

Nest Height and Vertical Vegetation Associated with Black-capped Vireo Breeding Success in Southwest Texas

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Abstract - *Vireo atricapilla* (Black-capped Vireo) is an endangered songbird whose habitat use has been well studied in central portions of its breeding range, which is characterized by successional vegetation communities. To expand our understanding of habitat use as it relates to reproductive success, we studied Black-capped Vireo habitat use at the territory and nest-site scales in southwest Texas in 2009 and 2010, an area characterized by xeric and stable vegetation communities. We measured vegetation in territories and at nests to evaluate the influence of habitat variables on nest parasitism and nest survival. Our results showed that Black-capped Vireo nest-site use in southwest Texas differed from that in breeding areas of central Texas and Oklahoma. Black-capped Vireos in southwest Texas used nest sites with a wide range of woody cover ($70 \pm 13\%$) and used *Juniperus* spp. (junipers) as a nest substrate proportionately more than its availability in territories, which is contradictory to previously published literature. Nest parasitism increased significantly with greater nest height, likely due to increased visibility to *Molothrus ater* (Brown-headed Cowbird). Increasing height of vertical cover above the nest was associated with decreased overall nest survival, likely because nests placed in habitat with taller vegetation are more susceptible to avian predators and Brown-headed Cowbird parasitism. Unlike the findings of studies conducted in the northern part of the species' breeding range, we found that parasitism did not increase the likelihood of depredation or abandonment. Our results indicate that Black-capped Vireo habitat structure and composition, as well as factors influencing nest success in Southwest Texas, differ from their breeding habitat in central Texas and Oklahoma, indicating that management guidelines need to be region-specific.

Introduction

Avian-habitat characteristics often vary across the range of a species due to multiple factors including habitat availability (Johnson 2007), vegetation species and structure (Rotenberry and Wiens 1980), predator assemblages (Conkling et al. 2012, Lima 1993), interspecific competition (Lockwood and Moulton 1994, Piper and Catterall 2003), and brood parasitism (hereafter, parasitism; Barber and Martin 1997). Habitat selection refers to a hierarchical process of behavioral responses that may result in the disproportionate use of habitat components (e.g., singing perches, plant species) to influence survival and fitness of individuals (Block and Brennan 1993, Hutto 1985, Jones 2001). However, habitat quality is not always positively

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associated with avian species density and, therefore, should be defined in terms of survival and reproductive rates (Maron et al. 2012, Van Horne 1983).

The habitat characteristics and environmental factors used by avian species as cues for selection at the territory scale may differ from those used for selection of nest sites (Latif et al. 2012, Orians and Wittenberger 1991, Reed and Dobson 1993). Understanding the dynamics of these factors across the breeding range and analyzing settlement patterns on multiple spatial scales (MacArthur and MacArthur 1961) is an essential part of effective management, especially for endangered species. Further, depredation is a main cause of decreased reproductive success in open-nesting birds (Martin 1993, Skutch 1949), and vegetation characteristics around the nest (e.g., vegetation density, nest height) have previously been linked to higher rates of depredation (Martin 1993). Both vegetation characteristics and predator assemblages often differ across a species' range; thus, it is likely that factors influencing reproductive success also vary.

Vireo atricapilla Woodhouse (Black-capped Vireo; hereafter Vireo) is a federally endangered migratory songbird (Ratzlaff 1987) with a current known breeding range that extends from central Oklahoma south through Texas to the Mexican states of Nuevo Leon and southwestern Tamaulipas (Fig. 1; González-Rojas et al. 2014, Graber 1961). The eastern limit of the Vireo breeding range in Texas follows the line of the Balcones Escarpment (Graber 1961), and small numbers of Vireos have been observed as far west as Big Bend National Park (Grzybowski 1995). Habitat selection varies across the breeding range (Farquhar and Gonzalez 2005, Graber 1961, Grzybowski et al. 1994). However, the majority of management efforts and research on Vireos has occurred in successional vegetation types of the Edwards Plateau in central Texas, which needs frequent disturbance to maintain Vireo habitat (Wilkins et al. 2006). Vireos in southwest Texas utilize Tamaulipan thornscrub, xeric vegetation typically found below 1000 m elevation, where the vegetation is patchy and low-growing (<3 m), is relatively stable, and tends to remain suitable for Vireos without disturbance by fire or grazing (Wilkins et al. 2006). However, limited research on Vireos has been conducted in the southwest Texas portion of the breeding range (Smith et al. 2012) despite a comparable abundance of Vireos occupying the area (McFarland et al. 2013).

Differences in both predator assemblages (Benson et al. 2010, Conkling et al. 2012) and reproductive behavior under varying parasitism pressure by *Molothrus ater* (Boddaert) (Brown-headed Cowbird, hereafter Cowbird; Grzybowski 1995, Pope et al. 2013) across the range may be influencing Vireo nest-survival rates differently in southwest Texas. Evidence is split on the influence of vegetation characteristics on Vireo nest survival in central Texas (Bailey 2005, Conkling 2010, Pope et al. 2013). For example, both Bailey (2005) and Conkling et al. (2012) found that Vireo nests placed higher in the canopy enjoyed higher nest-survival rates than nests placed nearer the ground. Additionally, Conkling (2010) found Vireo nest survival increased with increasing distance to edge. Another study, conducted farther south, found no relationship between vegetation characteristics and Vireo nest survival; however, Cowbird parasitism decreased nest survival due to higher

abandonment rates of parasitized nests (Pope et al. 2013), an observation also made for *Vireo* nests in Oklahoma (Grzybowski 1995, Pease and Grzybowski 1995).

Understanding *Vireo* habitat use and consequences on reproductive success in southwest Texas will allow for more informed management decisions and will improve conservation by providing knowledge of the *Vireo*'s habitat needs across

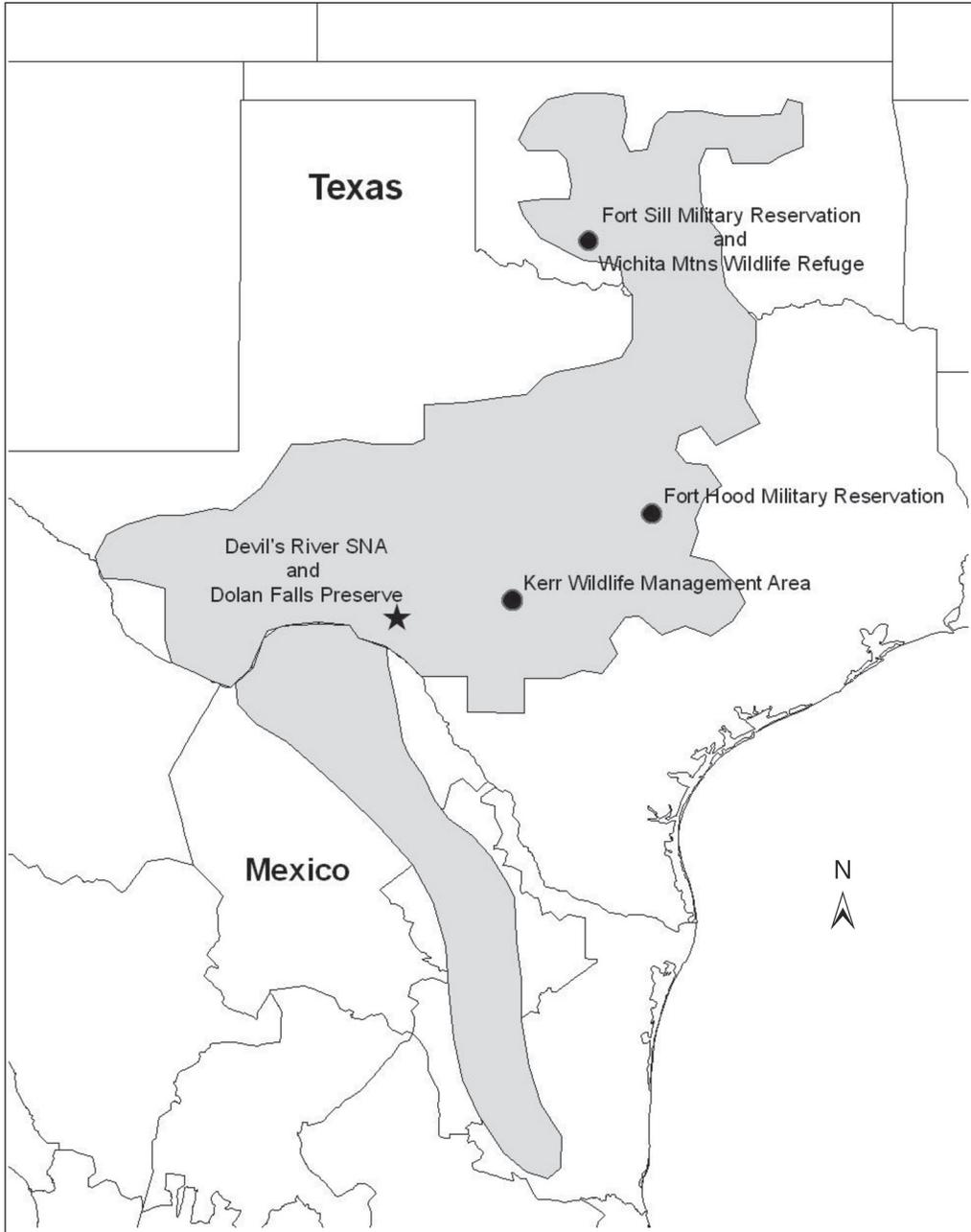


Figure 1. Black-capped Vireo breeding range (shaded), previously well-surveyed locations (circles), and location of 2009 and 2010 study area (star).

its breeding range. Our objectives were to describe and quantify habitat used by Vireos in southwest Texas, an under-described area of their breeding range, and to determine which vegetation characteristics, if any, were associated with reproductive success in 2009 and 2010. Specifically, we measured vegetation characteristics to (1) compare parasitized and not parasitized nests and (2) analyze nest survival to determine if habitat was associated with likelihood of parasitism or nest failure due to depredation or abandonment.

Field-site Description

Our study area was located in Val Verde County, TX, in the Devil's River region at the western edge of the Edwards Plateau. Our study area encompassed Devil's River State Natural Area (DRSNA), a state-owned property that encompasses 8090 ha of mostly unmanaged land, and Dolan Falls Preserve, a 1942-ha property owned and managed by The Nature Conservancy. The property has populations of non-native introduced mammals including *Ovis aries* L. (Feral Sheep), *Axis axis* (Erleben) (Axis Deer), and *Ammotragus lervia* (Pallas) (Aoudad). Adjacent properties were undeveloped and used for recreation, including hunting.

The natural plant communities at DRSNA and Dolan Falls Preserve exhibit elements of the mesquite–chaparral of the South Texas Plains, the oak–cedar of the central Edwards Plateau to the east, and the *Dasyilirion–Lechuguilla* (sotol–lechuguilla) of the Trans-Pecos to the west (Hedges and Poole 1999). Topographic features of DRSNA and Dolan Falls Preserve include high-domed rocky hills topped with plateaus and, hard-scrabble ridges with several large drainage systems that cut their way through canyons; elevation varies from ~409 m to 632 m (Hedges and Poole 1999). The upper portion of Dolan Creek is ephemeral, winding 20 km through DRSNA to Dolan Falls Preserve, where springs provide year-round waterflow to the Devil's River. Compared to historical averages for the months of the study, mean rainfall was slightly lower and temperatures were higher in 2009, whereas rainfall was significantly higher and temperatures were closer to average in 2010 (see Smith 2011 for details).

Methods

Study-site selection

Our sampling frame included DRSNA and Dolan Falls Preserve. There was little information about Vireo habitat use at these sites; thus, we initially sampled randomly across the study area to establish the location of specific study sites. We used ArcGIS 9.3 to create a grid comprised of 1-km² cells that covered our study area and then used Hawth's tools (Beyer 2004) to randomly select grid cells for sampling. We randomly selected 4 cells in 2009 and 3 in 2010. We visited each grid cell no earlier than local sunrise and no later than 4 h after sunrise 2–3 times during the early part of the breeding season (March and April); visits were >4 days apart. We systematically surveyed selected cells, concentrating on areas with sufficient vegetation to support Vireos (i.e., cover >20%) and walked within 200 m

of all locations within the cells. If we detected a singing male Vireo, we marked its coordinates with a global positioning system unit (GPS). If we did not detect Vireos after 3 visits, we visited the cell once a week for another month to be certain that no Vireos established territories. If we still observed no evidence of breeding, we randomly selected a new grid cell to replace the original cell. If we detected Vireos within a cell, we established that cell as a study site. Territorial male Vireos are highly detectable during the breeding season without the use of song playback (M.L. Morrison, unpubl. data).

We delineated our study sites once we had located all the territories that we were logistically capable of monitoring (8–12 territories) within and around each grid cell. We defined our individual study sites as contiguous areas that occurred in and around the randomly selected grid cells that contained Vireos. Size of the study site depended upon spacing of territories and the degree of difficulty of monitoring the territories at that particular site. We had 4 study sites in 2009 (2 along dry Dolan Creek and 2 in canyons) and 3 study sites in 2010 (2 along Dolan Creek and 1 in a canyon). Study sites ranged in size from 32 ha to 267 ha and were spaced from 3 km to 9 km apart. Canyon study sites were large because the vegetation suitable for Vireo territories exists in narrow strips along the bottoms of the canyons, causing the Vireo territories to be more spread out than in dry Dolan Creek.

Territory mapping and nest searching

We mapped adult male Vireo territories and searched for nests between 15 March and 15 July each year. After locating Vireos, we returned every 2–5 days to map singing locations by recording 3–6 GPS-location points during each of the first 4 visits. On subsequent visits, we recorded ≥ 3 territory points on every other visit. We considered 15 as the minimum number of points needed to provide a good representation of a territory (International Bird Census Committee 1970). After uploading territory points into ArcGIS, we used Hawth's tools to create minimum convex polygons (hereafter MCP) to represent territories used by each male we monitored. MCPs allowed us to encompass all of the potential vegetation the Vireos were using within territories and provided data comparable to that of other studies concurrently conducted in other areas of the Vireos range (Conkling 2010, Pope et al. 2013). We visited territories every 2–5 days and located nests using behavioral cues that characterize breeding adults (i.e., alarm calls, carrying nest material, carrying food, males singing on the nest). We marked nest locations by hanging flagging ≥ 15 m away and recorded locations using GPS units with accuracy of ± 5 m.

We monitored nests every 2–4 days until nestlings fledged or the nest failed. We added any Cowbird eggs and/or removed Cowbird nestlings at the time of their discovery and recorded the parasitism. We left Cowbird eggs in the nests because the presence of either real or artificial Cowbird eggs deters future parasitism (Ortega et al. 1993), and we allowed the parasitized nests to remain active and potentially fledge Vireo young while not influencing abandonment rates, thereby allowing us to observe nest survival in the context of depredation rates with maximum sample size. Vireo studies conducted farther north within the range also employed this protocol, which allowed us to compare nest survival across locations (Conkling et

al. 2012, Pope et al. 2013). If we observed an empty nest with no visible signs of fledging, we searched the territory for fledglings every 3–4 days for 2 weeks, within the time when the fledglings are the least mobile and still dependent on the adults (Pope et al. 2013), or until a fledgling was located. We considered a nest successful if at least one Vireo young fledged.

Vegetation sampling

Territory-scale. To quantify habitat used on the territory scale, we employed ArcGIS 9.3 to overlay a 20-m grid over each mapped territory. We used a GPS unit in the field to locate grid points (± 5 m accuracy) and we recorded the presence or absence of woody cover. If we observed woody cover (i.e., trees, shrubs, snags, brush piles), we recorded the plant species with the most foliage cover at that point. We used a 2.5-m measuring pole to determine the height at which the plant's foliage or branch cover began at the bottom (start height) and where its foliage cover ended at the top (maximum height) to the nearest decimeter.

Nest-scale. After a nest had either fledged or failed (Grzybowski 1995), we measured nest height (ground to rim), substrate height, and overstory height if present (different plant species above nest substrate), to the nearest 0.1 m. We measured foliage cover around the nest (hereafter, horizontal cover) in each cardinal direction by placing a 2 m x 0.10 m cover board 7 m away from the nest and estimating the proportion of 0.10-m squares covered (Guthery et al. 1981). We calculated cover above the nest (hereafter, vertical cover) as the overstory height minus the nest height or, if no overstory was present, the nest substrate height minus the nest height. We also recorded substrate species, and plant community (see below). We used a clinometer to measure the slope and, if a nest occurred on a slope, we also recorded aspect.

Vegetation communities were not homogenous across the study area or, occasionally, within territories; therefore, we classified nest location into 1 of 5 plant communities in order to evaluate the influence on Vireo nests due to potential variations in predator or Cowbird use. Hedges and Poole (1999) identified 9 non-grass/herbaceous plant communities at DRSNA that we used to delineate potential Vireo habitat and other plant communities. Three of these communities, *Fallugia paradoxa* (D. Don) Endl. (Apache plume), *Celtis reticulata* Torr. (Netleaf Hackberry)–*Juglans microcarpa* Bertlandier (Little Walnut), and *Platanus occidentalis* L. (Sycamore)–*Salix nigra* Marsh. (Black Willow), occur in the dry-river wash and streambed areas; we combined these communities for our purposes and called them wash communities. Three plant communities occur on dry, rocky slopes: *Juniperus ashei* J. Buchholz (Ashe Juniper)–*Quercus* spp. (oaks), *Acacia berlandieri* (Benth.) Britton & Rose (Guajillo), and *Agave lechuguilla* Torr. (Lechuguilla)–*Dasylyrion leiophyllum* Engelm. ex Trel. (Sotol); we combined these communities and referred to them as slope. Vegetation cover and oak dominance were considerably different along drainages and creeks; thus, we classified them separately as riparian. The Ashe Juniper–oak community also occurs in the deeper soils of the flat upland areas of the study area, which we classified as mesa. We combined the 2 communities

that occur on the low, flat, and gently sloping lower-elevation areas, *Leucophyllum frutescens* (Berland.) I.M. Johnst. (Ceniza) and *Prosopis glandulosa* Torr. (Mesquite)–*Aloysia gratissima* (Gillies & Hook.) Troncoso (Whitebrush), and called them low flat. The *Quercus fusiformis* Small (Plateau Live Oak)–Netleaf Hackberry series is the only mostly deciduous woodland community occurring at DRSNA, and we referred to these areas as woodland.

Statistical analyses

Habitat metrics. We calculated vegetation species diversity within territories using the Shannon–Wiener Index (Weaver and Shannon 1949). We detected no significant difference in vegetation measured in 2009 and 2010 ($P > 0.10$; Smith 2011); thus, we combined data from both years for analyses. We calculated mean and standard deviation for each variable recorded at territories and nests. We used a chi-square test to determine if nest-substrate use was equal proportionately to its availability within the territories. We calculated the proportion of substrate used by dividing number of nests in the substrate at a study site by the total number of nests at the study site. We determined the proportion of substrate available by dividing the number of times we detected a substrate at a point during territory-scale vegetation measurements, using only points falling within territories, by the total number of grid points visited within territories. In order to observe any changes in nest substrate used over time, we divided each season into 3 parts—early (days 1–25), middle (days 26–50), and late (days 51–75)—starting with the day the first egg was observed.

Parasitism. We performed logistic regression modeling in R 3.1.0 (R Development Core Team, Vienna, Austria) using package ‘MuMIn’ 1.10.0 (Bartón 2014) and used a generalized linear model with a logit link and a binomial distribution to determine factors that influenced parasitism by Cowbirds. The dependent variable was nest fate (0 = not parasitized, 1 = parasitized). Explanatory variables were nest height, vertical cover, mean horizontal cover, year, and 3 dummy variables to construct covariates for 4 different location types (low flat, riparian, wash, and slope). We also included mean cover variance, the variance of the horizontal cover, which was used as an additive variable with horizontal cover to convey variation of vegetation cover around the nest. In addition, including each variable in the regression, we used the interaction of year with each explanatory variable to determine if the influence of each on nest fate was consistent between 2009 and 2010.

We constructed additive models using a sequential model-fitting approach to examine variable effects on the probability of parasitism while limiting the number of models used. To determine which variables might be associated with the probability of parasitism, we entered variables in a forward stepwise-selection model if $P < 0.20$ and removed them if $P > 0.10$ (Pearce and Ferrier 2000). We also removed variables with low sample sizes (<10 occurrences in a year) and checked for variable correlation. We ranked models using small sample-size-corrected Akaike’s information criterion (AIC_c) values and weights (Burnham and Anderson 2002). We also used model averaging for beta estimates in the best-fitting models

($\Delta AIC < 2$) and examined the coefficients and 95% confidence intervals to determine the effects of each covariate (Arnold 2010). Finally, we used odds ratios to examine explanatory-variable effect and effect size of variables remaining in the model (Agresti 1996:107–108).

Nest survival. We analyzed nest survival, which we determined by whether or not the nest was lost to depredation or abandonment, using a logistic-exposure model in R using package RMark 2.1.3 (Laake and Rexstad 2008) to estimate daily survival rates (DSR). Cowbirds parasitized and depredated nests in both years (Smith et al. 2012), but we only used depredation events in this nest-survival analysis to signal the failure of a nest. We classified parasitized nests as active until the nest was successful, depredated (e.g., Vireo egg or nestling was removed without subsequent parasitism event), or abandoned. We used nest-specific covariates in our analyses, including linear date, nest height, vertical cover, horizontal cover, and if the nest was parasitized (yes/no). We also employed 3 dummy variables to construct covariates for 4 different location types (low flat, riparian, wash, and slope).

We constructed additive models using a sequential model-fitting approach to examine nest survival while limiting the number of models used. Our null model included year to control for effects between years because we were only interested in differences in nest survival resulting from differing vegetation structure. We initially fit our year-only model to determine if inclusion of linear date or vegetation structure (nest height or vertical cover height) best explained variation in nest survival. We subsequently used the best-fit model from the previous step to determine if models containing an interactive effect between horizontal cover and variance of horizontal cover improved the fit of the resulting model. We ranked models in each step based on AIC_c values and weights, used model averaging, and examined the coefficients and 95% confidence intervals to determine significance of effects for each covariate. We calculated odds ratios for significant covariates in the best-fit model by exponentiating the resulting parameter coefficients.

Results

Habitat metrics

We monitored and measured vegetation in 57 territories in 2009 and 2010 (Table 1). During both years, Vireo nests were located in wash ($n = 21$), slope ($n = 34$), riparian ($n = 35$), and low-flat ($n = 24$) communities; we found no nests in mesa or woodland communities. We measured vegetation at 78 nests in 2009 and 36 nests in 2010 (Table 1). Many territories had multiple nesting attempts in a season, primarily due to nest failures but occasionally because of second brood attempts. Nests built in slope plant communities had a mean slope of $21^\circ \pm 9^\circ$ (min–max = 7 – 45°). Nests occurred most often on slopes with a northerly aspect (33%) and least often on slopes with southwestern and southeastern aspects (<1%).

We located nests in 13 different substrates across the sampling frame. Four species made up 105 (88%) of the substrates used by Vireos for nests: *Juniperus* spp. (junipers; $n = 23$ [19%]), *Sophora secundiflora* (Ortega) Lag. ex DC. (Texas Mountain Laurel; $n = 34$ [29%]), *Diospyros texana* Scheele (Texas Persimmon; $n = 26$

[22%]), and *Quercus pungens* var. *vaseyana* Buckley (Vasey Shin Oak; $n = 22$ [19%]). The proportion of nest substrates used by Vireos changed throughout the breeding season, with Texas Mountain Laurel and juniper used during the early part of the season (38% and 25%, respectively) and Shin Oak proportionately more (33%) than others later in the season (Fig. 2). Use of Texas Persimmon increased considerably from the early to the middle part of the season; 15% to 30%, respectively; Fig. 2).

Table 1. Vegetation measurements in territories ($n = 57$) and around nests ($n = 114$) describing the overall mean (\pm SD), range of measurements observed, and mean (\pm SD) for both successful and failed territories and nests in the Devil’s River area during 2009 and 2010.

Parameter	Mean \pm SD	Variation	Successful	Failed
Territory				
Mean maximum height (m)	1.5 \pm 0.4	0.9–2.6	1.7 \pm 0.4	1.4 \pm 0.4
Mean start height (m)	0.5 \pm 0.2	0.2–0.8	0.5 \pm 0.2	0.5 \pm 0.2
Species diversity	2.60 \pm 0.45	1.42–3.53	2.7 \pm 0.4	2.5 \pm 0.5
Cover (%)	70 \pm 13	40–100	70 \pm 11	71 \pm 15
Juniper cover (%)	16 \pm 14	0–62	15 \pm 14	18 \pm 15
Year				
2009			33.3%	66.7%
2010			66.7%	33.3%
Nest				
Substrate height (m)	3.0 \pm 1.4	0.6–8.0	2.7 \pm 1.3	3.4 \pm 1.5
Nest height (m)	1.1 \pm 0.5	0.4–3.1	1.0 \pm 0.4	1.2 \pm 0.5
Horizontal cover (%)	85 \pm 11	48–100	85 \pm 11	85 \pm 10
Vertical cover (m)	2.8 \pm 1.2	0.7–6.6	2.5 \pm 1.1	2.9 \pm 1.3

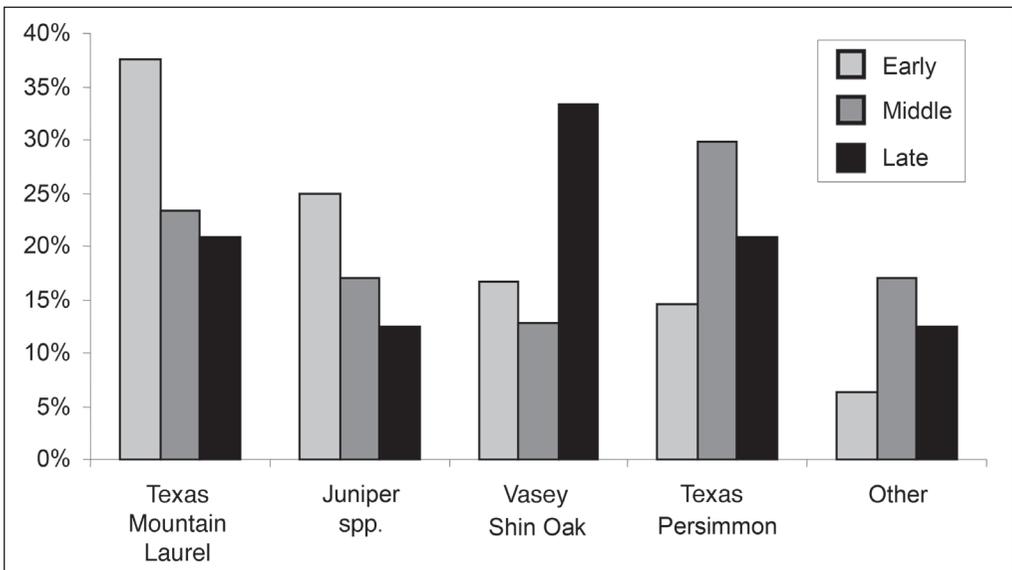


Figure 2. Percentage of nest substrates used by Black-capped Vireos in the Val Verde County, TX, during the early (days 1–25), middle (days 26–50), and late (days 51–76) periods of the 2009 and 2010 breeding seasons (Day 1 = 15 March).

Of the 4 most common nest substrates, Vireos used 3 substrates more than they were available within territories.. Vireos consistently used Vasey Shin Oak 3–25 times more than it was available and selected it over of other species in the canyons where it was widely available (Table 2). Juniper was used 2–6 times more often than it was available at 4 of the 7 study sites (Table 2). Texas Mountain Laurel was used more than it was available in all study sites and Texas Persimmon was used more than available in 6 of the 7 study sites (Table 2). The difference between used and available nest sites in Mountain Laurel and Texas Persimmon was even greater in habitat that ran along dry Dolan Creek (i.e., study sites 1, 3, 5, and 6) and where Vasey Shin Oak was not widely available for use by the Vireos.

Parasitism

Parasitism was lower in 2010 (26%) than 2009 (37%). We considered 10 models for our logistic-regression analysis of the probability of nest parasitism (Table 3). We did not include nests occurring in low-flat areas because of small sample size. We included cover variance and nest height in all the top models ($\Delta AIC_c < 2$). The top models also included site (i.e., canyon or dry creek), location type, and year, but the inclusion of these variables did not significantly improve the model (Table 3). The only significant variable in the best-fit models was nest height (Table 4), and it was positively associated with probability of parasitism. For every 1-m increase in nest height, the probability of parasitism increased 3.5 times (odds ratio = 3.45; 95% CI = 1.20–9.89).

Nest survival

We monitored 114 nests in our nest-survival analyses from 7 April to 10 July in 2009 and 2010 for a total of 99 sampling days. The majority of nest failures

Table 2. Percent of nest substrate used and available within Black-capped Vireo territories ($n = 57$) at dry-creek study sites and canyon study sites. An asterisk (*) denotes statistical difference ($P \leq 0.05$) between used and available substrate using chi-square test.

Substrate	Dry-creek study sites				Canyon study sites		
	1	3	5	6	2	4	7
Juniper spp.							
Used	12.5%	29.0%*	18.2%	6.7%	38.5%*	15.4%	16.7%
Available	13.9%	13.0%*	3.0%	15.7%	14.4%*	5.3%	18.0%
Texas Mountain Laurel							
Used	50.0%*	32.3%*	36.4%	46.7%*	7.7%	7.7%	8.3%
Available	11.4%*	7.8%*	12.1%	6.1%*	2.7%	4.2%	5.4%
Texas Persimmon							
Used	31.3%*	16.1%	45.5%*	40.0%*	7.7%	15.4%	8.3%
Available	10.8%*	9.3%	5.3%*	16.4%*	9.7%	3.4%	7.9%
Vasey Shin Oak							
Used	6.3%	6.5%	0.0%	0.0%	30.8%*	38.5%*	58.3%*
Available	0.0%	1.9%	1.5%	0.0%	2.8%*	1.5%*	10.7%*

was caused by depredation and only a few (<5%) were due to abandonment (see Smith et al. 2012). We considered 11 total models for our analyses (Table 5). Vertical cover and year best explained daily nest-survival (Table 5). All top models ($\Delta AIC_c < 2$) included vertical cover above the nest. The inclusion of linear date, nest height, horizontal cover, Cowbird parasitism, or location type did not improve the resulting model. Nest survival decreased with increasing vertical cover (Fig. 3), and 95% confidence intervals for individual covariates included in the top models were only significant for vertical cover; all other confidence intervals contained zero (Table 6). Daily-survival rates were 19% lower for every 1-m increase in vertical cover above the nest (odds ratio = 0.81; 95% CI = 0.66–0.99).

Table 3. Model-selection results for Black-capped Vireo parasitism from 2009 to 2010 in the Devil's River area of Texas. AICc = Akaike's information criterion with a correction for finite sample sizes. ΔAIC_c = change in AIC relative to the model with the smallest AIC value, ω = AIC model weight and Parameters = number of parameters.

Model	AICc	ΔAIC_c	ω	K
Cover variance + Nest height + Site + Riparian	138.5	0.00	0.18	5
Cover variance + Nest height + Site + Year + Riparian	138.7	0.15	0.16	6
Cover variance + Nest height + Site	139.3	0.79	0.12	4
Cover variance + Nest height + Site + Slope	139.6	1.07	0.10	5
Cover variance + Nest height + Slope	140.2	1.69	0.08	4
Cover variance + Nest height	140.4	1.89	0.07	3
Cover variance + Nest height + Site + Year	140.7	2.16	0.06	5
Cover variance + Nest height + Riparian	140.9	2.34	0.06	4
Nest height + Site	141.7	3.16	0.04	3
Nest height + Site + Slope	142.1	3.54	0.03	4
Nest height + Vertical cover + Site	142.4	3.89	0.03	4

Table 4. Model-averaged regression coefficient, $(\beta) \pm SE$ and 95% confidence intervals included in the best-fitting models ($\Delta AIC_c < 2$) for Black-capped Vireo (*Vireo atricapilla*) parasitism from 2009 to 2010 in the Devil's River area.

Parameter	Coeff. (β) \pm SE	95% Confidence Intervals	
		Lower	Upper
Intercept	-1.56 \pm 0.61	-2.76	-0.36
Cover variance	-0.002 \pm 0.001	-0.004	0.00
Nest height	1.24 \pm 0.53	0.18	2.29
Site	-0.95 \pm 0.51	-1.97	0.07
Riparian	0.90 \pm 0.52	-0.14	1.93
Year ^A	-0.67 \pm 0.54	-1.75	0.41
Slope ^A	-0.70 \pm 0.51	-1.71	0.30
Vertical cover ^A	0.20 \pm 0.17	-0.13	0.54

^ACoefficient not included in the best-fit model.

Discussion

Our study is the first to document habitat use and the influence of habitat characteristics on endangered Vireo nest-success and parasitism rates outside of Oklahoma and central Texas. Our results suggest that increased vertical cover (i.e., more vegetation above the nest) may have a negative influence on overall nest survival for Vireos in southwest Texas. The main cause of nest failure in 2009 and 2010 was predation, with avian species comprising 40% of documented nest predators

Table 5. Model-selection results for Black-capped Vireo nest survival from 2009 to 2010 in the Devil's River area of Texas. AICc = Akaike's information criterion with a correction for finite sample sizes. Δ AICc = change in AIC relative to the model with the smallest AIC value, ω = AIC model weight and K = number of parameters.

Model	AICc	Δ AICc	ω	K
Vertical cover + Year	411.88	0.00	0.29	3
Nest height + Vertical cover + Year	412.92	1.05	0.17	4
Vertical cover + Linear date + Year	413.30	1.42	0.14	4
Year (null)	413.83	1.95	0.11	2
Vertical cover + Year + Wash + Low-flat + Riparian	414.90	3.02	0.06	6
Linear date + Year	415.00	3.13	0.06	3
Nest height + Year	415.63	3.76	0.04	3
Year + Parasitized	415.79	3.92	0.04	3
Vertical cover + Year + Horizontal cover * Cover variance	415.88	4.01	0.04	6
Nest height + Vertical cover + Year + Horizontal cover * Cover variance	417.58	5.71	0.02	7
Year + Horizontal cover * Cover variance	418.47	6.60	0.01	5

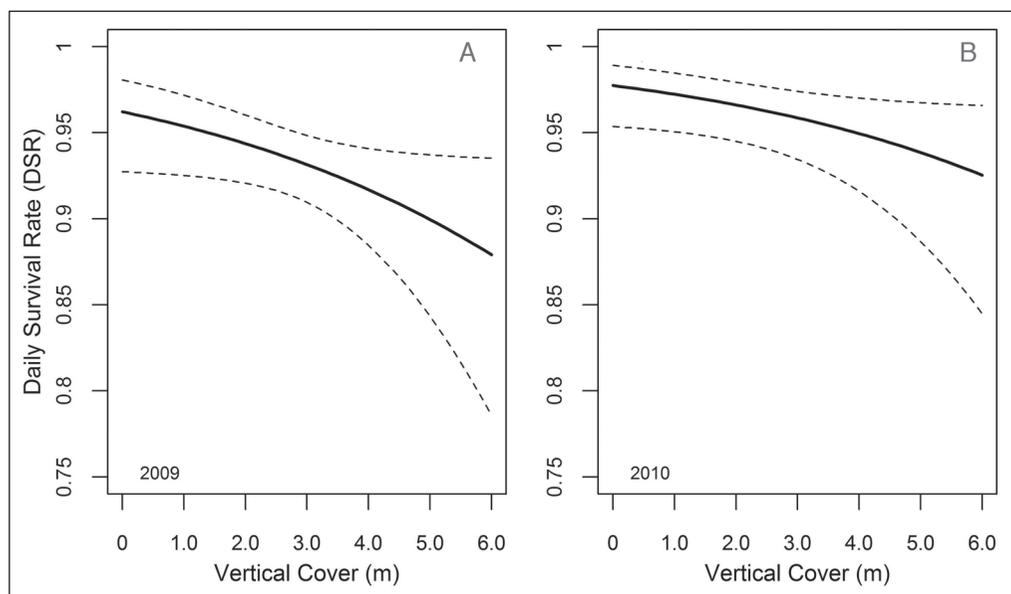


Figure 3. Daily nest survival (DSR) by vertical cover and year for Black-capped Vireo nests from 2009 (grey) and 2010 (black) at Devil's River State Natural Area and surrounding properties in Val Verde County, TX. Dotted lines represent 95% confidence intervals.

(Smith et al. 2012). Areas with higher vertical cover likely provide more perches for avian predators that rely on visual cues to locate nests (Howlett and Stutchbury 1996), including Cowbirds, a major predator of Vireo nests during 2009 and 2010 (Smith et al. 2012). Our results also indicated that Cowbirds located and parasitized nests that were placed higher in the vegetation, supporting the hypothesis that avian predators, which search for nests from above, are more likely to locate nests that are higher than those lower in the vegetation (Filliater et al. 1994).

In contrast with Vireo studies conducted farther north that employed identical nest-monitoring methods, in our study, nest survival did not decrease if the nest was previously parasitized (T.J. Conkling, Texas A&M University, unpubl. data; Pope et al. 2013). This difference may be because abandonment was much higher in those studies compared to ours, potentially due to the higher overall rates of parasitism in those areas, or it might be due to the more-diverse predator assemblage in the Devil's River area (Smith et al. 2012) compared to other Vireo breeding habitat in central Texas (Conkling et al. 2012). Barber and Martin (1997) looked at the number and size of stems surrounding Vireo nests and concluded that vegetation characteristics around Vireo nests were not different for parasitized and un-parasitized nests in central Texas. The stunted vegetation in the dry Devil's River area differs significantly from the vegetation in the wetter and deeper soils that make up Vireo habitat in central Texas; however, mean nest height is similar for Vireos across their range in Texas (Conkling et al. 2012). The shorter overall vegetation in southwest Texas may be allowing Cowbirds to locate higher Vireo nests, whereas more-concealed nests, which occur in the taller vegetation of central Texas, may be less detectable to Cowbirds.

Vireos may not be selecting territories based solely on the presence of Vasey Shin Oak, but they did select this species as a nest substrate when it was available, even in small quantities. Vireos primarily used the canyon riparian areas and slopes in the Devil's River area (Smith 2011). When Vasey Shin Oak, which occurs primarily in canyons, was readily available within the territory, Vireos used it for nesting more than other substrate species. When Vasey Shin Oak was not available early in the breeding season (i.e., before leaf-out), Vireos selected evergreen Texas Mountain Laurel and Ashe Juniper as nest substrates.

Table 6. Model-averaged regression Coefficient. (β) \pm SE and 95% confidence intervals included in the best-fitting models (Δ AICc < 2) for Black-capped Vireo (*Vireo atricapilla*) daily nest survival from 2009–2010 at Devil's River area of Texas.

Parameter	95% Confidence intervals		
	Coefficient (β) \pm SE	Lower	Upper
Intercept	3.25 \pm 0.574	2.13	4.36
Year	0.53 \pm 0.29	-0.03	1.09
Vertical cover	-0.21 \pm 0.10	-0.41	-0.01
Nest height ^A	0.22 \pm 0.28	-0.31	0.76
Linear date ^A	-0.005 \pm 0.006	-0.0017	0.007

^ACoefficient not included in the best-fit model.

Vireo nest-site characteristics in southwest Texas appear to differ from areas farther north. In contrast to other parts in the species' breeding range, Vireos in the Devil's River area used Ashe Juniper as a nest substrate proportionately more than is available in territories (Bailey and Thompson 2007, Grzybowski 1995, Grzybowski et al. 1986). Working in central Texas near the eastern boundary of the species' range, Bailey and Thompson (2007) found that Vireos were 283% more likely to nest in deciduous substrates than in Ashe Juniper. This finding may simply be because Ashe Juniper provides the structure and low cover preferred by Vireos for nesting, which is otherwise more difficult to find in southwest Texas compared to the ample oak available farther north and east. Until now, Texas Mountain Laurel was not listed as a nest substrate of Vireos, despite its presence in central Texas; however, Vireos used Texas Mountain Laurel more than any other substrate in the Devil's River area and used it proportionately more than other substrates during the early breeding season. Both Ashe Juniper and Texas Mountain Laurel are evergreens, providing cover early in the season before deciduous substrates have foliage.

Horizontal cover within territories was higher ($70 \pm 13\%$; $\bar{x} \pm SD$) than previous measurements taken in other parts of the Vireo's range (30–50%; Bailey and Thompson 2007, Grzybowski 1995). This result is likely due to the effects of the shallow soils present in southwest Texas that produce a stunted but dense climax vegetation community in the absence of disturbances (Hedges and Poole 1999). Bailey and Thompson (2007) showed that areas of high woody cover at Fort Hood Military Reservation in central Texas consisted of older vegetation that grew more vertically than horizontally, resulting in less foliage cover in the lower height zone. In contrast, vegetation in arid regions such as southwest Texas remains close to the ground and does not grow taller than the low stature used by Vireos over long periods in the absence of disturbance.

Predation and parasitism pressures on Vireos as well as nest-site preferences in southwest Texas are different from those reported from sites to the north and east. Therefore, Vireo breeding-habitat management needs are different in southwest Texas, an area where the vegetation remains relatively low and constant, except in areas that have a deeper soil layer due to periodic flooding events. Ashe Juniper was an important nest substrate for Vireos in our study and, unlike central Texas, is not extremely abundant on the landscape. Management guidelines may need to be amended to encourage preservation of Ashe Juniper in certain regions of the Vireo's range. Unlike areas to the north, managers do not need to create frequent disturbance in southwest Texas to maintain low-vegetation habitat for Vireos. On the contrary, fire in this area might destroy habitat which would be much slower to return than in areas of higher rainfall and deeper soils. More research is needed to better understand Vireo response to fire in southwest Texas. Conservation efforts might be more productive if focused in habitat with lower vegetation height as opposed to habitats in the region with deeper soils and taller vegetation because these areas may be functioning as population sinks.

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