Research Article

Demographic Differences of Black-Capped Vireos in 2 Habitat Types in Central Texas

LESLIE A. NOA,[1,2] *Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA*

DAVID H. HIRTH, *Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA*

THERESE M. DONOVAN, *United States Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit, Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA*

DAVID CIMPRICH, *The Nature Conservancy of Texas, P.O. Box 5190, Fort Hood, TX 76544, USA*

ABSTRACT To understand the effects of habitat selection, we analyzed differences in abundance, age structure, and nesting success of black-capped vireos (*Vireo atricapilla*) in 2 early successional habitat types found on Fort Hood, a 87,890-ha Military Reservation in central Texas, USA. These habitats were 1) large areas of continuously shrubby vegetation (both natural and mechanically made), referred to as shrubland habitat, and 2) anthropogenically created small patches of shrubby vegetation centered on one or several large trees, known locally as donut habitat. The objectives of our study were to determine whether there were differences in abundance, age structure, and daily nest survival in these 2 habitat types and to determine whether donut habitat is high- or low-quality habitat. Donut habitat had a lower abundance of vireos (half as many as shrubland/point count) and a higher percentage of second-year males, suggesting donut habitat was lower-quality habitat than shrubland. Analyses of daily nest survival indicated that habitat, nest height, and year were all important variables. Nests initiated in 2004, located in shrubland habitats, and higher from the ground were more likely to succeed. Our study provided evidence that habitat is a limiting factor for this federally endangered species. Because habitat is limiting, wildlife biologists at Fort Hood should focus on managing higher quality, contiguous shrubland habitat. Wildlife biologists should also continue to monitor areas of donut habitat to determine whether they represent potential population sinks. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1042–1049; 2007)

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Habitat selection occurs when an organism chooses among alternative habitats that influence survival and reproduction differently (Cody 1985). For species with declining populations, management strategies are driven by our knowledge of how individuals within a population select habitats and how these choices affect individual fitness and population-level growth rates. We would expect individuals to choose habitats that maximize fitness; however, there are cases where individuals choose habitats that negatively affect both their survival and productivity (Pulliam and Danielson 1991, Martin 1992, Robinson 1992, Donovan and Thompson 2001).

Many studies correlate abundance of individuals with habitat features, but the mere presence of individuals is not always indicative of either population health or habitat quality (van Horne 1983). Thus, in addition to abundance, measures of fitness are needed to assess habitat quality (Martin 1992). Fitness indicators include sex ratio (Gibbs and Faaborg 1990), age ratio (Holmes et al. 1996), and nesting success (Bowers 1994, Holmes et al. 1996). The assumption is that high-quality habitat will have equal sex ratios, age ratios dominated by older individuals, and high nesting success.

Understanding the fitness consequences of habitat selection for declining species will help direct conservation strategies. Fitness is particularly important in the case of the black-capped vireo (*Vireo atricapilla*), a federally endangered species that breeds only in central and southeastern Texas, USA, parts of Oklahoma, USA, and northeastern Mexico (Grzybowski 1995). Preferred black-capped vireo breeding habitat is characterized by low, scrubby vegetation, often oaks (*Quercus* spp.; Graber 1961, Grzybowski 1995). Fire historically created this early successional habitat or it occurred as a climax community in drier western areas. With the expansion of the livestock industry, dryland farming, and suppression of prairie fire, black-capped vireos have lost most of their former nesting habitat (Grzybowski 1995). In addition, brown-headed cowbirds (*Molothrus ater*) have negatively impacted the breeding success of these vireos (Ratzlaff 1987, United States Fish and Wildlife Service [USFWS] 1991).

Fort Hood Military Reservation in central Texas supports one of the largest known breeding populations of black-capped vireos under a single management entity, with an estimated 6,319 males in 2005 (Cimprich 2005). Little information exists on current population estimates of vireos throughout their range. However, a recent status review estimated that Fort Hood provides breeding habitat for approximately 33% of the range-wide population (Wilkins et al. 2006). The Nature Conservancy (TNC) has monitored vireo populations at Fort Hood since 1997, where efforts have focused on large expanses of shrubland habitat, which researchers traditionally considered the principal breeding habitat for vireos (Cimprich and Kostecke 2006). Shrubland habitat is a patchwork of low-lying shrubs with interdigitating, open pathways. Vegetation is rarely >3 m in height; trees occur rarely and are typically dead.

[1] *E-mail: lnoa@life.uiuc.edu*
[2] *Present address: University of Illinois, 102C Shelford Vivarium, Champaign, IL 61821, USA*

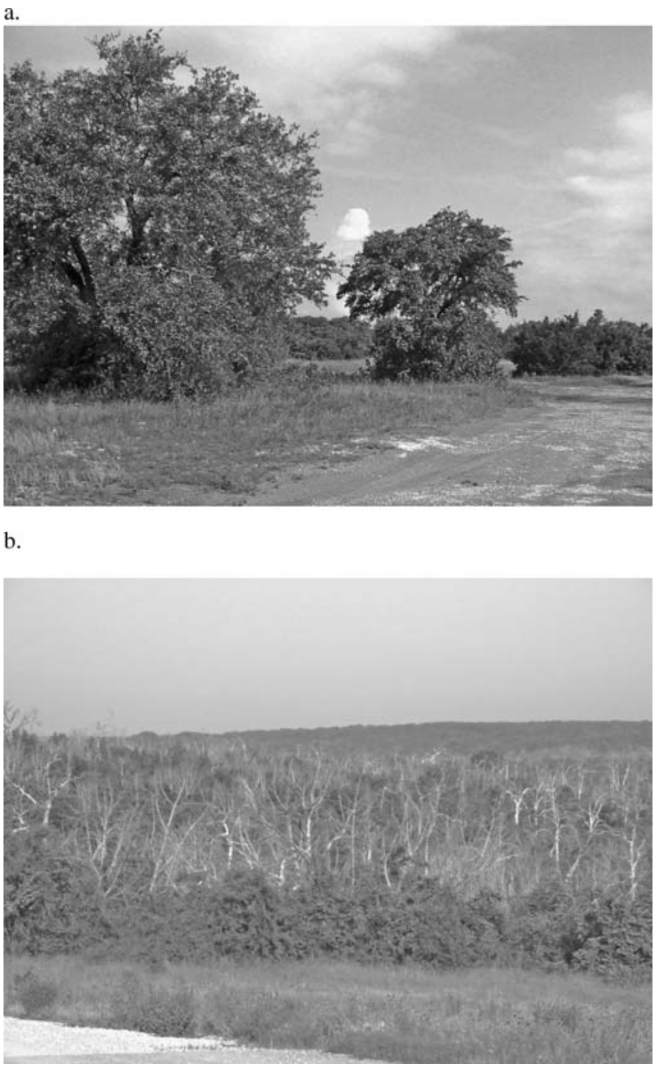

Figure 1. Black-capped vireo habitat on Fort Hood Military Reservation, Texas, USA: (a) donut habitat and (b) shrubland habitat.

However, in recent years researchers have recognized a second type of habitat on Fort Hood that supports nesting vireos. This habitat is known locally as donut habitat (Cimprich and Kostecke 2006). A donut is best described as an area of scrubby vegetation >2 m in height, predominately oaks, that grows up around a larger tree or group of trees and is usually surrounded by grass or barren ground; donut habitat consists of multiple donuts (Fig. 1; Cimprich and Kostecke 2006). Donuts range in size from 3 m to 10 m in diameter and are maintained when the vegetation around a tree or group of trees is crushed during military training exercises and allowed to grow back; the area between 2 donuts is typically at least large enough to allow vehicle passage. In contrast, shrublands consist of independent patches of shrubs 1–3 m in height, lack taller trees, and have a more random distribution due to the absence of military tracks. Both habitat types occur throughout the Fort Hood installation (Fig. 2), though donut habitat is concentrated to the west. Researchers identified donut habitat on Fort Hood by visually assessing vertical height, shrub height, and isolation caused by tanks. Shrubland represents about 70% of vireo habitat at Fort Hood, but donut habitat constitutes the majority of the remaining area occupied by vireos (Cimprich and Kostecke 2006).

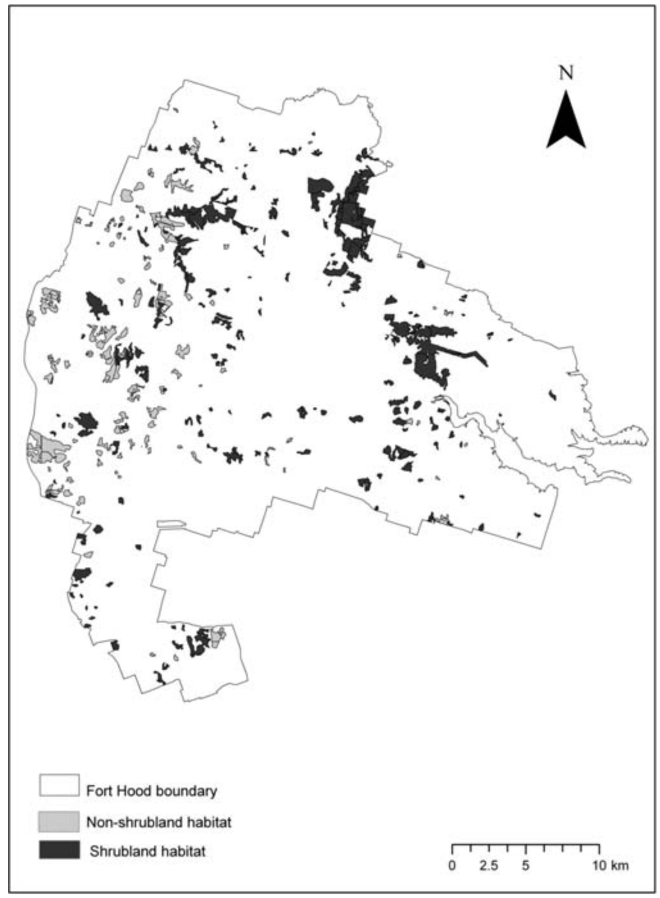

Figure 2. Black-capped vireo habitat distribution on Fort Hood Military Reservation, Texas, USA, 2005. Map data courtesy of The Nature Conservancy.

Researchers have not studied abundance, age structure, and productivity of black-capped vireos in donut habitat. Because this habitat type represents a significant area of Fort Hood, and because scrub-oak habitat in other parts of the vireo's range might also occur in small patches, it is important to determine the value of donut habitat to nesting vireos and to compare their productivity to that of shrubland habitat. Donuts might be suboptimal habitat and represent a sink for the local vireo population, but they may be as productive as shrublands, which are traditionally viewed as optimum habitat.

The objective of our study was to compare the relative abundance, age structure, and nesting success of black-capped vireos in donut habitat with shrubland habitat on Fort Hood. Understanding differences between the 2 habitat types will provide a better understanding of vireo habitat on Fort Hood and will serve as a management tool for Fort Hood and the region.

STUDY AREA

Fort Hood is an 87,890-ha military reservation located in central Texas. Under the guidelines of the Endangered

Species Act of 1973, federal agencies (including the United States Army) are required to manage for the recovery of endangered species (Pekins 2006). One-third of the Army's deployable heavy (armored tanks, etc.) forces trained at Fort Hood during the study period (S. Cannon, United States Army Forces Command, personal communication). Thus, Fort Hood must balance the requirements of training soldiers and protecting endangered species, including the black-capped vireo. Following recommendations in the Recovery Plan of 1991 (Eckrich et al. 1999, Hayden et al. 2000), an extensive brown-headed cowbird control program was implemented at Fort Hood in response to high rates of brood parasitism. This program included trapping and shooting adult cowbirds, and removal of cowbird eggs and young from vireo nests (Kostecke et al. 2005). We complied with this policy throughout the course of our study.

METHODS

We conducted our study during the 2003 and 2004 breeding seasons (Apr–Jul) in accordance with the University of Vermont's Institutional Animal Care and Use Committee (IACUC protocol 03–153). We collected donut-habitat data in 15 study sites. We randomly selected donut sites >3 ha from the mapped habitat on Fort Hood. Although all sites were accessible by tank, we removed 2 of the randomly selected sites that were inaccessible by conventional vehicle from the sampling scheme. We collected shrubland data in 8 study areas, and used identical data collection protocols in both donut and shrubland habitat (Ralph et al. 1993, Cimprich 2002).

Field Methods

Relative abundance.—To assess relative abundance of vireos in donut and shrubland habitat, we conducted 42 6-minute point counts in donut habitat and 152 counts in shrubland habitat. We conducted each 6-minute count by a single observer in favorable weather conditions (no rain, low wind). In total, 2 individuals surveyed donut habitat; 6 observers surveyed shrubland habitat in 2003, and 8 observers surveyed shrubland habitat in 2004. We did not use tape recordings to increase detection probability. All counts were separated by ≥250 m, and were replicated once a month from April to July in both 2003 and 2004. We broke counts into 3 time intervals (3 min, 2 min, and 1 min) for removal-method analyses and we recorded distances of vireos detected from the point location (Farnsworth et al. 2002, Moore et al. 2004).

Age structure.—To determine the age structure of the population, we captured and color-banded vireos through target mist-netting. We used plumage characteristics to age and sex vireos (Pyle 1997). We used 2 age classes for male vireos in each habitat: second-year (first breeding season) and after second-year.

Nesting success.—We located and monitored nests to estimate nesting success for vireos in donut and shrubland in each year. We used behavioral cues during searches of suitable nesting sites. Each observer was responsible for a study site or part of a study site in order to ensure familiarity with the sites (Martin and Geupel 1993). We monitored nests every 2–3 days, with nest contents and stage recorded at each visit until the nest fledged young or failed. We removed cowbird eggs or chicks from all nests in accordance with Fort Hood and TNC policy. When a nest was parasitized, we recorded this information and removed the cowbird egg when the clutch was complete. On rare occasions ($n = 3$), we found nests with cowbird chicks and these were also recorded as parasitized and cowbird chicks were removed. We made every effort to monitor the nest on the day young fledged, which gives the best measure of how many young have fledged. We considered a nest successful if ≥1 vireo young fledged (Ralph et al. 1993, Cimprich 2002).

Analysis Methods

Relative abundance.—Detection probability is the probability that an observer will detect an individual, given that it is present at a sampling point. Before conducting statistical tests to compare abundance in shrubland and donut habitat, we examined differences in detection probabilities between the 2 habitat types and between the early and late portions of the breeding season. We assumed observer differences were minimal because the target species has a loud and distinctive song (Graber 1961, Grzybowski 1995). We evaluated 3 models in program SURVIV (Farnsworth et al. 2002): 1) seasonal (early vs. late season), 2) habitat differences (shrubland vs. donut), and 3) seasonal and habitat differences. We used Akaike's Information Criterion (AIC) scores to select the best model and used the maximum likelihood estimates of detection probability from the best model to adjust the raw count data. With the corrected data, we tested for differences in relative abundance of vireos between shrubland and donut habitat with a Wilcoxon Rank Sum test (Proc Npar1way, SAS version 8.2; SAS Institute Inc, Cary, NC). We used this nonparametric statistical test because both the count data and their residuals were not normally distributed.

Age structure.—We compared age structure (the ratio of second-yr M to after-second yr M) between donut and shrubland habitat for both years with Fisher's Exact test (Proc Freq, SAS version 8.2). We only used males known to be breeding in either donut or shrubland habitat in the analysis. We did not use females in the analysis because the sample size was too small.

Nesting success.—To compare nesting success between habitats, we located and monitored 163 black-capped vireo nests in donut habitat and 177 nests in shrubland habitat. We evaluated 13 models (described below) to describe nest success and a global model to assess goodness-of-fit (Table 1) using an information-theoretic approach (Burnham and Anderson 2002). Daily nest survival was the response variable and was estimated following a generalized linear modeling approach outlined by Rotella et al. (2004) and Shaffer (2004) in SAS.

Habitat is an important factor in nesting success (Holmes et al. 1996), and one of our main objectives was to compare nesting success in 2 habitat types at Fort Hood. Therefore, the first 2 models in the model set included some

Table 1. Nest success models for black-capped vireos at Fort Hood, Texas, USA, 2003 and 2004 nesting seasons.

Model no.	Model	Description
1	$\beta_0 + \beta_1 \times$ Hab	Habitat main effects
2	$\beta_0 + \beta_1 \times$ Hab $+ \beta_2 \times$ Yr	Habitat and yr
3	$\beta_0 + \beta_1 \times$ Hab $+ \beta_2 \times$ Ht	Habitat and nest ht
4	$\beta_0 + \beta_1 \times$ Ht	Nest ht main effects
5	$\beta_0 + \beta_1 \times$ Hab$+ \beta_2 \times$ Ht $+ \beta_3$ (Hab $\times$ Ht)	Habitat $\times$ nest ht interaction
6	$\beta_0 + \beta_1 \times$ Hab $+ \beta_2 \times$ Ht $+ \beta_3 \times$ Yr	Habitat, yr, and nest ht (no interactions)
7	$\beta_0 + \beta_1 \times$ Hab $+ \beta_2 \times$ Ht $+ \beta_3$ (Hab $\times$ Ht) $+ \beta_4 \times$ Yr	Habitat $\times$ nest ht interaction and yr
8	$\beta_0 + \beta_1 \times$ Hab $+ \beta_2 \times$ Para	Habitat and parasitism
9	$\beta_0 + \beta_1 \times$ Hab $+ \beta_2 \times$ Para $+ \beta_3$ (Hab $\times$ Para)	Habitat $\times$ parasitism interaction
10	$\beta_0 + \beta_1 \times$ Para	Parasitism
11	$\beta_0 + \beta_1 \times$ Hab $+ \beta_2 \times$ Ht $+ \beta_3 \times$ Para $+ \beta_4$ (Hab $\times$ Ht) $+ \beta_5$ (Hab $\times$ Para)	Habitat $\times$ ht interaction and habitat $\times$ parasitism interaction
12	$\beta_0 + \beta_1 \times$ Hab $+ \beta_2 \times$ Ht $+ \beta_3 \times$ Para $+ \beta_4 \times$ Yr	Habitat, ht, parasitism, and yr
13	$\beta_0 + \beta_1 \times$ Yr	Yr
14	$\beta_0 + \beta_1 \times$ Hab $+ \beta_2 \times$ Ht $+ \beta_3 \times$ Yr $+ \beta_4 \times$ Para $+ \beta_5$ (Hab $\times$ Ht) $+ \beta_6$ (Hab $\times$ Para)	Full model (all variables and interaction terms)

combination of habitat, and habitat and year (Table 1). We used year (2003 and 2004) in the models because it is known that there are often year differences in nesting success rates (Holmes et al. 1986); TNC has also noted an alternating nesting success cycle in vireos (D. A. Cimprich, TNC, personal communication).

Donut habitat is structurally different from shrubland habitat and there may be differences in the height at which nests are placed. Nest height could be a factor in the probability of nest predation (Martin 1992, Burhans et al. 2002), and there may be interactions between habitat and nest-site characteristics (Burhans 1997). Models 3 and 5 focused on habitat and nest height, as well as interactions between them. Model 4 considered nest height alone. Model 6 focused on the 3 variables (habitat, yr, and nest ht) with no interaction between variables. Model 7 focused on the habitat and nest height interaction and year (no interaction with yr).

Brown-headed cowbird parasitism is known to have an effect on the reproductive success of song birds, and of vireos in particular (Ratzlaff 1987), and levels of parasitism may differ with habitat type (Robinson et al. 1995). Models 8, 9, and 10 examined habitat, parasitism occurrence, and their interaction. Model 11 focused on the interactions between habitat and nest height and the interaction between habitat and parasitism. Because we removed cowbird eggs and chicks from vireo nests in donut and shrubland habitat, models 8–11 evaluate whether the occurrence of a parasitism event (not cowbird eggs or chicks per se) affected the probability of nest survival. In addition, because cowbirds typically remove a vireo egg before parasitizing a nest, we compared the number of vireo young that fledge per successful nest for parasitized versus unparasitized nests as a second measure of the effect of parasitism on vireo fitness.

Model 12 focused on all 3 variables with no interactions, and model 13 evaluated year alone. Model 14 was the full model to assess goodness-of-fit of all the models and was not used in model selection.

RESULTS

Relative Abundance

Detection probability was influenced by both habitat and time of season; the SURVIV model that included both of these factors was best supported by the data (Table 2). In donut habitat, detection rates were 1.4× greater early in the season than late in the season. Shrubland had consistently high detection probability both seasons. The best model had a chi-square value of 0.69, indicating that the model was a reasonably good fit to the data. Therefore, we used the model that included both habitat and season to determine differences in detection probabilities. We used the maximum likelihood estimate detection probabilities from this model to adjust raw point-count data (Table 2).

We analyzed abundance in shrubland versus donut habitat. Results indicated that shrubland habitat had 2 times as many vireos as donut habitat ($P \leq 0.001$; 95% CI = 0.764–0.969 in shrubland and 95% CI = 0.366–0.583 in donut habitat). However, these estimates had large confidence intervals and, thus, were imprecise.

Age Structure

We caught and aged 63 males in donut habitat: 31 were second-year and 32 were after-second year. In shrubland habitat 115 males were caught and aged: 37 were second-year and 78 were after second-year. Donut habitat had a

Table 2. Probability of detection ($\hat{p}$) and standard errors for black-capped vireo point-count data from program SURVIV, Fort Hood, Texas, USA, 2003 and 2004 nesting seasons.

Parameter	$\hat{p}$	SE	95% CI Lower	95% CI Upper
Donut early season[a]	0.949	0.026	0.896	1.002
Donut late season[b]	0.687	0.182	0.328	1.045
Shrubland early season	0.853	0.314	0.791	0.915
Shrubland late season	0.841	0.355	0.771	0.911

[a] Early season = Apr and May.
[b] Late season = Jun and Jul.

Table 3. Model-selection results for black-capped vireo nesting success, Fort Hood, Texas, USA, 2003 and 2004 nesting seasons.[a]

Model no.	Model	Rank	K	Log likelihood	AIC_c	ΔAIC_c	w_i
6	$\beta_0 + \beta_1 \times Hab + \beta_2 \times Ht + \beta_3 \times Yr$	1	4	−651.86	1,319.74	0.00	0.692388
7	$\beta_0 + \beta_1 \times Hab + \beta_2 \times Ht + \beta_3 \times Yr + \beta_4 (Hab \times Ht)$	2	5	−651.30	1,322.62	2.88	0.1644044
12	$\beta_0 + \beta_1 \times Hab + \beta_2 \times Ht + \beta_3 \times Para + \beta_4 \times Yr$	3	5	−651.65	1,323.32	3.58	0.1156219

[a] K = the no. of parameters; AIC_c = Akaike's Information Criterion adjusted for small sample size; $\Delta AIC_c = AIC_c$ relative to the most parsimonious value; w_i = Akaike wt, Hab = habitat; Para = parasitism.

higher percentage of second-year males (49%) than shrubland habitat (32%; Fisher's Exact Test, $P < 0.019$; effective sample size 178).

Nesting Success

Of the 12 models tested, the data strongly supported model 6. Model 6 included the following variables with no interaction terms: habitat, nest height, and year. This was the best model according to the nesting success analysis described by Rotella et al. (2004); it had an Akaike weight (w_i) of 0.692, indicating that this model had the most support of the candidate set of models and had a 69.2% chance of being the best Kulback–Leibler model in the model set (Table 3). The next-best model (model 7, $\Delta AIC_c = 2.88$) simply added the habitat × nest height interactions to the variables in model 6 and had a w_i of 0.1644. A goodness-of-fit test of the global model (model 14) indicated that the model was a good fit (Pearson $\chi^2 = 2{,}275.4$, $\chi^2/df = 1.06$) and that there was support for the candidate set of models.

Clearly, habitat, nest height, and year were all important factors in determining nesting success (Table 4). Habitat had an effect on nesting success particularly in 2003 (Fig. 3a), where daily survival probability was lower in donut habitat than in shrubland habitat. Nest height also affected daily survival probabilities. Daily survival probabilities of a given nest increased as nest height increased in both habitats. However, in both 2003 and 2004 daily survival probability was lower in donut habitat than in shrubland habitat (Fig. 3b). The nesting success analysis indicated yearly differences in daily survival probabilities (Fig. 3c). In 2003, daily survival probability was much lower than in 2004. One difference between habitat types was brown-headed cowbird parasitism; donut habitat had a higher rate of parasitism (12.3% in donut and 2% in shrubland). The lack of a parasitism effect on nest success is not surprising because we systematically removed cowbird eggs and nestlings. However, it is well-documented that parasitized vireo nests will fail without intervention (USFWS 1991). Thus, in the absence of human intervention, the parasitism effects would become evident. Additionally, for successful nests, nests that were parasitized fledged fewer vireo chicks per nest ($\bar{x} = 2.0$, SD = 0), compared to unparasitized nests ($\bar{x} = 2.35$, SD = 1.0). Although not statistically different, these effects could very well have biological significance in terms of vireo population viability.

DISCUSSION

Black-capped vireos differed in abundance, age structure, and nest success between donut and shrubland habitats. Donut habitat had lower abundance of singing males than shrubland habitat, likely because donut habitat was more open than shrubland habitat and provided fewer nesting sites and foraging areas. The birds occupying donut habitat were dominated by less experienced breeders, potentially resulting in lower fitness compared to their older counterparts (Holmes et al. 1996, Petit and Petit 1996). Differences in daily nest survival of black-capped vireos between donut and shrubland habitat were more difficult to assess. Although habitat was consistently identified as an important factor, nest height placement (Martin 1993, Burhans 1997, Burhans et al. 2002, Bailey 2005) and year to year variation were also important determinants of nest success; the 2003 breeding season was much drier than the 2004 season and, thus, could influence the distribution of food (Holmes et al. 1986) and predators (Stake and Cimprich 2003) across Fort Hood. These results suggest that the per capita contribution of offspring to the overall vireo population, as well as the per habitat contribution, are lower for donut than shrubland habitats.

Based on data from abundance, age structure, and nesting

Table 4. Model 6 parameter estimates for black-capped vireo nesting success, Fort Hood, Texas, USA, 2003 and 2004 nesting seasons. We used estimates of zero as the reference point for categorical variables.

Description	Parameter[a]	Estimate	SE	Lower CL	Upper CL	P
$\beta_0 + \beta_1 \times Hab + \beta_2 \times Ht + \beta_3 \times Yr$	Intercept	3.5960478	0.2140504	3.17652	4.01558	2.44E−63
	Hab1	−0.103118	0.1559737	−0.4088	0.20259	0.508533
	Hab2	0	0	0	0	
	Yr1	−0.831760	0.142844	−1.111729	−0.551791	5.785E−09
	Yr2	0	0	0	0	
	Ht	0.0776379	0.2376155	−0.38808	0.5433557	0.7438663

[a] Hab1 = donut habitat; Hab2 = shrubland habitat; Yr1 = 2003; Yr2 = 2004; Ht = nest ht.

success, donuts represent lower quality habitat for black-capped vireos than shrubland habitat. These results have implications for both the Fort Hood vireo population and for the range-wide vireo population. Within Fort Hood, donut habitat represents 30% of potential vireo nesting habitat, and the remaining 70% occurs as shrubland habitat. Given these conditions, the Fort Hood population should persist as long as birds nesting on shrublands have a positive growth rate and as long as birds preferentially select shrubland habitat for breeding over donut habitat. Demographic models suggest that, under these conditions, populations should be able to persist as long as low-quality habitat does not constitute >40% of the total area (Donovan and Thompson 2001). However, if birds prefer donut habitats to shrubland habitats for nesting, then a higher percentage of shrubland habitat would be needed to offset the demographic losses associated with donut habitats (Donovan and Thompson 2001). Although we did not directly measure finite rate of population increase in either habitat type (λ), the nest success estimates in shrubland habitat, combined with abundance data, suggest that the presence of donut habitat may not detrimentally affect the Fort Hood population in spite of its low quality. In fact, donut habitat may provide important spillover habitat as shrubland habitat reaches its carrying capacity (Howe et al. 1991).

From a range-wide perspective, Fort Hood is a major contributor of birds to the global population of vireos, representing up to 33% of the known population. Controlling cowbird parasitism and determining how to manage habitats are 2 major priorities identified by the USFWS for recovery of this species (Ratzlaff 1987, USFWS 1991). Although donut habitat is strictly a military-based phenomenon, if the age ratios and abundances documented at Fort Hood are broadly reflective of small, isolated patches of habitat outside of Fort Hood, then these habitats may represent lower-quality habitat that are more vulnerable to predation and parasitism on a range-wide scale. Grzybowski et al. (1994) reported that second-year male vireos in the Edward's Plateau region of their range often occupied areas that were more open. A critical but missing piece of information is to understand if these same habitats suffer the predation and parasitism rates associated with donut habitat at Fort Hood. Importantly, these habitats may be increasing on the landscape due to rapid land-use change and increases in human population size in the central portion of the vireo range. The Edward's Plateau region in central Texas is the core of the vireo's range, and includes the cities of Austin and San Antonio, 2 rapidly growing population centers in terms of human population density and land development (Texas State Data Center and Office of the State Demographer 2007). Moreover, these open, secondary habitats may have much higher rates of nest failure than those documented on Fort Hood donut habitat because all parasitized nests will fail without intervention (Grzybowski 1995), and intervention is largely restricted to Fort Hood and areas managed by the state of Texas.

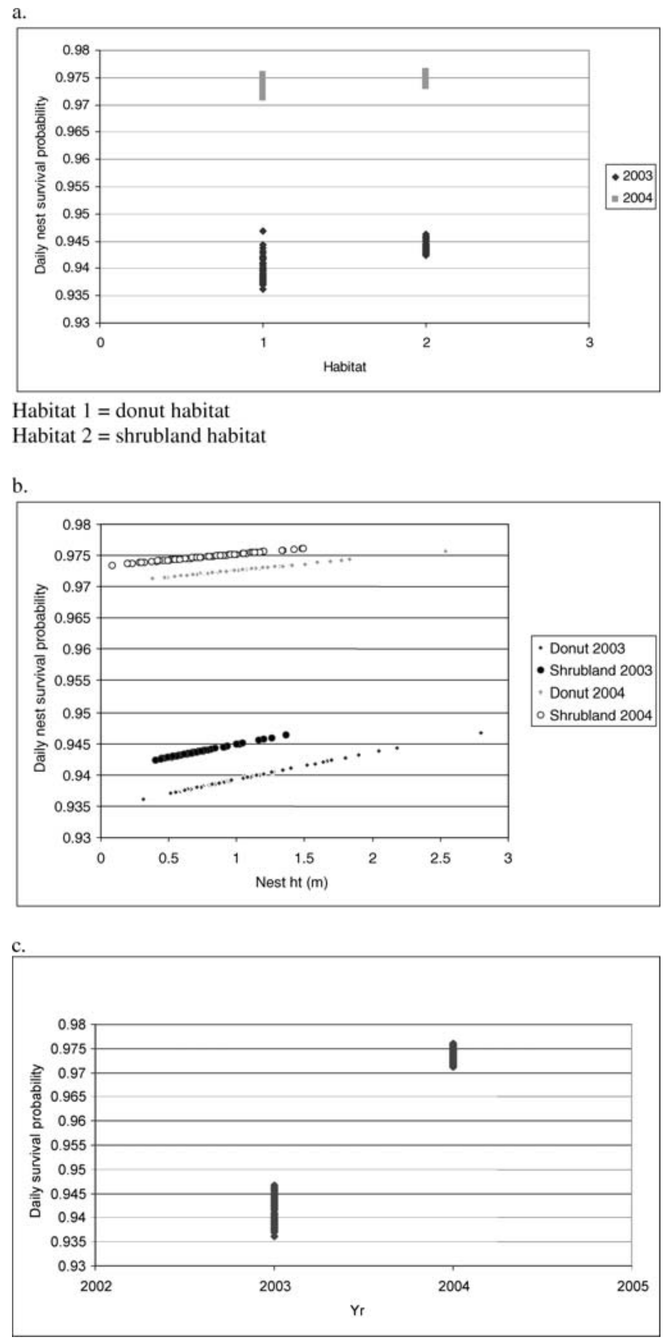

Figure 3. Nesting success plots for black-capped vireos at Fort Hood, Texas, 2003 and 2004 nesting seasons: (a) daily survival probability by habitat and year, (b) daily survival probability versus nest height, and (c) year differences in daily survival probabilities in donut and shrubland habitat.

MANAGEMENT IMPLICATIONS

Our study has 2 important implications for managing black-capped vireos. First, biologists should continue to manage for shrubland habitat on and around Fort Hood using prescribed burning and mechanical disturbance, keeping the caveat in mind that vireos may prefer burned areas to mechanical manipulated areas (Bailey 2005). Second, information about demography of vireos nesting in open, secondary habitats outside of Fort Hood, and the changes in the amounts of shrubland and secondary habitat is needed to determine the levels of habitat required to meet range-wide population objectives.

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LITERATURE CITED

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.

Bowers, M. A. 1994. Dynamics of age- and habitat-structured populations. Oikos 69:327–333.

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

Burhans, D. E., D. Dearborn, F. R. Thompson, III, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. Journal of Wildlife Management 66:240–249.

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

Cimprich, D. A. 2002. Monitoring of the black-capped vireo during 2002 on Fort Hood, Texas. Endangered species monitoring and management at Fort Hood, Texas: 2002 annual report. The Nature Conservancy, Fort Hood Project, Texas, USA.

Cimprich, D. A. 2005. Monitoring of the black-capped vireo during 2005 on Fort Hood, Texas. Endangered species monitoring and management at Fort Hood, Texas: 2005 annual report. The Nature Conservancy, Fort Hood Project, Texas, USA.

Cimprich, D. A., and R. M. Kostecke. 2006. Distribution of the black-capped vireo at Fort Hood, Texas, USA. Southwestern Naturalist 51: 99–102.

Cody, M. L. 1985. An introduction to habitat selection in birds. Academic Press, Orlando, Florida, USA.

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.

Eckrich, G. H., T. E. Koloszar, and M. D. Goering. 1999. Effective landscape management of brown-headed cowbirds at Fort Hood, Texas. Studies in Avian Biology 18:267–274.

Farnsworth, G. L., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer. 2002. A removal model for estimating detection probability from point count surveys. Auk 119:414–425.

Gibbs, J. P., and J. Faaborg. 1990. Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. Conservation Biology 4:193–196.

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

Grzybowski, J. A. 1995. Black-capped vireo (*Vireo atricapillus*). Account 181 *in* A. Poole and F. Gills, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologist 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.

Hayden, T. J., D. J. Tazik, R. H. Melton, and J. D. Cornelius. 2000. Cowbird control program at Fort Hood, Texas: lessons for mitigation of cowbird parasitism on a landscape level. Pages 357–370 *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, USA.

Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. Journal of Animal Ecology 65:183–195.

Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecological Monographs 56:201–220.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of 'sink' populations. Biological Conservation 57:239–255.

Kostecke, R. M., S. G. Summers, G. H. Eckrich, and D. A. Cimprich. 2005. Effect of cowbird removal on black-capped vireo nest success and population growth at Fort Hood, Texas. Ornithological Monographs 57: 28–37.

Martin, T. E. 1992. Breeding productivity: 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.

Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. Bioscience 43:523–533.

Martin, T. E, and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 63: 507–519.

Moore, J. E., D. M. Scheiman, and R. K. Swihart. 2004. Field comparison of removal and modified double-observer modeling for estimating detectability and abundance of birds. Auk 121:865–876.

Pekins, C. E. 2006. Armored military training and endangered species restrictions at Fort Hood, Texas. Federal Facilities Environmental Journal Spring:37–50.

Petit, L. J., and D. R. Petit. 1996. Factors governing habitat selection by prothonotary warblers: field tests of the Fretwell–Lucas models. Ecological Monographs 66:367–388.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137(Suppl.):50–66.

Pyle, P. 1997. Identification guide to North American birds. Part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California, USA.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. U.S. Forest Service Pacific Southwest Research Station, General Technical Report PSW-GTR-144, Albany, California, USA.

Ratzlaff, A. 1987. Endangered and threatened wildlife and plants: determination of the black-capped vireo to be an endangered species. Federal Register 52:37420–37432.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented landscape. Pages 408–417 *in* J. M. Hagan, III and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L. J. Petit, and J. A. Grzybowski. 1995. Ecology and behavior of cowbirds and their impact on host populations. Pages 428–460 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds: a synthesis and review of critical reviews. Oxford University Press, New York, New York, USA.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-

survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.
Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121: 256–540.
Stake, M. M., and D. A. Cimprich. 2003. Using video to monitor predation at black-capped vireo nests. Condor 105:348–357.
Texas State Data Center and Office of the State Demographer. 2007. Texas census data. <http://txsdc.utsa.edu/>. Accessed 29 Mar 2007.
United States Fish and Wildlife Service [USFWS]. 1991. Black-capped vireo (*Vireo atricapillus*) recovery plan. U.S. Fish and Wildlife Service, Austin, Texas, USA.
van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.
Wilkins, 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 U.S. Fish and Wildlife Service, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, USA.

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