a Swainson's Hawk (*Buteo swainsoni*) nest that contained one nestling, and one radio-marked fledgling was ingested by a New Mexico garter snake (*Thamnophis sirtalis dorsalis*). We also suspected that one Gray Vireo fledgling was depredated by a Loggerhead Shrike (*Lanius ludovicianus*) after we recovered a radio transmitter from a pile of feathers under a tree in which we observed a Loggerhead Shrike on the same day.

Fig. 2. Daily survival rate and frequency distribution of age at fledging of Gray Vireo (*Vireo vicinior*) fledglings (n = 90) at Sevilleta National Wildlife Refuge, New Mexico, from 2017 to 2019. Top curve includes only predation-related mortalities, which we included in habitat-related analyses; the bottom curve includes all mortalities (i.e., predation and environmental exposure). Both survival models included a random effect of brood and age from hatching as a covariate. Note that our period survival estimate (0.51 ± 0.08) accounted for variable ages at fledging and is not simply a product of survival from age 9 days onward.



Fledgling survival and habitat associations

Considering only mortalities attributed to predation, daily survival of fledglings was positively associated with age (Fig. 2). One model that included both age and hatch date slightly outperformed the age-only model (Table 1). This model suggested a tendency toward lower fledgling survival when hatching later in the season; however, from the earliest hatch date (2 June) to the latest hatch date (7 July), there was only a 3% reduction in survival, and the 95% confidence interval around the estimate of the effect of hatch date included zero (β = -0.40, CI = -1.08 to 0.11). Fledgling survival was lowest during the first 2 days post-fledging, i.e., 10-13 days after hatching, and we did not observe any mortality events after 11 days post-fledging, i.e., ~21–24 days after hatching. Seventeen fledglings were still observed with parents > 30 days post-fledging (maximum observed 45 days post-fledging, or ~58 days after hatching), and some radio transmitter batteries began expiring after ~28–36 days, often because tags were reused. We observed wing fluttering behavior, indicating begging, and adults feeding fledglings as late as 43 days post-fledging (~54 days after hatching). Therefore, we were unable to estimate the length of the dependent fledgling period for Gray Vireos.

Table 1. Logistic exposure models of Gray Vireo fledgling daily survival rate at Sevilleta National Wildlife Refuge, New Mexico, 2017–2019 (n = 579 observations). These models include only mortalities attributed to predation and excluded ages from hatching > 26 days (i.e., > 12 days post-fledging) after which we observed no mortalities. All models included a random effect of brood to account for interdependence among fledglings from the same nest. Age was the number of days from hatching (i.e., includes nestling and fledgling days).

Model	K	ΔAICc	AICc	w_i	LogLik
Age + Hatch date	4	0.00	161.73	0.23	-76.83
Age	3	0.38	162.11	0.19	-78.04
Age + 25-m tree cover	4	0.77	162.50	0.16	-77.21
Age + Lateral veg cover	4	1.78	163.51	0.10	-77.72
Age + Elevation	4	1.84	163.57	0.09	-77.75
Age + Age²	4	1.84	163.58	0.09	-77.75
Age + Height from ground	4	2.38	164.11	0.07	-78.02
Age + Site	5	3.87	165.60	0.03	-77.75
Null	2	16.36	178.10	0.00	-87.04

During the first 12 days post-fledging, Gray Vireo fledglings used areas with greater percent tree cover within a 25-m radius ($\bar{x}$ = 15 ± 9%) compared to random points ($\bar{x}$ = 9 ± 9%; ANOVA, $P < 0.001$; Fig. 3). At the same spatial scale, fledglings ($\bar{x}$ = 15 ± 9%) and nests ($\bar{x}$ = 15 ± 10%) were in areas of similar percent tree cover (ANOVA, $P = 0.83$; Fig. 3). Throughout the entire monitoring period, fledglings occupied juniper trees in 88% of observations ($n = 908$ of 1034 observations, $n = 62$ individuals; Fig. 4). Over the entire monitoring period, fledglings used microhabitats with 60 ± 24% SD lateral vegetation cover, which was similar to that of nest locations ($\bar{x}$ = 56 ± 26% SD, $n = 118$ nests; $t_{136} = -1.6$, $P = 0.11$). We estimated that fledglings used areas with approximately 90 ± 38 SD juniper trees per hectare during the first 12 days post-fledging ($n = 100$ locations).

Fledgling movements

Minimum daily distance traveled, distance from nests, and variance associated with these measures increased with age in Gray Vireo fledglings (Fig. 5). There was a notable increase in the variability in movements among fledglings at ~40 days after hatching. This variation was likely attributable to some fledglings starting to make relatively large movements of several hundred meters, whereas others did not, despite all of them still being accompanied by adults. Increased SE in movement distances is also attributable to the relatively small sample size of birds tracked > 40 days on account of mortalities, transmitter expirations, and random selection of one bird per brood for movement analysis.

Fig. 3. Percent tree cover (i.e., cover within 25-m radius buffers) at random, fledgling, and nest locations of Gray Vireos (*Vireo vicinior*) at Sevilleta National Wildlife Refuge, New Mexico, from 2017 to 2019. Thick horizontal bars represent median tree cover, boxes span first and third quartiles (inter-quartile range [IQR]), and whiskers denote 1.5 × IQR. Extreme values are shown as closed circles.

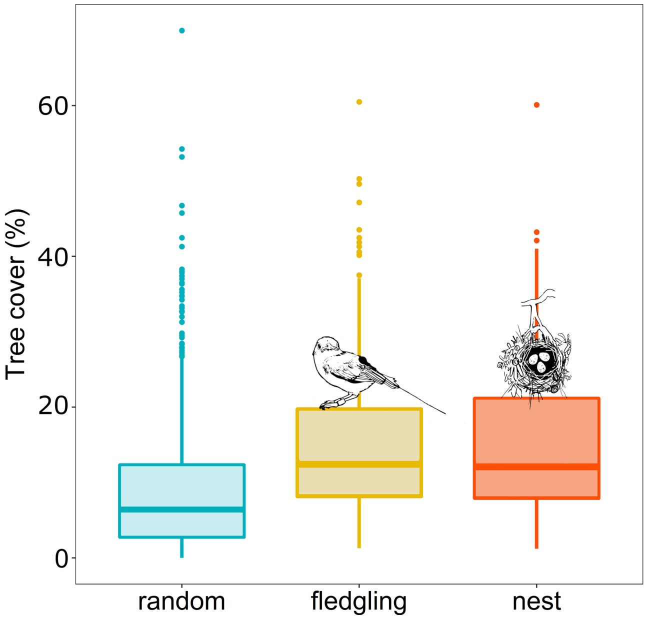


Fig. 4. Proportion of observations in vegetation substrates for Gray Vireo (*Vireo vicinior*) fledglings during the post-fledging period at Sevilleta National Wildlife Refuge, New Mexico, 2017–2019 (n = 1034 observations, n = 62 individuals).

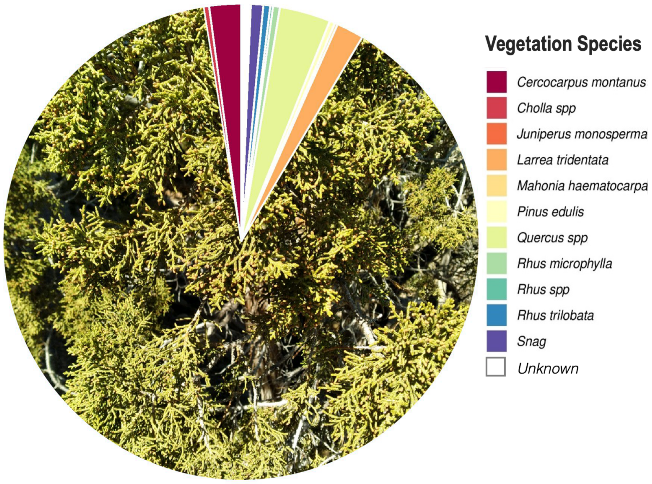
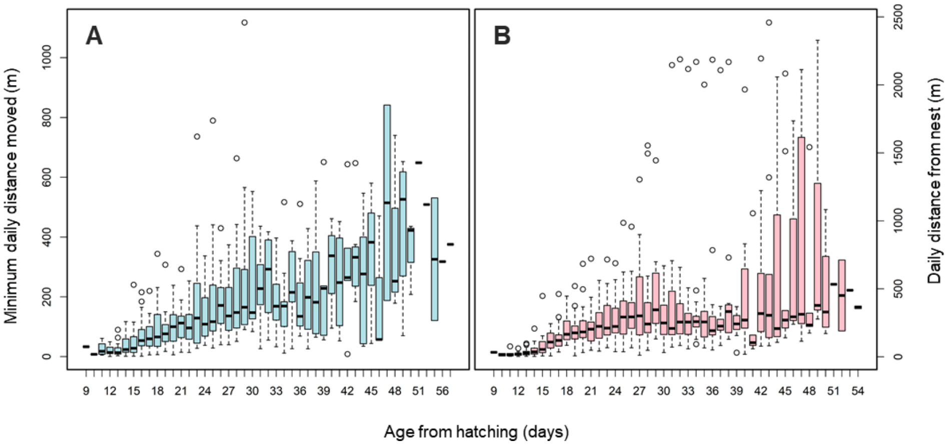


Fig. 5. (A) Minimum daily distance traveled (n = 45 fledglings and 591 locations) and (B) daily distance from nest (n = 34 fledglings and 697 locations) among Gray Vireo (*Vireo vicinior*) fledglings from 2017 to 2019 at Sevilleta National Wildlife Refuge, New Mexico, USA. Time is shown as fledgling age in days from hatching. Thick horizontal bars represent minimum median distance traveled at each age, boxes span first and third quartiles (interquartile range [IQR]), and whiskers denote 1.5 × IQR. Extreme values are shown as open circles.



DISCUSSION

Fledgling survival and habitat associations

The post-fledging ecology of Gray Vireos was similar in many ways to that of other songbirds. The fledgling survival rate (0.51) in Gray Vireos was approximately average among those reported for other Western North American migratory songbirds and Eastern North American migratory songbirds of similar size (Table 2) and similarly average among other fledgling songbirds (Cox et al. 2014). 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 for survival to stabilize; Cox et al. 2014). Age was the primary predictor of the survival rate with respect to predation among the covariates we considered, consistent with many other post-fledging studies in which the vast majority of mortality is from predation (Sullivan 1989, Naef-Daenzer et al. 2001, Wightman 2009, Naef-Daenzer and Grüebler 2016). Survival tended to be lower for fledglings hatching later in the breeding season, but 95% confidence intervals around this effect 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 Sevilleta NWR. Identifiable predators of fledglings included Swainson's Hawk, New Mexico garter snake, and likely Loggerhead Shrike (also documented in Barlow et al. 1999). Potential, but unconfirmed predators included small mammals such as white-throated woodrats (*Neotoma albigula*), Southern Plains woodrats (*N. micropus*), rock squirrels (*Otospermophilus 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 Woodhouse's Scrub Jays (*Aphelocoma woodhouseii*; documented predator of Gray Vireo nestlings, Fischer 2020), Northern Mockingbirds (*Mimus polyglottos*), Scott's Orioles (*Icterus parisorum*), desert striped whipsnakes (*Masticophis taeniatus taeniatus*), and several other snake species.

Lateral vegetation cover at fledgling locations and percent tree cover within 25-m radius buffers around fledgling locations were not associated with survival, suggesting that predation on Gray Vireo fledglings is either independent of lateral vegetation cover and percent tree cover or that it is associated with habitat characteristics we did not consider. Given the relatively homogeneous nature of vegetation across our study area, 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. Nests and fledglings were located in areas with denser percent tree cover compared to random points in our study area, consistent with nesting locations of Gray Vireos in 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 that there is an optimal maximum juniper density for the species. Based on our estimates, maintaining ~90 ± 38 juniper trees per hectare may optimize Gray Vireo post-fledging and nesting habitat in this portion of its range.

Table 2. A sample of dependent fledging period mean survival rates for migratory songbirds breeding in Western North America, and some Eastern North American migratory songbirds of similar body size to Gray Vireos, for comparison. Note that the dependent fledgling period length varies among species, but because survival is generally high following the first several days post-fledging, survival estimates from periods of various lengths should be comparable. Species are presented in order of descending mean survival estimates. For additional fledgling survival estimates from earlier studies and from studies of non-migrant songbirds, see Cox et al. (2014).

Species	Scientific name	Period survival	Method	Reference
Willow Flycatcher	*Empidonax trailii*	0.74	Band resighting	Vormwald et al. 2011
Golden-cheeked Warbler	*Setophaga chrysoparia*	0.73	Radio telemetry	Trumbo 2019
Dusky Flycatcher	*Empidonax oberholseri*	0.72	Band resighting	Vormwald et al. 2011
Spotted Towhee	*Pipilo maculatus*	0.69	Radio telemetry	Shipley et al. 2013
Grasshopper Sparrow	*Ammodramus savannarum*	0.55	Radio telemetry	Bernath-Plaisted et al. 2021
Golden-winged Warbler	*Vermivora chrysoptera*	0.52	Radio telemetry	Streby et al. 2016
Gray Vireo	*Vireo vicinior*	0.51	Radio telemetry	Fischer et al. this study
Hooded Warbler	*Setophaga citrina*	0.51	Radio telemetry†	Eng et al. 2011
Cerulean Warbler	*Setophaga cerulea*	0.48	Radio telemetry	Raybuck et al. 2020
Ovenbird	*Seiurus aurocapilla*	0.38	Radio telemetry	Streby and Andersen 2011
Lark Bunting	*Calamospiza melanocorys*	0.35	Radio telemetry	Yackel Adams et al. 2006
Henslow's Sparrow	*Centronyx henslowii*	0.35	Radio telemetry	Young et al. 2019
Sprague's Pipit	*Anthus spragueii*	0.29	Radio telemetry	Fisher and Davis 2011
Baird's Sparrow	*Centronyx bairdii*	0.25	Radio telemetry	Bernath-Plaisted et al. 2021
Hooded Warbler	*Setophaga citrina*	0.19	Radio telemetry†	Rush and Stutchbury 2008

†Radio-marked adults, not fledglings

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 include: Willow Flycatchers (riparian-obligate, *Empidonax traillii*; Vormwald et al. 2011), Sprague's Pipits (grassland-obligate, *Anthus spragueii*; Fisher and Davis 2011), Dickcissels (grassland-obligate, *Spiza americana*; Jones et al. 2017), Veeries (forest-obligate, *Catharus fuscescens*; Goguen 2019), and Black-capped Vireos (juniper-oak shrubland species, *Vireo atricapilla*; Martinez et al. 2019), species that could be considered habitat specialists like Gray Vireos. 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. The relative homogeneity and gradual transitions in tree density at our study sites rendered more categorical cover type selection analyses, e.g., discrete choice models (see Cooper and Millspaugh 1999), difficult to implement. To address the question of whether fledglings used areas similar to nesting locations or those randomly available, a simpler approach was sufficient. 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 congener Black-capped Vireo (Dittmar et al. 2014, 2016), because the fledglings we tracked were accompanied by adults throughout the study period. However, in our study area, there are few options of other cover types with trees or shrubs taller than creosote within 10 km of our sites, so changes in cover type associations would require large movements upon independence.

Fledgling movements and dependence on adult care

As in many other songbirds, Gray Vireo fledgling movements increased with age (Morton et al. 1991, Cox et al. 2014, Jenkins et al. 2017, Raybuck et al. 2020). The minimum daily distance and variation in distance traveled both increased 25–30 days post-fledging. Many other songbirds become independent from adult care at that time (e.g., 23–29 days in Ovenbirds [*Seiurus aurocapilla*]; Vitz and Rodewald 2010, Streby and Andersen 2013b, Jenkins et al. 2017; ~30–40 days in White-crowned Sparrows [*Zonotrichia leucophrys*], Morton et al. 1991) or disperse from the natal area (dispersal after ~31 days in White-throated Thrushes [*Turdus assimilis*]; Cohen and Lindell 2004). We observed greater variation in fledglings' distances from their nest compared to minimum daily distance traveled. We suspect this variation may be associated with brood division behavior, which we definitively observed in only two broods, with female-reared broods traveling farther from nests than male-reared broods (Fischer 2020).

We were unable to determine the length of the dependent period in Gray Vireos, given that we observed fledglings up to 45 days post-fledging begging and being fed by parents. Similarly, Cohen and Lindell (2004) observed older White-throated Thrush fledglings (> 60 days after leaving the nest) being fed by parents. However, the length of dependence on adult care in Gray Vireo fledglings seems to be longer than that of many other Nearctic-breeding songbirds that generally reach independence at ~30 days (Cox et al. 2014): we observed 17 fledglings with parents > 30 days post-fledging. Cohen and Lindell (2004) also suggested that there is variation in the length of the dependent period of White-throated Thrushes, which may also be the case in Gray Vireos. We hypothesize that this seemingly long and variable dependent period in Gray Vireos may be attributable to the relatively scarce resources available to fledgling songbirds in deserts compared to temperate forests where most post-fledging studies in North America have taken place (Cox et al. 2014). Future research on Gray Vireo fledgling survival, habitat associations, and movements during the independent period, though logistically challenging (Cox et al. 2014), would be valuable for filling additional full annual cycle knowledge gaps.

CONCLUSIONS

We intended to identify habitat characteristics associated with variation in fledgling survival to inform management to benefit Gray Vireos. Instead, we found that predation rates did not vary with measured habitat variables and were consistent among the three years of our study. Including all causes of mortality, we estimated 51% period survival for fledglings. That moderately high survival rate, combined with most pairs successfully nesting (even if requiring several nesting attempts; S. E. Fischer, *personal observation*), suggest that Gray Vireos at Sevilleta NWR may be a relatively highly productive population. Additional full-breeding-season research, including post-fledging ecology, 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) across its relatively limited and patchy breeding distribution, controlled experimental research with pre- and post-treatment data collection will be beneficial to determine their impacts on this species of conservation concern. Additional empirical estimates of Gray Vireo fledgling survival are needed across the breeding range, especially in locally declining populations and where habitat associations differ from Sevilleta NWR (e.g., southern California; Hargrove and Unitt 2017). More broadly, given the importance of fledgling survival to avian population growth, post-fledging studies are an urgent need in deserts, arid lands, and semi-arid lands, where many species have experienced long-term declines (Iknayan and Beissinger 2018).

Responses to this article can be read online at:
https://www.ace-eco.org/issues/responses.php/2053

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