EFFECTS OF HABITAT, NEST-SITE SELECTION, AND ADULT BEHAVIOR ON BLACK-CAPPED VIREO NEST AND FLEDGLING SURVIVAL

A Dissertation

by

THERESA LYNN POPE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2011

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of committee,	Michael L. Morrison
Committee members,	James Cathey
	Bret Collier
	William Rogers
Head of department,	John Carey

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ABSTRACT

Effects of Habitat, Nest-site Selection, and Adult Behavior on Black-capped Vireo Nest and Fledgling Survival. (August 2011)

Theresa Lynn Pope, B.S.F, Purdue University;

M.S.F., Northern Arizona University

Chair of Advisory Committee: Dr. Michael Morrison

Many factors affect the productivity of songbirds. Which vegetation types the birds inhabit, nest-site characteristics, and adult behavior at the nest may affect predation and parasitism frequencies, fecundity, and nest survival and fledgling survival. All of these metrics determine reproductive success of individuals and may influence population persistence, especially for threatened and endangered species. My research investigated factors that affected these metrics for endangered black-capped vireos (*Vireo atricapilla*). Shrubland is considered high quality vireo habitat, with woodland vegetation types considered marginal. I located and monitored nests, conducted nest behavior observations, recorded behavior and predation at nests using video cameras, and resighted fledglings in shrubland, oak-juniper woodland, and deciduous woodland during the 2008–2010 breeding seasons.

I monitored 302 black-capped vireo nests in 259 territories and resighted 350 fledglings with unique color combinations. Apparent nest success, nest survival, success of first nest attempts, parasitism and predation frequency, and fecundity did not differ statistically among vegetation types. Parasitism frequency was nearly twice as high in shrubland (22%) than in either woodland (12% in each) and varied by year. Nest-site characteristics differed among vegetation types, but nest survival was affected only by nest height and year; nests placed higher from the ground and nest attempts in 2008 and 2009 had lower survival. Fledgling survival was not affected by vegetation type or proximity of the nest to oak-juniper woodland. Nest behavior was not affected by vegetation characteristics, though nest attentiveness during incubation increased as average cover from 0 to 2 m increased. Females spent 80% more time on nests during incubation and 250% more time on nests during the nestling stage than males, but visitation was similar for each sex. Overall, the probability of nest success improved as male participation increased.

My results emphasize the importance of male participation in determining the outcome of nests for species exhibiting bi-parental care. Furthermore, woodland habitats previously considered marginal may be good quality habitat in areas with large populations of black-capped vireos. Recognizing woodlands as non-typical, yet still suitable, habitat will allow managers to incorporate these vegetation types into management plans and recommendations for landowner conservation incentive programs.

ACKNOWLEDGMENTS

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CHAPTER I

INTRODUCTION

HABITAT QUALITY

Wildlife habitat refers to an area that provides resources and conditions that allow a species to survive (Morrison et al. 2006). Habitat quality may vary among vegetation types, with high quality habitat providing the best resources for survival, reproduction, and population persistence (Morrison et al. 2006). Investigating differences in nest survival, success of first nest attempts, fecundity, and fledgling survival can determine if vegetation types are high or low quality habitat. Having a successful first nest attempt may lead to double brooding (Grzybowski 1995), reduce energetic costs related to renesting if unsuccessful (Haas 1998), and allow for more preparation time prior to fall migration (Morton 1992). Habitat loss is often a factor when listing endangered species, therefore identifying which vegetation types provide the highest quality habitat for endangered species will help direct management and conservation activities designed to recover these species.

One of these endangered species, listed in 1987 (Ratzlaff 1987), is the black-capped vireo (*Vireo atricapilla*); a small songbird whose historical breeding range once extended from Kansas south into Mexico (Graber 1961, Grzybowski 1995), with the majority of the currently known breeding population occurring in central and southwest Texas. At the time the black-capped vireo was listed as endangered, major threats

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This dissertation follows the style of the Journal of Wildlife Management.

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).

Suitable 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 higher 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). Where there is low-growing deciduous cover, black-capped vireos are more likely to occupy areas with sparser juniper cover (Grzybowski et al. 1994, Juarez 2004).

Even in suitable habitat, black-capped vireo nests are frequently lost to predation. Bailey and Thompson (in review) concluded that 87% of unsuccessful nests failed due to predation during their 2003–2004 study at Fort Hood. Predation was the greatest cause of nest failure at Fort Hood in 2010 as well, accounting for 79% of unsuccessful nests and 52% of all nests (Cimprich and Comolli 2010). A nest-monitoring study at Fort Hood from 1998 to 2001 found that snakes and fire ants (*Solenopsis* spp.) were the leading predators, accounting for 38% and 31%, respectively, of all depredated nests (Stake and Cimprich 2003). Other nest predators in the Fort Hood study included avian (19% of depredated nests) and mammalian predators (11%; Stake and Cimprich 2003). Conkling et al. (in review) used nest cameras to investigate the predator assemblage in black-capped vireo habitat north of Ft. Hood from 2008 to 2009 and found snakes and brown-headed cowbirds were the most frequent predators of black-capped vireo nests, combining for 75% of observed predation events.

Black-capped vireo habitat can be highly variable across the breeding range, with different species associations depending on location and past management activities, such as brush clearing and prescribed fire (Graber 1961, Grzybowski 1995). Yet the guidelines as to what constitutes suitable 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, Texas Parks and Wildlife Department) in Texas (Grzybowski 1995, Wilkins et al. 2006). Although vegetative characteristics of shrubland fit the description of suitable black-capped vireo habitat, black-capped vireos have been observed occupying other vegetation types such as deciduous and oak-juniper woodlands (Conkling 2010, T. Pope personal observation, D. Cimprich personal communication). In general, these woodland vegetation types are considered marginal, i.e., lower quality, habitat.

NEST BEHAVIOR

Parental care is a reproductive strategy used by many taxa, including fish, birds, and mammals. Over 90% of bird species use some form of parental care (Kendeigh 1952). Parental care can be separated into distinct categories, including nest building, incubation, and feeding young. For many bird species, males participate mainly in feeding young, though in some species they help build nests and bring food to incubating females (Erhlich et al. 1988, Barg et al. 2006). In the family *Vireonidae*, males are known to participate in incubation, sharing duties with the female during the day (Erhlich et al. 1988, Grzybowski 2001). Many studies investigating avian parental care have focused on species where females are the sole incubator, relating variables such as ambient temperature (Martin and Ghalambor 1999, Conway and Martin 2000, Londono et al. 2008), food availability (Eikenaar et al. 2003, Londono et al. 2008) and predation risk (Martin and Ghalambor 1999, Ghalambor and Martin 2002) to rates of incubation and feeding young.

Skutch (1949) proposed that nest predation increases with activity at the nest. The Skutch hypothesis assumes that predation occurs during the day or that predators remember the location of the activity and return later. However, adults may adjust the amount of time spent on and off of the nest during incubation as a means of predator defense (Conway and Martin 2000, Martin et al. 2000, Fontaine and Martin 2006). Adults may also adjust feeding rates, either males feeding incubating females or both adults feeding nestlings (Ghalambor and Martin 2002, Fontaine and Martin 2006) to avoid attracting attention when predators are present (Mullin and Cooper 1998, Conway and Martin 2000, Martin et al. 2000, Ghalambor and Martin 2002, Fontaine and Martin 2006, Eggers et al. 2008). Adult predator-defense behavior may also compensate for poor nest location (Cresswell 1997, Komdeur and Kats 1999, Weidinger 2002, Remes 2005, Eggers et al. 2008), depending upon the species (Weidinger 2002).

My research will help determine whether deciduous and oak-juniper woodlands are truly less suitable habitat for black-capped vireos than shrubland and whether black-capped vireo nest behavior affects nest success. Understanding these relationships will assist managers in making management plans and recommendations for landowner conservation incentive programs.

CHAPTER II

EFFECTS OF HABITAT AND NEST-SITE CHARACTERISTICS ON BLACK-CAPPED VIREO NEST AND FLEDGLING SURVIVAL

Wildlife habitat refers to an area that provides resources and conditions that allow a species to survive (Morrison et al. 2006). Habitat quality may vary among vegetation types, with high quality habitat providing the best resources for survival, reproduction, and population persistence (Morrison et al. 2006). Investigating differences in nest survival, success of first nest attempts, fecundity, and fledgling survival can determine if vegetation types are high or low quality habitat. Having a successful first nest attempt may lead to double brooding (Grzybowski 1995), reduce energetic costs related to renesting if unsuccessful (Haas 1998), and allow for more preparation time prior to fall migration (Morton 1992). Habitat loss is often a factor when listing endangered species, therefore identifying which vegetation types provide the highest quality habitat for endangered species will help direct management and conservation activities designed to recover these species.

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Tree species common in black-capped vireo habitat in central Texas include shin oak (*Quercus sinuata*), live oak (*Q. fusiformis*), Texas or Spanish oak (*Q. buckleyi*), sumac (*Rhus* spp.), Texas persimmon (*Diospyros texana*), roughleaf dogwood (*Cornus drummondi*), redbud (*Cercis canadensis*), Texas ash (*Fraxinus texensis*) and Mexican buckeye (*Ungnadia speciosa*; Graber 1961, Grzybowski 1995).

Even in suitable habitat, black-capped vireo nests are frequently lost to predation. Bailey and Thompson (in review) concluded that 87% of unsuccessful nests failed due to predation during their 2003–2004 study at Fort Hood. Predation was the greatest cause of nest failure at Fort Hood in 2010 as well, accounting for 79% of unsuccessful nests and 52% of all nests (Cimprich and Comolli 2010). A nest-monitoring study at Fort Hood from 1998 to 2001 found that snakes and fire ants (*Solenopsis* spp.) were the leading predators, accounting for 38% and 31%, respectively, of all depredated nests (Stake and Cimprich 2003). Other nest predators in the Fort Hood study included avian (19% of depredated nests) and mammalian predators (11%; Stake and Cimprich 2003). Conkling et al. (in review) used nest cameras to investigate the predator assemblage in black-capped vireo habitat north of Ft. Hood from 2008 to 2009 and found snakes and brown-headed cowbirds were the most frequent predators of black-capped vireo nests, combining for 75% of observed predation events.

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My objectives were to determine if deciduous and oak-juniper woodlands are truly less suitable habitat for black-capped vireos than shrubland. As such, I investigated survival of nests and fledglings in each vegetation type: shrubland, deciduous woodland, and oak-juniper woodland. I also evaluated whether certain vegetative characteristics at the nest site affected nest and fledgling survival. I incorporated annual and seasonal variation in survival estimates where appropriate. If shrubland was higher quality habitat for black-capped vireos than either woodland type, I expected to find lower predation and parasitism frequencies, more successful first nest attempts, higher fecundity, and higher daily and period survival for nests and fledglings in shrubland than deciduous and oak-juniper woodlands. I also expected to find differences in vegetative characteristics at nests sites (e.g., cover from 0 to 2 m) among vegetation types that may have influenced survival probabilities.

STUDY AREA

My study area was approximately 8,000 ha in Kerr County, Texas focused at Kerr Wildlife Management Area and adjacent private lands. In 2008, I monitored approximately 500 ha (6 pastures) on the eastern side of Kerr WMA. In 2009, I continued to monitor those pastures as well as approximately 700 ha on private properties surrounding Kerr WMA. I monitored approximately 90 ha (one pasture) of Kerr WMA in 2010.

Kerr County is representative of the Edwards Plateau Ecoregion of Texas and has a known population of breeding black-capped vireos. Within Kerr County there are 3 black-capped vireo vegetation types that 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, Ashe juniper (*Juniperus ashei*), Texas oak, shin oak, 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. In 2008, Kerr WMA was running 9 cowbird traps, with 39.4 cowbirds (19.1 females) caught per trap. Each of the subsequent years, Kerr WMA added 2 additional traps, and number of cowbirds caught per trap increased to 47.8 (20.3 females) in 2009 and 60.1 (22.5 females) in 2010. There was no cattle-grazing on Kerr WMA in 2010.

METHODS

Data collection

Territory mapping—I located black-capped vireo territories by surveying study areas for singing males. I visited each territory every 3–4 days. I used a GPS unit (Garmin Ltd., Olathe, KS) to mark 3–6 black-capped vireo locations (e.g., singing perch) per visit to a territory until I had at least 15 locations, enough to provide a good representation of each territory (International Bird Census Committee 1970). Each year I randomly selected up to approximately 30 territories to monitor per study area. In 2009 and 2010, I emphasized selecting territories in deciduous and oak-juniper woodland to increase sample sizes in those vegetation types.

Target mist-netting and banding—I banded adult black-capped vireos using target mist-netting techniques. I 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. I attached a USGS, size 0 aluminum band (silver in 2008, red anodized 2009 and 2010) on the tarsus of each adult. I also attached a unique color band combination (coordinated with The Nature Conservancy at Fort Hood) of Darvic or celluloid plastic bands (Avinet Inc., Dryden, NY). I banded nestlings with a silver or red USGS aluminum band and unique color combination at age 6–8 days.

Nest monitoring—I searched monitored territories for nests every 3–5 days, spending no longer than 1 hr in a territory per visit as stipulated in the federal permit. I used a combination of behavioral cues from adults and a search image to locate nests. After I located a nest, I checked the status of the nest every 2–4 days until the nest failed or fledged young. I used a nest mirror, binoculars, or direct observation to determine the contents of the nest, using the method that caused the least disturbance to the nest and nearby vegetation. I addled any brown-headed cowbird eggs in the nest to prevent hatching. I addled the egg instead of removing the egg from the nest because removing the egg could lead to abandonment of the nest. I removed brown-headed cowbird nestlings found in the nest. When a nest failed, I began searching the territory for another nesting attempt during the same visit.

Nest cameras—I used a continuously recording video camera system to identify predators and confirm the fate of nests. I selected nests based on availability of camera units, distribution of nests in each vegetation type (e.g., shrubland, oak-juniper woodland, and deciduous woodland) and nest stage. I only placed cameras on nests that had initiated incubation. If multiple nests were available, I preferentially chose nests earlier in the nesting cycle (i.e., day 2 of incubation vs. day 12) to be able to record activity at the nest for the longest period of time.

The camera system consisted of a weatherproof bullet camera with a 3.6 mm lens and infrared lighting (Rainbow, Costa Mesa, CA) to record activity at the nest 24 hours a day. I placed the video camera near enough to the nest to capture all activity, but not disturb the birds (approximately 1–2 m). A 15-m cable connected the camera unit to a digital video recorder (Detection Dynamics, Austin, TX) and a 12 v 26 ah battery (Batteries Plus, Hartland, WI). I used 4 GB (2008) or 8 GB (2009–10) SD memory cards and a time-lapsed recording of 5 frames per second to maximize data storage. I checked the camera system every 3–4 days to replace SD cards and batteries as needed and left the camera in place until the nest fledged or failed. In 2009 and 2010, I supplemented battery power with 20-watt solar panels (Suntech, San Francisco, CA). If I observed a loss of nest contents (i.e., eggs or nestlings) between consecutive nest checks, I viewed all nest video footage recorded during that time period to confirm nest fate and identify predators (if observed).

Resighting—If I determined a nest may have fledged young successfully, I returned to the territory every 3–5 days to attempt to relocate each individually color-banded fledgling to assess survival. I would spend at least 30 min attempting to locate the fledglings in the territory and surrounding area. If I located fledglings within 30 min, I would spend up to 30 additional minutes determining the color combinations of each fledgling seen. I attempted to relocate fledglings in each territory until the fledglings reached independence (approximately 35–45 days post-fledging) or until I was unable to locate fledglings for 3 consecutive visits.

Vegetation measurements—I recorded vegetation measurements at all nests in which at least one egg was laid. At each nest I recorded nest height; nest substrate species; height of the nest substrate plant; nest concealment (i.e., % visual obstruction) from 1 m away at 6 sides (each cardinal direction, above, and below); distance to nearest edge (i.e., horizontal distance from the nest to the nearest break in contiguous vegetation at nest height); and whether there was a canopy above the nest and if so, the species and height of the canopy plant(s). I used a coverboard to assess percent cover at the nest at each height class (0.1-m intervals) between 0–2 m, estimated 7 m from the nest in each cardinal direction (Guthery et al. 1981).

I marked the location of each nest using a GPS unit. I uploaded the nest point locations into ArcGIS 9.3 (Environmental System Research Institute, Redlands, CA) using DNRGarmin 5.3.2 (Minnesota Department of Natural Resources). I created a 25-m radius buffer around each nest point using the Buffer Features vector editing tool in Hawth's Analysis Tools 3.27 (Beyer 2004). I used the Iso Cluster Multivariate Spatial Analyst tool in ArcGIS 9.3 to perform an unsupervised classification of 1-m resolution National Agriculture Imagery Program (NAIP) Orthoimagery encompassing the study area (Seamless Data Warehouse, USGS) into two cover classes (cover or no cover; Figure 2.1). Using the thematic raster summary function of the raster tools in Hawth's Analysis Tools 3.27 (Beyer 2004), I calculated the percent cover in the 25-m radius buffer around each nest by dividing the number of cells classified as cover by the total number of cells in the buffer area.

Data analysis

For all analyses, I considered nests that were parasitized by brown-headed cowbirds as failures to remove the effect of manipulating the nests by addling brown-headed cowbird eggs or removing nestlings. The probability of a black-capped vireo nest fledging host young after being parasitized is very low (Graber 1961, Grzybowski

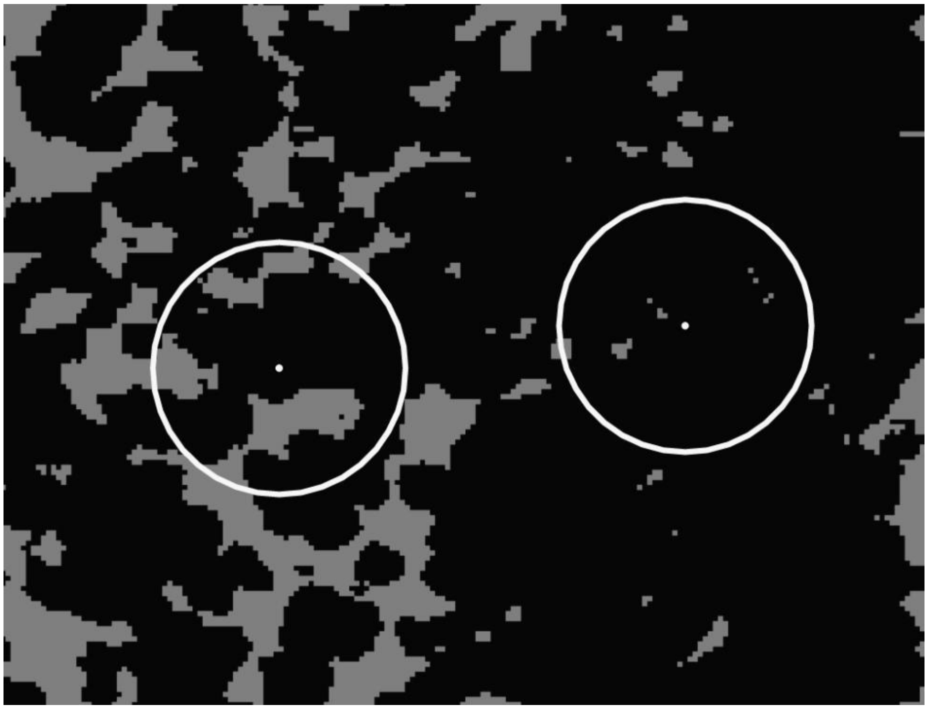

Figure 2.1. Examples of 25-m radius buffers around black-capped vireo nest locations in Kerr County, Texas, 2008–2010, showing percentage of woody cover (black) around the nest (77% left, 99% right).

1995). I also included only nests of known fates (fledged or failed) in analyses. I considered a nest successful if it fledged ≥ 1 host young.

Vegetation type—To determine if apparent nest success, success of first nesting attempts, parasitism frequency, and predation frequency varied among the vegetation types, I used SPSS 15.0 (SPSS Inc, Chicago, Illinois) to complete contingency tables and perform likelihood ratio tests (Agresti 1996: 27–34). I analyzed all years together because I was interested in differences between vegetation types and not annual differences. I performed a single-factor analysis of variance (ANOVA; Zar 1999: 178–189) using SPSS 15.0 to determine if fecundity (no. fledglings/female/year) in territories with a least one nest found with contents and of known fate was different in each vegetation type and year. I performed nest survival analysis using Program MARK (White and Burnham 1999) with a constant survival model to estimate daily and period survival for each vegetation type. Nest survival estimates are usually lower than apparent nest success because nest losses in early incubation are taken into account (Mayfield 1961, Dinsmore et al. 2002).

Nest-site selection—To determine if nest-site vegetation characteristics were different among shrubland, deciduous woodland, and oak-juniper woodland, I performed a single-factor ANOVA using SPSS 15.0 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), average cover from 0 to 2 m, and percent of woody cover within a 25-m radius of the nest. I did not include nest concealment in analyses because 1) I recorded nest concealment in categories in 2008 and could not compare 2008 directly to estimates from 2009 and 2010 and 2) nest concealment estimates in 2009 were abnormally low compared with 2010, due to differences in observers. I analyzed all years together because I was interested in differences between vegetation types and not annual differences.

I performed nest survival analyses using Program MARK to determine if nest-site vegetation characteristics influenced nest survival. Program MARK weights models using Akaike's Information Criterion (AIC) as a function of the equation:

$$\mathrm{AIC} = -2 \ln(L) + 2\mathrm{K}$$

where the model likelihood or fit of the model to the data is denoted as *L* while K is the number of parameters in the model. According to Williams et al. (2002), selecting the model with the lowest AIC weight out of all candidate models should result in the selection of the model best fitting the data to which it has been applied.

I created a list of candidate models that included covariates of interest for my objectives, including temporal effects of year and season, effect of vegetation type, effect of nest attempt, and effects of nest-site vegetation characteristics (Table 2.1). Initially, each model included the intercept and 1 covariate as a main effect. If the main-effect models had higher AIC values than the intercept-only model, I concluded that the covariate did not influence nest survival and removed it from further consideration. If any of the main-effect models had a lower AIC value than the intercept-only model, I included the covariate in additional candidate models that included the intercept and all possible combinations of the selected covariates and evaluated support for each model using AIC.

Program MARK provides estimates of daily survival with standard error and 95% confidence intervals. I 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) in the equation: period survival = daily survival^{28} (Mayfield 1961).

Table 2.1. List of covariates included in modeling black-capped vireo nest survival in Kerr County, Texas, 2008–2010.

Covariate	Description
Nest height	Height of nest from ground to nest rim (m)
Nest height by category	Nest height by category (average: 0.8-1.8 m; other: <0.8, >1.8 m)
Cover 0-2 m	Mean cover board measure from 4 directions at 7m from nest in 0-2 m height zone
% cover	Percent of woody cover w/in 25-m radius of nest
% cover by category	Percent of woody cover w/in 25-m radius of nest by category (average: 35-55%; other: <35%, >55%)
Substrate	Category of nest substrate (oak, deciduous, juniper)
Distance to edge	Distance to the nearest break in cover at nest height (m)
Overstory	Overstory present at nest (yes, no)
Year	Year of nest attempt (2008, 2009, 2010)
Habitat	Category of vegetation type where nest located (shrubland, deciduous woodland, oak-juniper woodland)
Attempt	Category of nest attempt (1st, 2nd, 3rd or more)
Date	Date of nesting season (day 1-108)

Fledgling survival—I analyzed fledgling survival using Cormack-Jolly-Seber (CJS) recapture models generated in Program MARK. I constructed a set of candidate models to examine the effect of several factors on fledgling survival. I included year (2008, 2009, and 2010), habitat (shrubland, deciduous woodland, and oak-juniper woodland), and whether the nest was located within 100 m of oak-juniper habitat. I included year as a covariate because survival may vary due to annual fluctuations in food resources or predator activity. I included habitat as a covariate to determine whether survival was influenced by vegetation type. Oak-juniper woodland may provide greater cover and food resources (Anders et al. 1998, Marshall 2011, D. Morgan personal communication), therefore I hypothesized that nests located relatively close (within 100 m) of oak-juniper woodland may positively affect fledgling survival. I considered a covariate as having an effect on fledgling survival if the model that included the covariate had a lower AIC value than a model that included constant survival.

I used capture histories that included 10 encounter occasions, representing weeks covering the post-fledging period. If I resighted a fledgling at any time during the week, I 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, I included models that allowed for 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, habitat, or located within 100 m of oak-juniper woodland was better supported than the model with constant survival, I also included this covariate in the models with seasonal variation in survival and resight probability.

RESULTS

Vegetation type

I monitored 101 black-capped vireo territories in 2008, 124 territories in 2009, and 34 territories in 2010. Apparent nest success was highest in shrubland (39%, n = 215) and deciduous woodland (38%, n = 61), and lowest in oak-juniper woodland (31%, n = 26); although these differences were not statistically significant ($\chi^2 = 0.682$, df = 2, $P = 0.711$). Daily and period nest survival estimates varied but were not significantly different among vegetation types (Table 2.2).

Table 2.2. Daily and period survival estimates and 95% confidence intervals using a constant survival model in MARK for black-capped vireo nests in three vegetation types in Kerr County, Texas, 2008–2010.

Habitat	Daily survival (95% CI)	Period survival (95% CI)
Shrubland	0.962 (0.955, 0.968)	0.342 (0.277, 0.407)
Deciduous woodland	0.957 (0.942, 0.969)	0.294 (0.186, 0.411)
Oak-juniper woodland	0.948 (0.919, 0.968)	0.227 (0.093, 0.399)

First nesting attempts in shrubland were not more likely to be successful than first nesting attempts in either woodland habitat ($\chi^2 = 0.596$, df = 2, $P = 0.742$). In shrubland and deciduous woodland, 41% and 43% of first nesting attempts fledged young, respectively. Oak-juniper woodland had the lowest percentage (34%) of first nesting attempts fledge young.

Fecundity did not differ among vegetation types ($n = 204$; $F = 0.471$, df = 2, $P = 0.625$). Fecundity was highest in shrubland (1.86 ± 1.82, $n = 144$), lower in deciduous woodland (1.63 ± 1.68, $n = 43$), and lowest in oak-juniper woodland (1.53 ± 1.74, $n = 17$). Fecundity was lowest in 2008 (1.56 ± 1.71, $n = 78$) and 2009 (1.61 ± 1.72, $n = 94$), increasing to 1.84 ± 1.80 ($n = 32$) in 2010.

Parasitism frequency was 22% ($n = 215$) in shrubland and 12% in each woodland ($n = 61$ in deciduous, $n = 26$ in oak-juniper). Parasitism was nearly twice as high in shrubland ($\chi^2 = 4.683$, df = 2, $P = 0.096$), with a tendency toward statistical significance because P was between 0.05 and 0.10. Parasitism frequency declined over the course of the study from a high of 31% ($n = 121$) in 2008, to 16% ($n = 124$) in 2009, and 0% ($n = 57$) in 2010.

Predation was the leading cause of failure for black-capped vireo nests in Kerr County, with > 60% of unsuccessful nests (*n* = 187) being lost to predation. 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. The differences in predation were not statistically significant ($\chi^2 = 2.975$, df = 2, $P = 0.226$).

Table 2.3. 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
Unknown 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

Avian species (18%) and snakes (15%) were the most common predators of nest contents, followed by mammalian and ant species (*n* = 61, Table 2.3). Brown-headed cowbirds depredated (i.e., killed or removed nestlings) 7% of nests with cameras. Brown-headed cowbirds did not lay eggs in nests (i.e., parasitize) after predation events. Though snakes typically depredate nest contents, I also recorded a snake depredating a female vireo and the nestlings she was brooding overnight. Although not included in the predator analysis, a gray fox (*Urocyon cinereoargenteus*) slept under a nest for approximately 4 hrs, which apparently resulted in the adults abandoning the nest during the incubation stage.

Nest-site selection

Vegetation characteristics at the nest site varied between different vegetation types (Table 2.4). Nest height, substrate height, and overstory height were lower in shrubland and distance to edge was closer in deciduous woodland (Table 2.5). Percent cover within 25-m radius of the nest increased from shrubland, to deciduous woodland, to oak-juniper woodland (Table 2.5). Average percent cover from 0-2 m was the only nest-site characteristic that did not vary among the vegetation types (Table 2.5).

Table 2.4. Results of ANOVA analysis comparing vegetation characteristics at black-capped vireo nest sites between shrubland, deciduous woodland, and oak-juniper woodland in Kerr County, Texas, 2008–2010. Bold values denote significance at α = 0.05.

Nest-site characteristic	*n*	*F*	df	*P*-value
Nest height (m)	302	4.62	2	**0.01**
Substrate height (m)	302	5.38	2	**0.01**
Overstory height (m)	205	8.73	2	**<0.001**
Distance to edge (m)	302	7.34	2	**0.001**
Average cover 0-2 m (%)	301	0.28	2	0.75
Cover w/in 25-m radius (%)	302	3.02	2	**0.05**

Table 2.5. Descriptive statistics for vegetation measurements at black-capped vireo nests within each vegetation type in Kerr County, Texas, 2008–2010.

	Shrubland				Deciduous woodland				Oak-juniper woodland			
	n	Mean ± SD	Min	Max	*n*	Mean ± SD	Min	Max	*n*	Mean ± SD	Min	Max
Nest height (m)	215	1.3 ± 0.53	0.4	3.2	61	1.5 ± 0.57	0.5	3.2	26	1.5 ± 0.94	0.6	4.0
Substrate height (m)	215	2.9 ± 1.48	0.8	11.0	61	3.6 ± 2.05	0.8	13.0	26	3.5 ± 1.71	0.7	7.5
Overstory height (m)	147	4.4 ± 1.62	1.0	11.0	39	5.0 ± 1.65	2.4	8.5	19	6.0 ± 2.20	2.1	12.0
Distance to edge (m)	215	1.5 ± 1.14	0.0	5.7	61	0.9 ± 1.08	0.0	4.8	26	1.5 ± 1.17	0.0	4.4
Average cover 0-2 m (%)	214	80 ± 15	30	100	61	80 ± 16	30	100	26	80 ± 15	40	90
Cover w/in 25-m radius (%)	215	47 ± 20	8	92	61	50 ± 21	8	99	26	56 ± 23	14	91

Only 3 covariates appeared in the models that were supported better than the intercept-only model: nest height, year, and cover at 0-2 m (Table 2.6). Of the 7 candidate models that included combinations of the 3 supported covariates, 4 models were < 2 ΔAIC_c of the best-supported model, demonstrating considerable model selection uncertainty. I selected the model with the lowest AIC value (nest height and year) for estimating nest survival. Daily nest survival was 0.960 (95 % CI: 0.954, 0.965) and period survival was 0.319 (95 % CI: 0.266, 0.374). Daily nest survival declined as the height of the nest increased and increased across each season (Figure 2.2).

Table 2.6. Model selection results for black-capped vireo nest survival in Kerr County, Texas, 2008–2010.

Model	K	AIC_c	ΔAIC_c	w_i
Nest height + year	4	1027.60	0.00	0.23
Cover 0-2 m + year	4	1027.89	0.28	0.20
Nest height + year+ cover 0-2 m	5	1028.29	0.69	0.17
Year	3	1028.32	0.72	0.16
Cover 0-2 m	2	1029.30	1.70	0.10
Nest height + cover 0-2 m	3	1030.25	2.65	0.06
Nest height	2	1031.22	3.62	0.04
Intercept only	1	1031.47	3.87	0.03

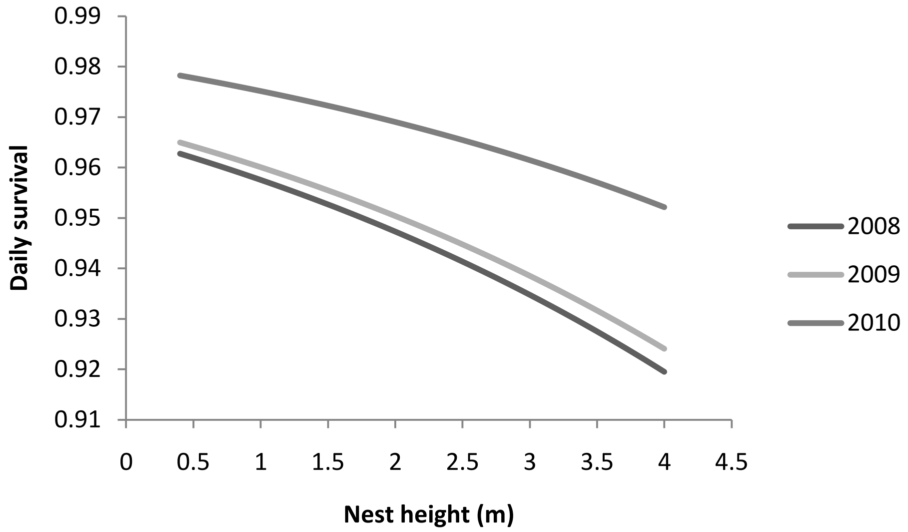

Figure 2.2. Predicted daily nest survival for black-capped vireo nests as a function of nest height in Kerr County, Texas, 2008–2010.

Fledgling survival

I used encounter histories for 350 individual fledglings from 111 potentially successful nests (i.e., showed signs of fledging) to determine fledgling survival. Of the 8 candidate models for fledgling survival, there was one model that was clearly best-supported (w_i = 0.91). The best-supported model included seasonal differences in survival and resight probability, with year affecting survival (Table 2.7). Models that included habitat and whether the nest was located within 100 m of oak-juniper woodland as covariates did not receive any support (Table 2.7). Fledgling survival was 0.570 (95 % CI: 0.446, 0.679) over the 10 week post-fledgling period. Seasonal differences in survival probabilities ranged from 0.751 to 0.892, and resight probabilities ranged from 0.431 to 0.575 (Table 2.8).

Table 2.7. Model selection results for black-capped vireo fledgling survival in Kerr County, Texas, 2008–2010.

Model	K	AIC_c	ΔAIC_c	w_i
Early/mid/late survival + year, early/mid/late recapture	8	2130.11	0.00	0.91
Survival + year, early/mid/late recapture	6	2134.77	4.66	0.09
Early/mid/late survival, early/mid/late recapture	6	2142.41	12.30	0.00
Survival, early/mid/late recapture	4	2148.25	18.14	0.00
Survival + year, constant recapture	4	2159.35	29.24	0.00
Survival, constant recapture	2	2171.51	41.40	0.00
Survival + habitat, constant recapture	4	2172.31	42.20	0.00
Survival + w/in 100m of juniper, constant recapture	3	2173.46	43.35	0.00

Table 2.8. Survival and resight probabilities for black-capped vireo fledglings during the early, mid, and late post-fledging periods in Kerr County, Texas, 2008–2010.

Post-fledging period	Survival probability (95% CI)	Resight probability (95% CI)
May 15 – June 11	0.850 (0.788, 0.896)	0.431 (0.364, 0.501)
June 5 – July 2	0.892 (0.845, 0.927)	0.575 (0.523, 0.625)
June 26 – July 23	0.751 (0.670, 0.818)	0.486 (0.405, 0.568)

DISCUSSION

Black-capped vireos occupied shrubland, deciduous woodland, and oak-juniper woodland in my study area. Factors that help determine if conditions provided by habitat are appropriate for population persistence (i.e., high quality), including apparent nest success, first nest attempt success, and daily and period nest survival were not significantly different in any of the vegetation types. Fecundity was highest in shrubland, and although the difference was not statistically significant, it may prove to be important biologically because fecundity affects the population growth rate. Parasitism frequency was nearly twice as high in shrubland as compared to woodland vegetation types. Robinson et al. (1999) also found higher parasitism in shrubland and savannas than forests in the Midwest. Other researchers found higher parasitism on forest edges than farther into the forest in Michigan (Gates and Gysel 1978) and Indiana (Winslow et al. 2000). Black-capped vireo nests in shrubland are easier for researchers to find than nests in woodland (personal observation); and therefore may be easier for female brown-headed cowbirds to find as well, especially if cowbirds are using similar behavioral cues from adult black-capped vireos to locate nests (Norman and Robertson 1975, Banks and Martin 2001). However, Burhans (1997) found indigo buntings (*Passerina cyanea*) nesting in Missouri had higher parasitism in forest (73%) than in nonforest (51%). Hahn and Hatfield (1995) also found higher parasitism in forest (32.3%) than in old-field and edge habitat (6.5%) in New York.

Recent studies at Fort Hood have shown high losses to predation (Bailey and Thompson, in review; Cimprich and Comolli 2010) as well. Major predators in and around Fort Hood include snakes and fire ants (Stake and Cimprich 2003, Conkling et al., in review). Snakes are also a major predator at Balcones Canyonlands National Wildlife Refuge near Austin, Texas (M. Colón, 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., in review). 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., in review; Smith 2011). Snakes were one of the major predators in my study area, though more nests were lost to avian predators, especially western scrub-jays and brown-headed cowbirds. As with parasitism, I did not record any brown-headed cowbird predation events in 2010.

Nest-site characteristics were different between the vegetation types, with the exception of average cover around the nest from 0 to 2 m. Differences in nest substrate height, overstory height, and percent cover within 25-m radius of the nest 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 I standardized recording the distance. I recorded distance to edge as the closest break in vegetation at nest height, though in deciduous woodland, there was often continuous cover at a height above the nest. 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. There was no difference in average percent cover within 25-m radius of the nest by vegetation type, indicating that the amount of cover preferred by black-capped vireos was provided in each vegetation type.

Despite the differences in nest-site characteristics between vegetation types, most nest-site characteristics did not have an effect on nest survival. Nest height and average percent cover from 0 to 2 m were the only nest-site characteristics to appear in the best-supported nest survival models. Cover around the nest is often considered an important factor in nest survival because it could conceal the nest from visual predators (Martin and Roper 1988, Martin 1992 and references therein). Nests depredated by western scrub-jays and hawks were 25% higher than nests of average height in my study area, therefore higher nests may be more susceptible to avian predators.

At Food Hood, Bailey and Thompson (in review) found nest height and substrate affected black-capped vireo nests survival, with nests in deciduous substrates and nests placed at typical heights and the greatest observed heights having higher survival. The negative relationship between nest height and survival in my study area that was not observed at Fort Hood may be due to the nests with the greatest observed heights at Fort Hood being relatively low (approximately 2 m) compared to Kerr County where nests were observed as high as 4 m. Avian predators also appear to have a greater impact on black-capped vireo nests in my study area, where 37% of depredated nests were lost to avian species. At Fort Hood, only 19% of depredated nests were lost to avian predators (Stake and Cimprich 2003).

Although differences in habitat quality between shrubland and woodland habitats were slight, there was evidence of yearly variation. Fecundity and nest survival were higher in 2010 than in 2008 and 2009, though not statistically significant. One explanation for finding higher fecundity is that due to logistical restraints, I focused on a smaller area (1 pasture) in 2010 which enabled me to find and monitor nearly all nesting attempts for each monitored territory. In 2008 and 2009, there was less emphasis placed on trying to monitor all nesting attempts at a given territory and I may have missed nesting attempts later in the season that fledged successfully.

Another explanation for higher fecundity and nest survival in 2010 could be the lack of brown-headed cowbird parasitism. None of the monitored nests were parasitized or depredated by brown-headed cowbirds that year. When I initiated this study in 2008, parasitism frequency was 31%. Each of the subsequent years, parasitism frequency declined to 16% and 0%, respectively. Interestingly, the highest numbers of cowbirds caught in traps came in 2010 despite the lack of cattle-grazing on Kerr WMA. Presumably, these birds were in the area because of the cattle and exotic wildlife grazing on the private lands in the vicinity.

Fledgling survival did not appear to be influenced by vegetation type, but was influenced by year. As with fecundity, focusing on a single pasture may have influenced year having an effect on fledgling survival. Due to monitoring a smaller area in 2010, I was 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 dropping 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 were lowest in May. During this time 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 (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 I think these estimates are conservative. Unlike other songbirds, such as willow flycatchers (*Empidonax trailii*) and western bluebirds that remain in family groups after fledging (Vormwald et al., in press; Wightman 2009); black-capped vireos may split broods between the adults (personal observation, Grzybowski 1995). Fledglings of species that remain in family groups are easy to relocate by finding the adults. Black-capped vireo fledglings are usually resighted after locating the singing male, and therefore fledglings remaining with the male are more likely to be encountered than fledglings being cared for by the quiet female.

Although I did not detect statistically significant differences among the vegetation types that would indicate differences in habitat quality, shrubland had the best results in all parameters except parasitism frequency, followed closely by deciduous woodland. Oak-juniper woodland consistently fell behind shrubland and deciduous woodland. Shrubland remains the most important habitat to maintain for the persistence of black-capped vireo populations because most black-capped vireos occupy and reproduce in shrubland, but deciduous and oak-juniper woodlands can also fulfill an important role. As wildlife habitat declines due to loss and degradation, there will be less high quality habitat across the landscape. In some situations, wildlife may need to utilize lower quality, or marginal, habitat that may be more widespread for wildlife populations to persist (Donovan and Thompson 2001). Shrubland is considered the highest quality habitat for black-capped vireos in central Texas, but this vegetation type has been declining due to 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). In the place of shrubland, there are woodlands with vegetation characteristic of later succession and with a higher proportion of juniper (Smeins and Merrill 1988, Fuhlendorf and Smeins 1997). For example, Wills (2005) found that woodland at Kerr WMA increased from 5.7% in 1884 to 80.0% in 2004 in Low Stony Hill ecosites and from 20.0% to 70.0% in Redland ecosites. Deciduous and oak-juniper woodlands also contribute individuals to black-capped vireo populations and may act as refuges as shrubland is lost to land use changes or during management activities, such as prescribed fire and brush clearing, designed to restore black-capped vireo habitat to shrubland.

MANAGEMENT IMPLICATIONS

Considering deciduous and oak-juniper woodlands appear to be suitable habitat for black-capped vireos in my study area, woodlands may also be suitable throughout the breeding range (Campomizzi 2009, Conkling 2010). Although it is best to maintain as much of the highest quality habitat (i.e., shrubland) as possible, knowing that black-capped vireos use and are reproductively successful in woodlands can aid in conservation efforts for 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 suitable habitat, especially if these areas are in close proximity to known large populations of vireos. Otherwise, managers and landowners may inadvertently remove vegetation that is suitable habitat for black-capped vireos because it does not adhere to current habitat descriptions. Recognizing woodlands as non-typical, yet still suitable, habitat will allow managers to incorporate these vegetation types into management plans and recommendations for landowner conservation incentive programs.

CHAPTER III

EFFECTS OF ADULT BEHAVIOR AND NEST-SITE CHARACTERISTICS ON BLACK-CAPPED VIREO NEST SUCCESS

Parental care is a reproductive strategy used by many taxa, including fish, birds, and mammals. Over 90% of bird species use some form of parental care (Kendeigh 1952). Parental care can be separated into distinct categories, including nest building, incubation, and feeding young. For many bird species, males participate mainly in feeding young, though in some species they help build nests and bring food to incubating females (Erhlich et al. 1988, Barg et al. 2006). In the family *Vireonidae*, males are known to participate in incubation, sharing duties with the female during the day (Erhlich et al. 1988, Grzybowski 2001). Many studies investigating avian parental care have focused on species where females are the sole incubator, relating variables such as ambient temperature (Martin and Ghalambor 1999, Conway and Martin 2000, Londono et al. 2008), food availability (Eikenaar et al. 2003, Londono et al. 2008) and predation risk (Martin and Ghalambor 1999, Ghalambor and Martin 2002) to rates of incubation and feeding young.

Skutch (1949) proposed that nest predation increases with activity at the nest. The Skutch hypothesis assumes that predation occurs during the day or that predators remember the location of the activity and return later. However, adults may adjust the amount of time spent on and off of the nest during incubation as a means of predator defense (Conway and Martin 2000, Martin et al. 2000, Fontaine and Martin 2006).

Adults may also adjust feeding rates, either males feeding incubating females or both adults feeding nestlings (Ghalambor and Martin 2002, Fontaine and Martin 2006) to avoid attracting attention when predators are present (Mullin and Cooper 1998, Conway and Martin 2000, Martin et al. 2000, Ghalambor and Martin 2002, Fontaine and Martin 2006, Eggers et al. 2008). Adult predator-defense behavior may also compensate for poor nest location (Cresswell 1997, Komdeur and Kats 1999, Weidinger 2002, Remes 2005, Eggers et al. 2008), depending upon the species (Weidinger 2002).

Black-capped vireos (*Vireo atricapilla*) are a federally endangered songbird whose historical breeding range once extended from Kansas south into Mexico, with the majority of the currently known breeding population occurring in central and southwest Texas (Graber 1961, Ratzlaff 1987, Grzybowski 1995). Previous studies have shown snakes to be a major predator of black-capped vireo nest contents (Stake and Cimprich 2003), and that these snakes may be using adult activity to help locate nests (Stake et al. 2005). Visits for exchanging incubation duties or feeding young may lead to an increased predation risk by attracting attention to the nest (Skutch 1949, Ghalambor and Martin 2002, Weatherhead and Blouin-Demers 2004). Nests that are more exposed may also attract attention of visual predators (Martin 1993, Benson et al. 2010). Therefore, I predicted that nest attentiveness (min/hr) would increase and visitation (trips/hr) would decrease as cover around the nest decreased. I also predicted that nest attentiveness and visitation would be predictors of nest success for black-capped vireos.

STUDY AREA

My study area consisted of study sites located in 3 Black-capped Vireo Recovery Regions (U.S. Fish and Wildlife Service 1991) in Texas. In Recovery Region 2 (Lampassas Cutplains), study sites were on private properties in Coryell Co. (2008–2009) and at Balcones Canyonlands National Wildlife Refuge (BCNWR, U.S. Fish and Wildlife Service) in Burnet, Williamson, and Travis counties (2010). The study site in Recovery Region 3 (Southeast Edwards Plateau) was at Kerr Wildlife Management Area (WMA, Texas Parks and Wildlife Department) and adjacent private lands (2008–2010) in Kerr Co. Devils River State Natural Area (SNA, Texas Parks and Wildlife Department) and Dolan Falls Preserve (The Nature Conservancy) in Val Verde Co. were the study sites in Recovery Region 5 (Stockton Plateau, 2009–2010).

The study area in Coryell County consisted of 11 private properties within a 140,000-ha area of the Leon River watershed in east-central Texas. Topography consists of rocky limestone hillsides and mesas. Vegetation consists of mid-successional woody vegetation similar to Lampasas Cut Plains and ecotones between mature oak–juniper (*Quercus–Juniperus*) woodland and grassland. Primarily land uses include ranching, farming, and hunting. Brown-headed cowbird (*Molothrus ater*) trapping is not a widely used practice in the area.

Balcones Canyonlands National Wildlife Refuge was created in 1992 to preserve the nesting habitats of the black-capped vireo and golden-cheeked warbler (*Dendroica chrysoparia*). The refuge covers approximately 12,000 ha across several noncontiguous land tracts in the Edwards Plateau, of which 2,000 ha were included in this study. The vegetation is characterized by several oak species, including shin oak (*Quercus sinuata*), plateau live oak (*Q. fusiformis*), and Texas oak (*Q. buckleyi*), as well as Ashe juniper (*Juniperus ashei*). Management activities at the refuge include cowbird trapping, prescribed burning, and invasive species control or removal.

The study area in Kerr County covers approximately 8,000 ha representative of the Edwards Plateau. This area supports a plant community of trees, shrubs, and grasses, including live oak, Ashe juniper, Texas oak, shin oak, 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 hunting, brown-headed cowbird trapping, and prescribed burning.

The Devils River area covers approximately 8,100 ha and includes features of multiple ecoregions including Edwards Plateau on the east, south Texas brush habitat in the southern section of the park, and Trans-Pecos habitat to the west. Vegetation includes stands of live oak and pecan trees (*Carya illinoinensis*) near the Devils River and xeric grassland on the surrounding ridges and slopes. Multiple springs provide the majority of water to the river. Primary land uses in the area are wildlife viewing and human recreation. There is no active brown-headed cowbird trapping at Devils River.

METHODS

Data collection

Territory mapping—I located black-capped vireo territories by surveying study areas for singing males. I visited each territory every 3–4 days. I used a GPS unit (Garmin Ltd., Olathe, KS) to mark 3–6 black-capped vireo locations (e.g., singing perches) per visit to a territory until I had at least 15 locations, enough to provide a good representation of each territory (International Bird Census Committee 1970). Each year I selected up to approximately 30 territories to monitor per study location, depending on the specific research objectives at each study location.

Nest monitoring—I searched each of the monitored territories for nests every 3–5 days, spending no longer than 1 hr in a territory per visit as stipulated in the federal permit. I used a combination of behavioral cues from adults and systematic searches to locate nests. After I located a nest, I checked the status of the nest every 2–4 days until the nest failed or fledged young. I used a nest mirror, binoculars, or direct observation to determine the contents of the nest, using the method that caused the least disturbance to the nest and nearby vegetation. I addled any brown-headed cowbird eggs in the nest to prevent hatching. I addled the egg instead of removing the egg from the nest because removing the egg could lead to abandonment of the nest and also to minimize the chance of a cowbird laying another egg. I removed brown-headed cowbird nestlings found in the nest. When a nest failed, I began searching the territory for another nesting attempt during the same visit.

Nest observations—Due to specific research objectives in Kerr Co., I only performed nest observations in this region. Each week, I randomly selected nests for observation from all of the active nests being monitored. I recorded the stage of the nest (incubation or nestling) and day of each stage in categories of 4-day intervals (i.e., 1–4, 5–8, 9–12, 13–16) for each observation. I stood or sat at least 10 m from the nest, hidden by vegetation so as not to disturb the adults, but still having the nest in view. I used binoculars or a spotting scope to observe the focal pair at the nest for 1 hr, recording all occurrences of visits to the nest (i.e., the time in 24-hr format an adult arrived or left the nest). I conducted all observations between sunrise and 13:00 EDT.

Nest camera observations—I used a continuously recording video camera system to observe adult behavior, identify predators, and confirm fate of nests. I only placed cameras on nests that had initiated incubation. If multiple nests were available, I preferentially chose nests earlier in the nesting cycle (i.e., day 2 of incubation vs. day 12) to be able to record activity at the nest for the longest period of time.

The camera system consisted of a weatherproof bullet camera with a 3.6 mm lens and infrared lighting (Rainbow, Costa Mesa, CA) to record activity at the nest 24 hours a day. I placed the video camera near enough to the nest to capture all activity, but not disturb the birds (approximately 1–2 m). A 15-m cable connected the camera unit to a digital video recorder (Detection Dynamics, Austin, TX) and a 12 v 26 ah battery (Batteries Plus, Hartland, WI). In 2009 and 2010, I supplemented battery power with 20-watt solar panels (Suntech, San Francisco, CA). I used 4 GB (2008) or 8 GB (2009–2010) SD memory cards and a time-lapsed recording of 5 frames per second to maximize data storage. I checked the camera system every 3–4 days to replace SD cards and batteries as needed and left the camera in place until the nest fledged or failed.

If I observed a loss of nest contents (i.e., eggs or nestlings) between consecutive nest checks, I viewed all nest video footage recorded during that time period to confirm nest fate and identify predators (if observed). In 2008, I watched every 3rd day of footage for 24 hrs to determine the number of trips to the nest and number of minutes spent on the nest per day. Initial analyses indicated that 2 sampling periods of 4 hrs each for 1 day during each stage day category per nest stage was the sampling strategy that best duplicated the actual daily observations. I used this sampling strategy in 2009 and 2010, beginning with the first full day of video recorded then every fourth day until the nest fledged young or failed. I randomly selected start times for each of the sampling periods using a random number table of possible hours of daylight. If the random number selected for the 2nd sampling period that day would cause the sampling periods to overlap, I selected the next random number that would not overlap. Therefore, I observed 8 hrs of daytime activity at the nest for each day sampled, resulting in 1–7 days of footage per nest. Only behavior observations from 2009 and 2010 are presented.

Vegetation measurements—I recorded vegetation measurements at all nests in which at least one egg was laid. I used a coverboard to assess percent cover at the nest at each height class (0.1-m intervals) between 0 and 2 m, estimated 7 m from the nest in each cardinal direction (Guthery et al. 1981). I averaged percent cover from one direction, and then all directions combined to estimate average cover at the nest from 0 to 2 m. Most black-capped vireo nests are placed in vegetation at heights of 0.5 to 2.0 m (Grzybowski 1995).

I marked the location of each nest using a GPS unit. I uploaded the nest point locations into ArcGIS 9.3 (Environmental System Research Institute, Redlands, CA) using DNRGarmin 5.3.2 (Minnesota Department of Natural Resources). I created a 25-m radius buffer around each nest point using the Buffer Features vector editing tool in Hawth's Analysis Tools 3.27 (Beyer 2004). I used the Iso Cluster Multivariate Spatial Analyst tool in ArcGIS 9.3 to perform an unsupervised classification of 1-m resolution National Agriculture Imagery Program (NAIP) Orthoimagery encompassing the study area (Seamless Data Warehouse, USGS) into two cover classes (cover or no cover). Using the thematic raster summary function of the raster tools in Hawth's Analysis Tools 3.27 (Beyer 2004), I calculated the percent cover in the 25-m radius buffer around each nest by dividing the number of cells classified as cover by the total number of cells in the buffer area.

Data analysis

Nest observations—For each observation, I determined nest attentiveness by calculating min/hr each adult was at the nest during the observation period, as well as the total min/hr an adult was present. I also determined visits to the nest by calculating trips/hr for each adult and total trips/hr, with a trip being each time an adult arrived at or exited from the nest (i.e., each visit was 2 trips). I used trips as a metric instead of visits because sometimes adults were already at a nest at the beginning of observation or remained on the nest at the end of an observation. I also used trips because each trip to the nest can attract the attention of predators. I grouped observations by nest stage, as either incubation or nestling. To avoid pseudoreplication (Hulbert 1984), I calculated the mean for nest attentiveness and visitation if I observed a nest more than once during a stage.

To determine if nest attentiveness and visitation for each stage, overall and by sex, varied by year, I performed a single-factor analysis of variance (ANOVA; Zar 1999: 178–189). I performed linear regression (Zar 1999: 324–337) to determine if nest attentiveness and visitation were related to average cover at nest from 0 to 2 m or percent cover within 25-m radius of the nest. To determine if nest attentiveness or visitation affected nest success (i.e., successful [fledged ≥ 1 host young] or failed); I compared binary logistic regression models (Agresti 1996: 103–144) using Akaike's Information Criterion (AIC), including only nests of known fates. I ran separate analyses for nest attentiveness and visitation, overall and by sex, for each stage. Candidate models for each analysis included terms for the main effect of the variable, interaction of the main effect with clutch size, interaction of the main effect with vegetation characteristics where appropriate (as determined from linear regression), and additive models of these terms. I used SPSS 15.0 (SPSS Inc, Chicago, Illinois) for all analyses.

Nest video observations—For each video segment, I determined nest attentiveness by calculating min/hr an adult was present during the observation period, and determined visitation by calculating total trips/hr. I did not calculate nest attentiveness and visits by sex because I could not always differentiate between individual adults on the video. I did not combine data from nest and video observations because I wanted to be able to investigate differences in parental effort by sex. Because I watched two segments per day, I calculated the mean of the segments for the value of nest attentiveness and visits for that day. I then grouped observations by nest stage, taking the average for all of the days watched at a nest during each stage.

I used the same methods as above to determine if nest attentiveness and visitation were related to average cover at nest from 0 to 2 m or percent cover within 25-m radius of the nest, if nest attentiveness or visitation affected nest success, and if nest attentiveness and visitation for each stage varied by year except I did not have separate analyses for each sex. I performed a single-factor ANOVA to determine if nest attentiveness and visitation for each stage varied by recovery region as well.

RESULTS

Nest observations

I recorded 37 nest observations at 19 nests in 2008, 53 nest observations at 36 nests in 2009, and 30 nest observations at 22 nests in 2010. I observed 67 nests during incubation and 53 during the nestling stage. Females spent 80% more time on nests during incubation and 250% more time on nests during the nestling stage than males, but visitation was similar for each sex (Figures 3.1 and 3.2). Attentiveness and visitation, by sex and total, did not differ significantly among years during either nest stage (Range: $F = 2.061$, df = 2, $P = 0.138$ to $F = 0.046$, df = 2, $P = 0.955$), so I did not separate further analyses by year.

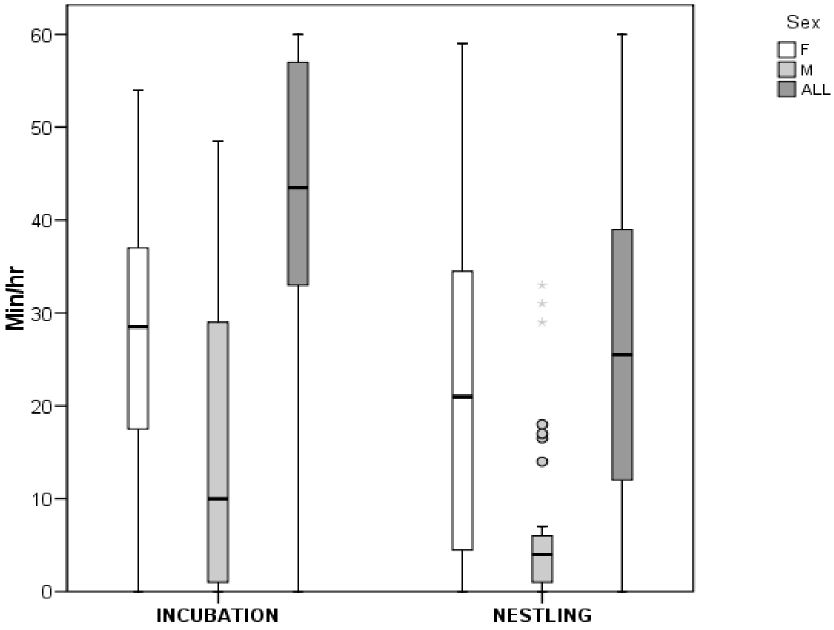

Figure 3.1. Nest attentiveness (min/hr) for incubation (*n* = 54) and nestling (*n* = 44) stages, by sex and combined, recorded during direct observations at black-capped vireo nests in Kerr County, Texas, 2008–2010.

Attentiveness during the nestling stage and attentiveness and visitation during both stages, for both sexes and total, were not affected by average cover from 0 to 2 m or percent cover within 25-m radius (see Appendix A). Female attentiveness ($\beta = 0.311$; $F = 4.988$, df = 1, $P = 0.030$) and total attentiveness ($\beta = 0.582$; $F = 14.018$, df = 1, $P < 0.001$) increased as average cover increased during incubation. Male attentiveness during incubation was close to being significant ($\beta = 0.263$; $F = 3.644$, df = 1 $P \leq 0.062$) and also increased as average cover increased. Therefore, I included average cover at the nest from 0 to 2 m in logistic regression models for nest attentiveness during incubation.

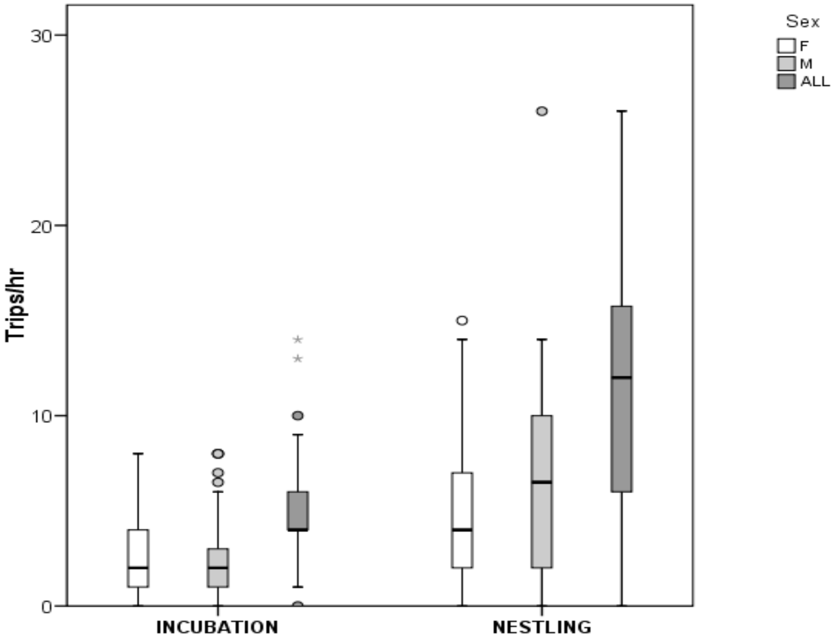

Figure 3.2. Visitation (trips/hr) for incubation (*n* = 54) and nestling (*n* = 44) stages, by sex and combined, recorded during direct observations at black-capped vireo nests in Kerr County, Texas, 2008–2010.

Black-capped vireo nest success was not affected by female visitation to nests during either nest stage because none of the logistic regression models including trips to the nest per hour were more supported (lower AIC$_c$) than the intercept only model (Table 3.1). During incubation, nest success was related to the time a female spent on the nest interacting with average cover from 0 to 2 m; whereas during the nestling stage, nest success was related to the time a female spent on the nest interacting with clutch size

(Table 3.1). The probability of a black-capped vireo nest being successful declined as female attentiveness increased during both nest stages (Figure 3.3A&C).

Table 3.1. Results of binary logistic regression models predicting the probability of success for black-capped vireo nests based on female activity at the nest during 1-hr observation periods in Kerr County, Texas, 2008–2010.

	Model	K	AIC$_c$	ΔAIC	w_i
Incubation					
Attentiveness	time on + time on × avg cover	3	62.91	0.00	0.39
	time on + time on × clutch + time on × avg cover	4	64.66	1.75	0.16
	intercept only	1	64.77	1.86	0.15
	time on	2	65.94	3.03	0.09
	time on × clutch	2	66.50	3.59	0.07
	time on × avg cover	2	66.87	3.96	0.05
	time on + time on × clutch	3	66.96	4.06	0.05
	time on × clutch + time on × avg cover	3	68.06	5.15	0.03
Visitation	intercept only	1	64.77	0.00	0.54
	trips	2	66.80	2.03	0.19
	trips × clutch	2	66.93	2.16	0.18
	trips + trips × clutch	3	68.39	3.62	0.09
Nestling					
Attentiveness	time on × clutch	2	52.73	0.00	0.52
	time on + time on × clutch	3	53.49	0.76	0.36
	time on	2	56.58	3.85	0.08
	intercept only	1	57.74	5.01	0.04
Visitation	intercept only	1	57.74	0.00	0.52
	trips × clutch	2	59.66	1.92	0.20
	trips	2	59.89	2.15	0.18
	trips + trips × clutch	3	61.01	3.27	0.10

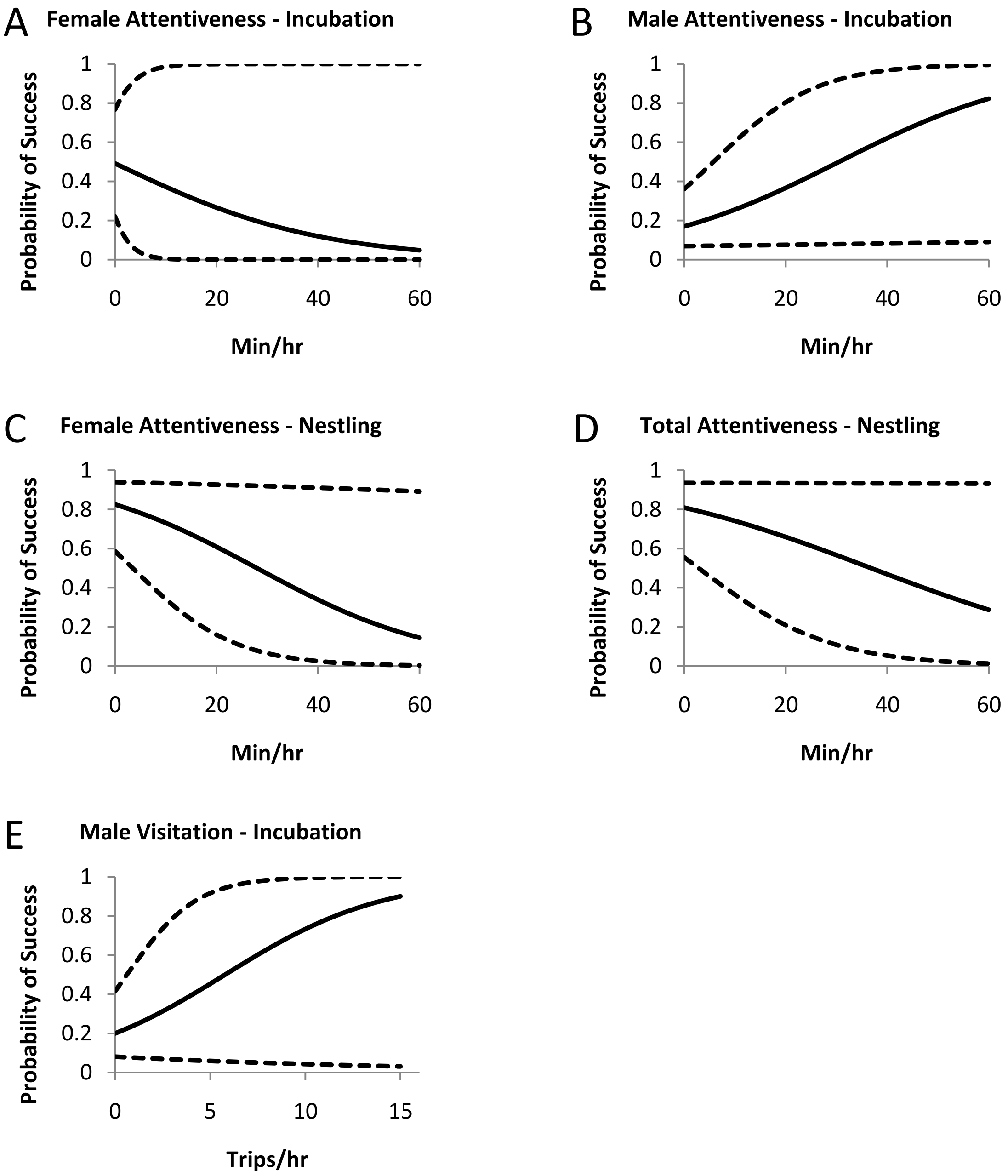

Figure 3.3. Predicted probability (solid line) with 95% confidence intervals (dashed lines) of a nest being successful based on the best (lowest AIC) logistic regression model from 1-hr nest observations at black-capped vireo nests in Kerr County, Texas, 2008–2010. Model equations: A. $y = -0.033 - 0.209(\text{min/hr}) + 0.002(\text{min/hr} \times \text{average cover [standardized at 80]})$; B. $y = -1.587 + 0.052(\text{min/hr})$; C. $y = -1.554 - 0.017(\text{min/hr} \times \text{clutch [standardized at 3.27]})$; D. $y = -1.444 - 0.012(\text{min/hr} \times \text{clutch [standardized at 3.27]})$; E. $y = -1.385 + 0.069(\text{trips/hr} \times \text{clutch [standardized at 3.48]})$.

Black-capped vireo nest success was not affected by male attentiveness or visitation to nests during the nestling stage because the best-supported logistic regression models were the intercept only models (Table 3.2). Nest success during incubation was related to the time a male spent on the nest and the number of trips to the nest by a male interacting with clutch size (Table 3.2). The probability of a black-capped vireo nest being successful increased as male attentiveness and visitation increased during incubation (Figure 3.3B&E).

Black-capped vireo nest success was not affected by total visitation during either nest stage or by total attentiveness during incubation because the best-supported logistic regression models were the intercept only models (Table 3.3). Nest success was related to the time on the nest by both adults interacting with clutch size during the nestling stage (Table 3.3). The probability of a black-capped vireo nest being successful declined as total attentiveness increased during the nestling stage (Figure 3.3D).

Table 3.2. Results of binary logistic regression models predicting the probability of success for black-capped vireo nests based on male activity at the nest during 1-hr observation periods in Kerr County, Texas, 2008–2010.

	Model	K	AIC$_c$	ΔAIC	w_i
Incubation					
Attentiveness	time on	2	61.76	0.00	0.25
	time on × avg cover	2	62.03	0.28	0.22
	time on × clutch	2	62.13	0.38	0.21
	time on + time on × clutch	3	63.97	2.22	0.08
	time on + time on × avg cover	3	64.02	2.27	0.08
	time on × clutch + time on × avg cover	3	64.27	2.51	0.07
	intercept only	1	64.77	3.02	0.06
	time on + time on × clutch + time on × avg cover	4	66.33	4.58	0.03
Visitation	trips × clutch	2	64.57	0.00	0.32
	intercept only	1	64.77	0.20	0.29
	trips	2	65.27	0.70	0.22
	trips + trips × clutch	3	65.76	1.19	0.17
Nestling					
Attentiveness	intercept only	1	57.74	0.00	0.56
	time on × clutch	2	59.94	2.21	0.19
	time on	2	59.95	2.21	0.19
	time on + time on × clutch	3	62.16	4.42	0.06
Visitation	intercept only	1	57.74	0.00	0.54
	trips	2	59.63	1.90	0.21
	trips × clutch	2	59.78	2.04	0.19
	trips + trips × clutch	3	61.97	4.23	0.06

Table 3.3. Results of binary logistic regression models predicting the probability of success for black-capped vireo nests based on activity of both adults at the nest during 1-hr observation periods in Kerr County, Texas, 2008–2010.

	Model	K	AIC_c	ΔAIC	w_i
Incubation					
Attentiveness	intercept only	1	64.77	0.00	0.23
	time on × avg cover	2	64.96	0.18	0.21
	time on × clutch	2	65.48	0.71	0.16
	time on	2	65.87	1.10	0.14
	time on + time on × avg cover	3	66.61	1.84	0.09
	time on × clutch + time on × avg cover	3	67.21	2.44	0.07
	time on + time on × clutch	3	67.66	2.89	0.06
	time on + time on × clutch + time on × avg cover	4	68.71	3.94	0.03
Visitation	intercept only	1	64.77	0.00	0.22
	trips × clutch	2	65.55	0.78	0.15
	trips	2	66.28	1.51	0.10
	trips + trips × clutch	3	66.99	2.22	0.07
Nestling					
Attentiveness	time on × clutch	2	54.88	0.00	0.50
	time on	2	56.85	1.97	0.19
	time on + time on × clutch	3	56.88	1.99	0.19
	intercept only	1	57.74	2.86	0.12
Visitation	intercept only	1	57.74	0.00	0.52
	trips	2	59.59	1.85	0.21
	trips × clutch	2	59.59	1.85	0.21
	trips + trips × clutch	3	61.89	4.15	0.07

Nest video observations

I recorded 63 predation events from video recorded 2008–2010. Avian predators (37%) and snakes (37%, *n* = 23) were the most common predators. Brown-headed cowbirds (*n* = 11), western scrub-jays (*Aphelocoma californica*, *n* = 7), and greater roadrunners (*Geococcyx californianus*, *n* = 3) were the most common avian predators. I observed all 3 of these species removing nestlings from nests (see also Stake and

Cavanagh 2001). Parasitism by cowbirds occurred before cameras were placed and I did not consider parasitism to be a predation event. Other predators included ants ($n = 5$), hawks ($n = 2$), gray fox (*Urocyon cinereoargenteus*, $n = 2$), fox squirrel (*Sciurus niger*, $n = 2$), coyote (*Canis latrans*, $n = 1$), ringtail (*Bassariscus astutus*, $n = 1$), bobcat (*Lynx rufus*, $n = 1$), raccoon (*Procyon lotor*, $n = 1$), and greater arid-land katydid (*Neobarrettia spinosa*, $n = 1$).

Table 3.4. Number of days of footage observed for behavior from black-capped vireo nest video recorded in 3 recovery regions of Texas in 2009 and 2010.

Year	Recovery Region	Nests	Days of Footage Observed
2009	2	16	51
	3	18	51
	5	38	118
2010	2	12	29
	3	19	88
	5	21	73
All Years	All Regions	122	410

I recorded 410 days of behavior observations from video recorded at 122 nests in 2009 and 2010 (Table 3.4). Total nest attentiveness and visitation were similar for video observations as compared to direct nest observations; however adults observed on video spent 29% more time on nests and therefore made fewer trips during incubation than adults observed directly at the nest (Figures 3.1, 3.2, 3.4, and 3.5). Nest attentiveness and visitation during incubation ($F = 0.259$, df = 2, $P = 0.772$; $F = 2.738$, df = 2, $P = 0.069$) and nestling ($F = 2.611$, df = 2, $P = 0.079$; $F= 2.146$, df = 2, $P = 0.123$) stages did not vary between recovery regions. Nest attentiveness and visitation did not vary among years during the nestling stage ($F = 0.821$, df = 1, $P = 0.368$; $F = 1.581$, df = 1, $P =$

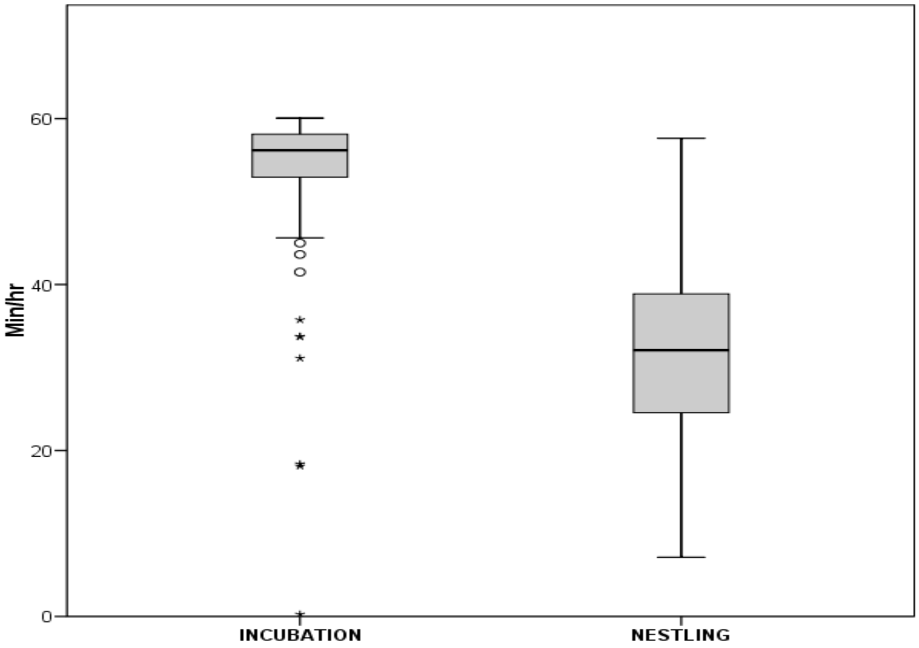

Figure 3.4. Nest attentiveness (min/hr) for incubation (*n* = 107) and nestling (*n* = 88) stages observed from video recorded at black-capped vireo nests in Burnet, Coryell, Kerr, Travis, Val Verde, and Williamson Counties, Texas, 2009–2010.

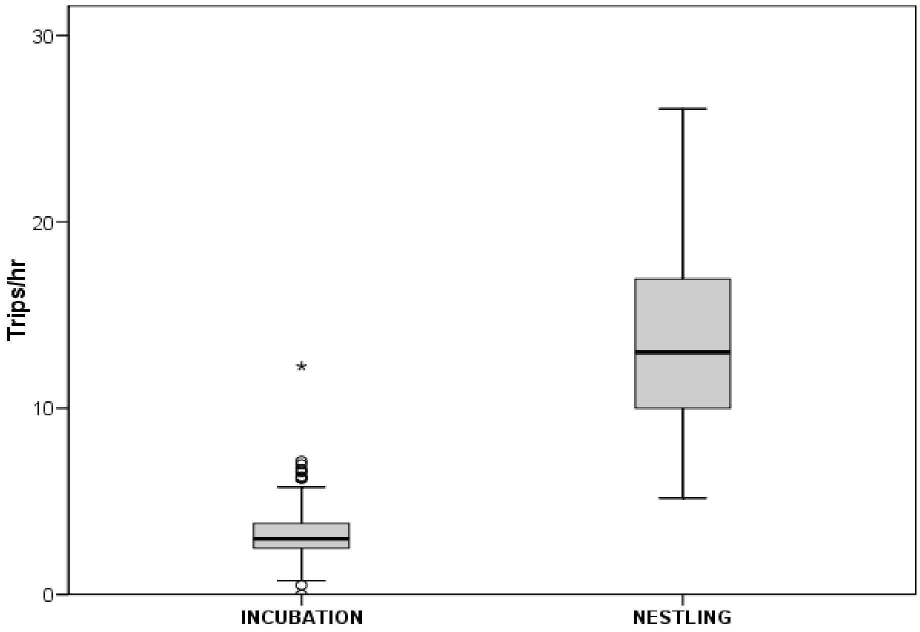

Figure 3.5. Visitation (trips/hr) for incubation (*n* = 107) and nestling (*n* = 88) stages observed from video recorded at black-capped vireo nests in Burnet, Coryell, Kerr, Travis, Val Verde, and Williamson Counties, Texas, 2009–2010.

0.212). Nest attentiveness also did not vary among years during incubation (*F* = 3.193, df = 1, *P* = 0.77), but visitation was slightly higher in 2009 than 2010 (*F* = 4.405, df = 1, *P* = 0.038). Therefore, I did not separate any further analyses by region; but I separated linear regression analyses by year for visitation.

Nest attentiveness was not influenced by percent cover within 25-m of the nest or average cover at the nest from 0 to 2 m during either nest stage (see Appendix B). Visitation was not influenced by average cover from 0 to 2 m during either stage or by percent cover within 25-m radius of the nest during incubation either year, nor during the nestling stage in 2010 (see Appendix B). Visitation during the nestling stage in 2009 increased as percent cover within 25-m radius of the nest increased ($\beta = 5.558$; *F* = 4.102, df = 1, *P* = 0.050), so I included percent cover within 25-m radius of the nest and year in logistic regression models for visitation during the nestling stage.

Black-capped vireo nest success was not affected by attentiveness or visitation to nests during incubation because the best-supported logistic regression models were the intercept only models (Table 3.5). During the nestling stage, nest success was related to time on the nest and the number of trips to the nest interacting with percent cover within 25-m radius of the nest (Table 3.5). The probability of a black-capped vireo nest being successful declined as attentiveness increased and amplified as visitation increased during the nestling stage (Figure 3.6A&B).

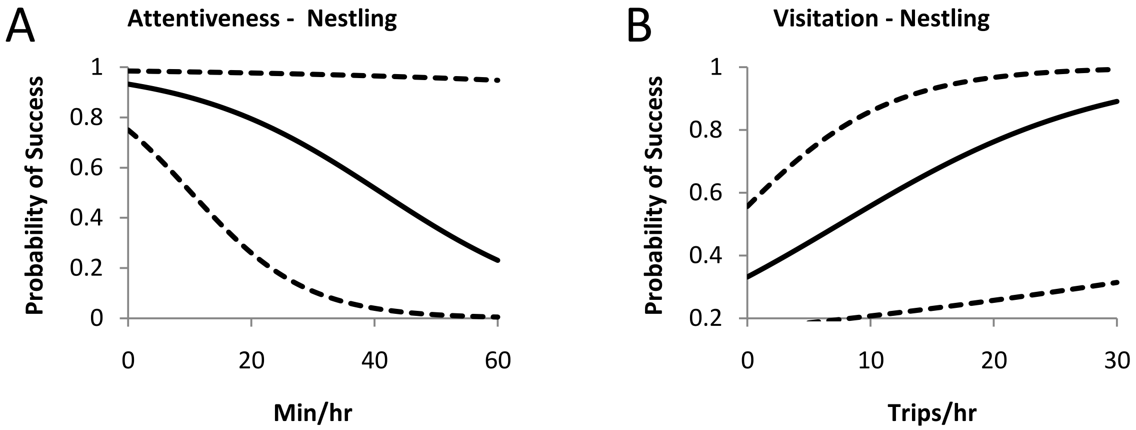

Figure 3.6. Predicted probability (solid line) with 95% confidence intervals (dashed lines) of a nest being successful based on the best (lowest AIC) logistic regression model from nest video observations at black-capped vireo nests in Burnet, Coryell, Kerr, Travis, Val Verde, and Williamson Counties, Texas, 2009–2010. Model equations: A. y = 2.632 – 0.064(min/hr); B. y = -0.700 + 0.160(trips/hr × % cover [standardized at 0.58]).

Table 3.5. Results of binary logistic regression models predicting the probability of success for black-capped vireo nests based on adult activity at the nest observed from nest video recorded in Burnet, Coryell, Kerr, Travis, Val Verde, and Williamson Counties, Texas, 2009–2010.

	Model	K	AIC$_c$	ΔAIC	w_{i}
Incubation					
Attentiveness	intercept only	1	141.51	0.00	0.35
	time on	2	141.72	0.21	0.31
	time on × clutch	2	142.30	0.79	0.23
	time on + time on × clutch	3	143.83	2.32	0.11
Visitation	intercept only	1	141.51	0.00	0.27
	trips × year	2	142.68	1.17	0.15
	trips × clutch + trips × year	3	142.72	1.21	0.15
	trips + trips on × year	3	143.08	1.56	0.12
	trips × clutch	2	143.42	1.90	0.11
	trips	2	143.56	2.04	0.10
	trips+ trips × clutch + trips × year	4	144.88	3.37	0.05
	trips + trips × clutch	3	144.96	3.44	0.05
Nestling					
Attentiveness	time on	2	105.23	0.00	0.38
	time on × clutch	2	105.53	0.30	0.32
	time on + time on × clutch	3	105.76	0.53	0.29
	intercept only	1	112.67	7.44	0.01
Visitation	trips × % cover	2	105.05	0.00	0.25
	trips × clutch + trips × % cover	3	105.61	0.55	0.19
	trips × % cover + trips × year	3	106.46	1.41	0.12
	trips + trips × % cover	3	106.55	1.50	0.12
	trips × clutch + trips × % cover + trips × year	4	106.81	1.76	0.10
	trips + trips × clutch + trips × % cover	4	107.24	2.19	0.08
	trips + trips × % cover + trips × year	4	107.84	2.79	0.06
	trips + trips × clutch + trips × % cover + trips × year	5	108.57	3.52	0.04
	trips + trips × clutch	3	112.65	7.60	0.01
	intercept only	1	112.67	7.62	0.01
	trips	2	112.72	7.67	0.01
	trips × year	2	113.04	7.99	0.00
	trips + trips × clutch, trips × year	4	113.59	8.54	0.00
	trips + trips × % cover + trips × year	4	107.84	2.79	0.06
	trips × clutch + trips × % cover + trips × year	4	106.81	1.76	0.10
	trips + trips × clutch + trips × % cover + trips × year	5	108.57	3.52	0.04

DISCUSSION

The Skutch hypothesis (1949) suggests the risk of nest predation should increase as adult activity at the nest increases. Support for the Skutch hypothesis has been ambiguous, with some studies finding that adult activity increases risk of nest predation (Martin et al. 2000, Muchai and du Plessis 2005) and others not finding the relationship (Roper and Goldstein 1997, Weidinger 2002, Fontaine et al. 2007, Chalfoun and Martin 2010). My results do not support the Skutch hypothesis because visitation did not have a detrimental effect on black-capped vireo nest success. In fact, despite visitation being higher during the nestling stage than during incubation, the probability of a nest succeeding improved as visitation increased in the nestling stage and as male visitation increased during incubation. The Skutch hypothesis also assumes that activity at the nest attracts attention of predators. For this to be true, predators should be diurnal and use visual cues to locate prey. I found that the major predators of black-capped vireo nests were birds and snakes, followed by mammals. All predation events by avian species occurred during daylight hours. However, most of the snake and mammal predation events occurred during crepuscular hours or at night when there are no behavioral cues to assist predators in locating nests. Given the diversity of the black-capped vireo nest-predator assemblage, nest-sites that provide protection from certain nest predators based on vegetation characteristics (e.g. cover) may be difficult to locate (Halupka and Greenley 2009).

In general, black-capped vireo nest behavior did not appear to be affected by the vegetation characteristics I considered. Nest attentiveness during incubation increased, however, as average cover around the nest from 0 to 2 m increased. Based on results from previous studies (Remes 2005, Eggers et al. 2008), I expected longer incubation bouts at more exposed nests where adults may be trying to avoid detection by visual predators. If that were the case, then visitation should be lower at exposed nests as adults would not switch incubation duties as often, which I did not observe. In 2009, video recordings revealed a tendency towards visitation during the nestling stage to increase as percent cover within 25-m radius of the nest increased. Woody cover provides more surface area for foliage-gleaning vireos to locate insects to feed to nestlings. Having more woody cover in the vicinity of the nest could allow vireos to spend less time searching for food, resulting in more food deliveries. This pattern would likely be more pronounced in years when food availability is reduced. I did not directly measure food availability, so I cannot determine if that was the case in 2009.

Although adult activity at black-capped vireo nests does not appear to be influenced much by vegetation characteristics or potential risk of nest predation, adult behavior may influence nest success. Despite nest attentiveness during the nestling stage apparently affecting success negatively, visitation during the nestling stage had a positive effect on nest success. Most visits to the nest during the nestling stage are to feed nestlings, so adults that are able to provide the most food increase chances for successfully fledging young. Nest attentiveness during incubation also affected the probability of success, with female attentiveness negatively affecting and male attentiveness positively affecting nest success. These results are complimentary considering female attentiveness should decline as male attentiveness increases due to sharing incubation duties. The probability of nest success also improved with male visitation during incubation, with visits often being food carries to the incubating female. Males sharing a larger proportion of incubation duties and bringing food to incubating females likely leads to better body condition of females. Adults in good condition can invest more energy into reproductive effort than self-maintenance. These results emphasize the importance of male participation in determining the outcome of nests for species exhibiting bi-parental care.

For many bird species, predation is the leading cause of nest failure (Nice 1957, Ricklefs 1969). Strategies for protecting nests from predation include placing nests where least exposed to predators discovery, active nest defense, and adjusting behavior to compensate for poor nest location (Weidinger 2002, Remes 2005, Eggers et al. 2008). Although black-capped vireos actively defend nests by alarm calling and mobbing predators discovered in the act of predation (personal observation, Grzybowski 1995, Stake and Cimprich 2003), these actions are not known to prevent nest failure. Due to the diverse black-capped vireo nest predator assemblage, managing for vegetation characteristics at nest sites that limit exposure to all types of predators will be difficult; therefore research should be focused on determining what vegetation characteristics provide the best resources for foraging and provisioning young. It will be important to protect and maintain habitat for vireos that provides these resources to ensure successful reproduction, a component necessary for the recovery of this endangered species.

CHAPTER IV

SUMMARY OF MANAGEMENT IMPLICATIONS

Wildlife managers within the black-capped vireo breeding range should be aware that this species could occur in areas that do not fit the current guidelines for suitable habitat, especially if these areas are in close proximity to known large populations of vireos. Otherwise, managers and landowners may inadvertently remove vegetation that is suitable habitat for black-capped vireos because it does not adhere to current habitat descriptions. Due to the diverse black-capped vireo nest predator assemblage, managing for vegetation characteristics at nest sites that limit exposure to all types of predators will be difficult; therefore research should be focused on determining what vegetation characteristics provide the best resources for foraging and provisioning young. It will be important to protect and maintain habitat for vireos that provides these resources to ensure successful reproduction, a component necessary for the recovery of this endangered species. Finally, recognizing woodlands as suitable habitat will allow managers to incorporate these vegetation types into management plans and recommendations for landowner conservation incentive programs.

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APPENDIX A

Bold values denote significance at α = 0.10.

	Incubation						Nestling					
	Avg. cover 0-2 m			% cover w/in 25 m			Avg. cover 0-2 m			% cover w/in 25 m		
	F	df	*P*-value	*F*	df	*P*-value	*F*	df	*P*-value	*F*	df	*P*-value
Attentiveness												
Female	4.988	1	**0.030**	1.501	1	0.226	0.001	1	0.978	0.008	1	0.931
Male	3.644	1	**0.062**	0.001	1	0.982	0.062	1	0.805	0.160	1	0.691
Total	14.018	1	**<0.001**	0.732	1	0.396	0.021	1	0.886	0.075	1	0.786
Visitation												
Female	2.020	1	0.161	<0.001	1	0.992	0.931	1	0.340	0.215	1	0.645
Male	0.311	1	0.580	0.688	1	0.411	0.082	1	0.777	0.056	1	0.814
Total	1.988	1	0.165	0.422	1	0.519	0.646	1	0.426	0.006	1	0.938

APPENDIX B

Bold values denote significance at α = 0.05.

	Incubation						Nestling					
	Avg. cover 0-2 m			% cover w/in 25 m			Avg. cover 0-2 m			% cover w/in 25 m		
	F	df	*P*-value	*F*	df	*P*-value	*F*	df	*P*-value	*F*	df	*P*-value
Attentiveness	0.891	1	0.347	1.330	1	0.251	0.971	1	0.327	0.140	1	0.710
Visitation												
2009	1.979	1	0.165	0.635	1	0.429	1.387	1	0.246	4.102	1	**0.050**
2010	2.728	1	0.106	0.003	1	0.955	1.933	1	0.172	0.020	1	0.889

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