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HABITAT SELECTION AND SURVIVAL OF JUVENILE BLACK-CAPPED VIREOS
DURING THE POST-FLEDGING PERIOD

BY

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THESIS

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ABSTRACT

Population declines of many species of songbirds have stimulated much research on breeding, migration, and wintering ecology. Until recently, the post-breeding season, the period from the completion of breeding and the onset of migration, has been overlooked. During this period, juvenile birds independent of parental care must find food to build up fat reserves for migration and simultaneously avoid predators. Many studies have reported low survival rates for juveniles as well as a shift in habitat selection during this time. If differences in ecological requirements result in juvenile birds using different habitats from breeding birds, then both breeding and post-breeding habitats need to be considered when managing species. Additionally, knowing how juvenile survival varies by age and sex is central to understanding population dynamics. My thesis examines habitat selection and survival of juvenile black-capped vireos (*Vireo atricapilla*) following their independence from parental care, from 2010-2013 in central Texas.

The black-capped vireo is a federally endangered migratory songbird that nests almost exclusively in shrub vegetation, but previous anecdotal observations suggest that juvenile vireos may move to riparian areas once reaching independence from parental care. In chapter 1, I used mist-net capture rates and radio-telemetry to determine the relative abundance of juvenile vireos across habitats and to quantify habitat selection. Further, I investigated how vegetation density and arthropod abundance influenced habitat selection by juvenile vireos. I captured juveniles at similar rates in shrub and riparian vegetation; however, radio telemetry data indicated that juveniles selected riparian vegetation over most other available vegetation types. Juveniles chose areas characterized by more canopy cover, denser foliage, and more arthropods than at random.

Riparian vegetation provides this combination of features more than other vegetation types, suggesting that cover and food are the basis for habitat selection by juveniles. My results suggest that habitat conservation strategies for black-capped vireos should include protection of riparian vegetation near breeding areas, and more generally, avian conservation strategies that focus only on breeding areas may potentially overlook other key habitats used by juveniles.

Knowing how survival varies by age is central to understanding population dynamics. Nearly all of the studies to date concerning juvenile bird survival have focused on the dependent period, between when juveniles leave the nest and the termination of parental care. Still relatively unstudied is survival during the period when juveniles are independent of parental care. In chapter 2, I used radio telemetry data to estimate survival rates of juvenile male and female black-capped vireos during the period following parental care. Additionally, I used behavioral observations to investigate how movement patterns, vocalizations, and associations varied by sex. I followed the fates of 71 juveniles and, using known-fate models in Program MARK, estimated overall post-fledging survival to be 55% (86% for females and 40% for males). Movement patterns varied among individuals and males tended to make more foray movements than females. Both sexes were frequently seen in association with conspecifics and heterospecifics. Half of the males we tracked were observed singing, both sexes were observed making many types of vocalizations, and frequency of vocalizations did not vary between sexes. My findings highlight the importance of age and sex-biased survival rates for population dynamics. Having accurate estimates of juvenile survival may assist biologists in predicting population estimates and help determine future management plans.

Dedicated to Peter Halash

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CHAPTER 1

HABITAT SELECTION BY JUVENILE BLACK-CAPPED VIREOS FOLLOWING INDEPENDENCE FROM PARENTAL CARE¹

ABSTRACT

If differences in ecological requirements result in juvenile birds using different habitats from breeding birds, then habitat management to protect those birds must protect both breeding and post-breeding habitats. Here we examined habitat selection by juvenile black-capped vireos (*Vireo atricapilla*) following their independence from parental care, in 2010-2013 on Fort Hood Military Reservation in central Texas, USA. The black-capped vireo is a federally endangered species that nests almost exclusively in shrub vegetation, but previous anecdotal observations indicate that juveniles may prefer riparian vegetation. We used mist-net capture rates and radio-telemetry to determine relative abundance of juvenile vireos across habitats, to quantify movement patterns and habitat selection, and to investigate how vegetation density and arthropod abundance influenced habitat selection. We captured juveniles at similar rates in shrub and riparian vegetation. Radio telemetry data indicated that juveniles selected riparian vegetation over most other available vegetation types, and tended to stay in riparian vegetation upon arrival. Juveniles selected areas characterized by more canopy cover, denser foliage, and more arthropods. Riparian vegetation provides this combination of features more than other vegetation types, indicating that cover and food are the basis for habitat selection by juveniles. Our results indicate that habitat conservation strategies for black-capped vireos should include protection of

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riparian vegetation near breeding areas, and more generally, that avian conservation strategies that focus only on breeding areas may potentially overlook other key habitats.

INTRODUCTION

The time from when a bird leaves the nest until it migrates is a potentially critical yet relatively understudied stage of a migratory bird's life. Most research conducted during the post-breeding period has focused on the time that fledglings are still dependent on parental care (e.g., Weatherhead and McRae 1990, Anders et al. 1997, Cohen and Lindell 2004, Rush and Stutchbury 2008), with little research during the time that juveniles have become independent. This independent period, prior to migration, can last up to 3 months and holds many challenges for juvenile birds. They must prepare for migration by building up fat reserves as well as satisfy the elevated energetic demands associated with preformative molt (Hall 1996). To exacerbate these challenges, young birds may be hindered by a lack of experience in foraging, navigating, and avoiding predators (Anders et al. 1997).

Differences in ecological requirements may result in juvenile birds using habitats differently from breeding birds. Habitat selection during the nesting season may differ from habitat selection during the post-fledging period (King et al. 2006). Indeed recent studies have demonstrated such differences for several migratory songbirds (King et al. 2006, Vitz and Rodewald 2010, Streby et al. 2011, Jenkins et al. 2013). Thus, the available evidence suggests that habitat shifts by juvenile birds following the termination of parental dependence may be common. Habitat conservation strategies generally focus on breeding areas and thus potentially overlook other habitats that could be important for juvenile birds (Faaborg et al. 1996, Cox et al. 2014).

In this study, we examine habitat selection by juvenile black-capped vireos (*Vireo atricapilla*; hereafter “vireo”) following their independence from parental care (35 to 45 days after fledging the nest; Grzybowski 1995). Previous work indicates that juvenile vireos may use different habitat than breeding adults. Grzybowski (1995) suggested that at Fort Hood, Texas there may be some movement by juvenile vireos into taller and more mesic woodlands, and mist-netting after the breeding season found that independent juvenile vireos were frequently found associated with riparian vegetation (D. A. Cimprich, Fort Hood Environmental Division, unpublished data). This evidence suggests that systematic investigation of habitat use by juvenile black-capped vireos was warranted, particularly given that gathering data on the habitat needs of this endangered species is a priority in its recovery plan (USFWS 1991). Effective population management requires knowing a species’ habitat needs. If newly independent vireos require habitat different from that used by breeding birds, it may be important to protect those habitats. Current habitat management efforts for this species focus almost exclusively on protecting early successional shrub vegetation where adults breed (Cornelius et al. 2007).

Our primary objective was to test the hypothesis that, following independence from their parents, juvenile vireos select areas with riparian vegetation. First, we used mist-netting to determine the relative abundance of independent juvenile vireos in riparian and shrub vegetation. We predicted that juveniles would be captured at greater rates in riparian than shrub vegetation. Second, we used radio telemetry to examine vegetation types used by individual juveniles. We predicted that juveniles captured in shrub vegetation would move to and remain in riparian vegetation and that juveniles captured in riparian vegetation would remain in that vegetation. Finally, we investigated how vegetation characteristics and food availability influenced habitat selection. When juvenile birds move out of breeding habitat, the switch may be a response to

vegetation characteristics and food availability, because juveniles of some species choose habitats with dense vegetation and high arthropod availability (McDermott and Wood 2010, Streby et al. 2011). We tested this hypothesis by comparing foliage density, canopy cover, and arthropod abundance in vegetation types used by juvenile vireos with randomly selected locations.

STUDY SITES

We conducted the study during the post-breeding season (mid-June to August) of the black-capped vireo from 2010-2013 on the Fort Hood Military Reservation in central Texas, USA. Military training is the primary land use on Fort Hood. Other uses include cattle grazing and maintenance of fish and wildlife habitat for conservation and recreation (Kostecke et al. 2005). Fort Hood has allowed landowners to graze cattle since 1942 (Fort Hood 2012), but recent assessments suggest that the combined effects of military training and continuous grazing have adversely impacted the condition and sustainability of the habitat (Fort Hood 2012). Impacts of cattle grazing include a reduction of vegetative communities to primarily shallow-rooted species, causing extensive soil erosion (Fort Hood 2012). Fort Hood has rigorous endangered species management practices, including habitat restoration, controlled burns, and cowbird trapping (Cornelius et al. 2007). Major vegetation cover types at Fort Hood are perennial grasslands (35%) and woodlands (49%) dominated by oak and juniper, whereas riparian vegetation is relatively rare (4%; Reemts and Teague 2007). We ignored the remaining 12% of cover types (water, bare ground, developed) because these areas are never used by vireos. For this study we categorized broad vegetation types in the study sites by their associated vegetation: grasslands, riparian areas, shrublands, and non-riparian forests. Hereafter we refer to

these general vegetation types as grass, riparian, shrub, and forest. Black-capped vireos nested in shrub vegetation types, which consisted primarily of shin oak (*Quercus sinuata*), plateau live oak (*Quercus fusiformis*), Texas ash (*Fraxinus texensis*), and Ashe juniper (*Juniperus ashei*; Cimprich and KostECKE 2006). This vegetation formed a matrix of dense shrubs with interspersed open areas of bare rock or ground, primarily on mesa tops and slopes. Riparian vegetation type was classified by association with rivers and streams, many of which were dry during the study due to drought conditions. Riparian vegetation was primarily giant ragweed (*Ambrosia trifida*), Roosevelt-weed (*Baccharis neglecta*), pecan (*Carya illinoensis*), honey-balls (*Cephalanthus occidentalis*), black willow (*Salix nigra*), and elm (*Ulmus* sp.). This vegetation formed both a dense understory and canopy adjacent to rivers, streams, and lakes. Dominant trees found in forests were Ashe juniper, plateau live oak, and Texas red oak (*Quercus buckleyi*). Grass vegetation types were comprised of little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum* sp.), sideoats grama (*Bouteloua curtipendula*), honey mesquite (*Prosopis glandulosa*), and tall dropseed (*Sporobolus compositus*). For more detailed descriptions of Fort Hood land uses and vegetation associations see Cornelius et al. (2007).

We chose 2 study sites with both riparian and shrub vegetation. Sites had similar grazing pressure (320 and 354 animal units; Fort Hood 2012). Because of the difficulty catching independent juvenile vireos, we chose large study sites (5,496 ha and 6,534 ha) with enough places to net birds. We chose sites in close proximity to long-term intensive study sites to increase our chances of capturing birds of known age (i.e., banded nestlings). Both sites had similar patch sizes and vegetation associations and were located on opposite sides of the military base, 18 km apart. Shrub vegetation was not adjacent to riparian vegetation in these areas, but separated by patches of grass and/or forest (4-123 ha patches).

METHODS

Juvenile Abundance in Riparian and Shrub Vegetation

To determine the relative abundance of independent juvenile vireos in each vegetation type, we conducted mist-netting 2-7 days a week from sunrise until about 10 am in shrub and riparian vegetation (2012-2013 only). The dense understory in both vegetation types concealed nets similarly (see results below) and thus, birds should have been equally vulnerable to capture in both. We chose netting sites so that all substantial patches of shrub and riparian vegetation in the study sites were sampled at least once before patches were re-sampled. We attempted to keep mist-net hours (one mist-net hour equals one 12-m net open for one hour) equal between riparian and shrub vegetation by alternating vegetation type each netting day. We used 6- and 12-m mist-nets with recordings of either black-capped vireos or eastern-screech owls (*Megascops asio*) broadcast near each net to increase capture rates. We determined the age, sex, and dependency status of each captured bird. Juveniles with greater coverts that are in heavy molt may still be dependent upon parental care (personal observation) so we considered juveniles independent only if their greater covert molt was complete or near completion. We did not observe any of the birds that we radio tracked being provisioned by adults (see results below), indicating that molt status provides a reasonably accurate measure of independence. We excluded juveniles whose dependency status was uncertain from analyses.

Individual Habitat Selection

To examine habitats used by individuals, we fitted independent juvenile vireos with 0.27-g radio transmitters (Model LB-2X, Holohil Systems Ltd, Ontario, Canada) using the backpack method (Hallworth et al. 2009). Backpacks weighed <4% of each bird's body mass. Radio

transmitters had a range of approximately 800 m. We attached transmitters to birds captured in riparian (29 birds) and shrub (42 birds) vegetation. Due to the limited battery life of transmitters (14 days on average), we could not track individual birds through their entire post-fledging period. Given the likelihood that the age of birds tracked varied, collectively the tracking data should cover most of the post-fledging, independent period. This assumption is supported by the fact that we recaptured and radio-tracked 9 individuals that were banded as nestlings in intensive study sites and these individuals ranged from 51 - 83 days old (65.7 ± 3.6) on their initial tracking day. We located radio-tagged birds twice a day, with at least 2 h between observations. We considered consecutive locations for an individual to be independent because the time between observations allowed sufficient opportunity for the birds to change vegetation type and because we witnessed juveniles traveling substantial distances during short durations (11 individuals moved at rates $>1,000$ m/h).

For most individuals (82%) we were able to obtain data on the proportion of time spent in each vegetation type and movement patterns within each type of vegetation. When tracking birds, we approached them on foot as discreetly as possible to avoid influencing natural movements. When a bird was first encountered, we recorded the GPS coordinates of each location. When an individual could not be re-sighted, usually because it was concealed by dense vegetation, we walked in a circle around the area with a strong radio signal in order to estimate the bird's location to ≤ 30 m. When juveniles were re-sighted, we observed them for at least 5 min and classified the dominant behavior as "foraging" if birds were seen making any gleaning maneuvers, "perching" if birds remained perched while under observation or "moving" if it flew from perch to perch without any gleaning. It is possible that juveniles may be excluded from shrub vegetation by territorial adult birds. To investigate if adult vireos were excluding juveniles

from shrub vegetation, when birds were re-sighted we noted if they were 1) in close association (≤ 30 m) with conspecific adults or 2) not in close association with adults (no adult detected or adult detected > 30 m from juvenile; 2012-2013 only).

Vegetation Characteristics and Arthropod Abundance

We conducted vegetation surveys at every other bird location (alternating between morning and afternoon locations, 2011-2013), as well as at random locations (2012-2013 only). Random points were generated in ArcGIS 10.1 (Esri, Redlands, California) from a 300-m grid of locations covering the study sites, based on the average distance birds moved between subsequent relocations. This allowed fine-scale surveys to be conducted in all habitats available to birds. We assessed vegetation characteristics at both the macro and microhabitat spatial scales. Vegetation was examined on a macro scale by determining the general habitat category (as described above) for each bird and random location. To quantify microhabitat, we sampled vegetation in 10-m-radius circles centered on bird and random locations. We measured percent canopy cover at 20 points - five along 10 m transects in each cardinal direction. We considered canopy to be any vegetation > 3 m above the ground and determined its occurrence using an ocular tube (James and Shugart 1970). To estimate understory foliage density, we collected data at three points, one in the center of the plot and two in random opposite cardinal directions, 10-m from the location center. Using a Robel pole, we gave foliage density scores ranging from 0 to 10; with 0 indicating no foliage and 10 indicating 100% foliage (see Robel et al. 1970 for details). We did this at two height intervals, 0-1 m and 1-2 m above the ground, which we then averaged to represent the foliage layer.

To measure food abundance we sampled arthropods at every other bird location and at most random locations in 2012-2013 using a hybrid version of the shake-cloth and branch-clipping method (Cooper and Whitmore 1990). We sampled two branches at each location; measured abundance by counting the number of arthropods collected in each sample, and averaged these numbers to get one estimate per location. We sampled branches between 0.5 and 2.0-m above ground. For each sample, we chose branches from either a locally dominant species or one on which we re-sighted the focal bird. This method captures prey that gleaning birds, foraging at shrub-height, may target, but is not suitable for collecting highly mobile arthropods or surveying inaccessible vegetation (e.g., high canopy). These samples do not necessarily represent the prey available to or eaten by vireos, but do provide a coarse estimate of arthropod abundance in the habitats in which the birds foraged. While banding, we collected fecal samples opportunistically to gather additional diet information. These we examined with a dissecting microscope and categorized the contents as fruit or arthropods.

Statistical Analysis

We conducted all analyses using Program SAS (SAS Enterprise Guide ver. 6.1, SAS Institute, Inc., Cary, NC) unless otherwise noted. To compare means, we used the Tukey-Kramer method and reported means \pm 1 SE, unless otherwise noted. To validate model assumptions, we examined residual and fit statistics. For the interpretation of estimates, we back-transformed variables that had been transformed. All factors were considered statistically significant at $P \leq 0.05$.

To determine if there was a difference between vireo captures in riparian and shrub habitats, we standardized captures for independent juvenile vireos by dividing the number of

individuals captured by the number of mist-net hours (referred to as birds/net hour). Separate analyses were conducted by year to estimate mean rates per year (PROC GLM). We then combined years and modeled birds/net hour by habitat type using a mixed linear model and accounting for year as a random effect (PROC MIXED).

To analyze habitat selection, we calculated the percent available and percent use of each habitat type for each individual juvenile vireo radio-tracked. Many studies use home range size to determine habitat selection. Due to the small number of locations obtained for each individual, and because birds were sometimes highly mobile, calculating habitat use at the home range scale was not appropriate. For each juvenile, we estimated the percent availability of each habitat by creating a 300-m buffer around each bird location and calculating the proportion of each habitat within the buffer (Geospatial Modeling Environment, Beyer 2012). We classified habitats based on ArcGIS vegetation polygon layers for Fort Hood (Reemts and Teague 2007). We used a 300-m buffer because it was the mean distance birds moved between consecutive locations. To compare proportions of habitats used with those available we used compositional analysis (program bycomp.sas, SAS version 9.3, 2010). We conducted separate analyses by year for the years in which we had large sample sizes (2012 and 2013). We found no yearly variation in habitat preference and combined years for final analysis of habitat selection. We calculated movement rates using the distance and time between consecutive locations. We then compared movement rate by habitat, with individuals and year included as random variables to account for individual and yearly variation (PROC MIXED). To meet the normality assumptions of mixed models, we log transformed rates.

Using general linear models (PROC GLM), we compared vegetation characteristics (percent foliage density and percent canopy cover) between bird and random locations. Because

both canopy and foliage were correlated (PROC CORR; Pearson Correlation Coefficient $r > 0.20$; $P < 0.001$), we included only 1 vegetation variable per model. Because random locations were not surveyed in 2010 and 2011 and because habitat variables did not differ by year in 2012 and 2013, we did not include year as a variable. We considered habitat types in all models. To determine if there was a difference in arthropod abundance between bird and random locations we developed a general linear model (PROC GLM). To examine if arthropod abundance varied over the course of the season, we developed linear regression models for each habitat and examined arthropod abundance over time (PROC REG). To meet the assumptions of general linear models, we log transformed arthropod numbers.

We conducted this study in accordance with the University of Illinois Institutional Animal Care and Use Committee Permit Number 12052, the Federal Fish and Wildlife Permit TE023643-7, Federal Bird Banding Permit 21999, and Texas Scientific Permit Number SPR-0409-079.

RESULTS

Juvenile Abundance in Riparian and Shrub Habitats

We accumulated 356 mist-net hours in shrub habitat and 245 in riparian habitat in 2012-2013. We captured similar numbers of birds/net hour in shrub and riparian habitats (0.25 and 0.26 respectively; $F_{1,77} = 0.04$, $P = 0.84$; Table 1). Capture rates did not differ statistically by year ($F_{1,77} = 0.89$, $P = 0.38$; Table 1).

Individual Habitat Selection

We radio-tagged and tracked 71 juvenile black-capped vireos in 2010-2013 and collected a total of 1,370 locations (mean of 19.3 ± 1.2 locations per individual).

Habitats within the study sites were available to juveniles in similar proportions (0.31 forest, 0.26 grass, 0.24 riparian, 0.19 shrub). When we compared habitats used by each individual to those available to each individual, juveniles did not use habitats in proportion to their availability (Wilks' Lambda: $F_{3,68} = 28.61$, $P < 0.001$; Fig. 1). Juveniles selected riparian over forest and grass habitats ($t_3 = 3.97$, $P = 0.001$; $t_3 = 7.92$, $P = 0.001$; respectively). Juveniles did not select riparian over shrub habitat ($t_3 = 0.02$, $P = 0.98$). Shrub was selected over forest and grass habitats ($t_3 = 3.67$, $P = 0.001$; $t_3 = 9.14$, $P = 0.001$; respectively). All other habitat types were selected over grass (all $P = 0.001$). Nearly all juveniles captured in riparian habitat remained in this habitat throughout the tracking period (24 of 26 individuals). In comparison, of the 32 juveniles captured in shrub habitat, 11 remained in shrub, 11 moved into riparian, 4 moved to forest, and 3 moved between shrub and forest habitats. The remaining 4 individuals showed variable movements across all habitat types, many moving continuously throughout the tracking period.

Juveniles moved an average of $4,898 \pm 445$ m throughout the time we tracked them. The mean distance between consecutive locations was 263 ± 11 m. The mean time between consecutive locations was 10.7 ± 0.2 h and movement rates averaged 80.3 ± 7.8 m/h. As predicted, movement rates varied by habitat ($F_{3,1,201} = 3.91$, $P = 0.001$), with juveniles moving more slowly in riparian than in other habitats (57.1 m/h riparian, 92.1 m/h grass, 106.2 m/h shrub, and 113.4 m/h forest).

We detected juveniles in close association with conspecific adults at 27% of bird locations. We witnessed juveniles closely associating with adults and occasionally begging for food from adults feeding dependent fledglings. (We did not witness any adults feeding the older juveniles that we were tracking.) When using playbacks for mist-netting, juveniles responded positively to male songs and other conspecific vocalizations. Overall, we did not observe any evidence that suggested hostile behavior between adult and juvenile birds.

Juveniles were usually foraging when re-sighted (407 of 473 locations where activity was documented). In the 111 fecal samples collected while banding vireos in 2012-2013, we found remains of arthropods in 103 samples, fruit in 3 samples, and 5 samples had no identifiable items, suggesting that arthropods make up the bulk of the juvenile diet during this time period.

Vegetation Characteristics and Arthropod Abundance

We surveyed foliage density and canopy cover at 702 bird locations and 408 random locations in 2011-2013. As predicted, vireos were associated with dense understory vegetation and canopy cover, in all habitats, relative to random locations (Fig. 2). Foliage density was higher at bird than at random locations ($F_{7,1,141} = 58.69$, $P < 0.001$; Fig. 2A). When analyzed by individual habitat type, this was true for both forest and shrub (both $P < 0.001$), but not grass ($P = 0.62$) or riparian habitat ($P = 0.06$). Canopy cover was also greater at bird locations than at random locations ($F_{7,1,141} = 57.21$, $P < 0.001$; Fig. 2B) and, by habitat type, was greater at bird locations than random locations in grass and riparian (both $P < 0.001$) but not in forest ($P = 1.00$) or shrub habitat ($P = 0.61$).

To determine whether juvenile vireos select riparian habitat because of higher density vegetation, we compared canopy cover and foliage density among habitat types using only data

from random locations. Canopy cover was higher in forest ($P < 0.001$) than all other habitat types (forest: 0.57 ± 0.03 ; grass: 0.04 ± 0.01 ; riparian: 0.33 ± 0.04 ; shrub: 0.26 ± 0.02) but did not differ between riparian and shrub habitats ($P = 0.47$). Foliage density did not differ between riparian, shrub, and forest habitats (all $P > 0.05$), but was greater in those habitat types than in grass (all $P < 0.001$; forest: 0.50 ± 0.02 ; grass: 0.16 ± 0.01 ; riparian: 0.45 ± 0.04 ; shrub: 0.45 ± 0.02).

We sampled arthropods at 583 bird locations and 518 random locations from 2012-2013. We found no significant seasonal trend in arthropod abundance in forest, grass, or shrub habitat ($R^2 < 0.001$, $P = 0.83$; $R^2 < 0.001$, $P = 0.54$; $R^2 = 0.003$, $P = 0.37$, respectively) but a weak negative relationship was found in riparian habitat ($R^2 = 0.07$, $P < 0.001$). We found no significant variation in arthropod numbers between bird and random locations ($F_{1,3} = 0.06$, $P = 0.81$). However, arthropod abundance did differ by habitat ($F_{1,3} = 8.74$, $P < 0.001$; Fig. 3) and was highest in riparian habitat.

DISCUSSION

Collectively our results suggest that juvenile black-capped vireos often move out of the shrub habitat in which they were produced and into other habitat types, particularly riparian habitat. We captured juveniles at similar rates in shrub and riparian habitats, even though vireos nest almost exclusively in shrub habitat (Grzybowski 1995; but see Pope et al. 2013) and radio-tracked individuals demonstrated selection for riparian over most other available habitat types. Use of riparian habitat is likely a function of increased cover and food compared to other available habitat types. These results suggest that riparian habitat may be important for juvenile

black-capped vireos, thus expanding what is considered necessary habitat for this endangered species.

Movement patterns of radio-tracked vireos provide insight into how juveniles appear to select habitat. Birds captured in shrub did not all move directly to riparian habitat as might be expected if they had an innate preference for that habitat. Rather, they moved extensively and used denser vegetation in all habitats. Those that did move into riparian habitat remained there, as did nearly all the vireos that were already in riparian habitat when captured. Thus, it is possible that birds keep sampling areas until they encounter the features they prefer (e.g., vegetation structure, food) and then restrict further movements. In our study sites, riparian habitat provides more of the preferred attributes than do other habitats.

Our results contribute to the growing evidence that habitat selection for birds may differ seasonally, likely due to the different ecological requirements for birds in the breeding season compared with the post-breeding season (Vega Rivera et al. 1998, King et al. 2006, Akresh et al. 2009, Vitz and Rodewald 2010). Juvenile vireos tend to choose areas characterized by dense canopy and foliage, suggesting that vegetative cover may be important in choosing habitats. Dense vegetation may provide cover and protection from the elements, which may be particularly important for young, inexperienced birds. Juvenile vireo selection of riparian habitat did not appear to be solely a function of dense vegetation, but rather a combination of cover and food abundance. Given that foraging was the predominant activity observed, it is likely that habitat selection decisions incorporate food abundance. Arthropods were most abundant in riparian habitat, even though we found a slight decrease in abundance over the season. Previous work in other systems has demonstrated that riparian areas have more arthropods than other habitats (Vega Rivera et al. 1998, Iwata et al. 2010). Because juveniles are highly mobile and are

not constrained by territoriality, they may be able to respond to variation in arthropod abundance and choose foraging areas accordingly (Uesugi and Murakami 2007).

A potential difficulty in determining habitat selection by juveniles is the possibility that they are forced to use those habitats by adults. Our observations suggest this does not explain why many juvenile vireos leave shrub habitat and end up in riparian habitat, however, because we captured many juveniles in mist-nets when we were broadcasting adult male song and regularly observed juveniles in close proximity to conspecific adults. These observations suggest adults tolerate juveniles, particularly later in the season when adult territories have dissolved.

MANAGEMENT IMPLICATIONS

Current conservation strategies on Fort Hood focus entirely on protecting and monitoring shrub habitat and do not consider riparian habitat. Management efforts that incorporate both breeding and post-breeding habitat requirements should be more effective. Fort Hood lies within three major watersheds. If riparian habitat provides key resources used by juvenile vireos, it is important to protect these areas, particularly those near shrub habitat. Cattle grazing appears to be a particular threat to the quality of riparian habitat. Grazing has been found to alter vegetation structure along small streams and rivers, reducing foliage density and canopy cover, reducing vegetation diversity, and cause habitats to be unsuitable for riparian-dependent species (Kauffman and Krueger 1984, Belsky et al. 1999, Hough-Snee et al. 2013). Additionally, grazing decreases invertebrate abundance, particularly caterpillars and other arthropods eaten by gleaning birds (Allombert et al. 2005). A decrease in grazing disturbance can positively impact riparian vegetation and increase avian species abundance and diversity (Dobkin et al. 1998,

Earnst et al. 2012, Hough-Snee et al. 2013). Due to the ephemeral nature of shrub habitat, controlled burns and mechanical clearing of vegetation are necessary to maintain breeding habitat for black-capped vireos. Prioritizing areas in proximity to riparian habitat may add value to breeding habitat.

CHAPTER 2

SURVIVAL AND BEHAVIOR OF JUVENILE BLACK-CAPPED VIREOS *VIREO*

*ATRICAPILLA*²

ABSTRACT

Survival estimates for juvenile birds are rarely empirically derived and have been typically estimated as some percentage of adult survival. In particular, little information is available on survival when juveniles are independent of parental care or whether juvenile survival is sex biased. Additionally, little information is available about behaviors of juvenile birds that might be relevant to their survival. We used radio telemetry to estimate survival of independent juvenile male and female black-capped vireos (*Vireo atricapilla*), and observed behaviors while tracking individuals. From 2010 to 2013, we tracked 71 juvenile vireos in central Texas. Using a known-fate model in program MARK, we calculated overall survival during the independent period to be 55% (86% for females and 40% for males). Movement patterns varied among individuals and males tended to make more foray movements than females. Both sexes were frequently seen in association with conspecifics and heterospecifics. Half the males we tracked were observed singing, both sexes made many types of vocalizations, and the frequency of vocalizations did not differ between sexes. Whether behavioral differences contributed to survival differences between males and females will require further research. Our results indicate that juvenile mortality is likely important for the population dynamics of this species and emphasize the need for studies of juvenile survival across a range of species and regions.

²This chapter has been submitted in its entirety in the Journal of Avian Biology. Dittmar, E. M., D. A. Cimrich, J. H. Sperry, and P. J. Weatherhead. 2014. Sex-specific survival and behavior of juvenile black-capped vireos *Vireo atricapilla*. Journal of Avian Biology (in review).

INTRODUCTION

Juvenile survival is likely a critical factor affecting population dynamics and persistence. For birds, determining survival of juveniles can be difficult because mortality is often confounded with dispersal (Akresh et al. 2009). Consequently, juvenile survival rates in birds are often estimated indirectly through band returns or as some percentage of adult survival, without a good empirical basis for the estimates (Ricklefs 1973). Miniaturized radio transmitters now make it possible to obtain more accurate age-specific survival rates. For songbirds, it was previously assumed that survival during the post-fledging period (between fledging the nest and the initiation of migration) was low, but recent evidence suggests that this is highly dependent on fledgling age, with relatively high survival after about 20 days post-fledging (see Cox et al. 2014 for complete review).

Nearly all of the studies to date documenting juvenile survival in birds have focused on the dependent period, between when juveniles fledge from the nest and the termination of parental care. Still relatively unstudied, however, is the period when juveniles are independent of parental care. Once family groups break apart, juvenile birds often move out of adult territories and therefore become difficult to monitor. This period of independence, which for migratory species can last up to three months before the start of migration, may hold many challenges for young birds. Juveniles must prepare for migration by building up fat reserves, while meeting the energetic demands associated with preformative molt (Hall 1996). While juveniles are finding food, they must also avoid predators, both of which were activities previously done with parental assistance, potentially making independent juveniles more vulnerable to predators (Anders et al. 1997). In addition to meeting survival needs, juveniles may engage in other behaviors relevant to

future needs (i.e., prospecting for territories, socializing, learning vocalizations; Vega Rivera et al. 1999, Mitchell et al. 2010). Previously it was thought that mortality rates remained high even after juveniles gained independence, because of inexperience in foraging and evading predators (Lack 1954). Contrary to this assumption, however, several recent studies have reported relatively high estimates of daily survival for independent juveniles, ranging from 0.988 to 1.000 for 6 species (Anders et al. 1997, King et al. 2006, Wightman 2009, Ausprey and Rodewald 2011, Vitz and Rodewald 2011, Dybala et al. 2013, Streby et al. 2013), indicating that independent juveniles may exhibit behaviors that decrease the risk of mortality. However, survival estimates may vary among species and locations. Additionally, reported samples are low, ranging from 16-37 individuals and few of the studies followed birds beyond the first 2 weeks of independence, revealing an obvious gap in our knowledge regarding juvenile ecology.

Our goal in this study was to use radio telemetry to estimate the survival of juvenile black-capped vireos (*Vireo atricapilla*; hereafter “vireo”) during the period following independence from parental care. Because juvenile vireos are sexually dimorphic (i.e., males have gray-black caps and white breast plumage, females have olive-gray caps and buffy-peach breast plumage; Cimprich 2007), we were able to determine whether survival differed between males and females. For most birds, juvenile males and females are not sexually dimorphic, making it difficult to estimate sex-specific survival. The few reports of juvenile mortality by sex found that sex did not influence survival (Tarwater et al. 2011, Cox and Kesler 2012). We also quantified the behavior of the vireos we tracked to determine whether any sex differences in survival could be associated with differences in behavior. If juvenile survival is low we expect that juveniles would behave in ways that maximize survival (i.e., minimize movements, vocalize infrequently, associate with groups). Alternatively, if survival is high, then juveniles might

exhibit behaviors that serve purposes other than maximizing immediate survival (i.e., broad-scale movements, frequent vocalizations, solitary behavior). Under this alternative scenario, sex differences in behavior might be associated with sex differences in survival.

METHODS

We conducted this study during the post-breeding season (mid-June to August) of the vireos from 2010-2013 on the Fort Hood Military Reservation in central Texas, USA. The federally endangered vireo is a Neotropical-Nearctic migrant passerine, threatened by habitat degradation/loss and severe brood parasitism by brown-headed cowbirds (*Molothrus ater*; Kostecke et al. 2005). Vireos breed in low, shrubby, deciduous vegetation (Grzybowski 1995), predominantly on mesa tops and slopes at Fort Hood. Military training is the primary land use on Fort Hood. Other uses include cattle grazing and maintenance of fish and wildlife habitat for conservation and recreation (Kostecke et al. 2005). Fort Hood has rigorous endangered species management practices, including habitat restoration, controlled burns, and cowbird removal (Cornelius et al. 2007). For more detailed descriptions of Fort Hood land uses and management practices see Cornelius et al. (2007). We conducted fieldwork at two large study sites (5,496 ha and 6,534 ha), approximately 18 km apart. Study sites were chosen to maximize netting locations in a variety of habitat types (see Dittmar et al. in press for more details on study sites and habitats).

Survival and behavioral data

To capture vireos for radio tracking, we conducted mist-netting 2-7 days a week, for approximately 4 hours starting at sunrise, from June 5–August 22. We used 6- and 12-m mist-

nets with recordings of either black-capped vireos or eastern-screech owls (*Megascops asio*) broadcast near each net. We noted the sex and dependency status of each captured individual and attached radio transmitters only to vireos that we classified as independent. Based on previous observations, we considered juveniles to be independent of parental care if their preformative molt had progressed at least to the stage that all juvenile greater coverts had been replaced. During this study, we did not observe any of the vireos that we radio tracked being provisioned by adults, indicating that our criterion for independence was reliable.

We fitted vireos with 0.27-g radio transmitters (Model LB-2X, Holohil Systems Ltd, Ontario, Canada) using the backpack method (Hallworth et al. 2009). Backpacks weighed <4% of each vireo's body mass. Due to the limited battery life of transmitters (14 days on average), we could not track individual vireos through their entire post-fledging period. Given the likelihood that the age of vireos tracked varied and that we captured vireos to attach transmitters over most of the post-breeding season, collectively the tracking data should represent most of the post-fledging, independent period. We located vireos twice a day, with at least 2 h between observations and considered consecutive behavioral observations at locations for an individual to be independent. When tracking vireos, we approached them on foot as discreetly as possible to avoid influencing natural movements. When juveniles were re-sighted, we observed them for at least 5 min and classified flocking behavior as "alone" if individuals were not seen in association with other birds or "flocking" if birds were seen in close association with conspecifics or heterospecifics. We considered birds in close association if they were observed interacting with others or remained in close proximity (<10m) while foraging or moving around. When possible we documented the species and number of other flock members. We also noted if juveniles made any vocalizations while under observation and classified vocalizations as adult calls (adult-

specific vocalizations such as kinglet calls, shree calls, and contact notes), fledgling calls (fledgling-specific location calls, soft peeps, or squeaks), shrads (given in alarm or when scolding), or songs (see Grzybowski 1995 for details about vocalization types). We confirmed mortality by finding the carcass or inferred it from the condition of transmitter (i.e., evidence of blood, scratch marks, or numerous feathers found in the vicinity).

Statistical analysis

All analyses were conducted using R 3.02 (R Core Team 2013). To validate model assumptions, we examined residual and fit statistics. All factors were considered statistically significant at $P \leq 0.05$.

We estimated daily survival rate (DSR) and cumulative survival rate for each sex covering the 75-day tracking period using known-fate models in Program MARK (White and Burnham 1999) by converting field telemetry data into encounter histories for each juvenile. From 5 June to 2 August, each vireo had a daily survival history during which it lived, died, or was not tracked. Known-fate models assume the encounter probability of an individual is 1.0 and are preferred over the Kaplan-Meier product-limit estimator because they allow for the inclusion of covariates. We used an information-theoretic framework to compare models using Akaike's information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002). To account for possible effects of temporal variables on survival, we compared several models including a null model, a time-dependent model, a model including Julian date on initial tracking day, and both time and Julian dates (Appendix). Because the time-dependent model had the most support (AIC_c value = 52.233 and $\omega_i = 0.718$), we only present survival estimates from this model for all subsequent analyses. We used a Student t-Test to test the difference between male and female overall survival.

To analyze behavioral observations we constructed generalized linear mixed models (Bates et al. 2014) accounting for individual vireo and year as random effects. For movements, we tested the difference in distances traveled between consecutive locations by sex, using a Poisson variance function with log link. We classified broad-scale movements as movements >1,100 m (a frequency distribution of movement distances showed a bimodal pattern with a break at this distance) and compared the number of these movements made by individuals. For association behavior, we estimated by sex, the probability of juveniles being 1) solitary versus in a group, 2) associated with conspecifics, and 3) associated with heterospecifics. For these models, we used the binomial variance function and withlogit link. Additionally, we examined the difference in flock size by sex using a Poisson variance function with log link. For vocalizations, we estimated the probability of vocalizing by sex and used the binomial variance function with logit link. We then separated vocalizations by type (adult calls, fledgling calls, shrads and songs) and tested differences in call types by sex using a Poisson variance function with log link.

RESULTS

Survival

We followed the fates of 33 females and 38 males from 2010-2013. Of the 71 vireos tracked, 7 individuals (6 male, 1 female) did not survive the tracking period. One predation event occurred where a vireo was ingested by a copperhead (*Agkistrodon contortrix*), although it is unknown whether the snake killed the vireo or if the vireo had died prior to ingestion. The remaining 6 juveniles were recovered fully intact or as complete skeletons cleaned by ants, with transmitters still attached and no signs of depredation, suggesting they may have died from

exposure or starvation. Two of these individuals showed signs of physical trauma (i.e., hematoma under skull), which suggests they sustained an injury that may have caused mortality. Three individuals were found dead immediately following a storm that lasted several days.

We estimated combined DSR for both sexes to be 0.993 ± 0.005 and survival over the 75-day tracking period to be 0.554 ± 0.125 . DSR was greater for females (0.998 ± 0.002) than males (0.989 ± 0.008), with cumulative survival over the 75-day period greater for females than males ($t_{74} = -2.271$, $P = 0.03$; Fig. 4).

Behaviors

We located vireos with transmitters 1,370 times (19.3 ± 1.2 locations per individual). Vireos traveled an average of 266.3 ± 11.2 m between consecutive locations. Half the vireos we tracked remained in approximately the same area for the duration of the tracking period, while the others were observed making broad-scale movements. These large movements included forays away from and back to a previous location, as well as movements from one location to another. Males moved further than females between consecutive locations (294.9 m 95% CI [248.4, 350.1] and 240.5 m CI [202.8, 285.3], respectively; $F_{1,1291} = 5.885$, $P = 0.02$). More males than females made broad-scale movements (17 vs. 10 individuals) and the total number of these movements per individual tracked was higher for males than for females (0.92 vs. 0.61) but did not differ significantly ($F_{1,66} = 1.690$, $P = 0.20$).

We recorded presence or absence of vocalizations 689 times that we relocated juveniles (377 for females, 312 for males). Juveniles vocalized on 25% of these occasions and were heard making an array of vocalizations. The majority (61%) of these were shrads or warning calls, 23% were fledgling-specific vocalizations, 10% were songs, and 6% of vocalizations were adult-specific calls, which include chips and an adult call typically made during courtship or nest-

building. We observed 12 males (50%) singing, with songs ranging from crude and slurred, to being indistinguishable from those of adults. We did not detect a difference in frequency of vocalization by sex ($F_{1,686} = 0.083$, $P = 0.77$) and fledgling-specific vocalizations, shrad, and adult-specific calls did not vary by sex ($F_{1,686} = 0.001$, $P = 0.98$, $F_{1,686} = 0.003$, $P = 0.96$; $F_{1,686} = 0.000$, $P = 1.00$, respectfully; Fig. 5).

At 715 juvenile locations (382 for females, 333 for males) we documented whether juveniles were solitary or in close association with other birds. Although not statistically different, we found that males were more likely to be solitary than females ($F_{1,710} = 1.983$, $P = 0.16$; Fig. 6A). Juveniles were seen with groups of from 1 to >50 birds (both conspecifics and heterospecifics). Group size did not vary by sex ($F_{1,713} = 0.001$, $P = 0.98$). Vireos were commonly seen in close association with both conspecifics and heterospecifics. Association with conspecifics varied by sex ($F_{1,713} = 3.759$, $P = 0.05$), with females more likely to be near conspecifics (Fig. 6B). Juvenile vireos were commonly seen associating with other juveniles and singing adult vireos. Association with heterospecifics did not vary by sex ($F_{1,713} = 0.840$, $P = 0.34$). The most common heterospecific species radio-tagged vireos were observed in association with were northern cardinals (*Cardinalis cardinalis*), white-eyed vireos (*Vireo griseus*), painted buntings (*Passerina ciris*), and blue-grey gnatcatchers (*Polioptila caerulea*).

DISCUSSION

Juvenile survivorship is often lower than that of adults and may have direct effects on population viability (Blomberg and Shine 2001, Sandercock et al. 2005, Gardali et al. 2003). Our results suggest that low juvenile survival could be a factor contributing to the endangered status

of vireos. Previous model-based estimates of juvenile vireo yearly survival ranged broadly from 0.12 to 0.71 (Beardmore et al. 1995, Grzybowski 2005). An analysis of mark-recapture data over a 10-year period estimated juvenile vireo survival, from post-fledging independence to the following spring, to be about 0.38 (Kostecke and Cimprich 2008). Although this estimate is likely biased low due to the confounding effect of natal dispersal, our data indicate that survival prior to migration may be low for independent juvenile vireos, suggesting that the estimate by Kostecke and Cimprich (2008) may be reasonably accurate. The daily survival rate we estimated is the lowest documented for any species during this period. Juvenile survival rates are thought to level off after about 20 days after fledging (Cox et al. 2014) but due to the limited data available for survival rates of independent juveniles, this may not hold true for all birds.

Although we tracked 9 individuals of known age (58-83 days old on initial tracking day), the majority of the birds we tracked were of unknown age and we could not interpret if younger juveniles had lower survival than older juveniles. Additionally, poor body condition during the nestling and fledging period has been found to lead to low survival rates (Perrins 1963, Dhondt 1979, Krementz et al. 1989, Tarwater and Brawn 2010, Ausprey and Rodewald 2011, Vitz and Rodewald 2011). Due to the small body size of vireos, we selectively attached transmitters to only relatively larger birds, preventing us from determining if body condition was a significant factor influencing survival. Therefore, in this regard, our survival estimate may be biased high.

The male bias we observed in juvenile mortality is potentially important if it proves to be a general feature of juvenile vireo ecology. Male vireos were more likely to engage in potentially risky behaviors such as longer distance forays and reduced likelihood of flocking with conspecifics. Because our estimates are based on only seven individuals that died, however, further evidence is needed before concluding that male survival is lower than female survival. If

mal mortality is higher, we would expect that adult sex ratios would be female biased unless female mortality exceeds that of males at some other life stage (e.g., predation of incubating females; Reidy et al. 2009). It was previously thought that adult vireo sex ratios are male biased (Grzybowski 1995); although that could be a function of lower female recapture rates (Kostecke and Cimprich 2008).

Despite relatively low survival, we found that independent juveniles behaved in ways that seem unlikely to maximize survival. These behaviors included making exploratory movements, vocalizing, and socializing. Presumably, these behaviors benefit juveniles in some way by meeting either current or future needs. Our data are consistent with growing evidence that juvenile birds may explore the landscape and prospect for future breeding sites prior to migration (Mauersberger 1957, Berndt and Winkel 1979, Adams and Brewer 1981). Juvenile vireos (particularly males) often made forays, to and from breeding habitat, despite a general preference for riparian habitat (Dittmar et al. in press). We frequently observed both males and females associating with conspecifics and heterospecifics as has been observed in other species (Morton et al. 1991, Vega Rivera et al. 1998, Templeton et al. 2012). Juveniles may use other birds to find good habitat (Kersher et al. 2004). Birds in flocks may also benefit from collective vigilance (Elgar 1989, Powell 1974) or risk dilution (Cresswell 1994, Roberts 1996). Additionally, we observed juveniles making an array of vocalizations. We do not know whether juveniles of other species vocalize to a similar extent. Females vireos do not sing but the calls they (and males) make could have some value in allowing them to become or remain members of social groups. Call notes by juveniles might increase rather than reduce survival if these vocalizations are used as social cues or as alarm calls. Juvenile males likely benefit from early development of song (Searcy 1992, Catchpole and Slater 2003, Gil and Gahr 2002) and interacting with many adult

males may serve to increase song repertoires. For vireos, the question of interest would seem to be what advantage juveniles gain from moving so extensively, vocalizing, and socializing frequently, given the apparent costs of low survival during this time.

Our study provides further evidence that post-breeding ecology is important for understanding avian population dynamics. Knowing how survival varies throughout all life phases is crucial for predicting population growth rates and viability. The juvenile stage may be the most limiting avian life stage (Crouse et al. 1987), yet only a small number of post-fledging survival studies have been conducted for passerines (Cox et al. 2014). With the recent miniaturization of tracking devices, obtaining accurate survival estimates is becoming more accessible. There is a need for more research focused on juvenile survival, across a variety of species and habitats, as well as on the factors that influence survival, as this information may serve an important role in identifying conservation strategies for at-risk species.

CHAPTER 3

THESIS SUMMARY

Collectively my results highlight the importance of post-breeding ecology for the management of migratory songbirds. Management practices that consider only the breeding season may not improve population productivity, because ecological factors outside the breeding season affect population dynamics. Like similar studies, I found that juvenile vireos independent of parental care did not all remain in breeding habitat. Although vireos moved through a variety of vegetation types, they showed selection for riparian areas, which provided a combination of dense vegetation cover and high arthropod abundance. Additionally, I found that survival of independent juveniles was relatively low, with a cumulative survival rate of 55%. Additionally, behavioral observations suggest that despite relatively low survival, juveniles may behave in ways that seem unlikely to maximize survival. I observed a variety of behaviors, including frequent exploratory forays, vocalizations, and socializing. Presumably these behaviors benefit juveniles in some way by meeting either current or future needs.

Survival during the juvenile life stage is the most variable for short-lived animals (Wisdom et al. 2000) and juvenile survival is a key factor for the productivity of a population. My estimated survival rates for independent juvenile vireos, combined with those of dependent juveniles (Kostecke and Cimprich 2008) suggests that survival rates prior to migration are low (10-20%) and indicate that productivity of vireo populations are likely affected by post-breeding ecology. My survival estimates should be incorporated into demographic models to more accurately predict population trends for this species. Future research focused on dispersal and survival of juvenile vireos during migration and on the wintering grounds will increase our

understanding of the juvenile life stage and improve conservation and management of this endangered species.

Current conservation strategies for the vireo focus almost exclusively on protecting and monitoring shrub-breeding habitat and do not consider riparian areas. Due to the ephemeral nature of shrub, mechanical clearing of vegetation and controlled burns are necessary to maintain breeding habitat for vireos. My results suggest that when choosing areas to manage for breeding vireos, proximity to riparian habitat should be incorporated into those decisions. Prioritizing areas in proximity to riparian areas would add value to breeding habitat because it increases the likelihood that young raised there might benefit by finding the post-breeding habitat they prefer.

On Fort Hood, continuous grazing by cattle has negatively affect vegetation structure and soil erosion in many areas (Fort Hood 2012). Overgrazing has been found to particularly alter vegetation structure along small streams and rivers by reducing foliage density and canopy cover and reducing vegetation diversity (Kauffman and Krueger 1984, Belsky et al. 1999, Hough-Snee et al. 2013). A decrease in grazing disturbance may positively impact overgrazed areas and increase avian species abundance and diversity (Earnst et al. 2012, Dobkin et al. 1998, Hough-Snee et al. 2013). Adding riparian buffer zones that exclude livestock is not an option on Fort Hood, due to military training practices, so alternative cattle management practices need to be implemented. Providing alternative upland water troughs or decreasing stocking rates should improve the quality and slow down degradation of vegetation due to overgrazing.

FIGURES AND TABLES

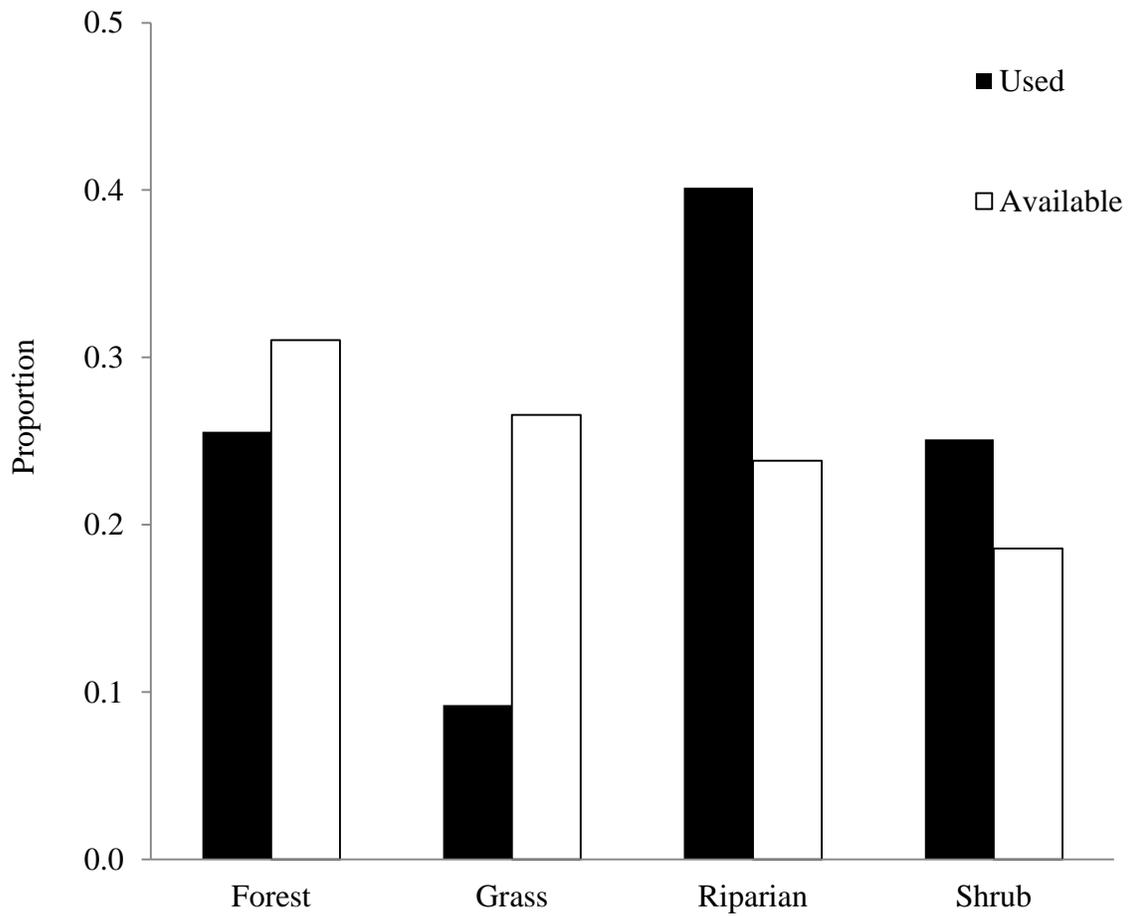


Fig. 1. The proportion of used versus available vegetation types for juvenile black-capped vireo locations at Fort Hood, TX, 2010-2013.

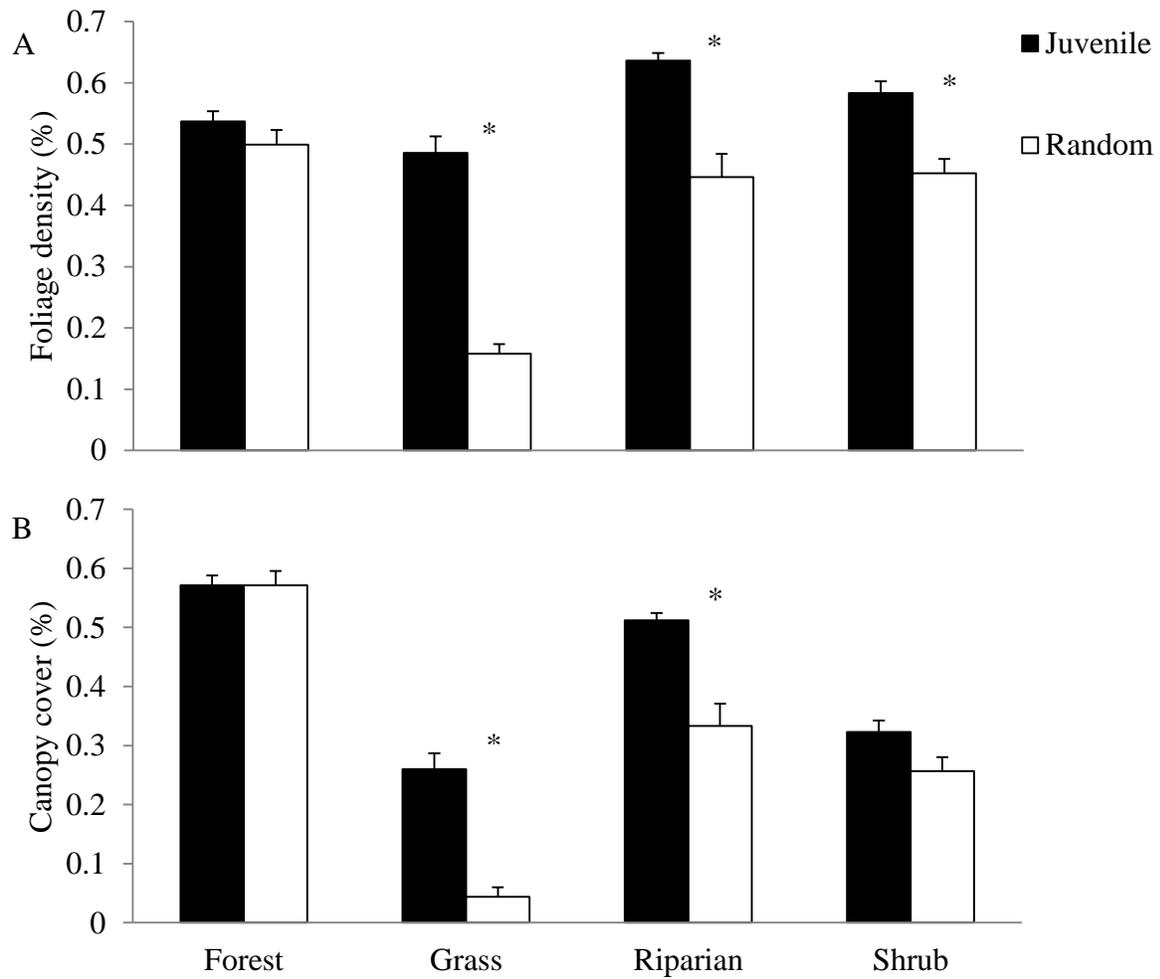


Fig. 2. Mean \pm 1 SE foliage density (A) and canopy cover (B) at juvenile black-capped vireo locations and random locations at Fort Hood, TX, 2011-2013. Statistically significant differences ($P < 0.05$) denoted by asterisks.

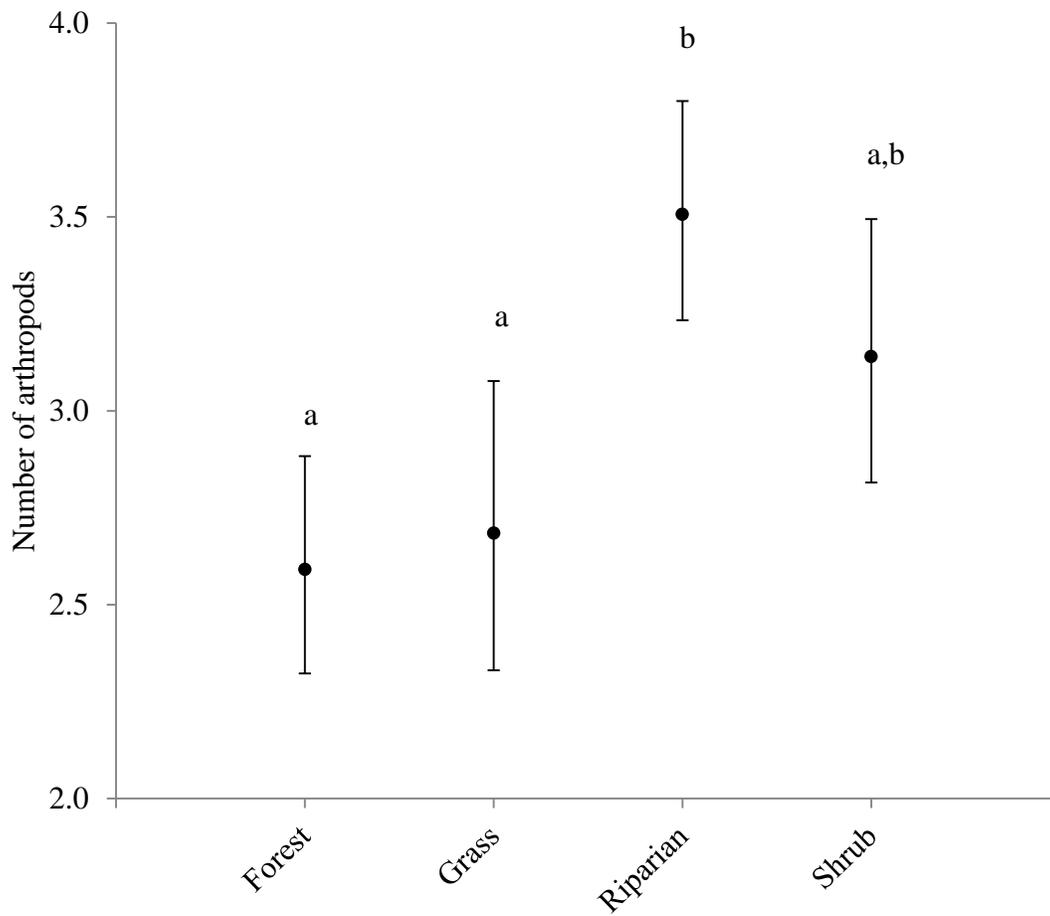


Fig. 3. Mean (\pm 95% CI) arthropod abundance by vegetation type across all sites at Fort Hood, TX, 2012-2013. Different letters signify statistically significant differences ($P < 0.05$).

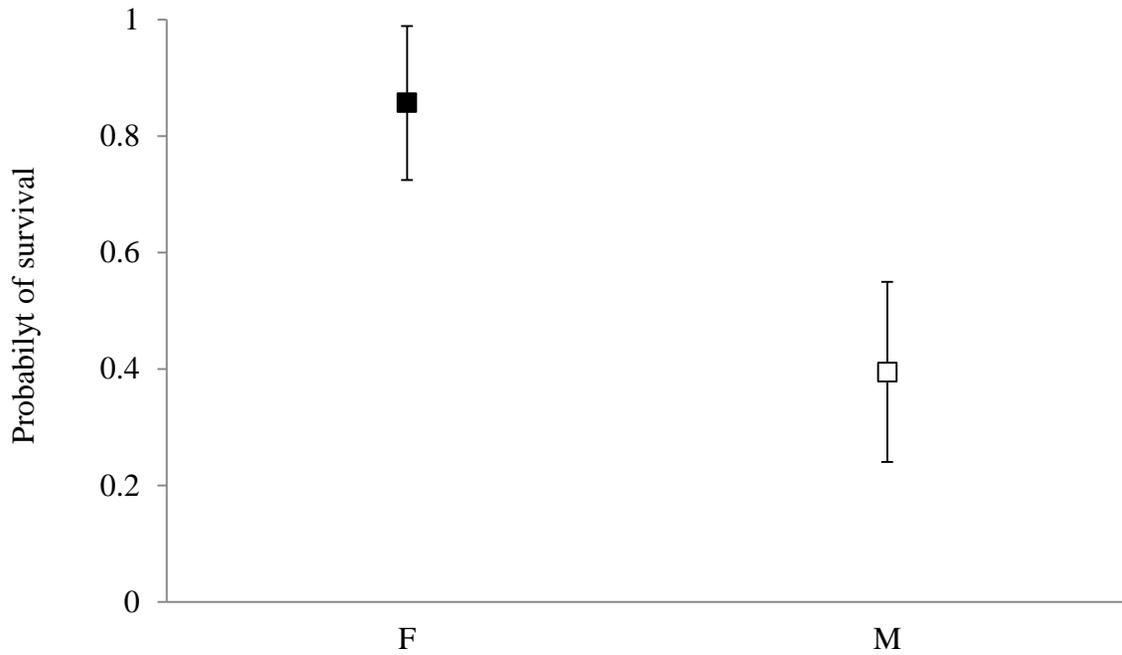


Fig 4. Cumulative probability of survival (± 1 SE) over the 75-day independent period for female and male juvenile black-capped vireos, from 2012-2013 at Fort Hood, TX. Female and male survival rates differ significantly ($t_{74} = -2.271$, $P = 0.03$).

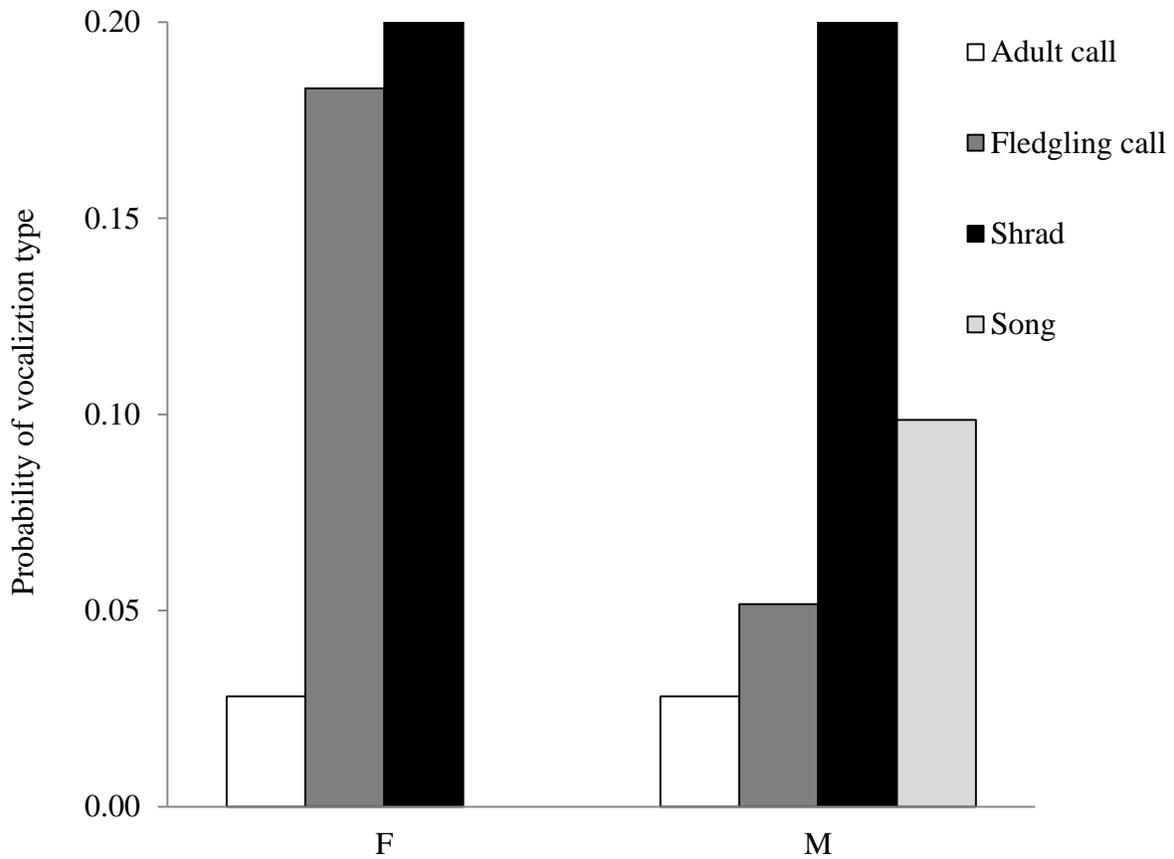


Fig 5. Probability of type of juvenile black-capped vireo vocalization by individuals from 2012-2013 at Fort Hood, TX. Adult calls are adult-specific vocalizations such as kinglet calls, shree calls, or contact notes, fledgling calls are fledgling-specific location calls, soft peeps, or squeaks, and shrads are calls given in alarm or when scolding.

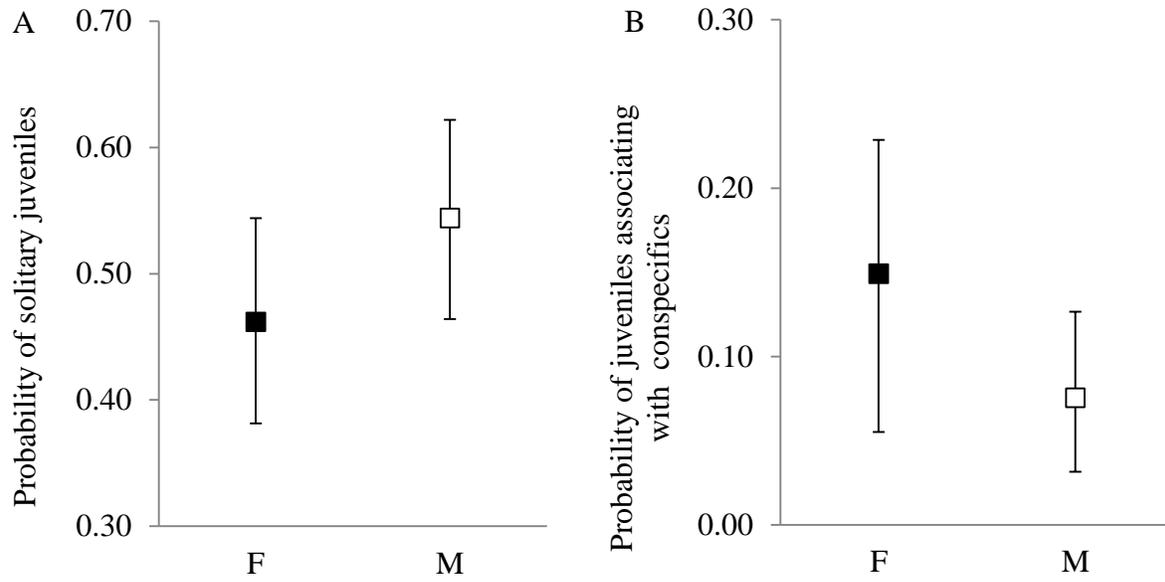


Fig 6. Probability (\pm 95% CI) of individual juvenile black-capped vireo males and females observed A) solitary and B) associated with conspecifics from 2012-2013 at Fort Hood, TX.

Table 1. Capture rates (birds per net hour) and SE of independent juvenile black-capped vireos in riparian and shrub habitats at Fort Hood, TX, 2012-2013. Number of individuals (*n*) given in parenthesis.

Age	Habitat	2012			2013			Years combined		
		Capt rate	SE	(<i>n</i>)	Capt rate	SE	(<i>n</i>)	Capt rate	SE	(<i>n</i>)
Juveniles	Riparian	0.24	0.33	(15)	0.21	0.20	(43)	0.25	0.10	(58)
	Shrub	0.47	0.48	(20)	0.14	0.16	(47)	0.26	0.10	(67)

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APPENDIX

Known-fate models deriving survival estimates for juvenile black-capped vireos ($n = 71$) at Fort Hood TX, 2012-2013. Models were generated in program MARK and ranked by Akaike's information criterion corrected for small sample sizes (AIC_c), where ΔAIC_c represents the difference in the AIC_c value relative to the top model, ω_i is the Akaike weight, and k is the number of parameters. Model set includes a time-dependent model (ϕ_t), a model accounting for the effect of Julian date (ϕ_{julian}), a model accounting for both time-dependence and Julian date ($\phi_{t + \text{julian}}$), and a constant survival model (ϕ).

Model	AIC_c	ΔAIC_c	ω_i	k
ϕ_t	52.233	0.000	0.718	5
$\phi_{t + \text{julian}}$	54.100	1.868	0.282	6
ϕ	81.170	28.938	0.000	1
ϕ_{julian}	83.054	30.821	0.000	2