NESTING ECOLOGY AND MULTI-SCALE HABITAT USE OF THE BLACK-CAPPED VIREO

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ABSTRACT

NESTING ECOLOGY AND MULTI-SCALE HABITAT USE OF THE BLACK-CAPPED VIREO

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Ecology and habitat use can vary substantially across a species breeding range. Most of the intensive studies on black-capped vireos have been in central Texas and Oklahoma. However, there is little information about black-capped vireo habitat use in the southern and western region of their breeding range. I monitored black-capped vireo territories and nests in 2009 and 2010 and utilized nest cameras to identify nest predators. I compared habitat used with what was available to the vireos at the landscape, territory and nest-site scale and determined if habitat used was adaptive on the territory and nestsite scale.

From March through July in 2009 and 2010 I territory mapped and monitored 64 Black-capped Vireo territories and 119 nests across 7 study sites. I observed 69 nests with cameras to determine nest predators. Nest success was 18.5% in 2009 and 44.7% in 2010. Both nest depredation and parasitism was >10% higher in 2009 than it was in 2010. Clutch size differed statistically in 2009 (3.4 + 0.09) from clutch size in 2010 (3.8 + 0.09)0.07). There was a large variety of nest predators compared to other areas of the blackcapped vireo's range that has been sampled. The most common nest predators were Brown-headed Cowbirds (n=4), snakes (n=4), and greater roadrunners (n=3). New predators identified that have not previously observed as Black-capped Vireo nest predators included bobcat (Lynx rufus), raccoon (Procyon lotor), Greater Roadrunner (Geococcyx californianus), and the greater arid-land katydid (Neobarrettia spinosa). Black-capped vireos primarily selected riparian areas and slopes of canyons and did not select mesas, low flats, or woodlands. The other areas highly used by BCVIs are the slopes of canyons and drainages, but unlike the riparian areas, slope habitat is widely abundant within the study area. Low woody cover is fundamental for black-capped vireos territories in the Devil's River area, as it is in all other areas of their breeding range; however, mean cover within territories was higher in my study area (70%).

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INTRODUCTION

The study of habitat use describes the way in which an individual or species uses habitats to meet its life history needs (Block and Brennan 1993), and habitat selection refers to a hierarchical process of behavioral responses that may result in the disproportionate use of habitat components to influence survival and fitness of individuals (Hutto 1985, Block and Brennan 1993, Jones 2001). The availability of a component is its accessibility to the consumer and the *selection* of that component is a process in which the consumer actually chooses the component. Usage is said to be selective if components are used disproportionately to their availability (Johnson 1980). Further, these habitat characteristics often vary substantially across the range of a species, which can be due to many factors (Morse 1974, Cody 1978) including: (1) habitat availability (Johnson 2007), (2) predator assemblage (Lima 1993), (3) interspecific competition (Lockwood and Moulton 1994, Piper and Catterall 2003), and (4) brood parasitism (Barber and Martin 1997). The habitat characteristics and environmental factors used by species as cues for selection at the territory scale may differ from those used for selection of nest site (Orians and Wittenberger 1991). Understanding the dynamics of these factors across breeding locations and analyzing settling patterns on different spatial scales (MacArthur and MacArthur 1961) is an essential part of effective management, especially for endangered species.

The presence of individuals in a location is not necessarily positively related to habitat quality (Van Horne 1983, Pulliam 1988, Jones 2001). For example, Misenhelter and Rotenberry (2000) found that sage sparrows (*Amphispiza belli*) in southern California

settled in areas in which they did worse reproductively because of anthropogenic changes to their historical habitat. Many factors may be influencing territory settlement such as population density as it relates to habitat availability (Orians and Wittenberger 1991), presence of other avian species, and conspecific attraction (Campomizzi et al. 2008). These factors may be causing individuals to settle in low quality areas and may be reducing the odds of successful reproduction by these individuals. To determine whether territory and nest-site selection is adaptive for a given species, vegetation measurements and reproductive success must be measured in each vegetation type being used.

The black-capped vireo (BCVI, *Vireo atricapilla*) is a federally endangered migratory songbird (Ratzlaff 1987) with a current known breeding range that extends from central Oklahoma south through Texas to the Mexican states of Nuevo Leon and southwestern Tamaulipas (Graber 1961, Farquhar and Gonzalez 2005, Wilkins et al. 2006). The eastern limit of the BCVI breeding range in Texas follows the line of the Balcones Escarpment (Graber 1961), and small numbers of BCVIs have been observed as far west as Big Bend National Park (Grzybowski 1995). Breeding habitat for BCVI is characterized by patchy distributions of low, scrubby growth made up mostly of deciduous woody shrubs and trees of irregular height (Graber 1961). Black-capped vireos establish territories in areas with high vegetation density between 0 and 2 m (Grzybowski 1995) and build the majority of their cup nests in this height zone (Graber 1961, Wilkins et al. 2006). Because of the BCVI's endangered species status, research is needed on their biology, habitat needs, management, and threats (USFWS 1991).

Surveys and monitoring have been conducted to better understand the breeding ecology and productivity of BCVIs; however, the majority of intensive surveys have occurred in few select locations in the Edwards Plateau region of Texas and in Oklahoma (Wilkins et al. 2006). To date, about 75 percent of the known population in the breeding range is found on four well-surveyed areas: Fort Hood Military Reservation and Kerr Wildlife Management Area (WMA) in Texas, and in two adjacent areas in Oklahoma (Wichita Mountains Wildlife Refuge and Fort Sill Military Reservation). These areas, concentrated in recovery regions 1 and 2 (Fig. 1, USFWS 1996), contain most of the present known breeding population, yet only comprise 1 percent of the total area in the Texas/Oklahoma range of the BCVI (Wilkins et al. 2006). Kerr WMA is the furthest location south and west that has been intensively surveyed (Dufault 2004, Grzybowski et al. 1994).

The few geographical studies that exist for the BCVI suggest that, despite the relatively restricted range of the BCVI compared to that of most North American passerines, habitat selection can vary substantially across their breeding range (Farquhar and Gonzalez 2005, Graber 1961, Grzybowski et al. 1994). Regions 1 and 2, located in the Edwards Plateau, are characterized primarily by oak-juniper (*Quercus-Juniperus*) woodlands and live oak (*Quercus virginiana*) savannahs in the west and are structurally very similar to BCVI habitat in Oklahoma (Graber 1961, Grzybowski et al. 1994). Much of the vegetation suitable for BCVIs across the Mexican breeding sites has been characterized as either Tamaulipan thornscrub or submontane pine-oak chaparral (Farquhar and Gonzalez 2005). Tamaulipan thornscrub is a xeric habitat typically found

Figure 1. Known breeding and wintering ranges for the black-capped vireo with recovery regions as suggested for revision by the Population and Habitat Viability
Assessment Report (USFWS 1996). Ranges are generalized for all known locations since time of listing. Note: Black outlines in the Texas range of the species represent recovery units (Wilkins et al. 2006).





below 1,000 meters where the vegetation is patchy and low-growing (<3 m) as in large areas of west Texas, including Dolan Falls Preserve and Devil's River State Natural Area (SNA) in Val Verde County, Texas (Wilkins et al. 2006).

Very little is currently known about BCVI's ecology and threats in the drier, scrubbier habitat of southwest Texas (region 4, Fig. 1) and central Mexico. It has been asserted that the BCVIs at Kickapoo Caverns State Park in Kinney and Edwards counties may form part of a more extensive metapopulation or series of populations extending southward and westward in canyons traversing from the upper bend of the Rio Grande River, which includes canyons of the Devil's River, where the status of the BCVI is still not well determined (Bryan and Stuart 1990, USFWS 1991, Grzybowski 1995, USFWS). Data collected in region 4 may also be applicable to the ecology of BCVIs in Mexico and will add to our understanding of the ecology of BCVIs and their habitat requirements across their entire range. To efficiently and accurately manage BCVIs in region 4, we must fill the gaps in the current knowledge about their nesting ecology and habitat use. Identification of potentially critical or consistently present habitat conditions can be an essential part of effective management for the species (Grzybowski et al. 1994).

In contrast to the successional vegetation types in regions 1 and 2, the xeric vegetation utilized by BCVIs in region 4 is relatively stable and tends to remain suitable for BCVIs without disturbance by fire or grazing. Cattle and goat overgrazing in fact destroys the low scrubby growth needed for BCVI breeding habitat. It appears that the main threats to BCVIs in the Southwest and Trans-Pecos regions of their breeding range are grazing and browsing animals; however, densities of domestic livestock have

decreased substantially in region 4. Goat numbers, in particular, declined 58 percent in the region from 1987 to 2002 (Wilkins et al. 2006). Because of the lack of information, it is relatively unknown the degree to which these factors (i.e., grazing and browsing animals, nest parasitism) are currently affecting BCVIs in region 4.

Because predation is the major cause of nest failure for many bird species, determining how selection of nest sites relates to nest predation is important to understanding habitat needs, reproduction, and survival of avian species (Martin 1993). Conservation and management efforts to mitigate high nest predation require knowledge of predators and predator-specific management (Thompson and Burhans 2003). However, very little is known about nest predators of BCVIs and almost nothing is known about BCVI nest predators outside of regions 1 and 2. Monitoring of BCVI nests at Fort Hood Military Reservation revealed that snakes and imported fire ants (*Solenopsis invicta*) were the primary predators from 1998 to 2001 (Stake and Cimprich 2003). In the same region and further south at Kerr WMA, Brown-headed cowbirds (*Molothrus ater*, BHCO) and snakes were observed to be the primary predators (Conkling 2010) of BCVI nests in 2008 and 2009. Determining predation rates, as well as primary nest predators in region 4 is another important aspect in understanding black-capped vireo ecology across their breeding range.

Brown-headed cowbird parasitism was widely observed as the primary factor contributing to the low reproductive success of BCVIs at the time of their listing as an endangered species (USFWS 1991). Since listing, the relative abundance of brownheaded cowbirds declined or remained the same in the BCVI's recovery regions 1, 2, and 3 in Texas; however, breeding season brown-headed cowbird abundance has shown a slight to moderate increase in region 4 (Fig. 1, Wilkins et al. 2006). Brood parasitism rates on BCVIs also appear to be correlated with the densities of other more conspicuous host species; this suggests BCVI nests experience higher parasitism rates in areas where populations of more abundant host species (e.g. northern cardinals [*Cardinalis cardinalis*]) have higher densities (Barber and Martin 1997, Wilkins et al. 2006). Farrell et al. (2011) found a positive relationship between parasitism frequency and the abundance of several other individual bird species, suggesting that the abundance of other host species may be useful predictors of parasitism frequency for BCVI. The vegetation structure surrounding the host species' nest has been shown to directly affect the probability of parasitism (Clotfelter 1998, Saunders et al. 2003). Because of local vegetation structure, BCVIs in recovery region 4 may be more or less susceptible to parasitism depending on avian species diversity, composition, and abundance in comparison to regions 1 and 2.

Due to appropriate research and recovery programs, several endangered species such as the bald eagle (*Haliaeetus leucocephalus*), Kirtland's warbler (*Dendroica kirtlandii*), and peregrine falcon (*Falco peregrinus*) have recovered. A combination of actions are required for successful conservation efforts including: 1) research on distribution, population size and trends, ecology and threats; 2) monitoring; 3) identification of a network of key population sources; 4) safeguarding and managing of these sites under a range of governance mechanisms; 5) public awareness and education; and 6) policy interventions at multiple scales (Butchart et al. 2006). My study will contribute many of these required actions by researching the ecology of and the threats to black-capped vireos in an under-studied region of their breeding range and possibly identifying a key breeding site that was not previously acknowledged. My objectives were to (1) describe nesting ecology and nest success, (2) identify the causes of nest failures, (3) quantify habitat use by black-capped vireos at the landscape, territory, and nest-site scales, (4) determine if characteristics of habitat used by BCVIs influence territory success and/or nest success, and (5) use these results to provide management recommendations for BCVIs in the Devil's River area, Texas.

MATERIALS AND METHODS

Study area

My study area was located in Val Verde County, Texas in the Devil's River region on the western edge of the Edwards Plateau. Average rainfall from 1997 to 2008 for the Devil's River area during the BCVI breeding season (March through July) was approximately 5.0 cm, and average mean temperatures ranged from 17.6° Celsius (C) in March to 30.0° C in July (NOAA 2010). The study area encompassed Devil's River State Natural Area (DRSNA) and Dolan Falls Preserve, a 1,942-hectare property owned and managed by The Nature Conservancy. The DRSNA encompasses 8,090 hectares, with mostly unmanaged land. The property has a large population of feral sheep (*Ovis* spp.) and aoudad (*Ammotragus lervia*) and a modest number (30-40; TPWD 2010) of aoudad are killed during public hunts that take place several times a year. There is currently no management of feral sheep on the property. Adjacent properties were undeveloped, recreational, or used for wild game hunts.

The natural plant communities at Devil's River SNA and Dolan Falls Preserve exhibit elements of the mesquite-chaparral of the South Texas Plains, the oak-cedar of the central Edwards Plateau to the east, and the sotol-lechuguilla of the Trans-Pecos to the west (Hedges and Poole 1999). Topographic features of Devil's River SNA include a nearly level plateau that is frayed into high-domed hills and flat-topped, hard scrabble ridges as well as several large drainage systems that cut their way through canyons. Elevation ranges from approximately 632 m at the northeastern park boundary to

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approximately 409 m at the southwestern corner of the property where it connects to Dolan Falls Preserve (Hedges and Poole 1999). Dolan Creek, dry the majority of the year, winds 20.1 km from the north end of Devil's River SNA and exits in the southwestern portion of the park. Dolan Creek then travels through Dolan Falls Preserve where it is contains water year-round, the result of constantly running springs. Topography at Dolan Falls Preserve is similar to the State Natural Area, differing only in the fact that Dolan Falls Preserve contains more property adjacent to the Devil's River.

Hedges and Poole (1999) identified 9 non-grass/herbaceous plant communities at Devil's River SNA: apache plume (*Fallugia_paradoxa*), ashe-juniper-oak (*Juniperus ashei - Quercus* spp.), ceniza (*Leucophyllum frutescens*), guajillo (*Acacia berlandieri*), lechuguilla-sotol (*Agave_lechuguilla - Dasylirion leiophyllum*), mesquite-whitebrush (*Prosopis glandulosa - Aloysia_gratissima*), netleaf hackberry-little walnut (*Celtis reticulata - Juglans microcarpa*), plateau live oak-netleaf hackberry (*Quercus fusiformis - Celtis reticulate*), and sycamore-willow (*Platanus occidentalis - Salix nigra*). Three of these communities, apache plume, netleaf hackberry-little walnut, and sycamore-willow, occur in the dry river wash and stream bed areas. Plant species composition varies between these communities, but all occur in the gravely stream beds with scattered woody vegetation. Therefore, I combined these communities for my purposes and call them "wash" communities.

Three plant communities occur on dry, rocky slopes: ashe juniper-oak, guajillo, and lechuguilla-sotol. Different plant species are dominant in these communities, but all include similar woody species, including Texas persimmon (*Diospyros texana*). I combined these communities and referred to them as "slope". The ashe juniper-oak community not only occurs on slopes, but also along dry creeks and drainages where the oaks are much more dominant. Because vegetation cover and oak dominance are considerably different along these drainages and creeks, I classified them separately as "riparian". The ashe juniper-oak community also occurs in the deeper soils of the flat upland areas of the study area which I qualified as "mesa". The two communities that occur on the low flat and gently sloping areas of lower elevation are ceniza and mesquitewhitebrush. Both of these communities contain a variety of shrubs (e.g., Texas persimmon, juniper spp.). I combined these and called them the "low flat" communities. The plateau live oak-netleaf hackberry series is the only forest community occurring at Devils River SNA. This evergreen to mostly deciduous woodland is limited in occurrence to areas with deeper soils. I referred to these areas as the "woodland" vegetation community.

Site selection

My sampling frame included Devils River SNA and Dolan Falls Preserve. Because there was little information about what habitat BCVIs are using within the sampling frame, I sampled randomly across the study area. I used ArcGIS 9.3 to create a grid comprised of 1 km² grid cells that covered my study area and then used Hawth's tools (Beyer 1994) to randomly select grid cells. I randomly selected 4 cells in 2009 and 3 in 2010. I visited each grid cell no earlier than local sunrise and no later than 4 hours after sunrise 2-3 times during the early part of the breeding season (March and April), each visit was at least 4 days apart. I systematically walked through each of the 1 km²

grid cells, concentrating on those areas with enough vegetation to support BCVIs (i.e., cover >20%) and walking within 200 m of all locations within the grid cells. If I detected a BCVI singing male, I marked its coordinates with a Garmin Rino 120 global positioning system unit (GPS). If there were no detections of BCVIs after 3 visits then I visited the cell only 1 time a week for a month to be certain that no BCVIs established territories in that cell. I randomly selected a new grid cell to replace the cells that had no detections after 3 visits. My individual study sites were contiguous areas within my study area that occurred in and around the cells that I had randomly selected and also contained BCVIs. I delineated my study sites once I located all the territories that I was logistically capable of monitoring. Study sites included areas near monitored territories that were also searched but within which no BCVIs were detected. Size of the study site depended upon spacing of territories and the degree of difficulty of monitoring the territories at that particular site. I had 4 study sites in 2009, 2 along dry Dolan Creek, 1 in East Canyon, and 1 in Leon Springs Canyon. I had 3 study sites in 2010, 2 along Dolan Creek and 1 in northern Rough Canyon.

Territory mapping and nest searching

I territory mapped adult male BCVIs and searched for BCVI nests between 15 March and 15 July. Once I had the general locations of the vireos, I returned every 2 to 5 days to territory map the singing locations of the males. I mapped territories by recording 3 to 6 GPS location points during the first 4 visits. Following the 4th visit, I recorded \geq 3 territory points on every other visit. I considered 15 the minimum number of points to identify a territory. After uploading territory points into ArcGIS, I used Hawth's tools to create minimum convex polygons to spatially represent territories used by each male I monitored. I located nests using behavioral cues that signify breeding of adults (i.e., alarm calls, carrying nest material, carrying food, males singing on the nest). I marked nests with flagging \geq 15 m away and recorded locations using GPS units with accuracy of \leq 10 m with Universal Transverse Mercator coordinates.

I monitored nests every 2 to 4 days until the nestlings fledged or the nest failed. At each visit to the nest, I recorded the date, time, contents of the nest, and general activity at the nest (e.g., incubation, brooding, adult shradding). I promptly addled any cowbird eggs and/or removed cowbird nestlings at the time of their discovery and recorded the parasitism. I did not remove cowbird eggs from the nests because studies have shown that the presence of either real or artificial cowbird eggs deters future parasitism (Ortega et al. 1993). I placed a numbered aluminum band on each nestling 7 to 9 days after hatching as well as a unique combination of plastic color bands in order to identify individuals after fledging. If I thought a nest had fledged, I searched the territory for fledglings every 3-4 days for 2 weeks or until a fledgling was located to be more certain that the nest did in fact fledge. I considered a nest successful if at least one young fledged.

I used nest cameras (see below) to help classify causes of nest failure as: (1) parasitized, (2) abandoned, or (3) predated. I categorized nests as parasitized if there was at least one cowbird egg present at any stage of the nest. I counted all parasitized nests as failures because parasitized BCVI nests fledge only 0.2 to 0.9 fledglings per nest (Grzybowski 1995, Tazik 1991, Wilkins et al. 2006). I classified nests as abandoned if at least one egg was laid and there was no further attendance by an adult.

Nest predators

I used camera units in 2009 and 2010 to determine nest fate. I used Rainbow Weatherproof IR Bullet cameras (Costa Mesa, CA) and Digital Event Recorders ([DVR], Detection Dynamics, Austin, TX) with high capacity SD cards to monitor BCVI nests 24 hours a day. Cameras were powered by a 12v 26 ah battery (Batteries Plus, Hartland, WI) and supplemented by a 20 - watt solar panel (Suntech, San Francisco, CA). I kept the cameras evenly distributed between each of the vegetation communities (i.e., low flats, slopes, riparian, washes) where I located BCVI nests and each of the study sites monitored each year. I put up the cameras as early as possible in the nesting cycle, but only after incubation had begun to avoid forced abandonment of the nest. After I placed the camera, I observed the nest until the adults returned to normal behavior and removed the camera if the adults did not return to normal behavior within 30 minutes. Once the nest fledged or failed, I randomly chose a new nest location in the same vegetation community to deploy the camera in order to observe as many nest depredations as possible.

Habitat use

I employ the term *habitat use* and not *habitat selection* in this section because my study focused on the distributional aspects of BCVIs within my sampling frame and not the behavioral aspect.

Landscape-scale use.--- In 2009, I studied BCVI nest-site and territory use at a restricted number of locations with my study area. However, this did not explain how

BCVIs were using habitat across the larger landscape of my study area. In 2010 I added the landscape scale aspect of BCVI habitat use to my study to better understand the distribution of BCVIs across my sampling frame. I observed black-capped vireo territories in 5 general areas throughout the sampling frame: on steep slopes adjacent to Dolan Creek, in the wash area of dry Dolan Creek, in riparian areas along Dolan Creek and canyon drainages, on rocky canyon slopes, and in low flat areas. Infrequently, I detected BCVIs on the mesas.

To determine which vegetation communities BCVIs were using at the landscape scale, I relied on point counts of BCVIs that were conducted from 8 April to 30 June within my study area in 2010. Five minute point counts began no earlier than local sunrise and occurred no later than 13:00. I did not survey during inclement weather or when winds exceeded 5.4 m/s. I laid a 300 m grid over my study area using ArcGIS and surveyed 652 points one time across 7,471 ha within my study area. If I detected a black-capped vireo during the 5 minute point count, I recorded its distance and direction from the observer to the detected BCVI, as well as vegetation community being used (i.e., low flat, slope, canyon slope, riparian, wash, mesa). Distance, direction, and vegetation community were also recorded for BCVIs detected in between points and if I could accurately determine that they were not the same birds detected at a point.

I determined the proportion of the different vegetation communities available to BCVIs in the study area by performing a supervised classification using a maximum likelihood algorithm in ArcGIS 9.3. I used 2008 National Agriculture Imagery Program (NAIP, 1 m resolution) imagery, soil data collected 1997 to 2009 by the U.S. Department of Agriculture, and 10 m resolution 2005 National Elevation Data (NED) as my input rasters. I created a signature file by delineating areas based on my on-the-ground knowledge of the locations of the vegetation communities that I identified previously (i.e., low flat, slope, riparian, wash, woodland, mesa, river). I identified these areas using ArcGIS across the study area in a 25 m resolution output raster file based on soil type, elevation, slope, and vegetation cover. I delineated the area that surrounded the points that were visited during the point count by placing a 150 m circular buffer around the points. This distance was based on maximum distance of sound attenuation in the area. I then calculated the proportions of each vegetation community available to the BCVIs only within the buffered area that surrounded the visited points. I then calculated proportion of the area used by BCVIs as the number of BCVIs found in each vegetation communities during point counts divided by the total number of BCVIs detected, and compare it with the proportion available for use.

*Territory-scale habitat use and productivity.---*To quantify habitat used on a territory scale, I used ArcGIS 9.3 to generate 20 m gridded points within each mapped territory and 80 m gridded points within each study site. In the field, I used a GPS unit to locate the gridded points. Once I arrived at the point within 5 m accuracy, I stopped and sampled that exact point location using a 2.5 m measuring pole. I recorded the presence of woody cover (Y/N). If woody cover was detected (i.e., trees, shrubs, snags, brush piles), I recorded the dominant plant species. I then recorded the height at which the plant's foliage or branch cover began at the bottom (start height) and where its foliage cover ended at the top (max height) to the nearest decimeter. I recorded the same

information for any secondary woody species if present. I calculated vegetation cover by dividing the number of times a woody species was present at a point by the number of gridded points we visited within that territory. To determine if plant diversity, vegetation cover, and/or vegetation height affected territory outcome, I statistically compared these parameters, described below, in territories that were successful with territories that did not fledge young.

Nest-scale habitat use and productivity.---After a nest had either fledged or failed I measured nest height (ground to rim), substrate height, and distance of the nest to the nearest edge (outside of rim of nest to the nearest leafy edge), all to the nearest 0.1 meter. I measured foliage cover around the nest by estimating the proportion of cover of 0.10 m squares on a 2 m coverboard that was observed from 7 m away in each cardinal direction. I also recorded substrate species, topographic location of the nest (i.e., riparian, slope, low flat, wash), and degree of slope at the nest. If a nest occurred on a slope, I also recorded aspect. I then used these nest site characteristics to determine their effect on nest success, depredation, and parasitism.

I determined if nest substrates were being used in proportion to their availability by comparing the counts of substrates used with the amount available to vireos within their territories at each study site. To determine if BCVIs were using areas with more or less vegetation cover around their nests compared to what was available within their territories, I performed an unsupervised classification in ArcGIS 9.3. I created 20 m diameter circles around nests and at points randomly selected within the same territory. The 1 m raster cells within the circles were classified as either cover or no cover according to NAIP imagery and percent cover was subsequently calculated for each of the used and not used circles.

Statistical analyses

I evaluated nest success using the Mayfield method (1961, 1975) and program MARK to calculate daily nest survival. I only used data from nests in which eggs and/or nestlings were observed in calculating daily survival rate. I used SAS 9.2 (SAS Institute, Cary, NC, USA) for statistical analyses. I calculated mean and standard error by year for clutch size and host eggs hatched. I performed chi-square analyses to determine if percent parasitism, percent depredation, or percent nest success was different between years.

*Landscape-scale use.---*I descriptively compared habitat used with the proportion available at the landscape scale. I calculated proportion used by dividing the total number of times a BCVI was detected in a particular vegetation community by the total number of BCVI detections during point counts. I calculated proportion of vegetation community available by dividing the amount of each vegetation community that was determined by the supervised classification by the total cells classified within the area where the point counts were conducted in 2010.

*Territory-scale habitat use and productivity.---*I calculated vegetation species diversity using the Shannon-Wiener Index (Weaver and Shannon 1949) within territories and study sites. To take into account the potentially large degree of variance in vegetation measurements taken in territories and within study sites, I tested for

homogeneity of variance using two-sampled *t*-tests for variance in SAS 9.2. I used two sample *t*-tests assuming unequal variance (Zar 1999:122-129) to compare vegetation used and vegetation available (i.e., height start, max height, cover, and species diversity) at each study site. I also used two-sample *t*-tests assuming equal variance (Zar 1999:122-129) to compare successful territories with territories that did not fledge young. I considered the differences to be statistically different if the *P*-value was ≤ 0.05 .

*Nest-scale habitat use and productivity.---*I calculated mean and standard deviation for each measurement taken at nests. To determine if nest substrate use is equal proportionately to its availability within the territories I used the equation presented by Zar (1999:555-557) for comparing two proportions:

$$Z_{c} = \frac{|\hat{p}_{1} - \hat{p}_{2}| - \frac{1}{2} \left(\frac{1}{n_{1}} + \frac{1}{n_{2}}\right)}{\sqrt{\frac{\overline{p}\overline{q}}{n_{1}} + \frac{\overline{p}\overline{q}}{n_{2}}}}$$

Proportion of substrate used was compared to the proportion of that substrate available within the territories at each study site. Proportion of substrate used was calculated by dividing number of times a nest substrate was used at a study site by the total nests at the study site. Proportion of substrate available was determined by dividing the number of times a substrate was detected at a point during territory-scale vegetation measurements, using only points falling within territories, by total grid points visited within territories. To determine the difference in cover around nests compared with random locations within the territory, I used a paired *t*-test to compare the average cover around each nest with mean cover at a random point within the same territory.

I performed 3 logistic regression analyses to determine factors that influenced nest success, parasitism, and depredation. The dependent variable was nest fate (0=failed, 1=fledged; 0=not parasitize, 1=parasitized; 0=not depredated, 1=depredated). Explanatory variables included nest height, substrate (coded as dummy variable [1,0] Vasey shin oak, Texas mountain laurel, juniper spp., Texas Persimmon), substrate height, presence of an overstory, distance of nest to the nearest edge, slope, mean foliage cover at nest, and topographic location of the nest (coded as a dummy variable [1,0] low flat, riparian, slope, wash). The four nest substrates included in the analyses were the most abundantly used substrates in the study area. In addition to each variable being included in the regression, I crossed year with each explanatory variable to determine if the influence of each explanatory variable on nest fate was consistent between 2009 and 2010. I entered variables in a forward stepwise selection model if P < 0.20 and removed if P > 0.10 to determine which were associated with the probability of nest success, parasitism, or depredation (Pearce and Ferrier 2000). I also removed variables with low sample sizes (<10 occurrences in a year). I used odds ratios to examine explanatory variable effect and effect size of those variables that remained in the model (Agresti 1996: 107-108).

RESULTS

Nesting ecology and nest success

I located and monitored 81 and 38 nests in 2009 and 2010, respectively. The earliest date of incubation was 7 April 2010, despite early nest building in mid-March in 2009. The latest date a nest was known to be active was 14 July 2010. Mean of the monthly rainfall totals averaged 3.6 cm/month (SD = 2.9 cm) in 2009, 1.1 cm/month below normal, and 7.0 cm above normal in 2010, averaging 11.7 cm/month (SD = 10.1 cm) from March to July. In 2009, the average daily temperatures were above normal ranging from 18.6° C in March to 32.2° C in July. In 2010, the mean temperature ranged from 16.2° C in March to 29.4° C in June (NOAA 2010).

Of the 119 nests located, 26 (22%) were located in low flat areas, 35 (29%) in riparian areas, 37 (31%) on slopes, and 21 (18%) in wash areas. Clutch size in 2009 (3.4 \pm 0.09) was different from mean clutch size in 2010 (3.8 \pm 0.07; t_{117} = -3.278, P = 0.0014). Proportion of BCVI eggs that hatched were not different between years (t_{62} = -0.697, P = 0.4881; Table 1). Proportion of nests parasitized and depredated varied between years by 10.7% and 11.8%, respectively. These differences between years were not statistically different according to the chi-square test for parasitism (χ^2 = 1.3324, P = 0.2484, df = 1) or depredation (χ^2 = 1.4250, P = 0.2326, df = 1). The first record of BHCO parasitism in 2009 occurred 21 April. In 2010, nest parasitism was not recorded until 3 May and regular parasitism of nests did not begin to occur until the end of May. I did not observe bronzed cowbird (*Molothrus aeneus*) parasitism in either year. Table 1. Clutch size and host eggs hatched (mean \pm SE) and *t*-statistics for black-capped

	2009	2010	Р	df
Clutch Size	3.4 ± 0.09	3.8 ± 0.07	< 0.001	117
BCVI Eggs Hatched	0.84 ± 0.04	0.88 ± 0.04	0.4881	62

vireo nests in the Devil's River area during 2009 and 2010.

Nest success also varied statistically between the two years, increasing from only 18.5% in 2009 to 44.7% in 2010 ($\chi^2 = 9.0439$, P = 0.0026, df = 1). Mayfield estimates of daily survival rate ($\overline{X} \pm SE$) for incubation and nestling nest periods were 0.947 \pm 0.007 (95% CI 0.931-0.959) and 0.968 \pm 0.007 (95% CI 0.950-0.980) in 2009 and 2010, respectively. Nest success was higher in 2010, primarily because nest success was higher in the first half of the breeding season (Fig. 2). In 2009, one monitored pair attempted a second brood that subsequently failed. Six monitored territories attempted second broods in 2010 and 2 of those fledged young. An additional second brood attempt was found in a territory that had not been previously monitored (male feeding fledgling while also building new nest), but was later parasitized and abandoned.

Causes of nest failure

Nest depredation was the leading cause of nest failure in 2009 and 2010 followed by parasitism (Fig. 3). Other causes of nest failure were abandonment, nest falling down because of poor construction, eggs not hatching, and destruction by flooding. Both occasions of the nest falling down and eggs not hatching occurred in 2009 and the nest failing because of flooding occurred in 2010.

I recorded nest video at 43 nests in 2009 and 26 nests in 2010. Cameras identified 20 depredation events and I was able to identify 10 predator species (Table 2). Of the 20 depredations caught on video, 7 (35%) were in the incubation stage of the nest cycle and 13 (65%) were in the nestling stage. Eight depredations took place at night and 12 took place during daylight hours. Most snake depredations took place at night, all avian depredations took place during the day, and mammal depredations were mainly

Figure 2. Proportion of nests that fledged young to the date of initiation across the breeding season in 2009 compared to 2010 in the Devil's River area.


Figure 3. Percentage of black-capped vireo nests that failed by cause of failure in 2009 and 2010 in the Devil's River area.



Table 2. Count of nest predators identified depredating black-capped vireo nests in the

Predator	2009	2010	Total
Ants	2	0	2
Brown-headed cowbird (Molothrus ater)	4	0	4
Bobcat (<i>Lynx rufus</i>)	0	1	1
Gray fox (Urocyon cinereoargenteus)	2	0	2
Greater arid-land katydid (Neobarrettia spinosa)	0	1	1
Raccoon (<i>Procyon lotor</i>)	0	1	1
Ringtail (Bassariscus astutus)	1	0	1
Greater roadrunner (Geococcyx californianus)	2	1	3
Western scrub-jay (Aphelocoma californica)	1	0	1
Snakes	2	2	4

Devil's River area for 2009 and 2010.

crepuscular except for the ringtail depredation which occurred at night. The species depredating BCVI nests most often were brown-headed cowbirds (n = 4) and snakes (n = 4). Brown-headed cowbirds were only recorded depredating nests in 2009. Three snakes were identified to species level, 2 Baird's rat snakes (*Elaphe Bairdi*) and 1 Trans-Pecos rat snake (*Bogertohis subocularis*). Avian predators accounted for 40% (n = 8) of nest depredation events caught on video. Insects (ants and greater arid-land katydid [*Neobarrettia spinosa*]) accounted for 15%. (n = 3) of depredation events recorded and all occurred during the nestling stage. Katydids were only observed in the study area in 2010 and one pulled a nestling from the nest at night after startling the adult female and causing her to flush off the nest. Mammals were identified as the nest predator 25% of the time (n = 5). All 5 mammal depredation events occurred on nests within riparian areas. All other predator species were distributed across all 4 vegetation communities.

Habitat use

Landscape-scale use.---Three hundred and five BCVI locations were recorded during point counts in 2010. BCVIs detected were located primarily in the riparian areas (47%) and on slopes (46%). Approximately 5% of the BCVIs detected were in low flat areas, and 3% were on the mesas.

Subsequent comparisons of the supervised classification output map with NAIP imagery and topographic maps, as well as my knowledge of habitat within the study area, indicated that the classification had an overall accuracy of roughly 80%. The majority of the error was due to underestimation of riparian areas. The supervised classification

created 403,587 raster pixels with 25 m resolution (Fig. 4). The dominant vegetation community was the canyon slope, comprising 52% of the delineated area, riparian (17%), low flat (11%), woodland (1%), and water (<1%). Riparian habitat is the only habitat used more than its availability (Fig. 5) in areas where point counts were conducted within the study area. Slope habitat is used approximately equal to its availability while mesa and low flat habitat is used less than available within the study area (Fig. 5).

Territory-scale habitat use and productivity.---Cover within used territories (n = 64) ranged from 40% to 100% with a mean cover (\pm SD) of 70% \pm 7%. Cover in study sites ($62\% \pm 12\%$) was not significantly different (t = 1.993, P = 0.093, df = 6) from cover within territories (Fig. 6). When all study sites were pooled, mean minimum height the vegetation cover starts from the ground within the territories was 0.5 ± 0.2 m and mean maximum height of the vegetation was 1.5 ± 0.4 m. When the minimum height vegetation cover starts from the ground was compared by study site (Fig. 7), only 2 of the 7 study sites showed territories having significantly shorter start heights than the vegetation available. Mean maximum height of vegetation also differed significantly in 2 of the 7 study sites (Fig. 8). Vegetation species diversity within territories ranged from H = 1.49 to 3.78, with a mean diversity of $H = 2.60 \pm 0.44$ and was lower than species diversity in areas available but not used by BCVIs within the study site ($H = 3.37 \pm 0.22$, P < 0.0001).

In 2009, 11 of 33 territories (33.3%) with known productivity fledged at least one young. In 2010, the proportion of successful territories was nearly double with 16 of 24 territories (66.7%) fledging young. Because productivity was different in 2009 and 2010,

Figure 4. A zoomed in view of a portion of the study area comparing NAIP imagery (above) with the supervised classification (below). The blue stars represent BCVIs detected during the 2010 point counts.



Figure 5. Percent of habitat used by black-capped vireos, determined by point counts conducted in 2010, in the study area compared to the percent of the habitat available.



Figure 6. Proportion of vegetation cover within the study site (S) and within the blackcapped vireo territories (T) in the Devil's River area in 2009 and 2010.



Study Site (S) vs. Territory

Figure 7. Height vegetation starts from the ground within the study site (S) and within the black-capped vireo territories (T) at each study site in the Devil's River area in 2009 and 2010.



Study Site (S) vs. Territory

Figure 8. Maximum height of vegetation within the study site (S) and within the blackcapped vireo territories (T) at each study site in the Devil's River area in 2009 and 2010.



Study Site (S) vs. Territory

I analyzed each year separately when comparing territory success. Vegetation cover in territories that were successful was not different from territories that were not successful in 2009 (t = 1.153 P = 0.2577, df = 31) or 2010 (t = -0.831, P = 0.4147, df = 22).

Mean height of vegetation did not differ between successful and unsuccessful territories in 2009 (t = 0.203, P = 0.8402, df = 31); however, mean vegetation height was higher (t = -2.251, P = 0.0347, df = 22) in successful territories (1.8 ± 0.4 m) than in those territories that did not fledge young (1.4 ± 0.4 m) in 2010 (Fig. 9). Mean height from the ground that foliage starts was not different in territories that fledged young or did not fledge young in 2009 (t = 0.920, P = 0.3646, df = 31) or 2010 (t = -0.313, P = 0.07575, df = 22). Vegetation diversity was not different between successful and unsuccessful territories in 2009 (t = -0.305, P = 0.7623, df = 31) or in 2010 (t = -1.415, P = 0.1710, df = 22; Fig. 10).

Nest-scale habitat use and productivity.---I measured vegetation at 119 nests in 2009 and 2010. Nests were located in 13 different substrates across the study area (Table 3). Four species made up 88% (n = 105) of the substrates used by Black-capped Vireos for nesting: juniper spp. (n = 23; 19.3%), Texas mountain laurel (n = 34; 28.6%), Texas persimmon (n = 26; 21.8%), and Vasey shin oak (n = 22; 18.5%). The proportion of total use of nest substrate also changed throughout the breeding season. Mountain laurel and juniper were the substrates most used during the early part of the season (38% and 25%) and shin oak was used proportionately more (33%) than others later in the season. Use of Texas persimmon increased considerably from the early part of the season to the middle (15% to 30%; Fig. 11). Three of the four nest substrates used most often were also used

Figure 9. Maximum height of vegetation within the black-capped vireo territories that fledged young (1) and did not fledge young (0) during 2009 and 2010 in the Devil's River area.



Figure 10. Vegetation species diversity (H) in black-capped vireo territories that were successful (1) and not successful (0) in 2009 and 2010 in the Devil's River area.



Common Name	Scientific Name	Count
Agarita	Berberis trifoliate	1
Evergreen Sumac	Rhus virens	3
Gum Bumelia	Sideroxylon lanuginosum	2
Juniper	Juniperus spp.	23
Little Walnut	Juglans microcarpa	1
Mexican Buckeye	Ungnadia speciosa	1
Texas Mountain Laurel	Sophora secundiflora	34
Netleaf Foresteria	Forestiera reticulate	2
Plateau Live Oak	Quercus fusiformis	1
Sycamore	Platanus occidentalis	1
Texas Colubrina	Colubrina texensis	1
Texas Persimmon	Diospyros texana	26
Vasey Shin Oak	Quercus pungens	22
Unknown		1

and 2010.

Figure 11. Percentage of nest substrates used by black-capped vireos in the Devil's River area during the early (days 1-25), middle (days 26-50), and late (days 51-76) periods of the 2009 and 2010 breeding seasons.



consistently more than they were available within the territories. Vasey shin oak was consistently used 3 to 25 times more than it was available and was selected ahead of other species in the canyons where it was widely available (Table 4). Juniper was used 2 to 6 times more than it was available at 4 of the 7 study sites (Table 4). Texas mountain laurel was used more than it was available in all study sites and Texas Persimmon was used more than available in 6 of the 7 study sites (Table 4). The difference between used and available for mountain laurel and Texas persimmon was even greater in study sites that ran along dry Dolan Creek (i.e., study sites 1, 3, 5, and 6) and where shin oak was not widely available for use by the vireos.

Mean nest substrate height ($\overline{X} \pm SD$) was 3.0 ± 1.4 m (range = 0.6 – 8.0). Mean nest height was 1.1 ± 0.5 m (range = 0.4 - 3.1). Mean distance between nest and edge of vegetation clump in which the nest was located was 1.8 ± 2.9 m (range = 0 – 25.0). Mean cover from 0.5 – 1.5 m as measured by the coverboard from 7 m was 85.1% ± 10.5%. I only used cover measurements from 0.5 – 1.5 m because that is where the vast majority of the nests were located, as mentioned above. Of the 119 nests, 51% (n = 61) had no overstory and 49% (n = 58) had an overstory. Nests built in slope habitat (n = 37) had a mean slope of 21° ± 9° (range=7° – 45°). Nests most often occurred on slopes with a northerly aspect (32.8%) and least often on slopes with southwestern and southeastern aspects (Table 5). Vegetation cover around nests ($62 \pm 27\%$) did not differ statistically (t= 1.178, P = 0.2418, df = 100) from cover in randomly selected locations (58 ± 29%) within the territories. Table 4. Percent of nest substrate used and available within BCVI territories at dry Dolan

Creek study sites and canyon study sites. Bold percentages denote statistical

	Dry Creek Study Sites				Canyon Study Sites			
Substrate	1	3	5	6	2	4	7	
Juniper spp.								
used	12.5%	29.0%	18.2%	6.7%	38.5%	15.4%	16.7%	
available	13.9%	13.0%	3.0%	15.7%	14.4%	5.3%	18.0%	
Mountain								
laurel								
used	50.0%	32.3%	36.4%	46.7%	7.7%	7.7%	8.3%	
available	11.4%	7.8%	12.1%	6.1%	2.7%	4.2%	5.4%	
Texas								
persimmon								
used	31.3%	16.1%	45.5%	40.0%	7.7%	15.4%	8.3%	
available	10.8%	9.3%	5.3%	16.4%	9.7%	3.4%	7.9%	
V. shin oak								
used	6.3%	6.5%	0.0%	0.0%	30.8%	38.5%	58.3%	
available	0.0%	1.9%	1.5%	0.0%	2.8%	1.5%	10.7%	

Table 5. The aspect associated with BCVI nests that occurred on slopes in the

Aspect	Count
North	19
South	11
Northeast	8
East	7
Northwest	6
West	4
Southwest	2
Southeast	1

Devil's River area in 2009 and 2010.

The logistic regression included 119 nests found in 2009 and 2010. I removed low flat as an explanatory variable because there were only 4 nests located in low flat areas in 2010 and all failed. Besides the difference between years, higher nest success was associated with riparian areas ($B = 0.5629 \pm 0.2744$, P = 0.0402); however, the odds ratio confidence interval overlapped one (90% CIs, 0.13-1.04), indicating a lack of evidence for effects. There were several variables associated with probability of parasitism by BHCOs across both years (Table 6). For every 1 m increase in nest height the probability of parasitism increased by 7.6 times (odds ratio = 7.60; 90% CI = 2.70 -21.40). Percent cover around the nest was also positively associated with likelihood of parasitism ($B = 0.0574 \pm 0.245$, P = 0.0193); probability of parasitism increased by 6% (odds ratio = 1.06; 90% CI = 1.02 - 1.10) for every 1 percent increase in cover. Nests with an overstory were 58% (Odds ratio 0.42; 90% CI 0.20 - 0.87) less likely to be parasitized than those without an overstory (Table 6). Nests were 21% (90% CI = 0.65 -0.97) less likely to be parasitized with every 1 m increase in distance to the edge of the vegetation clump (Table 6). None of the explanatory variables were associated with the probability of nest depredation.

Table 6. Descriptive statistics and logistic regression results for habitat variables measured at black-capped vireo nests that were

	Descriptive Statistics			Logistic Regression					
		2009		2010					
	me	an \pm SD	mea	$m \pm SD$			90% Confidence	Wald	
				Not		Odds			
Habitat Variable	Parasitzed	Not Parasitized	Parasitized	Parasitized	Coeff. (B) \pm SE	ratio ^a	Interval ^b	statistic	P-value
Nest substrate									
v. shin oak					0.3919 ± 0.3042	2.19	0.81 - 5.96	1.660	0.1976
Overstory					-0.4346 ± 0.2202	0.42	0.20 - 0.87	3.896	0.0484
% Cover	86 ± 9	83 ± 12	89 ± 10	88 ± 9	0.0574 ± 0.0245	1.06	1.02 - 1.10	5.476	0.0193
Nest Height (m)	1.3 ± 0.5	1.1 ± 0.5	1.1 ± 0.4	0.9 ± 0.4	2.0279 ± 0.6296	7.60	2.70 - 21.40	10.373	0.0013
Distance to edge (m)	1.3 ± 1.2	1.4 ± 2.4	2.3 ± 2.1	2.8 ± 4.6	-0.2309 ± 0.1207	0.79	0.65 - 0.97	3.659	0.0558

parasitized (n=40) and not parasitized (n=79) in 2009 and 2010 in the Devil's River area.

^aOdds ratios >1 indicate positive relationship; <1 indicate negative relationship.

^bConfidence intervals not including 1 indicate evidence of effects.

DISCUSSION

There were substantial differences in vegetation used by BCVIs in the Devil's River area compared to other areas in their breeding range in central Texas and Oklahoma. This is likely due to the effects of the shallow soils present in southwest Texas that produce a stunted climax vegetation community (Hedges and Poole 1999). Cover within territories was higher ($70\% \pm 7\%$) than previous measurements taken in other parts of the BCVIs range (30 - 50%; Grzybowski 1995, Bailey et al. 2007). Bailey et al. (2007) showed that areas of high woody cover at Fort Hood Military Reservation in central Texas consist of older vegetation that grows more vertically than horizontally. The effect of this is less cover for BCVIs in the lower height zone. Because vegetation in southwest Texas does not grow more vertically than horizontally over time, vegetation cover is maintained close to the ground which is the consistent characteristic of vegetation in BCVI territories across their range.

Bailey and Thompson (2007) also found that BCVI nest patch use decreased with increasing percent woody cover, and BCVIs were 283% more likely to nest in deciduous substrates than in ashe juniper at Fort Hood Military Reservation. In my study area, BCVIs used nest sites with a wide variety of cover ($62\% \pm 27\%$). No difference was detected in the cover around nest points and non-nest points within the same territory. Black-capped vireos in the Devil's River area also used juniper as a nest substrate proportionately more than it is available to them which is contradictory to previously published literature (Grzybowski et al. 1986, Grzybowski 1995, Bailey and Thompson 2007). Texas mountain laurel has not been listed as a nest substrate of BCVIs in any previously published literature; however, BCVIs used Texas mountain laurel more than any other substrate in the Devils River area and used it the most, proportionately to other substrates, during the early breeding season. The information my study found about BCVI nest-site selection indicated that they are using other criteria to select for nest locations in the Devil's River area than they are using in central Texas and Oklahoma.

Black-capped vireo nesting ecology in southwest Texas is similar in many ways to their nesting ecology in other areas of their range. Average clutch size (3-4) is the same as recorded in Oklahoma and central Texas (Graber 1961, Grzybowski 1995). Nest building begins earlier in the Devil's River area, but incubation begins at approximately the same time as other areas in central Texas. Final nesting attempts cease earlier in the season in the Devil's River area than other areas of their range (Grzybowski 1995, Pope pers. comm). Heights of nests (1.1 m) are also similar to those in other areas of their range (1.0 m, Graber 1961, Grzybowski 1995). Low growing, woody cover is fundamental for BCVI territories in the Devil's River area, as it is in all other areas of their breeding range (Grzybowski et al.1994, Wilkins et al. 2006, Bailey and Thompson 2007).

Productivity of Black-capped Vireos in the Devils River area appeared to be heavily influenced by weather, particularly precipitation, before and during the breeding season. Other studies of avian productivity have indicated increased rainfall during the breeding season directly affects avian populations in semi-arid regions (Bolger et al. 2005, Djerdali et al. 2008). Many studies indicated that food supply was the main cause of increased nest success when precipitation increased (Nott et al. 2002, Illera and Diaz 2006). However, Coe and Rotenberry (2003) showed that supplying water to Blackthroated Sparrows (*Amphispiza bilineata*) increased clutch size independent of food availability. The increase in mean clutch size in 2010 may have been caused by one or both of these factors, both relating to precipitation.

There is a diverse assemblage of BCVI nest predators in the Devils River region in comparison to other locations where predators have been identified in the past (Stake and Cimprich 2003, Conkling 2010). New predators identified that have not previously observed as BCVI nest predators included bobcat (*Lynx rufus*), raccoon (*Procyon lotor*), greater roadrunner (*Geococcyx californianus*), and the greater arid-land katydid (*Neobarrettia spinosa*). Avian predators (i.e., BHCO, greater roadrunner, and western scrub-jay) were the most common, comprising 40% of all predation events recorded.

All mammal depredations occurred in riparian areas. This may be because the mammals are using dry Dolan Creek and washes as corridors that occur between BCVI habitat to move around in the study area. Riparian corridors are an important landscape element for predators and guide animal movement (Noss 1991). Many predators, particularly mammalian predators, are known to forage along travel lanes such as habitat edges (Small and Hunter 1998, Marini et al. 1995, Barding and Nelson 2008). Most of the vegetation outside the wash areas is thick and difficult for mammals to move through and the washes serve as habitat edges in the study area. It may be less costly for mammals to travel in the sparsely vegetated dry washes; therefore, they would more often forage in riparian areas and, consequently, more often come into contact with nests built in the riparian habitat.

The main predator of BCVI nests in 2009 was BHCOs. It is likely that BHCOs are depredating nests in order to force hosts to re-nest and subsequently parasitize the new host nest attempt. The presence or absence of cattle may not be a good indicator for the impact of parasitism in a particular area; other factors may be contributing to BHCO use of an area for breeding. There were no cattle within the study area or on the surrounding properties during this study; however, there is a substantial population of feral sheep and aoudad that may be attracting BHCOs. Also, BHCOs may be attracted to the food supply created by supplemental deer feeding occurring on many of the adjacent properties; some deer feeders occur only a couple of meters away from the DRNSA fence line (pers. obs.). Brown-headed cowbird females have been shown to travel up to 13 km from their feeding areas to their breeding range (Curson et al. 2000) but typically travel no more than 7 km (Thompson 1994, Goguen and Mathews 2000). The deer feeders are providing an increase in food availability for BHCO females and likely increasing the number of breeding BHCOs. Black-capped vireo habitat at DRSNA occurs within the typical distance that BHCO have been observed to commute between feeding and breeding areas thus potentially increasing depredation and parasitism pressure on BCVIs breeding within the study area.

The influence of cowbirds, both as nest predators and parasites, was much less significant in 2010. It is unclear how or if higher precipitation and/or flooding affected BHCO behavior and abundance in 2010. It is possible that the abundance of water across the landscape allowed BHCOs to disperse into areas where water availability typically prevents them from occurring thereby decreasing the number of BHCOs around

perennially wet Dolan Creek and the Devil's River. I also observed fewer cowbirds early in the season in 2010 than 2009 and there was a low number of BCVI nests parasitized at Kerr WMA and Balcones Canyonlands Preserve (Austin, TX) in 2010 (T.L. Pope and M.R. Colon, pers. comm.). There may be an unknown factor, independent of the higher precipitation that caused this delay in arrival from their winter habitat. Further long-term study of the variation in nest success, depredation, and parasitism is needed to answer the questions regarding year to year differences.

Only 3% of the BCVIs that were detected during point counts in mesa habitat, comprised mainly of juniper and oak spp., compared to its availability (18%). Vegetation structure and substrate species on the mesas is very similar to areas used by BCVIs within my study area and in other parts of their range (i.e., low scrubby growth, open space between vegetation clumps; Grzybowski et al. 1994, Bailey et al. 2007). The lack of mesa use by BCVIs could be a result of wind. The wind in southwest Texas can be very strong; for example, the average wind speed during the 2009 and 2010 breeding season was 16 km/h and gusted to between 80 and 100 km/h (NOAA 2010). There is little to no protection from wind on the mesas and the energy needed to cope with it may be more than BCVIs can afford during the breeding season. No BCVIs were detected in the woodland areas despite the similarity of the vegetation structure to areas used by BCVIs in the central Texas (Conkling 2010), but they are using woodlands during the post-breeding season (K.N. Smith, pers. obs.).

Only 5% of BCVIs were detected in low flat areas compared to 11% availability. These areas most often occur adjacent to riparian areas and use could possibly be overflow of territories from the highly used riparian areas because of conspecific attraction and clumping of the vireo territories. Many low flat areas have become overgrown with thick vegetation, primarily *Acacia* spp. and pricklypear cactus (*Opuntia* spp.); these areas were not used by BCVIs.

BCVIs are selecting to use riparian areas at the landscape scale. Most of the detections during point counts occurred in riparian/wash areas and they appear to be using these areas in much higher proportion than their availability both along dry Dolan Creek and in the canyons. It is likely that the classification underestimated the amount of riparian habitat available within the study area. This is because riparian vegetation can occur in small areas and thin strips that may not be distinguished with the raster resolution that was used. The other areas highly used by BCVIs are the slopes of canyons and drainages, but unlike the riparian areas, slope habitat is widely abundant within the study area.

Black-capped vireos are using vegetation very similar to what is available to them at the territory scale. Cover within territories was highly variable across the study area and did not affect success or failure of the territory. Proximity of vegetation cover to the ground was also the same as what was available to the vireos at the study site. Most vegetation occurs close to the ground across the entire study area due to the shallow soil layer in the region and so one would not expect a difference in used and available areas. Similarly, no difference was detected for height of vegetation in used and available areas. Height vegetation started from the ground did not influence success or failure of BCVI territories in 2009 or 2010. Vegetation height was significantly higher in successful territories than in failed territories in 2010 but not in 2009. It appears that the vireos are equally successful in the entire range of vegetation that they use, but may be more likely to fledge young in territories with taller trees and shrubs.

Vegetation species diversity was lower in BCVI territories than across the study sites. This may indicate that BCVIs are selecting for areas that have a few vegetation species that they use for foraging and/or nesting. High species diversity across the study site could also be the result of the sampling at the study site scale being distributed over a larger amount of area than territories and, therefore, points were located in a variety of vegetative communities. Species diversity was not significantly different in successful or failed territories in either year of the study.

Black-capped vireos are building many of their nests on slopes and appear to be placing them on slopes with particular aspects. Slopes with a northerly aspect were used dominantly and slopes with a westerly aspect were not used as regularly. These trends are probably due to two reasons: sunlight exposure and vegetation availability, which are not mutually exclusive. Temperatures can reach 38° C and higher during a large proportion of the breeding season in this area of the BCVI's range. Northern slopes receive less direct sunlight than any of the other directions. Cottle (1932) stated that the differences in the vegetation on the north and south slopes of mountains in southwest Texas was attributable to higher levels of soil moisture, less evapotranspiration, lower soil temperatures, higher humidity, and lower wind velocity on the north slope. Southern and western slopes not only receive direct sunlight, they are exposed directly in the afternoon when the heat is most intense and are more exposed to winds from the southwest; these factors lead to a relatively smaller amount of vegetation available for use for foraging and nesting by BCVIs than northern or eastern facing slopes.

Black-capped vireos nested in 13 different substrate species in 2009 and 2010. The majority of their nests were located in 4 of these species – Texas mountain laurel, juniper spp., Texas persimmon, and Vasey shin oak. The first three species listed previously are consistently available to BCVIs at all 7 seven study sites and were used more than available in at least 2 of the 7 study sites. When shin oak, which occurs in the canyon study sites, was readily available to BCVIs, they used it more than other substrate species (Table 4). This indicates that BCVIs may not be using the presence of Vasey shin oak to select where they choose to settle on the landscape but they are choosing to use shin oak as a nest substrate when it is available, even in small quantities. When shin oak is not available, mountain laurel and Texas persimmon were used as nest substrates when compared across the entire breeding season.

There was no significant correlation of habitat variables I measured around the nests and increased nest success or increased depredation; however, it appears that brown-headed cowbirds more efficiently locate BCVI nests that are placed in particular habitat conditions. Nests that were more concealed tended to have a slightly higher probability of being parasitized. Mean cover around the nest tended to be high ($85\% \pm 11\%$) which could indicate that BCVIs are choosing to use nest locations that will increase the likelihood of parasitism. Nests that had an overstory were less likely to be parasitized; however, presence of an overstory did not appear to be a factor influencing nest placement by BCVIs given that the number of nests with an overstory was

approximately 50%. Finally, nest height had a large impact on likelihood of parasitism and the majority of BCVI nests were built 1.1 m high and below.

MANAGEMENT IMPLICATIONS

Black-capped vireo breeding habitat needs to be managed differently in southwest Texas than the way it is managed in the areas with deeper soils that have successional vegetation communities. Frequent disturbance is not needed in the Devil's River area to create habitat for black-capped vireos; therefore, the typical management techniques used for creating and maintaining BCVI habitat do not apply. Regular flooding appears to be maintaining BCVI habitat in riparian areas in this region and natural fires may also be resetting vegetation communities and providing new habitat for BCVIs.

No vegetation management, predator control, or BHCO control is currently being conducted in the area. Because of the xeric stable nature of the vegetation in the southwest portion of the BCVI's range in Texas, available habitat remains relatively constant in the absence of the rare occasions of outright removal or overgrazing by domesticated or feral livestock. There is a substantial number of feral sheep (*Ovis spp.*) and aoudad (*Ammotragus lervia*) and at Devil's River SNA, particularly in the canyons, and focused population control may be necessary in the future to minimize overgrazing and destruction of black-capped vireo habitat on the property. Regular burning in habitat that will get overtaken by catclaw and prickly pear would also likely promote use by black-capped vireos. More research in to BCVI response to burning in the region would be beneficial.

Brown-headed cowbirds are also impacting black-capped vireo productivity because of both depredation and parasitism of nests in this region despite the steady decrease in cattle and goat ranching in the area. There is a large population of black64

capped vireos at Devil's River SNA and Dolan Falls Preserve. According to local landowners, a growing number of properties in the vicinity are being sold and converted into high-fenced hunting ranches. Supplemental deer feeding is common on hunting properties in Texas and could possibly be providing regular food sources for BHCOs. Research into deer feeder affects on BHCO behavior and populations and the potential influence on BCVI nest parasitism rates is needed to assemble any conclusions.

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