

FORAGING BEHAVIOR OF THE BLACK-CAPPED VIREO
IN CENTRAL TEXAS

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ABSTRACT

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Habitat loss, through urbanization and habitat degradation, is a major component threatening endangered Black-capped Vireo populations. Acquisition and management of breeding habitat are identified as the main objectives for recovering populations to a viable level. In order to identify attributes of suitable habitat for Black-capped Vireos, it is essential to understand the way they use their habitat. I examined Black-capped Vireo foraging behavior for adults and fledglings and identified differences that existed between the sexes at four study sites in Central Texas. G-test of Independence and Fisher's Exact test were used to compare frequency distributions of males and females for foraging height, height of tree used, tree species, substrate and foraging maneuvers.

I found males and females foraged at different proportions relative to various height classes with males foraging at all levels but primarily greater than 3 m and females foraging almost exclusively below 3 m. Males used taller vegetation proportionally more than females, which consequently, influenced the use of different tree species. No intersexual difference was found for substrate and maneuvers during foraging attempts. All Black-capped Vireos primarily gleaned from foliage. Fledglings foraged generally below 2 m but were observed using vegetation >3 m 50% of the time. Due to the use of tree canopies for foraging by males and taller vegetation by fledglings, greater vertical strata may be an important component commonly overlooked when identifying a heterogeneous landscape for Black-capped Vireos. Additional fledgling dispersal studies are recommended to identify detailed fledgling habitat use prior to migration.

CHAPTER I

INTRODUCTION

The Black-capped Vireo, *Vireo atricapilla*, is a Neotropical passerine that was once locally common throughout the south-central United States and northern Mexico. Historically, the species occupied a breeding range as far north as Kansas, southward through central Oklahoma, central Texas into northern Mexico. During the 1900s, however, Black-capped Vireo abundance began to decline, with extirpation from Kansas in the 1930s, while populations in Oklahoma, Texas and Mexico continued to fragment and dwindle in size (USFWS 1991). The Black-capped Vireo is currently restricted to three remnant populations in Oklahoma, while in Texas breeding habitat is primarily confined to isolated regions within the Edwards Plateau, the Lampasas Cut Plains and southeastern Trans-Pecos (Campbell 1995). The breeding range in northern Mexico extends into southwestern Tamaulipas. Due to the continuous decline in abundance and reduced geographical range, the Black-capped Vireo was listed as a federally endangered species in 1987 by the U.S. Fish and Wildlife Service (USFWS 1991). Habitat loss, through urban expansion and land management practices, was identified as the primary threat to the continued survival of Black-capped Vireos.

The Black-capped Vireo occupies wooded areas of low shrubby deciduous growth of irregular height and distribution, interspersed with open or grassy areas. Optimal habitat consists of 35%-55% shrub cover with Ashe juniper (*Juniperus ashei*) comprising no more than 10% of total vegetation; however, in the Edwards Plateau Ashe junipers may contribute important cover (Grzybowski 1994). Various oak species (*Quercus* sp.) and other deciduous vegetation, generally dominate Black-capped Vireo breeding habitat. This early successional stage of scrubland habitat provides adequate nest concealment, and is speculated to afford sufficient forage substrate for this insectivorous species (Grzybowski 1994). In contrast to structurally specific breeding habitat for Black-capped Vireos, a moderately diverse plant species composition is suitable foraging habitat within these constraints across their range (Graber 1961, Grzybowski 1995). Although dense shrub vegetation is a critical constituent of nesting habitat, conventional descriptions of suitable habitat deemphasize the presence of taller habitat elements that are sporadically situated.

In the 19th Century, the introduction of cattle ranching to Texas in conjunction with fire suppression altered the community floristic successional trend. Consequentially, deciduous brush advanced into a mature successional stage with taller shrubs and trees that provided inadequate cover for nests. This condition left eggs or hatchlings vulnerable to predation. Disruption of the natural fire regime also allowed Ashe Juniper to invade and dominate the vegetative landscape.

Indiscriminant brush removal to accommodate grazing livestock also contributed to the destruction of breeding habitat, while continued livestock grazing pressure inhibited the regrowth of understory vegetation. The detrimental effects of agricultural

land use on habitat loss were compounded by the attraction of Brown-headed Cowbirds, *Molothrus ater*, to cattle pastures. Brown-headed Cowbirds are nest parasites and have been found to parasitize 90% of Black-capped Vireo nests within a study site on Fort Hood Military Reservation (Weinberg et al. 1998).

Recommended management procedures for Black-capped Vireo habitat include various measures to disrupt succession, reinforce growth of deciduous plant species, and remove Brown-headed Cowbirds from the breeding habitat (USFWS 1991). A regime of prescribed burning appears to provide optimal regrowth of a diverse deciduous plant community with development of suitable habitat for Black-capped Vireos; however, for management areas in close proximity to urban or suburban residential communities, prescribed burning is not practical. The selective brush removal method is often used within these areas, often referred to as the “wildland-urban interface” (Texas Forest Service 2007).

When land managers are challenged with mechanically sculpting the landscape for Black-capped Vireo habitat, the selection process should incorporate various factors relating to how the species uses its habitat. Although numerous vegetative analyses of breeding territories have refined habitat management objectives, data on foraging behavior within territories are lacking (Wilkins et al. 2006). Foraging ecology of targeted species should be tied to the objectives of habitat management (Bolen and Robinson 2003).

The primary assumption of foraging theory is to maximize caloric intake while minimizing energy expenditure in obtaining food items. Thus, the size of breeding territories must incorporate a balance by providing sufficient foraging habitat with

respect to the cost of energy needed to defend boundaries from competing conspecifics (Hixon 1980).

Territories of breeding birds include the minimum area necessary to provide sufficient foraging habitat (Greenberg and Gradwohl 1997). Within these areas males and females may exhibit behavioral divergence in use of foraging substrates, foraging heights, and maneuvers (Selander 1966, Williams 1971, Holmes 1986). There are several possible explanations for these intersexual differences of foraging ecology in bird species including 1) reduction of intersexual foraging competition, 2) improvement of reproductive success by broadening the resource base within territories, and 3) conservation of energy by foraging in locations close to gender related activity centers (Morse 1968, Recher and Holmes 2000).

Intersexual foraging behavior is primarily documented for structurally dimorphic species, particularly woodpeckers, where one sex is much larger than the other or the shape and size of the bill differ between males and females (Selander 1966, Mueller and Meyer 1985, Morrison and With 1987). This, in turn, directs how and where prey is taken. However, intersexual foraging behavior may also occur in structurally similar passerines (Morse 1968, Williamson 1971, Holmes 1986).

Several morphologically similar vireo species known to exhibit differing intersexual foraging behaviors include the Red-eyed Vireo (*Vireo olivaceus*) and Philadelphia Vireo (*Vireo philadelphicus*) where the females forage at lower vertical strata than males, and Red-eyed Vireo females use different substrate-maneuver combinations than males (Williamson 1971, Holmes 1986).

Although Black-capped Vireos have dichromatic plumage they are also morphologically similar like other vireos exhibiting intersexual foraging behavior. However, no quantitative studies have investigated Black-capped Vireo foraging patterns and anecdotal accounts describe their foraging behavior differently. Grzybowski (1995) suggested males and females foraged at all heights but males tended to forage more frequently than females above 2 m while Graber (1961) noted all Black-capped Vireos foraged primarily from upper portions of vegetation.

The objectives of my study were to investigate (1) foraging ecology of the Black-capped vireo within breeding habitat, (2) differences that may exist between male and female foraging patterns, and (3) implications of foraging behavior for management strategies.

CHAPTER II

STUDY AREA

The study area consisted of four sites with known Black-capped Vireo breeding populations on the Edwards Plateau in central Texas. Two sites, the Vireo Ridge tract and Cortaño tract, are in the Balcones Canyonlands Preserve (BCP) on the edge of the Jollyville Plateau in western Travis County. The Eckhardt tract is located on the Balcones Canyonlands National Wildlife Refuge in Burnet County, and the Kerr tract at the Kerr Wildlife Management Area in northwestern Kerr County. All sites have plant species commonly found throughout central Texas; however, they differ in structural features of vegetation, such as vertical strata and spatial composition.

The Cortaño Tract is a 685-ha portion of the BCP owned and managed by the City of Austin. In 1995, approximately 40 ha were manipulated mechanically and by hand clearing to remove invasive Ashe juniper and to restore the vegetative landscape associated with early successional stages as suitable breeding habitat for Black-capped Vireos. This upland landscape is characterized as a shrubland dominated by shin oak (*Quercus sinuata*) and live oak (*Quercus fusiformis*) interspersed with taller shade trees and open grassy areas or bare rock. Texas red oak (*Quercus texana*), red bud (*Cercis canadensis*), flameleaf sumac (*Rhus lanceolata*), and Ashe juniper are also dispersed in

the restored area. Larger oak stands are situated in the center of the tract. The terrain subtly slopes downward toward the periphery of the restored area with a steep wooded canyon located along the western edge. The Cortaña Tract has historically supported three to five Black-capped Vireo territories.

The Vireo Ridge Tract of the Travis County portion of BCP has also been mechanically manipulated using a frail mower and hand clearing to create roughly 50 ha of Black-capped Vireo habitat. The first restoration effort began in 2002 and has continued annually. The tract consists of a matrix of oak shrubland, deciduous motts exceeding 4m in height and open grassy areas. The variety of plant species found on Vireo Ridge creates a heterogeneous landscape. The restored area is upland of steep wooded canyons dominated by Ashe juniper. Although Vireo Ridge covers an area exceeding 200 ha, approximately 40 ha of the tract was used for my study. Generally, Black-capped Vireos have established seven to eight territories annually on Vireo Ridge during the past decade.

The Balcones Canyonlands National Wildlife Refuge acquired the Eckhardt Tract in 1995. The Eckhardt tract was historically used for cattle ranching; however, the details of land management practices are unknown. When the tract was acquired the early successional physiognomy was in place for Black-capped Vireo breeding habitat. The vegetative landscape is dominated by thickets of shin oak with scattered trees of hackberry (*Celtis laevigata*), Texas ash (*Fraxinus texensis*) and several oak species, which rise above the lower shrub canopy. The Eckhardt tract still maintains optimal vegetative structure for Black-capped Vireos. This tract has subtle slopes with no

adjacent canyons. It is the smallest study site, approximately 28 ha, but it had the most Black-capped Vireo territories (23) within the Balcones Canyonlands area.

The Kerr Wildlife Management Area, a 2628 ha-faculty, was obtained by the state of Texas in 1950 for research and management of white-tailed deer (*Odocoileus virginianus*). A regime of prescribed burning to control the invasion of Ashe juniper began in 1979. As a result, optimal breeding habitat for Black-capped Vireos developed in a patchwork of open grassy areas, contiguous shrubland and deciduous motts, comprised of oaks and a rich heterogeneity of other species. Remnant corridors of Ashe juniper snake through portions of Black-capped Vireo habitat. The Kerr Wildlife Management Area has a high density population of Black-capped Vireos with approximately 450 territories and sustains one of the largest known source populations on the Edwards Plateau. For my study about 40 ha of Bobcat Pasture was used for foraging observations which supported 22 breeding territories.

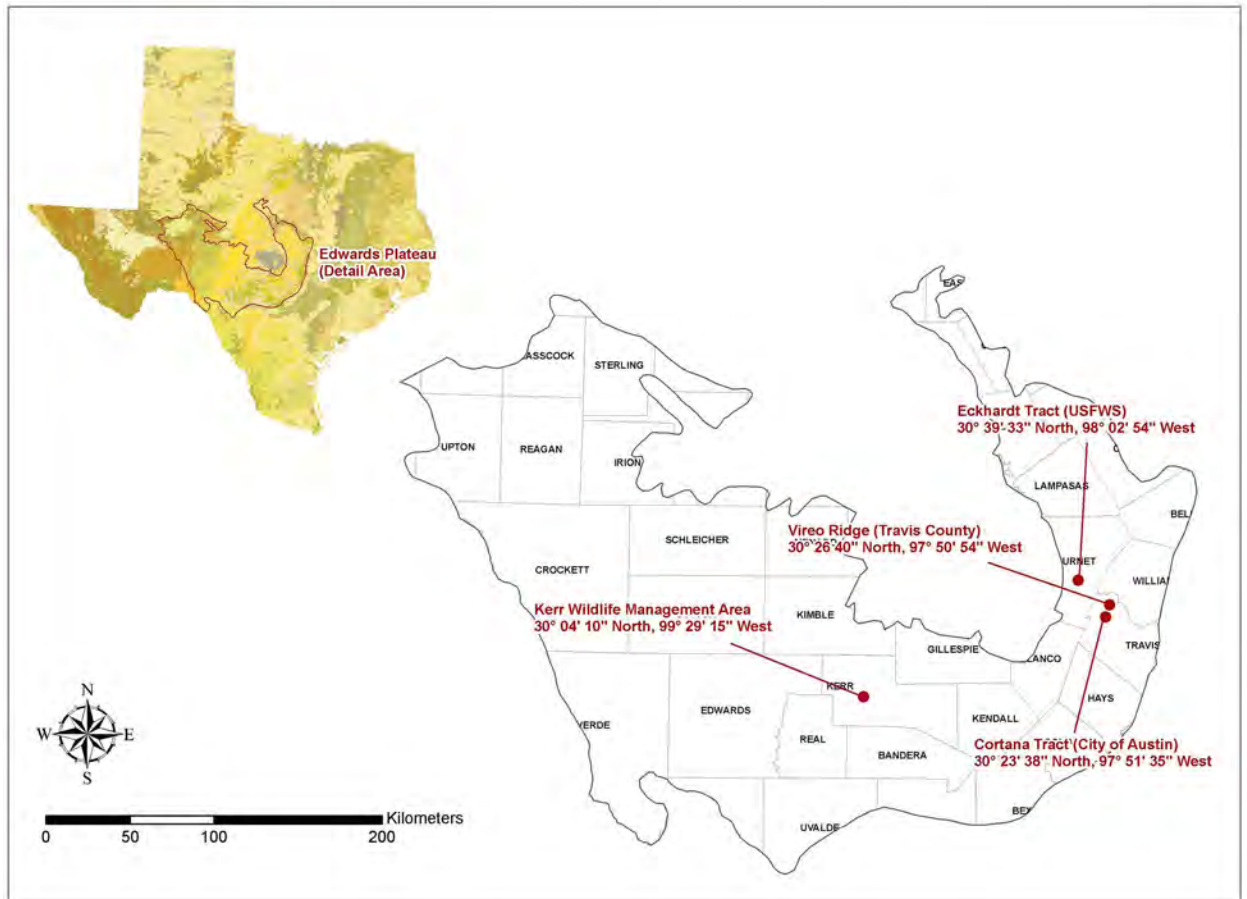


Figure 1. Map of study site locations on the Edwards Plateau in central Texas.

CHAPTER III

METHODS

I studied foraging ecology of Black-capped Vireos in April-July 2004 and April-August 2005. Descriptive foraging observations were collected both years, while quantitative data were collected during the 2005 breeding season only. During the 2005 breeding season, each study site was visited a minimum of 10 times between 0630 h and 1500 h. Foraging behaviors were recorded for each member of a focal pair when possible.

Spot mapping was used at each site to ensure an even sampling distribution for foraging behaviors (Beal and Khamis 1990). Territories were determined by monitoring movements of Black-capped Vireo pairs and noting the location of interactions between neighboring males and females (Bibby et al. 2003).

Each territory was randomly walked until a Black-capped Vireo was detected visually or audibly. Once a vireo was observed foraging, I followed it for at least 10 sec before data for the first foraging attempt were recorded. This allowed the bird to resume normal foraging behavior in the presence of an observer and also minimized the recording of conspicuous behaviors (Hejl and Verner 1990). For each foraging attempt, multiple variables were recorded including: 1) foraging height, 2) height of tree used, 3) tree species used, 4) substrate, 5) maneuvers, and 6) sex. Up to five sequential foraging attempts were recorded for each bird before termination of an observation.

Substrate was characterized as foliage (leaf, flower, or seed), branch, or trunk of a tree. Foraging maneuver described the attack method used to carry out the foraging attempt. Foraging maneuvers were categorized as glean (picking food items from nearby substrates while remaining perched without fluttering wings), aerial jump (a launch into the air to reach a food item while fluttering wings), and sally (flight from a perch to catch a food item and return to the perch) (Remsen and Robinson 1990). I used the dichromatic coloration of male and female Black-capped Vireos to identify sex.

After a sequence of up to five foraging observations was recorded for each member of a focal pair, the process was repeated in the neighboring territory. Females were more difficult to locate during territory visits and consequentially uniform data by sex were not always collected for each pair.

In addition, opportunistic foraging observations of Black-capped Vireo fledglings were recorded, however, due to inconsistent and infrequent encounters, inferential statistics were not used for comparison with adults.

Sequential observations allow the researcher to gather a greater amount of data particularly for species which are difficult to locate (Sturman 1968, Hertz et al. 1976, Recher and Gebiski 1990); however, consecutive observations on the same individual are not independent posing problems for statistical analysis (Wagner 1981, Morrison 1984, Bradley 1985). Although sequential foraging attempts were recorded for individual birds, only initial observations were used for statistical analyses. Because data were sometimes collected from the same individual of a pair, site visits were spaced at least seven days apart to reduce bias.

Data were categorized for each foraging variable to create frequency distributions for each sex. Foraging height and height of tree used were divided classes: 0-2.9 m to reflect foraging in the shrub layer and ≥ 3 m to indicate foraging in higher vertical strata normally not referred to as habitat. Tree species used by males and females with frequencies ≥ 10 were identified while those with frequencies < 10 were pooled and categorized as “other”. For substrate, trunks of trees were not used in any initial observations, thus, all substrate data were categorized as foliage or branches. Maneuvers were categorized into gleaning or aerial maneuvers. Aerial jump and sally were combined due to the lack of sallying events recorded for females.

Each behavior or foraging category was pooled across study sites and tested separately. I used the G- test of Independence with William’s Correction to compare frequency distributions of foraging height, height of tree, and tree species used by male and female Black-capped Vireos (Sokal and Rohlf 1995). I used Fisher’s Exact test to compare substrates and maneuvers between males and females because some cell frequencies in contingency tables were < 5 (Sokal and Rohlf 1995). A significance level of $P < 0.05$ was used for all statistical comparisons.

I calculated niche overlap from frequency distributions of all foraging variables to assess the degree of resource overlap between sexes (Schoener 1970). Values ranged from 0 to 1. A value of 1 represented complete overlap between the sexes for a given variable and 0 indicated complete separation.

CHAPTER IV

RESULTS

I observed 224 foraging attempts by Black-capped Vireos at four study sites; Kerr tract ($n = 69$), Eckhardt tract ($n = 56$), Corta a tract ($n = 55$), and Vireo Ridge tract ($n = 44$). I used 116 initial observations (male, $n = 69$; female, $n = 47$) to calculate means and standard errors of foraging height and height of trees used and to compare frequency distributions of foraging attributes between males and females.

Males foraged proportionally at different heights than females ($G_I = 31.94$, $P < 0.001$) (Table 1). Females foraged primarily in the shrub layer at a mean height of 1.65 m (SE = 0.14) with 90% of foraging observations occurring at <3 m; whereas, males used a broader range of vertical strata. Males foraged predominately in tree canopies, ≥ 3 m (60%) and in the shrub layer, <3 m, 40% of the time (Fig. 2). Mean height of foraging males was 3.23 m (SE = 0.19). Niche overlap for intersexual foraging height was moderate at 0.50.

Table 1. Frequency of foraging height (m) classes for foraging attempts of male and female Black-capped Vireos in central Texas in 2005.

		0 – 0.9	1– 1.9	2 – 2.9	3 – 3.9	> 4
Male	n	2	19	7	23	19
	%	3	27	10	33	27
Female	n	9	28	5	4	1
	%	19	60	11	8	2

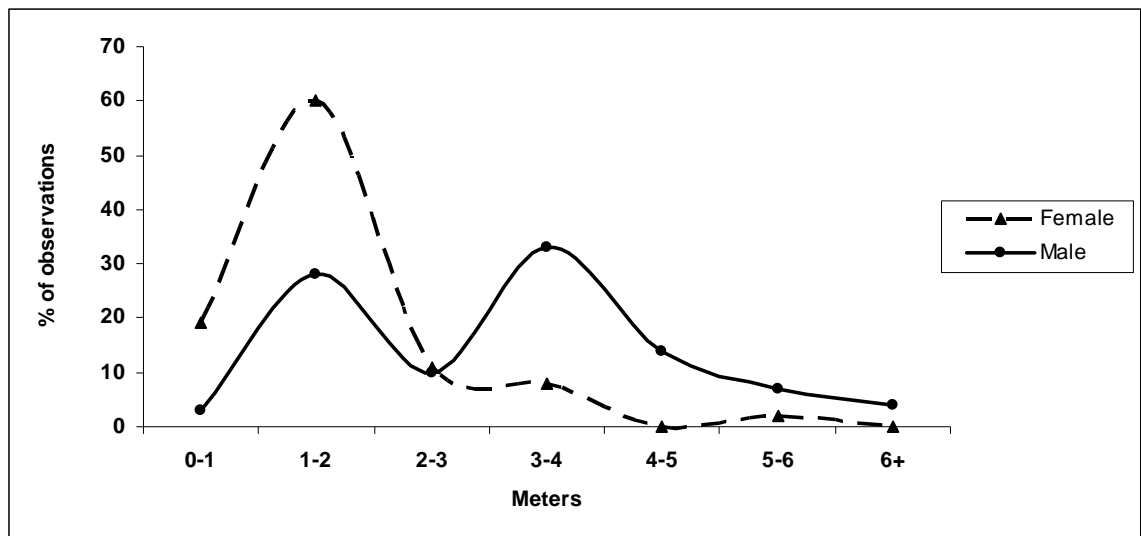


Figure 2. Frequency distribution of foraging height for male and female Black-capped Vireos in central Texas in 2005.

Eighty percent of male foraging attempts ($n = 55$) occurred in trees ≥ 3 m in height compared to 40% of attempts ($n = 19$) by females in trees ≥ 3 m in height ($G_I = 18.56$, $P < 0.001$) (Fig. 3). Females foraged more in low shrubs 0-2.9 m in height ($n = 28$, 60%) than males ($n = 14$, 20%). The mean height of trees used for foraging by males was 5.00 m (SE = 0.26) and 2.73 m (SE = 0.20) for females. Niche overlap of heights of trees used for foraging for males and females was 0.60.

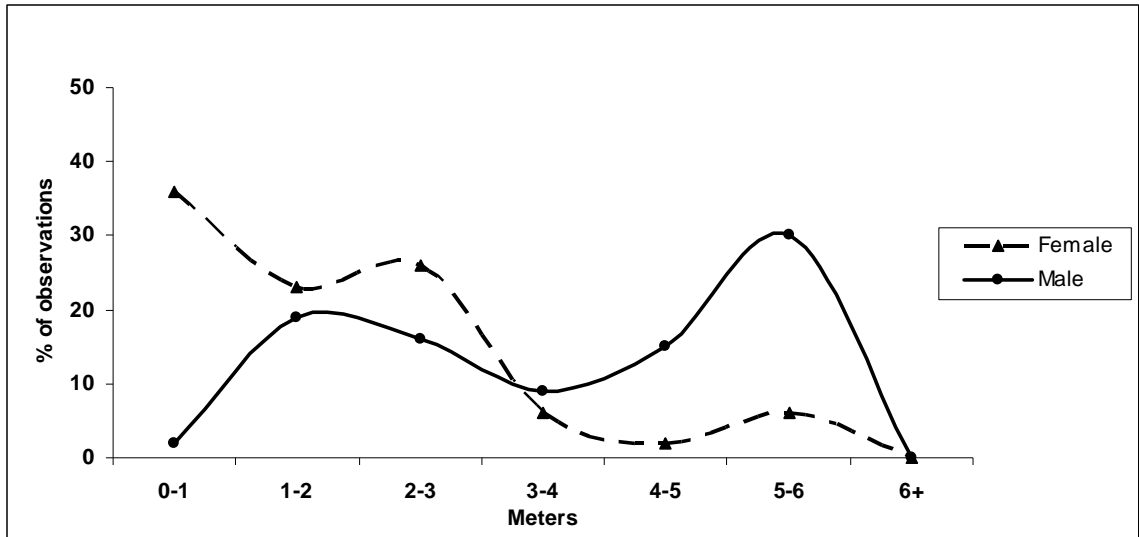


Figure 3. Frequency distribution of tree height used for male and female Black-capped Vireos in central Texas in 2005.

Based on foraging attempts, males and females foraged in different species of trees ($G_4 = 11.44$, $P = 0.02$), however, niche overlap value was relatively high (0.74) (Table 2). Males and females foraged mostly in live oak, 46% and 34%, respectively. Males used more Texas red oak (16%) than females (2%). Additionally, females used shin oak (28%) more than males (13%). Ashe juniper was used for foraging 7% of the time by males and 13% of the time by females. Combinations of other species were used more by females (23%) than by males (18%). These species included cedar elm, hackberry, flameleaf sumac, Texas ash, Texas persimmon (*Diospyros texana*), evergreen sumac (*Rhus virens*) trees and dead tree snags.

Table 2. Frequency of tree species used for foraging attempts of male and female Black-capped Vireos in central Texas in 2005.

		Live oak	Red oak	Shin oak	Ashe juniper	Other
Male	n	32	11	9	5	12
	%	46	16	13	7	18
Female	n	16	1	13	6	11
	%	34	2	28	13	23

Males and females foraged on a similar substrate (odds ratio = 0.2964, $df = 1$, $P = 0.0974$, niche overlap = 0.87) and used similar foraging maneuvers ($P = 0.737$). Most foraging attempts by males ($n = 56$, 81%) and females ($n = 44$, 94%) were directed at foliage ($n = 100$, 86%). Males, however, used branches ($n = 13$, 19%) more than females ($n = 3$, 6%).

Foraging maneuvers used by males and females had the highest niche overlap of all foraging variables (0.97). Gleaning was the predominant maneuver by both sexes (odds ratio = 0.7179, $df = 1$, $P = 0.737$) being used 92% ($n = 63$, 91% for males and $n = 44$, 94% for females) of the time. Aerial jump and hovering were used 8% of the time ($n = 6$, 9% for males and $n = 3$, 6% for females).

Fledglings ($n = 18$) primarily foraged in shrubs at heights <3 m (89%, $\bar{X} = 1.57$ m, $SE = 0.24$, $n = 16$) and used trees <3 m in height equally with those >3 m (50%, $\bar{X} = 3.59$ m, $SE = 0.37$, $n = 9$). They foraged in shin oak (39%, $n = 7$), live oak (28%, $n = 5$), Texas red oak (11%, $n = 2$) and equally (5.5% each, $n = 1$) in Ashe juniper, cedar elm, Texas persimmon and Western soapberry (*Sapindus drummondii*). They primarily used gleaning (94%, $n = 17$) in foraging from foliage (89%, $n = 16$).

CHAPTER V

DISCUSSION

For many morphologically similar songbirds, the most frequently documented intersexual foraging difference has been that males generally forage higher than females (Morse 1968, Williamson 1971, Franzreb 1978, Hutto 1981, Morrison and With 1987, Recher and Holmes 2000). Black-capped Vireos in central Texas followed this same pattern of foraging behavior between the sexes. Grzybowski (1995) speculated that male Black-capped Vireo did not forage exclusively in the shrub layer but foraged across a range of vertical strata. Although males foraged mostly at heights >3 m, the foraging height distribution (Fig. 1) produced a bimodal frequency curve with two distinct peaks occurring <2 m and >3 m with a trough between these two height classes. Females foraged primarily in the shrub layer <2 m with decreasing frequency of use at heights >2 m. This trough, demonstrated by both sexes, may be attributed to vegetative structure in breeding habitats where foliage and arthropod density profiles may be bimodal (MacArthur and MacArthur 1961, Williamson 1971) with shrub layer ≤ 2 m, and emergent upper canopy layer ≥ 3 m. The lack of vegetative structure between the 2 m to 3 m height class may be explained by the effects of fire or mechanical manipulation mimicking the effects of fire on vegetative structure in breeding habitat. Studies on the effect of prescribed burning in Black-capped Vireo breeding territories at the Kerr

Wildlife Management Area revealed the influence of fire on the morphology of small mottes composed primarily of live oak (Baccus 1981, 1982, 1983, 1984, O'Neal et al. 1996). High moisture content in the litter under mottes prevents the curing of vegetation necessary to carry fire through mottes (Baccus 1981, 1982, 1983, 1984, Fonteyn et al. 1988). This inhibits the higher strata from being subject to a ladder effect where fire travels vertically upward through the vegetative structure. Consequentially, fire will bypass mottes allowing interior trees to grow into the emergent canopy layer. This process creates a gap between tree canopies and the regrowth of understory, thus, restricting foraging to two disjunctive height classes.

The decrease of foraging activity at the 2 m- to 3 m-height interval for both male and female Black-capped Vireos may alternatively be attributed to foraging height preference. In Least Bell's Vireos (*Vireo bellii*) foraging height distribution is a function of foraging height preference despite availability of vegetative structure at all heights (Miner 1989).

Intersexual difference in the height of trees used for foraging appears to be interconnected to heights at which the sexes forage. Low foraging females tended to use low shrubby vegetation while males used predominately taller trees. In turn the height of trees used for foraging appears to influence the use of specific tree species.

Variation in tree species use by the sexes may be a function of tree morphology which influences availability within each vegetative height class. Shin oak, used more frequently by females than males, generally grows no more than 3 m in height forming thickets as a result of certain growing conditions, such as root disturbance or fire. This allows more foraging opportunities for females than in tree species which do not provide

abundant substrate >2 m, such as the Texas red oak. The Texas red oak generally attains heights >9 m producing a primary trunk with the crown of the tree found above the shrub layer. Consequently, male Black-capped Vireos used Texas red oaks more often than females.

Although individual males and females tended to forage in specific tree species, as a whole they produced a relatively high niche overlap for tree species use. Live oak was used predominately by both males and females. This may be explained by the variety of height classes of live oak available and used by Black-capped Vireos. Live oak occurred on my study tracts in multiple growth forms, ranging from low growing thickets to large canopy trees reaching heights up to 15 m (Texas A&M University 2007).

Male and female Black-capped Vireos used similar substrates for foraging and flight maneuvers while foraging. Gleaning was the primary foraging maneuver used by both sexes. It had the highest niche overlap of all foraging variables. This is a maneuver characteristic of small insectivorous birds and has been documented as the predominant means of acquiring prey for other Vireonidae including Bell's Vireo (Salata 1983), Black-whiskered Vireo, *Vireo altiloquus*, (Lack 1976, Cruz 1980), Cassin's Vireo, *Vireo cassinii*, (Airola and Barret 1985), Gray Vireo, *Vireo vicinior*, (Orenstein and Barlow 1981, Griffin 1986), Plumbeous Vireo, *Vireo plumbeus*, (Cruz 1975), White-eyed Vireo, *Vireo griseus*, (Crowder 1976, Greenberg et al. 1993) and the Yellow-throated Vireo, *Vireo flavifrons* (Rodewald and James 1996).

Gleaning enables birds to capture a variety of small, cryptic prey that would probably be missed when using other search tactics (Robinson and Holmes 1982). It is also recognized as the most cost efficient foraging maneuver in terms of energy

expenditure (Remsen and Robinson 1990) and is consequentially used by most passerines in contrast to more energy demanding foraging tactics such as aerial maneuvers (Whelan 2001).

The substrate used most often in foraging by both Black-capped Vireo males and females was foliage. Other vireos primarily forage on foliage, such as the Black-whiskered Vireo (Lack 1976), Cassin's Vireo (Airola and Barrett 1985), Hutton's Vireo (*Vireo huttoni*) (Davis 1995), Warbling Vireo (*Vireo gilvus*) (Bent 1950, Petit et al. 1990) and the White-eyed Vireo (Greenburg et al. 1993). Although not statistically significant, males foraged on branches more than females. Robinson and Holmes (1982, 1984) found birds that forage at different heights may encounter different foraging opportunities which in turn may affect the way birds exploit food resources. In emergent tree canopy layers of Black-capped Vireo habitat, lateral branches were readily exposed and more abundant than in shrubby vegetation. Males foraged into crevices in bark and from lichen covered branches which were often associated with mature branches in the upper canopy layer. These substrates on larger branches were not available to females in the shrub layer where smaller branches and twigs were abundant.

Tree canopies rising above the shrub layer are not always available in Black-capped Vireo territories. It can then be expected that intersexual foraging differences may not be expressed in response to varying resource availability and the change in vegetative structure and composition (Ligon 1968, Robinson and Holmes 1982, Recher and Holmes 2000). When comparing intersexual foraging behavior of Red-eyed Vireos in a mature forest and younger forest, there was little reaction to foliage changes in their use of substrate, foraging maneuvers, and even tree species (Maurer and Whitmore 1981).

Foraging height of Red-eyed Vireos differed, however, with males foraging higher in the more mature forest where greater vertical strata were available (Maurer and Whitmore 1981).

There are several hypotheses explaining intersexual difference of foraging patterns in passerines. One hypothesis presumes that resource partitioning reduces intersexual competition where males and females have either evolved to alleviate competition (Rand 1952, Selander 1966) or diverged in foraging behavior during periods of limited resources (Selander 1966). Differences in foraging behavior of birds are often found in dimorphic species where morphological structures dictate where and how prey are taken. Black-capped Vireos, however, are morphologically similar and exhibit a large degree of overlap for foraging variables such as use of substrate and maneuver. Although the distributions of foraging height, tree height and tree species differ between males and females in my study, complete divergence of these foraging variables were not found, which suggests competition for resources is unlikely (Kelly and Wood 1996). In addition, I did not observe aggressive behavior between breeding males and females within territories.

Another hypothesis accounting for intersexual foraging differences is that individuals are associated with centers of activity during the breeding season. The proposed advantage for foraging near sex-specific activities is that energy and time are spent more efficiently (Morse 1968). For example, males forage at greater heights nearer to singing posts (Morse 1968, Franzreb 1978). Vireos in particular sing while foraging (Barlow 1962, James 1976, Barlow and Nash 1985), including Black-capped Vireos (Grabor 1961, Grzybowski 1995). During the breeding season Black-capped Vireos are

highly territorial and boundary disputes are not uncommon, therefore, singing perches are often used as a means to communicate with neighboring conspecifics (Grzybowski 1995). Furthermore, trees used as song posts are the object of aggressive bouts between neighboring Black-capped Vireos. In colonized areas where canopy trees were sparsely spaced and were not available within each territory, males frequently displayed territorial behaviors seemingly to claim and incorporate the perch tree within their territory.

These birds are unique among vireos by being sexually dichromatic with females having an overall duller plumage than males and also showing delayed plumage maturation for males (Graber 1961). Dichromatic differences in avian ecology are hypothesized to be a function of social recognition and sexual selection (Butcher and Rohwer 1989, Savalli 1995). Black-capped Vireos also possess the most sophisticated repertoire of syllables compared to other members of the genus. Both dichromatic features and complex repertoires of this species may indicate the significance of visual and audible conspicuousness for males within their habitat (Krebs et al. 1978, Beck and George 2000). Taller perch sites rising above shrublands may facilitate males to communicate with conspecifics by enabling males to be seen and heard at greater distances while foraging.

Despite the role of Black-capped Vireo males in maintaining territory boundaries, their reproductive responsibilities are not restricted to territory singing but also involve nest construction, incubation, and care of hatchlings and fledglings. The range of breeding related activities for males may explain foraging in the shrub layer and in tree canopies. Females, conversely, forage primarily in lower strata where they are closer to nests, which are typically built 1 m from ground level (Grabor 1961). Foraging in the

shrub layer may also be a means for females to expend less energy by avoiding vertical flights to tree canopies (Morse 1968) and may also reduce the risk of predation by remaining inconspicuous (Baccus, personal communication).

Fledgling Black-capped Vireos shared similar foraging patterns with adults by gleaning prey from leaves. They tended to forage in vegetation <2 m in height similar to females, however, almost half of the foraging observations occurred in trees >3 m in height resulting in greater canopy cover than in trees used by male and female adults. Although not reflected in my data, fledgling use of greater canopy cover may be greater than represented in the foraging height statistic due to the observed use of low shrubs adjacent to or beneath trees with large canopies.

These results are not conclusive to determine behavioral trends for fledglings; however, they may be indicative of habitat use not previously documented for Black-capped Vireos. At three research sites, I observed fledglings moving freely within territories soon after fledgling. They often moved from the vicinity of their nests in shrubby vegetation to more heavily wooded areas when available. On the Cortaña tract, a nest located and monitored within a shrubland area produced three fledglings. Within 14 days of hatching, the fledglings were repeatedly found with the adult male on the edge of their territory at <2 m in a woodland cluster with an average height >4 m. They were observed conducting a variety of activities within an area of 10 m including foraging, preening, resting, and fluttering from branch to branch presumably strengthening locomotive skills. As the fledglings matured they continued to use this area. The only fledgling recorded for the 2005 breeding season at the Vireo Ridge tract was seen foraging along the periphery of a restored area at the canyon ridge dominated by Ashe

juniper with lateral branches beginning at ground level and exceeding 3 m in height.

Previous and subsequent observations of fledgling habitat use on this tract have generally been located in the juniper woodland along the canyon slopes which surround upland nesting habitat (Fushille, personal communication). Locations of fledglings foraging in areas normally not associated with nesting habitat were also recorded at the Kerr tract where narrow strips of mature Ashe juniper and oaks snaked through multiple Black-capped Vireo territories. Adults with foraging fledglings were observed within these bands of woodland during several consecutive visits.

In areas where woodland clusters or mottes of emergent canopy trees are present, Black-capped Vireo fledglings forage and may prefer these patches of multi-tiered vegetation to low growing nesting shrubland. During the course of a life cycle, bird species may require multiple habitat types depending on specific behaviors and needs associated with each life stage (Law and Dickman 1998, Graham 2001, Cohen and Lindell 2004). Nesting and wintering grounds of many species, including Black-capped Vireos, have been studied extensively; however, few studies have investigated the postfledgling stage and habitat requirements associated with that period (Anders et al. 1997). After leaving the nest, fledglings must be able to survive independently from their parents while building substantial fat reserves to ensure successful migration to wintering grounds (Moore et al. 1993). This period may be an integral factor for understanding population viability (Cohen and Lindell 2004) and thus essential for management of a species.

Fledglings may move from natal habitats to adjacent areas where nesting adults may not normally be found. Wood Thrush (*Hylocichla mustering*) fledglings dispersed

from even-aged oak-hickory forests to areas composed of a mosaic of early and mid-successional pine forest, and mature riparian forest. Philadelphia Vireo fledglings moved from canopy tops to sapling and shrub layers of a late successional hardwood forest and White-throated Robin (*Turdus assimilis*) fledglings moved from agricultural lands to forests (Robinson 1981, Anders et al. 1997, Cohen and Lindell 2004).

A shift in fledgling habitat use may be attributed to more favorable foraging opportunities in newly occupied areas than at nest sites where the supply of food may have been “depressed” by foraging adults tending their young (Charnov et al. 1976, Robinson 1981). Cover is also a crucial constituent of these areas. During the fledgling period, young birds are more susceptible to mortality than during any other stage of life (Parsons et al. 1976, Greenwood and Harvey 1982, Magrath 1991, Vega Rivera et al. 1998, Monrós et al. 2002, Wheelwright et al. 2003) due to their limited ability to move long distances and efficiently evade potential predators or inclement weather. These areas composed of greater plant and structural diversity may provide fledglings with greater cover from potential dangers where they are able to learn essential life skills once they are no longer dependent on their parents (Anders et al. 1997, Kershner et al. 2004).

CHAPTER VI

MANAGEMENT IMPLICATIONS

Coupled with cowbird control measures, habitat management is identified as a major criterion in restoring Black-capped Vireo populations to a viable threshold (USFWS 1991). A recent genetic study characterizing the heterozygosity and population structure of existing Black-capped Vireo colonies found no depletion of genetic variability among the species across its range (Fazio et al. 2004). Therefore, the acquisition, creation and maintenance of habitat remain a priority for Black-capped Vireo recovery.

Optimal Black-capped Vireo habitat is conventionally described as early successional deciduous shrubland which varies in spatial arrangement. Although structural heterogeneity of vegetation is identified as a chief constituent of breeding habitat, vegetative stratification above 3 m is generally not included within these parameters. For example, the Black-capped Vireo Recovery Plan describes desired habitat with spatial heterogeneity between vegetation and open areas, with no mention of diverse vertical strata (USFWS 1991). Taller vegetation within breeding habitat, however, may play an important role in foraging ecology for males and juveniles.

Despite the use of vegetation at all height levels, I observed male Black-capped Vireos foraging predominately at heights over 3 m in trees with a mean height of 5 m.

The use of greater vertical strata by male Black-capped Vireos is likely a result of breeding related centers of activity, however, expanding the foraging habitat beyond the shrubland may consequently improve reproductive success by broadening the resource base within territories (Recher and Holmes 2000).

Taller vegetation may also be an important attribute within shrubland habitat for fledglings. Although fledglings foraged below 2 m, the vegetation used was >3 m 50% of the time. This means height statistic for vegetation used may actually be underrepresented at the landscape level. Although not quantified, I observed fledglings on numerous occasions adjacent to or beneath taller trees presumably for additional cover canopies would provide from overhead.

When mechanically manipulating the vegetative landscape, vertical heterogeneity coupled with spatial heterogeneity of shrubland should be preserved in Black-capped Vireo habitat. Emergent tree canopies sporadically situated throughout the shrubland as well as clusters of taller vegetation along perimeters of territories should not, however, compromise the growth of dense early successional vegetation. Heterogeneity of vertical strata in Black-capped Vireo habitat can benefit other species as well. In central Texas, particularly on the BCP, Black-capped Vireo habitat is often juxtaposed with mature oak-juniper woodlands which support the endangered Golden-cheeked Warbler (*Dendroica chrysoparia*). Golden-cheeked Warbler territories occasionally overlap at habitat interfaces (Grzybowski 1995) and Golden-cheeked Warblers have been observed using canopy trees in the shrubland for foraging.

Although knowledge of habitat use for all stages of a species life cycle is essential for understanding population dynamics, little research has investigated the postfledgling

period (Cohen and Lindell 2004) and its implications for habitat management. In order to definitively determine whether taller vegetation is an important component of habitat use for Black-capped Vireos, I recommend more research on fledgling dispersal.

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