The Journal of Wildlife Management 77(5):994–1001; 2013; DOI: 10.1002/jwmg.539

Habitat Relations

Woodlands as Quality Breeding Habitat for Black-Capped Vireos

THERESA L. POPE,[1,2] *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA*
MICHAEL L. MORRISON, *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA*
R. NEAL WILKINS,[3] *Texas A&M Institute of Renewable Natural Resources, College Station, TX 77843, USA*

ABSTRACT Identifying vegetation types that result in the highest quality habitat will help direct management and conservation activities designed to recover endangered species. Shrubland is considered to result in high quality habitat for black-capped vireos (*Vireo atricapilla*), whereas deciduous and oak-juniper woodlands are considered to result in marginal habitat (i.e., lower quality). We investigated differences in nest and fledgling survival among shrubland and woodland vegetation types. We monitored 302 black-capped vireo nests in 259 territories from 2008 to 2010 in Kerr County, Texas and collected vegetation data at each nest. We also resighted 350 fledglings to estimate individual survival. Nest survival and fecundity did not differ statistically among vegetation types. Although nest-site characteristics differed among vegetation types, none affected nest survival. Nests that were parasitized were less likely to survive and parasitism was the only variable to affect survival of those measured. Parasitism frequency was nearly twice as great in shrubland (22%) than in either woodland type (12% in each) and varied by year (31% in 2008 to 0% in 2010). Vegetation type and proximity of the nest to oak-juniper woodland did not affect fledgling survival. Our results suggest woodlands may result in good quality habitat in areas with large populations of black-capped vireos. Recognizing woodlands as non-typical, yet good quality, habitat will allow managers to incorporate these vegetation types into management plans and make recommendations for conservation incentive programs directed at private landowners. © 2013 The Wildlife Society.

KEY WORDS black-capped vireo, fledgling survival, habitat quality, nest-site characteristics, nest survival, *Vireo atricapilla*.

Habitat refers to an area that provides resources and conditions that allow a species to survive (Morrison et al. 2006:10). In bird species, investigating differences in nest survival, fecundity, and fledgling survival can reveal whether vegetation types consistently result in high or low quality habitat. Habitat loss is often a factor when listing endangered species; therefore, identifying which vegetation types can provide the highest quality habitat for endangered species will help direct management and conservation activities designed to recover these species.

Listed as endangered in 1987 (Ratzlaff 1987), the black-capped vireo (*Vireo atricapilla*) is a small songbird with a historical breeding range that once extended from Kansas south into Mexico (Graber 1961, Grzybowski 1995); most of the currently known breeding population occurs in central and southwest Texas. At the time of listing as endangered, major threats included habitat loss through land use conversion, vegetation succession, grazing and browsing by domestic and wild herbivores, and parasitism by brown-headed cowbirds (*Molothrus ater*; Ratzlaff 1987, Wilkins et al. 2006). Habitat for black-capped vireos is characterized by a patchy distribution of low, scrubby growth consisting of mostly deciduous woody shrubs and trees of irregular height (Graber 1961, Grzybowski 1995). According to Grzybowski et al. (1994), black-capped vireo territories had a greater density of deciduous vegetation under 2-m tall than adjacent areas. Furthermore, deciduous cover around black-capped vireo nests was typically 30–45% and total woody cover was 35–55% (Grzybowski et al. 1994). In landscapes with low-growing deciduous cover, black-capped vireos are more likely to occupy areas with sparser juniper (*Juniperus* spp.) cover (Grzybowski et al. 1994, Juarez 2004).

Black-capped vireo habitat can be highly variable across the breeding range, with different plant species associations depending on location (e.g., soil type, climate) and past management activities (e.g., brush clearing, prescribed fire; Graber 1961, Grzybowski 1995). Yet the guidelines as to what constitutes high quality black-capped vireo habitat have been molded by vegetative characteristics that are prevalent in a few, well-studied locations with relatively large populations of black-capped vireos, including Wichita Mountains National Wildlife Refuge and Fort Sill in Oklahoma, and Fort Hood and Kerr Wildlife Management Area (WMA) in

Received: 11 October 2011; Accepted: 14 December 2012
Published: 8 April 2013

[1] *E-mail: tpope@utah.gov*

[2] *Present address: Utah Division of Wildlife Resources, 1594 W. North Temple, Suite 2110, Salt Lake City, UT 84116, USA.*

[3] *Present address: East Wildlife Foundation, 700 Everhart Road, Suite G-21, Corpus Christi, TX, 78411, USA.*

Texas (Grzybowski 1995, Wilkins et al. 2006). Although vegetative characteristics of shrubland fit the description of high quality black-capped vireo habitat, researchers have observed black-capped vireos occupying other vegetation types such as deciduous and oak-juniper (*Quercus-juniperus*) woodlands (Conkling 2010, Pope 2011, Morgan 2012), that are typically considered to result in marginal habitat.

Black-capped vireo nests are frequently lost to predation. Studies at Fort Hood (79–87%; Bailey 2005, Cimprich and Comolli 2010) and Devil's River State Natural Area, Texas (Smith et al. 2012) found that predation was the greatest cause of nest failure for unsuccessful nests. Multiple studies have shown snakes, brown-headed cowbirds, and red imported fire ants (*Solenopsis invicta*) were the leading predators of black-capped vireo nests in central Texas (Stake and Cimprich 2003, Conkling et al. 2012). Nest-site vegetation characteristics can affect nest vulnerability differently depending on the major nest predators in an area (Benson et al. 2010, Conkling et al. 2012). Therefore, managers must understand the predator assemblage at a location, given that assemblages can vary widely across the range of a species (Conkling et al. 2012).

Failure of resource managers to recognize that black-capped vireos are using certain vegetation types for successful breeding could inadvertently lead to a substantial loss of breeding locations. We investigated differences in fecundity and nest survival in shrubland, deciduous woodland, and oak-juniper woodland vegetation types. Structural differences among the vegetation types could affect vegetation characteristics at nests (e.g., average cover), which may affect survival. For example, higher nests (Bailey 2005, Conkling et al. 2012), nests with more cover (Martin 1992 and references therein), and nests with greater distance to edge (Conkling 2010) may have better nest survival. In addition, nests located closer to juniper may enhance fledgling survival by providing increased cover and food resources (Anders et al. 1998, Marshall 2011, Morgan 2012). If shrubland resulted in higher quality habitat for black-capped vireos than either woodland type, we expected to find greater fecundity and daily and period nest survival rates in shrubland than deciduous and oak-juniper woodlands.

STUDY AREA

Our study area was approximately 8,000 ha in Kerr County, Texas centered at Kerr WMA and including adjacent private lands. In 2008, we monitored vireos on approximately 500 ha (6 pastures) on the eastern side of Kerr WMA. In 2009, we continued to monitor vireos on those pastures as well as approximately 700 ha on private properties surrounding Kerr WMA. During 2010, we reduced the monitored area to approximately 90 ha (1 pasture) of Kerr WMA because of logistical constraints.

Kerr County is representative of the Edwards Plateau Ecoregion of Texas and has a known population of breeding black-capped vireos. Within Kerr County, 3 vegetation types inhabited by black-capped vireos are distinguished by topography, soils, and past management activities: shrubland, which consists of oak and other deciduous patches surrounded by a matrix of grassland; deciduous woodland, which has taller trees, more canopy cover, and is typically found along drainages; and oak-juniper woodland. Kerr County supports a plant community of trees, shrubs, and grasses, including live oak (*Q. fusiformis*), Ashe juniper (*J. ashei*), Texas oak (*Q. buckleyi*), shin oak (*Q. sinuata*), cedar elm (*Ulmus crassifolia*), greenbrier (*Smilax* spp.), prickly pear (*Opuntia* spp.), little bluestem (*Schizachyrium scoparium*), Texas grama (*Bouteloua rigidiseta*), and curly mesquite (*Hilaria belangeri*). Management activities in the area include cattle grazing, native and exotic game hunting, prescribed burning, and brown-headed cowbird trapping. Grazing on the properties in our study area was light enough that it did not significantly alter the shrub layer (T.L. Pope, Texas A&M University, personal observation).

METHODS

Data Collection

We delineated vegetation types in Kerr County by performing a supervised classification using the Spatial Analyst toolbox in ArcGIS 9.3 (Environmental System Research Institute, Redlands, CA). We used 2008 National Agriculture Imagery Program (NAIP, 1-m resolution) imagery and Natural Resources Conservation Service ecological site descriptions as input rasters. We created a signature file by delineating 3–4 training area polygons per vegetation type (i.e., shrubland, deciduous woodland, and oak-juniper woodland) based on on-the-ground knowledge. We used a maximum likelihood algorithm to create a 25-m resolution output file, with each raster assigned to 1 of the vegetation types. We initially assigned nests to vegetation type by overlaying the nest location on the output raster file, and then confirmed vegetation-type designation in the field.

We mapped territories to identify locations to search for nests. We located black-capped vireo territories by surveying study areas for singing males. We visited each territory every 3–4 days and recorded coordinates for 3–6 black-capped vireo locations (e.g., singing perch) per visit. When we had at least 15 locations, enough to provide a representation of each territory (International Bird Census Committee 1970), we created minimum convex polygons using ArcGIS 9.3 to represent territory boundaries. Each year, we randomly selected at least 30 territories to monitor. In 2009 and 2010, we emphasized selecting territories in deciduous and oak-juniper woodland to increase sample sizes in those vegetation types. Additionally, we banded adult male and female black-capped vireos using target mist-netting techniques to assist with territory delineation and establishing breeding success. We set up a 6-m mist-net (Avinet Inc., Dryden, NY) in the territory and used an mp3 player (RCA, New York, NY) and 2 mini audio amplifiers (Radio Shack, Fort Worth, TX) to play back recordings of black-capped vireo vocalizations to lure adults into the net. We placed nets in shaded locations, kept nets under observation during playback, and released birds at the spot of capture after banding (Animal Use Protocols [AUP] 2006-67 and 2009-83). We attached an aluminum band and unique color combination of plastic bands (Avinet Inc.) to each adult. We also banded nestlings with an aluminum band and unique color band combination at age 6–8 days. We handled nestlings only in the middle of the day when temperatures were adequate to prevent chilling (AUP 2006-67 and 2009-83).

From early April to mid-July, we searched for nests in monitored territories every 3–5 days and spent no longer than 1 hour in a territory per visit. We used a combination of behavioral cues from adults and a search image to locate nests. Although differences among vegetation types can affect detectability of nests, we standardized effort for locating nests and attempted to find every nest in monitored territories. After locating a nest, we checked the status of the nest every 2–4 days until it was no longer active. We used a nest mirror, binoculars, or direct observation to view contents of the nest; we used the method that caused the least disturbance to the nest and nearby vegetation. We addled any brown-headed cowbird eggs in the nest to prevent hatching and removed brown-headed cowbird nestlings found in the nest.

We used a continuously recording video camera system to identify predators and confirm the fate of nests. We selected nests based on availability of camera units, distribution of nests in each vegetation type, and nest stage. We only placed cameras on nests that had initiated incubation (i.e., once the penultimate egg was laid). We used weatherproof bullet cameras (Rainbow, Costa Mesa, CA) with a 3.6-mm lens and 940-nm infrared lighting that was invisible to predators to record activity at the nest 24 hours a day. We typically placed video cameras approximately 1 m from nests, which was near enough to capture all activities, but far enough away so as not to disturb the birds. We connected the camera unit to a digital video recorder (Detection Dynamics, Austin, TX) and a 12-v 26-ah battery (Batteries Plus, Hartland, WI) using a 15-m cable. In 2009 and 2010, we supplemented battery power with 20-watt solar panels (Suntech, San Francisco, CA). We used 4 GB or 8 GB secure digital (SD) memory cards and a time-lapsed recording of 5 frames per second to maximize data storage. We checked the camera system every 3–4 days to replace memory cards and batteries as needed and left the camera in place until after the nest fledged or failed. If we observed a loss of nest contents (i.e., eggs or nestlings) between consecutive nest checks, we viewed all nest video footage recorded during that period to identify predators and confirm nest fate.

From late May to mid-July, if we suspected a nest fledged young successfully, we returned to the territory every 3–5 days to attempt to locate each individually color-banded fledgling. We spent 30 minutes attempting to locate the fledglings in the territory and surrounding area. If we located fledglings within 30 minutes, we would spend 30 additional minutes determining the color combinations of each fledgling seen. We attempted to locate fledglings in each territory until they reached independence (approx. 35–45 days post-fledging) or until we were unable to locate any individuals for 3 consecutive visits.

We recorded vegetation measurements at all nests in which at least 1 egg was laid. At each nest, we recorded nest height (from ground to nest rim), nest substrate species (categorized as oak, juniper, or other for analyses), height of the nest substrate plant, distance to nearest edge (i.e., horizontal distance from the nest to the nearest break in contiguous vegetation at nest height), and whether the nest was under a canopy and if so, the species and height of the canopy plant(s). Black-capped vireos generally place nests in vegetation at heights of 0.5–2.0 m (Grzybowski 1995), so we assessed percent cover at nests using a 2-m coverboard. We stood approximately 7 m from a nest in each cardinal direction to estimate the percent cover at each height class (0.1-m intervals) between 0 m and 2 m (Guthery et al. 1981). We averaged percent cover from each direction separately, and then combined averages from all directions to estimate average cover at the nest from 0 m to 2 m.

Data Analysis

To evaluate if nest-site vegetation characteristics were different among vegetation types, we performed a single-factor analysis of variance (ANOVA; Zar 1999:178–189) using SPSS 15.0 (SPSS Inc, Chicago, IL) for nest height, height of the nest substrate, height of the overstory (if present), distance to the nearest edge (i.e., break in vegetation at nest height), and average cover from 0 m to 2 m.

Nest survival.—We performed nest survival analysis using Program MARK (White and Burnham 1999) to estimate daily and period survival for each vegetation type. Program MARK provides estimates of daily survival with standard error and 95% confidence intervals. We considered a nest successful if it fledged ≥ 1 host young. For nests with cameras, we confirmed fledging from video footage. For all other nests, we considered a nest fledged if we observed adult behavior indicating the presence of fledglings (e.g., food carries and alarm calls) or, most commonly, by resighting a banded fledgling from the nest. We considered a nest failed if eggs remained but there was no adult activity, all contents were missing prior to typical age of fledging, or we had video footage of predation (not including partial predation). If we observed an empty nest that was close to fledging age at last check but could not confirm fledging from the criteria above, we considered the nest fate unknown and did not include the nest in analyses. We extrapolated period survival and 95% confidence intervals using a 28-day nesting cycle (3-, 14-, and 11-days for laying, incubation, and nestling stages, respectively; Grzybowski 1995) by raising daily survival to the 28th power (Mayfield 1961).

For all models, we grouped encounter histories for nests by vegetation type. We created a list of candidate models that included covariates of interest for our objectives, including temporal effects of year and season, brown-headed cowbird parasitism, nest attempt, and nest-site vegetation characteristics. We incorporated nest attempt into nest survival estimates because having a successful first nest attempt may lead to double brooding (Grzybowski 1995), may reduce energetic costs related to renesting if unsuccessful (Haas 1998), and may allow for more preparation time prior to fall migration (Morton 1992). Our candidate models included the intercept-only (null) model, 9 models that included the intercept and 1 covariate as a main effect, a model that included all nest-site vegetation characteristics, a model that included all nest-site vegetation characteristics plus year, a model that included both temporal covariates, a model that included parasitism and date, a model that included parasitism and year, a model that included parasitism and average cover, a model that included parasitism and nest attempt, a model that included parasitism and all vegetation covariates, a model that included parasitism and all vegetation covariates plus year, and the global model that included all covariates. For all models, we standardized vegetation covariates and used the mean of individual covariate values for estimating real parameters. We used model averaging for parameter estimates and examined coefficients and 95% confidence intervals for significance of effects. We evaluated models using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and model weights (w_i; Burnham and Anderson 2002).

Fledgling survival.—We analyzed fledgling survival using Cormack-Jolly-Seber (CJS) recapture models generated in Program MARK. We constructed a set of candidate models to examine the effect of several factors on fledgling survival. We included as covariates year (2008, 2009, or 2010), vegetation type of the nest location (shrubland, deciduous woodland, or oak-juniper woodland), and whether the nest was located within 100 m of oak-juniper woodland. We included year as a covariate because survival may vary because of annual fluctuations in food resources or predator activity. Oak-juniper woodland may provide greater cover and food resources (Anders et al. 1998, Marshall 2011, Morgan 2012); therefore, we predicted that nests located relatively close (<100 m) to oak-juniper woodland might positively affect fledgling survival.

We used capture histories that included 10 encounter occasions, representing weeks covering the post-fledging period. If we resighted a fledgling at any time during the week, we recorded a positive recapture. The first encounter occasion included the week of 15 May through 21 May and continued for the next 10 weeks, so that the last encounter occasion covered the week of 17 July through 23 July. Additionally, we included models that allowed survival and resight probability to vary across the season (early, mid, and late), so that each period included 3 weekly intervals. If a model containing year, vegetation type, or location within 100 m of oak-juniper woodland was better supported ($\Delta AIC_c \leq 2$) than the model with constant survival, we also included this covariate in the models with seasonal variation in survival and resight probability.

RESULTS

We monitored 101 black-capped vireo territories in 2008, 124 territories in 2009, and 34 territories in 2010. Fecundity (mean ± SD) did not differ among shrubland (1.86 ± 1.82, $n = 144$), deciduous woodland (1.63 ± 1.68, $n = 43$), and oak-juniper woodland (1.53 ± 1.74, $n = 17$). We monitored 121 nests in 2008, 124 nests in 2009, and 57 nests in 2010. Parasitism frequency was 22% ($n = 215$) in shrubland and 12% in each woodland type ($n = 61$ in deciduous, $n = 26$ in oak-juniper). Parasitism frequency declined over the course of the study from a high of 31% in 2008, to 16% in 2009, and 0% in 2010. The percentage of nests that were partially (i.e., contents removed but still fledged ≥1 young) or fully depredated was 37% ($n = 208$) in shrubland, 42% ($n = 59$) in deciduous woodland, and 54% ($n = 26$) in oak-juniper woodland.

Predation was the leading cause of failure for black-capped vireo nests, with >60% of the 187 unsuccessful nests being lost to predation. For nests with cameras ($n = 61$), birds (39%) and snakes (32%) were the most common predators of nest contents, followed by mammals and ants ($n = 28$, Table 1). Brown-headed cowbirds killed or removed nestlings from 7% of nests with cameras. Parasitism by cowbirds occurred before we placed the cameras and we did not consider parasitism to be a predation event. Though snakes commonly depredate eggs and nestlings, we also recorded a snake depredating an adult female vireo and the 1-day-old nestlings she was brooding overnight. Although not included in the predator analysis, a gray fox (*Urocyon cinereoargenteus*) slept under a nest for approximately 3 hours, which apparently resulted in the adults abandoning the nest during the incubation stage.

Vegetation characteristics at the nest site varied between different vegetation types (Table 2). Nest height, substrate height, and overstory height were lower in shrubland and distance to edge was closer in deciduous woodland (Table 2). Average percent cover from 0 m to 2 m was the only nest-site characteristic that did not vary among vegetation types (Table 2).

Nest Survival

Parasitism was the only covariate that had a clear effect on black-capped vireo nest survival; it appeared in all of the top models ($\Delta AIC_c \leq 2$; Table 3). Parasitism negatively affected nest survival ($\beta = -0.79$, 95% CI: −1.15 to −0.42). Parasitism decreased the probability of nest survival by 64% (95% CI: 21–97%) in shrubland, 76% (95% CI: 26–99%) in deciduous woodland, and 80% (95% CI: 28–100%) in oak-juniper woodland. Daily (DSR) and period (PSR) nest survival rates were numerically greater in shrubland (DSR = 0.97, 95% CI: 0.96–0.97; PSR = 0.41, 95% CI: 0.33–0.48) than in deciduous woodland (DSR = 0.96, 95% CI: 0.94–0.97; PSR = 0.28, 95% CI: 0.17–0.41) and oak-juniper woodland (DSR = 0.95, 95% CI: 0.92–0.97; PSR = 0.23, 95% CI: 0.09–0.41), but differences were not statistically significant because 95% confidence intervals overlapped.

Fledgling Survival

We used encounter histories for 350 individual fledglings from 111 potentially successful nests (i.e., showed signs of fledging) to estimate fledgling survival. Of the 8 candidate models for fledgling survival, 1 model was clearly best supported ($w_i = 0.91$; Table 3). The best-supported model included seasonal differences in survival and resight probability, with year affecting survival (Table 3). Models that included vegetation type and whether the nest was located within 100 m of oak-juniper woodland as covariates did not

Table 1. Black-capped vireo nest predators observed from nest video cameras in Kerr County, Texas, 2008–2010.

		2008 ($n = 20$)	2009 ($n = 20$)	2010 ($n = 21$)
Snake spp.	*Elaphe* spp.	4	1	4
Brown-headed cowbird	*Molothrus ater*	2	2	0
Western scrub-jay	*Aphelocoma californica*	2	2	1
Cooper's hawk	*Accipiter cooperii*	0	0	1
Unidentified hawk		0	1	0
Ant spp.		0	2	0
Coyote	*Canis latrans*	0	1	0
Fox squirrel	*Sciurus niger*	0	0	2
Unknown		1	2	0

Table 2. Descriptive statistics and results of analysis of variance for vegetation measurements at black-capped vireo nests within each vegetation type in Kerr County, Texas, 2008–2010.

	Shrubland			Deciduous woodland			Oak-juniper woodland					
	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.	F	df	P-value
Nest height (m)	1.3 ± 0.5	0.4	3.2	1.5 ± 0.5	0.5	3.2	1.5 ± 0.9	0.6	4.0	4.62	2	0.01
Substrate height (m)	2.9 ± 1.4	0.8	11.0	3.6 ± 2.1	0.8	13.0	3.5 ± 1.7	0.7	7.5	5.38	2	0.01
Overstory height (m)	4.4 ± 1.6	1.0	11.0	5.0 ± 1.7	2.4	8.5	6.0 ± 2.2	2.1	12.0	8.73	2	<0.001
Distance to edge (m)	1.5 ± 1.1	0.0	5.7	0.9 ± 1.1	0.0	4.8	1.5 ± 1.2	0.0	4.4	7.34	2	0.001
Average cover 0–2 m (%)	80 ± 15	30	100	80 ± 16	30	100	80 ± 15	40	90	0.28	2	0.75

Table 3. Model selection results for black-capped vireo nest and fledgling survival in Kerr County, Texas, 2008–2010. Models are ranked from most supported ($\Delta\mathrm{AIC}_c = 0$) to least supported; K is the number of parameters in each model. The Akaike weight (w_i) is the weight of the evidence for model i, given the data. The model likelihood indicates the support of the model, given the data.

Model	K	$\Delta\mathrm{AIC}_c$[a,b]	w_i	Model likelihood
Nest survival				
β_0 + parasitism	4	0.00	0.29	1.00
β_0 + parasitism + average cover	5	0.09	0.27	0.96
β_0 + parasitism + date	5	1.11	0.17	0.58
β_0 + parasitism + year	6	1.27	0.15	0.53
β_0 + parasitism + 1st attempt	5	1.94	0.11	0.38
β_0 + parasitism + average cover + distance to edge + overstory + height + substrate	10	7.50	0.01	0.02
β_0 + parasitism + year + average cover + distance to edge + overstory + height + substrate	12	9.23	0.00	0.01
β_0 + all	13	11.19	0.00	0.00
β_0 + year	5	12.66	0.00	0.00
β_0 + average cover	4	13.79	0.00	0.00
β_0	3	14.58	0.00	0.00
β_0 + date	4	15.95	0.00	0.00
β_0 + distance to edge	4	16.32	0.00	0.00
β_0 + overstory	4	16.43	0.00	0.00
β_0 + height	4	16.48	0.00	0.00
β_0 + 1st attempt	4	16.52	0.00	0.00
β_0 + date + year	5	17.12	0.00	0.00
β_0 + substrate	5	17.29	0.00	0.00
β_0 + year + average cover + distance to edge + overstory + height + substrate	11	21.28	0.00	0.00
β_0 + average cover + distance to edge + overstory + height + substrate	9	22.06	0.00	0.00
Fledgling survival				
Early/mid/late survival + year, early/mid/late resight	8	0.00	0.91	1.00
Survival + year, early/mid/late resight	6	4.66	0.09	0.10
Early/mid/late survival, early/mid/late resight	6	12.30	0.00	0.00
Survival, early/mid/late resight	4	18.14	0.00	0.00
Survival + year, constant resight	4	29.24	0.00	0.00
Survival, constant resight	2	41.40	0.00	0.00
Survival + habitat, constant resight	4	42.20	0.00	0.00
Survival + within 100 m of juniper, constant resight	3	43.35	0.00	0.00

[a] Akaike's Information Criterion corrected for small sample sizes (AIC_c) of best model for nest survival was 1008.21.

[b] AIC_c of best model for fledgling survival was 2,130.11.

Table 4. Survival and resight probabilities with 95% confidence intervals for black-capped vireo fledglings during the early, mid, and late post-fledging periods at Kerr Wildlife Management Area, 2008–2010.

Post-fledging period	Survival probability (95% CI)	Resight probability (95% CI)
15 May–11 June	0.85 (0.79, 0.90)	0.43 (0.36, 0.50)
5 June–2 July	0.89 (0.85, 0.93)	0.58 (0.52, 0.63)
26 June–23 July	0.75 (0.67, 0.82)	0.49 (0.41, 0.57)

receive any support (Table 3). Fledgling survival was 0.57 (95% CI: 0.45–0.68) over the 10-week post-fledgling period. Seasonal differences in survival probabilities ranged from 0.75 to 0.89, and resight probabilities ranged from 0.43 to 0.58 (Table 4).

DISCUSSION

This study emphasizes the multiple negative effects of brown-headed cowbirds on a host species. Nest parasitism adversely affects nest survival, perhaps because parasitized nests are more susceptible to predation (McClaren and Sealy 2000, Kosciuch and Sandercock 2008, Hannon et al. 2009). Black-capped vireos will also abandon parasitized nests (Grzybowski 1995, Pease and Grzybowski 1995). In our study, we observed nest abandonment due to parasitism was especially high for first nest attempts. Parasitism can also reduce fecundity because host eggs can be removed or damaged during the parasitism event and nestlings may die when larger brown-headed cowbird nestlings outcompete for resources (Graber 1961, Grzybowski 1995). Ours and other studies (Arcese et al. 1996, Hoover and Robinson 2007, Conkling et al. 2012) have shown that unparasitized host nests also fail as a direct result of predation by brown-headed cowbirds.

Disproportionate use of certain vegetation types by brown-headed cowbirds may skew parasitism effects on host nests toward vegetation types more commonly used by cowbirds. Robinson et al. (1999) found greater parasitism rates in shrubland and savannas than forests in the Midwest. Other researchers found greater parasitism rates on forest edges than farther into the forest in Michigan (Gates and Gysel 1978) and Indiana (Winslow et al. 2000). In contrast, researchers found parasitism by cowbirds to be associated with interior forests as well (Hahn and Hatfield 1995, Burhans 1997, Gustafson et al. 2002, Knutson et al. 2004). We observed proportionately more parasitized nests in shrubland than woodlands in our study, though we did not collect data to quantify cowbird habitat use.

Predation was the greatest cause of nest failure in our study. Recent studies at Fort Hood also have shown high losses to predation (Bailey 2005, Cimprich and Comolli 2010). Major predators in and around Fort Hood include snakes and fire ants (Stake and Cimprich 2003, Conkling et al. 2012). Snakes are also a major predator at Balcones Canyonlands National Wildlife Refuge near Austin, Texas (M. L. Morrison, Texas A&M University, unpublished data). To the north of Fort Hood where trapping for brown-headed cowbirds is less intensive than at Fort Hood, brown-headed cowbirds are also a major predator of black-capped vireo nests (Conkling et al. 2012). The predator assemblage in the western portion of the black-capped vireo breeding range is quite diverse, though avian and mammalian species were the most common predators (Conkling et al. 2012, Smith et al. 2012). Snakes were one of the major predators in Kerr County; however, more nests were lost to avian predators, especially western scrub-jays (*Aphelocoma californica*) and brown-headed cowbirds.

Nest-site characteristics were different between the vegetation types, with the exception of average cover around the nest from 0 m to 2 m. Differences in nest substrate height and overstory height are most likely due to differences in vegetative structure found between shrubland and woodlands. Distance to nearest edge may have been smaller in deciduous woodland than shrubland or oak-juniper woodland because of how we standardized recording the distance. We recorded distance to edge as the closest break in vegetation at nest height; although, in deciduous woodland, nests were often located under continuous cover. Nests in deciduous woodland were often in small saplings and therefore the nearest break in vegetation could be at the end of leaves directly surrounding the nest. Remarkably, average cover around the nest from 0 m to 2 m was nearly identical for each vegetation type.

Vegetation type did not appear to influence fledgling survival, although year did. Focusing on a single pasture may have influenced year having an effect on fledgling survival. Because we monitored a smaller area in 2010, we were more likely to encounter fledglings while observing other territories, which likely inflated resight probability. Probabilities of survival and resighting fledglings varied throughout the post-fledgling period, increasing in June before decreasing again in July. The decline in survival and resight probability at the end of the season is most likely due to fledglings from earlier nest attempts reaching independence and dispersing away from the area. Resight probabilities are lowest in May. During this period, only fledglings from early nest attempts are available for resighting and these fledglings are still very young. Black-capped vireo fledglings are more difficult to resight during the first couple of weeks post-fledging because they stay well hidden in the vegetation and stop moving and making begging calls once the adults discover the observer and persist in incessant alarm calling (T.L. Pope, personal observation).

Black-capped vireo fledgling survival estimates in Kerr County are similar to other songbirds (e.g., western bluebirds [*Sialia mexicana*; Wightman 2009], dickcissels [*Spiza americana*; Suedkamp Wells et al. 2007], and eastern meadowlarks [*Sturnella magna*; Kershner et al. 2004]), though we think our estimates for vireo fledgling survival are conservative. Unlike other songbirds, such as willow flycatchers (*Empidonax trailii*) and western bluebirds that remain in family groups after fledging (Wightman 2009, Vormwald et al. 2011), black-capped vireos may split broods between the adults (T. L. Pope, personal observation; Grzybowski 1995). Fledglings of species that remain in family groups are easier to relocate by finding the adults. When brood splitting occurs, fledglings remaining with a singing male are more likely to be encountered than fledglings being cared for by a quiet female.

Shrubland remains the most important vegetation type to maintain for the persistence of black-capped vireo populations because most black-capped vireos occupy and reproduce in shrubland, but this vegetation type has been declining because of anthropogenic land use changes that include fire suppression and overgrazing, as well as afforestation of rangelands (Archer 1994, Fuhlendorf and Smeins 1997, Van Auken 2000, Briggs et al. 2005). Woodlands with vegetation characteristic of later succession and with a greater proportion of juniper have replaced shrubland (Smeins and Merrill 1988, Fuhlendorf and Smeins 1997). For example, Wills (2005) found that woodland at Kerr WMA increased from 6% in 1884 to 80% in 2004 in Low Stony Hill ecosites and from 20% to 70% in Redland ecosites. Wildlife habitat, including high quality habitat, will likely decrease because of loss and degradation. In some situations, wildlife may need to use areas that result in lower quality habitat, which could challenge persistence of certain wildlife populations (Donovan and Thompson 2001).

Shrubland is potentially the highest quality habitat for black-capped vireos breeding in central Texas, though deciduous and oak-juniper woodlands can also provide beneficial habitat requirements. Prescribed fire and brush clearing are popular management activities in the black-capped vireo breeding range for improving forage for cattle and wild ungulates as well as restoration of black-capped vireo habitat (Texas Parks and Wildlife Department 2012). Woodlands may act as a refuge for displaced vireos while these activities are occurring or in areas where the highest quality habitat is lost. Black-capped vireos can reproduce successfully in deciduous and oak-juniper woodlands and therefore contribute individuals to populations. Deciduous and oak-juniper woodlands appear to result in good quality habitat for black-capped vireos in Kerr County and may result in good quality habitat in other areas of the breeding range as well (Campomizzi et al. 2009, Conkling 2010). Examining demographic parameters for black-capped vireos in non-typical habitat throughout the breeding range should be a focus of further research. In addition, future research might focus on differences in other vital rates, such as adult and juvenile survivorship among vegetation types.

MANAGEMENT IMPLICATIONS

Although maintaining the highest quality habitat is preferred, focusing solely on shrubland might limit opportunities for conserving black-capped vireo habitat. Knowing that black-capped vireos use and are reproductively successful in woodlands as well as shrubland can aid in efforts to conserve this endangered species. Wildlife managers within the breeding range of this species should be aware that black-capped vireos could occur in areas that do not fit the current guidelines for high quality habitat, especially if these areas are in close proximity to known large populations of vireos. Otherwise, managers and landowners may inadvertently remove vegetation that results in good quality habitat for black-capped vireos because it does not adhere to current habitat descriptions. However, because the general trend favored shrubland over woodland, management should not promote conversion from shrubland to woodland. Nevertheless, recognizing woodlands as non-typical, yet potentially good quality, habitat will allow managers to incorporate these vegetation types into management plans and make recommendations for conservation incentive programs directed at private landowners.

ACKNOWLEDGMENTS

We thank Texas Parks & Wildlife Department and Kerr WMA for providing housing and access to field sites. We especially thank all of the private landowners that allowed access to their properties. We thank the Institute of Renewable Natural Resources for logistical support and K. Smith, P. Santema, M. Lackey, M. Hutchinson, P. Falatek, M. Burck, S. Cancellieri, E. McCann, L. Pulliam, and C. Ondracek for their field assistance. B. Collier provided advice for statistical analyses. F. Thompson, W. A. Cox, A. Rodewald, L. Kearns, and T. Conkling provided technical support and advice regarding nest camera setups. The U.S. Army Integrated Training Area Management (ITAM) Program, Office of the Secretary of Defense—Department of Defense and Texas Parks & Wildlife Department provided funding. T. Pope also earned support from the Tom Slick Senior Graduate Fellowship. Comments from anonymous referees substantially improved the paper.

LITERATURE CITED

Anders, A. D., J. Faaborg, and F. R. Thompson, III. 1998. Post-fledgling dispersal, habitat use, and home range size of juvenile wood thrushes. Auk 115:349–358.

Arcese, P., J. N. M. Smith, and M. I. Hatch. 1996. Nest predation by cowbirds and its consequences for passerine demography. Proceedings of the National Academy of Sciences of the United States of America 93:4608–4611.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns, and proximate causes. Pages 13–68 *in* M. Vavra, W. A. Laycock, and R. D. Pieper, editors. Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, Colorado, USA.

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

Benson, T. J., J. D. Brown, and J. C. Bednarz. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology 79:225–234.

Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. Bioscience 55:243–254.

Burhans, D. E. 1997. Habitat and micro-habitat features associated with cowbird parasitism in two forest edge cowbird hosts. Condor 99:866–872.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Campomizzi, A. J., M. L. Morrison, S. L. Farrell, R. N. Wilkins, B. M. Drees, and J. M. Packard. 2009. Red imported fire ants can decrease songbird nest survival. Condor 111:534–537.

Cimprich, D. A., and K. Comolli. 2010. Monitoring of the black-capped vireo during 2010 on Fort Hood, Texas. Endangered species monitoring and management at Fort Hood, Texas: 2010 annual report. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, USA.

Conkling, T. J. 2010. Analysis of the black-capped vireo and white-eyed vireo nest predator assemblages. Thesis, Texas A&M University, College Station, USA.

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

Donovan, T. M., and F. R. Thompson. III 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecological Applications 11:871–882.

Fuhlendorf, S. D., and F. E. Smeins. 1997. Long-term importance of grazing, fire and weather patterns on Edwards Plateau vegetation change. Pages 7.19–7.20 *in* C. A. Taylor editor. 1997, Juniper Symposium Texas Agricultural Experiment Station, The Texas A&M University System. Technical Report 97-1. January 9–10, San Angelo, Texas, USA.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883.

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

Grzybowski, J. A. 1995. Black-capped vireo (*Vireo atricapilla*). Account 181 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists Union, Washington, D.C., USA.

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

Gustafson, E. J., M. G. Knutson, G. J. Niemi, and M. Friberg. 2002. Evaluation of spatial models to predict vulnerability of forest birds to brood parasitism by cowbirds. Ecological Applications 12:412–426.

Guthery, F. S., T. B. Doerr, and M. A. Taylor. 1981. Use of a profile board in sand shinnery oak communities. Journal of Range Management 34:157–158.

Haas, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. Auk 115:929–936.

Hahn, D. C., and J. S. Hatfield. 1995. Parasitism at the landscape scale: cowbirds prefer forests. Conservation Biology 9:1415–1424.

Hannon, S. J., S. Wilson, and C. A. McCallum. 2009. Does cowbird parasitism increase predation risk to American redstart nests? Oikos 118:1035–1043.

Hoover, J. P., and S. K. Robinson. 2007. Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. Proceedings of the National Academy of Sciences of the United States of America 104:4479–4483.

International Bird Census Committee, 1970. An international standard for a mapping method in bird census work recommended by the international bird census committee. Audubon Field Notes 24:722–726.

Juarez, E. A. 2004. Habitat relationships of seven breeding bird species in the Leon River Watershed investigated at local scales. Thesis, Texas A&M University, College Station, USA.

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

Knutson, M. G., G. J. Niemi, W. E. Newton, and M. A. Friberg. 2004. Avian nest success in midwestern forests fragmented by agriculture. Condor 106:116–130.

Kosciuch, K. L., and B. K. Sandercock. 2008. Cowbird removals unexpectedly increase productivity of a brood parasite and the songbird host. Ecological Applications 18:537–548.

Marshall, M. E. 2011. Effects of tree species composition and foraging effort on the productivity of golden-cheeked warblers. Thesis, Texas A&M University, College Station, USA.

Martin, T. E. 1992. Breeding productivity considerations; what are the appropriate habitat features for management. Pages 455–473 *in* J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

McClaren, C. M., and S. G. Sealy. 2000. Are nest predation and brood parasitism correlated in yellow warblers? A test of the cowbird predation hypothesis. Auk 117:1056–1060.

Morgan, D. T. 2012. Foraging ecology and forage availability for the black-capped vireo. Thesis, Texas State University, San Marcos, USA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 2006. Wildlife-habitat relationships: concepts and applications. Third edition. Island Press, Washington, D.C., USA.

Morton, M. L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain white-crowned sparrow. Condor 94:117–133.

Pease, C. M., and J. A. Grzybowski. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. Auk 112:343–363.

Pope, T. L. 2011. Effects of habitat characteristics and adult behavior on black-capped vireo nest and fledgling survival. Dissertation, Texas A&M University, College Station, USA.

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

Robinson, S. K., J. D. Brawn, S. F. Morse, and J. R. Herkert. 1999. Use of different habitats by breeding brown-headed cowbirds in fragmented Midwestern landscapes. Studies in Avian Biology 18:52–61.

Smeins, F. E., and L. B. Merrill. 1988. Long-term change in a semiarid grassland. Pages 101–114 *in* B. B. Amos and F. R. Gehlbach, editors. Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor University Press, Waco, Texas, USA.

Smith, K. N., J. W. Cain, III, M. L. Morrison, and R. N. Wilkins. 2012. Nesting ecology of the black-capped vireo in southwest Texas. Wilson Journal of Ornithology 124:277–285.

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

Suedkamp Wells, K. M. S., M. R. Ryan, J. J. Millspaugh, F. R. Thompson, III, and M. W. Hubbard. 2007. Survival of postfledging grassland birds in Missouri. Condor 109:781–794.

Texas Parks and Wildlife Department [TPWD], 2012. Management guidelines for black-capped vireo. <http://www.tpwd.state.tx.us/publications/pwdpubs/media/pwd_bk_w7000_0013_black_capped_vireo_mgmt.pdf> Accessed 19 Oct 2012.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197–215.

Vormwald, L. M., M. L. Morrison, H. A. Mathewson, M. C. Cocimano, and B. A. Collier. 2011. Survival and movements of fledgling willow and dusky flycatchers. Condor 113:834–842.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

Wightman, C. S. 2009. Survival and movements of fledgling western bluebirds. Southwestern Naturalist 54:248–252.

Wilkins, R. N., R. A. Powell, A. A. T. Conkey, and A. G. Snelgrove. 2006. Population status and threat analysis for the black-capped vireo. Prepared for the U.S. Fish and Wildlife Service Region 2. Texas A&M University, College Station, USA.

Wills, F. H. 2005. Structure of historic vegetation on Kerr Wildlife Management Area, Kerr County, Texas Texas Journal of Science 57:137–152.

Winslow, D. E., D. R. Whitehead, C. F. Whyte, M. K. Koukal, G. M. Greenberg, and T. B. Ford. 2000. Within-landscape variation in patterns of cowbird parasitism in the forests of south-central Indiana. Pages 298–310 *in* J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin, Texas, USA.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Associate Editor: Peter Coates.