Black-capped Vireos and White-eyed Vireos: How two birds adapt to challenges of living in Central Texas

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A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science
University of Washington
2016

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Program Authorized to Offer Degree:
School of Environmental and Forest Sciences

University of Washington

Abstract

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Abstract: Black-capped vireos (*Vireo atricapilla*) and white-eyed vireos (*Vireo griseus*) are closely related songbirds, which occupy the same landscape in Central Texas. While white-eyed vireos are common and widespread, black-capped vireos are federally endangered with a restricted distribution. Both species are vulnerable to brown-headed cowbird (*Molothrus ater*) parasitism, and brood parasitism has been implicated in the decline of black-capped vireos. Here we use a comparative approach to investigate the divergent species responses to elucidate causes of the black-capped vireos imperiled status. From 2011 to 2015 we studied black-capped and white-eyed vireos across a range of six study sites, which represented a spectrum of vegetation types and levels of cowbird control regimes. We monitored 404 black-capped vireo territories and 813 nests and 141 white-eyed vireo territories and 268 nests. We collected vegetation measurements in breeding adult vireo territories to test for differences in vegetation use. We performed 34 nest observations to examine nest building behaviors as they relate to cowbird parasitism. We performed n = 229 nest vegetation surveys to examine differences in nest placement and potential influences on cowbird parasitism. We tracked 122 juvenile black-capped and 25 juvenile white-eyed vireos during the pre-migration period to estimate survival, dispersal, and vegetation use. We documented higher levels of brood parasitism in black-capped vireos than white-eyed vireos and identified vireo’s singing rate within 15m of the nest during the building stage as being associated with parasitism risk. We found white-eyed vireos exhibited a wider range of vegetation use than black-capped vireos, including areas with higher levels of canopy cover, which is associated with lower levels of cowbird parasitism. We found that compared to the white-eyed vireo, black-capped vireos seem to be especially prone to brood parasitism from brown-headed cowbirds, and cowbird control will likely remain an important factor in black-capped vireo conservation.

Acknowledgements

The Fort Hood Natural Resources Management Branch, Texas Parks and Wildlife at Colorado Bend State Park, and the U.S. Fish and Wildlife at Balcones Canyonlands National Wildlife Refuge, and private landowners in San Saba, Texas, provided support and access. In particular, Paula Cimprich, Nathan Grigsby, Gil Eckrich, Daniel Kovar, Erika Dittmar, Scott Summers, Beth Gardner, Laura Prugh provided a range of much needed support. I especially thank Dr. David Cimprich, for mentoring me and giving me a fantastic opportunity that led to more. Simon Kiacz, Stephen Tyndel, Samatha Wolfe, Hannah Beyl, Alex Glass, and Joel Throckmorton provided excellent field support in the toughest of working conditions. Paul, Mary, and Ben Heimbuch for putting up with my wanderings.

My committee: Josh Lawler and Aaron Wirising for extremely helpful comments. My advisor: John Marzluff, for pushing me, always.

My lab, who is always there for me: Loma Pendergraft, Avery Meeker, Amber Mount, Jorge Tomasevic, Jack DeLap, Kaeli Swift, and Leif Hansen. My honorary lab mates: Mitch Parsons, Michael Freeman, Shannon Kachel, Carolyn Shores, and Laurel Peelle.

Also, Ben, Lauren, and Maggie Walker (no relation) for always supporting me.

Funding: This work was funded by the Strategic Environmental Research and Development Program (SERDP) as part of project RC-2120.

This work was approved and permitted by the U.S. Fish and Wildlife Service (Federal Fish and Wildlife Permit TE023643, Special Use Application and Permit 21561-75699 and 75678), the U.S. Geological Survey (Federal Bird Banding Permit 21999), the Texas Parks and Wildlife Department (Scientific Research Permit No. SPR-0409-079), and by the University of Washington IACUC protocol 3077-01.

Introduction

Over 60% of all species considered by the International Union for the Conservation of Nature's Red List are threatened by either exploitation or agricultural practices and over 80% of species are harmed by multiple stressors (Maxwell et al 2016). Despite the devastation wrought by such human practices on many species, other organisms persist and even thrive in anthropogenic settings. The brown-headed cowbird (*Molothrus ater*), for example has adapted to agricultural practices that threaten other North American birds (Lowther 1993). Cowbirds historically had a commensal relationship with bison, following their herds and using them to flush arthropods that they ate (Friedmann 1929). This unique life cycle and foraging strategy is believed to have led to the cowbird's even more unique breeding strategy. An obligate brood parasite, cowbirds do not build nests or care for their young, they exclusively lay eggs in other species' nests (host species) leaving them for the host to raise. Cowbirds have been known to parasitize the nests of over 220 host species, some of which are threatened or endangered (Lowther 1993). Cowbirds have been implicated in the decline of several species including the federally endangered Kirtland's warbler (*Setophaga kirtlandii*) and least Bell's vireo (*Vireo bellii pusillus)* (Bocetti et al. 2014, Kus et al. 2010). Since the extirpation of bison from much of their previous range, domestic livestock have become the de facto surrogate for cowbirds (Mayfield 1965), with cowbirds demonstrating a strong association and increased abundance near livestock (Goguen, and N. E. Mathews 1999 and 2000).

The compounding effects of landscape change and agricultural practices, particularly fire suppression and overgrazing on arid ranchlands, differentially affect the avifauna of North America. In central Texas, for example, two vireo species appear to respond in opposite fashion to such change. The black-capped vireo (*Vireo atricappilla*) has declined range-wide and was listed as federally endangered in 1987 (Ratzlaff 1987, USFWS 1991). In contrast, the white-eyed vireo (*Vireo griseus*), a closely related species (Slager et al. 2014) that co-occurs with the black-capped vireo, is abundant and widely distributed (Hopp et al.1995). Differential sensitivity to ranch practices and land conversion as well as susceptibility to nest parasitism by brown-headed cowbirds may explain why one vireo succeeds where the other cannot.

White-eyed vireos suffer lower-rates of parasitism than black-capped vireos (Kovar 2015, Campomizzi et al. 2013, Barber and Martin 1997). This disparity does not appear to be due to nest site selection or concealment (Campomizzi et al. 2013). Moreover, white-eyed vireos and black-capped vireos do not seem to compete with each other, despite their co-occurrence (Kovar 2015). Increased host density, especially the northern cardinal (*Cardinalis cardinalis*) that is a common species within the black-capped vireo's range, has been associated with increased cowbird parasitism (Barber and Martin 1997), but this alone does not explain why within the same landscape white-eyed and black-capped vireos should experience different levels of parasitism.

Changes to the black-capped vireo's typical scrub habitat provide advantages to the white-eyed vireo. Scrub is traditionally fire-mediated and is naturally fragmented, open, and patchy (Grzybowski 1995). Suppression of fire throughout the black-capped vireo's range has resulted in natural plant succession and tree encroachment, reducing the suitability for black-capped vireos (Campbell 2003). White-eyed vireos demonstrate a wider use of habitat and are able to take advantage of later successional vegetation with increased tree and canopy cover (Hopp et al. 1995).The use of treed land by white-eyed vireos may also provide productive breeding grounds as cowbird parasitism has been shown to decrease with increasing canopy cover (Howell et al. 2007, Rothstein et al. 1984, Young and Hutto 1999).

Through a comparative study of the black-capped vireo and the white-eyed vireo, we sought to elucidate the causes of this divergent response to human threats within the same landscape, which may in turn help guide the management and conservation of the endangered black-capped vireo. Little is known about the factors that make white-eyed vireos so common and black-capped vireos rare within the same landscape (Kovar 2015). Black-capped vireo nest concealment has not been shown to impact parasitism rates (Campomizzi et al. 2013), so we hypothesized differential behavior during the nest-building stage may increase the conspicuousness of black-capped relative to white-eyed vireo nests (Banks and Martin 2001, Sharp and Kus 2006). Microhabitat selection within the same landscape, through differences in canopy cover or shrub cover, may also be an important behavior employed by white-eyed vireos to mitigate parasitism risk and thus we hypothesized that white-eyed vireos would place their home ranges and nests in areas of greater cover than black-capped vireos. With black-capped vireos' more isolated populations and patchwork habitat, habitat connectivity may be a factor in this species' decline (USFWS 1991). Therefore, we hypothesized that juvenile white-eyed vireos would have greater survival, ease of movement, and use of productive riparian vegetation than juvenile black-capped vireos.

Methods

Study Sites

From 2011 to 2015, we monitored six sites representing a spectrum of habitat characteristics and brown-headed cowbird control regimes across central Texas, USA (Fig. 1). Cowbird control was considered 'complete' if it included trapping and targeted shooting of birds;

‘moderate’ if either shooting or trapping occurred; and ‘none’ if no cowbird control methods were implemented at the site (Table 2).

Fort Hood – Fort Hood military installation is a large (~88,500 ha) US Army base located in central Texas, USA. From 2011 to 2015, we surveyed black-capped vireos on three study sites located across the installation with varying degrees of cowbird control. The Fort Hood Natural Resources Management Branch performs intensive brown-headed cowbird control efforts across much of the installation using both trapping and targeted shooting to remove cowbirds. In 2006, Fort Hood began an experimental cessation of cowbird control efforts in the northwestern portion of the base to study the impact of cowbird control on black-capped vireo populations. The West Range study site is located within the cowbird cessation area where cowbirds are ubiquitous. Taylor Valley is located on the eastern portion of the installation and has had continuous cowbird control since 1991. The Maxdale study area is located in the southwestern portion of Fort Hood and has had continuous cowbird control, but cowbirds remain prevalent, as there are no nearby traps. During the 2014 and 2015 field seasons, white-eyed vireos were surveyed on West Range, Taylor Valley, and Maxdale study sites. The study areas on Fort Hood are composed primarily of scrub habitat dominated by a mix of deciduous vegetation and ashe juniper (*Juniperus ashei*, hereafter ‘juniper’).

Colorado Bend State Park – Colorado Bend is a 2156-ha state park located in San Saba County along the western edge of the Colorado River. We monitored black-capped vireos from 2011 through 2014 in mesa-top scrub habitat, dominated by plateau live oak (*Quercus fusiformis)* and juniper along the Tie Slide, Heller Brakes, and Gorman Falls trails. As no white-eyed vireos bred within the bounds of the black-capped vireo monitoring area, we expanded our monitoring during the 2014 and 2015 season to include the nearby Gorman Springs trail. The

Gorman Springs area is a riparian woodland comprised mostly of deciduous vegetation. No cowbird control occurred in the park from 2011 to 2013, but control efforts began mid-way through the 2014 breeding season and continued through 2015.

Balcones Canyonlands National Wildlife Refuge –Balcones Canyonlands is a 9638-ha refuge comprised of 65 tracts of land located at the intersection of Burnet, Williamson, and Travis Counties, approximately 72 km southwest of Fort Hood. Vireo surveys were conducted on two tracts in 2011 and three tracts from 2012 to 2015, with white-eyed vireo monitoring occurring during the 2014 season. Balcones Canyonlands was not intensively monitored in 2015 due to habitat modifications that were performed on portions of the refuge to support black-capped vireo recovery. Whereas cowbird traps were located across the refuge, none were located on our study sites until 2015, when no intensive monitoring occurred.

San Saba – We monitored black-capped vireos on portions of two neighboring private properties in San Saba County from 2012 through 2015 and added white-eyed vireo monitoring during 2014 and 2015. The site is comprised of hillside, covered primarily in dense persimmon (*Diospyros texana*) and juniper. The site covered approximately 25-ha and was located about 19 km southwest of San Saba, TX. Brown-headed cowbird control was initiated on the properties mid-way through the 2014 breeding season and was continued through the 2015 season, though the cowbird trap was moved farther from the study site in 2015.

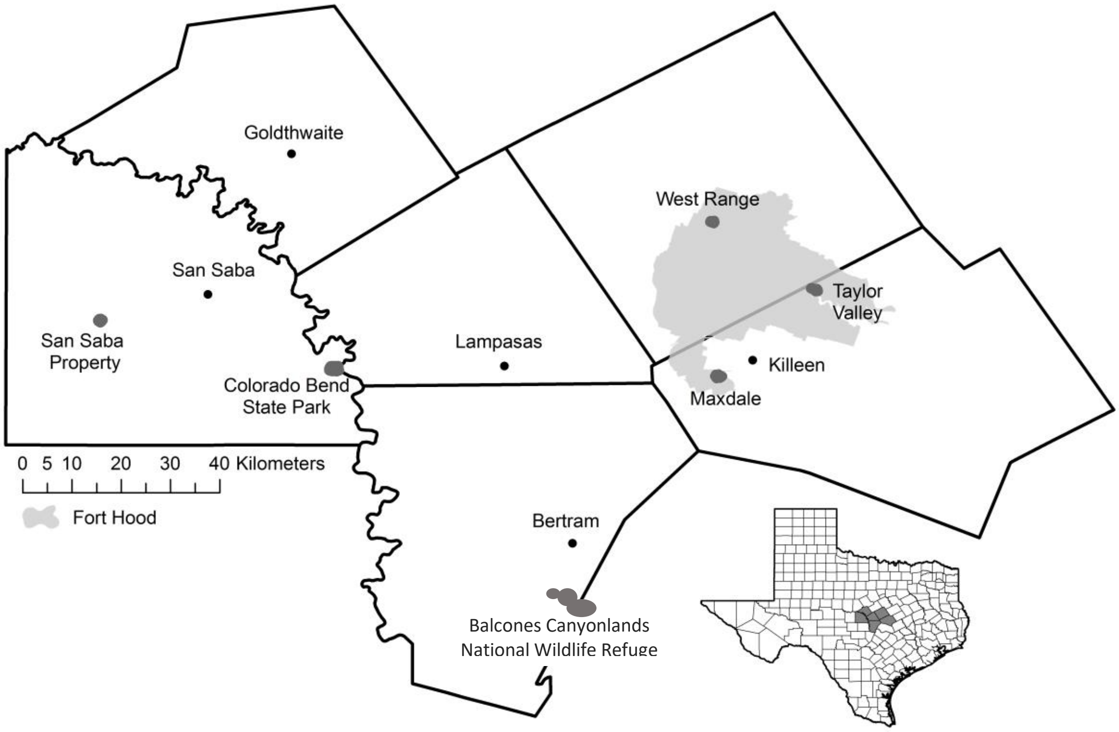

Fig. 1. **-** Black-capped and white-eyed vireo study sites monitored in central Texas from 2011 to 2015. Maxdale, Taylor Valley, and West Range are located within Fort Hood (shaded figure) within Bell and Coryell counties. Our study area at Balcones Canyonlands National Wildlife Refuge is located in Burnet County approximately 70km southwest of Fort Hood. Colorado Bend State Park and San Saba properties are located in San Saba County approximately 60km and 100km west of Fort Hood respectively. In 2015, black-capped vireos were not monitored in Colorado Bend State park and neither species of vireo was monitored in Balcones Canyonlands National Wildlife Refuge during that season. Figure adapted from Walker (2015).

	Year				
	2011	2012	2013	2014	2015
Fort Hood - Bell/Coryell Counties					
Maxdale	Moderate	Moderate	Moderate	Moderate	Moderate
Taylor Valley	Complete	Complete	Complete	Complete	Complete
West Range	None	None	None	None	None
San Saba County					
Colorado Bend	None	None	None	Moderate	Moderate
San Saba	--	None	None	Moderate	Moderate
Burnet County					
Balcones Canyonlands	Moderate	Moderate	Moderate	Moderate	--

Table 1. Levels of cowbird control management on each study site by year. Complete control involved both trapping and targeted shooting of cowbirds; moderate control consisted of either trapping or targeted shooting; and none, if no cowbird control efforts were implemented. The San Saba study site was not monitored in 2011 and the Balcones Canyonlands site was not monitored in 2015. During the 2015 season, only white-eyed vireos were intensively monitored at the Colorado Bend study site.

Presence-Absence Survey

To better understand vegetation used by vireos within our study region, we surveyed for vireo presence across Fort Hood in 2014 and 2015 within four vegetation types that could be used by vireos. We identified vegetation types using the 2011 National Land Cover Database (NLCD 2011): deciduous forest, evergreen forest, scrub, and woody wetlands (Homer et al., 2015). We excluded vegetation types not used by vireos (e.g. herbaceous, developed, open water). We selected 10 random survey start locations in each of the four vegetation types using the ‘random point’ tool of ESRI ArcMap 10.2 and 10.3 (ESRI, Redlands, California). We excluded potential survey locations from areas where the vegetation patch was too small to completely contain the survey route. During each count, we conducted a line transect survey using the randomized starting point and following a triangular path with one vertex established 100 meters north and another 100 meters east of the starting location. Surveys lasted 30 minutes (a period long enough for partners to change nest attendance duties and increase our detection) or ended when both black-capped and white-eyed vireos were detected during the survey time; we considered a species to be present only when birds were observed along the transect route or within the transect triangle. We detected vireo presence primarily through male vocalizations, but also used visual sightings when possible. Surveys were conducted within 4hrs of sunrise, as vireo vocalization intensity is greatest in the morning (Grzybowski 1995 and Hopp et al. 1995). To minimize observer bias, a single observer conducted all surveys. Prior to each survey, we confirmed that the NLCD vegetation designation was consistent with the actual vegetation conditions within the survey area. If landscape modifications or succession changed the vegetation classification of a survey, we chose a new survey location with the appropriate vegetation type.

Territory and Nest Monitoring

We visited each study site two to three times per week during the vireo breeding season, late March through July, to survey and monitor territories of adult vireos. We captured adult vireos using mistnests and banded them with a combination of U.S. Geological Survey aluminum bands and a unique arrangement of colored-plastic leg bands to make birds individually identifiable. We resighted banded vireos with binoculars and collected territory locations with a handheld GPS unit (Garmin eTrex varieties). As vireo territory use shifts slightly over the course of a season, we collected no more than five territory locations in a single day to reflect a more complete home-range the bird used throughout the season. We collected territory locations at least five minutes apart to allow birds time to move more naturally throughout their territory.

We observed vireos and used behavioral cues to locate their nests. We monitored nests by visiting them two to three times per week and recording the number of host eggs and brown-headed cowbird eggs (if present), number and estimated age of nestlings, and parental presence/absence at the nest. When nestlings were between 6-8 days old, we banded them with a U.S. Geological Survey aluminum band and a combination of colored bands unique to the study site. We considered nests successful if a fledgling was seen or if parental behaviors indicating success were observed (i.e. observed adults carrying food or observed persistent and intense adult scolding for several days post-fledging; Christoferson and Morrison 2001).

Juvenile Vireo Radio Telemetry

To help understand juvenile survival, vegetation use, and dispersal, we used radio telemetry to track independent juvenile vireos during the 2012-2015 field seasons; juvenile white-eyed vireo were tracked only during 2014 and 2015. From late June through August, we captured juvenile vireos with mistnests and banded them with a unique identifying combination. We then attached a radio transmitter using a leg-loop harness affixed to the bird. The cotton harnesses were designed to degrade and fall off within several months to decrease the impact on the birds (Hallworth et al. 2009). The transmitters had an average mass of 270 mg, which was approximately 3% of the bird’s mass or less for juveniles of both species captured on our sites (black-capped vireos: 8.92g ± 0.05, n = 166; white-eyed vireos: 11.13g ± 0.04, n = 335).

We targeted our netting attempts in territories with banded fledglings from monitored nests. Due to difficulties capturing banded juvenile vireos, we also affixed transmitters to unbanded juveniles incidentally captured. We tracked birds daily until the individual died, the transmitter battery died, or they could no longer be found. We resighted birds when possible and collected their location using a handheld GPS unit. If a bird moved to a location that could not be accessed (e.g. private property), we estimated the birds location using triangulation with GPS locations and compass bearings.

Home Range Estimation

We use fixed-kernel density estimation to create utilization distributions from adult territory locations and juvenile tracking locations following methods described by Worton (1989). In brief, using location points we created utilization distributions with a 10m resolution and converted distributions to percent volume contours.

We collected 4-86 locations from breeding adult male black-capped vireos and 8-49 locations from breeding adult male white-eyed vireos. We estimated home range sizes for all vireos (black-capped vireo: $n = 377$, white-eyed vireos: $n = 151$) and found significant correlations between the number of locations and home range size (black-capped vireos: $r = 0.21$, $t_{375}= 4.18$, $P < 0.001$; white-eyed vireos: $r = 0.15$, $t_{149} = 1.86$, $P = 0.065$). When we considered black-capped vireo territories with at least 40 locations ($n = 120$) and white-eyed vireo territories with at least 25 locations ($n = 116$) we found no correlation between the number of locations and home range size (black-capped vireos: $r = 0.14$, $t_{120}= 1.55$, $P = 0.12$ (Walker 2015); white-eyed vireos: $r = 0.10$, $t_{114} = 1.05$, $P = 0.30$), we only considered these territories in further analyses.

We collected 3-34 locations from juvenile black-capped vireo ($n = 113$) and 1-45 locations from juvenile white-eyed vireos ($n = 25$). To balance sample size with kernel accuracy, we limited analysis to vireos with at least 15 locations (black-capped vireos: $n = 73$; white-eyed vireos: $n = 18$) for vegetation sampling surveys.

Vegetation Sampling Surveys

We divided vireo home ranges into multiple strata based on a birds' relative use of areas within their home range and conducted vegetation surveys within each strata. We divided adult territories into high (0-25% kernel density estimate), moderate (25-75%) and low-use (75-100%) strata using percent volume contours from utilization distributions. We divided juvenile home ranges into high (0-25% kernel density estimate) and moderate to low-use (25-100%) strata. We selected survey points using a random point generator in ArcGIS (10.2 and 10.3) from within home range strata. We generated two survey points within each adult territory's strata and four points from within each strata of a juvenile's home range. Survey points were at least 15 from the edge of a strata boundary and at least 30 m apart to accommodate the dimensions of the vegetation survey plot.

We conducted vegetation sampling using the methods described by Walker (2015). Briefly, we measured canopy cover, shrub cover, and foliage density in plots centered on a survey point, with additional survey points extending 15 m in each of the cardinal directions. We measured four characteristics of vegetation structure that would together summarize the amount of low cover (foliage density from 0-1 m and 1-2 m), low woody plants (shrub cover), and high woody vegetation (canopy cover).

Nest Vegetation Sampling

During the 2014 and 2015 seasons we conducted vegetation surveys at the nests of both vireo species on four study sites. In 2014 we measured nests only on our West Range study site on Fort hood. In 2015 we measured nests at our three Fort Hood sites (Maxdale, Taylor Valley, and West Range) in addition to nests on our San Saba study site. We monitored all nests to completion and conducted vegetation sampling after the vireo breeding season had concluded. Centered at the nest, we collected foliage density measurements (from 0-1m and 1-2m) at a distance of 3m in each cardinal direction to summarize nest concealment. Foliage densities were highly correlated ($r = 0.73$, $t_{231} = 16.45$, $P < 0.001$) and we used their average in further analysis. We measured the height of the nest's substrate and the canopy over the nest, classifying it as being 'short' (< 2m), 'medium' (2-5m), 'tall' (5-10m), or 'very tall' (> 10m).

Nesting Behavior

We performed nest observations on black-capped vireo and white-eyed vireo nests during the 2014 and 2015 field seasons to collect behavioral information during the nest building stage. A single, camouflaged observer watched each nest from a concealed location. We initiated observations between 0630 and 1200 h from May 22 to June 24, in both 2014 and 2015, with an average start of 2h 51min after sunrise (range 00:13 to 5:23). Cowbirds utilize different habitats for breeding and foraging; cowbirds lay eggs and locate nests in breeding habitat earlier in the day and later commute to their preferred foraging habitat (Rothstein et al. 1984). We conducted nest observations before 1200h because this is the time cowbirds are likely locating and parasitizing nests (Rothstein et al. 1984). Observations occurred an average of 12m (se = 0.85) from the nest and lasted an average of 73min (se = 2.95). To ensure observer presence was not affecting vireo behavior, we initiated observations after adults resumed behaviors near the nest (building, singing within 15m, etc.). The average duration between observation set-up and start was 12min (se = 3.34).

We recorded the duration and number of building events (building trips to and from the nest and duration of building), vocalizations at/around the nest (number and duration), and other behaviors (movement, perching, preening, scolding, etc.) during the observation period. When possible, we distinguished adult male and females and recorded their behaviors separately. We recorded behaviors occurring within 15m of the nest, documenting behavior start and end times to calculate the total duration of each behavior. To calculate the song rate and build rate, we divided the total behavior duration by the nest observation to achieve a rate in min/hr. We used song rate and rate of nest building in future analysis because the song rate and time spent near the nest has been identified as important factors used by cowbirds to locate nests with other vireo species (Banks and Martin 2001). Moreover, the number of song bouts (defined here as a song separated by at least 5 seconds of no singing) was correlated with song rate ($r = 0.48$, $t_{32} = 3.10$, $P = 0.004$) and the number of building trips was correlated with the rate of nest building ($r = 0.84$, t32 = 8.57, $P < 0.001$) in our study.

Statistical Analyses

Vegetation Use

Presence-Absence Surveys – To understand the distribution of black-capped and white-eyed vireos in our study region and across vegetation type we conducted a $\chi 2$ test of species association (Whittaker, 1975) and generated a coefficient of association (Cole, 1949). This test allowed us to examine whether the two vireo species were using the same vegetation types in our study region or if they were independently distributed with species specific vegetation use patterns.

Territory Size – Differences in territory size between adult male black-capped and white-eyed vireos were analyzed using a linear mixed-effects model fitted with restricted maximum likelihood with species as the predictor and territory size as the response; prior to analysis, territory sizes were log-transformed to normalize their distribution. We tested for differences in territory sizes between study sites separately for each vireo species and found significant differences in territory size between study sites (black-capped vireo: $F_{5,371} = 10.25$, $P < 0.001$; white-eyed vireo: $F_{6,144} = 5.88$, $P < 0.001$). Our study sites varied in multiple ways, including geographical location and vegetation characteristics; differences between study sites were not of interest in our analysis as we seek to understand how these vireo species behave broadly over our study region. We used a linear mixed-effects model that allowed us to account for differences between season and at the study site level; we designated each study site within a season (year) as random effects in the model to account for these differences.

Vegetation Sampling- We assessed the correlation between vegetation characteristics (shrub cover, canopy cover, and foliage density 0-1m and 1-2 m) and found foliage density measurements (0-1m and 1-2 m) to be highly correlated (Adult Territories: $r = 0.88$, $t_{2288} = 90.79$, $P < 0.001$; Juvenile Home Ranges: $r = 0.90$, $t_{587} = 51.26$, $P < 0.001$). Therefore, we averaged foliage density measurements from 0-1 m and 1-2 m in all further analyses.

To test differences if vegetation use between breeding adult vireo species and between relative use strata (0-25%, 25-75%, and 75-100%) we used ordinal regression through a cumulative link mixed model fitted with the Laplace approximation and logit link. Ordinal regression was used as the relative use strata is categorical and has a ranked order We set strata as the response variable and used the interaction of species and vegetation characteristics (canopy cover, shrub cover, averaged foliage density) as predictor variables; we included year as a predictor to test for seasonal effects. To examine if vireo species are adjusting their vegetation use in response to cowbird control regimes (at levels of complete, moderate, and none), we also used the interaction of species and level of cowbird control as predictors in the model. As we were not interested in vegetation use differences between study sites and individuals, we designated study site and individual vireos as random effects in the model.

To test differences in juvenile vegetation use between vireo species and relative use strata (0-25% and 25-100%) we used generalized linear mixed model fit with the Laplace approximation using a binomial distribution and logit link. We used the interaction of species and vegetation characteristics along with year and predictors in the model and strata (0-25% and 25-100%) as the response variable. Again, we used study site and individual vireo as random effects in the model.

Nesting

Nest Monitoring- We calculated daily mortality and survival, period survivals (egg laying, incubation, and nestling periods), and total survival using the Mayfield method (Mayfield, 1975) and used methods described by Johnson (1979) to calculate period survival standard errors. As sites were visited only two to three times per week, we chose the Mayfield method to accommodate differences in the stage a nest was found (building, egg laying, incubation, or nestling) and account for likely biases in nest detection between sites due to differences in habitat characteristics, which likely influenced our ability to find nests. We calculated 95% confidence intervals of period survival for each site, and all sites together, to compare differences in nest survival between species and nest period.

Nest Placement – We tested for differences in nest heights using a linear mixed effects model fitted with restricted maximum likelihood. We used the same statistical technique to analyze whether nest height impacted parasitism risk, setting parasitism fate (parasitized or not) and used species, nest height, and their interaction as the response; prior to analysis, nest height was log-transformed to normalize the distribution. We found significant differences in nest height between study sites for each vireo species (black-capped vireo: $F_{4,555} = 4.89$, $P < 0.001$; white-eyed vireo: $F_{4,197} = 5.32$, $P < 0.001$). Therefore, to account for site, individual, and seasonal variation we nested individual within a study site within a season (year) as random effects in the model.

We analyzed nest vegetation sampling for differences between species using a generalized linear model with Laplace Approximation and binomial distribution and logit link for both species. Nest vegetation measurement were only collected on West range in 2014, and all study sites in 2015. We selected this model to account for random effects of study site and the individual bird. We used nest height, canopy height, substrate height, and average foliage density as predictor variables with species as the response variable. We converted the substrate height to a continuous variable by selecting the mid-point of the classification (e.g. 3.5m for 'medium' 2-5m) to aid with model convergence.

To analyze what nest variables may contribute to brood parasitism, we separately analyzed black-capped and white-eyed vireo nests. We excluded our Taylor Valley study site from this analysis as it had no parasitism in 2014 or 2015. We again used a generalized linear model with Laplace Approximation and binomial distribution and logit link for both species. We used nest height, substrate height (categorical converted to continuous), and canopy height (categorical converted to continuous), and average foliage density as our predictor variables and parasitism fate (parasitized or not) as our response variable. To account for variation between study site and individual vireos, we again set site and individual as random effects in the model.

Brood parasitism - To test for differences in parasitism rate between species, we calculated parasitism rates at the site level for each species per year. We then used a linear mixed-effects model fit with restricted maximum likelihood with parasitism rate as the response and species as the predictor. As parasitism varied by site and year we nested site within year to use as random effects in the model. To test the effect of nest placement on parasitism rates, we ran a generalized linear mixed-effects model using a binomial distribution and logit link with parasitism as the response and the interaction of species and nest height as predictors. We accounted for seasonal and site differences by designating site within year as random effects.

Nest Observations – To investigate behavioral factors that may influence parasitism risk, we used a generalized linear model with a binomial distribution to model nest parasitism from vireo behaviors near (< 15m) or at the nest site. We used song rate (min/hr) and building rate (min/hr) as predictor variables with parasitism fate as the response variable. We then tested differences between vireo species, again using a generalized linear model with binomial distribution. We used song rate and building rate as predictors with species as the response variable.

Juvenile Survival and Movement

Survival - Using observations from vireos tracked using telemetry, we calculated daily survival probabilities using the Kaplan-Meier method (Kaplan and Meier 1958). Birds can be lost through faulty transmitters, by moving outside our search area, or by the natural end of a transmitter's battery life; we used the Kaplan-Meier approach as it allowed us to include data from birds with unknown fates (birds we could not confirm alive or dead) to create survival probabilities. We then tested for differences in survival between vireo species using a log rank test (Rich et al. 2010).

Movement – Using locations collected from juvenile vireos tracked with telemetry, we used ESRI ArcMap 10.2 and 10.3 to calculate movement distances for each vireo per day (ESRI, Redlands, California). If we were unable to locate a bird one day and subsequently found the bird, we averaged the distance between the two points and assigned the average movement to the days we were unable to locate the bird. We log transformed the movement distance to normalize the distribution for our analysis. We then used a linear mixed-effects model fitted with restricted maximum likelihood to test for differences in movement between species. We used site within year as random effects to account for geographic and seasonal variability and the log transformed distance (m) as the response variable with species as the predictor variable.

All analyses were conducted in program R version 3.2.2 unless otherwise noted (R Core Team 2015).

Results

Differences in species occurrence - We found white-eyed vireos in a greater variety of vegetation than black-capped vireos (Table 2). Testing for association between species, we found white-eyed and black-capped vireos to be independently distributed across vegetation types (χ^2 = 0.23, P = 0.63, DF = 1; coefficient of association: C_a = 0.05). These differences in distribution seemed to be primarily driven by white-eyed vireo use of woody wetland vegetation. Namely, removing the woody wetland vegetation type from our analysis, resulted in greater similarity in both species' association with deciduous forest, evergreen forest, and scrub (χ^2 = 2.51, P = 0.11, DF = 1, C_a = 0.29).

	Deciduous Forrest	Evergreen Forest	Scrub	Woody Wetlands
White-eyed vireo (Only)	6	5	3	20
Black-capped vireo (Only)	0	3	4	0
Both Species Detected	13	7	10	0
Neither Species Detected	1	5	3	0
Total Surveys Conducted	20	20	20	20

Table 2. Results of white-eyed vireo and black-capped vireo presence absence surveys. 20 surveys were conducted in each of the four vegetation types (Deciduous Forest, Evergreen Forest, Scrub, and Woody Wetlands), with 10 being conducted per year during 2014 and 2015. Rows indicate possible survey outcomes with one vireo species, both, or neither species being detected. Numbers indicate the total number of surveys conducted in a vegetation type that had the corresponding species detection outcome (see row categories). A total of 80 presence absence surveys were conducted. No black-capped vireos were detected during any of the woody wetland surveys.

Territory Monitoring- From 2011 to 2015 we monitored 404 black-capped vireo territories across six study sites. We found and monitored 813 nests and banded 418 adults and 985 nestling black-capped vireos (Table 3). From 2014 to 2015 we monitored 141 white-eyed vireo territories across six study sites. We found and monitored 268 nests and banded 340 and 360 adult and nestling white-eyed vireos respectively (Table 3). Nests were sometimes found, but were never observed containing eggs, these nests are excluded from all of our analyses.

Study Site	Species	Banded		Territories Monitored	Nests Monitored
		Adults	Nestlings		
Balcones Canyonlands	BCVI	55	100	44	56
	WEVI	46	30	12	17
Colorado Bend	BCVI	66	85	69	185
	WEVI	24	44	29	65
San Saba	BCVI	47	132	48	122
	WEVI	33	70	21	34
Maxdale (Ft.Hood)	BCVI	84	181	81	158
	WEVI	58	59	21	45
Taylor Valley (Ft. Hood)	BCVI	76	267	86	140
	WEVI	100	95	28	60
West Range (Ft. Hood)	BCVI	90	220	76	152
	WEVI	79	62	30	47
Total	BCVI	418	985	404	813
	WEVI	340	360	141	268

Table 3. Summary of black-capped vireo (BCVI) and white-eyed vireo (WEVI) territory and nest monitoring across six study sites from 2011-2015. Rows show monitoring effort by study site seperated by species, with overall totals also provided. Columns show the number of adult and nestlings banded, territorties monitored, and nests found/monitored per study site and species with totals provided.

Across our study sites, black-capped vireos (mean = 3.54 ha, se = 0.21, n = 121) had significantly larger territories than white-eyed vireos (mean = 1.09 ha, se = 0.08, n = 116; t_{212} = -12.67, p < 0.001; Table 4.).

	Value	Std. Error	DF	t-value	p-value
Species	-0.560	0.04	212	-12.67	*< 0.001

Table 4. Results of a linear mixed-effects model fitted with restricted maximum likelihood. We used species as a predictor variable and log-transformed values of territory sizes (in ha) with study site nested within year as random effects to account for variation between season and sites. Value shows the relative direction and influence of the predictor variable (species) on the response variable (territory size).

Vegetation Sampling: Adult Territories- We conducted vegetation surveys in the territories of 274 breeding adult black-capped vireos and 119 white-eyed vireos. Black-capped and white-eyed vireos had significant differences in vegetation use within their territories ($z = 2.20$, $P = 0.03$), though both species of vireo had significantly higher shrub cover and foliage density in the core of their territories compared to lower use strata (Shrub Cover: $z = -4.05$, $P < 0.001$; Foliage Density: $z = -3.23$, $P = 0.001$; Table 5 and 6). White-eyed vireos had significantly more canopy cover throughout their territory than black-capped vireos ($z = -3.32$, $P < 0.001$, Table 5 and 6), with the highest percent canopy cover in the core of their territory (Table 5 and Fig. 2). We found no difference in vegetation use of either vireo species associated with level the level cowbird control regime (None: $z = -0.46$, $P = 0.65$; Moderate: $z = -0.37$, $P = 0.71$; Table 5). Additionally we found no year effects on vegetation use for either vireo species (2013: $z = 0.24$, $P = 0.81$; 2014: $z = -0.32$, $P = 0.75$; 2015: $z = 0.04$, $P = 0.97$; Table 5). For all model output: Vegetation Surveys: $n = 2253$, Predictor Variables = 14, Random Effects = 2 (Table 5).

Predictor Variables	Estimate	Std. Error	z value	Pr(>|Z|)
Species: White-eyed vireo (WEVI)	0.824	0.38	2.20	*0.03
Canopy Cover	0.351	0.26	1.35	0.18
Shrub Cover	-1.354	0.33	-4.05	*< 0.001
Ave. Foliage Density	-0.983	0.30	-3.23	*0.001
Year: 2013	0.027	0.12	0.24	0.81
Year: 2014	-0.039	0.12	-0.32	0.75
Year: 2015	0.008	0.20	0.04	0.97
Cowbird Control: Moderate	-0.069	0.19	-0.37	0.71
Cowbird Control: None	-0.084	0.18	-0.46	0.65
WEVI * Canopy Cover	-1.393	0.42	-3.32	*< 0.001
WEVI * Shrub Cover	-0.154	0.60	-0.26	0.80
WEVI * Ave. Foliage Density	0.648	0.59	1.09	0.27
WEVI * Cowbird Control: Moderate	-0.010	0.25	-0.04	0.97
WEVI * Cowbird Control: None	-0.224	0.28	-0.80	0.42

Threshold coefficients

	Estimate	Std. Error	z value	Pr(>|Z|)
0-25% | 25-75 %	-2.098	0.24	-8.86	* < 0.001
25-75% | 75-100 %	-0.568	0.23	-2.45	*0.01

Table 5. Model output for territory vegetation surveys using ordinal regression through a cumulative link mixed model fitted with the Laplace approximation and logit link. Estimates are given to show relative influence in the model as well as standard errors, z values and their associated p-value ($\alpha = 0.05$). The model included species, canopy cover, shrub cover, average foliage density, year, and level of cowbird control as predictor variables. We include interaction terms of species with canopy cover, shrub cover, average foliage density and level of cowbird control. P-values for statistically significant model variables are starred. The model found significant differences in threshold coefficients, which shows significant differences between each strata, showing greater density of foliage and shrubs in the cores of both species. There are significant difference in vegetation use between species, though both species had greater shrub cover and foliage density in the cores of their territories. Additionally, white-eyed vireos have significantly greater canopy cover use than black-capped vireos across their entire territory. Estimates show the relative direction and influence of a predictor variable on the response variable (relative use strata: 0-25%, 25-75%, 75-100%).

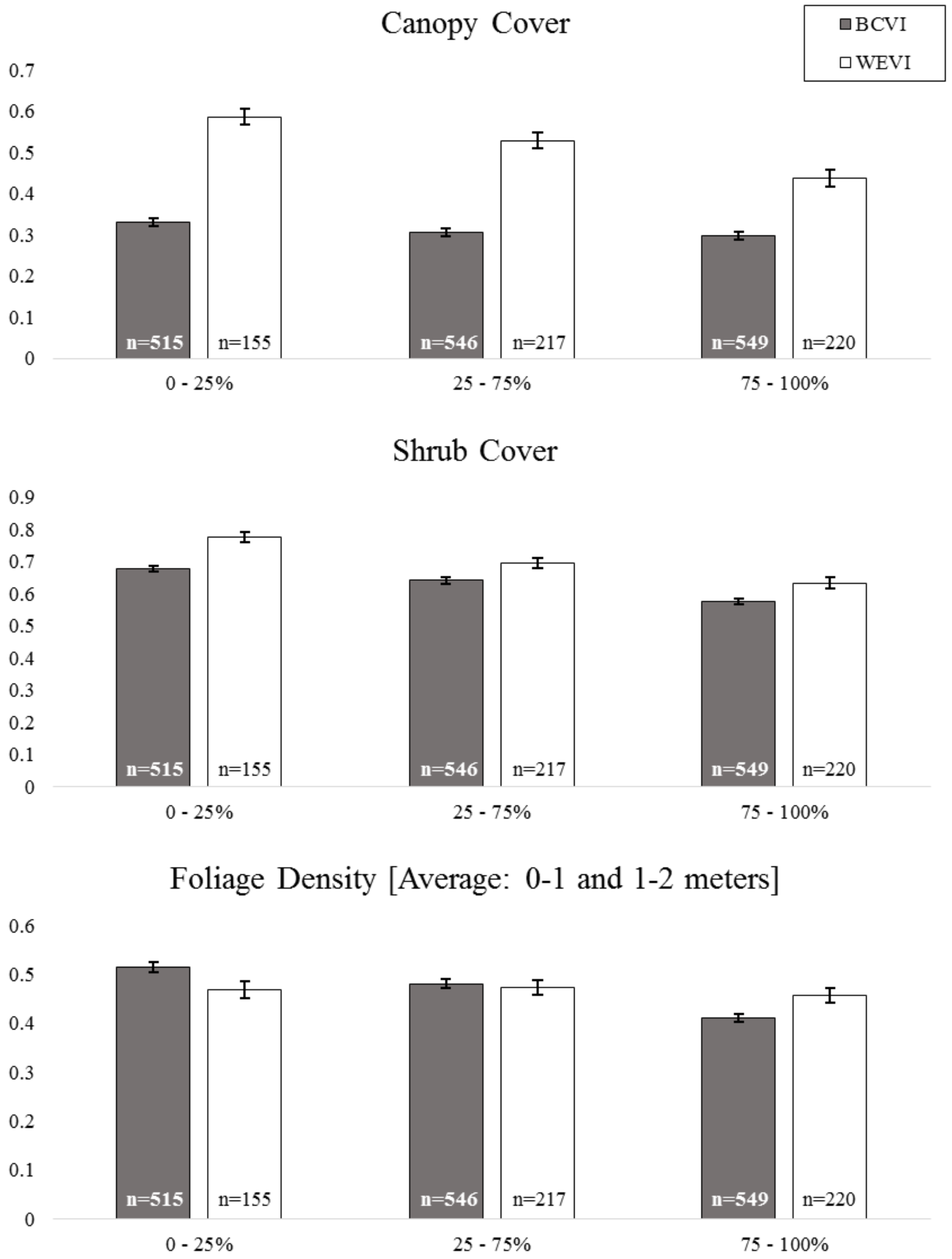

Fig. 2. Average measurements for vegetation characteristics across territory use strata of black-capped (BCVI) and white-eyed vireos (WEVI) with standard error bars. X-axis are seperated by the relative use strata (0-25%, 25-75% and 75-100%), y-axis lables are percent coverage (0 - 1) of a a given vegetation measurement. White-eyed vireos have higher use of canopy cover within their entire home range and both vireo species have higher shrub cover and average foliage denisty, which increases as with relative use (0-25% highest use and 75-100% lower relative use).

Black-capped Vireo				White-eyed Vireo			
Canopy Cover							
Strata	Mean	SE	n	Strata	Mean	SE	n
0 - 25%	0.33	0.01	515	0 - 25%	0.59	0.02	155
25 - 75%	0.31	0.01	546	25 - 75%	0.53	0.02	217
75 - 100%	0.30	0.01	549	75 - 100%	0.44	0.02	220
Shrub Cover							
Strata	Mean	SE	n	Strata	Mean	SE	n
0 - 25%	0.68	0.01	515	0 - 25%	0.78	0.02	155
25 - 75%	0.64	0.01	546	25 - 75%	0.69	0.02	217
75 - 100%	0.58	0.01	549	75 - 100%	0.63	0.02	220
Average Foliage Density							
Strata	Mean	SE	n	Strata	Mean	SE	n
0 - 25%	0.51	0.01	515	0 - 25%	0.47	0.02	155
25 - 75%	0.48	0.01	546	25 - 75%	0.47	0.02	217
75 - 100%	0.41	0.01	549	75 - 100%	0.46	0.01	220

Table 6. Average percent canopy cover, shrub cover, and foliage density for each relative use strata within adult black-capped and white-eyed vireo territories. Standard errors and sample sizes provided; these values are visualized in Figure 2. White-eyed vireos have higher levels of canopy cover throughout their territory compared to black-capped vireos. Both vireo species had higher levels of shrub cover and foliage density in the core (0-25%) of their territory with cover/density decreasing with decreasing relative use within their territory.

Vegetation Sampling: Juvenile Home Ranges – We conducted vegetation surveys in home ranges of 74 black-capped and 18 white-eyed vireo juveniles. To balance accuracy with sample size, we did not conduct vegetation sampling in home ranges of juvenile birds with fewer than 15 locations. Juvenile vireos, of both species, selected significantly higher foliage density in the core of their home range compared to lower relative use areas (z = -1.87, P = 0.06, Table 7). Juvenile white-eyed vireos tended to use areas with higher levels of canopy cover throughout their home range relative to black-capped vireos, but the trend was not significant (z = -1.45, P =

0.15, Table 7 and 8, Fig. 3). Shrub cover and foliage density did not differ between species (shrub cover: z = 0.63, P = 0.53; foliage density: z = -0.11, P = 0.91, Table 7), though output values show both species tended to have higher densities in the cores of their home range, also seen in Fig. 3 (Table 8). We found no effect of year on juvenile vireo home ranges (2013: z = 0.80, P = 0.42; 2014: z = 0.49, P = 0.62; 2015: z = 0.28, P = 0.78). For all model output: Vegetation Survey: n = 589, Predictor Variable = 10, Random Effects = 2 (Table 7).

Predictor Variables	Estimate	Std. Error	z value	Pr(>|Z|)
Species	0.456	0.63	0.73	0.47
Canopy Cover	-0.186	0.43	-0.43	0.67
Shrub Cover	-0.374	0.60	-0.62	0.53
Average Foliage Density	-1.005	0.54	-1.87	*0.06
Year: 2013	0.195	0.24	0.80	0.42
Year: 2014	0.106	0.22	0.49	0.62
Year: 2015	0.141	0.50	0.28	0.78
Species * Canopy Cover	-1.282	0.88	-1.45	0.15
Species * Shrub Cover	0.895	1.43	0.63	0.53
Species * Ave. Foliage Density	-0.157	1.40	-0.11	0.91

Table 7. Results of a generalized linear mixed model fit by Laplace approximation with a binomial distribution and logit link. Vegetation characteristics (canopy cover, shrub cover, foliage density) were modeled considering interactions with species and year to test for year effects. To account for site and individual differences between birds, we included site and individual as random effects in the model. Both species selected denser foliage in the core of their home range and white-eyed vireos tended to use more canopy cover throughout their home range. Estimates show the relative direction and influence of a predictor variable on the response variable (relative use strata: 0-25% and 25-100%).

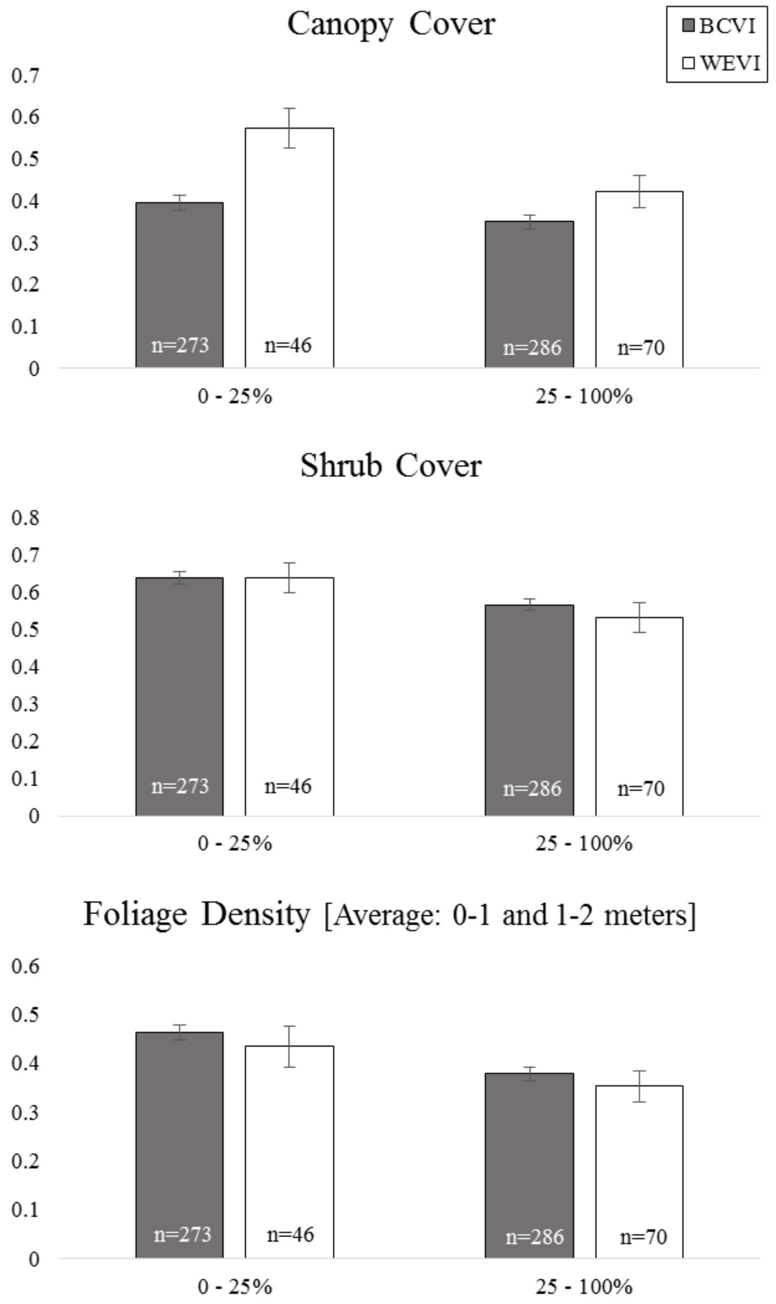

Fig. 3. Average measurements for vegetation characteristics (canopy cover, shrub cover, average foliage density) across home range strata of juvenile black-capped (BCVI) and white-eyed vireos (WEVI) with error bars and sample sizes. The x-axis is separated by relative use strata with 0-25% representing the core of the home range and 25-100% lower relative use areas. The y-axis is the percent coverage of vegetation measurements, with 1 being 100% coverage. Foliage density was significantly greater in the core areas of both vireo species and both species tended to have higher levels of canopy cover and shrub cover in their core use areas. White-eyed vireos home ranges tended to have greater canopy cover throughout their home range than black-capped vireos.

Black-capped Vireo				White-eyed Vireo			
Canopy Cover							
Strata	Mean	SE	n	Strata	Mean	SE	n
0 - 25%	0.39	0.02	273	0 - 25%	0.57	0.05	46
25 - 100%	0.35	0.02	286	25 - 100%	0.42	0.04	70
Shrub Cover							
Strata	Mean	SE	n	Strata	Mean	SE	n
0 - 25%	0.64	0.02	273	0 - 25%	0.64	0.04	46
25 - 100%	0.57	0.02	286	25 - 100%	0.53	0.04	70
Average Foliage Density							
Strata	Mean	SE	n	Strata	Mean	SE	n
0 - 25%	0.46	0.01	273	0 - 25%	0.43	0.04	46
25 - 100%	0.38	0.01	286	25 - 100%	0.35	0.03	70

Table 8 Average percent canopy cover, shrub cover, and foliage density for each relative use strata within juvenile black-capped and white-eyed vireo home ranges. Standard errors and sample sizes provided; these values are visualized in Figure 3. Core use areas of both vireo species contained significantly greater foliage density with trends for more canopy and shrub cover at the core of both species' home range. White-eyed vireos had higher levels of canopy cover throughout their home range.

Nests: Survival and Placement- From 2011 to 2015 we monitored 813 black-capped vireo of which 268 were parasitized and 230 succeeded at producing at least one black-capped vireo fledgling (Table 3 and 11). From 2014 to 2015, we monitored 268 white-eyed vireo nests of which 43 nests were parasitized and 91 were successful at producing at least one white-eyed vireo (Table 3 and 9). Black-capped vireos had an overall parasitism rate of 33.17% (se = 0.05), whereas 16.60% (se = 0.03) of white-eyes vireo nests were parasitized (for site specific parasitism rates see Table 10). Controlling for seasonal and site variation, black-capped vireos had significantly higher parasitism rates than white-eyed vireos (t_9 = -2.32, P = 0.05).

	Estimate	Std. Error	DF	t-value	p-value
Species	-0.093	0.04	9	-2.32	*0.05

Table 9 – Results of a linear mixed-effect model fitted with restricted maximum likelihood. Species was used as the predictor variable with parasitism rate (specific to species, year, and study site) as the response. Study site within year was used as random effects in the model to account for variant among sites and between years. The estimates shows the relative direction and influence of the predictor variable (species) on the response variable (parasitism rate).

Site	Species	Parasitized Nests	Total Nests	Parasitism Rate	SE
San Saba	BCVI	55	122	45.08%	0.12
	WEVI	4	33	12.12%	0.07
Balcones	BCVI	9	56	16.07%	0.03
	WEVI	2	15	13.33%	---
Colorado Bend	BCVI	127	181	70.17%	0.07
	WEVI	18	64	28.13%	0.02
Maxdale (Ft. Hood)	BCVI	40	157	25.48%	0.07
	WEVI	5	44	11.36%	0.09
Taylor Valley (Ft. Hood)	BCVI	1	140	0.71%	0.00
	WEVI	0	60	0.00%	0.00
West Range (Ft. Hood)	BCVI	36	152	23.68%	0.07
	WEVI	14	43	32.56%	0.01

Table 10. Parasitism rates for black-capped (BCVI) and white-eyed vireos (WEVI) across all study sites, with standard errors. Black-capped vireos had higher rates of parasitism on all sites except West Range on Fort Hood. Taylor Valley has a complete cowbird control regime and West Range has no cowbird control. The remaining sites have moderate levels of cowbird control.

Despite differences in parasitism, black-capped vireos had a 28.29% apparent nest success and white-eyed vireos had a slightly higher 33.96% apparent success rate. Nest survival during the egg laying, incubation, and nestling stages did not differ between black-capped and white-eyed vireos within sites in most cases (Table 11). Black-capped vireos had an overall nest survival of 30.11% and white-eyed vireos had a slightly lower 27.65% nest survival probability for the egg laying, incubation, and nestling stages. At our Colorado Bend and San Saba sites, black-capped vireos (Colorado Bend: 23.95%, 95% CI: 0.18-0.31; San Saba: 45.40%, 95% CI: 0.36-0.57) had a significantly lower survival during the incubation period compared to white-eyed vireos (Colorado Bend: 57.41%, 95% CI: 0.46- 0.72; San Saba: 71.79%, 95% CI: 0.55-0.93; Table 11).

Site	Species	Lay		Incubation		Nestling	
		Period	95% CI	**Period**	95% CI	**Period**	95% CI
San Saba	BCVI	84.93%	0.76 - 0.95	45.40%	0.36 - 0.57	54.43%	0.42 - 0.70
	WEVI	63.39%	0.31 - 1.00	71.79%	0.55 - 0.93	63.95%	0.48 - 0.85
Balcones NWR	BCVI	91.69%	0.83 - 1.00	71.45%	0.59 - 0.86	58.55%	0.46 - 0.75
	WEVI	78.80%	0.47 - 1.00	63.07%	0.40 - 0.98	67.98%	0.44 - 1.00
Colorado Bend	BCVI	82.21%	0.76 - 0.89	23.95%	0.18 - 0.31	45.27%	0.33 - 0.61
	WEVI	96.36%	0.90 - 1.00	57.41%	0.46 - 0.72	44.46%	0.31 - 0.63
Taylor Vally (Ft. Hood)	BCVI	89.35%	0.83 - 0.96	72.35%	0.64 - 0.81	64.16%	0.55 - 0.75
	WEVI	73.37%	0.57 - 0.93	70.69%	0.59 - 0.85	55.40%	0.42 - 0.72
Maxdale (Ft. Hood)	BCVI	83.77%	0.77 - 0.91	49.22%	0.41 - 0.59	44.61%	0.34 - 0.58
	WEVI	82.70%	0.66 - 1.00	46.64%	0.33 - 0.66	43.38%	0.28 - 0.67
West Range (Ft. Hood)	BCVI	90.81%	0.84 - 0.97	58.31%	0.50 - 0.68	67.68%	0.58 - 0.79
	WEVI	89.26%	0.76 - 1.00	67.73%	0.55 - 0.83	46.90%	0.32 - 0.69
Overall	BCVI	87.70%	0.84 - 0.91	58.13%	0.54 - 0.63	58.96%	0.54- 0.64
	WEVI	79.60%	0.70 - 0.89	64.27%	0.57 - 0.72	53.86%	0.46 - 0.63

Table 11. Period-specific survival rates for egg laying, incubation, and nestling stages of black-capped (BCVI) and white-eyed vireo (WEVI) nests with 95% confidence intervals. Overall period survivals do not differ between species, but at San Saba and Colorado Bend study sites, white-eyed vireos had higher percent survival during the incubation stage.

Black-capped vireos nested at an average height of 1.12m (se = 0.02, n = 560) and white-eyed vireos nested at an average height of 1.59m (se = 0.05, n = 202) across our study sites. We tested nest heights as a predictor of parasitism, and while we found white-eyed vireos nest significantly higher than black-capped vireos (z = -1.97, P = 0.05, Nests: n = 1081, Predictor Variables = 3, Random Effects = 2), we found no significant impact of nest height on parasitism (z = 0.72, P = 0.47, Nests: n = 1081, Predictor Variables = 3, Random Effects = 2) or an interaction between species and nest height (z = -0.41, P = 0.68, , Nests: n = 1081, Predictor Variables = 3, Random Effects = 2) (see Table 12).

	Estimate	Std. Error	z value	Pr(>|z|)
Species	-0.603	0.31	-1.97	*0.05
Nest Height	0.389	0.54	0.72	0.47
Species * Nest Height	-0.465	1.13	-0.41	0.68

Table 12 – Results of a generalized linear mixed model fit with a Laplace approximation with a binomial distribution and logit link. We used species and the log-transformed nest height as predictors with parasitism fate as the response, also testing for interactions between species and nest height. To account for seasonal and site variation we included site within year as random effects in the model. Estimates show the relative direction and influence of a predictor variable on the response variable (parasitized or not).

We conducted nest vegetation measurements on 113 black-capped vireo nests and 116 white-eyed vireo nests during the 2014 and 2015 season. We conducted nest vegetation measurement on our West Range study site in 2014 and added Maxdale, Taylor Valley, and San Saba in 2015. White-eyed vireos nested in locations with ‘very tall’ (>10m) canopy significantly more than black-capped vireo (z = 4.80, P < 0.001, Nests: n = 239, Predictor Variables = 6, Random Effects = 2, Table 13). There was no difference in nest height, nest substrate height, or foliage density between vireo species (see Table 13).

	Estimate	Std. Error	z value	Pr(>|z|)
Nest Height	1.020	1.17	0.87	0.38
Nest Substrate Height	-0.150	0.46	-0.33	0.74
Canopy Height: Short	-1.751	5.77	-0.30	0.76
Canopy Height: Tall	0.509	1.52	0.34	0.74
Canopy Height: Very Tall	21.797	4.54	4.80	*< 0.001
Average Foliage Density	0.029	0.37	0.08	0.94

Table 13 – Results of a generalized linear mixed-model fit with a Laplace approximation with a binomial distribution and logit link. To test for differences between species, we set species as the response variable and nest height, substrate height, canopy height (categorical: short, medium, tall, very tall), and average foliage density as predictors. To account for individual difference and site differences we designated the individual (adult male associated with the nest) and study site as random effects in the model. Estimates show the relative direction and influence of a predictor variable on the response variable (species).

We modeled parasitism separately for each vireo species to test for species-specific differences in nest placement between parasitized and un-parasitized nests. We excluded our Taylor Valley study site from this analysis as there were no nests parasitized in the years we conducted the nest vegetation measurements. We found black-capped vireo nests in taller substrates are significantly more likely to be parasitized (z = 2.83, P = 0.005, Nests: n = 113, Predictor Variables: n = 4, DF = 36, Table 14). We found no impact of nest height, canopy height over the nest, or foliage density (concealment) around the nest on parasitism (Table 14). We found no nest placement variables to be significant in predicting parasitism in white-eyed vireos (Nests: n = 116, Predictor Variables = 4, DF = 36, Table 15).

	Estimate	Std. Error	z value	Pr(>|z|)
Nest Height	-0.813	0.58	-1.41	0.16
Substrate Height	0.526	0.19	2.83	*0.005
Canopy Height	-0.027	0.11	-0.24	0.81
Average Foliage Density	0.109	0.14	0.78	0.43

Table 14 – Results of a generalized linear mixed-model fit with a Laplace approximation with a binomial distribution and logit link modeling black-capped vireo nests. We set parasitism as the response variable to test if nest placement variables (nest height, substrate height, canopy height, or foliage density) had any influence on parasitism risk. We found a significant influence of substrate height on parasitism risk, with taller substrates positively influencing parasitism risk. To account for individual difference and site differences we designated the individual (adult male associated with the nest) and study site as random effects in the model. Estimates show the relative direction and influence of a predictor variable on the response variable (black-capped vireo nest: parasitized or not).

	Estimate	Std. Error	z value	Pr(>|z|)
Nest Height	0.765	0.62	1.24	0.22
Substrate Height	-0.185	0.23	-0.80	0.42
Canopy Height	0.032	0.16	0.20	0.84
Average Foliage Density	-0.122	0.22	-0.55	0.59

Table 15 – Results of a generalized linear mixed-model fit with a Laplace approximation with a binomial distribution and logit link modeling white-eyed vireo nests. We set parasitism as the response variable to test if nest placement variables (nest height, substrate height, canopy height, or foliage density) had any influence on parasitism risk. We found no nest placement variables to have a significant impact on parasitism risk. To account for individual difference and site differences we designated the individual (adult male associated with the nest) and study site as random effects in the model. Estimates show the relative direction and influence of a predictor variable on the response variable (white-eyed vireo nest: parasitized or not).

Parental Behavior: Nest Building- We conducted nest observations on 17 black-capped vireo and 19 white-eyed vireo nests during the building stage. We excluded two white-eyed vireo nests from analysis as we never observed either nest with eggs, and thus were not considered in our analysis as nest fate could not be determined. Of the 17 black-capped vireo nests observed, six were successful, 11 failed, and four were parasitized (Table 16). Of the 17 white-eyed nests considered for our analysis, four were successful, 13 failed, and two were parasitized (Table 16).

	Black-capped Vireo	White-eyed Vireo	Totals
Nest Observations	17	17	34
Successful Nests	6	4	10
Failed Nests	11	13	24
Parasitized Nests	4	2	6

Table 16 - Summary of nest and parasitism fates for black-capped and white-eyed vireos included in our nest observation analysis.

During nest observations black-capped vireo males sang an average of 11.40 song bouts per hour (se = 2.20) and at a rate of 4.68 min/hr (se = 2.20). White-eyed vireo males made and average of 7.70 song bouts (se = 2.06) and sang at a rate of 2.43 min/hr (se = 0.63). Black-capped vireos made an average of 6.56 building trips/hr (se = 1.44) and white-eyed vireos make and average of 5.66 trips/hr (se = 1.66). Black-capped vireo adults built at a rate of 3.41 min/hr (se = 0.84) and white-eyed vireos built at an average rate of 3.69 min/hr (se = 1.28) (Table 17). Of the 395 individual black-capped vireo behaviors recorded, there were 38 (10.13%) we could not determine the sex of the bird. Of the 273 white-eyed vireo behaviors observed, we could not determine the sex of 51 (18.68%). Due to small sample sizes and limitations in identifying the sex of individual vireos we did not attempt to factor the sex of the adult into our analyses, though song rate and song bouts are behaviors exclusive to male vireos.

	Black-capped Vireo		White-eyed Vireo	
Behavior	Average	se	Average	se
Song Bouts / Hour	11.40	2.20	7.70	2.06
Song Rate (min/hr)	4.67	2.20	2.43	0.63
Building Trips / Hour	6.56	1.44	5.66	1.66
Nest Building rate (min/hr)	3.41	0.84	3.69	1.28

Table 17- Summary of black-capped and white-eyed vireo behaviors from nest observations. Behavior averages with standard errors are given for each species. Sample size is n = 17 for both species.

Male black-capped vireos had significantly higher rates of singing than male white-eyed vireos (z = -2.03, P = 0.04, Observations = 36, Predictor Variables = 2, Table 18), though there was no difference in building rate between species (z = 0.44, P = 0.66, Observations = 36, Predictor Variables = 2, Table 18).

	Estimate	Std. Error	z value	Pr(>|z|)
Song Rate (min/hr)	-0.266	0.13	-2.03	*0.04
Build Rate (min/hr)	0.038	0.09	0.44	0.66

Table 18 - Results from a generalized linear model with a binomial distribution. We used song rate and build rate as predictor variables and species as our response variable. We found significant differences in song rate between species, with black-capped vireos singing at a higher rate than white-eyed vireos. Estimates show the relative direction and influence of a predictor variable on the response variable (species).

We found significant differences in song rate (z = -2.03, P = 0.04, Observations= 36, Predictor Variables= 2 Table 19), but no difference in building rate between parasitized and un-parasitized nests (z = 0.44, P = 0.66, Observations = 36, Predictor Variables = 2, Table 19). Song rate positively influenced parasitism response in our model (Table 19).

	Estimate	Std. Error	z value	Pr(>|z|)
Song Rate (min/hr)	0.331	0.16	2.03	*0.04
Build Rate (min/hr)	-0.103	0.14	-0.74	0.46

Table 19- Results of a generalized linear model with binomial distribution using song rate and building rate as predictors of parasitism fate. Song rate was significantly different between parasitized and un-parasitized nests and the positive estimate associated with song rate shows that higher song rates had a positive effect on parasitism (i.e. the chance of getting parasitized). Estimates show the relative direction and influence of a predictor variable on the response variable (parasitized or not).

Juvenile Telemetry: Survival and Movement- We tracked 122 recently fledged, independent black-capped vireos during the pre-migration periods of 2012, 2013, and 2014. In 2014 and 2015, we additionally tracked 25 juvenile white-eyed vireos. Of the vireos with transmitters, 9 black-capped and 3 white-eyed vireos were lost soon after the start of tracking due to either the individual moving beyond our search area or through a transmitter malfunction. Excluding birds with transmitters that failed or were lost soon after the start of tracking, transmitters lasted an average of 27 days for white-eyed vireos and 17 days for black-capped vireos. One white-eyed vireo and 8 black-capped vireos died during the tracking period. The longest we were able to track a black-capped vireo was 40 days with a maximum of 45 days for white-eyed vireos. Black-capped vireos (mean = 330. 58m, se = 44.31, n = 111) made significantly farther daily movements, on average, than white-eyed vireos (mean = 216.59m, se = 20.38, n = 22) (t_{108} = -3.09, p = 0.003).

	Value	Std. Error	DF	t-value	p-value
Species	-0.230	0.07	108	-3.09	*0.003

Table 20 - Results of linear mixed-effects model fitted with restricted maximum likelihood. We set species as the response variable with the log-transformed daily movement the response. We accounted for year and site differences by setting study site within a year as random effects in the model. Black-capped vireos move significantly farther per day than white-eyed vireos. The value shows the relative direction and influence of a predictor variable (species) on the response variable (daily movement).

Juvenile vireos had high survival regardless of species. Juvenile white-eyed vireos had a 95% probability of surviving more than two weeks of independence, whereas black-capped vireos had a 91.3% chance of survival two weeks or more post-fledgling. There was no significant difference in juvenile survival between species ($\chi^2 = 0.2$, df = 1, P = 0.66) during the tracking period.

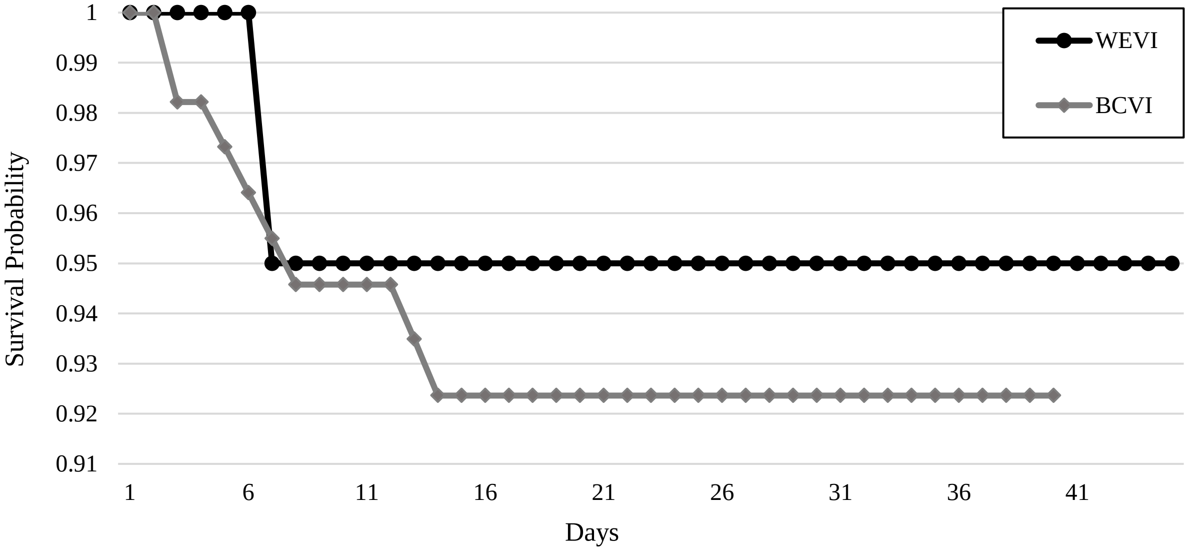

Fig. 5. Post-independence survival probabilities of white-eyed (WEVI) and black-capped vireos (BCVI) from 2012-2015. X-axis is the number of days and the y-axis is the percent probability of surviving to a given day. White-eyed vireos had a 95.0% survival over 40 days of independence and black-capped vireos had a 91.3% survival over the same period.

Discussion

It may seem paradoxical to inform the management of an endangered species by studying a related, abundant species, but in so doing one is able to better understand how a suite of interrelated threats challenge a species. For example, in our study, compared to the relatively common white-eyed vireo, we found that the threatened black-capped vireo exhibited a more constrained niche breath in vegetative preference, was prone to higher rates of brood parasitism, exhibited nest building behaviors associated with higher parasitism risk, and that adult selection of nesting habitat imposed a dispersal cost on juveniles. These insights suggest that, while management of cowbirds is important for the recovery of black-capped vireos, its success may be limited because of inherent preference for a portion of the vegetation available throughout its range.

We are not the first to find great value in the comparative approach, especially when concerning endangered or threatened species, as it allows for the study of sensitive species through less invasive methods. Recent work by Cinner et al. (2016), for example, illustrates the power and broad applicability of a comparative approach by applying techniques traditionally used in the field of human health to identify important factors in coral reef conservation. The approach, originally developed to combat childhood malnutrition, involved observing what ‘worked’ and applying that knowledge to other communities (Wollinka et al.1997). This ‘Bright Spot’ analysis involves identifying ecosystems (or species) that do substantially better than average and ‘dark spots’, which do substantially worse. Using this technique researchers were able to find common themes among ‘bright spots’ and ‘dark spots’ in coral reefs and allowed the authors unique insights into factors that led certain reefs to be healthier than others, leading to management strategies that would not have been apparent through direct investigation (Cinner et al. 2016).

A common ‘dark spot’ we detected involved the species’ vulnerability to nest parasitism. Across our study sites, we found that black-capped vireos had nearly twice the parasitism rate as white-eyed vireos, which parallels findings from other research in our study region (Kovar 2015, Campomizzi et al. 2013, Barber and Martin 1997). Overall we found cowbird parasitism to be a primary suspect for population differences between vireo species, and due to the likely causes of these differences (i.e. habitat preferences, nest site selection, behaviors near the nest, timing of arrival on breeding grounds), cowbird management will likely retain a vital role in the management of this species.

Territory vegetation surveys indicated that white-eyed vireos selected for higher percent canopy cover throughout their territory, with the core of their territory containing significantly higher levels of canopy cover than those of black-capped vireos. Core areas corresponded with nesting sites because territorial males spend much of their time in close proximity to their nests due to vireos' shared roles in nesting (Grzybowski 1995, Hopp et al. 1995), which is supported by our finding that white-eyed vireos had significantly higher canopy over their nest sites. As higher levels of canopy cover have been shown to be negatively correlated with cowbird parasitism (Rothstein et al. 1984, Howell et al. 2007, Young and Hutto 1999), white-eyed vireos' selection of higher levels of canopy cover at their nesting sites may be a mechanism for decreasing the risk of cowbird parasitism within the same landscape. As the level of cowbird control regime did not affect the vegetation use within a territory, black-capped vireos do not appear to adjust their vegetation use in response to the threat of cowbird parasitism.

At study sites with nearby riparian vegetation, vireos tended to segregate themselves with few overlapping territories between species. White-eyed vireos primarily occupied riparian areas characterized by greater canopy cover, despite readily available scrub vegetation. Species segregation at these sites is likely driven by habitat preferences rather than any competitive exclusion or competition, because other researchers found no evidence of competition between black-capped and white-eyed vireos (Kovar 2015). The black-capped vireos' conspicuous absence from riparian or woody wetland vegetation on our study sites as well as from the woody wetland vegetation type during our presence absence surveys, indicates a potential ‘bright spot’ in understanding how white-eyed vireo are thriving in this region. Riparian vegetation may act as a refuge for white-eyed vireos, providing them with natural areas of lower parasitism due to higher levels of canopy cover and possibly buffering nearby populations with its reproductive output. This trend was typified at our Colorado Bend and San Saba study sites, where black-capped to white-eyed vireo parasitism rates were 70.2% to 28.1% and 45.1% to 12.1%, respectively. At these sites, white-eyed vireos had significantly higher survival during the incubation period. This difference in survival was likely driven by parasitism, as black-capped vireos will often abandon their nest shortly after being parasitized (Boves et al. 2014) whereas white-eyed vireos rarely abandoned in our study. Whereas we found that black-capped and white-eyed vireos had similar overall nest success and survival, populations of white-eyed vireos in riparian areas and denser forested areas may supplement white-eyed vireo populations in more open and scrubby areas.

We found no difference in foliage density (a proxy for nest concealment) between nests of vireo species, and though white-eyed vireos nested significantly higher than black-capped vireos, we found no correlation between nest height and parasitism. These findings likely indicate factors, other than nest placement, as the primary drivers for the differences in parasitism rates between these species. Structurally, the songs of black-capped and white-eyed vireos are quite different, with black-capped vireo song consisting of longer phrases sung over longer periods compared to white-eyed vireos’ short repeated phrases and shorter song durations. Cowbirds locate nests primarily through host behaviors, focusing on vocalizations and movement near the nest site (Lowther 1993, Rothstein 1984, Banks and Martin 2001). Black-capped vireos are likely broadcasting more signals to cowbirds compared to white-eyed vireos simply through their greater song rate as increased host vocalizations near their nest correlates with an increase in parasitism risk (Rothstein 1984, Banks and Martin 2001).

White-eyed vireos arrive on the breeding grounds and initiate nests earlier than black-capped vireos in this region, with white-eyed vireos initiating nests an average of 8 days earlier than the earliest black-capped vireo nests (Kovar 2015). By initiating nests earlier, white-eyed vireos decrease their risk of cowbird parasitism (Boves et al. 2014) and reduce the risk of nest depredation by snakes (Sperry et al. 2008), both of which increase as the breeding season progresses. White-eyed vireos also continue to breed later (Kovar 2015), which may allow them to effectively expand their breeding season compared to black-capped vireos. During the 2015 field season, we observed several white-eyed vireo territories that successfully fledged three broods of nestlings, which has not been documented in black-capped vireos. This additional reproductive capacity, especially during productive years, may buffer white-eyed vireo populations during less productive breeding seasons.

Black-capped vireos had significantly larger territory sizes across all study sites. The reduced territory size may allow white-eyed vireos to occupy smaller habitat patches, which may provide additional buffers to their populations also increasing the connectivity between larger populations. By contrast, black-capped vireos may have a minimum home range size that prevents them from occupying smaller patches even if they are otherwise suitable for nesting. Combined with broader habitat use, white-eyed vireos likely have a more interconnected network of populations within our study range, allowing for easier dispersal of individuals, which may in turn protect sink populations from local extirpation. This may be an important factor as black-capped vireo’s patchy distribution makes them especially vulnerable to local extirpation, with isolated populations being lost from Oklahoma as recently as the mid-90's (Grzybowski et al. 1986, Grzybowski 1995).

Though we detected no differences in survival between juvenile vireos during the pre-migration period, black-capped vireos made significantly farther daily movements than white-eyed vireos. Vegetation measurements of juvenile vireo home ranges showed that both species had higher levels of foliage density in the core of their range, with white-eyed vireo's trending towards more canopy cover throughout. Other researchers working in this study system found similar trends, with juvenile black-capped vireos selecting habitat differing from adult breeding habitat, characterized by higher levels of canopy cover, shrub cover, and foliage density. Specifically, they found that juvenile black-capped vireos captured in riparian areas did not leave them and if they moved into riparian areas, they remained there (Dittmar et al. 2014). Riparian areas, with higher levels of canopy cover and foliage density, also have greater arthropod abundance (Dittmar et al. 2014, Vega Rivera et al. 1998, Iwata et al. 2010). Accordingly, differences in daily movement between black-capped and white-eyed vireos may be caused by food availability, with black-capped vireos moving farther from natal territories to find more preferred juvenile habitat with higher vegetation density. Meanwhile, white-eyed vireos, which fledge from territories with significantly higher levels of canopy cover, may not be required to travel as far for preferred pre-migration habitat. The increased movement of black-capped vireos, potentially caused by searching for suitable foraging habitat, may impose a survival cost that we were unable to detect due to relatively short tracking periods.

Our study highlights several 'bright spots' working in conjunction and to the white-eyed vireo's favor. White-eyed vireo populations appear to be more robust due to the species' innately broader habitat requirements, which effectively increase potential breeding habitat within the same range. Additionally, their broader vegetation use likely offers protection from the effects of cowbird parasitism as white-eyed vireos tend to use riparian vegetation when available and where the increased canopy cover decreases parasitism risk (Howell et al. 2007, Rothstein et al. 1984, Young and Hutto 1999). This additional habitat likely provides a buffer for this species to overcome seasonal variability in nest success in addition to refuges from cowbird parasitism. By initiating nests earlier, white-eyed vireos decrease their risk of both parasitism (Boves et al. 2014, Campomizzi et al. 2013) and nest depredation by snakes (Sperry et al. 2008), and a longer breeding season may allow them additional nesting attempts. Additionally, white-eyed vireo song is likely weaker signal for cowbirds to cue in on and locate nests. Our work on white-eyed vireos highlights the importance of continued cowbird management on Fort Hood and other important breeding populations, as black-capped vireos appear to be particularly vulnerable to nest parasitism even among closely related species. Furthermore, riparian habitat provides important refuges for juvenile vireos during their pre-migratory phase (Dittmar et al. 2014) and protecting these areas, especially those in close proximity to adult breeding habitat, may decrease dispersal costs of juvenile black-capped vireos as they leave their natal territory. Future studies, of longer duration, could examine how habitat characteristics influence subsequent daily movements to elucidate the cause of the differential dispersal distances between black-capped vireos and white-eyed vireos and better understand this critical life stage.

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