Population Dynamics of the Endangered Black-capped Vireo (*Vireo atricapilla*)

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Abstract

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Landscape heterogeneity and fragmentation create local populations that differ in habitat availability and predator communities and present unique tradeoffs between reproductive success and survival. Varying demography across the landscape can result in a metapopulation structure and the recognition of source-sink dynamics could have far-reaching implications for wildlife management, particularly of endangered species. The black-capped vireo (*Vireo atricapilla*; vireo) is an endangered songbird that suffers from high rates of parasitism by the brown-headed cowbird (*Molothrus ater*) across its breeding range from northeastern Mexico to southern Oklahoma. The largest population located on the Fort Hood Military Reservation in central Texas is well-studied, but its role in landscape-level vireo population dynamics is largely unknown. From 2011 through 2014, we monitored seven vireo populations on Fort Hood and nearby private and state lands that varied in vegetation and nest parasitism rates. We calculated measures of fecundity and survival and assessed populations as sources or sinks using population matrices. Sites with cowbird control had greater overall nest success and the most successful source population had complete cowbird control in all study years. To investigate tradeoffs in habitat selection, we monitored breeding territories and tracked juvenile vireos using radio-telemetry. Vireos in general selected shrubland and forest habitats; canopy cover may present a tradeoff that improves juvenile survival but reduces breeding success. We recorded vocalizations at vireo nests and found little evidence for tradeoffs in social communication and mediation of parasitism or predation risk. Vireos did benefit, however, by optimizing temporal patterns in vocalizations. Finally, we documented some flexibility in mating strategy through an observation of polygyny in a territorial male vireo. Land managers of vireo breeding populations should consider habitat needs across the entire reproductive cycle: cowbird control will increase nest success and breeding sites that provide nearby or adjacent forested areas may improve survival of recently independent juveniles.

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POPULATION DYNAMICS OF THE ENDANGERED BLACK-CAPPED VIREO (VIREO ATRICAPILLA)

INTRODUCTION

Many wildlife species exist in metapopulations across heterogeneous and fragmented landscapes and the question of how populations persist under unique local conditions is central to population ecology. Natural selection shapes species' behaviors to optimize reproductive success but, due to gene flow (Lenormand 2002), unique tradeoffs (Futuyma and Moreno 1988, Agrawal et al. 2010), or limited plasticity (DeWitt et al. 1998), demography may remain variable across a diverse landscape. Endangered species are frequently restricted in range and habitat and researchers, out of necessity, often focus on the largest or most densely inhabited patches to conduct demographic studies. Populations of highly mobile species, such as birds, however, may interact over long distances and wide-spread metapopulation dynamics may ultimately affect the stability of individual populations (Tittler et al. 2006). Thus, a broad perspective on landscape heterogeneity and recognition of source-sink dynamics could have broad implications, particularly for the management of endangered birds.

For songbirds, natural selection balances nest success with adult and juvenile survival to maximize overall reproductive success (Pianka 1976). Breeding site selection may present tradeoffs if habitat features that benefit nest success ultimately lower juvenile survival (Streby et al. 2014a, 2014b). Similarly, tradeoffs may exist in social communication if vocalizations near nests that benefit pair bonding and increase nest defense also attract predators and nest parasites, cuing them into the nest location (Clotfelter 1998, Banks and Martin 2001). A species' behavioral flexibility may therefore affect their ability to persist across a heterogeneous landscape.

The black-capped vireo (*Vireo atricapilla*) is a small migratory songbird that winters in western Mexico and breeds locally from northeastern Mexico through southern Oklahoma. In 1987, the species was listed as endangered by the U.S. Fish and Wildlife Service, which cited declines in shrubland breeding habitat and high rates of brood parasitism by brown-headed cowbirds (*Molothrus ater*) (Ratzlaff 1987, USFWS 1991). Intense habitat and cowbird management on the Fort Hood Military Reservation have bolstered the local vireo population from 85 individuals at the time of listing (Tazik et al. 1993) to an estimated 5000 pairs in 2011 (Cimprich and Heimbuch 2011). Today, Fort Hood has the largest breeding population of black-capped vireos but its role in landscape-level vireo population dynamics remains largely unknown. Relatively small vireo populations on state and private lands across central Texas may be sinks, dependent on immigration from Fort Hood for population persistence.

Across their range, vireo breeding habitat varies in vegetation and in predator and nest parasite communities, perhaps driving differences in population demographics. Although vireo breeding habitat varies in specific vegetation communities, it is consistently described as patchy deciduous shrublands (Grzybowski et al. 1994). On Fort Hood, juvenile vireos select riparian areas over other habitat types (Dittmar et al. 2014), but in general habitat selection by juvenile vireos is poorly understood. Thus, differences in habitat availability across the breeding range could result in variable tradeoffs between nest success and juvenile survival. Vireo populations across central Texas also differ in local land management practices and cowbird control efforts; the ability of vireos to adapt to variable parasitism pressure likely plays an important role in vireo population stability.

The primary objective of this study was to broaden the perspective on black-capped vireo population dynamics and investigate the source-sink status of vireo populations across central Texas. From 2011 through 2014, I monitored vireo populations at seven sites on Fort Hood and on nearby private and state lands to assess populations that varied in habitat characteristics and parasitism regimes as sources or sinks (Chapter 1). To uncover potential tradeoffs in vireo breeding habitat selection, I monitored territorial and juvenile black-capped vireos and documented patterns in nest success, juvenile survival, and habitat use and selection by both age classes (Chapter 2). I recorded vocalizations at vireo nests and compared them to eventual depredation or parasitism fate as well as local cowbird density to investigate the tradeoffs between social communication and nest success (Chapter 3). Providing limited evidence of some flexibility in mating strategy, I observed a single instance of polygyny by a territorial male vireo (Chapter 4). Finally, I provide management recommendations for vireo breeding populations that focus on habitat availability and cowbird control.

CHAPTER 1

Parasite-driven Population Dynamics in an Endangered Songbird, the Black-capped Vireo

Since its introduction by Pulliam (1988), the source-sink model of metapopulation structure has broadened our theoretical understanding of ecology and conservation, while also informing management. Source habitats are reproductively successful and produce young that, due to density regulation, must disperse to other patches (Pulliam 1988). In contrast, sinks are populations that have insufficient reproduction to balance local mortality and thus depend on immigration from sources to avoid local extinction or rescue them thereafter (Brown and Kodric-Brown 1977). The presence of source-sink dynamics in fragmented metapopulations has been used to explain the persistence of local populations in low-quality habitat (Foppen et al. 2000, Murphy 2001), argue for conservation of source areas (Robinson et al. 1995), and identify threats to population persistence (Balogh et al. 2011). For endangered species management in particular, the recognition of source-sink dynamics could have great impacts on conservation and recovery efforts. Populations of endangered species are frequently restricted in range and relatively small in size, forcing researchers concerned with the practicality of data collection to study only the largest or most densely inhabited locales. However, monitoring populations across a heterogeneous landscape may yield a more accurate representation of the overall status of the population. Distinguishing particular subpopulations as either sources or sinks may help both highlight spatially-specific conservation needs and create more accurate long term predictions of population viability.

The establishment of source-sink dynamics results from heterogeneous landscapes where survival, reproduction, or both are spatially variable and where the movement of individuals from productive source populations at least temporarily sustains sink populations. Habitat fragmentation often results in patches that vary in size and degree of isolation and habitat variability along edges as well as within and between patches can impact risk of predation (Andren 1992, Paton 1994, Heithaus and Dill 2006) or brood parasitism (Paton 1994, Vasseur and LeBerg 2015), prey availability (O'Donnell 2000), and resource competition with con- and heterospecifics (Fagan et al. 1999, Amarasekare 2003, Piper and Caterall 2003). For birds that are able to fly long distances and are less likely to face physical impediments to dispersal, source-sink dynamics are often attributed to annual fluctuations in resource abundance (Bock and Bock 1974, Stacey and Taper 1992), or locally high predator or brood parasite populations that reduce survival (Balogh et al. 2011) or nest success (Robinson et al. 1995, Barabas et al. 2004, Jewell and Arcese 2008) below what is necessary for the population to remain sustainable without immigration.

The black-capped vireo (*Vireo atricapilla*; vireo) is a migratory songbird that breeds in local populations throughout northeastern Mexico, Texas, and southern Oklahoma. The species was listed as endangered in 1987 by the U.S. Fish and Wildlife Service due to habitat loss and high rates of brood parasitism by the brown-headed cowbird (*Molothrus ater*; cowbird; Ratzlaff 1987, USFWS 1991). Today, the largest, and best studied, local breeding population of black-capped vireos is located on the Fort Hood Military Reservation (Fort Hood) in central Texas. Although the local population at the time of listing was estimated at only 85 male vireos (Tazik et al. 1993), intensive cowbird control efforts (initiated in the early 1990's and ongoing; Kostecke et al. 2005) have brought the total Fort Hood population to approximately 5000 males

(Cimprich and Heimbuch 2011). While the Fort Hood population has been well-studied, and monitoring also occurs on a National Wildlife Refuge to the southeast, small breeding vireo populations on state and private lands in the areas surrounding Fort Hood have garnered less focus. Thus, our primary objective is to broaden our perspective on the central Texas vireo metapopulation and better understand the contributions of individual breeding populations, including Fort Hood, to landscape-level patterns in vireo population dynamics.

Although their breeding habitat is generally described as consisting of patchy shrublands, across their breeding range black-capped vireos use habitats that vary in structure and species composition. Locally, there is evidence for variable reproductive success and survivorship, correlated with habitat differences such as vegetation and parasitism by cowbirds. In habitats structured by military activity on Fort Hood, vireos are found in lower abundance and with a greater proportion of second year males than in shrublands managed for vireos (Noa et al. 2007). Similarly, vireos are more successful in breeding patches that have been structured through fire rather than by mechanical disturbance on Fort Hood (Bailey 2005). Vireo nest success is also higher in natural shrublands, particularly those with deciduous cover (Bailey 2005), perhaps due to reduced rates of parasitism (Noa et al. 2007). Across habitat types, vireo nests located higher above the ground had greater daily survival probabilities (Noa et al. 2007), indicating that habitat structure may also be an important factor in reproductive success. The annual survival of adult vireos on Fort Hood varies between local breeding patches and may reflect differences in habitat quality (Kostecke and Cimprich 2008).

On Fort Hood and throughout central Texas, vireos exhibit differential reproductive success between habitat types and parasitism regimes. Dispersal events between breeding populations are rarely observed, however, and evidence of source-sink dynamics is inconclusive.

Some genetic investigations into vireo population structure observed significant differences in genetic variation within subpopulations, effectively ruling out gene flow and the possibility of source-sink dynamics (Barr et al. 2008). However, Zink et al. (2010) found similar measures of genetic variation, but argued that the differences between populations were not biologically significant. The vireo population structure proposed by Zink et al. (2010) does not exclude the possibility of source-sink dynamics and, ultimately, additional investigation remains important.

Successful management, conservation, and recovery of the black-capped vireo across its range would benefit from a more complete understanding of the population dynamics across large spatial extents. Vireo population growth was the basis for a 2007 recommendation by the U.S. Fish and Wildlife Service to downgrade the species from endangered to threatened status (USFWS 2007). The presence of source-sink dynamics, however, could have repercussions for the stability of vireo metapopulations and the species as a whole. For example, if other small populations are largely sinks, it could indicate that the central Texas vireo metapopulation is highly dependent on the success of the Fort Hood subpopulation. This study measured vireo demography and survival on and around Fort Hood and assessed breeding sites across central Texas as sources or sink populations. We also ranked the relative importance of fecundity and adult and juvenile survival to identify the demographic measures driving vireo population dynamics. We predicted that the predominant driver of vireo population dynamics would be variable fecundity and areas with consistent cowbird control would serve as source populations. We expected populations with relatively little cowbird control and high rates of cowbird parasitism to be sinks.

METHODS

Study Sites

The largest breeding vireo population is on Fort Hood, near Killeen, TX in Coryell and Bell Counties. We chose study sites on Fort Hood and in nearby areas to the south and west that vary in vegetative characteristics and cowbird control regimes (Figure 1.1). The habitat is largely characterized by shortgrass communities and cattle rangeland although many areas that were once grasslands are now woodlands due to fire suppression and the range expansion of the native evergreen Ashe juniper (*Juniperus ashei*). The climate is semi-arid with an average of 33 inches of rainfall annually and average high temperatures between 58°F (14.4°C) in January and 96°F (35.6°C) in August.

Fort Hood. We monitored three study sites on Fort Hood from 2011 through 2014 (Figure 1.1). West Range, a 120 acre site dominated by mixed juniper and deciduous woodlands, had comprehensive cowbird control until 2006 when Fort Hood began an experimental cessation of cowbird control in the northwest area of the base. East Range, about 150 acres, is located on the eastern side of the installation where cowbirds have been continually controlled via shooting and trapping since 1991. The 250 acre West Fort Hood site is located near the southern edge of the Fort Hood installation and, although cowbirds are removed from the site when they are reported, there are no nearby traps and cowbird presence remains high. Both East Range and West Fort Hood are characterized by a mix of grasslands and deciduous woodlands.

Balcones Canyonlands National Wildlife Refuge. Balcones Canyonlands is a 23,815 acre reserve comprised of 65 individual tracts of land, located approximately 45 miles southwest of Fort Hood near the intersection of Burnet, Williamson, and Travis Counties (Figure 1.1). We focused our monitoring efforts on three tracts along the northern edge of the refuge. In 2011, we monitored approximately 160 acres and, from 2012-2014, expanded our survey efforts to cover an additional 200 acres. Vegetation cover varies between tracts from tall dense shin oak (*Quercus sinuata* var. *breviloba*) to juniper woodlands to open grasslands with scattered low shin oak and flame-leaf sumac (*Rhus lanceolata*). Cowbird traps were present across the refuge, although they were not located directly on our study tracts.

San Saba. From 2012 through 2014, we surveyed portions of two neighboring private ranches, nearly 12 miles southwest of San Saba, TX, in San Saba County (Figure 1.1). About 60 acres, the site is composed of a northwest-facing hillside, largely covered in dense persimmon (*Diospyros texana*), juniper, hog plum (*Colubrina texensis*), honey mesquite (*Prosopis glandulosa*), allthorn (*Koeberlinia spinosa*), catclaw mimosa (*Mimosa biuncifera*), and green condalia (*Condalia viridis*). The top of the hill is characterized by open patchy persimmon and the bottom flattens out into grassland, then slopes downward again in dense juniper, persimmon, cedar elm (*Ulmus crassifolia*), and bee brush (*Aloysia gratissima*). There were no cowbird control efforts at the San Saba property in either 2012 or 2013 but a cowbird trap was established mid-way through the 2014 breeding season.

Colorado Bend State Park. Colorado Bend is a 5328 acre state park located along the west side of the Colorado River in San Saba County (Figure 1.1). From 2011 through 2014, we monitored vireo territories along the Tie Slide, Heller Brakes, and Gorman Falls trails, an area comprising approximately 300 acres. The site was characterized by a mix of open grasslands and patchy juniper and live oak (*Quercus fusiformis*) woodlands. There was no effective cowbird control in the state park from 2011 through 2013 but trapping efforts began mid-way through the 2014 breeding season.

Goldthwaite. From 2012 through 2014, we monitored a privately owned ranch approximately 9.5 miles west of Goldthwaite, Texas in Mills County (Figure 1.1). In the northeastern corner of the ranch, our 82 acre study site was comprised of an open and patchy hilltop with densely vegetated south-facing slopes. Shrub and tree vegetation was primarily persimmon, juniper, elbow bush (*Forestiera pubescens*), and mesquite. There were no cowbird control efforts when we began monitoring the Goldthwaite site in 2012. However, in 2013, traps were placed near the study site mid-way through the breeding season and, in 2014, both traps and shooting were used to control local cowbird populations.

Cowbird Control Efforts

In each study year, we classified each study site by their level of cowbird control (Table 1.1). We designated sites with both trapping and shooting as having “complete” cowbird control. If cowbirds were either trapped *or* regularly removed by shooting, we designated the site with “moderate” cowbird control. We labeled all other sites as having no cowbird control. For adult survival analyses, we used the cowbird control level at the site in the year that the bird was initially caught.

Monitoring Efforts

We visited study sites two to three days per week throughout the vireo breeding season, from late March through early July, and searched for all territorial males. We target-netted territorial vireos and banded them with USFWS aluminum bands and unique color band combinations. We visited each territory between one and three times per week, recording locations of territorial male vireos using a handheld GPS unit. We recorded no more than five locations a day for each territory and each observation was separated by at least five minutes.

We monitored pairs to locate all nests. Although we attempted to document all nesting attempts, we may have missed some unsuccessful nests. We believe this happened infrequently, however, as relatively few nests were located post-fledging (2.0%) or post nest failure (1.4%). We visited known nest locations every three to four days until failure or fledging and recorded the number of vireo and cowbird eggs (if present), the number and approximate age of nestlings, and parental presence at the nest. If a nest survived to the nestling stage, we banded nestlings between 6 and 8 days post hatching with a USFWS aluminum band and a color combination unique to each study site. We considered a nest to be successful (*n* =223) if we observed at least one fledgling with parents away from the nest (*n* =150) or if we observed at least one vireo nestling in the nest on day 11 (average fledge day) and we observed behaviors by the adults to suggest they had fledglings (scolding, carrying food; *n* = 73).

Analyses

Nest Success and Fecundity. We calculated nesting success using the Mayfield (1975) method. Based on exposure days, we calculated separate daily survival rates for nests in the egg-laying, incubation, and nestling stages, as well as the probability of surviving each individual nest stage (stage survival) and nest survival from egg-laying to fledging (overall nest survival). Following standards used by Fort Hood Natural Resource biologists (Cimprich and Heimbuch 2011), we considered the egg laying stage to begin in the middle of the first day an egg was observed in the nest, with a maximum exposure period of 2.5 days. Incubation, a period of 14 days, began at the beginning of the day the last egg was laid. We assumed the beginning of the nestling stage to be half way between the last check with eggs alone and the first check with nestlings present. The nestling stage lasted 11 days. In parasitized nests where the cowbird hatched but the host eggs did not, we considered failure to occur at the midpoint of the incubation stage. We considered nests to be successful if they fledged at least one host young.

Using several two-way ANOVAs, we evaluated the relationships between study site, study year, level of cowbird control, and nest stage and their effects on both daily and nest stage survival. We used *post hoc* Tukey tests to further investigate the source of significant ANOVA results.

Based on nest survival estimates for each site, we calculated fecundity (the mean number of female offspring produced by each adult female each year) following Donovan et al. (1995). We assumed that, if the first breeding attempt was successful, a vireo pair would make one second brood attempt. If the first breeding attempt was unsuccessful, we assumed pairs would make up to three total nesting attempts. (Although we have observed pairs making up to seven nesting attempts, few pairs were ever successful beyond a third attempt.) We assumed that young produced exhibited a 50:50 male:female ratio and that nest success and fecundity were constant throughout the breeding season.

Adult Survival. We used banding and resighting data from color-banded adult vireos to calculate average dispersal distances (mean ± SE) and estimate apparent survival (φ) and recapture probabilities (p). We defined φ as the probability an adult vireo survived and returned to one of our sites in a subsequent breeding season and p as the probability of encountering a vireo given its survival and presence on one of our sites. We used the package "RMark" (Laake 2013) in R v 3.1.1 (R Core Team 2014) to estimate φ considering the effects of individual study site, location on or off Fort Hood, or average level of cowbird control (none, moderate, complete). Because of a limited sample size, we could not consider the effects of combinations of variables that might interactively affect survival. For recapture models, we considered single variable models of study site, location, cowbird control, and sex. Including null survival and recapture models, we considered 20 combinations of adult vireo survival and recapture probabilities and compared them using Akaike's Information Criterion adjusted for small sample size (AIC_c; Akaike 1974) and model weights (w_i).

Juvenile Survival. We defined juvenile survival as the probability a vireo banded as a nestling survived to return to one of our study sites in a subsequent season and estimated apparent survival (φ) and recapture probabilities (p) using the package "RMark" (Laake 2013) in R v 3.1.1 (R Core Team 2014). Because we had relatively few birds banded as nestlings return to our study sites in subsequent field seasons, we additionally included banding and resighting data of nestlings banded on four long-term study sites on Fort Hood monitored by Fort Hood's Division of Natural Resources from 2011 through 2014. We considered the effects of individual study site, location on or off Fort Hood, and average level of cowbird control (none, moderate, complete) on both φ and p. Including null survival and recapture models, we considered 16 combinations of juvenile vireo survival and recapture probabilities and compared them using Akaike's Information Criterion adjusted for small sample size (AIC_c; Akaike 1974) and model weights (w_i).

Population Assessments and the Relative Importance of Survival and Reproduction. To determine the status of vireo populations in central Texas at each of our study sites, we followed methods outlined by Caswell (2001) and Pulliam (1988). We built simple two stage population matrices (Caswell 2001) for each individual site, sites on and off of Fort Hood, and across all sites to calculate the growth rate, λ, of each population. We labeled populations where $\lambda > 1$ as sources and populations where $\lambda < 1$ as sinks. Matrix elements were largely based on population-specific data from field observations. We calculated fecundity from nesting data collected from 2011 through 2014 (see *Nest Success and Fecundity* above) and estimated adult and juvenile survival from an analysis of banding (2011-2014) and resighting data (2012-2015; see *Adult Survival* and *Juvenile Survival* above).

We projected population growth at each individual study site, on and off Fort Hood, and across all sites using the simple projection model,

$N_{(t+1)} = \mathrm{A}^{*}N_t$,

where N is the population size at time t and A is the population matrix (Caswell 2001). Our intent was not to predict future population size or viability but to demonstrate current rates of population decline or growth without the effects of immigration, emigration, or stochasticity. For all projections, we used a starting population of N_0 = 100 adults and time frame of 30 years.

To better define the relationship between matrix elements and population growth rate, we plotted growth rate against a range of fecundity values (0 – 3.0 young fledged/year) and adult and juvenile survival rates (0 - 100%) and calculated the slope, or the sensitivity, for each demographic parameter (fecundity, adult survival, and juvenile survival). Sensitivity is the rate of change in the population growth rate with respect to a numerical change in a matrix element (Caswell 2001). Survival and fecundity are measured on different scales, however, making comparisons between the sensitivity of fecundity and either measure of survival uninformative. Therefore, we also calculated the elasticity, or *proportional* sensitivity, for fecundity and survival matrix elements. We compared the effects of individual demographic parameters across sites using sensitivity and compared the effects of different parameters within sites using elasticity. We used the package "popbio" (Stubben and Milligan 2007) in R v 3.1.1 (R Core Team 2014) for all matrix calculations and populations projections.

RESULTS

Monitoring Efforts

Between 2011 and 2014, we banded over 1600 black-capped vireos, including 426 adult males and 303 adult female vireos (Table 1.2). We monitored 384 vireo territories across seven study sites (Table 1.2); 195 territories had at least one successful nest. In total, we located and monitored 754 nests and found evidence of an additional 28 nesting attempts, including nests which had already failed ($n = 12$) and pairs with fledglings ($n = 16$; Table 1.2). Two-hundred and thirty-three nests (30%) were successful in fledging at least one vireo nestling (Table 1.2, Figure 1.2). Of unsuccessful nests with known fate ($n = 520$), 61.9% ($n = 322$) were depredated, 30.6% ($n = 159$) were abandoned, and 2.5% ($n = 13$) were destroyed.

Of nests with a known fate and known parasitism status ($n = 742$), 34.5% ($n = 256$) were parasitized (Figure 1.2). Although only 10.2% of parasitized nests ($n = 26$) fledged a cowbird, no nests that fledged a cowbird were also able to successfully fledge any vireo young (Figure 1.2). The most common nest fate for parasitized nests was to be abandoned (42.9%; Figure 1.2). Of pairs that abandoned parasitized nests ($n = 71$), 43 pairs (60.6%) went on to have a later non-parasitized nesting attempt and 16 pairs (22.5%) were successful in fledging a later brood. Nineteen parasitized nests were successful in fledging vireo young either because the cowbird egg failed to hatch ($n = 17$) or the cowbird nestling died shortly after hatching ($n = 2$). Successful parasitized nests fledged 2.53 young/nest (SE = 0.23), significantly less than the average productivity of successful non-parasitized nests (3.26 young/nest, SE = 0.06; $t_{214} = 3.42$, $P < 0.001$).

Nest Survival

Daily nest survival varied by site ($F_{6,57} = 2.54$, $P = 0.03$) but not by nest stage ($F_{2,57} = 1.21$, $P = 0.31$) and *post hoc* tests revealed that daily nest survival was greater at the most productive East Range than at the least productive Goldthwaite property ($q = 4.35$, $P = 0.05$; Table 1.3). Stage survival for nests varied among sites ($F_{6,57} = 3.08$, $P = 0.01$) and between nest stages ($F_{2,57} = 17.63$, $P < 0.001$). There were no significant differences among sites but survival during egg laying was greater than during either the incubation ($q = 7.99$, $P < 0.001$) or nestling stages ($q = 6.23$, $P < 0.001$).

Cowbird control affected both daily ($F_{2,69} = 3.79$, $P = 0.03$) and nest stage survival ($F_{2,69} = 5.30$, $P = 0.01$; Table 1.4). *Post hoc* tests revealed that, when both cowbird control methods were implemented, both daily ($q = 3.81$, $P = 0.02$) and nest stage survival ($q = 4.52$, $P = 0.01$) estimates were greater than when there was no cowbird control. Furthermore, when no cowbird control methods were used, nest stage survival during egg laying was greater than in either the incubation ($q = 5.58$, $P < 0.001$) or nestling stages ($q = 4.92$, $P = 0.003$). When moderate cowbird control was implemented, egg laying stage survival was greater than only incubation ($q = 5.22$, $P = 0.001$) and, under complete cowbird control, there were no differences between nest stage survival estimates.

Adult Survival

Resightings. We banded 729 adult black-capped vireos from 2011 through 2014, including 426 males and 303 females. Of those banded individuals, we resighted 214 in at least one subsequent field season (2012-2015). Most resightings ($n = 157$) were of male vireos, but we also resighted 57 females. Site fidelity was high and the average adult breeding dispersal distance from one season to the next was only 258 m. Females tended to disperse farther than males ($\bar{x}_{\text{female}}$ = 386 ± 76 m, $\bar{x}_{\text{male}}$ = 222 ± 41 m; t_{300} = 1.91, P = 0.06). We did not observe any adults dispersing between study sites.

Modelled Survival. The best model of adult survival included the effects of location (on or off Fort Hood) on survival and sex on recapture rate (Table 1.5 and 1.6). This model had a weight of 0.64 and was significantly better than the second best model (ΔAIC_c = 3.03, w_i = 0.14) and we used the survival estimates from the top model to assess population status at our study sites (Tables 1.5 and 1.6). For the assessment of the overall population status across all study sites, we used the adult survival estimate from the φ(~1),p(~sex) model (φ = 0.43, SE = 0.02).

Juvenile Survival

Resightings. We banded 907 nestling black-capped vireos from 2011 through 2014 and resighted only 14 (8 males and 6 females) in subsequent breeding seasons. On average, vireos dispersed 7135 m (SE = 5180 m) between their natal territory and where they later settled to breed and one male vireo dispersed from Balcones Canyonlands to Fort Hood, a distance of nearly 74 km. There was no difference in dispersal distance between males and females ($\bar{x}_{\text{male}}$ = 11043 ± 9022 m, $\bar{x}_{\text{female}}$ = 1925 ± 1160 m; t_7 = 1.00, P = 0.35) even if we did not include the long-distance disperser ($\bar{x}_{\text{male}}$ = 2059 ± 895 m, $\bar{x}_{\text{female}}$ = 1925 ± 1160 m; t_{10} = 0.09, P = 0.93).

Modelled Survival. In addition to our banding efforts, 1245 nestlings were banded on four long-term study sites on Fort Hood from 2011-2014 (D. Cimprich, pers. comm.). In total, researchers resighted 94 vireos in at least one subsequent field season (2012-2015). The best model of juvenile survival included only the effects of study site on recapture rate, φ(~1),p(~site), and had a weight of 0.64 (Table 1.7 and 1.8). Although this model was only marginally better than the second best model (φ(~location),p(~site); ΔAIC_c = 1.88, w_i = 0.25), we used the survival estimates from the top model to assess population status at individual study sites and across all sites (Tables 1.7 and 1.8).

Population Assessment

Current Population Status. Four of seven surveyed populations had negative population growth and are sinks (Tables 1.9 and 1.10; Figure 1.3). Two sites on Fort Hood, East Range and West Range, and the surveyed population at Balcones Canyonlands National Wildlife Refuge had positive population growth and could be defined as a source after averaging fecundity across all four study years (Tables 1.9 and 1.10; Figure 1.3). East Range, the only site with consistent and comprehensive cowbird control, had the strongest rate of population growth. Additionally, only East Range was a source population during all four individual study years (Table 1.9; Figure 1.3). Most other sites varied in their population status between years; only Colorado Bend State Park and West Fort Hood were sink populations in every study year (Table 1.9). Notably, when we considered all sites together, the population was unsustainable without immigration across all study years and in each individual study year (Tables 1.9 and 1.10; Figure 1.3).

Effects of Survival and Fecundity on Population Growth Rates. To achieve a positive growth rate for the central Texas vireo population as a whole, average fecundity would need to reach 1.25 young fledged/year (Figure 1.4), a level reached only at East Range and West Range (Tables 1.9 and 1.10). Fecundity at East Range averaged 1.66 young fledged/year, which was also greater than the minimal fecundity for positive population growth on Fort Hood alone (1.35 young fledged/year; Figure 1.4). West Range on Fort Hood just equaled this average minimum required fecundity (Tables 1.9 and 1.10). Off of Fort Hood, an average fecundity of 1.15 young fledged/year would enable positive population growth (Figure 1.4) and this was almost achieved at Balcones Canyonlands where fecundity averaged 1.22 across the four study years (Tables 1.9 and 1.10).

Holding fecundity and adult survival at baseline rates, we found that allowing juvenile survival to reach 58% enabled a positive growth rate on average across our study sites (Figure 1.4). On Fort Hood, a juvenile survival rate of 50% would allow for positive growth while off of Fort Hood, juvenile survival would need to reach 73% (Figure 1.4). A positive growth rate could not be achieved on Colorado Bend; even allowing for 100% juvenile survival, the population at Colorado Bend would decline at a rate of 7.5% (Figure 1.4). At West Fort Hood, juvenile survival would need to be very high (84%) to allow for positive growth without improving either adult survival or fecundity.

Across all sites, an increase in adult survival to 54% would enable a positive growth rate and, on Fort Hood, adult survival rates of 42% would allow for positive growth (Figure 1.4). Off of Fort Hood, 67% adult survival would allow for positive growth rates across all sites on average and all individual sites except for Colorado Bend which would require 81% adult survival (Figure 1.4).

Growth rates were most sensitive to changes in juvenile survival at East Range and West Range and least sensitive to juvenile survival at Colorado Bend and West Fort Hood (Table 1.10). By contrast, growth rates were most sensitive to fecundity and adult survival at Colorado Bend and least sensitive to these factors at East and West Range (Table 1.10). Elasticity of growth rates in response to changes in adult survival was greater than elasticity to juvenile survival or fecundity at Colorado Bend and the property at San Saba (Table 1.10).

DISCUSSION

We found that populations of the endangered black-capped vireo across central Texas are mostly sinks although some peripheral sites could become sources with increased cowbird control efforts. Our results suggest that cowbird parasitism is the *most* important limiting factor in vireo population growth across our study sites. At individual breeding sites, however, the most important demographic driver of population growth varied between survival and fecundity, highlighting the need for informed land management.

Cowbirds, Nest Success, and Fecundity

Parasitism rates of vireo nests was highest at sites with little cowbird control effort suggesting that, without control, cowbird parasitism would be high at breeding sites across central Texas. Daily and nest stage survival also increased with degree of cowbird control, both overall and within specific nest stages. When nests were parasitized, however, vireo pairs commonly responded by abandoning their nest. Pairs which abandon a parasitized nest relatively early in the season may be able to renest successfully. However, nest abandonment after parasitism may not always be the best strategy, especially if cowbird eggs frequently do not hatch allowing vireos the potential to raise their own young (Boves et al. 2014). Parasitized nests that were not abandoned faced high rates of depredation and relatively few went on to fledge either vireo or cowbird young. Additionally, parasitized nests that succeeded in producing young fledged nearly one less nestling/nest on average than successful nests that were not parasitized, likely because cowbirds typically remove one host egg when they parasitize a vireo nest. Thus, selection for abandonment may be dependent on local conditions including cowbird and predator densities.

Fecundity varied across sites and was greatest at East Range where there was complete cowbird control. In general, vireo populations at sites with high parasitism rates were more sensitive to increases in fecundity compared with sites with relatively low parasitism rates. Sensitivity to fecundity was lowest on East Range, where cowbirds parasitized only one of 126 monitored nests.

Adult Survival

In agreement with patterns observed in many songbirds (Greenwood 1980, Pampus et al. 2005, Cline et al. 2013) as well as other bird taxa (Friedrich et al. 2015, Terraube et al. 2015), male vireos exhibited more breeding site fidelity than females. We also resighted more adult males than adult females and, thus, our adult survival estimates may be biased to better reflect male survival. Previous studies, however, have found no evidence for differences in adult male and female survival among black-capped vireos (Kostecke and Cimprich 2008) or other vireo species (Budnik et al. 2000; Gardali and Ballard 2000), and a sex bias may have only minimally impacted our survival estimates. Better survival data from long-term data sets with larger sample sizes may elucidate sex-specific differences in survival that may affect our population assessments and population growth projections.

Our estimates of adult vireo survival were generally in agreement with previous estimates both on and off of Fort Hood that range between 36 and 75% (Graber 1961, Tazik and Cornelius 1993, Grzybowski 1995, USFWS 1996, Weinberg et al. 1998, Grzybowski 2005; see Kostecke and Cimprich 2008 for summary). The most comprehensive estimation of adult survival across Fort Hood considered data from several long-term study sites (1997-2006) and survival estimates varied between 45 and 56% (Kostecke and Cimprich 2008), notably higher than our estimate for our Fort Hood sites (38%). However, Kostecke and Cimprich (2008) found that survival varied significantly between years and in some years was as low as 36%. Our survival estimates could simply reflect survey years with relatively poor survival on Fort Hood (because our surveys did not overlap areas surveyed by Kostecke and Cimprich (2008)) or, alternatively, our Fort Hood sites could represent relatively poor vireo breeding habitat compared with long-term sites elsewhere on the base. Differences in habitat could affect adult survival directly, for example through local increases in predator populations. Additionally, adult survival estimates may be biased low in general because of incomplete breeding site-fidelity (Marshall et al. 2004), but this bias might differ between sites that vary in habitat quality if birds more frequently disperse away from low quality sites in favor of better breeding habitat. Dispersal-biased adult survival on Fort Hood may also explain why we observed higher survival at sites off of Fort Hood. Although birds that breed on Fort Hood have considerable nearby habitat to choose from and may disperse outside our search areas between subsequent breeding seasons, birds in relatively isolated patches of habitat, such as those off of Fort Hood, may simply have nowhere else to go. Age-specific analyses that compare adult survival between the first and second breeding season with survival in subsequent seasons may help elucidate these patterns.

Population growth at sites with high parasitism and low nest success was more sensitive to adult survival than population growth at sites with high nest success. Additionally, proportional changes in adult survival benefited sites with low nest success more than increases in reproductive success. Thus, biases in our estimates of adult survival may have the greatest impact on population projections for sites with low nest success.

Juvenile Survival

Because we resighted a relatively small number of juvenile vireos from our own study sites, we included banding and resighting records of vireos on long-term sites monitored by Fort Hood. We found no evidence that juvenile survival differed between populations on or off of

Fort Hood or between individual sites. Juvenile survival is notoriously difficult to estimate because it is often impossible to distinguish between dispersal and true mortality. To compensate, many researchers instead assign juvenile survival as a percentage, often 50%, of adult survival (Greenberg 1980, Temple and Cary 1988, Noon and Sauer 1992, Donovan et al. 1995). In contrast, our estimate of 46% juvenile survival is relatively high, even greater than our estimates of adult survival on some study sites, and is higher than previous estimates of juvenile survival on Fort Hood (Kostecke and Cimprich 2008). Our estimate is, however, consistent with juvenile vireo survival estimates from the Wichita Mountains (Grzybowski 2005) and is further bolstered by evidence of high survival of independent juvenile vireos from radio-telemetry during the post-breeding season (Chapter 2). In fact, high juvenile dispersal and low return rates may have resulted in underestimates of juvenile survival. Biases cannot, however, account for negative population growth projected for our site with high cowbird parasitism (Colorado Bend). Furthermore, they are unlikely to explain negative projections for West Fort Hood or sites off of Fort Hood as the sensitivity of population growth rates to juvenile survival was relatively low in populations with poor nest success and high rates of parasitism compared with other sites.

Importance of Sink Habitats

We found that many of the populations we monitored were sink habitats, although low adult survival estimates may have biased population growth projections on sites with low nest success. Though efforts to conserve endangered and threatened species often focus on the creation and preservation of high quality habitat patches, low quality habitat may also contribute to the stability and long-term survival of metapopulations (Foppen et al. 2000, Murphy 2001) and may buy time for management of declining populations (Heinrichs et al. 2015). Although populations located in lower quality habitat may individually be more vulnerable to a poor reproductive year or catastrophic event due to isolation and relatively small size, low quality habitat is often found in greater abundance and reproduction in these patches may still contribute to overall metapopulation size (Foppen et al. 2000). Sinks may also positively affect the overall population if individuals eventually leave and disperse to higher quality habitat (Howe et al. 2001, Gaona et al. 1998). Importantly, many populations we assessed as sinks overall were stable or source populations in some individual years and young produced during source years may disperse to supplement populations in higher quality habitat or help establish new populations in uninhabited fragments.

Dispersal

We were unable to quantify the amount of immigration and emigration between study populations and, ultimately, the role of dispersal in the persistence of these populations. Dispersal events between high and low quality habitat patches could help alleviate demographic pressures placed on less productive populations and, although we did not directly observe any adult dispersal between breeding sites, we know from our estimates of population growth that migration must occur for many of these populations to have persisted through the course of this study. Vireo dispersal events as far as 78 km have been rarely documented from the resighting of uniquely banded individuals (Kostecke and Cimprich 2008) but future studies would likely benefit from the use of molecular techniques to identify and elucidate genetic relationships between seemingly disparate subpopulations. Although previous genetic analyses of black-capped vireo populations across their range have been inconclusive in identifying source-sink population dynamics (Barr et al. 2008, Zink et al. 2010), no investigation has analyzed the genetic makeup of vireo populations on the relatively local, metapopulation scale.

Implications to Management

Vireo populations with low nest success and high parasitism rates respond more to proportional changes in adult survival than fecundity or juvenile survival. Elasticity, however, does not necessarily translate directly to management and, in addition to evaluating measures of elasticity, managers must assess their ability to affect change on demographic parameters (Heppel 1998, Mills et al. 1999). Although we know predation, food availability, and climate are likely to influence adult songbird mortality during the breeding season (Sherry and Holmes 1995), specific drivers of adult vireo mortality are unknown and probably vary across breeding populations. By contrast, much research (including results of this study) has suggested that effective cowbird control can dramatically impact nest success and fecundity (e.g. Kostecke et al. 2005, Kus and Whitfield 2005). Ultimately, management action to improve reproductive success is likely to be both more feasible and much more effective than attempts to improve adult survival, particularly at sites with high parasitism rates. For example, for the vireo population at Colorado Bend, let's assume management action can either (A) improve adult vireo survival by 10% through habitat restoration or (B) double fecundity by enacting complete cowbird control efforts. Plan A would result in a 5% increase to population growth, changing λ from 0.72 to 0.76. In contrast, Plan B would improve population growth by 50% and make Colorado Bend a self-sustaining population with a growth rate of 1.08. Thus, cowbird control remains the primary objective of managing vireo breeding habitat. Additionally, cowbird control can be easily and immediately implemented, while improvements to habitat quality may take several years. Importantly, our results suggest that cowbird removal programs are most effective when they utilize both shooting and trapping strategies, although the relative contribution of each control method is difficult to tease out. Previous research on Fort Hood suggests that shooting alone may be more effective than trapping alone because managers can target cowbirds that are the most likely to parasitize nests (Kostecke et al. 2005). Shooting, however, requires a relatively intensive management presence and, for many land managers, trapping may be the best cowbird removal strategy because it covers a broader area with less effort.

Metapopulation Dynamics

Dynamics between the subpopulations of wildlife species may vary temporally (e.g. shift between breeding seasons) and researchers must properly understand the drivers of these shifts (e.g. through sensitivity and elasticity analyses) to accurately predict the likelihood of population persistence. Additionally, using averages across several years to project population growth may not sufficiently describe metapopulation status in cases where population dynamics shift significantly or frequently. Furthermore, an understanding of the drivers of fine scale shifts in metapopulation status can help identify unforeseen management strategies. In many cases, sinks may be converted to stable or source populations with relatively minimal management action.

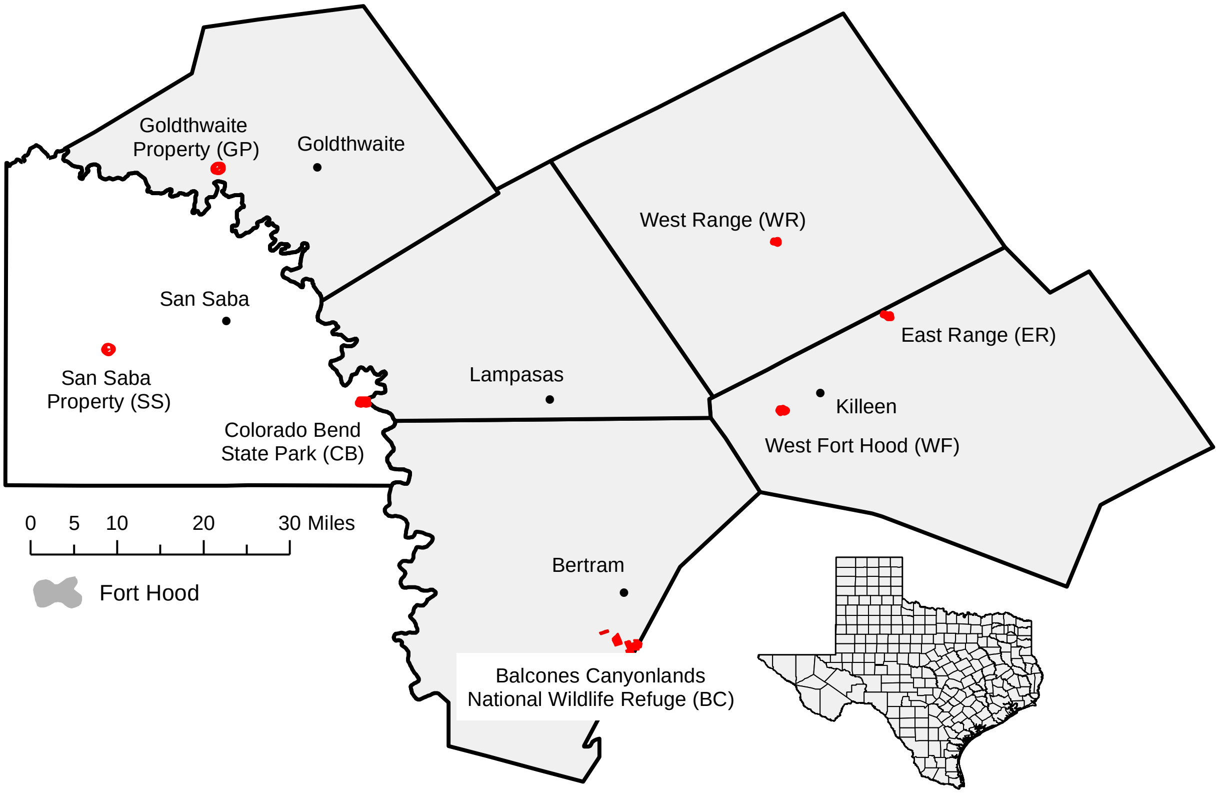


Figure 1.1. Black-capped vireo study sites in central Texas, 2011-2014.

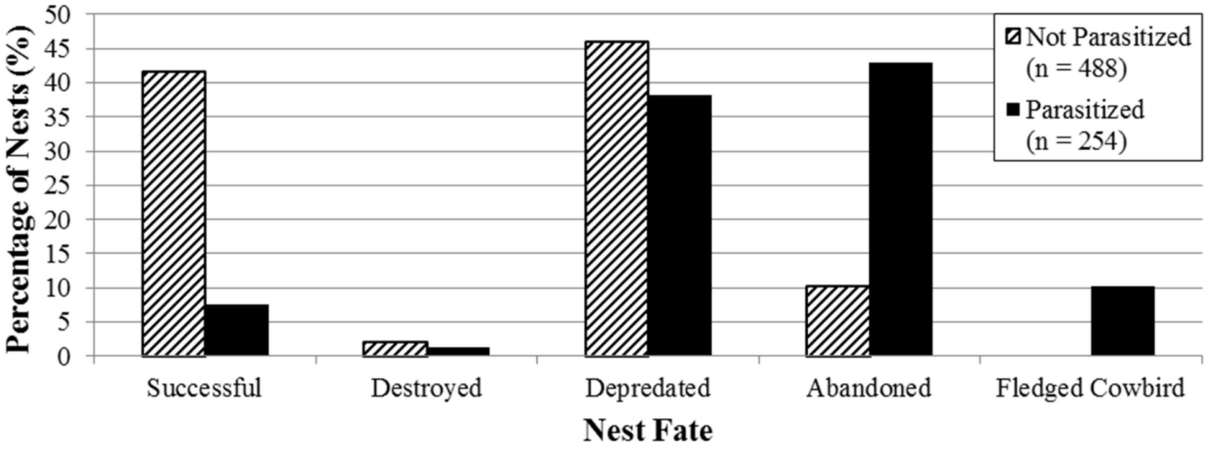


Figure 1.2. Summary of nest fate and parasitism status of vireo nests in central Texas from 2011-2014 with known fate and parasitism status (*n* = 742).

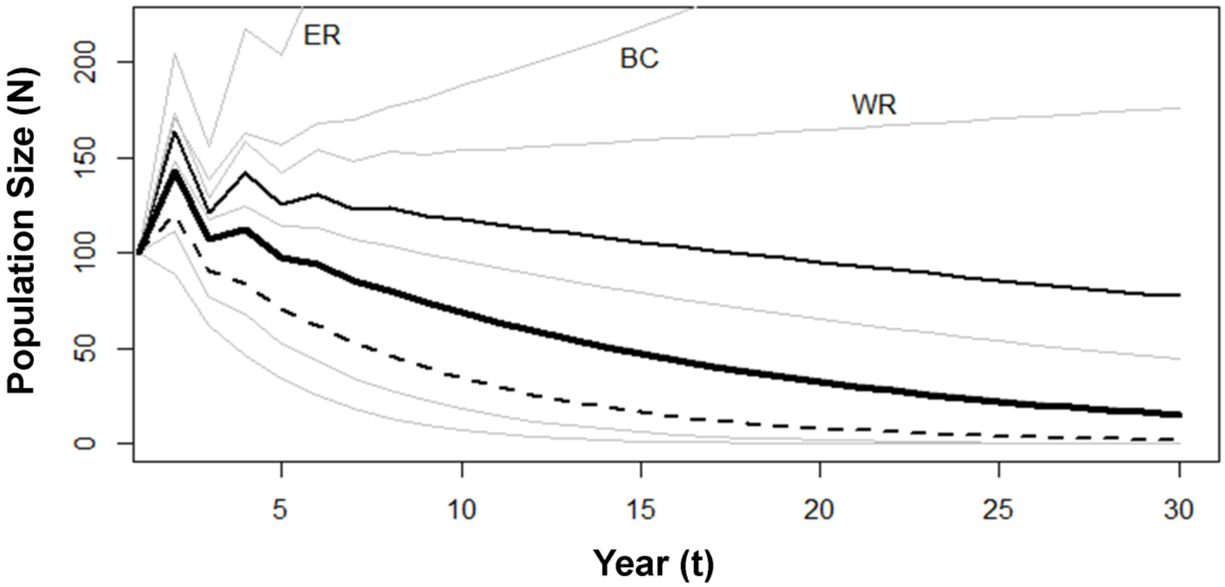


Figure 1.3. Vireo population projections (N_0 = 100 adults) based on population matrices (Caswell 2001) of demographic parameters at vireo populations across central Texas. Projections reflect calculations of fecundity, adult survival, and juvenile survival based on field observations. The bold black line is the average growth rate across all sites, thin black lines are averages for sites on (solid) and off Fort Hood (dashed), and gray lines are projections for individual sites (sites with positive population growth are labelled).

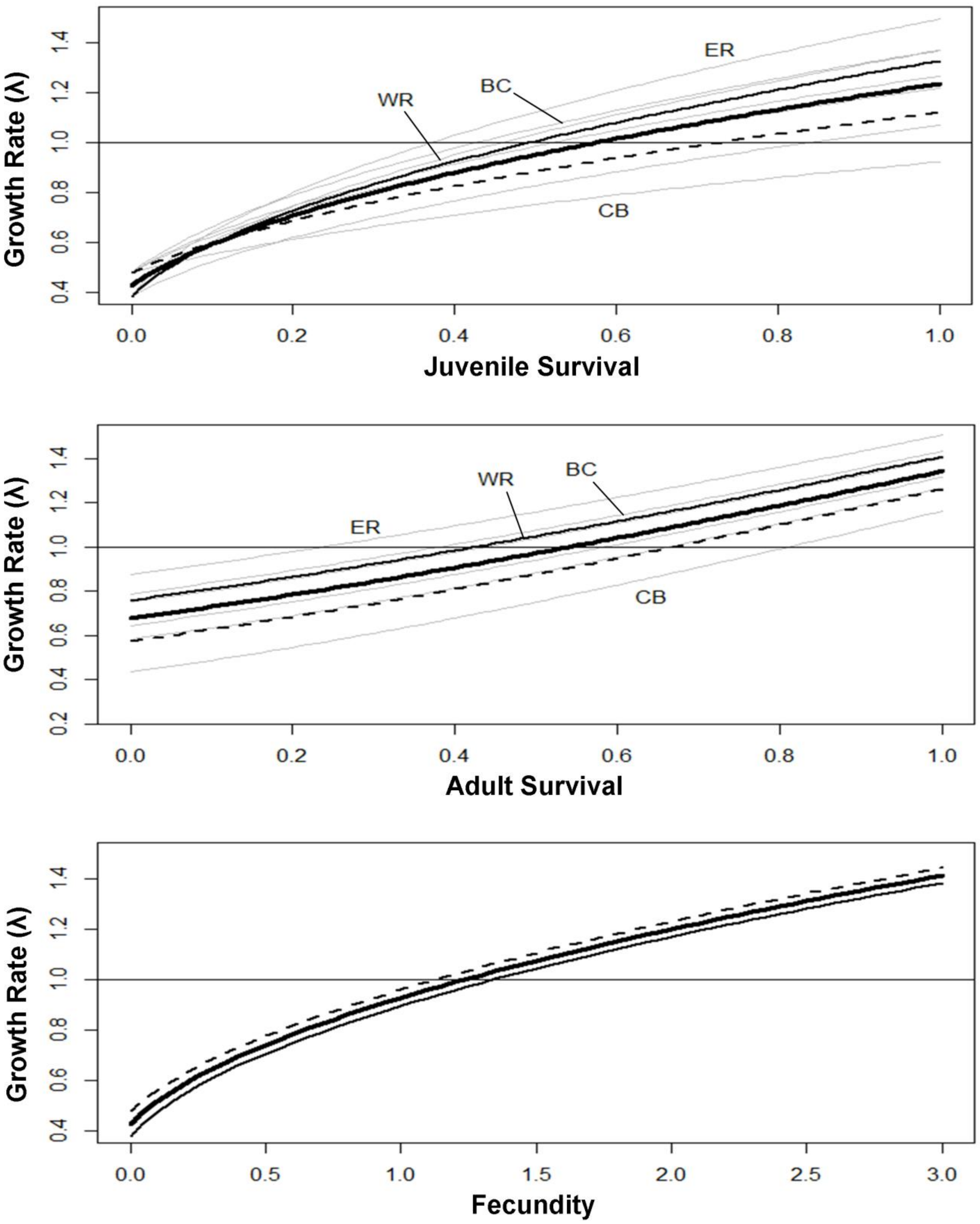


Figure 1.4. Variation in growth rate (λ) at vireo populations across central Texas considering a range of juvenile survival, adult survival, and fecundity. The bold black line is the average growth rate across all sites, thin black lines are averages for sites on (solid) and off Fort Hood (dashed), and gray lines are projections for individual sites.

Table 1.1. Level of cowbird control at vireo breeding sites across central Texas from 2011-2014. At sites with complete control, managers used both shooting and trapping to remove cowbirds. At moderately controlled sites, cowbirds were controlled with either trapping or shooting. The properties in Goldthwaite (GP) and San Saba (SS) were not monitored in 2011.

	Year			
Site	2011	2012	2013	2014
BC	Moderate	Moderate	Moderate	Moderate
CB	None	None	None	Moderate
GP	---	None	Moderate	Complete
SS	---	None	None	Moderate
ER	Complete	Complete	Complete	Complete
WF	Moderate	Moderate	Moderate	Moderate
WR	None	None	None	None

Table 1.2. Summary of vireo banding and monitoring efforts across central Texas breeding sites, 2011-2014.

	Total	BC	CB	GP[a]	SS[a]	ER	WF	WR
Vireos Banded	1635	176	175	28	216	407	267	351
Terr. Monitored	384	44	68	13	39	78	74	68
% Terr. Success	0.51	0.45	0.32	0.54	0.54	0.62	0.42	0.68
Nests[b]	782	58	185	21	109	128	144	137
% Nest Success[c]	0.30	0.40	0.15	0.38	0.28	0.41	0.22	0.44
% Parasitism	0.34	0.18	0.69	0.35	0.46	0.01	0.28	0.21

[a] Monitored in 2012-2014 only.
[b] All known nesting attempts, including those discovered while no longer active.
[c] Apparent success.

Table 1.3. Daily and stage survival of vireo nests (Mayfield 1975) at breeding sites across central Texas from 2011-2014.

Site	*n*		Nest Stage			Overall Survival
			Egg Laying	Incubation	Nestling	
BC	56	Daily Survival	0.97	0.98	0.95	
		Stage Survival	0.92	0.72	0.59	0.38
CB	181	Daily Survival	0.93	0.90	0.93	
		Stage Survival	0.82	0.24	0.45	0.09
GP[a]	20	Daily Survival	0.88	0.96	0.96	
		Stage Survival	0.73	0.53	0.64	0.25
SS[a]	106	Daily Survival	0.94	0.95	0.95	
		Stage Survival	0.85	0.45	0.54	0.21
ER	126	Daily Survival	0.96	0.98	0.96	
		Stage Survival	0.89	0.72	0.64	0.42
WF	140	Daily Survival	0.93	0.95	0.93	
		Stage Survival	0.84	0.49	0.46	0.19
WR	133	Daily Survival	0.96	0.96	0.97	
		Stage Survival	0.91	0.58	0.68	0.36
All	762	Daily Survival	0.94	0.95	0.95	
		Stage Survival	0.86	0.50	0.57	0.25

[a] Monitored in 2012-2014 only.

Table 1.4. Average daily and stage survival of vireo nests (Mayfield 1975) at sites varying in level of cowbird control across central Texas from 2011-2014.

	Daily Survival		Stage Survival	
Cowbird Control	Mean	SE	Mean	SE
Complete	0.97	0.01	0.78	0.04
Egg Laying	0.98	0.01	0.95	0.03
Incubation	0.97	0.01	0.70	0.07
Nestling	0.96	0.01	0.68	0.05
Moderate	0.94	0.01	0.67	0.04
Egg Laying	0.93	0.02	0.83	0.04
Incubation	0.95	0.01	0.53	0.06
Nestling	0.96	0.01	0.66	0.07
None	0.92	0.02	0.58	0.05
Egg Laying	0.90	0.04	0.80	0.07
Incubation	0.94	0.01	0.45	0.05
Nestling	0.91	0.03	0.49	0.08

Table 1.5. Top models of adult vireo survival and recapture. We compared 20 models in total and, for the 16 models not shown, $\Delta AIC_c > 26.00$ and $w_i < 0.001$.

Model	k	AIC_c	ΔAIC_c	w_i
φ (~location), *p* (~sex)	4	1126.04	0.00	0.64
φ (~cowbird control), *p* (~sex)	5	1129.07	3.03	0.14
φ (~site), *p* (~sex)	9	1129.07	3.04	0.14
φ (~1), *p* (~sex)	3	1130.36	4.33	0.07

Table 1.6. Parameter estimates from top model of adult vireo survival, considering the effects of location on survival (φ; probability of a vireo surviving and returning to one of our study sites in a following breeding season) and sex on recapture probability (*p*; probability of encountering a vireo given its survival and that it returned to one of our sites).

			95% Confidence Interval	
Parameter	Estimate	SE	Lower	Upper
φ (On Fort Hood)	0.38	0.03	0.33	0.44
φ (Off Fort Hood)	0.48	0.03	0.42	0.54
p (Female)	0.46	0.07	0.35	0.61
p (Male)	0.94	0.03	0.88	0.98

Table 1.7. Top models of juvenile vireo survival and recapture. We compared 16 models in total and, for the 11 models not shown, $\Delta AIC_c > 10.00$ and $w_i < 0.005$.

Model	k	AIC_c	ΔAIC_c	w_i
φ (~1), *p* (~site)	12	881.20	0.00	0.64
φ (~location), *p* (~site)	13	883.07	1.88	0.25
φ (~cowbird control), *p* (~site)	14	885.24	4.04	0.08
φ (~site), *p* (~1)	12	889.54	8.34	0.01
φ (~site), *p* (~location)	13	891.07	9.87	0.005

Table 1.8. Parameter estimates from top model of juvenile vireo survival, considering the effects of location on survival (φ; probability of a vireo surviving and returning to one of our study sites in a following breeding season) and sex on recapture probability (p; probability of encountering a vireo given its survival and that it returned to one of our sites). Sites labelled "Fort Hood" are long-term sites monitored by biologists with the Fort Hood Division of Natural Resources.

			95% Confidence Interval	
Parameter	Estimate	SE	Lower	Upper
φ (null)	0.46	0.07	0.35	0.61
p (Balcones NWR)	0.03	0.02	0.01	0.10
p (Colorado Bend)	< 0.001	< 0.001	< 0.001	< 0.001
p (Goldthwaite)	0.11	0.11	0.01	0.49
p (San Saba)	0.05	0.03	0.01	0.13
p (East Range)	0.02	0.01	0.004	0.05
p (West Fort Hood)	0.04	0.02	0.01	0.11
p (West Range)	0.01	0.01	< 0.001	0.04
p (Fort Hood - Site A)	0.12	0.03	0.07	0.19
p (Fort Hood - Site B)	0.02	0.02	0.001	0.08
p (Fort Hood - Site C)	0.10	0.03	0.06	0.16
p (Fort Hood - Site D)	0.06	0.02	0.03	0.12

Table 1.9. Annual variation in sources and sinks at specific sites across central Texas from 2011-2014.

Site	Year	*n*	Young/Successful Nest	Fecundity/Female/Year	Population Status
BC	2011	8	2.00	1.25	Source
	2012	17	3.00	0.95	Sink
	2013	7	2.20	1.46	Source
	2014	24	3.22	1.39	Source
	Total	56	2.68	1.22	Source
CB	2011	9	3.67	1.17	Source
	2012	54	3.17	0.65	Sink
	2013	83	2.75	0.16	Sink
	2014	35	3.75	0.51	Sink
	Total	181	3.26	0.41	Sink
GP	2012	4	0.00	0.00	Sink
	2013	8	2.67	0.37	Sink
	2014	8	3.50	2.01	Source
	Total	20	3.14	1.00	Sink
SS	2012	24	3.00	0.35	Sink
	2013	44	3.50	0.35	Sink
	2014	38	3.33	1.59	Source
	Total	106	3.29	0.91	Sink
ER	2011	13	3.60	1.61	Source
	2012	25	3.67	2.47	Source
	2013	47	3.16	1.54	Source
	2014	41	3.46	1.33	Source
	Total	126	3.42	1.66	Source
WF	2011	14	2.80	0.69	Sink
	2012	25	3.57	1.16	Sink
	2013	50	2.86	0.66	Sink
	2014	51	2.75	0.58	Sink
	Total	140	3.00	0.74	Sink
WR	2011	10	2.50	0.84	Sink
	2012	28	3.36	1.69	Source
	2013	40	3.35	1.75	Source
	2014	55	2.83	1.02	Sink
	Total	133	3.13	1.35	Source
All	2011	67	2.83	0.90	Sink
	2012	177	3.39	1.17	Sink
	2013	279	3.08	0.81	Sink
	2014	252	3.19	1.06	Sink
	Total	762	3.17	1.00	Sink

Table 1.10. Growth rates (λ) and sensitivity and elasticity of demographic parameters at vireo populations across central Texas, 2011-2014. Sensitivity is the response of lambda to a numerical change in an individual parameter while elasticity reflects a proportional change.

Site	Growth Rate (λ)	Parameter	Sensitivity	Elasticity
BC	1.031	Fecundity	0.29	0.35
		Juvenile Survival	0.77	0.35
		Adult Survival	0.65	0.30
CB	0.738	Fecundity	0.47	0.26
		Juvenile Survival	0.41	0.26
		Adult Survival	0.74	0.48
GP[a]	0.962	Fecundity	0.32	0.33
		Juvenile Survival	0.69	0.33
		Adult Survival	0.67	0.33
SS[a]	0.931	Fecundity	0.34	0.33
		Juvenile Survival	0.65	0.33
		Adult Survival	0.67	0.35
ER	1.092	Fecundity	0.26	0.39
		Juvenile Survival	0.92	0.39
		Adult Survival	0.61	0.21
WF	0.808	Fecundity	0.38	0.34
		Juvenile Survival	0.60	0.34
		Adult Survival	0.66	0.31
WR	1.007	Fecundity	0.28	0.38
		Juvenile Survival	0.83	0.38
		Adult Survival	0.62	0.24
Off Fort Hood	0.866	Fecundity	0.37	0.31
		Juvenile Survival	0.58	0.31
		Adult Survival	0.69	0.38
On Fort Hood	0.979	Fecundity	0.29	0.38
		Juvenile Survival	0.80	0.38
		Adult Survival	0.62	0.24
All	0.928	Fecundity	0.32	0.35
		Juvenile Survival	0.70	0.35
		Adult Survival	0.65	0.30

[a] Monitored in 2012-2014 only.

CHAPTER 2

Habitat Use by Adult and Juvenile Black-capped Vireos: Natural Selection and the Importance of Considering a Broader Definition of Breeding Habitat

Natural selection, the fundamental mechanism of evolution, favors heritable traits of individuals that enhance reproduction and survival. Although much avian research has focused on understanding the characteristics guiding success of the actual reproductive event (e.g. nest or territory success within a single breeding season; see Streby and Andersen 2011), natural selection operates on the timescale of an individual's entire reproductive life. Natural selection, therefore, may guide not only the qualities that successfully produce young but also those that allow those young to survive long enough to reproduce themselves. Research that focuses on understanding the qualities of breeding sites alone (e.g. nest placement or territory composition) may not fully document the way in which natural selection fashions the choice of where a species nests.

Aspects of the breeding site that affect post-independence juvenile survival vary across species and life history strategies. For relatively wide-ranging species such as raptors and seabirds, juvenile survival may be limited by temporal and spatial variation in prey availability (Rohner and Hunter 1996, Wiens et al. 2006, Riotte and Weimerskirch 2013), environmental conditions (Fay et al. 2015), and interactions with humans (Votier et al. 2008, Stoychev et al. 2014). Juvenile survival for many passerines, however, is limited primarily by the ability to avoid predators and forage effectively (Sullivan 1989, Kershner et al. 2004), and foraging proficiency might be particularly important for birds preparing for an arduous fall migration.

For many young songbirds, the greatest threats to survival are predation shortly after fledging (Anders et al. 1997, Yackel Adams et al. 2001, Rush and Stutchbury 2008, Vitz 2008, Ausprey and Rodewald 2011) and the myriad challenges of migration (Owen and Black 1989, Sillett and Holmes 2002, Menu et al. 2005). Thus, parents may increase their reproductive output by selecting breeding territories with both sufficient cover to protect young birds from predators (Vega Rivera et al. 1998) and food resources that enable juveniles to store sufficient fat reserve for migration (White et al. 2005, Vitz and Rodewald 2007, Streby et al. 2011). Shrublands or habitats with dense understory vegetation may meet those requirements for many species. Juvenile yellow-breasted chats (*Icteria virens*) and gray catbirds (*Dumetella carolinensis*) that fledged from shrublands remained in early-successional habitat after they became independent (Maxted 2001). Young ovenbirds (*Seiurus aurocapilla*; King et al. 2006, Vitz 2008, Streby and Andersen 2013), worm-eating warblers (*Helmitheros vermivorum*; Vitz 2008), and white-throated robins (*Turdus assimilis*; Cohen and Lindell 2004) used post-fledging habitat with relatively dense understory vegetation compared with typical breeding habitat for those species. However, Streby and Andersen (2013) found that juvenile ovenbirds remained in their nesting habitat (mature forest) when dense understory cover was also available.

Tensions between the selection of a breeding territory that optimizes the production of fledglings versus one that maximizes offspring survival prior to migration should be reflected in differential habitat use by adults and juveniles (Figure 2.1). Furthermore, nest site selection that considers juvenile habitat requirements might result in sub-optimal nest success whereas habitat that optimizes nest success alone may endanger juveniles. Thus, a full understanding of how natural selection shapes the choice of a breeding site is necessary for both researchers aiming to fully understand the life history and ecology a species and land managers wishing to properly conserve or restore appropriate breeding habitat. This is perhaps particularly important for the management of endangered species already limited by habitat loss or restricted breeding ranges. To evaluate the role of juvenile habitat requirements on breeding site selection, we surveyed habitat use by territorial and juvenile birds of an endangered shrubland species, the black-capped vireo (vireo; *Vireo atricapilla*).

Vireos are small songbirds that breed locally throughout northeastern Mexico, Texas, and southern Oklahoma in early successional shrub habitat and winter along the western Mexican coast. In 1987, the species was listed as endangered by the U.S. Fish and Wildlife Service, which cited declines in breeding habitat due to the disruption of disturbance regimes (i.e. fire suppression), invasive vegetation (e.g. Ashe juniper; *Juniperus ashei*), and increased ranching, agriculture, and urbanization, which convert shrublands and increase brood parasitism by brown-headed cowbirds (*Molothrus ater*) (Ratzlaff 1987, USFWS 1991). Vireo reproductive success is limited by cowbird parasitism because vireos are generally unable to fledge their own young from parasitized nests and areas with high cowbird presence may represent lower quality or even sink habitat (Chapter 1). Today, the largest breeding population of vireos, approximately 5000 pairs, is located on the 88478 hectare Fort Hood Military Reservation (Fort Hood), where cowbird populations are controlled to improve vireo productivity (Kostecke et al. 2005) and large patches of shrubland habitat remain undeveloped.

Although the characteristics of vireo breeding habitat have been well documented (Grzybowski et al. 1994, Conkling et al. 2012), relatively little is understood about the habitat requirements for juvenile vireos or the tradeoffs, if any, between these requirements and those favored by nesting adults. Across their breeding range, adult vireos use habitats with high densities of deciduous shrub cover (Grzybowski et al. 1994). Vireo nest success is also higher in natural shrubland than in habitat modified by military activity (Bailey 2005, Noa et al. 2007). On Fort Hood, juveniles use riparian vegetation near water sources more than the shrub habitat characteristic of breeding territories (Dittmar et al. 2014). Young birds on Fort Hood also use areas with greater canopy cover and foliage density compared with random nearby locations (Dittmar et al. 2014). However, juvenile habitat use and survival has not been assessed across broader scales or in areas without nearby or easily accessible riparian vegetation.

In this chapter, we compared the use of vegetation by adult and juvenile vireos across central Texas during the breeding season and during the post-breeding/pre-migration period, respectively. We compared vegetative characteristics of nest sites, breeding territories, and places visited by juveniles using direct field measurements of structure as well as remotely sensed aspects of the landscape. We expected that both breeding and juvenile vireos would most frequently use areas with at least moderate shrub cover and dense cover near the ground due to previous observations of habitat associations for vireos (Grzybowski 1995, Bailey 2005, Dittmar et al. 2014). We predicted, however, that areas with relatively high amounts of low structural cover and high proportions of shrub and deciduous forest land cover would not necessarily benefit nest success (Bailey 2005, Chalfoun and Martin 2009) but would improve juvenile survival (Vitz 2008, Dittmar et al. 2014). We anticipated one important tradeoff in breeding site and juvenile habitat: to reduce risk of nest parasitism in areas without cowbird control, breeders may favor areas with less canopy cover relative to juveniles. Cowbirds may use perches within the canopy to survey and search for nest locations (Hauber and Russo 2000). In contrast, canopy cover may benefit juvenile birds by providing cover from predators (Streby et al. 2015). We also expected juveniles to concentrate habitat use and have greater survival in vegetation with abundant understory cover, including shrublands and mixed deciduous forest land covers.

Finally, we predicted that juveniles would concentrate their use in wetland habitats, as found by Dittmar et al. (2014), but that there would be no association with wetlands in breeding territories.

METHODS

Study Sites

We chose study sites on Fort Hood and in nearby areas to the south and west, all within what is commonly called the Hill Country of central Texas (Figure 2.2). The habitat is largely characterized by shortgrass communities and cattle rangeland. Many areas that were once native grass or shrublands have transitioned to woodlands due to fire suppression regimes and the range expansion of the native evergreen Ashe juniper.

Fort Hood Military Reservation. We monitored three study sites on Fort Hood from 2011 through 2014 (Figure 2.2). West Range, approximately 50 hectares, is dominated by mixed juniper and deciduous woodlands. The East Range site, about 60 hectares, and West Fort Hood, 100 hectares, are both characterized by a mix of grasslands and deciduous woodlands.

Balcones Canyonlands National Wildlife Refuge. Balcones Canyonlands is a 9638 hectare reserve comprised of 65 individual tracts of land, located approximately 45 miles southwest of Fort Hood near the intersection of Burnet, Williamson, and Travis Counties (Figure 2.2). We focused our monitoring efforts on three tracts along the northern edge of the refuge. In 2011, we monitored approximately 65 hectares and, from 2012-2014, expanded our survey efforts to cover an additional 80 hectares. Vegetation cover varies between tracts from tall dense shin oak (*Quercus sinuata* var. *breviloba*) to juniper woodlands to open grasslands with scattered low shin oak and flame-leaf sumac (*Rhus lanceolata*).

San Saba. From 2012 through 2014, we surveyed portions of two neighboring private ranches, nearly 12 miles southwest of San Saba, TX, in San Saba County (Figure 2.2). About 25 hectares, the site is comprised of a northwest-facing hillside, largely covered in very dense persimmon (*Diospyros texana*), juniper, hog plum (*Colubrina texensis*), honey mesquite (*Prosopis glandulosa*), allthorn (*Koeberlinia spinosa*), and green condalia (*Condalia viridis*). The top of the hill is characterized by open patchy persimmon and the bottom flattens out into grassland, then slopes downward again in dense juniper, persimmon, cedar elm (*Ulmus crassifolia*), and bee brush (*Aloysia gratissima*).

Colorado Bend State Park. Colorado Bend is a 2150 hectare state park located along the west side of the Colorado River in San Saba County (Figure 2.2). From 2011 through 2014, we searched for vireo territories and attempted to mistnet and band vireos in the Gorman Falls area, along the Tie Slide, Heller Brakes, and Gorman Falls trails, an area comprising approximately 120 hectares. The site was characterized by a mix of open grasslands and patchy juniper and live oak (*Quercus fusiformis*) woodlands.

Effects of Cowbird Control

In each study year, we classified each study site by their level of cowbird control (Table 2.1). We designated sites with both trapping and shooting as having “complete” cowbird control. If cowbirds were either trapped *or* regularly removed by shooting, we designated the site with “moderate” cowbird control. We labeled all other sites as having no cowbird control.

Monitoring Efforts

Adults. We visited study sites two to three days per week throughout the vireo breeding season, from late March through early July, and searched for all territorial males. We identified males by individual color band combination and visited each territory from one to three times per week, recording locations of territorial male vireos using a handheld GPS unit. We recorded no more than five locations per day for each territory and each observation was separated by at least five minutes.

We monitored pairs to locate all nests. Although we attempted to document all nesting attempts, we likely missed some unsuccessful nests. We believe this happened infrequently, however, as relatively few nests were located post-fledging (2.0%) or post nest failure (1.4%). We visited known nest locations every three to four days until failure or fledging and recorded the number of vireo and cowbird eggs (if present), the number and approximate age of nestlings, and parental presence at the nest. We considered a nest to be successful (n = 223) if we observed at least one fledgling with parents away from the nest (n = 150) or if we observed at least one vireo nestling in the nest on day 11 (average fledge day) and we observed behaviors by the adults to suggest they had fledglings (scolding, carrying food) (n = 73).

Juveniles. In late June through August of 2012-2014, we caught juvenile black-capped vireos and attached radio-transmitters weighing approximately 270 mg (or about 3% of a vireo's body weight) using leg loop harnesses. We aimed netting attempts at young vireos banded as nestlings so we could be certain of their exact age and natal location; we attached transmitters to 27 banded juveniles recaptured between 32 and 64 days post-fledging. However, we also attached transmitters to unbanded juvenile vireos (n = 86) that we caught incidentally. We assumed that all juveniles were fledged from breeding territories at their capture location. We followed and recorded locations of each radio-tagged bird daily until the bird could no longer be found. We lost contact with 51 birds that appeared to have moved beyond our search area (although their transmitters may have failed suddenly and earlier than expected) and 53 birds because the transmitter batteries died.

Home Range Estimation

We used a fixed-kernel density estimator in Geospatial Modeling Environment (version 0.7.3.0; GME; Beyer 2012) to create utilization distributions at 10 m resolution covering the points used by breeding adults and juveniles. We used the plug-in algorithm to estimate the optimal bandwidth and 1.5 as a starting point for the iterative smoothing factor algorithm for each home range. We then converted utilization distributions to percent volume contours and considered the home range equal to the area circumscribed by the 99 percent contour.

We obtained 4-86 locations on breeding adult males and 3-34 on juveniles. We estimated the home range area for all breeders (n = 377) and found a significant correlation between the number of location points and the size of the home range ($r = 0.21$, $t_{376} = 4.18$, $P < 0.001$). When we considered only territories represented by at least 40 location points (n = 121), however, the number of points and the size of the territory were no longer correlated ($r = 0.14$, $t_{120} = 1.55$, $P = 0.12$) and we considered only these territories in further analyses. Across all juveniles tracked (n = 113), juvenile range size was not correlated with the number of location points ($r = 0.02$, $t_{112} = 0.20$, $P = 0.84$). Thus, we compared range composition (land-cover area and proportion within the home range) among all juveniles. To balance kernel accuracy while achieving a sufficient sample size, however, we considered only juveniles with at least 15 location points (n = 73) in analyses of use (concentration of use and resource utilization functions) as well as structural vegetation plots.

Structural Vegetation Plots

Locations. We divided each home range into multiple strata reflecting relative use within which we established vegetation plots. For each territory, we split the utilization distribution into high (0-25% kernel density estimate), moderate (25-75%), and low-use (75-99%) strata. For each juvenile bird, we split the home ranges into high (0-25% kernel density estimate) and moderate/low-use (25-99%) strata. We used a random point generator in ArcGIS (v.10.0) to establish vegetation plot locations (two per territory stratum and four per juvenile stratum) that were at least 30 m apart and at least 15 m from the stratum edge.

Field Measurements. We measured vegetation in plots centered on a survey point, with five additional points extending along axes in each of the four cardinal directions, each separated by 3 m. We measured four characteristics of vegetation structure that would together summarize the amount of low cover (foliage density from 0-1 m and 1-2 m), low woody plants (shrub cover), and high woody vegetation (canopy cover).

We measured foliage density in each plot using a 2 m cover pole, divided into 10 cm sections, and separately measured the foliage density within 1 m of the ground and between 1 and 2 m above the ground. At each of three points, the center point, 15 m north, and 15 m south, an observer knelt and sighted the cover pole at a distance of 4 m in each of the cardinal directions. The observer noted the number of 10 cm sections which were at least 50% obscured in each of the height zones (0-1 m and 1-2 m). Thus, we collected 12 samples of foliage density in each height zone and we considered the plot's foliage density in each zone to be the average percent of obscured pole segments.

To assess the presence of shrub cover, we placed a vertical 2-m pole at each survey point and marked shrub cover as present if any shrub branches or foliage were within 20 cm of the pole. We considered the canopy and shrub cover of the plot to be the percent of points with canopy or shrub presence. Finally, to sample canopy cover at each point, we looked straight upward through an ocular tube (2 cm in diameter, 30 cm in length). We considered canopy cover to be present if we observed any branches or foliage at or above 3 m.

*Analyses***.** We assessed differences between the vegetation structure in each use strata within breeding and juvenile home ranges across all study sites using ANOVAs. We also conducted an ANOVA to assess the impacts of vegetation structure and use-strata and their interaction on juvenile survival. We then conducted *post hoc* Tukey HSD tests and used the studentized range distribution (*q*) to determine specific differences between strata, age class, and success. To assess territory success, we used a generalized linear model of vegetation, strata, level of cowbird control, and all two-way interactions and used *post hoc* chi-square tests to identify specific differences. For all tests, we used an alpha of 0.05 to indicate significance but we additionally report results that approach significance (are within the 90% confidence interval).

Land-cover Classification

We determined the composition of adult and juvenile ranges with land-cover data from the 2011 National Land Cover Database (NLCD; Homer et al. 2015), a national dataset that classifies land cover in the conterminous United States into 16 categories at 30 m resolution. A 2011 NLCD layer also provided percent canopy cover at 30 m resolution (Homer et al. 2015). We identified 14 NLCD land-cover classifications within vireo territories that, to focus on habitat types biologically relevant to the black-capped vireo, we simplified into five land-cover types:

(1) Water/Wetlands: areas with perennial open water and woody wetlands where forest or shrubland vegetation is periodically saturated or covered by water;

(2) Open/Developed: areas with little structural vegetation, including developed areas, herbaceous grasslands and wetlands, pastures and agricultural land, and areas identified as barren;

(3) Mixed/Deciduous Forest: mix of deciduous and evergreen trees with a canopy height greater than 5 m tall and comprising greater than 20% of the total vegetative cover;

(4) Evergreen Forest: primarily evergreen forest (at least 75%), trees are greater than 5 m tall and comprise more than 20% of the vegetative cover;

(5) Shrubland: shrubs and early successional trees with a canopy less than 5 m in height and greater than 20% of the total vegetative cover.

Home-Range Composition. Within both breeding and juvenile home ranges, we calculated the area and the proportion of total area covered by each land-cover type. Then, using ANOVAs and *post hoc* Tukey tests, we compared the area and land-cover composition of breeding home ranges with those of juvenile vireos. Finally, we assessed the effects of land-cover composition and the level of cowbird control on the reproductive success of territorial birds using a binomial generalized linear model. We assessed the importance of home range area and land-cover composition to juvenile survival using Cox proportional hazards regression and the package "coxph" in R (v.3.1.1; R Core Team 2014).

Nest Characteristics. For each vireo nest, we recorded the plant species supporting the nest and the height of the nest above ground level. We also overlaid nest locations onto land-cover maps (Homer et al. 2015) and identified the land-cover type surrounding the nest and the distance to the nearest edge using ArcGIS (v.10.2.2; Environmental Systems Research Institute, Inc., Redlands, CA). Finally, we determined the average canopy cover over the nest location using the NLCD canopy-cover dataset (Homer et al. 2015). Using a binomial generalized linear model, we compared the effects of cowbird control and each of four nest characteristics (nest height, distance to edge, canopy cover, and land-cover type), as well as their interaction, on nest success.

Concentration of Use. Using GME (Beyer 2012), we created a regular grid of points, each separated by 30 m, across the utilization distribution of each home range and sampled use and land-cover type at each point. We then used Fragstats (v.4.2.1; McGarigal et al. 2012) to evaluate the area of each land-cover type within each bird's home range. Finally, we calculated concentration of use for each habitat type within each vireo's home range for both territorial and juvenile birds. Concentration of use (COU), a measure of selectivity within the home range, is the ratio of the total volume of the utilization distribution within each land-cover type to the area of that land cover within the home range (Neatherlin and Marzluff 2004). We compared concentration of use among the five land-cover types and between breeding and juvenile birds using an ANOVA. Finally, we assessed the relationship between COU and territory success using a generalized linear model that considered success as a dependent binomial variable and the independent variables: COU, land-cover type, cowbird control effort, and all two-way interactions.

Resource Utilization Functions. Because low use cells are more abundant in utilization distributions than high use cells (Johnston 2013), we expected some problems with the fit of resource utilization functions (RUFs). To evaluate model fit, we examined residual plots from univariate RUFs from a sample of five breeding and five juvenile birds and found, in many cases, that the response variable was right-skewed (Supplementary Material Figure 2.S1). We were able to improve residual normality in our test RUFs by log-transforming the response variable (use) and thereafter applied this transformation to all breeding and juvenile birds. We did not transform any predictor variables.

Using the package "ruf" in R (v.2.13.1; Handcock 2004, R Core Team 2014), we calculated resource utilization functions (RUFs; Marzluff et al. 2004, Kertson and Marzluff

2011) to relate territorial and juvenile vireo space use with spatial predictor variables, including land-cover type and canopy cover.

RESULTS

Home Range Composition

Of 121 territories with at least 40 location points, the average territory size was 6.96 ha (SE = 0.39 ha). Juvenile birds (n = 113) used much larger areas ($\bar{x}$ = 195.82 ha; SE = 27.56 ha) than were defended by adults.

Across all birds, home ranges differed in their relative composition of land-cover types ($F_{4,960}$ = 72.12, $P < 0.001$; Tables 2.2 and 2.3, Figure 2.3). Both breeding birds and juveniles had home ranges with proportionally more shrubland and evergreen forest than open or developed land (shrub: q = 5.08, P = 0.003; evergreen: q = 4.35, P = 0.02), mixed and deciduous forest (shrub: q = 10.73, $P < 0.001$; evergreen: q = 10.00, $P < 0.001$), or wetlands (shrub: q = 20.55, $P < 0.001$; evergreen: q = 19.82, $P < 0.001$; Tables 2.2 and 2.3). Home ranges also had relatively more open habitat than mixed forest (q = 5.64, $P < 0.001$) or wetlands (q = 15.46, $P < 0.001$) and more mixed forest than wetland habitat (q = 9.82, $P < 0.001$; Tables 2.2 and 2.3).

Breeding territories differed in land-cover composition from juvenile home ranges ($F_{4,960}$ = 6.31, $P < 0.001$; Tables 2.2 and 2.3, Figure 2.3). Breeding birds used areas with proportionally more shrubland (q = 4.83, $P < 0.001$), less open or developed areas (q = 3.73, P = 0.01), and less wetland habitat (q = 3.29, P = 0.02) than in juvenile home ranges (Tables 2.2 and 2.3, Figure 2.3). Average canopy cover in home ranges, however, did not differ between breeding and juvenile vireos (t_{192} = 0.09, P = 0.93). Juvenile home ranges had a smaller variance in the proportion of each land-cover type, as well as canopy cover, compared with breeding birds (Bartlett Test of Homogeneity of Variance; water: k = 414.38, $P < 0.001$; open: k = 5.88, P =

0.02; mixed forest: $k = 38.41$, $P < 0.001$; evergreen forest: $k = 3.62$, $P = 0.06$; shrub: $k = 40.04$, $P < 0.001$; canopy cover: $k = 5.75$, $P = 0.02$; Figure 2.3).

Nest Sites

Over four breeding seasons, we located and monitored 784 vireo nests. Canopy cover over nests averaged 42.5% (SE = 0.89%) and nests were located 1.10 m off the ground (SE = 0.02 m). On average, nests were located 15.59 m (SE = 0.55 m) from the nearest patch edge.

We found nests in all land-cover types, although most were located in shrublands (32.4%; Table 2.4). Nests in different land-cover types differed in distance to edge ($F_{4,779} = 3.83$, $P = 0.004$), height off the ground ($F_{4,770} = 3.90$, $P = 0.004$), as well as canopy cover ($F_{4,779} = 142.59$, $P < 0.001$; Table 2.5). Nests in mixed forests were located closer to the patch edge than nests in either evergreen forest ($q = 4.72$, $P = 0.007$) or open habitat ($q = 4.73$, $P = 0.007$). Nests in evergreen forests were higher off the ground than nests in either shrublands ($q = 4.73$, $P = 0.007$) or open land cover ($q = 3.82$, $P = 0.05$).

Concentration of Use

Breeding pairs ($n = 121$) and juveniles ($n = 73$) varied their concentration of use in five land-cover types ($F_{4,960} = 40.84$, $P < 0.001$; Table 2.6). Birds within both reproductive stages used forests and shrublands more than open or developed areas (mixed/deciduous forest: $q = 4.17$, $P = 0.03$; evergreen forest: $q = 4.33$, $P = 0.02$; shrubland: $q = 5.59$, $P < 0.001$) and more than water/wetlands (mixed/deciduous forest: $q = 14.14$, $P < 0.001$; evergreen forest: $q = 14.31$, $P < 0.001$; shrubland: $q = 15.56$, $P < 0.001$), even after considering availability. Vireos also used open or developed areas more than wetlands open/developed: $q = 9.97$, $P < 0.001$). Breeding birds, but not juveniles, also used shrub more than mixed forests although the difference was not quite significant ($q = 3.55$, $P = 0.09$). There was no significant interaction between concentration of use in a particular land-cover type and reproductive stage ($F_{4,960} = 1.59$, $P = 0.17$).

Resource Utilization Functions

We found no consistent association between canopy cover or any land-cover type and juvenile use of the landscape, although a negative association with open and developed areas was nearly significant (Table 2.7, Supplemental Material Table 2.S1). Relative use of areas within the home range of breeding vireos was positively associated (95% CI around RUF coefficients did not include zero) with both deciduous and evergreen forest as well as shrublands (Table 2.7, Supplemental Material Table 2.S1).

Vegetation Structure

From 2012-2014, we measured vegetation in 113 vireo territories with greater than or equal to 40 location points, totaling 671 vegetation plots. Additionally, we measured vegetation at 477 plots representing areas used by 62 juvenile vireos. Across all study sites, we observed similar patterns in vegetation characteristics in breeding territories and in areas used by juveniles (Table 2.8).

Comparing reproductive stage and use level together, we found that, for both breeding and juvenile vireos, high-use areas of the home range had greater shrub cover ($F_{1,1144} = 19.63$, $P < 0.001$) as well as areas with greater foliage density between 0 and 1 m ($F_{1,1140} = 25.38$, $P < 0.001$; Table 2.8). Canopy cover differed between breeding and juvenile birds but not between strata; juveniles had home ranges with greater canopy cover than territorial birds ($F_{1,1144} = 48.70$, $P < 0.001$). Foliage density from 1 to 2 m differed between both breeding and juvenile birds and use strata; breeding birds used areas with greater foliage density from 1 to 2 m than juvenile birds ($F_{1,1144} = 5.05$, $P = 0.03$) but both breeding birds and juveniles concentrated use in areas of their home ranges with relatively high foliage density from 1-2 m ($F_{1,1144} = 26.82$, $P < 0.001$).

Correlates of Reproductive Success

Of pairs with home ranges represented by at least 40 location points, 52% ($n = 63$) successfully fledged at least one vireo. Cowbird control had a strong relationship with territory success ($\chi^2 = 36.35$, df = 2, $P < 0.001$). Even after accounting for cowbird control, however, territory success was also related to the area and proportion of land-cover types (Table 2.2; area: $\chi^2 = 10.26$, df = 4, $P = 0.04$; proportion: $\chi^2 = 9.41$, df = 4, $P = 0.05$). *Post hoc* tests, however, found no significant differences in the amount (area or proportion) of individual land-cover types between successful and unsuccessful territories.

Territory success was not related to any measure of vegetation structure within the home range (canopy: $\chi^2 = 0.04$, df = 1, $P = 0.83$; shrub: $\chi^2 = 1.91$, df = 1, $P = 0.17$; foliage density 0-1 m: $\chi^2 = 2.40$, df = 1, $P = 0.12$; foliage density 1-2 m: $\chi^2 = 0.07$, df = 1, $P = 0.79$), even when considering differences between use-strata (canopy: $\chi^2 = 3.21$, df = 2, $P = 0.20$; shrub: $\chi^2 = 1.74$, df = 2, $P = 0.42$; foliage density 0-1 m: $\chi^2 = 2.45$, df = 2, $P = 0.29$; foliage density 1-2 m: $\chi^2 = 0.001$, df = 2, $P = 0.99$). Territory success was, however, affected by interactions between the level of cowbird control and both canopy cover ($\chi^2 = 6.60$, df = 2, $P = 0.04$) and shrub cover ($\chi^2 = 6.23$, df = 2, $P = 0.04$). The effect of canopy cover on territory success varied between areas with moderate levels of cowbird control and those with none ($\chi^2 = 6.73$, df = 1, $P = 0.03$). At sites with moderate cowbird control, successful territories had less canopy cover than territories which failed to fledge any young ($\bar{x}_{\text{successful}} = 0.25 \pm 0.02$; $\bar{x}_{\text{failed}} = 0.29 \pm 0.02$). Successful territories in areas without cowbird control, however, had more canopy cover than unsuccessful territories ($\bar{x}_{\text{successful}} = 0.31 + 0.02$; $\bar{x}_{\text{failed}} = 0.27 \pm 0.01$). Territories in areas without cowbird control were also more likely to successfully fledge young when they contained more shrub cover ($\bar{x}_{\text{successful}}$ = 0.62 + 0.02; $\bar{x}_{\text{failed}}$ = 0.56 ± 0.02).

Of the 784 nests we monitored, only 28.3% (*n* = 223) were successful. The success of individual nests was not related to the nearby canopy cover (χ^2 = 0.57, df = 1, *P* = 0.45), nest height (χ^2 = 0.001, df = 1, *P* = 0.97), or distance from the nest to the nearest patch edge (χ^2 = 0.33, df = 1, *P* = 0.56). Nest success nearly differed between land-cover types (Table 2.4; χ^2 = 8.98, df = 4, *P* = 0.06) and there was a significant interaction with the degree of cowbird control (χ^2 = 24.84, df = 7, *P* < 0.001). In areas with moderate cowbird control, nest success was greater in evergreen forests than in mixed forests (*z* = 1.98, *P* = 0.05) or in shrublands (*z* = 2.72, *P* = 0.01). At sites with no cowbird control, nests in open areas were more likely to succeed than nests in forests (evergreen: *z* = 4.46, *P* < 0.001; mixed/deciduous: *z* = 2.19, *P* = 0.03) and shrublands (*z* = 4.03, *P* < 0.001); nest success was also greater in mixed forests than in evergreen forests (*z* = 2.43, *P* = 0.02).

Correlates of Juvenile Survival

Excluding birds that immediately moved beyond our search area or whose transmitters malfunctioned shortly after attachment, we tracked 113 recently fledged, independent black-capped vireos during the pre-migration periods of 2012, 2013, and 2014. Excluding transmitters on birds that were lost immediately and one transmitter that obviously malfunctioned (failed almost immediately upon release), the transmitters lasted on average 17 days. The longest we were able to track a vireo was 40 days. Nine birds died during tracking.

Based on observations of tracked juveniles, we calculated daily survival probabilities (Kaplan and Meier 1958) and found that juvenile vireos had a 91.3% chance of surviving two weeks or more of independence (Figure 2.4). Juvenile survival was not correlated with total home range size (Cox Proportional Hazards Regression, Wald $\chi^2 = 0.83$, df = 1, $P = 0.36$) or with the area of individual land-cover classes (Wald $\chi^2 = 3.47$, df = 5, $P = 0.63$). However, survival was positively related to the proportion of mixed deciduous forest (Wald $\chi^2 = 11.02$, df = 1, $P < 0.001$) in the juvenile's home range and negatively related to the proportion of shrub therein (Wald $\chi^2 = 4.96$, df = 1, $P = 0.03$; Table 2.3).

DISCUSSION

Across a diversity of wildlife taxa, researchers recognize numerous potential tradeoffs in the selection of an optimal breeding location that consider successful reproduction, adult survival, and survival of dependent young (Pianka 1976). Despite acknowledging these tradeoffs, however, it is often difficult to find habitat characteristics that are good predictors of breeding success, particularly for birds (Chalfoun and Schmidt 2012). We propose that, for some species, survival of independent young may also shape selection of breeding habitat and may help explain some apparent discrepancies between the selection of breeding locations and ultimate reproductive success. Tradeoffs between breeding success and independent juvenile survival may exist when habitat features benefit either success or survival but not both (Streby et al. 2014a, 2014b).

Independent juveniles may face periods of high mortality risk before they reach reproductive age, a risk that for some species might be mediated by selection of breeding habitat. Among species that provide no parental care, for example, juveniles are highly vulnerable when leaving the nest and nest site selection may have a great impact on juvenile survival (e.g. sea turtles; Whelan and Wyneken 2007). For migratory avian taxa, juveniles face a stressful migration shortly after independence that is thought to be a period of high mortality (Sillett and Holmes 2002) and habitat that enables juveniles to adequately prepare for their first migration may benefit overall juvenile survival. Adult migratory songbirds may improve their genetic legacy by selecting breeding areas that include or are adjacent to habitat that will provide their independent offspring with cover from predators to improve immediate survival and abundant food resources to better prepare them for stressful migration.

Breeding and Juvenile Habitat Selection and Use

Breeding habitat selection must optimize a variety of factors to maximize an individual's lifetime reproductive success. Breeding birds specifically must ultimately balance numerous factors that influence nest success, survival of young fledglings, and survival of independent juveniles as well as themselves. Home ranges of breeding and juvenile vireos, although similar in many characteristics, differed in several aspects of land-cover composition and vegetation structure, indicating a complicated relationship between territory and nest site selection and juvenile survival. It is also possible that, due to habitat loss, vireos have only limited availability of optimal breeding sites and this might be particularly true at breeding sites off of Fort Hood that are relatively small and isolated. First time breeders arrive on the breeding grounds later than older birds and, if optimal habitat is limited, may be forced to choose territories that do not match juvenile habitat needs.

Tradeoffs in Nest Success. Similarities in breeding and juvenile home ranges that were not in congruence with higher nest success may exist as a tradeoff to improve juvenile survival. Both juvenile and breeding vireos concentrated use in deciduous and evergreen forests, perhaps due to the association between forest land cover and the presence of canopy cover. Juveniles with greater proportions of mixed forest were more likely to survive and, matching our predictions, juveniles also used areas with more canopy cover than breeding birds. Although we also predicted that breeding birds would avoid areas with canopy cover, high use areas within breeding territories had greater canopy cover than low use areas in general. Additionally, in areas with some cowbird control, neither nest success nor territory success was affected by canopy cover or the presence of forest. In accordance with our predictions, however, territories and nests at sites without cowbird control, and thus with greater risk of parasitism, were more successful in areas with less canopy cover. Although canopy provides perches for cowbirds and increases rates of parasitism among some host species (Hauber and Russo 2000), abundant canopy may also provide cover for nests (Fiorini et al. 2012, Vasseur and Leberg 2015). Thus, for breeding vireos, selection against canopy cover may be relatively weak in areas with less parasitism risk, allowing adult birds to select areas that better reflect juvenile habitat requirements.

Selection for breeding territory characteristics that do not appear to benefit either nest success or independent juvenile survival may instead reflect habitat features that optimize the survival of adults or of very young dependent fledglings. Both breeding and independent juvenile vireos in central Texas used shrublands more than other land-cover types and open areas relatively infrequently, a result that closely followed expectations set by previous research (Grzybowski 1995). These habitat associations, however, proved detrimental to nest and territory success as well as independent juvenile survival. Thus, shrub cover might present an alternative tradeoff with either adult survival or survival of young dependent fledglings. We did not track habitat use by young fledglings or family groups, however, and so the selective forces behind use of shrublands are difficult to tease out from our data. We suspect, however, that fledgling survival may benefit from habitat with shrubby understory based on research of other songbird species (e.g. King et al. 2006).

Juvenile Habitat Selection. Although adults must select breeding habitats that present multiple tradeoffs in reproductive success that might vary across their breeding range, juveniles can choose from available habitats to optimize only their own survival. We predicted that juveniles would focus on particular habitat features that provide the right balance of cover and food availability. Juvenile vireos selected habitats with a relatively narrow range of shrubland availability compared with breeding adults and, while low levels of shrubland may not provide enough cover, landscapes dominated by shrublands alone may not have enough food resources to support birds preparing for migration. Similarly, juvenile home ranges contained a narrower range of forest proportion and canopy cover than breeding territories. Home ranges dominated by forested areas may not provide the understory vegetation for sufficient refuge from predators but some canopy cover may be necessary to supply juveniles with sufficient food availability. Additionally, older juveniles are less vulnerable to predation than young fledglings and may risk exposure in favor of finding additional food resources (Jenkins et al. 2013, Small et al. 2015). Independent juvenile Swainson's thrush (*Catharus ustulatus*) in Oregon selected habitats with abundant ants and beetles without regard to shrub cover (Jenkins et al. 2013). Similarly, independent juvenile grasshopper sparrows (*Ammodramus savannarum*) use relatively open areas with more bare ground and easier foraging opportunities compared with dependent fledglings that stayed in areas with more shrubby cover (Small et al. 2015). We observed no evidence of disproportionate use of wetlands by juvenile vireos across a broader range of central Texas although past research on Fort Hood indicated that juvenile vireos spent the most time in riparian habitats due to increased insect availability (Dittmar et al. 2014).

Habitat Prospecting by Juveniles. We assumed that juvenile vireo habitat use was driven by survival pressures such as the availability of food and cover from predators, an assumption bolstered by the results of previous juvenile habitat selection observations on Fort Hood (Dittmar et al. 2014). For many juvenile birds, however, the post-breeding period may also be used to prospect for potential future breeding sites (Schjorring et al. 1999, Nicolaus et al. 2012). For some species, prospecting birds assess the quality of a potential breeding site based on the success of local breeding pairs (Part and Doligez 2003). Although no studies have evaluated black-capped vireos for post-breeding season prospecting behavior, we often observed juvenile vireos in association with adults and other hatch year birds. Additionally, there is evidence that first time breeders are thought to be attracted to conspecific vocalizations after spring migration, during the early breeding season (Ward and Schlossberg 2004). This tendency toward conspecific attraction suggests that our observations of juvenile habitat use may reflect a need to balance survival with potential future breeding success. This may also partially explain why we observed similarity between juvenile and breeding habitat selection of shrub and forest land-cover types.

Juvenile Survival

We observed high survival of juvenile vireos during the post-breeding/pre-migration period, making associations between habitat selection and juvenile survival difficult to interpret. For many migratory songbirds, much of post-independence juvenile mortality may occur during migration itself (Sillett and Holmes 2002). Thus, it is not surprising that survival might be relatively high during the pre-migration period and this pattern has been observed in other neotropical migrants (Vitz 2008, Whittaker and Marzluff 2009, Jenkins et al. 2013, Streby et al. 2015). Our study of juvenile mortality was limited by the lifespan of small transmitter batteries, however, and it is possible we were simply unable to track juveniles vireos long enough to capture many pre-migration mortality events. With the advent of new technologies, longer tracking periods would enable researchers to better define overall juvenile mortality as well as associate patterns of survival with land-cover availability and use.

Management Implications

Management guidelines for vireo breeding habitat maintenance and restoration often focus on the provision of moderate shrub cover needed to provide sufficient nesting sites and nest cover (e.g. Reemts and Cimprich 2014). Restoration guidelines pay little attention, however, to the provision of optimal habitat requirements for young vireos after they have become independent from their parents. To most benefit this endangered species, land managers should conserve and even restore habitats vital for reproduction and survival throughout the annual cycle, not just during periods of active breeding.

Our results suggest that, in addition to low vegetative cover, abundant canopy cover may be the most important structural feature relevant to juvenile habitat selection. Deciduous and mixed deciduous and evergreen forest may provide habitat with both good understory cover and high canopy, thus providing both sufficient food availability and cover from predators. Although vireo reproductive success was inversely related to the availability of evergreen forest in territories, breeding sites that provide nearby or adjacent forested areas with abundant canopy cover may improve juvenile survival and aid in the establishment of larger breeding populations.

What is Breeding Habitat?

For all wildlife species, the ideal breeding habitat is based on a combination of factors that contribute to the successful passing on of the parent’s genes. Although wildlife researchers often characterize breeding habitat based on areas used by actively breeding individuals, the availability of habitats used by family groups or independent juveniles in the post-breeding season might be just as vital for offspring survival. In fact, sites that provide good habitat for nesting or denning but do not also offer sufficient habitat for dependent and newly independent young may act as ecological traps (see Dwernychuk and Boag 1972). The redefinition of breeding habitat to include these additional habitat considerations would expand the requirements on land managers and stake-holders seeking to provide quality breeding habitat for a given wildlife species but might ultimately improve breeding success, juvenile survival, and population persistence (Battin 2004).

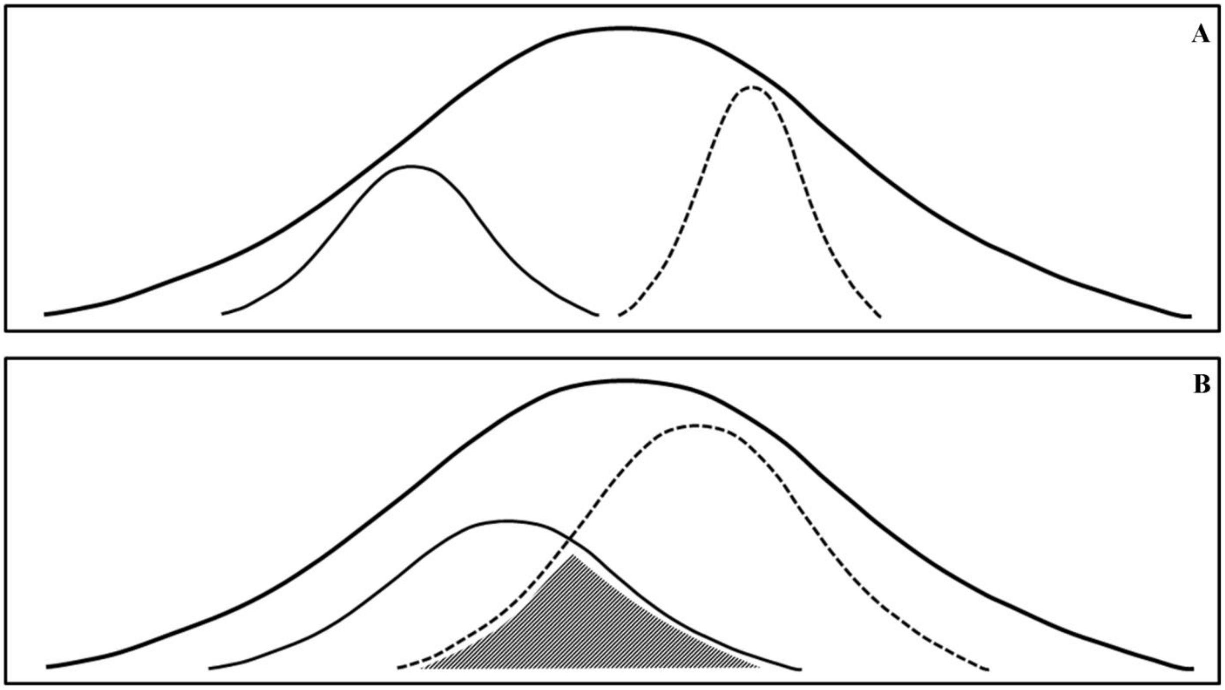


Figure 2.1. A hypothetical gradient of breeding habitat (large bold curve) with optimal nesting (area under thin solid line) and juvenile habitat (area under dashed line). In (A), habitat requirements for each reproductive stage are relatively narrow and breeding individuals must accept tradeoffs in selecting breeding habitat. In (B), overlap between nesting and juvenile habitat requirements prevents the need for tradeoffs in habitat selection.

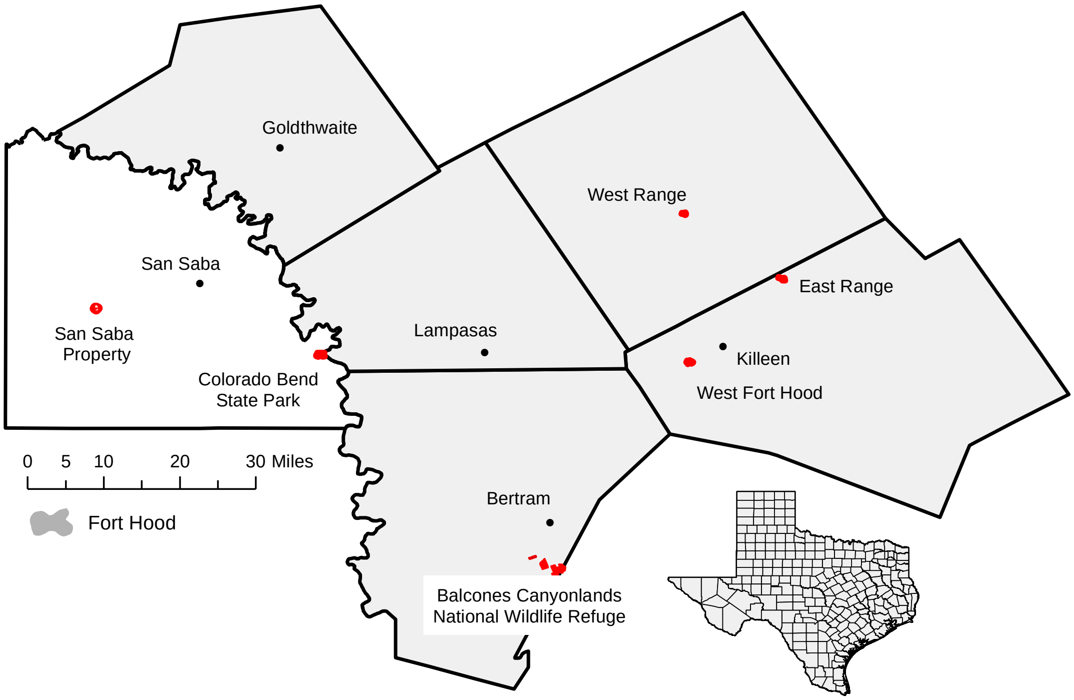


Figure 2.2. Black-capped vireo study sites across central Texas, 2011-2014.

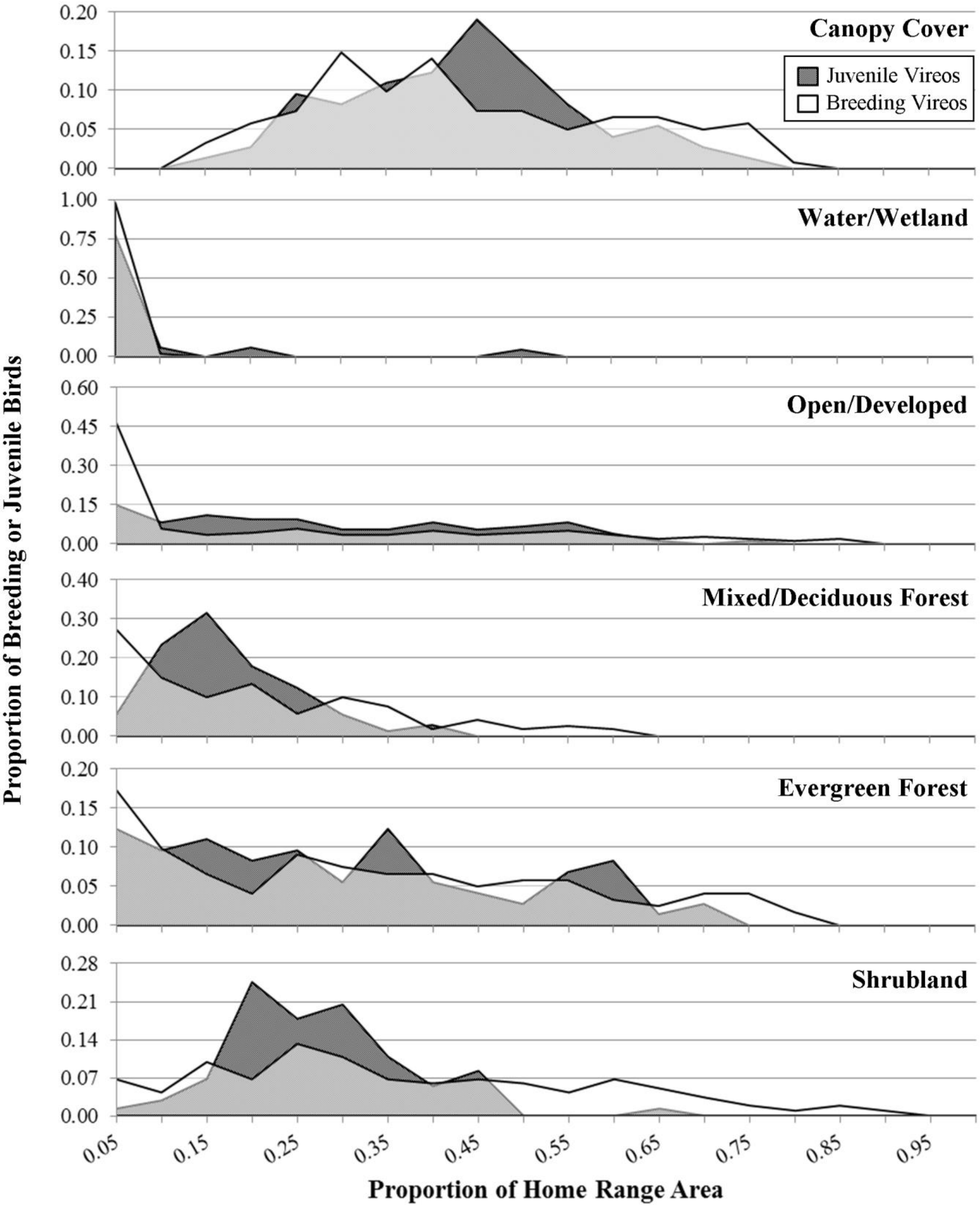


Figure 2.3. Canopy cover and land-cover composition of juvenile and breeding vireo home ranges in central Texas, 2011-2014.

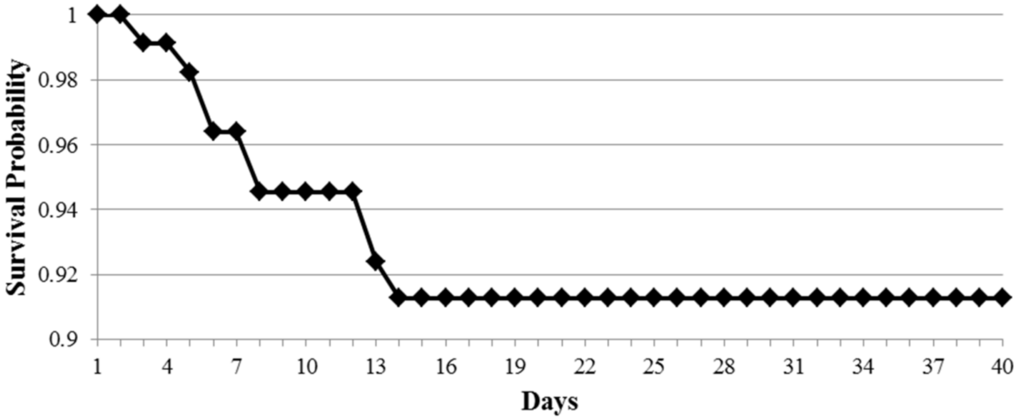
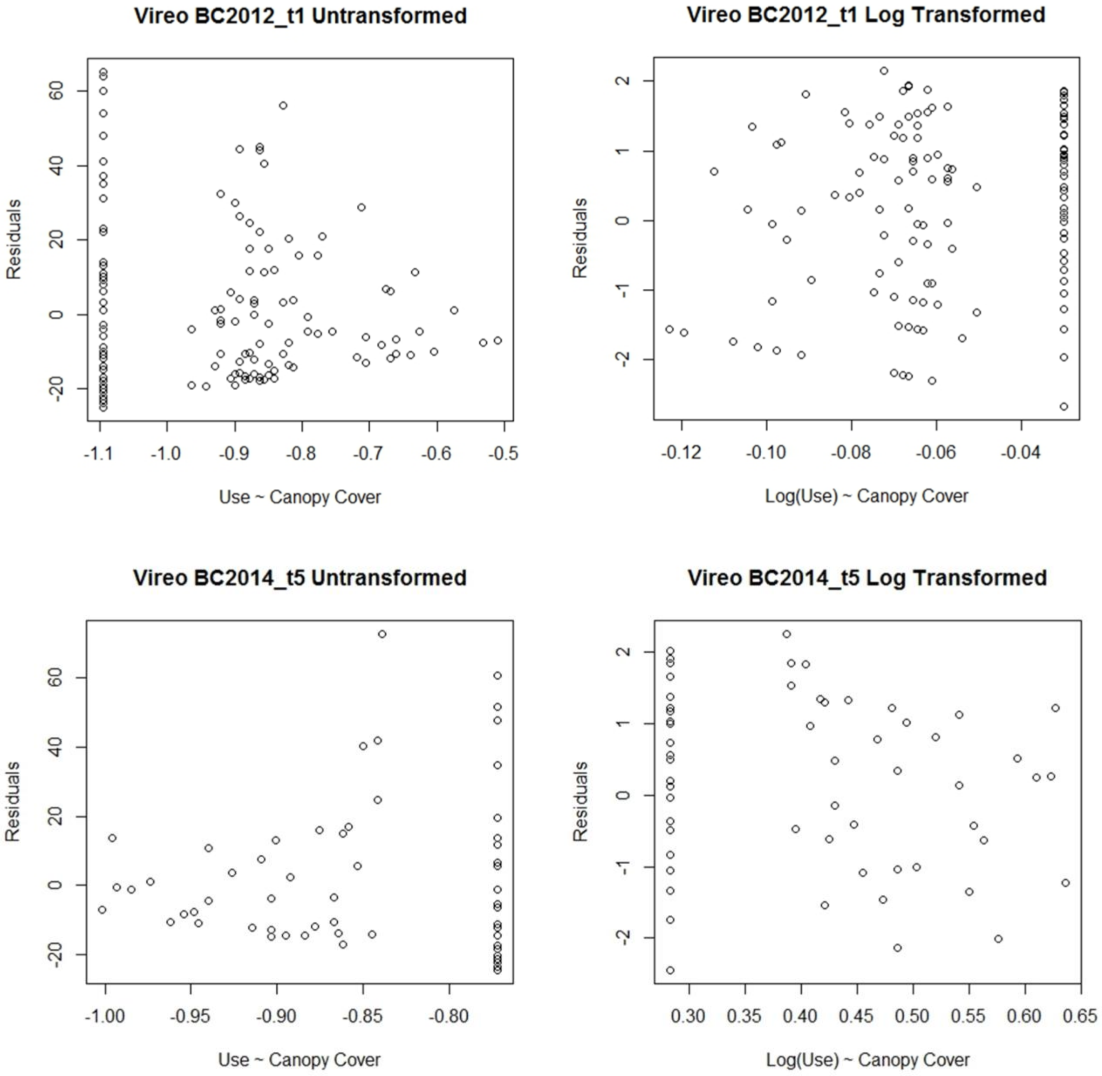
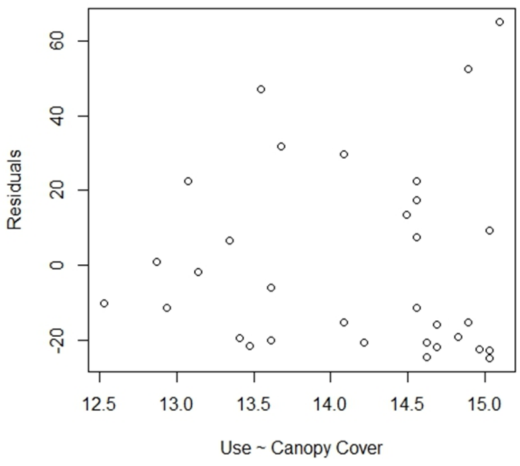


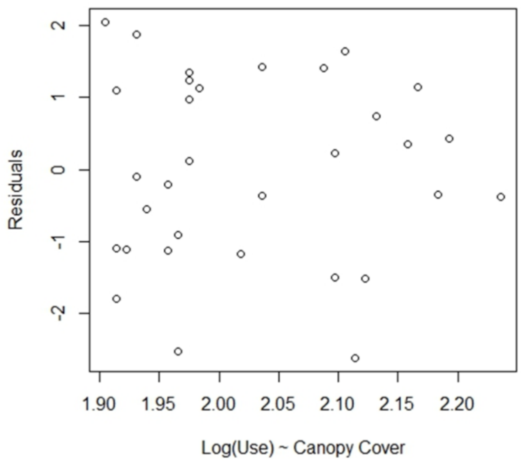
Figure 2.4. Post-independence daily survival probabilities of juvenile vireos across central Texas from 2012-2014.

Supplementary Material Figure 2.S1. Residual plots from resource utilization functions (RUFs) for ten vireos, including five randomly selected breeding vireos and five randomly selected independent juvenile vireos, before and after log transformation of the response variable: use. RUFs considered the univariate predictor variable canopy cover.

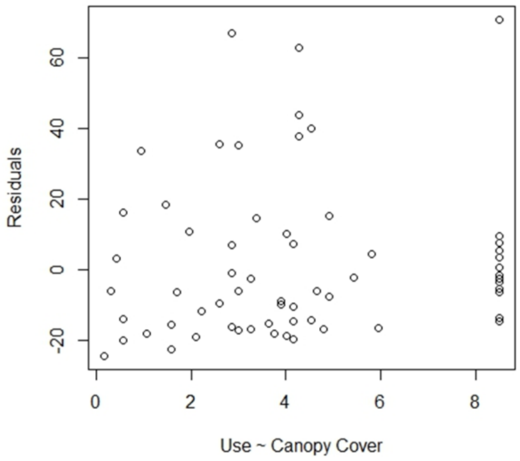




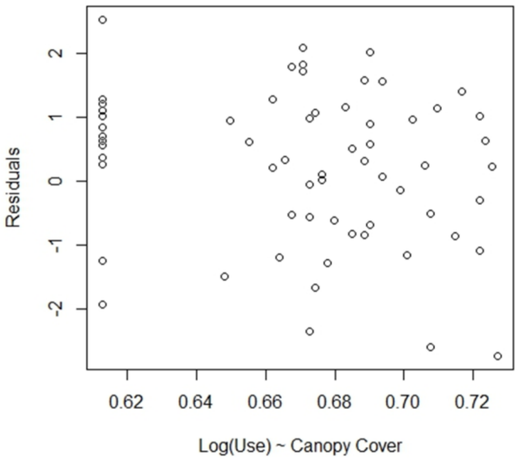
Vireo CB2013_t16 Untransformed



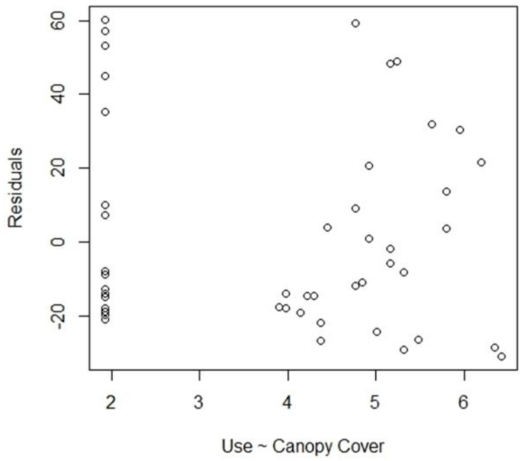
Vireo CB2013_t16 Log Transformed



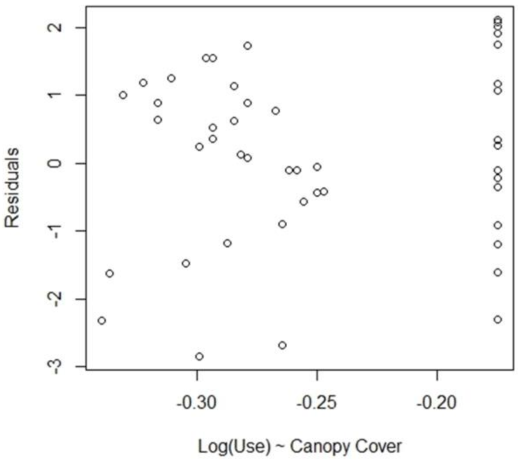
Vireo WF2012_t7 Untransformed



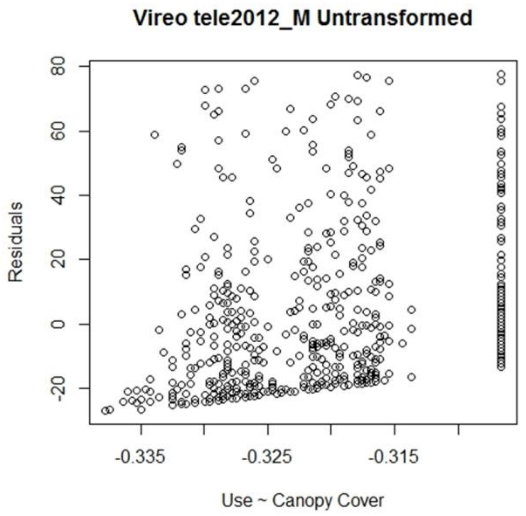
Vireo WF2012_t7 Log Transformed

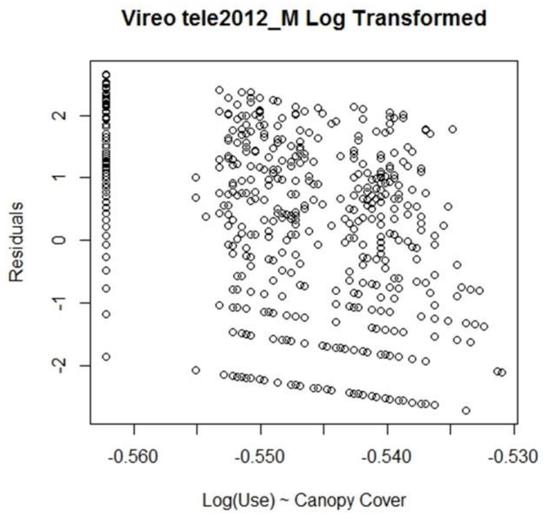


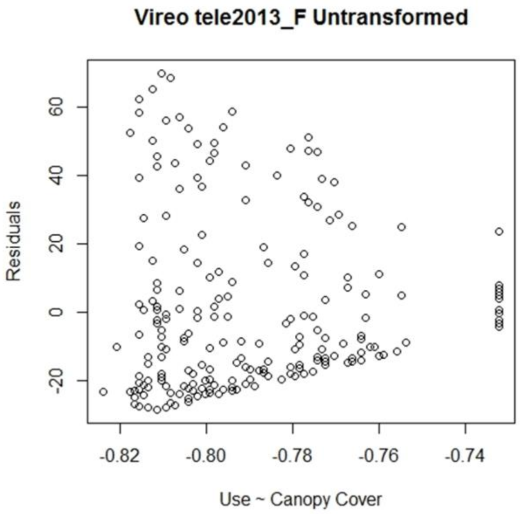
Vireo WR2013_t5 Untransformed

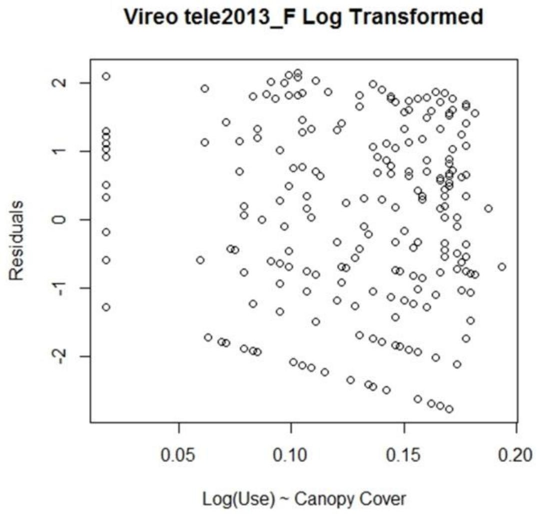


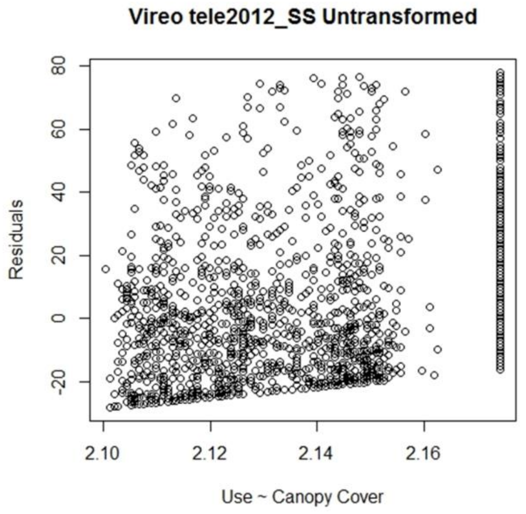
Vireo WR2013_t5 Log Transformed

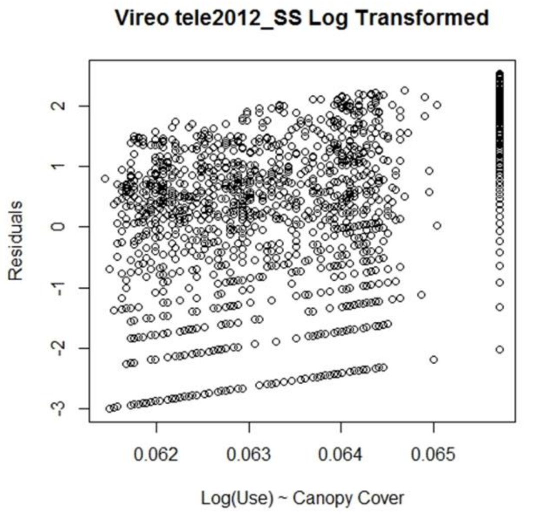

Vireo tele2012_M Untransformed
Residuals
80
60
40
20
0
-20
-0.335
-0.325
-0.315
Use ~ Canopy Cover

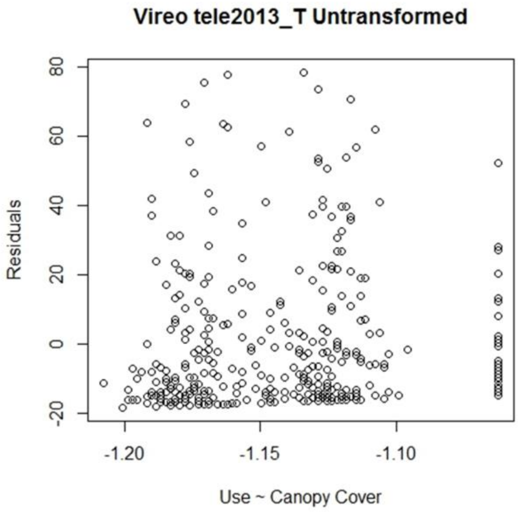

Vireo tele2012_M Log Transformed
Residuals
2
1
0
-1
-2
-0.560
-0.550
-0.540
-0.530
Log(Use) ~ Canopy Cover

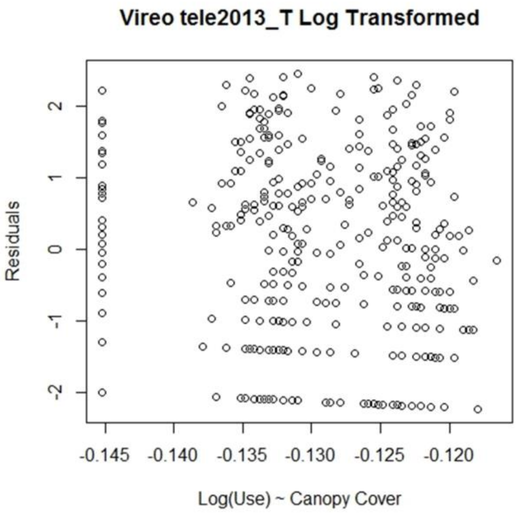

Vireo tele2013_F Untransformed
Residuals
60
40
20
0
-20
-0.82
-0.80
-0.78
-0.76
-0.74
Use ~ Canopy Cover

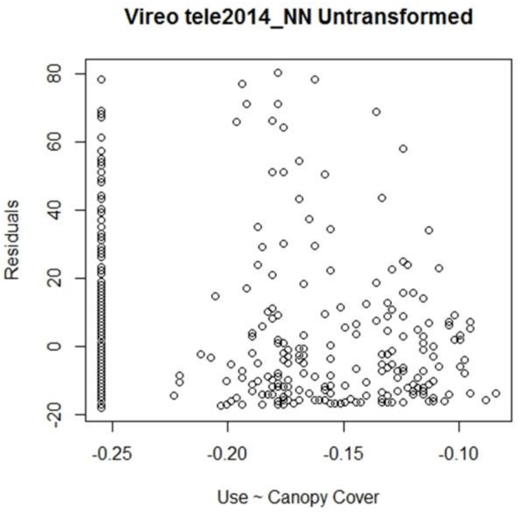

Vireo tele2013_F Log Transformed
Residuals
2
1
0
-1
-2
0.05
0.10
0.15
0.20
Log(Use) ~ Canopy Cover


Vireo tele2012_SS Untransformed
Residuals
80
60
40
20
0
-20
2.10
2.12
2.14
2.16
Use ~ Canopy Cover


Vireo tele2012_SS Log Transformed
Residuals
2
1
0
-1
-2
-3
0.062
0.063
0.064
0.065
Log(Use) ~ Canopy Cover


Vireo tele2013_T Untransformed
Residuals
-20
0
20
40
60
80
-1.20
-1.15
-1.10
Use ~ Canopy Cover


Vireo tele2013_T Log Transformed
Residuals
-2
-1
0
1
2
-0.145
-0.140
-0.135
-0.130
-0.125
-0.120
Log(Use) ~ Canopy Cover


Vireo tele2014_NN Untransformed
Residuals
-20
0
20
40
60
80
-0.25
-0.20
-0.15
-0.10
Use ~ Canopy Cover

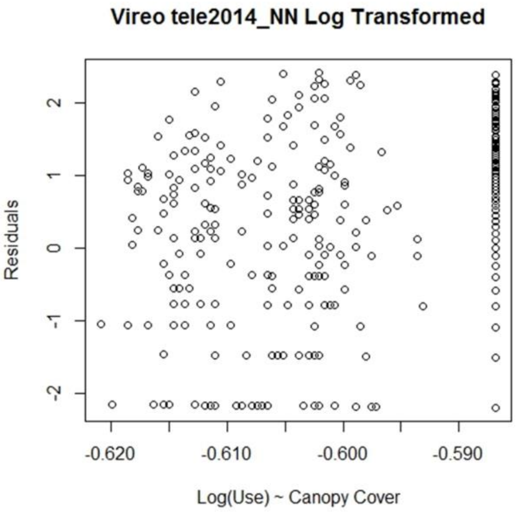

Vireo tele2014_NN Log Transformed
Residuals
-2
-1
0
1
2
-0.620
-0.610
-0.600
-0.590
Log(Use) ~ Canopy Cover

Table 2.1. Level of cowbird control at vireo breeding sites across central Texas from 2011-2014. At sites with complete control, managers used both shooting and trapping to remove cowbirds. At moderately controlled sites, cowbirds were controlled with either trapping or shooting. The properties in Goldthwaite (GP) and San Saba (SS) were not monitored in 2011.

	Year			
Site	2011	2012	2013	2014
BC	Moderate	Moderate	Moderate	Moderate
CB	None	None	None	Moderate
GP	---	None	Moderate	Complete
SS	---	None	None	Moderate
ER	Complete	Complete	Complete	Complete
WF	Moderate	Moderate	Moderate	Moderate
WR	None	None	None	None

Table 2.2. Average area and proportion of total area of five landcover types within the home ranges of breeding birds that were (*n* = 63) and were not successful in fledging young (*n* = 58), 2011-2014.

	All Territories				Non-Successful				Successful			
Landcover	Area (ha)	SE	Prop.	SE	Area (ha)	SE	Prop.	SE	Area (ha)	SE	Prop.	SE
Water/Wetland	0.02	0.006	0.003	< 0.001	0.02	0.01	0.003	0.002	0.009	0.006	0.002	0.001
Open/Developed	1.24	0.15	0.20	0.02	0.90	0.18	0.15	0.03	1.56	0.23	0.24	0.03
Mixed/Deciduous Forest	1.00	0.08	0.17	0.01	0.88	0.12	0.14	0.02	1.12	0.11	0.19	0.02
Evergreen Forest	2.20	0.25	0.29	0.02	2.77	0.44	0.33	0.03	1.68	0.24	0.26	0.03
Shrubland	2.50	0.20	0.34	0.02	2.93	0.32	0.38	0.03	2.11	0.24	0.30	0.02

Table 2.3. Average area and proportion of total area of five landcover types within the home ranges of independent juveniles that did ($n = 104$) and did not survive the tracking period ($n = 9$), 2011-2014.

	All Juveniles				Did Not Survive				Survived			
Landcover	Area (ha)	SE	Prop.	SE	Area (ha)	SE	Prop.	SE	Area (ha)	SE	Prop.	SE
Water/Wetland	7.84	2.18	0.05	0.01	15.22	14.69	0.03	0.02	4.93	1.71	0.03	0.008
Open/Developed	58.05	10.08	0.25	0.02	33.39	23.00	0.25	0.08	60.18	10.77	0.25	0.01
Mixed/Deciduous Forest	25.04	3.38	0.16	0.01	15.87	7.97	0.31	0.10	25.79	3.59	0.15	0.007
Evergreen Forest	55.58	8.78	0.29	0.02	25.22	17.13	0.23	0.06	60.52	9.61	0.32	0.01
Shrubland	49.33	7.29	0.25	0.01	24.31	17.12	0.18	0.03	51.49	7.77	0.25	0.01

Table 2.4. Success and associated land cover of black-capped vireo nests in central Texas, 2011-2014.

Land Cover	n_{total}	Proportion of Total Nests	$n_{\text{successful}}$	Percent Successful
Water/Wetland	2	0.03%	0	0%
Open/Developed	160	20.4%	60	37.5%
Mixed/Deciduous Forest	158	20.2%	50	31.6%
Evergreen Forest	210	26.8%	56	26.7%
Shrubland	254	32.4%	57	22.4%

Table 2.5. Characteristics of black-capped vireo nests across five land-cover types in central Texas, 2011-2014.

	Canopy Cover (%)		Distance to Edge (m)		Height (m)	
Land Cover	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Water/Wetland	86.00	5.00	6.16	2.00	1.08	0.16
Open/Developed	24.96	1.69	17.48	1.28	1.07	0.03
Mixed/Deciduous Forest	60.55	0.96	11.78	0.67	1.13	0.04
Evergreen Forest	58.40	1.46	17.13	1.16	1.21	0.03
Shrub	28.82	1.19	15.57	1.03	1.04	0.03

Table 2.6. Concentration of use (COU) by breeding (n = 121) and juvenile (n = 73) vireos across five land-cover types in central Texas, 2011-2014.

	Breeding Territory COU		Juvenile COU	
Land Cover	$\bar{x}$	SE	$\bar{x}$	SE
Water/Wetland	5.01	3.26	166.30	28.90
Open/Developed	132.33	13.14	321.78	30.83
Mixed/Deciduous Forest	191.38	13.14	380.85	33.46
Evergreen Forest	195.17	11.79	381.84	34.51
Shrubland	253.17	11.10	359.33	29.75

Table 2.7. Means and standard errors of unstandardized maximum likelihood coefficients of juvenile and breeding vireo resource utilization functions.

	Juveniles			Breeding		
Habitat Measure	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
Canopy	72	3.8E-04	2.1E-04	121	-6.9E-05	0.001
Water/Wetland	37	-0.02	0.09	8	-0.26	0.29
Open/Developed	71	-0.12	0.07	69	0.06	0.09
Mixed/Deciduous Forest	72	-0.11	0.07	103	0.26	0.11
Evergreen Forest	69	-0.10	0.07	106	0.33	0.12
Shrubland	72	-0.12	0.06	120	0.20	0.09

Table 2.8. Structural characteristics of vegetation in breeding and juvenile vireo home ranges in central Texas, 2011-2014.

		Canopy		Shrub		Foliage Density		Foliage Density	
Juveniles	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
High Use	233	0.40	0.02	0.66	0.02	0.48	0.02	0.44	0.02
Low Use	244	0.37	0.02	0.59	0.02	0.41	0.02	0.37	0.02
Breeding Birds									
High Use	219	0.28	0.01	0.65	0.01	0.51	0.02	0.48	0.02
Moderate Use	226	0.29	0.01	0.62	0.02	0.48	0.02	0.44	0.01
Low Use	226	0.28	0.02	0.55	0.02	0.39	0.01	0.36	0.01

Supplemental Material Table 2.S1. Number of resource utilization functions with significant unstandardized coefficients for juvenile and breeding vireos.

	Juveniles				Breeding			
	Positive		Negative		Positive		Negative	
Habitat Measure	Total	Significant	Total	Significant	Total	Significant	Total	Significant
Canopy	28	5	23	4	64	23	57	14
Water/Wetland	9	5	17	17	4	0	4	3
Open/Developed	14	7	36	35	35	15	34	16
Mixed/Deciduous Forest	13	7	38	34	53	25	50	23
Evergreen Forest	14	7	34	32	56	27	50	26
Shrubland	12	7	39	36	63	30	57	29

CHAPTER 3

Reticence or vigilance at the nest: a cruel bind for the endangered black-capped vireo

Animal communication is critical for locating conspecifics, establishing territories, obtaining a mate, and coordinating social activities (Bradbury and Vehrencamp 2011). Breeding birds in particular use songs and calls to attract mates and repel rivals (Catchpole 1987, Kroodsma and Byers 1991) and song quality can directly contribute to mating success as well as mate quality (Nowicki and Searcy 2005). Additionally, vocalizations of a particular frequency or quality, such as scold calls, may attract neighboring birds for group defense or social learning (Cornell et al. 2012). Frequent or loud vocalizations near the nest, however, may also cue nest predators or brood parasites to the location of the caller's nest. Avian brood parasites rely on pairs of other breeding birds to incubate their eggs and raise their young, often inducing reproductive and energetic costs on their hosts (Rothstein 1975, Payne 1977). Thus, although defense strategies could favor increased communication between pairs, risk of predation or parasitism might induce alternative selective pressures on vocalization near the nest. Nesting birds might benefit from secretive behavior with fewer vocalizations in proximity to their developing brood (Marzluff and Balda 1992). The need to remain attentive and coordinated without attracting undo attention puts nesting birds in a cruel bind. Natural selection presumably solves this bind by considering the combined influence of communication on parental actions that benefit the development of their nestlings while enabling detection and appropriate responses to the threats of parasites and predators.

The strength and direction of selection on vocalization frequency during the breeding season may depend on a variety of community features, including the predator guild or the presence of brood parasites. Avian predators and brood parasites cue in to auditory and other behavioral signals to locate nests (McLean et al. 1986, Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001, Haff and Magrath 2011), whereas many mammalian or reptilian nest predators are more reliant on olfaction (Conover 2007). For example, loud vocalizations by American robins (*Turdus migratorius*) during the breeding season attract crows (McLean et al. 1986) and begging calls by nestlings attract a wide variety of avian predators (Skutch 1976, McDonald et al. 2009, Haff and Magrath 2011). Pairs of willow flycatchers (*Empidonax traillii*) that were relatively noisy during egg laying and early incubation experienced higher rates of brood parasitism by brown-headed cowbirds than did quiet birds (cowbirds; *Molothrus ater*; Uyehara and Narins 1995). Similarly, red-winged blackbird females whose nests were later parasitized by cowbirds gave more vocalizations during the egg laying period than females who were not parasitized (Clotfelter 1998). In a comparison of four songbird species, Banks and Martin (2001) also found that the frequency of cowbird parasitism increased among species with males that were more vocal and active near their nests during the nest-building period. By contrast, some species may benefit from remaining vigilant and actively defensive of their nests. Bell's vireos (*Vireo bellii*) that vocalized more during nest building and incubation were parasitized less by cowbirds than relatively quiet pairs (least Bell's vireo, *V. b. pusillus*: Sharp and Kus 2006; Arizona Bell's vireo, *V. b. arizonae*: Steckler and Conway 2012).

A temporal shift in vocalizations could allow for a combination of behavioral adaptations that would accommodate both sexual selection and natural selection to reduce parasitism or predation risk. Cowbirds often locate nests during the host's building stage and then return to parasitize the nest early in the morning while the host is laying or in early incubation (Friedmann 1929, Hann 1941, Lowther 1993). Thus, hosts may benefit from stage-specific vocalization, e.g. being relatively secretive during building but vigilant in nest defense in laying or incubation stages. Birds may also alter their songs in frequency (Hz), structure, or in the timing of their vocalizations throughout the day in response to changes in their acoustic environment (Patricelli and Blickley 2006, Warren et al. 2006, Fuller et al. 2007), and some birds may be able to similarly adjust the timing of vocalizations to avoid temporally-specific threats without losing the social benefits of conspecific communication. Although there is little information about the specific time of day when nest predators are most likely to depredate nests, some nesting birds demonstrate behavioral plasticity near their nests when predation pressures are perceived to be high (Marzluff and Balda 1992, Ghalambor and Martin 2000, Eggers et al. 2005). Nuthatches (*Sitta* sp.) responded to experimentally enhanced stage-specific predation risk by making less frequent visits to the nests and by aborting more visits altogether (Ghalambor and Martin 2000). In areas with high predator presence, Siberian jays (*Perisoreus infaustus*) visited their nests less frequently during the afternoon, when their nest predators were more active, and compensated by making more frequent visits when predators were less active (Eggers et al. 2005).

We investigated the vocal response of black-capped vireos (vireo; *Vireo atricapilla*) to predation and parasitism risk, considering different nesting stages and time of day. The vireo is an endangered songbird threatened by high rates of brood parasitism by cowbirds (Ratzlaff 1987). Vireo recovery to date has focused on the removal of cowbirds from vireo breeding habitat, creating several large managed populations, including the Fort Hood Military Reservation (Fort Hood) in central Texas (Kostecke et al. 2005). Nest parasitism, however, continues to significantly contribute to the ongoing low reproductive rate of vireos in areas without cowbird control (Chapter 1). Thus, vireo populations on and around Fort Hood provide a unique opportunity to investigate vocalization behavior at the nest across a gradient of parasitism risk, as they weigh potential trade-offs with a relatively stable risk of predation.

We tested two hypotheses regarding the relationship of host vocalizations and predator/parasite attraction: the predator-attraction hypothesis (Aviles et al. 2006, Steckler and Conway 2012) and the parasite-assessment hypothesis (Forsman and Martin 2009, Steckler and Conway 2012). The predator-attraction hypothesis assumes that the primary predators of eggs and nestlings use auditory cues to locate nests and that brood parasites use information on perceived predation risk to make decisions about which nests to parasitize (Aviles et al. 2006, Steckler and Conway 2012). The predator-attraction hypothesis predicts that individuals who vocalize frequently near their nests should have a greater probability of incurring nest predation and a lower probability of brood parasitism (Aviles et al. 2006, Steckler and Conway 2012). Conversely, the parasite-assessment hypothesis predicts that nesting individuals perceive parasitism risk based on local parasite densities and that host vocalization rate will be inversely correlated with local parasite density (Forsman and Martin 2009, Steckler and Conway 2012). We expect that, in our study system, risk of predation or parasitism may be dependent on nest stage or time of day and we suspect that vocalization rates of black-capped vireos will respond to parasitism and predation risk during at least some nesting stages. Nest predation is not likely to be affected by vocalizations in the building stage but selection to reduce predation pressure may affect vocalization rate in later nesting stages. Cowbirds locate nests during building and laying (Lowther 1993) and we therefore expect that vireos will benefit from being relatively quiet and secretive during these nest stages, especially in areas with high cowbird densities. We also hypothesized that vireos breeding in areas where cowbirds are common may make fewer nesting vocalizations in the morning and more in the afternoon or evening relative to vireos breeding in areas with lower parasitism risk.

METHODS

Study Sites

We chose five study sites in central Texas, on Fort Hood and in nearby areas to the west, that reflect a gradient of cowbird control effort and offer vireos a range of tradeoffs relevant to nest communication (Figure 3.1). The habitat within the Hill Country of central Texas is semi-arid and largely characterized by shortgrass communities and cattle rangeland. Many ungrazed areas that were once grass or deciduous shrublands are now woodlands due to fire suppression and the range expansion of the native evergreen Ashe juniper (*Juniperus ashei*).

On Fort Hood, we chose three study sites that represent a range of cowbird control: East Range, West Range, and West Fort Hood. West Range, dominated by mixed juniper and deciduous woodlands, had comprehensive cowbird control until 2006 when Fort Hood began an experimental cessation of cowbird control in the northwest area of the base. East Range is located on the eastern side of the installation where cowbirds have been continually controlled via shooting and trapping since 1991. West Fort Hood is located near the southern edge of the Fort Hood installation and, although cowbirds are removed from the site when they are reported, there are no nearby traps and cowbird presence remains high. East Range and West Fort Hood are characterized by a mix of grasslands and deciduous woodlands.

The San Saba study site is comprised of portions of two neighboring private ranches southwest of San Saba, Texas, approximately 60 miles west of Fort Hood. Moderate cowbird control efforts began at San Saba in 2014 but cowbirds remained common on the site throughout this study.

Colorado Bend State Park is a 5328 acre state park located about 36 miles west of Fort Hood, along the west side of the Colorado River in San Saba County, Texas. The study site, along the northeastern boundary of the park, consists of a mix of grassland and patchy juniper and live oak woodlands (*Quercus fusiformis*). During the course of this study, there was no effective cowbird control in the state park except for minimal trapping efforts in 2014.

Cowbird Density Estimation

Cowbird density may be reliably estimated using point counts (Miles and Buehler 2000). Thus, to assess the level of cowbird presence on each study site, we conducted 10-minute variable distance point counts at several locations within each study site. We based the number of point count locations roughly on the relative area of each site; we conducted counts at seven locations on East Range, nine on West Fort Hood, five on West Range, five on San Saba, and 13 on Colorado Bend. Point count locations were at least 200 m apart. At each location, we conducted three rounds of counts in 2013 and three in 2014 noting the distance to any cowbirds we detected.

Using the point count data, we conducted detection-dependent density modelling using the packages “Distance” and “mrds” in R v.3.1.1 (Laake et al. 2014, Miller 2014, R Core Team 2014). We compared models with half-normal or hazard-rate key functions and cosine or simple polynomial adjustment functions with an optimized number of adjustment terms. We compared models with 1) no binning or truncation of the data, 2) truncated but unbinned data, and 3) seven variations of bin structure and data truncation. Thus, in total, we compared thirty-six models using AIC_c (Akaike’s Information Criterion corrected for small sample size; Akaike 1974) and model weights, which we evaluated using Chi-square.

Using the best model, (hazard rate key function, simple polynomial adjustment function with two adjustment terms; Goodness of Fit: $\chi^2 = 1.94$, df = 7, $P = 0.96$) we estimated cowbird density on each study site (Table 3.1) as an indication of the relative level of cowbird abundance.

Nest Monitoring

We monitored black-capped vireos at each study site in 2013 and 2014. We visited study sites three times a week from late March through mid-July and searched for territorial males. Upon identifying territories, we visited each territory two or three times a week to identify nesting behavior and locate nests. We visited known nest locations every three to four days until the nest either failed or fledged; during each visit, we recorded the number of host eggs and cowbird eggs (if present) and the number and approximate age of nestlings.

Audio Recordings

Nest Recordings and Site Selection. We recorded vireo vocalizations at nests between sunrise and sunset from mid-April through late June during multiple nest stages: building, egg-laying, and early incubation (days 1-4 of incubation; Table 3.1). Parasitism events typically occur during the egg-laying or early incubation stages and, to avoid unnecessary disruption of the nesting cycle, we did not record vocalizations at nests during later periods of vireo incubation or after eggs hatched. We also avoided recording on days with rain or high wind. Minimizing disturbance of the nest, we attached a Sennheiser condenser microphone to a branch at the approximate height of the nest three to five meters away and, using a Sony digital voice recorder, recorded vocalizations for the battery life of the recorder (about 23 hours). We concealed recorders in vegetation below the microphone.

We selected nests to record at random within each site (Table 3.1). We located most nests we recorded during the building stage (88%, $n = 46$) but 12% ($n = 6$) were located during lay. East Range was the only site with very low to zero cowbird presence and we recorded nests at this site in both 2013 and 2014. In 2013, we also conducted nest recordings at West Fort Hood and Colorado Bend and, in 2014, we recorded nests at West Range and San Saba.

Vocalization Rates. To calculate vocalization rates, we divided each day's recording into morning (sunrise to 9 am), midday (noon to 3 pm), and evening (6 pm to sunset) time periods and randomly selected one 30 minute section from each time period. We then counted the number of male song vocalizations in each 30 minute section, categorizing the singer's approximate distance from the nest as "near" (within approximately 15 m of the nest) or "far" (greater than 15 m from the nest) based on the relative volume of vocalizations. We then calculated a "near nest" vocalization rate (songs/minute). Vocalizations distant from the nest are unlikely to cue a cowbird or predator to the nest location and, in some cases, may represent a vocalization from a neighboring male. Therefore, we discarded vocalizations determined to be "far from the nest" and they were not included in further analyses. A single observer listened to all recordings and categorized all vocalization distances. Across nests, we also calculated average vocalization rates (mean ± SE).

Analyses. To test the predator-attraction (Aviles et al. 2006, Steckler and Conway 2012) and parasite-assessment hypotheses (Forsman and Martin 2009, Steckler and Conway 2012), we conducted three analyses of "near nest" vocalizations. To assess the predator-attraction hypothesis, we compared generalized linear models defined *a priori* considering combinations of nest stage, time of day, and (1) depredation fate (whether the nest was eventually depredated or not) and (2) parasitism fate (whether the nest was eventually parasitized or not). To analyze the parasite-assessment hypothesis, we compared models considering nest stage, time of day, and (3) estimated cowbird density.

To explain vocalization rates at vireo nests, we compared seven models in each of three analyses including a null model, a model considering only nest stage, time of day, and their interaction, and additional analysis-specific models that considered either parasitism fate, depredation fate, or cowbird density. We ranked candidate models defined *a priori* using AIC_c (Akaike 1974) and assigned a relative probability to each model (Burnham and Anderson 1998). We compared model weights (w_i), which measure relative support for a particular model within the model set, and considered a model to be competitive if its ΔAIC_c was less than 2 (Burnham and Anderson 1998).

After defining our best model for each analysis, we conducted *post hoc* tests of factor interactions to determine the relationship between nest stage, time of day, and measures of nest fate and cowbird density. All analyses were conducted in R v.3.1.1 (R Core Team 2014); we used the packages "AICcmodavg" (Mazerolle 2015) to calculate AIC_c (Akaike, 1974), and "phia" for all *post hoc* evaluations (De Rosario-Martinez 2015).

RESULTS

We recorded vocalizations at 52 nests during the 2013 and 2014 seasons (Tables 3.1 and 3.2). Fifteen nests (28.8%) were eventually parasitized and 19 (36.5%) were depredated. Four parasitized nests (26.7%) were also eventually depredated. On average, nests which were eventually parasitized and depredated had more vocal males ($\bar{x}$ = 1.13 ± 0.32 songs/minute) than nests which were only depredated ($\bar{x}$ = 0.59 ± 0.16 songs/minute), only parasitized ($\bar{x}$ = 0.59 ± 0.19 songs/minute), or were neither depredated nor parasitized ($\bar{x}$ = 0.62 ± 0.14 songs/minute), but these differences were not significant ($F_{3,151} = 0.84$, $P = 0.47$).

Predator-Attraction Hypothesis

Depredation Fate. After comparing seven models relating vocalization rate to combinations of nest stage, time of day, and depredation fate, the best supported model included all main effects and two-way interactions (Tables 3.3 and 3.4); there were no other competitive models (Table 3.3). More vocal males were less likely to be eventually depredated overall ($\chi^2 = 21.84$, $P < 0.001$) but this varied by nest stage and time of day (Table 3.4). *Post hoc* evaluations determined that nests were more likely to eventually experience nest predation when males vocalized more frequently in the early incubation stage ($\chi^2 = 31.29$, $P < 0.001$; Figure 3.2). Conversely, nests were less likely to be depredated when males vocalized more during building ($\chi^2 = 51.60$, $P < 0.001$) and laying ($\chi^2 = 45.72$, $P < 0.001$; Figure 3.2). Depredation was also more likely when males vocalized less in the evening ($\chi^2 = 54.27$, $P < 0.001$) and more during the middle of the day ($\chi^2 = 7.24$, $P = 0.01$; Figure 3.2).

Parasitism Fate. The best model of vocalization rate considering parasitism fate included all three main effects (nest stage, time of day, and parasitism fate) and all two-way interactions (Tables 3.5 and 3.6). Across all nest recordings, there was no significant relationship between parasitism fate and vocalization rate ($\chi^2 = 0.01$, $P = 0.94$) but differences among nest stages and periods of the day were evident (Table 3.6). *Post hoc* analyses of these interactions revealed that, during the laying period, eventual parasitism was associated with less frequent vocalizations ($\chi^2 = 96.61$, $P < 0.001$; Figure 3.3). Conversely, in the building and early incubation stages and during the midday, vocalizations were positively correlated with eventual parasitism (building: $\chi^2 = 29.76$, $P < 0.001$; incubation: $\chi^2 = 144.89$, $P < 0.001$; midday: $\chi^2 = 8.17$, $P = 0.01$; Figure 3.3).

Parasite-Assessment Hypothesis

Cowbird Density. The best and only competitive model of vocalization rate considering cowbird density included all three main effects (nest stage, time of day, and estimated cowbird density) as well as all two-way interactions (Tables 3.7 and 3.8). *Post hoc* analyses revealed that vocalization rates varied with cowbird density within each nest stage (building: $\chi^2 = 95.14$, $P < 0.001$; laying: $\chi^2 = 144.62$, $P < 0.001$; incubation: $\chi^2 = 102.33$, $P < 0.001$) and during the morning ($\chi^2 = 73.91$, $P < 0.001$) and midday hours ($\chi^2 = 36.02$, $P < 0.001$), but not in the evening ($\chi^2 = 0.57$, $P = 0.45$; Figure 3.4). Vocalization rates decreased with increasing cowbird densities during the laying period (Figure 3.4). During the building and early incubation stages, however, vocalization rate was positively correlated with cowbird density. Vocalization rates increased with high cowbird densities in the morning and midday hours.

Importance of Nest Stage and Time of Day

Nest stage, time of day, and their interaction were important in all analyses described above and better explained patterns in vireo vocalizations than either depredation fate, parasitism fate, or cowbird density alone (Tables 3.3, 3.5, and 3.7). In the midday, male song rate at nests was greatest in the incubation and building stages and relatively low during laying (Table 3.2, Figure 3.5). During building and incubation, vocalization rates were lowest in the evening and highest in the midday. Song rates in the morning were moderate but significantly greater than in the evening and less than in midday. During the laying stage, “near nest” vocalizations were most frequent in the morning. These vocalization patterns in response to nest stage and time of day were consistent across all final models that tested the predator-attraction and parasite-assessment hypotheses (although χ^2 values varied between analyses, all $P < 0.001$).

DISCUSSION

Vocalizations near nests are known to attract predators and brood parasites for some host species (Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001) and reduce rates of parasitism for others (Sharp and Kus 2006, Steckler and Conway 2012). For the endangered black-capped vireo, we found only limited, stage-specific evidence for both the predator-attraction and parasite-assessment hypotheses across landscapes that vary in parasitism risk. Thus, we suggest that neither hypothesis adequately captures the selection pressures that shape vireo vocalization patterns. Black-capped vireos face a cruel bind in navigating the risks of predation and brood parasitism risk, a bind that they solve through temporal plasticity in vocalization rates near the nest.

Predator-Attraction Hypothesis

Patterns in black-capped vireo vocalizations near their nests do not support the predictions outlined by the predator-attraction hypothesis. Across all recordings, the relationships observed between song rate and depredation and parasitism fate were in contrast to the expectations of this hypothesis; namely, nests with more vocal males were less likely to be depredated and there was no relationship between parasitism and song rate. Additionally, although we found some temporal variation between vireo defense strategies, patterns relating vocalization rate and depredation or parasitism fate were generally consistent suggesting that vireos experience minimal trade-offs in mediating parasitism or predation risk through vocalizations. We suspect that, during the early stages of the nesting cycle, selection for optimal vireo vocalization rates at the nest might focus most on the threat of cowbird parasitism. Had we observed nests during nestling development, we may have garnered more support for the predator attraction hypothesis.

Although the predator-attraction hypothesis assumes that nest predators cue in to parental behaviors such as vocalizations, this may not be true for vireos, particularly during the early nesting stages. Across the breeding range, vireo nests are susceptible to a suite of nest predators, including ants, snakes (*Elaphe* sp.), and avian predators (Stake and Cavanagh 2001, Stake and Cimprich 2003, Conkling et al. 2012). Snakes and fire ants (*Solenopsis* sp.) are the most common predators of vireo nests on Fort Hood (Stake and Cimprich 2003) but do not respond to aural cues such as vocalizations. Whereas avian predators, such as western scrub-jays (*Aphelocoma californica*), locate nests based on parental cues (Curry et al. 2002), predation events by birds other than cowbirds are most often of nestlings and are relatively uncommon in the early nesting stages (Stake and Cimprich 2003). Although cowbirds may be important nest predators at some vireo breeding sites (Conkling et al. 2012), their primary motivation for locating nests is brood parasitism and partial predation events do not always lead to nest failure (Stake and Cavanagh 2001). Cowbirds are most likely to depredate nests that are located late in the nesting cycle (Conkling et al. 2012), in some cases forcing the host pair to renest and giving the cowbird another parasitism opportunity (Arcese et al. 1992, Stake and Cavanaugh 2001).

Parasite-Assessment Hypothesis

In central Texas, black-capped vireo vocalization rates are, on average, only weakly correlated with local cowbird density. During the building and incubation stages, vireo vocalization rates near the nest were slightly higher at sites with higher estimates of cowbird density. During the laying stage, however, vocalization rates were highest in areas where cowbird density is low, providing some stage-specific evidence for the parasite-assessment hypothesis. Cowbirds typically parasitize nests near the end of the laying stage and vireos may reduce vocalization rates in response to increases in perceived parasitism risk during this nest stage (Lowther 1993, Forsman and Martin 2009). Alternatively, high cowbird densities may induce nest vigilance by vireos during the building or early incubation stages, although the mechanism for this phenomenon is not obvious.

Reticence or Vigilance: Alternative Strategies for Nest Success

Although we observed little evidence of trade-offs between the mediation of risk for predators and brood parasites, some stage-specific patterns provide clues as to how vireos balance the risks and benefits of social communication. Temporally specific behavioral adaptations by vireos may alleviate some conflicts in nest defense strategy and ultimately optimize nest success. Cowbirds often locate nests while hosts are building and then return to parasitize the nest during the host laying or early incubation period (Friedmann 1929, Hann 1941, Lowther 1993). Vireos may minimize their risk of eventual nest parasitism by remaining quiet during the building stage to prevent cowbirds from finding the nest location. Nests that are discovered by cowbirds may be abandoned before laying occurs because vireos are less invested in the particular nest location. Once laying begins, however, vireos are more invested in their nest and benefit by remaining vigilant to ward off potential brood parasites. Previous studies found that vireo nests suffer higher rates of predation during the nestling stage compared with incubation (Stake and Cimprich 2003, Conkling et al. 2012), but these studies did not evaluate predation rates during laying or early incubation periods. In general, avian predators of vireo nests on Fort Hood, including cowbirds, act diurnally (Stake and Cimprich 2003). Stake and Cavanagh (2001) observed that cowbirds depredating vireo nests during the nestling stage most frequently acted during the midday between 10 am and 3 pm. Scrub-jays and other corvids are generally active throughout the day although the specific timing of predation events is unreported (Luginbuhl et al. 2001, Eggers et al. 2005). Thus, vireos may minimize depredation threat by being relatively quiet during the middle of the day when avian predators are most active; this proved an especially effective strategy during early incubation.

Although patterns demonstrate that, in general, parasitism and predation risks do not require conflicting defense strategies during the early nesting stages, some differences in risk mediation suggest that, in cases of conflict, vireos minimize loss by optimizing behavior to defend against nest predation. During the building stage, for example, vigilant and more vocal vireos reduced their susceptibility to eventual nest depredation but increased their likelihood of parasitism despite increasing cowbird densities. In the evenings, vireos that remained vigilant were able to reduce their probability of nest depredation. Vocalizations in the evening had no impact on parasitism fate, however, and increasing cowbird densities did not affect the frequency of vocalizations in the evening.

Although vireos demonstrate some flexibility in the timing of vocalizations, selection pressures for pair bonding and territory defense may limit plasticity in social communication. In areas with high cowbird densities, vireos became more vigilant during the building stage, when cowbirds typically locate nests, and more secretive during laying, when brood parasitism generally occurs (Lowther 1993). These were not, however, effective defense strategies against parasitism; birds that vocalized more during building and less during the laying stage were also more often parasitized. Additionally, these patterns may amplify one another; if cowbirds are able to follow aural cues and locate a nest during the building stage (Friedmann 1929, Hann 1941, Lowther 1993), vireo reticence during laying may inadvertently aid cowbirds by allowing them more uninterrupted access to the nest. Although vigilance during building may reflect a trade-off with predation risk, we did not observe evidence for such a trade-off during the laying stage; during laying, frequent vocalizations near the nest increased the likelihood of both parasitism and depredation. Instead, vireo territory density and trade-offs with territory defense may help explain these apparent conflicts. High host density may favor selection for territory defense and increased vocalization rates. Indeed, previous studies have positively correlated vireo densities with parasitism rates (Barber and Martin 1997). Thus, at sites with high cowbird densities, vocalization rates may reflect selection for territory defense rather than parasitism risk. Alternatively, at high cowbird densities, building vireos may be more likely to become incidentally discovered by a cowbird, regardless of vocalization rate. Under those circumstances, mate communication may outweigh reticence as an effective defense against parasitism.

In contrast to our results, nest parasitism in a similar species, Bell's vireo, was negatively correlated with vigilance and increased vocalization near the nest during the building and incubation stages but not during laying (Steckler and Conway 2012). Bell's vireo vocalizations during laying were positively correlated with eventual parasitism, although the difference was not significant. This contrast between two very similar species may suggest that, in some cases, parasitism is affected by variables or behaviors not captured well by audio recordings (e.g. female presence on the nest; Neudorf and Sealy 1994). Alternatively, trade-offs with predation risk may differ across habitat types and predator guilds (e.g. Kotler et al. 1991), resulting in different vocalization patterns in response to risk of brood parasitism.

Vocalization behavior and parasitism risk have an interactive relationship that is made increasing complex by the additional consideration of nest predation. Although in many species more vocal individuals suffer higher rates of brood parasitism (Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001), adaptation of vocalization behaviors that minimize parasitism risk may be outweighed by selection for behaviors that enable individuals to maintain important conspecific bonds or minimize risk of nest predation. Species that do not have nest predators cued by auditory signals, however, may be able to more readily adapt vocalization patterns that minimize parasitism risk. Without the complications of additional trade-offs with predation, some species may develop more temporal flexibility and avoid vocalizing during periods of the day or stages of the nesting cycle when they are most vulnerable to brood parasitism.

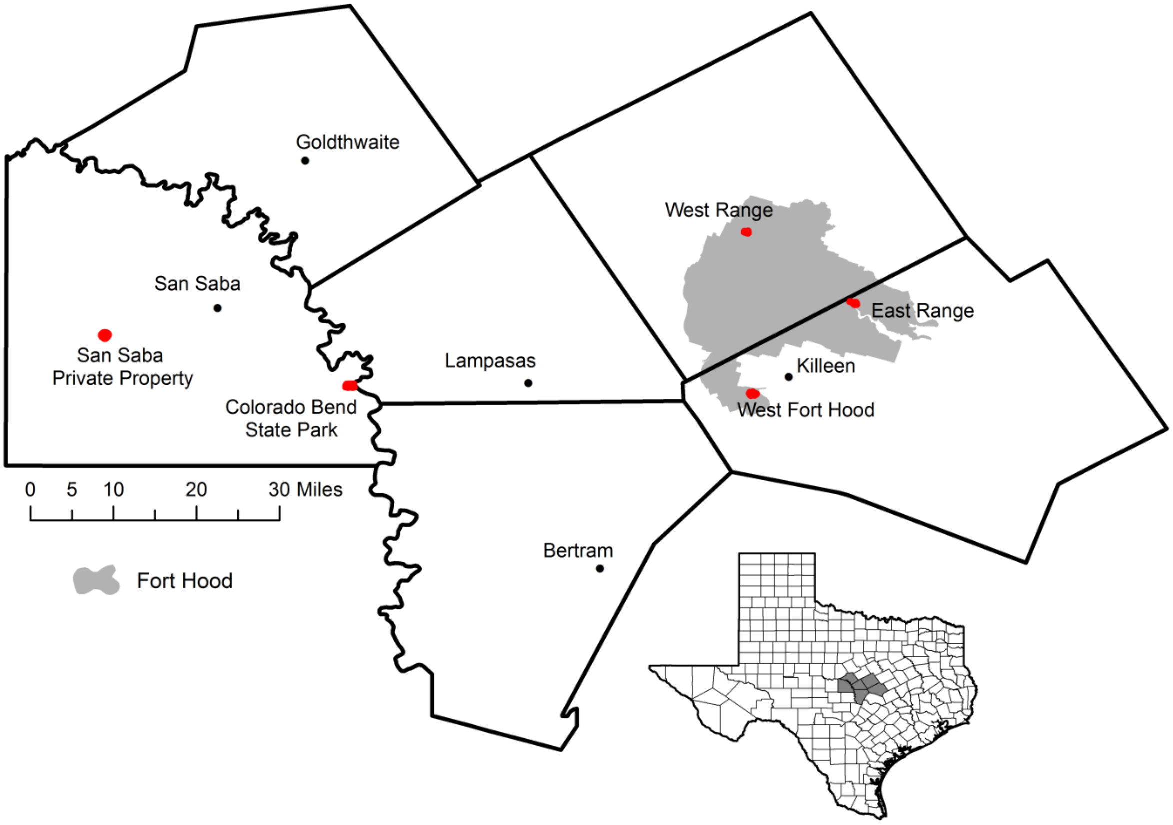


Figure 3.1. Study site locations for black-capped vireo nest recordings in central Texas, 2013-2014.

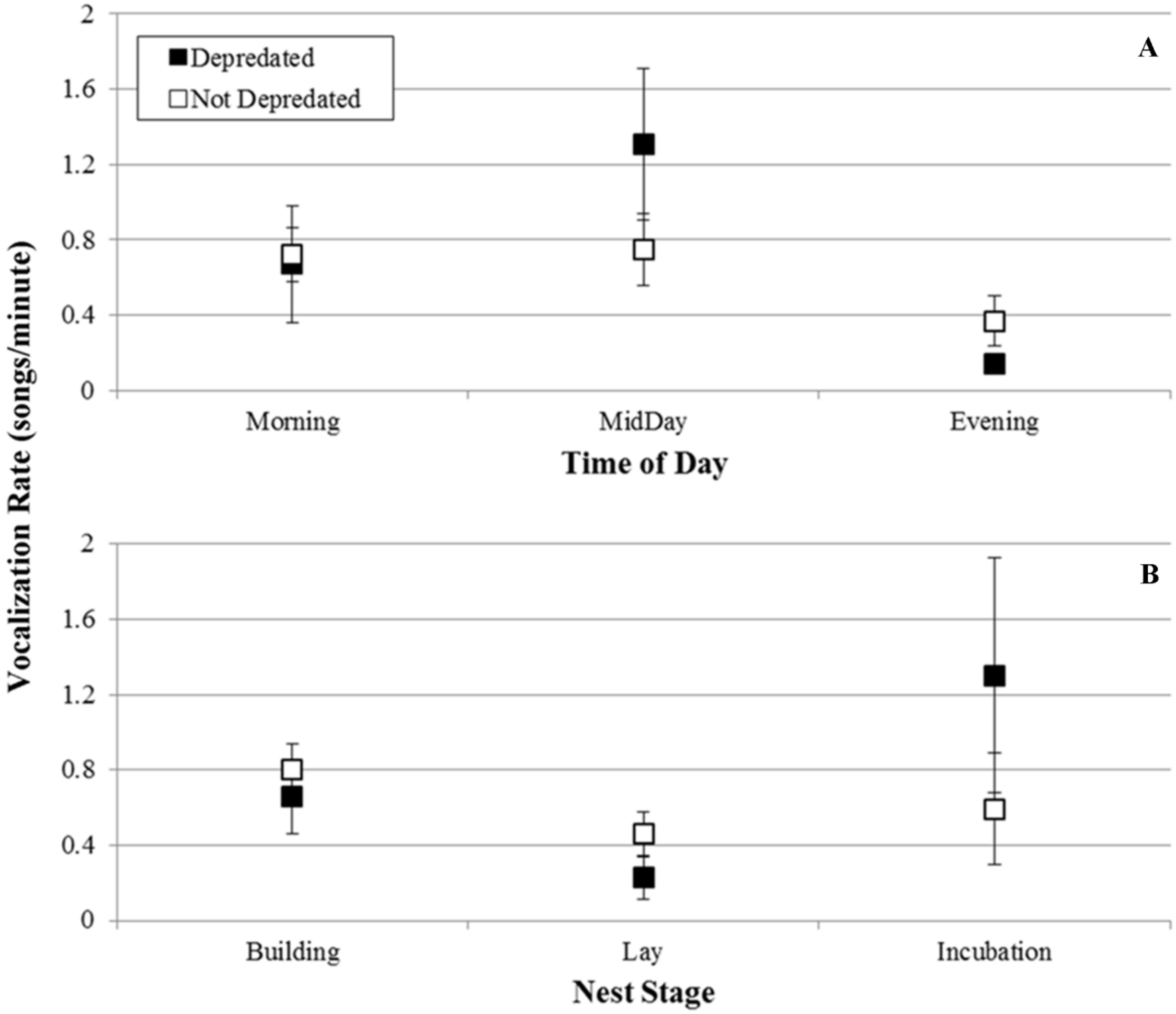


Figure 3.2. Interaction between vocalization rates at vireo nests in central Texas, 2013-2014, depredation fate, and (A) time of day and (B) nest stage. Adjusted averages and standard errors are shown.

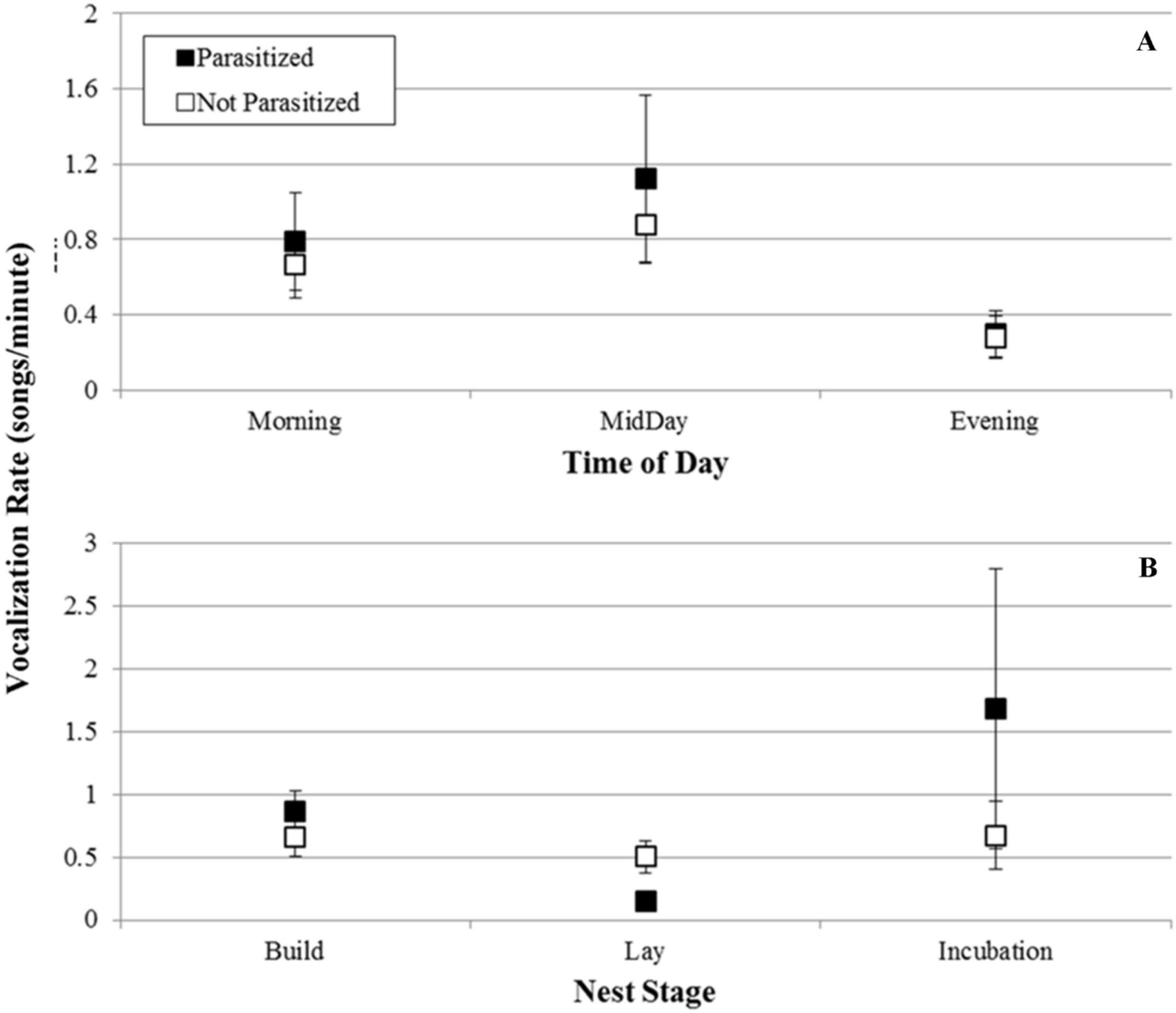


Figure 3.3. Interaction between vocalization rates at vireo nests in central Texas, 2013-2014, parasitism fate, and (A) time of day and (B) nest stage. Adjusted averages and standard errors are shown.

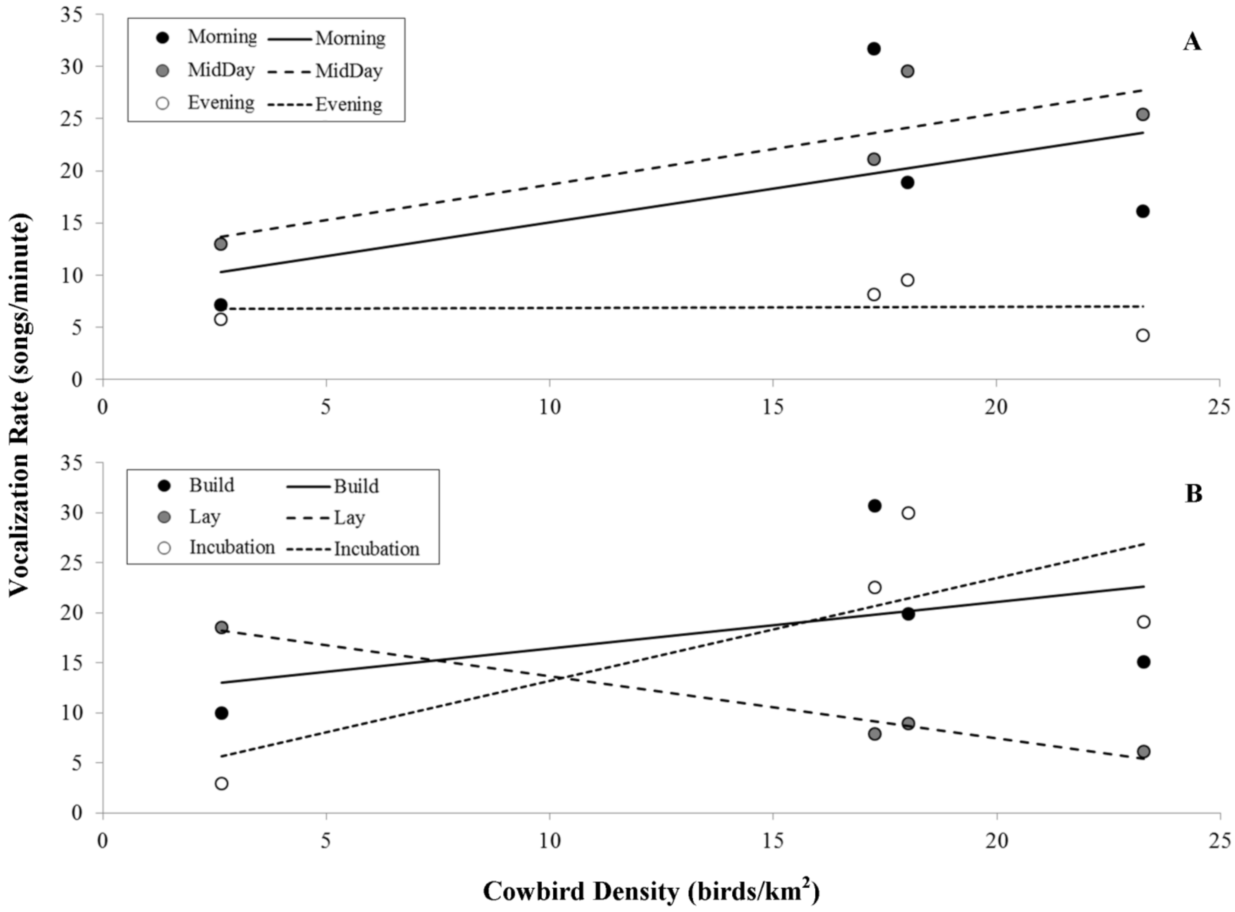


Figure 3.4. Linear trends relating vocalization rates at vireo nests in central Texas, 2013-2014, cowbird density, and (A) time of day and (B) nest stage.

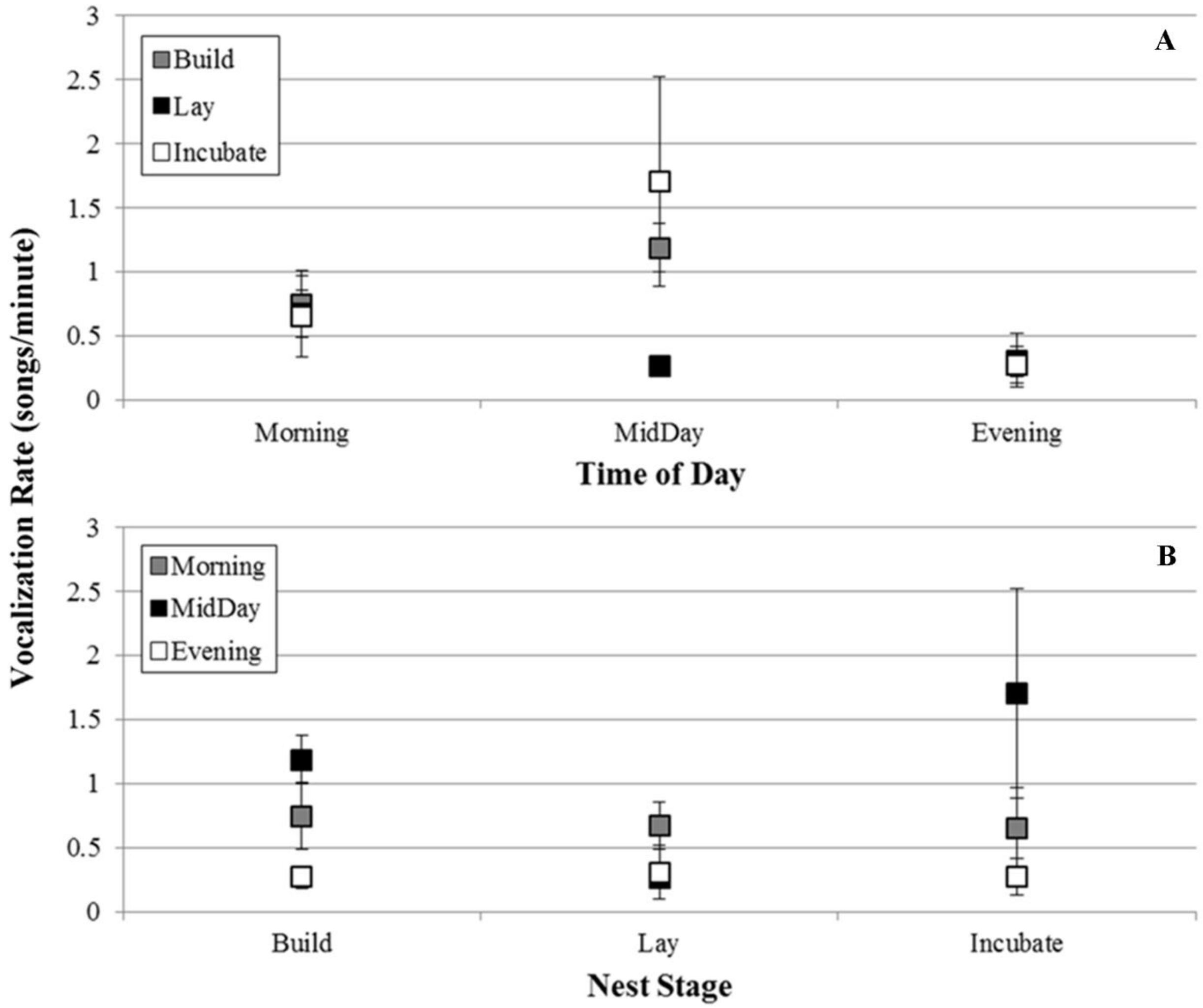


Figure 3.5. Interaction between vocalization rates at vireo nests in central Texas, 2013-2014, and (A) time of day and (B) nest stage. Adjusted averages and standard errors are shown.

Table 3.1. Cowbird density (birds/km^2) and number of audio recordings made at black-capped vireo breeding sites in central Texas.

	Cowbird Density		Sample Size by Nest Stage			
Site	Estimate	SE	Building	Laying	Early Incubation	Total
Colorado Bend	18.02	22.90	4	4	3	11
East Range	2.64	3.55	9	6	2	17
San Saba	17.26	22.49	2	3	1	6
West Fort Hood	23.29	29.50	4	4	2	10
West Range	17.26	22.24	4	2	2	8
		Total	23	19	10	52

Table 3.2. Male black-capped vireo vocalization rates (songs/minute) near nests.

	Nest Stage							
Time of Day	Building	SE	Laying	SE	Early	SE	Total	SE
Morning	0.75	0.26	0.67	0.19	0.65	0.32	0.70	0.15
MidDay	1.19	0.19	0.27	0.08	1.71	0.82	0.95	0.19
Evening	0.27	0.09	0.31	0.21	0.27	0.15	0.28	0.09
Total	0.73	0.12	0.41	0.10	0.88	0.31	0.64	0.09

Table 3.3. Models used to evaluate the predator-attraction hypothesis and the role of nest stage (Stage), time of day (Time), and depredation fate (Depr) on vocalization rates by male vireos near their nests.

Parameters	ΔAIC_c	w_i
Stage + Time + Depr + Stage*Time + Stage*Depr + Time*Depr	0.00[a]	1.00
Stage + Time + Depr + Stage*Time + Stage*Depr	69.23	< 0.001
Stage + Time + Depr + Stage*Time + Time*Depr	126.04	< 0.001
Stage + Time + Stage*Time	223.53	< 0.001
Stage + Time + Depr + Stage*Time	225.80	< 0.001
Depr	1409.56	< 0.001
(null)	1421.39	< 0.001

[a] $AIC_c = 4934.35$

Table 3.4. Parameter estimates for best model of vocalization rates considering nest stage, time of day, and depredation fate.

β	Estimate	SE	*z*	*P*
Intercept	-0.20	0.06	-3.65	< 0.001
Nest Stage (Lay)	-0.10	0.08	-1.30	0.20
Nest Stage (Incubation)	-0.57	0.10	-5.86	< 0.001
Time of Day (MidDay)	0.37	0.07	5.40	< 0.001
Time of Day (Evening)	-0.72	0.10	-7.52	< 0.001
Depredation Fate	-0.20	0.08	-2.64	0.008
Nest Stage (Lay)*Time of Day (MidDay)	-1.32	0.12	-11.45	< 0.001
Nest Stage (Incubation)*Time of Day (MidDay)	0.50	0.10	4.93	< 0.001
Nest Stage (Lay)*Time of Day (Evening)	0.01	0.13	0.12	0.91
Nest Stage (Incubation)*Time of Day (Evening)	0.28	0.16	1.76	0.08
Nest Stage (Lay)*Depredation Fate	-0.38	0.13	-2.88	0.004
Nest Stage (Incubation)*Depredation Fate	0.91	0.09	9.96	< 0.001
Time of Day (MidDay)*Depredation Fate	0.20	0.09	2.27	0.02
Time of Day (Evening)*Depredation Fate	-0.94	0.15	-6.43	< 0.001

Table 3.5. Models used to evaluate the predator-attraction hypothesis and the role of nest stage (Stage), time of day (Time), and parasitism fate (Para) on vocalization rates by male vireos near their nests.

Parameters	ΔAIC_c	w_i
Stage + Time + Para + Stage*Time + Stage*Para + Time*Para	0.00[a]	0.99
Stage + Time + Para + Stage*Time + Stage*Para	8.54	0.01
Stage + Time + Para + Stage*Time	264.60	< 0.001
Stage + Time + Para + Stage*Time + Time*Para	266.89	< 0.001
Stage + Time + Stage*Time	283.68	< 0.001
Para	1459.86	< 0.001
(null)	1481.54	< 0.001

[a] $AIC_c = 4874.20$

Table 3.6. Parameter estimates for best model of vocalization rates considering nest stage, time of day, and parasitism fate.

β	Estimate	SE	*z*	*P*
Intercept	-0.47	0.06	-8.32	< 0.001
Nest Stage (Lay)	0.28	0.08	3.60	< 0.001
Nest Stage (Incubation)	-0.29	0.09	-3.15	0.002
Time of Day (MidDay)	0.59	0.07	8.71	< 0.001
Time of Day (Evening)	-1.00	0.10	-9.66	< 0.001
Parasitism Fate	0.44	0.08	5.68	< 0.001
Nest Stage (Lay)*Time of Day (MidDay)	-1.50	0.12	-12.90	< 0.001
Nest Stage (Incubation)*Time of Day (MidDay)	0.53	0.10	5.27	< 0.001
Nest Stage (Lay)*Time of Day (Evening)	0.21	0.13	1.60	0.11
Nest Stage (Incubation)*Time of Day (Evening)	0.15	0.16	0.96	0.34
Nest Stage (Lay)*Parasitism Fate	-1.61	0.14	-11.26	< 0.001
Nest Stage (Incubation)*Parasitism Fate	0.64	0.09	7.09	< 0.001
Time of Day (MidDay)*Parasitism Fate	-0.32	0.09	-3.46	0.001
Time of Day (Evening)*Parasitism Fate	-0.04	0.13	-0.31	0.76

Table 3.7. Models used to evaluate the parasite-assessment hypothesis and the role of nest stage (Stage), time of day (Time), and local cowbird density (Cowbird) on vocalization rates by male vireos near their nests.

Parameters	ΔAIC_c	w_i
Stage + Time + Cowbird + Stage*Time + Stage*Cowbird + Time*Cowbird	0.00[a]	1.00
Stage + Time + Cowbird + Stage*Time + Stage*Cowbird	32.03	< 0.001
Stage + Time + Cowbird + Stage*Time + Time*Cowbird	285.06	< 0.001
Stage + Time + Cowbird + Stage*Time	353.26	< 0.001
Stage + Time + Stage*Time	450.21	< 0.001
Cowbird	1549.24	< 0.001
(null)	1648.06	< 0.001

[a] $AIC_c = 4707.67$

Table 3.8. Parameter estimates for best model of vocalization rates considering nest stage, time of day, and local cowbird density.

β	Estimate	SE	*z*	*P*
Intercept	-1.11	0.09	-11.85	< 0.001
Nest Stage (Lay)	1.13	0.11	10.18	< 0.001
Nest Stage (Incubation)	-1.00	0.17	-5.87	< 0.001
Time of Day (MidDay)	0.71	0.11	6.44	< 0.001
Time of Day (Evening)	-0.34	0.14	-2.49	0.01
Cowbird Density	0.06	0.01	11.02	< 0.001
Nest Stage (Lay)*Time of Day (MidDay)	-1.47	0.12	-12.72	< 0.001
Nest Stage (Incubation)*Time of Day (MidDay)	0.60	0.10	5.85	< 0.001
Nest Stage (Lay)*Time of Day (Evening)	0.01	0.13	0.11	0.91
Nest Stage (Incubation)*Time of Day (Evening)	0.31	0.16	1.93	0.05
Nest Stage (Lay)*Cowbird Density	-0.09	0.01	-14.51	< 0.001
Nest Stage (Incubation)*Cowbird Density	0.04	0.01	4.95	< 0.001
Time of Day (MidDay)*Cowbird Density	-0.02	0.01	-2.60	0.009
Time of Day (Evening)*Cowbird Density	-0.05	0.01	-6.06	< 0.001

CHAPTER 4

Simultaneous Polygyny by a Male Black-capped Vireo in Central Texas

Avian species exhibit a wide variety of mating systems. Birds that produce altricial young are most often socially monogamous because both parents are required for proper care of the young. However, approximately 5% of North American passerines practice regular simultaneous polygyny (hereafter polygyny; Verner and Willson 1966), whereby a male maintains pair bonds with more than one female at the same time. Additionally, several passerine groups are known to occasionally or rarely practice polygyny, including hummingbirds (Batchelder et al. 2012), sparrows (Petrinovich and Patterson 1978, Smith et al. 1982, Wheelwright et al. 1992), warblers (Barg et al. 2006, Peak et al. 2010), and wrens (Verner 1964, Leonard 1990). Here, we report an observation of polygyny in the endangered black-capped vireo (*Vireo atricapilla*), to our knowledge only the second instance of true polygyny within the Vireonidae (see Mountjoy 1997).

Black-capped vireos are small neotropical migrants that winter along western Mexico and breed locally from northeastern Mexico through Texas and southern Oklahoma (Graber 1961, Grzybowski 1995). Males begin arriving on the breeding grounds in late March, followed shortly by females. Their mating system is typically socially monogamous: males establish territories and pair with a single female. Females and males build nests together and share incubation duties and both parents care for nestlings and young fledglings. On average, eggs are incubated for 14-16 days and nestlings fledge after 11 days. Clutch size is typically four eggs (three is regular, five is rare) and pairs may renest several times if their initial efforts are unsuccessful. Cup-shaped nests are located along forked branches of low vegetation (often below 2 m) and, once found, are often easy to access and monitor.

METHODS

We observed simultaneous polygyny in the black-capped vireo while conducting a broad-scale investigation of vireo population dynamics across central Texas from 2011-2014. We visited study sites throughout the vireo breeding season, from late March through early July, and searched for all territorial males. We identified males by individual color band combination and visited each territory at least once a week (often more), recording locations of territorial male vireos using a handheld GPS unit. We recorded no more than five locations a day for each territory and each observation was separated by at least five minutes.

When nesting activity was observed, we carefully monitored pairs and attempted to locate all nests. We visited known nest locations every three to four days until failure or fledging and recorded the number of host eggs and cowbird eggs (if present), the number and approximate age of nestlings, and parental presence at the nest. We considered a nest to be successful if we observed evidence that at least one vireo nestling had fledged.

OBSERVATIONS

On 19 May 2014, we located a vireo nest with four eggs incubated by an unbanded female paired with a color-banded male. The nest was located on the Mullen tract of Balcones Canyonlands National Wildlife Refuge, 0.48 meters off the ground in a low patch of shin oak (*Quercus sinuata* var. *breviloba*; Figure 4.1). Although male vireos typically help incubate their nests, we checked this nest four times and never observed this male incubate or brood. We were, however, scolded by the male when we discovered the nest on 19 May and when we banded the nestlings on 28 May. On 30 May, we found the nest empty and presumably depredated. On 2

June, we discovered a nearby vireo nest (178 meters away), 1.28 meters off the ground in a tall shin oak under high live oak canopy. An unbanded female and the same color-banded male were brooding this second nest with three eggs and a single 1-day-old nestling. Four fledglings successfully fledged from this second nest on 14 June 2014. Because we carefully monitored and spotmapped all territories, we were able to identify both nests as solidly within the male's territory (Figure 4.1). Although we did not locate the male's second nest until after the first had been depredated, the presence of nestlings on 2 June allows us to reconstruct a timeline; the second nest was initiated (first egg likely laid around 17 May) while the first was still active. As both nests were being incubated simultaneously, we believe the nests were likely laid by two separate females.

There was only one adjacent territory (Figure 4.1) and that male was not paired during these observations. Although we did not directly assess paternity, we never observed this second male within the primary male's territory during 15 visits. We monitored 377 territories across four breeding seasons and seven study sites in central Texas and this was the only observed case of polygyny.

DISCUSSION

Occasional polygyny has been observed in a number of otherwise monogamous species and is thought to be associated with a variety of species-specific, or perhaps case-specific, drivers. While the benefits of polygyny are obvious for the male (he may be able to produce more young), benefits to the females are less apparent and the shift to polygyny may be explained by the presence of unbalanced sex ratios (Liker et al. 2014), asynchronous settlement (Leonard 1990), uneven distribution of resources such as nesting sites or food availability (the polygyny-threshold model; Verner 1964, Verner and Willson 1966, Orians 1969), or individual male quality (the sexy son hypothesis; Weatherhead and Robinson 1979).

We suspect that differences in habitat quality between the two adjacent territories were drivers in this instance of polygyny among black-capped vireos. During the 2014 breeding season, we found two territorial males and two females on the Mullen tract of Balcones Canyonlands National Wildlife Refuge. Thus, we did not observe any unbalance in the sex ratio of the local breeding population. Although we do not know the settlement date for each of the females, the timing of their nests overlapped significantly and thus asynchronous settlement seems unlikely. We have only limited means of comparing the quality of individual males but both males were second year birds, in their first breeding season. We observed small differences in body condition metrics including mass/wing chord or mass/tarsus length (the polygynous male had a 2% larger mass/wing and a 3% larger mass/tarsus ratio) but these metrics are not always a reliable measure of fitness (Schamber et al. 2008). Thus, territory quality seems the most likely driver. The territory of the polygynous male had more open land cover and less canopy cover than the adjacent male, habitat features that may be associated with territory success (see Chapter 2). Anecdotally, the location of the polygynous territory was also occupied in the 2011-2013 breeding seasons and successfully produced young each year. The other territory was occupied in 2011 and 2012, but not 2013, and fledged young only in 2011.

This is the first documented occurrence of simultaneous polygynous nesting in the endangered songbird, the black-capped vireo. Simultaneous nesting has implications at multiple scales. Individual birds that produce simultaneous nests may be able to successfully fledge more young. This phenomenon may also boost productivity at the population level, potentially aiding in long term viability and population persistence. Although polygyny appears rare in this species, this example demonstrates flexibility in mating strategy that may be important in the face of potential habitat changes due to land management or climate change. Such flexibility in individuals may aid in the persistence of populations, especially important for endangered species with limited population strongholds.

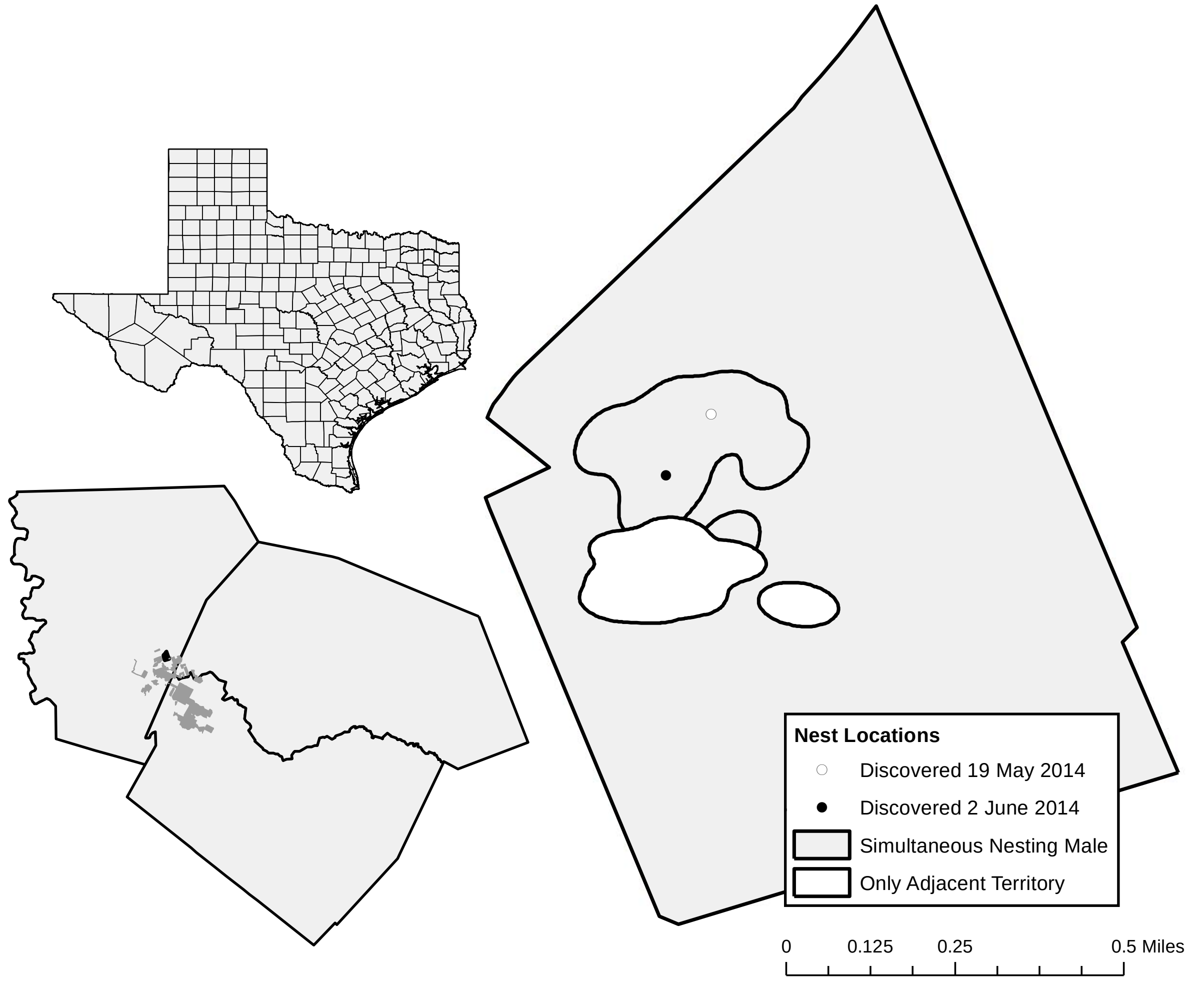


Figure 4.1. Location of polygynous black-capped vireo territory on Balcones Canyonlands National Wildlife Refuge in 2014.

LITERATURE CITED

Agrawal, A. A., J. K. Conner, and S. Rasmann. 2010. Tradeoffs and negative correlations in evolutionary ecology. In: Bell, M., W. Eanes, D. Futuyma, and J. Levinton, editors. Evolution after Darwin: the first 150 years. Sinauer, Sunderland, Massachusetts. pp. 243-268.

Akaike, H. 1974. A new look at the statistical model identification. Institute of Electrical and Electronics Engineers Transactions on Automatic Control 19:716-723.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6:1109-1122.

Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson. 1997. Juvenile survival in a population of neotropical migrant birds. Conservation Biology 11:698-707.

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. Ecology 73:794–804.

Arcese, P., J. N. M. Smith, W. M. Hochachkac, M. Rogers, and D. Ludwig. 1992. Stability, regulation and the determination of abundance in an insular song sparrow population. Ecology 73:805-822.

Ausprey, I. J., and A. D. Rodewald. 2011. Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. Auk 128:293-302.

Aviles, J. M., B. G. Stokke, and D. Parejo. 2006. Relationship between nest predation suffered by hosts and brown-headed cowbird parasitism: a comparative study. Evolutionary Ecology 20:97-111.

Bailey, J. W. 2005. Hierarchical nest-site selection and the effects of habitat characteristics on black-capped vireo nest survival. Thesis. University of Missouri, Columbia, Missouri.

Balogh, A. L., T. B. Ryder, and P. P. Marra. 2011. Population demography of gray catbirds in the suburban matrix sources, sinks and domestic cats. Journal of Ornithology 152:717-726.

Banks, A. J., and T. E. Martin. 2001. Host activity and the risk of nest parasitism by brown-headed cowbirds. Behavioral Ecology 12:31-40.

Barabas, L., B. Gilicze, F. Takasu, and C. Moskat. 2004. Survival and antiparasite defense in a host metapopulation under heavy brood parasitism: a source-sink dynamic model. Journal of Ethology 22:143-151.

Barber, D. R., and T. E. Martin. 1997. Influence of alternate host densities on brown-headed cowbird parasitism rates in black-capped vireos. Condor 99:595-604.

Barg, J. J., J. Jones, M. K. Girvan, and R. J. Robertson. 2006. Within-pair interactions and parental behavior of cerulean warblers breeding in eastern Ontario. Wilson Journal of Ornithology 118:316–325.

Barr, K. R., D. L. Lindsay, G. Athrey, R. F. Lance, T. J. Hayden, S. A. Tweddale, and P. L. Leberg. 2008. Population structure in an endangered songbird: maintenance of genetic differentiation despite high vagility and significant population recovery. Molecular Ecology 17:3628-3639.

Batchelder, N., G. Batchelder, D. A. Livezey, and J. S. Marks. 2012. Simultaneous multiple nests of calliope hummingbird and rufous hummingbird. Wilson Journal of Ornithology 124:640-643.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482-1491.

Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.7.3.0). (software). URL: http://www.spatialecology.com/gme.

Bock, C. E., and J. H. Bock. 1974. Geographical ecology of the acorn woodpecker: diversity versus abundance of resources. American Naturalist 108:694-698.

Boves, T. J., J. H. Sperry, K. Comolli, and P. J. Weatherhead. 2014. Brood parasitism of black-capped vireos: frontline and post-laying behavioral responses and effects on productivity. Journal of Field Ornithology 85:364-378.

Bradbury, J. W., and S. L. Vehrencamp. 2011. Principles of animal communication, Second Edition. Sinauer, Sunderland, Massachusetts.

Brown, J. H., and A. Kodric Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445-449.

Budnik, J. M., M. R. Ryan, and F. R. Thompson III. 2000. Demography of Bell’s vireos in Missouri grassland-shrub habitats. Auk 117:925–935.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information theoretic approach. Springer-Verlag, New York, New York.

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts.

Catchpole, C. K. 1987. Bird song, sexual selection and female choice. Trends in Ecology and Evolution 2:94-97.

Chalfoun, A. C., and T. E. Martin. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497-503.

Chalfoun, A. D., and K. A. Schmidt. 2012. Adaptive breeding-habitat selection: is it for the birds? Auk 129:589-599.

Cimprich, D. A., and M. Heimbuch. 2011. Monitoring of the black-capped vireo during 2011 on Fort Hood, Texas. In: Endangered species monitoring and management at Fort Hood, Texas: 2011 annual report. Fort Hood Natural and Cultural Resources Management Branch, Fort Hood, Killeen, Texas.

Cline, M. H., A. M. Strong, T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes. 2013. Correlates and consequences of breeding dispersal in a migratory songbird. Auk 130:742-752.

Clotfelter, E. D. 1998. What cues do brown-headed cowbirds use to locate red-winged blackbird host nests? Animal Behaviour 55:1181-1189.

Cohen, E. B., and C. A. Lindell. 2004. Survival, habitat use, and movements of fledgling white-throated robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. Auk 121:404-414.

Conkling, T. J., T. L. Pope, K. N. Smith, H. A. Mathewson, M. L. Morrison, R. N. Wilkins, and J. W. Cain. 2012. Black-capped vireo nest predator assemblage and predictors for nest predation. Journal of Wildlife Management 76:1401-1411.

Conover, M. R. 2007. Predator–prey dynamics: the use of olfaction. Taylor and Francis, Boca Raton, Florida.

Cornell, H. N., J. M. Marzluff, and S. Pecoraro. 2012. Social learning spreads knowledge about dangerous humans among American crows. Proceedings of the Royal Society B 279:499-508.

Curry, R. L., A. T. Peterson, and T. A. Langen. 2002. Western scrub jay (*Aphelocoma californica*). Account 712 in The Birds of North America Online (A. Poole, Editor). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/712.

De Rosario-Martinez, H. 2015. Phia: post-hoc interaction analysis. R package version 0.2-0. http://CRAN.R-project.org/package=phia.

DeWitt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology and Evolution 13:77-81.

Dittmar, E. M., D. A. Cimprich, J. H. Sperry, and P. J. Weatherhead. 2014. Habitat selection by juvenile black-capped vireos following independence from parental care. Journal of Wildlife Management 78:1005-1011.

Donovan, T. M., F. R. Thompson, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380-1395.

Dwernychuk, L. W., and D. A. Boag. 1972. Ducks nesting in association with gulls: an ecological trap? Canadian Journal of Zoology 50:559-563.

Eggers, S., M. Griesser, and J. Ekman. 2005. Predator-induced plasticity in nest visitation rates in the Siberian jay (*Perisoreus infaustus*). Behavioral Ecology 16:309-315.

Fagan, W. E., R. S. Cantrell, and C. Cosner. 1999. How habitat edged change species interactions. American Naturalist 153:165-182.

Fay, R., H. Weimerskirch, K. Delord, and C. Barbraud. 2015. Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. Journal of Animal Ecology 84:1423-1433.

Fiorini, V. D., D. T. Tuero, and J. C. Reboreda. 2012. Dense canopy cover over house wren (*Troglodytes aedon*) nests increases latency of brood parasitism by shiny cowbirds (*Molothrus bonariensis*). Emu 112:55-59.

Foppen, R. P. B., J. P. Chardon, and W. Liefveld. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. Conservation Biology 14:1881-1892.

Forsman, J. T., and T. E. Martin. 2009. Habitat selection for parasite-free space by hosts of parasitic cowbirds. Oikos 118:464-470.

Friedmann, H. F. 1929. The cowbirds: a study in the biology of social parasitism. Charles C. Thomas, Springfield, Illinois.

Friedrich, M. J., K. L. Hunt, D. H. Catlin, and J. D. Fraser. 2015. The importance of site to mate choice: mate and site fidelity in piping plovers. Auk 132:265-276.

Fuller, R. A, P. H. Warren, and K. J. Gaston. 2007. Daytime noise predicts nocturnal singing in urban robins. Biology Letters 3:368-370.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology, Evolution, and Systematics 19:207-234.

Gaona, P., P. Perreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). Ecological Monographs 68:349-370.

Gardali, T., and G. Ballard. 2000. Warbling vireo (*Vireo gilvus*). Account 551 in The Birds of North America Online (A. Poole, Editor). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/551.

Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behavior 60:263-267.

Graber, J. W. 1961. Habitat requirements and life history of the black-capped vireo (*Vireo atricapilla*). Ecological Monographs 31:313-336.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28:1140-1162.

Grzybowski, J. A. 1995. Black-capped vireo (*Vireo atricapilla*). Account 181 in The Birds of North America Online (A. Poole, Editor). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/181.

Grzybowski, J. A. 2005. An estimate of juvenile survival in black-capped vireos and its implications to source-sink analyses of songbirds. USDA Forest Service General Technical Report PSW-GTR-191.

Grzybowski, J. A., D. J. Tazik, and G. D. Schnell. 1994. Regional-analysis of black-capped vireo breeding habitats. Condor 96:512–544.

Haff, T. M., and R. D. Magrath. 2011. Call at a cost: elevated nestling calling attracts predators to active nests. Biology Letters 7:493-495.

Handcock, M. S. 2004. Ruf: an R package for the estimation of the resource utilization function. http://csde.washington.edu/~handcock/ruf.

Hann, H. W. 1941. The cowbird at the nest. Wilson Bulletin 53:211-221.

Hannon, S. J. 1984. Factors limiting polygyny in the willow ptarmigan. Animal Behavior 32:153–161.

Hauber, M. E., and S. A. Russo. 2000. Perch proximity correlates with high cowbird parasitism of ground nesting song sparrows. Wilson Bulletin 112:150-153.

Heinrichs, J. A., D. J. Bender, D. L. Gummer, and N. H. Schumaker. 2015. Effects of landscape and patch-level attributes on regional population persistence. Journal for Nature Conservation 26:56-64.

Heithaus, M. R., and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480-491.

Heithaus, M. R., and L. M. Dill. 2006. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? Oikos 114:257-264.

Heppel, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 2:367-375.

Homer, C.G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345-354.

Howe, R. W., G. J. Davis, and G. J. Mosca. 1991. The demographic significance of sink populations. Biological Conservation 57:239-255.

Jenkins, S. R., M. G. Betts, M. M. Huso, and J. C. Hagar. 2013. Habitat selection by juvenile Swainson's thrushes (*Catharus ustulatus*) in headwater riparian areas, Northwestern Oregon, USA. Forest Ecology and Management 305:88-95.

Jewell, K. J., and P. Arcese. 2008. Consequences of parasite invasion and land use on the spatial dynamics of host populations. Journal of Applied Ecology 45:1180-1188.

Johnston, A. N. 2013. Eastern gray squirrel ecology and interactions with western gray squirrel. Dissertation, University of Washington, Seattle, Washington.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457-481.

Kempenaers, B. 1994. Polygyny in the blue tit: intra- and inter-sexual conflicts. Animal Behavior 49:1047–1064.

Kershner, E. L., J. W. Walk, R. E. Warner, and D. A. Haukos. 2004. Postfledging movements and survival of juvenile eastern meadowlarks (*Sturnella magna*) in Illinois. Auk 121:1146-1154.

Kertson, B. N., and J. M. Marzluff. 2011. Improving studies of resource selection by understanding resource use. Environmental Conservation 38:18-27.

King, D. I., R. M. Degraaf, M. L. Smith, and J. P. Buonaccorsi. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). Journal of Zoology 269:414-421.

Kostecke, R. M., and D. A. Cimprich. 2008. Adult and juvenile survival of black-capped vireos within a large breeding population in Texas. Condor 110:251-259.

Kostecke, R. M., S. G. Summers, G. H. Eckrich, and D. A. Cimprich. 2005. Effects of brown-headed cowbird (*Molothrus ater*) removal on black-capped vireo (*Vireo atricapilla*) nest success and population growth at Fort Hood, Texas. Ornithological Monographs 57:28-37.

Kotler, B. P., J. S. Brown, and O. Hasson. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249-2260.

Kroodsma, D. E., and B. E. Byers. 1991. The function(s) of bird song. American Zoologist 31:318-328.

Kus, B. E., and M. J. Whitfield. 2005. Parasitism, productivity, and population growth: response of least Bell’s vireos (*Vireo bellii pusillus*) and southwestern willow flycatchers (*Empidonax traillii extimus*) to cowbird (*Molothrus* spp.) control. Ornithological Monographs 57:16-27.

Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with Mark. AFSC Processed Rep 2013-01. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

Laake, J., D. Borchers, L. Thomas, D. Miller, and J. Bishop. 2014. Mrds: mark-recapture distance sampling (mrds). R package version 2.1.10. http://CRAN.R-project.org/package=mrds.

Lenormand, T. 2002. Gene flow and the limits to natural selection. Trends in Ecology and Evolution 17:183-189.

Leonard, M. L. 1990. Polygyny in marsh wrens: asynchronous settlement as an alternative to the polygyny-threshold model. American Naturalist 136:446–458.

Liker, A., R. P. Freckleton, and T. Szekely. 2014. Divorce and infidelity are associated with skewed adult sex ratios in birds. Current Biology 24:880-884.

Lima, S. L., T. J. Valone, and T. Caraco. 1985. Foraging-efficiency-predation-risk trade-off in the grey squirrel. Animal Behaviour 33:155-165.

Llambias, P.E. 2012. How do southern house wrens *Troglodytes aedon musculus* achieve polygyny? An experimental approach. Journal of Ornithology 153:571–578.

Lowther, P. E. 1993. Brown-headed cowbird (*Molothrus* ater), Account 47 in The Birds of North America Online (A. Poole, Editor). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/047.

Luginbuhl, J. M., J. M. Marzluff, J. E. Bradley, M. G. Raphael, and D. E. Varland. 2001. Corvid techniques and the relationship between corvid relative abundance and nest predation. Journal of Field Ornithology 72:556-572.

Marshall, M. R., D. R. Diefenbach, L. A. Wood, and R. J. Cooper. 2004. Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: study designs that may help. Animal Biodiversity and Conservation 27:59-72.

Marzluff, J. M., and R. P. Balda. 1992. The pinyon jay, behavioural ecology of a colonial and cooperative corvid. T & AD Poyser Ltd, London, England.

Marzluff, J. M., J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Resource utilization by an avian nest predator: relating resources to a probabilistic measure of animal space use. Ecology 85:1411-1427.

Maxted, A. M. 2001. Post-fledging survival, dispersal, and habitat use in two migratory shrubland bird species. Thesis, Purdue University, West Lafayette, Indiana.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

Mazerolle, M. J. 2015. AICcmodavg: model selection and multimodel inference based on (Q)AIC©. R package version 2.0-3. http://CRAN.R-project.org/package=AICcmodavg.

McDonald, P. G., D. R. Wilson, and C. S. Evans. 2009. Nestling begging increases predation risk, regardless of spectral characteristics or avian mobbing. Behavioral Ecology 20:821-829.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html

McLean, I. G., J. N. M. Smith, and K. G. Stewart. 1986. Mobbing behaviour, nest exposure, and breeding success in the American robin. Behaviour 96:171-185.

Menu, S., G. Gauthier, and A. Reed. 2005. Survival of young greater snow geese (*Chen caerulescens atlantica*) during fall migration. Auk 122:479-496.

Miles, R. K., and D. A. Buehler. 2000. An evaluation of point counts and playbacks as techniques for censusing brown-headed cowbirds. In: Smith, J. N. M., T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin, Texas. pp. 63-68.

Miller, D. L. 2014. Distance: a simple way to fit detection functions to distance sampling data and calculate abundance/density for biological populations. R package version 0.9.2. http://CRAN.R-project.org/package=Distance.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13:815-829.

Mountjoy, D. J. 1997. A probable case of polyterritorial polygyny in the red-eyed vireo, *Vireo olivaceus*. Canadian Field-Naturalist 1114: 628-630.

Murphy, M. T. 2001. Source-sink dynamics of a declining eastern kingbird population and the value of sink habitats. Conservation Biology 15:737-748.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1435-1441.

Neatherlin, E. A., and J. M. Marzluff. 2004. Responses of American crow populations to campgrounds in remote native forest landscapes. Journal of Wildlife Management 68:708-718.

Neudorf, D. L., and S. G. Sealy. 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96:162-169.

Nicolaus, M., S. P. M. Michler, K. M. Jalvingh, R. Ubels, M. van der Velde, J. Komdeur, C. Both, and J. M. Tinbergen. 2012. Social environment affects juvenile dispersal in great tits (*Parus major*). Journal of Animal Ecology 81:827-837.

Noa, L. A., D. H. Hirth, T. M. Donovan, and D. Cimprich. 2007. Demographic differences of black-capped vireos in two habitat types in central Texas. Journal of Wildlife Management 71:1042-1049.

Noon, B. R., and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. In: McCullough, D. R., and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science, New York. pp. 441-464.

Nowicki, S., and W. A. Searcy. 2005. Song and mate choice in birds: how the development of behavior helps us understand function. Auk 122:1-14.

O’Donnell, C. F. J. 2000. Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). New Zealand Journal of Zoology 27:207-221.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist 103:589-603.

Owen, M., and J. M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology 58:603-617.

Pampus, M., K. H. Schmidt, and W. Wiltschko. 2005. Pair bond and breeding success in blue tits *Parus caeruleus* and great tits *Parus major*. Ibis 147:92-108.

Part, T., and B. Doligez. 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. Proceedings of the Royal Society B 270:1809-1813.

Paton, P. W. C. 1994. The effect of edge on avian nest success – how strong is the evidence. Conservation Biology 8:17-26.

Patricelli, G. L., and J. L. Blickley. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. Auk 123:639-649.

Payne, R. B. 1977. The ecology of brood parasitism in birds. Annual Review of Ecology, Evolution, and Systematics 8:1-28.

Peak, R. G., D. J. Lusk, and J. D. Peppers. 2010. Polygyny in the golden-cheeked warbler. Bulletin of the Texas Ornithological Society 43:44–47.

Petrinovich, L., and T. L. Patterson. 1978. Polygyny in the white-crowned sparrow (*Zonotrichia leucophrys*). Condor 80:99-100.

Pianka, E. R. 1976. Natural selection of optimal reproductive tactics. American Zoologist 16:775-784.

Pilastro, A., L. Biddau, G. Marin, and T. Mingozzi. 2001. Female brood desertion increases with number of available mates in the rock sparrow. Journal of Avian Biology 32:68–72.

Piper, S. D., and C. P. Caterall. 2003. A particular case and a general pattern: hyperaggressive behavior by one species may mediate avifaunal decreases in fragmented Australian forests. Oikos 101:602-614.

Pulliam, H. P. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-661.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/.

Ratzlaff, A. 1987. Endangered and threatened wildlife and plants: determination of the black-capped vireo to be an endangered species. Federal Register 52:37420-37423.

Reemts, C. M., and D. A. Cimprich. 2014. Restoring early-successional shrubland habitat for black-capped vireos using mechanical mastication. Natural Areas Journal 34:400-407.

Riotte-Lambert, L., and H. Weimerskirch. 2013. Do naïve juvenile seabirds forage differently from adults? Proceedings of the Royal Society B 280: 20131434.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.

Rohner, C., and D. B. Hunter. 1996. First-year survival of great horned owls during a peak and decline of the snowshoe hare cycle. Canadian Journal of Zoology 74:1092-1097.

Rothstein, S. I. 1975. Evolutionary rates and host defenses against avian brood parasitism. American Naturalist 109:161-176.

Rush, S. A., and B. J. M. Stutchbury. 2008. Survival of fledgling hooded warblers (*Wilsonia citrina*) in small and large forest fragments. Auk 125:183-191.

Schamber, J. L., D. Esler, and P. L. Flint. 2008. Evaluating the validity of using unverified indices of body condition. Journal of Avian Biology 40:49-56.

Schjorring, S., G. Gregersen, and T. Bregnballe. 1999. Prospecting enhances breeding success of first time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. Animal Behavior 57:647-654.

Searcy, W. A., and K. Yasukawa. 1995. Polygyny and sexual selection in red-winged blackbirds. Princeton University Press. Princeton, New Jersey.

Sharp, B. L., and B. E. Kus. 2006. Factors influencing the incidence of parasitism of least Bell's vireos. Journal of Wildlife Management 70:682-690.

Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence? In: Martin, T. E., and D. M. Finch, editors. Ecology and management of neotropical migratory birds. Oxford University Press, New York, New York. pp. 85-120.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296-308.

Skutch, A. F. 1976. Parent birds and their young. University of Texas Press, Austin, Texas.

Small, D.M., P. J. Blank, and B. Lohr. 2015. Habitat use and movement patterns by dependent and independent juvenile grasshopper sparrows during the post-fledging period. Journal of Field Ornithology 86:17-26.

Smith, J. N. M., Y. Yom-Tov, and R. Moses. 1982. Polygyny, male parental care, and sex ratio in song sparrows: an experimental study. Auk 99:555-564.

Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations. Ecological Applications 2:18-29.

Stake, M. M., and P. M. Cavanagh. 2001. Removal of host nestlings and fecal sacs by brown-headed cowbirds. Wilson Bulletin 113:456-459.

Stake, M. M., and D. A. Cimprich. 2003. Using video to monitor predation at black-capped vireo nests. Condor 105:348-357.

Steckler, S. E., and C. J. Conway. 2012. Frequent vocalizing is negatively associated with brood parasitism in a host of the brown-headed cowbird. Condor 114:219-226.

Stoychev, S., D. Demerdzhiev, S. Spasov, B-U Meyburg, and D. Dobrev. 2014. Survival rate and mortality of juvenile and immature eastern imperial eagles (*Aquila heliaca*) from Bulgaria studied by satellite telemetry. Slovak Raptor Journal 8:53-60.

Streby, H. M., and D. E. Andersen. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. Ecosphere 2(78):1-15.

Streby, H. M., and D. E. Andersen. 2013. Movements, cover-type selection, and survival of fledgling ovenbirds in managed deciduous and mixed coniferous-deciduous forests. Forest Ecology and Management 287:9-16.

Streby, H. M., S. M. Peterson, and D. E. Andersen. 2011. Invertebrate availability and vegetation characteristics explain use of non-nesting cover types by mature-forest songbirds during the postfledging period. Journal of Field Ornithology 82:406-414.

Streby, H. M., S. M. Peterson, G. R. Kramer, and D. E. Andersen. 2015. Post-independence fledging ecology in a migratory songbird: implications for breeding-grounds conservation. Animal Conservation 18:228-235.

Streby, H. M., J. M. Refsnider, and D. E. Andersen. 2014a. Redefining reproductive success in songbirds: moving beyond the nest success paradigm. Auk 131:718-726.

Streby, H. M., J. M. Refsnider, S. M. Peterson, and D. E. Andersen. 2014b. Retirement investment theory explains patterns in songbird nest-site selection. Proceedings of the Royal Society B 281: 20131834.

Stubben, C. J., and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:11.

Sullivan, K. 1989. Predation and starvation: age-specific mortality in juvenile juncos *Junco phaenotus*. Journal of Animal Ecology 58:275-286.

Tazik, D. J., J. D. Cornelius, and C. Abrhamson. 1993. The black-capped vireo on the lands of Fort Hood, Texas, Volume 1: distribution and abundance. Technical Report EN-94/01, US Army Corps of Engineers, CERL, Champaign, Illinois.

Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2:340-347.

Terraube, J., V. Vasko, and E. Korpimaki. 2015. Mechanisms and reproductive consequences of breeding dispersal in a specialist predator under temporally varying food conditions. Oikos 124:762-771.

Tittler, R., L. Fahrig, and M. A. Villard. 2006. Evidence of large-scale source-sink dynamics and long-distance dispersal among wood thrush populations. Ecology 87:3029-3026.

U.S. Fish and Wildlife Service. 1991. Black-capped vireo (*Vireo atricapillus*) recovery plan. Austin, TX.

U.S. Fish and Wildlife Service. 1996. Black-capped vireo population and habitat viability assessment report. Compiled and edited by C. Beardsmore, J. Hatfield, and J. Lewis in conjunction with workshop participants. Report of a September 18-21, 1995 workshop arranged by the U.S. Fish and Wildlife Service in partial fulfillment of U.S. National Biological Service Grant No. 80333-1423. Austin, Texas. 57 pp.

U.S. Fish and Wildlife Service. 2007. Black-capped vireo (*Vireo atricapilla*) 5-year review: summary and evaluation. Arlington, Texas.

Uyehara, J. C., and P. M. Narins. 1995. Nest defense by willow flycatchers to brood-parasitic intruders. Condor 97:361-368.

Vasseur, P. L., and P. L. LeBerg. 2015. Effects of habitat edges and nest-site characteristics on painted bunting nest success. Journal of Field Ornithology 86:27-40.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood thrush postfledging movements and habitat use in northern Virginia. Condor 100:69-78.

Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evolution 18:252-261.

Verner, J., and M. F. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47:143-147.

Vitz, A. C. 2008. Survivorship, habitat use, and movements for two species of mature forest birds. Dissertation, The Ohio State University, Columbus, Ohio.

Vitz, A. C., and A. D. Rodewald. 2007. Vegetative and fruit resources as determinants of habitat use by mature-forest birds during the postbreeding period. Auk 124:494-507.

Votier, S. C., T. R. Birkhead, D. Oro, M. Trinder, M. J. Grantham, J. A. Clark, R. H. McCleery, and B. J. Hatchwell. 2008. Recruitment and survival of immature seabirds in relation to oil spills and climate variability. Journal of Animal Ecology 77:974-983.

Ward, M. P., and S. Schlossberg. 2004. Conspecific attraction and the conservation of territorial songbirds. Conservation Biology 18:519-525.

Warren, P. S., M. Katti, M. Ermann, and A. Brazel. 2006. Urban bioacoustics: it's not just noise. Animal Behaviour 71:491-502.

Weatherhead, P. J., and R. J. Robertson. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis". American Naturalist 113:201-208.

Weinberg, H. J., T. J. Hayden, and J. D. Cornelius. 1998. Local and installation-wide black-capped vireo dynamics on the Fort Hood, Texas Military Reservation. U.S. Army Construction Engineering Research Laboratories Technical Report 98/54, Champaign, IL.

Wheelwright, N. T., C. B. Schultz, and P. J. Hodum. 1992. Polygyny and male parental care in savannah sparrows: effects on female fitness. Behavioral Ecology and Sociobiology 31:279-289.

Whelan, C. L., and J. Wyneken. 2007. Estimating predation levels and site-specific survival of hatchling loggerhead sea turtles (*Caretta caretta*) from south Florida beaches. Copeia 2007:745-754.

White, J. D., T. Gardali, F. R. Thompson, and J. Faaborg. 2005. Resource selection by juvenile Swainson's thrushes during the postfledging period. Condor 107:388-401.

Whittaker, K. A., and J. M. Marzluff. 2009. Species-specific survival and relative habitat use in an urban landscape during the postfledging period. Auk 126:288-299.

Wiens, J. D., B. R. Noon, and R. T. Reynolds. 2006.. Post-fledging survival of northern goshawks: the importance of prey abundance, weather, and dispersal. Ecological Applications 16:406-418.

Yackel Adams, A. A., S. K. Skagen, and R. D. Adams. 2001. Movements and survival of lark bunting fledglings. Condor 103:643-647.

Zink, R. M., A. W. Jones, C. C. Farquhar, M. C. Westberg, and J. I. Gonzales Rojas. 2010. Comparison of molecular markers in the endangered black-capped vireo (*Vireo atricapilla*) and their interaction in conservation. Auk 127:797-806.