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COMPARATIVE REPRODUCTIVE BIOLOGY OF CO-OCCURRING ENDANGERED
AND COMMON SHRUBLAND BIRDS

BY

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THESIS

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ABSTRACT

Black-capped vireos (*Vireo atricapilla*) and white-eyed vireos (*Vireo griseus*) are closely related and ecologically similar. Despite these similarities, white-eyed vireos are widely distributed and common, whereas the black-capped vireo has a restricted breeding range and is federally endangered. Here I address this apparent paradox with a comparative ecological study of co-occurring black-capped and white-eyed vireos. I studied vireos in shrublands and woodlands in central Texas, USA in 2013 and 2014. I used point count surveys (n = 256) and nest monitoring (n = 145) to determine arrival dates, settlement patterns, nest site selection, and, ultimately, nest survival relative to temporal and habitat factors. Additionally, I conducted reciprocal playback trials (n = 16) to test for the presence of interspecific aggression. White-eyed vireos arrived first and established territories in shrub and woodland habitat with equal probability. Black-capped vireos arrive after white-eyed vireos and settled in greater numbers in shrubland habitat. White-eyed vireos begin initiating nests earlier than black-capped vireos and selected nest sites surrounded by taller, more mature, and more densely wooded vegetation. Playback trials failed to detect evidence of interspecific aggression, suggesting that competition with white-eyed vireos is not currently limiting black-capped vireos. For both species, nest survival declined as the season progressed, and was greater for nests in taller, more mature habitat. Accordingly, overall nest survival appeared greater for white-eyed vireos than black-capped vireos suggesting that the flexibility demonstrated by white-eyed vireos in where and when they nest confers a reproductive advantage.

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INTRODUCTION

What determines the distribution and abundance of imperiled species relative to more common but ecologically similar species? Comparisons between species with restricted ranges and their widespread, sympatric congeners can provide insight into this fundamental question of ecology as well as yield valuable information for species distributions, abundances and, ultimately, conservation. Such comparisons have been historically used to address ecological, evolutionary, and genetic questions within a wide range of taxa (e.g. Shine 1986, Hansson and Richardson 2005, Burne et al. 2003, Young et al. 2007). For birds, nest success is a likely candidate for congeneric comparisons as it can be a key demographic parameter influencing population dynamics (e.g. Sæther and Bakke 2000, Stahl and Oli 2006, Sherry et al. 2015). Here I compare breeding-season ecology of an endangered and geographically restricted species, the black-capped vireo, and a widespread congener, the white-eyed vireo. By comparing these two species, we can determine what habitat and temporal factors differentially impact reproductive success, and use this knowledge to better guide conservation and management efforts for these species.

The endangered black-capped vireo (*Vireo atricapilla*) is a small Nearctic-Neotropical migrant songbird that breeds almost exclusively in shrub habitats. Populations of black-capped vireos have experienced drastic declines, primarily due to habitat loss and low reproductive rates (USFW 1991). Although the species was likely never widespread, its breeding range previously extended south from central Kansas, through Oklahoma and Texas, into Mexico. Declines were evident by the 1950s (Graber 1961) and by the time the species was federally listed in 1987, it had been completely extirpated from Kansas, was restricted to just three small breeding populations in Oklahoma, and had been extirpated from northern and eastern Texas. Its

remaining range in central Texas had become increasingly fragmented and was primarily composed of isolated patches of habitat (Grzybowski 1995). The black-capped vireo breeds in a relatively specialized early successional habitat, characterized by a patchy distribution of deciduous shrubs interspersed with areas of open ground or rock (Graber 1961). This habitat has been lost throughout its range due to overgrazing, fire suppression, and development (Campbell 2003). High rates of nest predation and brood parasitism by brown-headed cowbirds (*Molothrus ater*, hereafter cowbird), which have reduced reproductive rates, have also contributed to the decline (Grzybowski 1995, Kostecke et al. 2005).

The white-eyed vireo (*Vireo griseus*), a closely related species (Slager et al. 2014), co-occurs with the black-capped vireo in central Texas. Like the black-capped vireo, this species breeds in shrub or scrub habitats, and constructs nest of similar structure and height in shrubby vegetation. Both species have experienced the same recent landscape changes and increased cowbird abundance in central Texas. However, in contrast to the endangered black-capped vireo, the white-eyed vireo has an extensive breeding distribution, ranging from Texas north and east as far as Iowa, New York, and Massachusetts, and is abundant in many areas throughout this range (Hopp et al. 1995). Breeding Bird Survey data show that white-eyed vireo population levels within the range of the black-capped vireo have remained stable or increased (Sauer et al. 2014, Wilkins et al. 2006) while black-capped vireo numbers continued to decline.

Why has the black-capped vireo declined while the white-eyed vireo thrived? One possibility is that the two species, while broadly similar, differ subtly in their breeding ecology, and these differences have an impact on reproductive output. Differences between the species in habitat use during and the timing of the breeding season has not been previously quantified, but anecdotal information suggests that white-eyed vireos arrive at the breeding sites earlier and

exhibit more generalist habitat tendencies. In central Texas, deciduous shrubland and Ashe juniper (*Juniperus ashei*, hereafter, juniper) woodlands often occur as adjacent habitat types. Reports from field personnel suggest these woodlands are suitable habitat for white-eyed vireos but are less often used by black-capped vireos. Juniper woodlands have closed canopies and often contain fewer edges and openings, which possibly confers safety from predators (Blouin-Demers and Weatherhead 2001) and cowbirds (Howell et al. 2007). However, it is not known whether white-eyed vireos select more densely wooded nest sites and experience greater daily nest survival.

Arrival date at breeding sites and length of the breeding season can influence productivity for avian species. Black-capped vireo nests initiated earlier in the season have lower rates of predation (Sperry et al. 2008) and brood parasitism (Boves et al. 2014, Campomizzi et al. 2013). White-eyed vireos typically arrive earlier in Texas than black-capped vireos (eBird 2015), although earlier arrival may not indicate earlier initiation of breeding. In addition, longer nesting seasons can allow additional nesting attempts following nest failure which numerous studies have shown influences variation in reproductive output (Pease and Grzybowski 1995, Dececco et al. 2000). If white-eyed vireos arrive earlier at the breeding sites and initiate nests prior to black-capped vireos, they may have an increased opportunity for renesting as well as decreased risk of predation and parasitism, thereby increasing reproductive output relative to black-capped vireos.

A second, non-mutually exclusive possibility is that the more common white-eyed vireo is limiting the black-capped vireo through interspecific competition. Interspecific aggression and territoriality is known to occur between other vireos (Rice 1978, Robinson 1981), and black-capped and white-eyed vireos overlap significantly in their use of nest sites and food resources, with both birds constructing similar nests in the shrub layer and primarily consuming insects

during the breeding season. White-eyed vireos (10.0 – 12.5 g) are slightly larger than black-capped vireos (8.8 – 9.2 g), and so may be competitively dominant (Hopp et al. 1995, Grzybowski 1995). However, evidence indicating direct competition between black-capped and white-eyed vireos is conflicting. Early research detected no evidence of aggression between the two species, even when territories overlapped (Graber 1961). However, a later review noted instances of mutually exclusive territories and cautioned against overlooking the prospect of interspecific territoriality mediated by agonistic encounters (Grzybowski 1995). The use of juniper woodland, in addition to shrubland, by white-eyed vireos could be explained by a despotic distribution where white-eyed vireos are able to monopolize higher-quality habitat due to their earlier arrival and larger size, thereby reducing the reproductive potential of the black-capped vireo. A true test for interspecific competition between these two species (e.g. a removal experiment) was not possible here due to logistical constraints. However, widespread or strong displays of aggressive behavior between the species would be a strong indication that interspecific competition is possible, while conversely, absence of such aggression would suggest that these two vireos are not in direct exploitative competition.

While previous studies have used white-eyed vireos as a comparison species when studying black-capped vireos (Barber and Martin 1997, Farrell et al. 2011, Campomizzi et al. 2013) little work has addressed the central question of what factors make one of these species common and the other rare. Campomizzi et al (2013) found that black-capped vireos had higher parasitism rates and lower nest success relative to co-occurring white-eyed vireos, which could explain the differences we see in the abundance and distribution of the two species, but did not identify which ecological factors explain this difference. Here I examine the reproductive ecology of these two species, in sites where their ranges and territories overlap, in order to assess

potential ecological factors that might explain this difference. I first aim to determine whether the timing of breeding or the selection of habitat differs between the species. Second, I examine how differences in timing or breeding habitat influence nest survival in the two species. Finally, I experimentally test whether interspecific aggression (which could implicate interspecific competition) is occurring between black-capped and white-eyed vireos.

METHODS

Field Methods

Study sites – All field work was conducted at the Fort Hood military installation, a large (~88,500 ha) US Army base in central Texas. Fort Hood likely houses the largest population of black-capped vireos under a single management agency (Cimprich and Kostecke 2006), as well as a substantial number of white-eyed vireos (D. Cimprich, unpublished data). Fort Hood's large population of black-capped vireos is attributed to large amounts of undeveloped areas, including shrublands, and to an intensive cowbird removal program. In 2013, I conducted all field work on a single study site on the eastern portion of the base ("East Range"). This study site is within the area of cowbird control, and so nest parasitism is rare. In 2014, I collected data at the East Range site as well as an additional site ("Royalty Ridge") located on the western side of the base. This study site is outside the area of cowbird control, and consequently, cowbirds are much more common. Both sites contained areas of early successional, primarily deciduous, shrubland as well as closed canopy woodland dominated by mature juniper trees (typically >5 m in height). At these study sites, as well as throughout Fort Hood and the surrounding landscape, these two habitat types exist in relatively well-defined habitat patches which are easily distinguished on the ground and through aerial imagery.

At both the East Range and Royalty Ridge sites, I conducted point count surveys to document settlement patterns in shrubland and woodland habitats, searched for and monitored nests to assess nest survival, measured vegetation characteristics at nest sites to determine if nest placement differed between the species, and conducted interspecific reciprocal playback trials to test for the presence of interspecific aggression.

Point count surveys – I conducted repeated point count surveys in the early spring of 2014 to collect data on arrival dates and territory-scale settlement patterns with respect to habitat. For each study site, I used ArcGIS (ESRI 2011) to create a grid of points 200 m apart with a random starting point. From this grid, I selected 16 points on and around each study site (for a total of 32 points) to serve as point count survey stations. These stations covered a range of open shrubland to closed canopy woodland. Because I were interested in how birds selected habitats, I balanced the number of stations between shrub and wooded habitats at each site.

A single experienced observer (DGK) conducted point count surveys at each point count station at least once per week from 12 March to 29 April. This time period spans from before any vireos were present to when settlement of both species appeared to be approaching an asymptote. I surveyed the set of points at one site in a morning, and typically surveyed the set of points at the other site the following morning (this set of surveys of both sets of points within a short period of time constituted a “visit”). All surveys were conducted within four hours of sunrise. I counted and recorded the distance to singing male black-capped and white-eyed vireos during a 3-minute count period. I measured distances with a laser range-finder when I could see the bird or identify the shrub or tree the bird was singing from, and estimated distances by ear only when a direct line of sight could not be established. I also recorded weather variables for use as detection covariates (Table 1).

While I did not conduct formal point count surveys in 2013, I did note when the first individuals of each vireo species were detected on the East Range study site. To examine how the arrival dates I observed on my sites during the two years of my study compared to a wider range of years, I examined eBird records (Sullivan et al. 2009) from the period 2010 to 2015 in Bell and Coryell counties (the two counties in which Fort Hood is located). I compared the

earliest reported occurrences of each species in either of the two counties for each year, and calculated an average recorded arrival date for each species over this period.

Nest searching and monitoring – I searched for and monitored nests of both species in both years. I considered nests failed if they contained only dead nestlings, if evidence of depredation (destroyed nest, egg shell fragments) was present, or if they were empty before the nestlings could be expected to survive outside the nest. I tested for clutch abandonment when an incubating adult was not seen on a nest with eggs two checks in a row, or when a cowbird egg appeared in a vireo nest. I considered nests successful if any of the following observations were made in the vicinity of the nest: young fledglings detected, adults carrying food, or adults scolding intensely on at least 2 separate days after the presumed fledging.

I recorded the parasitism status at nest checks. Cowbird eggs and nestlings are readily distinguished from vireos. Cowbird eggs are noticeably larger, and heavily speckled with brown, whereas black-capped vireo eggs are usually unmarked and white-eyed vireo eggs are only lightly marked with brown or black spots. Cowbird nestlings are covered in down after hatching, while nestlings of both vireo species never appear downy. I continued monitoring parasitized nests until they failed or fledged young of any species, although I considered these nests failed due to parasitism if all host young died.

Vegetation sampling – After nests became inactive, I returned and measured vegetation characteristics following a modified version of the BBIRD protocol (Martin et al. 1997). I measured habitat variables at the nest site and within three circular plots (5 m, 11.3 m, and 30 m radii) centered on the nest. The full list of characteristics measured is collected in Table 2.

I estimated canopy closure at the nest site using an ocular sighting tube by standing at the nest site and pointing the tube upward ($>45^\circ$ angle) in a random direction 20 times and recording the number of times the crosshairs “hit” foliage. For ground cover within the 5 m plot, the ocular tube was pointed in a random direction at the ground within the plot 50 times, and I recorded the number of “hits” in various categories of vegetation <0.25 m high, bare soil, or bare rock. Within the 11.3 m plot, I counted all trees (based on DBH size classifications) and collected an index of shrub cover. I operationally defined shrub cover as any branches or stems with leaf cover within the zone between 0.25 and 2.0 m high, which represents vegetation that vireos could potentially nest in. Shrub cover was quantified as the percent of the length of two transects which intersected with shrub cover. These two transects were along two perpendicular diameters of the 11.3 m plot.

Playback trials – I conducted playback experiments in 2014 to assess the response of territorial male black-capped and white-eyed vireos to the presence of conspecifics and heterospecifics. I observed male vireos to assess the approximate location and boundaries of the male’s territory and then carried out the playback experiment within each territory. Each trial tested a single male vireo over the course of two sessions, separated by at least 1.5 hours and not more than two days. Each session consisted of a northern cardinal (*Cardinalis cardinalis*, hereafter “cardinal”) song to act as a control, followed by a song from either a conspecific or heterospecific male vireo, determined at random. The second session of a trial consisted of another period of cardinal song, followed by song of the species not played during the first session. Individual sessions each consisted of a total of 6 minutes of song playback, with a 1

minute pause (to observe and record behavior) in the middle of the playback for each species and between cardinal and vireo song playback.

For each playback trial, I randomly selected playback tracks from a pool of six black-capped vireo songs, seven white-eyed vireo songs, and three northern cardinal songs. All playback tracks were recorded locally at Fort Hood and contained no heterospecific vireo song or scolding calls in the background. Songs were played back using a cell phone music player application (Apple iPhone 4) and a portable, 9-volt battery powered speaker (RadioShack mini audio amplifier/speaker) which was placed on the ground and obscured by vegetation approximately 6 m away from the observer. All playback tracks were broadcast at volume levels approximately matching that of an actual bird of the appropriate species.

During a session, I recorded when the target vireo displayed any of the following aggressive behaviors: counter-singing with the playback, approaching within 6 m of the playback speaker, and approaching within 1 m of the speaker. Because I considered it an unambiguous sign of aggression, and to avoid unnecessary harassment of breeding vireos, I concluded trials immediately when the target approached within 1 m of the speaker.

Statistical Analyses

Point count surveys – I used distance sampling methods to model the point count data in R 3.1.3 (R Core Team 2015) using the package unmarked. This allowed me to estimate vireo abundances at different times and in different habitat types during the settlement and early breeding periods. This package uses N-mixture models to model abundance and detection probability simultaneously (Fiske and Chandler 2011, Royle et al. 2004). Because point count

stations were located 200 m apart, I truncated detections at 100 m to increase the independence of individual counts.

I compiled a list of 8 variables that I suspected might influence detection probability, abundance, or both (Table 1). These variables were divided into four categories: habitat, spatial, temporal, and weather. Habitat type was a categorical factor based on whether area surrounding the point count station was primarily woodland or shrubland. I derived this variable by examining digital aerial orthophotos in ArcGIS and classifying a point based on the appearance of the vegetation within 100 m of the point count station. Visit number represented the temporal aspect of my surveys.

I analyzed the point count data for each species separately. In order to avoid comparing all possible combinations of detection and abundance variables, I took a hierarchical model selection approach. In the first stage, I identified the detection function and covariates that best described the observation process. In the second stage, I compared models to identify which habitat and temporal variables were important in predicting the abundance of black-capped and white-eyed vireos. Because I conducted surveys before the vireos arrived, several visits resulted in no detections of any vireos. I therefore only included data from visits where I detected >1 vireo of the species in the current analysis. I removed only the first visit for white-eyed vireos and removed the first three visits for black-capped vireos.

I evaluated the effects of habitat type, point count visit number, and study area on abundance. Because I hypothesized that abundance might differ between habitats at different times in the season, I also compared additive and interaction models of the temporal and habitat effects. I took an information theoretic approach to compare the relative support for the models based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002). I also used a

bootstrapped goodness-of-fit χ^2 test to assess overall fit of any models I drew inferences from. I estimated mean and 95% confidence intervals for vireo abundance at points within the two habitat points over the course of the settlement period.

Nest Monitoring – I modeled daily survival of nests using PROC GENMOD in SAS 9.4 (SAS Institute, Cary, North Carolina) using Shaffer's (2004) method of logistic exposure. I compiled an *a priori* list of variables I suspected might influence daily survival. I considered 6 habitat variables, including 4 composite variables derived from a principal component analysis (PCA; Table 3) of nest vegetation (see below) as well as categorical habitat variables that could not be incorporated into the PCA. The categorical habitat variables were the nest substrate category (broadleaf or juniper) and coarse habitat type (shrubland or woodland). Julian date and year (2013 or 2014) were included as temporal variables in my models. I also evaluated the effect of study area (representing parasitism risk) on daily survival and the species the nest belonged to.

I took two steps to reduce the number of candidate models ultimately considered. First, I used a hierarchical variable selection approach. I assessed relative support for a set of six single-variable habitat models, moving those within $2\Delta AIC_c$ of the top model forward, and removing habitat variables represented by the low ranked models from consideration. Second, where I hypothesized interaction effects where plausible, I evaluated pairs of additive and interaction models and only retained the best supported of a pair (Anderson 2007, Arnold 2010).

The four interaction models I examined included three models in which species interacted with another variable (Julian date, the composite variable representing habitat maturity, and study area), and a fourth model where day of season interacted with habitat maturity. These

models represented the hypotheses that the effects of day of season, habitat maturity, and study area on the daily survival rate differed depending on the species, any of which would be evidence of differing ecological specialization between the two species. I evaluated the interaction between day of season and habitat maturity to examine support for the hypothesis that the safety of a habitat may change throughout the season.

Next I constructed a final candidate model set composed of combinations of variables that were retained from the habitat subset and the other variables from my *a priori* list (Table 4). I examined only models which had biologically plausible underpinnings, and compared support for these models based on AIC_C (Burnham and Anderson 2002). I also included an intercept-only, or constant-survival model. I used a χ^2 test of the global model to assess overall model fit. Using this final candidate model set, I calculated model-averaged parameter values as well as unconditional variance (Burnham and Anderson 2002, Grueber et al. 2011). I calculated both daily survival rates (DSR, the probability that a nest survives one day) and nest survival rates (NSR, the probability that a nest survives the entire nesting period) for the parameters of interest across the ranges in which I observed them.

I used species-specific averages of incubation and nestling periods in my calculation of nest survival rates. For nests in which I observed the entire incubation or nestling stages, I calculated the total length of these periods. When eggs hatched between checks, I used the size and development of the nestlings as a guide to determine their age. If I were unsure how old the nestlings were, I used the midpoint between the two nest checks as the presumed hatch date. I calculated the average length of the entire nesting cycle for each species by combining the average lengths of the incubation and nestling periods and adding two days to account for the

laying period, as the median clutch size for each species was 4 eggs, and each species typically begins incubation when the penultimate egg is laid (Grzybowski 1995, Hopp et al. 1995).

Vegetation sampling –I selected 24 numerical vegetation variables to use in my analyses of nest vegetation characteristics (Table 2). I chose the characteristics that I judged had the most potential to influence nest success, represented predicted differences in habitat selection between the species, or were expected to typify the different habitat types in which I searched for nests (woodland and shrubland). I conducted all of my vegetation analyses in R 3.1.3 (R Core Team 2015). Prior to analyses, I log transformed data which did not meet normality and variance assumptions. I examined pairwise correlations and, from pairs that were highly correlated ($r > 0.6$), I removed one variable.

First, I used MANOVA (multivariate analysis of variance) to determine whether the two species differed in overall nest site characteristics. I followed this with univariate linear modeling to test for differences between individual nest-site characteristics. I adjusted the alpha level using the Dunn-Sidak method to control the experiment-wide false discovery rate (Gotelli and Ellison 2004). For vegetation characteristics which differed significantly between the species, I examined means and standard deviations.

I also employed PCA, in order to construct composite nest site vegetation variables for use in the nest survival analysis, as described above (psych package; Revelle 2015). Based on a scree plot of the eigenvalues of each component in order of extraction, I retained four principal components (PC1 to PC4) as composite variables (McGarigal et al. 2000). These four components represented 42.2% of the variability of the original set of nest site characteristics. I examined the loadings of each original variable on the retained components in order to attribute

biological meaning to the components (Tabachnick and Fidell 1989). Based on these loadings, PC1 represents a gradient from shorter, mid-successional vegetation to taller more mature vegetation (Table 3). PC2 to PC4 were ultimately poor predictors of nest survival, and so their interpretations are not further described here. I output a score for each nest on each retained principal component, and used these scores as variables in my nest survival analysis, as described above.

Reciprocal Playback Trials – I used PROC GLIMMIX in SAS 9.3 to fit a logistic regression model with a binomial distribution and a logit link to the playback trial data. I used the target vireo's behavior (presence/absence of aggressive response) as the response variable. I parametrized the model with the additive effects of song type and species of the target vireo. To avoid pseudoreplication (Hurlbert 1984) due to repeatedly testing the individual target males with different playback types, I specified vireo identity as a random effect. I calculated parameter estimates and standard errors for the effects of species and song type and examined p-values for Type III tests of fixed effects.

RESULTS

In 2014, I conducted a total of 256 point count surveys over the course of seven weeks, representing eight sets of surveys each at the Royalty Ridge and East Range study sites. In 2014, the first white-eyed vireo was detected on 17 March and the first black-capped vireo was detected on 28 March. In 2013, I first detected white-eyed vireos on 12 March, and the first black-capped vireo on 16 March. eBird records of arrival dates in Bell and Coryell counties from the period 2010 to 2015 were similar to mine (Figure 1).

Habitat and temporal effects were present in the best supported models of black-capped vireo abundance (Table 5). Across all visits, black-capped vireo abundance was greater in shrubland than in wooded habitats (Figure 2). Habitat type appeared in the two top models, which were the only competitive models (ΔAIC of < 2.0). In contrast, white-eyed vireo settlement was primarily a function of time (Table 5), and estimated abundance was similar in both habitat types (Figure 2). Although habitat type was present in the second most supported model (ΔAIC of 1.71), the single-variable model for habitat type ranked very poorly (ΔAIC 69.47).

Nest site characteristics differed between black-capped and white-eyed vireos (MANOVA; Pillai's Trace = 0.413, $p \ll 0.001$). Univariate linear modeling identified differences between nests of the species in seven of the 24 habitat characteristics I compared (at the Dunn-Sidak adjusted alpha level of 0.002), all of which were associated with vegetation height and/or successional maturity (Table 6). Many of the nest site characteristics which differed were also strongly associated with the PC1 composite variable constructed for my nest survival analysis (Table 3). As predicted, the differences indicated that white-eyed vireos tended to nest in taller,

more closed, later successional (i.e. more woodland-like) habitats, although I saw considerable overlap in habitat use.

I found 145 black-capped vireo (n=82) and white-eyed vireo nests (n=63). These nests are broken down by study site and habitat type in Table 7. The apparent survival rate for black-capped vireos nests was 29.1% compared to 47.6% for white-eyed vireo nests. On the East Range study site (with active cowbird control), I observed no instances of nest parasitism, for each species, in either year (0 of 91 nests). In 2014 on the Royalty Ridge study site, I observed cowbird eggs or nestlings in 54.3% of black-capped vireo nests (19 of 35), while only 5.6% white-eyed vireo nests I found contained a cowbird egg (1 of 18). Of the 19 parasitized black-capped vireo nests, 9 were abandoned (47.4%), 5 accepted the egg but were depredated (26.3%), 1 failed due to direct effects of the cowbird nestling (5.3%), 3 successfully produced fledgling cowbirds (15.8%), and 1 nest, in which the cowbird egg failed to hatch, successfully produced black-capped vireo fledglings (5.3%). The parasitized white-eyed vireo nest was depredated during the incubation stage. At East Range, in the absence of cowbird parasitism, the apparent survival rate for white-eyed vireo nests was 46.7% (21 of 45) while that for black-capped vireos was 32.6% (15 of 46).

I observed complete incubation periods for 34 black-capped and 28 white-eyed vireo nests, and complete nestling periods for 19 black-capped vireo nests and 22 white-eyed vireo nests. For black-capped vireos, the mean incubation period lasted 14.8 days, and the mean nestling period was 11.0 days, resulting in an overall nesting cycle length of 27.8 days. For white-eyed vireos, the mean incubation period lasted 13.9 days, and the mean nestling period was 10.6 days, resulting in an overall nesting cycle length of 26.5 (~1 day shorter).

I know the precise initiation date for 99 nests which I monitored during the laying period. Using the nesting cycle lengths described above, I were able to estimate nest initiation dates for 35 additional nests. White-eyed vireos began initiating clutches earlier than black-capped vireos, and the pulse of first nesting attempts for white-eyed vireos was earlier than that for black-capped vireos (Figure 3). The first 10% of white-eyed vireo nests were initiated 8 days earlier than the first 10% of black-capped vireo nests (Julian day 99 for white-eyed vireos, compared to day 107 for black-capped vireos).

Of the total nests found, 143 were used in logistic exposure analysis (n=2195 exposure days). Daily survival was best explained by the effects of day of season and the composite variable representing habitat maturity (PC1), with these variables included in all top ranked models (Table 4). Day of season had a negative effect on survival ($\beta = -0.011$, 95% CI: -0.021 to -0.001), while habitat maturity (as measured by PC1) had a positive effect ($\beta = 0.255$, 95% CI: 0.009 to 0.501). Consequently, the daily survival rate of nests decreased over the course of the season, and was higher for nests in areas characterized by later successional vegetation (Figure 4). Species was also present in competitive models, although the confidence interval for this effect encompassed zero ($\beta = -0.402$, 95% CI: -1.205 to 0.400). Estimated daily survival for white-eyed vireo nests was numerically higher at all values of day of season and PC1, although the confidence intervals of the daily survival rates for the two species overlapped (Figure 5). The model-averaged daily survival rate for black-capped vireos was 0.954 (95% CI: 0.940 to 0.965) while white-eyed vireos had a daily survival rate of 0.966 (95% CI: 0.952 to 0.976). Factoring in the average lengths of the nesting cycle for the two species magnifies this difference. Using model-averaged daily survival rates and my species-specific estimates of nest cycle length, I estimated overall nest survival at 26.9% (95% CI: 17.8% to 36.8%) for black-

capped vireos compared to a 40.2% (95% CI: 27.3% to 52.8%) for white-eyed vireos. Study area, which is related to cowbird abundance and parasitism risk, and year did not appear in any highly ranked models.

I tested $n = 16$ male vireos (8 of each species) for the presence of interspecific aggression. There was no significant overall difference in responses to playback stimuli between black-capped and white-eyed vireos ($\beta = -1.96$, 95% CI: -4.54 to 0.61). Vireo responses to heterospecific playback were indistinguishable from responses to control playback (cardinal song; $\beta = -0.749$, -3.712 to 2.215). I observed an aggressive response at only 1 of 16 (6.3%) of heterospecific and 1 of 32 (3.1%) of control playback trials. In contrast, vireos responded strongly to conspecific playback as compared with heterospecific playback ($\beta = 4.50$, 95% CI: 1.66 to 7.35). I observed an aggressive response at 12 of 16 conspecific playback trials (75.0%).

DISCUSSION

I found that, compared to the widespread and common white-eyed vireo, imperiled black-capped vireos arrived later at the breeding grounds, exhibited more restricted nest habitat preference, and suffered higher rates of brood parasitism. Black-capped vireo apparent and estimated nest success was numerically lower, and although the difference I observed was not statistically significant, others have documented significantly lower daily nest survival rates for black-capped co-occurring with white-eyed vireos in central Texas (Campomizzi et al. 2013). White-eyed vireos were more likely to nest earlier in the season and in more wooded habitats, both of which have been shown to have reduced risk of predation (Sperry et al. 2008) and parasitism (Boves et al. 2014). The difference in nest survival between the two species (~13% estimated, and ~19% apparent) may seem minor, but even relatively small differences in reproductive output at individual nests could be magnified over the course of the lifetime of bird. Even if both species have comparable adult survival rates, small differences in reproductive output could have substantial impacts on population viability.

The earlier and extended breeding season exhibited by white-eyed vireos could confer numerous advantages. The activity of ratsnakes (*Elaphe* spp.), the major predator of black-capped vireo nests (Stake and Cimprich 2003), is constrained by temperature and early season nests are less likely to be depredated (Sperry et al. 2008). Early season nests are also rarely parasitized by cowbirds (Boves et al. 2014, Campomizzi et al. 2013) likely because cowbirds at Fort Hood do not begin laying eggs until mid-April (S. Summers, personal communication). My data show that white-eyed vireos arrive at the breeding site earlier than black-capped vireos, initiate nests earlier, and have an earlier pulse in clutch initiations. Consequently, proportionately

more white-eyed vireo nests were initiated during the safest part of the breeding season. In addition, white-eyed vireos continued initiating new clutches at least as late in the season as black-capped vireos, suggesting that their breeding season is actually longer and not just shifted (Figure 3). Although daily survival declined across the season, some of the late season and second brood nests I monitored of both species did successfully fledge young. By extending their nesting season, white-eyed vireos may be able to attempt more nests and thereby increase productivity.

White-eyed vireos also exhibited a broader range of habitat use than black-capped vireos, both at the territory and nest site scale. My data suggest that white-eyed vireos selected territories without apparent preference to habitat type, settling in relatively equal numbers in shrubland and woodland habitats. The more specialized black-capped vireo, which settled in greater numbers in shrubland habitat, may be more habitat limited. Shrubland birds have experienced declines across the US (Askins 1998, Brawn et al. 2001) and habitat loss has been implicated as one of the primary threats to black-capped vireo populations (USFW 1991). White-eyed vireos' ability to nest in a variety of habitat types likely buffers them from the otherwise deleterious impacts of reduced shrubland habitats.

Black-capped vireo nests were parasitized at a higher rate than white-eyed vireo nests on my study site which lacked cowbird control. Previous studies also found higher parasitism rates for black-capped vireos compared to co-occurring white-eyed vireos (Campomizzi et al. 2013, Barber and Martin 1997), although the magnitude of the difference was not as great. The difference I saw in parasitism rates could be due to the cowbird's preference for habitats with openings and edges (such as shrublands) over closed canopy forests (Howell et al. 2007, Brittingham and Temple 1983), which more closely aligns with the black-capped vireo's

tendency to nest in shrubland habitats. On my study area, female cowbirds were often seen in shrubland areas perched on top of snags and other tall objects. These perches provide good visibility and may allow cowbirds to find nests more easily in shrubland. My results reinforce the idea that cowbird control programs are effective at greatly reducing the parasitism rate of black-capped vireo nests, and can be a valuable tool in black-capped vireo recovery.

In spite of the dramatic difference in parasitism rates I saw between the species, parasitism risk was not highly supported as a factor influencing daily nest survival. This suggests that the effect of predation was more important than parasitism in driving nest success on my study sites. I saw relatively few nests fail due to direct effects of parasitism (e.g. abandonment of nests or starvation of vireo nestlings) and many parasitized nests were ultimately depredated, which may explain this pattern. Unfortunately, I was only able to collect data on parasitism rates at one site in one year, and so care must be taken in interpreting my results on parasitism. However, white-eyed vireo nest survival appeared higher even at the study site with cowbird control. This also indicates that, while parasitism undoubtedly plays a role, additional factors are contributing to the reduced nest success of the black-capped vireo relative to its common congener.

I did not find evidence of direct interference competition between white-eyed vireos and black-capped vireos. The absence of aggressive behaviors in the presence of simulated heterospecific intruders suggests that any interspecific competition, if present, is not mediated by agonistic interaction. Without the presence of aggressive interactions or evidence of exclusion, direct exploitative competition is unlikely. Scramble competition and apparent competition, however, could conceivably still be involved. A more rigorous evaluation of competition would require experimental manipulation (e.g. a removal experiment), which was logistically

prohibitive for this project. While I cannot conclude that no form of interspecific competition is affecting black-capped vireos, my results do suggest that interspecific interference competition is unlikely to be the major force currently limiting the black-capped vireo.

What constrains the reproductive timing and habitat use of black-capped vireos? The fact that black-capped vireos do not arrive and begin breeding earlier, despite the reproductive advantage this could confer, would suggest that some cost is limiting their reproductive timing. One possibility is that conditions on the black-capped vireo's wintering grounds constrains arrival on the breeding grounds. Body condition and fat reserves, which allow birds to initiate migration and arrive on the breeding grounds earlier, can be influenced by conditions on the wintering grounds (Marra et al. 1998, Bearhop et al. 2004). The wintering range of the black-capped vireo (the Pacific coast of Mexico; (Grzybowski 1995) does not overlap with that of the white-eyed vireo (Hopp et al. 1995), and so differing conditions at the wintering grounds for the two species may impact arrival times. Another, non-mutually exclusive possibility is that white-eyed vireos, with their higher body mass and lower surface area to volume ratio, may be able to withstand cold weather better than black-capped vireos. Consequently, early arrival may be less risky and energy intensive for white-eyed vireos, which would allow them to better take advantage of the part of the nesting season where the risk of predation is lowest.

Research into why black-capped vireos appear to select lower quality habitat may also be a productive area of future research. One possibility is that the black-capped vireo's habitat preference is a conserved trait, shaped under conditions which differ from the present. Modern shrublands likely differ from historical shrublands in several important ways, which may make them more risky nesting habitat. Parasitism and predation pressures have likely increased due to expanding cowbird populations (Lowther 1993) and the combined effects of loss and

fragmentation of shrubland habitat. It is also possible that black-capped vireos are specialized to exploit aspects of shrubland habitat that are not related to nest safety, and these counterbalance the selection pressure of increased predation and parasitism. For instance, black-capped vireos consume notable amounts of orthopterans (Graber 1961, Grzybowski 1995), which make up only a minor part of the diet of white-eyed vireos (Hopp et al. 1995). Orthopterans may be more abundant in shrublands with grassy openings, and black-capped vireos could take this or other benefits into account when selecting breeding habitat.

I believe these results have several important implications for conservation of black-capped vireos. My results further support carefully designed and executed cowbird control programs as effective means of decreasing brood parasitism rates for black-capped vireos. Because black-capped vireos appear to suffer particularly high rates of cowbird parasitism, cowbird control can be an effective conservation tool. Instituting cowbird control programs similar to the one in place at Fort Hood at other locations with significant vireo habitat would also likely increase local reproductive rates. Additionally, my results reinforce the importance of habitat in the conservation of black-capped vireos. Given that black-capped vireos demonstrate a strong preference for shrubland habitats, reducing further fragmentation of existing shrubland and increasing the patch size of newly created habitat would confer reproductive benefits and may be the best way to aid in achieving population recovery goals.

SUMMARY

Black-capped vireos and white-eyed vireos are closely related and ecologically similar. Despite their similarities, white-eyed vireos are widely distributed and common, whereas the black-capped vireo has a restricted breeding range and is federally endangered. In this thesis, I address this apparent paradox with a comparative ecological study of co-occurring black-capped and white-eyed vireos. I studied vireos in shrublands and woodlands in central Texas, USA in 2013 and 2014. I used point count surveys and nest monitoring to determine arrival dates, settlement patterns, nest site selection, and, ultimately, nest survival relative to temporal and habitat factors. Additionally, I conducted reciprocal playback trials to test for the presence of interspecific aggression. White-eyed vireos arrived first and established territories in shrub and woodland habitat with equal probability. Black-capped vireos arrive after white-eyed vireos and settled in greater numbers in shrubland habitat. White-eyed vireos begin initiating nests earlier than black-capped vireos and selected nest sites surrounded by taller, more mature, and more densely wooded vegetation. Playback trials failed to detect evidence of interspecific aggression, suggesting that competition with white-eyed vireos is not currently limiting black-capped vireos. For both species, nest survival declined as the season progressed, and was greater for nests in taller, more mature habitat. Black-capped vireo nests were also parasitized at a higher rate by cowbirds, except where cowbird control programs were in place. Accordingly, overall nest survival appeared greater for white-eyed vireos than black-capped vireos suggesting that the flexibility demonstrated by white-eyed vireos in where and when they nest confers a reproductive advantage. Based on my results, several management recommendations can be made. First, as well designed cowbird control programs are effective at reducing parasitism rates

of black-capped vireo nests, their implementation should be considered at significant patches of habitat. Second, I conclude that the comparatively narrow habitat preferences demonstrated by the imperiled black-capped vireo necessitates a focus on habitat conservation and improvement as a means to increase populations and meet management goals.

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TABLES AND FIGURES

Tables

Table 1. Variables used in models explaining vireo detection and abundance at point count stations in central Texas in 2013 and 2014, categorized by type. Marks in “p” and “λ” indicate that variables were included in analyses as covariates of detection or abundance, respectively.

Variable name	<i>p</i>	<i>λ</i>	Description
Habitat	✓	✓	Major habitat type within 100 m (shrubland or woodland)
StudyArea		✓	East Range or Royalty Ridge study area
Visit		✓	Visit number, a measure of seasonality
Time	✓		Minutes after local sunrise
Wind	✓		Approximate wind speed according to Beaufort Scale
Temp	✓		Air temperature (°C)
Precip	✓		Precipitation (none or light)
Sky	✓		Cloud cover (clear, scattered, broken, overcast)

Table 2. Vegetation characteristics measured at vireo nests in central Texas in 2013 and 2014.

Characteristic	Description
<u>Nest site</u>	
NstHt	Nest height, measured from ground to rim of nest cup
ForkDiam	Diameter of nest fork
Supp	Number of supporting branches the nest was woven into
DistCntr	Distance from nest to center of substrate shrub or trunk of substrate tree
DistOpn	Distance from nest to nearest opening. Typically either edge of shrub clump in open areas or a gap >1.5 m across extending from canopy to ground in woodland areas.
AbvCvr	Percent of nest obscured from 1 m above
SCvrAvg	Average percent of nest obscured from 1 m away in the 4 cardinal directions
SubstHt	Height of nest substrate
CanClo	Percent canopy closure at nest site, as measured with ocular tube
<u>5 m plot</u>	
Grass	Percent of ground covered by grass
Log	Percent of ground covered by dead wood
Litter	Percent of ground covered by leaf litter
Bare	Percent bare earth
Shrub	Percent of low shrub cover (<0.25 m high)
Rock	Percent bare rock
<u>11.3 m plot</u>	
CanHt	Canopy height of 11.3 m plot
ShrbCvrBrd	Amount of broadleaf shrub cover (leafy vegetation 0.5-2 m high) present
BrdTrees	Total number of broadleaf trees (>10 cm in DBH) present
JunTrees	Total number of Juniper trees (>10 cm basal diameter) present
DeadTrees	Total number of snags and stumps (>10 cm in diameter) present
<u>30 m plot</u>	
LogDist	Distance from nest to nearest log (>10 cm in diam)
LogDiam	Diameter of log nearest to nest
TreeDist	Distance from nest to nearest tree (>10 cm in diam)
TreeDiam	Diameter of tree nearest to nest

Table 3. Results from principal component analysis of black-capped and white-eyed vireo nest placement and vegetation at Fort Hood, Texas in 2013 and 2014. Loadings of original habitat variables on the first four principal components (PC1-PC4) are listed. Significant loadings are indicated in bold.

Variable	PC1	PC2	PC3	PC4
<u>Nest site</u>				
NstHt	0.63	-0.12	0.08	0.10
ForkDiam	-0.11	-0.01	0.45	-0.06
Supp	-0.12	-0.22	0.03	-0.16
DistCntr	0.12	0.24	0.63	0.31
DistOpn	0.64	-0.31	-0.15	-0.12
AbvCvr	-0.04	-0.04	-0.03	-0.08
SCvrAvg	-0.25	0.13	0.27	-0.16
SubstHt	0.40	-0.05	0.46	0.43
CanClo	0.64	0.01	0.18	0.32
<u>5 m plot (ground cover)</u>				
Grass	-0.43	0.53	0.30	0.04
Log	0.10	0.38	-0.49	0.25
Litter	0.32	-0.79	0.27	0.09
Bare	0.02	0.66	0.25	-0.19
Shrub	-0.32	0.26	-0.57	0.03
Rock	0.23	0.04	0.16	-0.51
<u>11.3 m plot</u>				
CanHt	0.72	0.34	-0.16	-0.01
ShrbCvrBrd	-0.23	-0.58	-0.19	0.34
BrdTrees	0.43	0.43	-0.14	0.28
JunTrees	0.65	-0.16	-0.15	-0.53
DeadTrees	0.50	0.15	-0.21	0.09
<u>30 m plot</u>				
LogDist	-0.15	-0.1	0.32	-0.50
LogDiam	0.13	-0.03	0.01	-0.04
TreeDist	-0.57	-0.31	0.00	0.32
TreeDiam	0.13	0.27	0.26	0.11

Table 4. Final set of candidate models explaining nest survival of black-capped and white-eyed vireos in 2013 and 2014 at Fort Hood, USA, ranked by AIC_c. Models indicated by * were compared to models including an interaction term of the same variables. Only the model with the lower AIC_c of a corresponding additive/interaction pair was included in the final candidate set.

Model	Deviance	K	AIC _c	ΔAIC _c	Weight
DOS+PC1*	621.731	3	627.742	0	0.36
Species+DOS+PC1	621.060	4	629.079	1.34	0.18
Species+DOS*	624.520	3	630.531	2.79	0.09
PC1+SubstTyp	624.836	3	630.847	3.11	0.08
Species	627.750	2	631.756	4.01	0.05
Species+Study Area*	625.963	3	631.974	4.23	0.04
PC1	628.228	2	632.234	4.49	0.04
SubstTyp	628.512	2	632.518	4.78	0.03
Species+PC1*	626.515	3	632.526	4.78	0.03
DOS	628.844	2	632.850	5.11	0.03
StudyArea	629.439	2	633.444	5.70	0.02
DOS+Year	627.457	3	633.468	5.73	0.02
Constant survival	632.258	1	634.260	6.52	0.01
Year	630.338	2	634.343	6.60	0.01

Table 5. Models of vireo abundance at Fort Hood, Texas in 2014. Covariates of abundance are indicated by $\lambda(\cdot)$, whereas those modifying detection are indicated by $p(\cdot)$. Number of parameters estimated (K), AIC values, model and cumulative weights are reported.

Black-capped vireo abundance and detection models						
Model	K	AIC	ΔAIC	Weight	Cumulative	
$\lambda(\text{Habitat}) p(\text{Habitat})$	4	450.71	0	0.60	0.60	
$\lambda(\text{Visit+Hab}) p(\text{Habitat})$	8	452.20	1.49	0.28	0.88	
$\lambda(\text{StudyArea}) p(\text{Habitat})$	4	454.18	3.47	0.11	0.98	
$\lambda(\text{Visit*Hab}) p(\text{Habitat})$	12	458.42	7.70	0.01	1	
$\lambda(\cdot) p(\text{Habitat})$	3	461.77	11.06	0	1	
$\lambda(\text{Visit}) p(\text{Habitat})$	7	463.26	12.54	0	1	
White-eyed vireo abundance and detection models						
Model	K	AIC	ΔAIC	Weight	Cumulative	
$\lambda(\text{Visit}) p(\text{Wind})$	13	930.70	0	0.69	0.69	
$\lambda(\text{Visit+Hab}) p(\text{Wind})$	14	932.41	1.71	0.30	0.99	
$\lambda(\text{Visit*Hab}) p(\text{Wind})$	20	939.16	8.46	0.01	1	
$\lambda(\text{StudyArea}) p(\text{Wind})$	8	990.14	59.44	0	1	
$\lambda(\cdot) p(\text{Wind})$	7	999.19	68.49	0	1	
$\lambda(\text{Habitat}) p(\text{Wind})$	8	1000.16	69.47	0	1	

Table 6. Mean and standard deviation nest placement and vegetation characteristics measured at black-capped (n=82) and white-eyed (n=63) vireo nests at Fort Hood, Texas in 2013 and 2014. Characteristics that differ significantly between species ($p < 0.002$, alpha corrected for 24 comparisons) are indicated in bold.

Variable	Black-capped Vireo		White-eyed Vireo		<i>p</i>
	Mean	SD	Mean	SD	
<u>Nest site</u>					
NstHt	1.07 m	0.38 m	1.45 m	0.39 m	<<0.0001
ForkDiam	4.70 mm	1.29 mm	4.79 mm	1.31 mm	0.6826
Supp	3.01	0.90	2.69	0.69	0.0213
DistCntr	1.11 m	0.58 m	1.08 m	0.51 m	0.7174
DistOpn	3.66 m	3.15 m	5.88 m	3.19 m	<0.0001
AbvCvr	57%	29%	51%	31%	0.2833
SCvrAvg	24%	15%	20%	14%	0.1262
SubstHt	2.66 m	1.07 m	3.64 m	1.57 m	0.0001
CanClo	68%	21 %	79%	14%	0.0009
<u>5 m plot (ground cover)</u>					
Grass	7%	11%	2%	4%	0.0001
Log	5%	6%	6%	7%	0.2134
Litter	55%	15%	62%	14%	0.0069
Bare	2%	4%	2%	4%	0.7853
Shrub	14%	11%	11%	8%	0.0959
Rock	6%	7%	7%	7%	0.7172
<u>11.3 m plot</u>					
CanHt	4.34 m	1.26 m	5.74 m	2.24 m	<0.0001
ShrbCvrBrd	56%	19%	60%	15%	0.1122
BrdTrees	1.99	2.67	4.64	6.35	0.0078
JunTrees	12.36	15.26	17.34	16.22	0.0600
DeadTrees	1.19	1.70	2.50	2.91	0.0008
<u>30 m plot</u>					
LogDist	6.90 m	4.63 m	5.68 m	4.29 m	0.0970
LogDiam	14.35 cm	5.99 cm	15.05 cm	6.29 cm	0.4941
TreeDist	5.22 m	5.15 m	3.88 m	4.50 m	0.1024
TreeDiam	19.9 cm	9.36 cm	20.83 cm	9.88 cm	0.5614

Table 7. Number of black-capped (BCVI) and white-eyed (WEVI) vireo nests monitored at Fort Hood, Texas broken down by study site and habitat type, with totals and subtotals indicated in bold. Nests were monitored at East Range in 2013 and 2014 and at Royalty Ridge in 2014.

Study Site	n
East Range	91
BCVI	46
Woodland	13
Shrubland	33
WEVI	45
Woodland	21
Shrubland	24
Royalty Ridge	54
BCVI	35
Woodland	12
Shrubland	23
WEVI	19
Woodland	16
Shrubland	3
Total	145

Figures

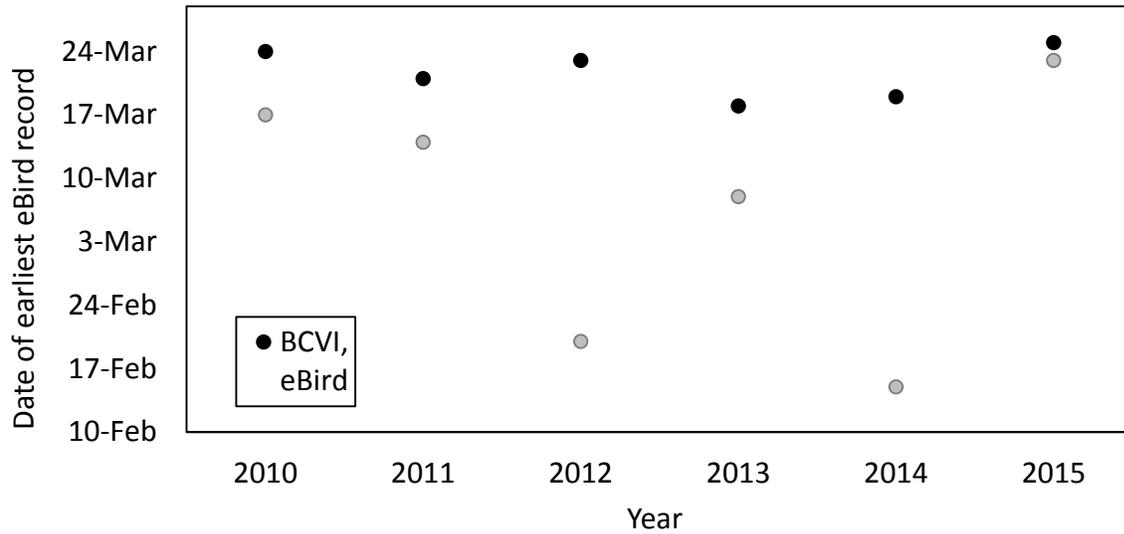


Figure 1. Date of the first sightings of black-capped (BCVI) and white-eyed (WEVI) vireos as reported to eBird for the period 2010 – 2015 (eBird 2015). Points represent the earliest reported sightings for a particular year in either Bell or Coryell counties in Texas. On average, white-eyed vireos were reported by 6 March, while black-capped vireos were not reported until 21 March (15 days later).

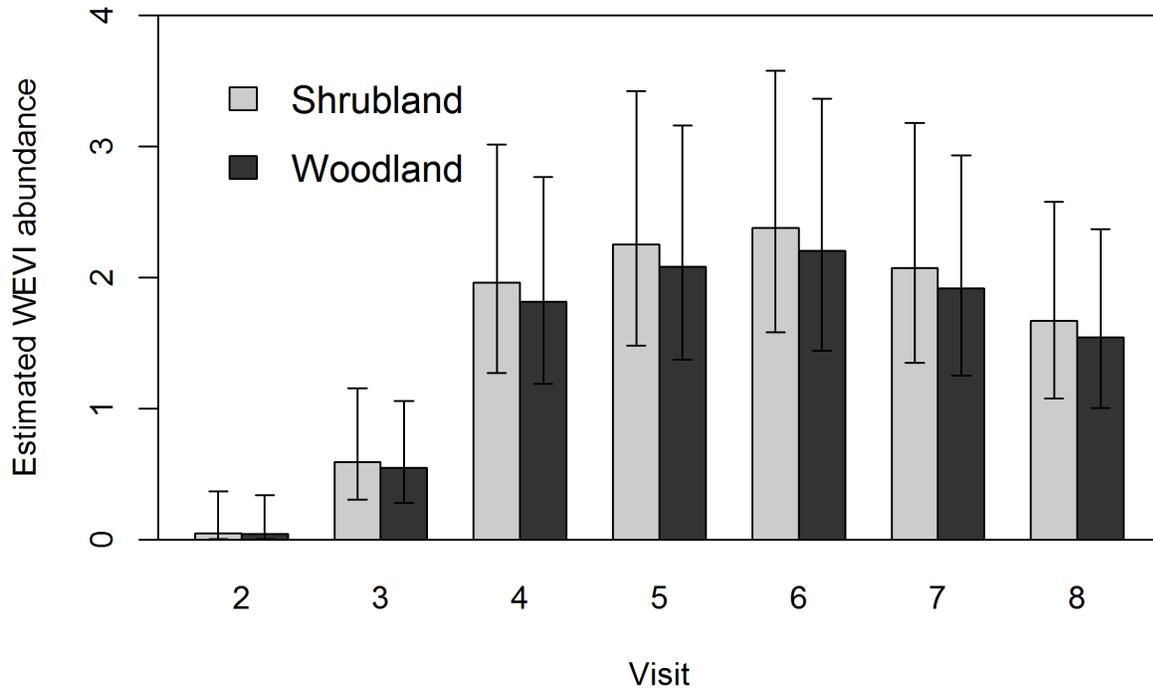


Figure 2. Estimated abundance (with 95 % confidence intervals) of white-eyed vireos (top) and black capped vireos (bottom) within 100 m of point count stations in shrubland and woodland habitats. Visits represent repeated point count surveys (~7 days apart) over the period of time from 17 March to 26 April at Fort Hood, Texas. Abundance estimates for each species were produced from models incorporating additive effects of visit number and habitat type, using the “lsmeans” package in R (Lenth and Herva 2015).

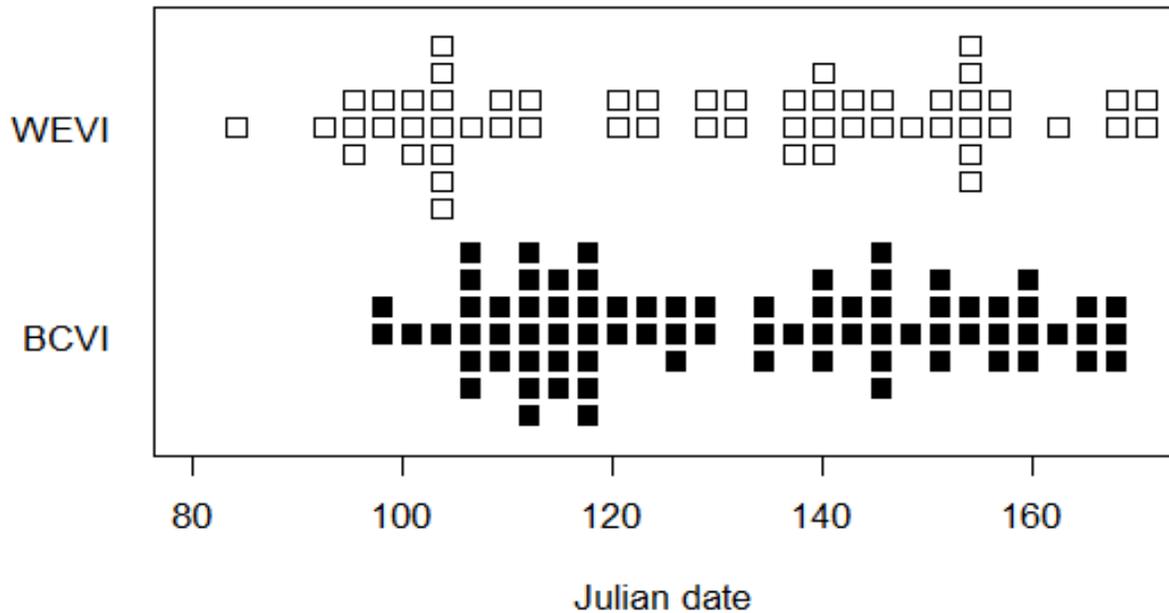


Figure 3. Clutch initiations by Julian date for white-eyed (WEVI) and black-capped (BCVI) vireos at Fort Hood, Texas in 2013 and 2014. Each square represents the initiation of a clutch and each bin on the horizontal axis represents ~2.5 days. Plot created with the “beeswarm” package in R (Eklund 2015).

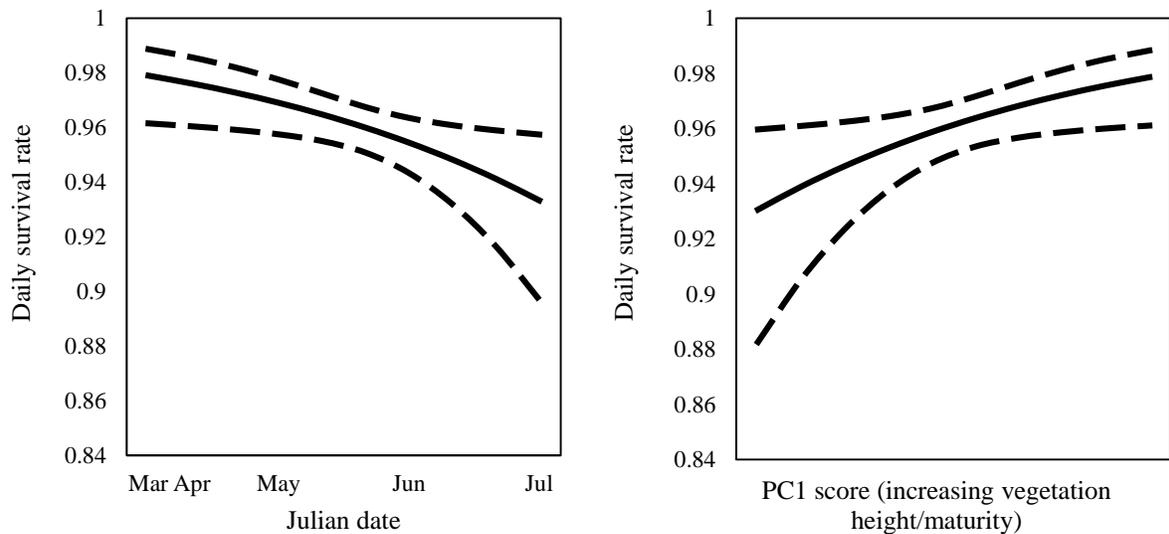


Figure 4. Model averaged predictions of daily survival rate for black-capped and white eyed vireo nests (species combined) as a function of Julian date (left) and habitat height and maturity (PC1 score; right). These sets of predictions were created by varying the values for day of season or PC1 while holding other variables at their mean values.

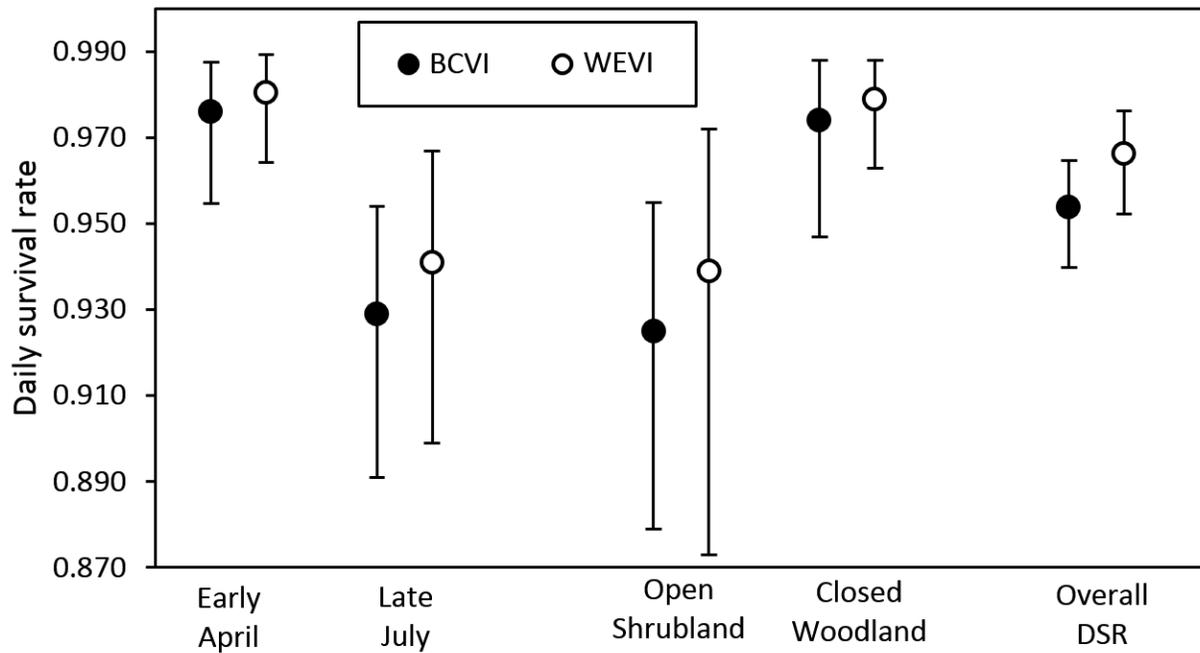


Figure 5. Estimates of daily survival rates (DSR) for black-capped and white-eyed vireo nests at Fort Hood, Texas in 2013 and 2014. Estimates were calculated by varying the parameter of interest while holding other variables at their mean values. The estimates for overall DSR are model averaged over the entire candidate model set (Table 4) while the others were produced from the model incorporating the additive effects of day of season, PC1, and species.