MULTI-SCALE HABITAT USE OF FLEDGLING BLACK-CAPPED VIREOS ACROSS TWO TEMPORAL SCALES

A Thesis

by

MARISA TAKADA MARTINEZ

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

MASTER OF SCIENCE

Chair of Committee,	Michael L. Morrison
Committee Members,	Heather A. Mathewson
	Sorin Popescu
Head of Department,	Michael P. Masser

August 2015

Major Subject: Wildlife and Fisheries Science

ABSTRACT

Knowledge of post-fledging habitat needs is limited for avian species. To better understand this life stage I examined how fledgling black-capped vireos (*Vireo atricapilla;* hereafter vireo) respond to woodland landcover by assessing habitat use at a landscape scale (>100 ha) and local scale (0.04 ha circular plot) at sites with low, medium, and high woodland availability (WA). I used post-fledging season and post-fledging age as scales to identify temporal trends in habitat use at the two spatial scales.

I established study sites across Balcones Canyonlands National Wildlife Refuge and private properties in central Texas. During the 2013 and 2014 vireo breeding seasons, I located and monitored fledglings, conducted behavioral surveys, and conducted vegetation sampling at fledgling locations, study site-wide locations, and nest locations. Though fledglings occupied woodland areas, fledglings used non-woodland areas considerably more than woodland areas. Probability of post-fledging woodland use was greatest at sites where woodland availability was high (>60%). Fledglings used non-woodland areas significantly more than woodland areas regardless of the post-fledging season or their age. Although woodland use varied over the post-fledging season and with age class, the differences were not statistically significant.

Fledglings used areas with higher canopy, shrub cover, and compositions of Ashe juniper, live oak, and shin oak than what was average at the site. The vegetation characteristics of post-fledging habitat differed significantly between low, medium, and high WA sites, which suggest post-fledging habitat is highly variable across the landscape. Young fledglings used areas with 10% more shrub cover than old fledglings, and shrub cover at nest locations was about 10% higher than fledgling locations.

These results indicate the importance of non-woodland areas like shrublands for vireo fledglings. Landowners should be aware of fledgling activity before implementing management practices that would modify or remove vegetation in these areas such as prescribed burning, understory thinning, or grazing. Recognizing vegetation characteristics of post-fledging habitat and how they change across the landscape will help landowners manage and conserve vireo populations.

DEDICATION

I dedicate this work to all of the individuals who are striving to make Earth a sustainable habitat for everyone and everything living on it. Never give up.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Morrison, and my committee members, Dr. Mathewson and Dr. Popescu, for their guidance throughout my thesis research and expertise in their respective fields. I would like to thank all of the members of Dr. Morrison's lab for their assistance for their constructive feedback, and enthusiasm for everything and anything to do with avian ecology. I would like to thank Texas A&M University Institute of Renewable Natural Resources and the Department of Wildlife and Fisheries Science for their financial, administrative, and logistic support. I would like to thank the staff at the Balcones Canyonlands National Wildlife Refuge for allowing me access, resources, and housing for both field seasons, as well as private landowners for their generous authorization of property access. I would like to thank the Joint Fire Science Foundation and Braun & Gresham, PLLC Texas EcoLab for their funding which made this research possible. Lastly, I would like to thank my friends and Soka Gakkai International members for their unwavering support, and my parents for their love and constant faith in me since day one.

NOMENCLATURE

USFWS	U.S. Fish and Wildlife Service
BCNWR	Balcones Canyonlands National Wildlife Refuge
cm	centimeter
ha	hectare
km	kilometer
m	meter
hr	hour
min	minute

TABLE OF CONTENTS

Page

ABSTRACT ii

DEDICATION iv

ACKNOWLEDGEMENTS v

NOMENCLATURE vi

TABLE OF CONTENTS vii

LIST OF FIGURES ix

LIST OF TABLES x

CHAPTER I INTRODUCTION AND LITERATURE REVIEW 1

- Landscape-scale Habitat 1
- Local-scale Habitat 5
- Research Objectives 10

CHAPTER II LANDSCAPE-SCALE POST-FLEDGING HABITAT USE 11

- Introduction 11
- Study Objectives 15
- Study Area 16
- Methods 19
- Results 27
- Discussion 34

CHAPTER III LOCAL-SCALE POST-FLEDGING HABITAT USE 38

- Introduction 38
- Study Objectives 42
- Study Area 43
- Methods 43
- Results 46
- Discussion 59

CHAPTER IV CONCLUSION AND MANAGEMENT RECOMMENDATIONS 64

REFERENCES 68

APPENDIX A 75

APPENDIX B 77

LIST OF FIGURES

Page

Figure 1. Hypothetical relationships demonstrating three possible drivers of post-fledging habitat (adapted from Garshelis 2000) 9

Figure 2. Map of the study area (2013–2014) within the black-capped vireo's breeding range in the U.S. 19

Figure 3. Mean proportions of available woodland and woodland and associated standard error bars at low, medium, and high woodland availability (WA) sites at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 29

Figure 4. Observed distance (m) and associated 95% confidence intervals between black-capped vireo fledgling locations and woodland cover over the post-fledging season and at low, medium, and high woodland availability (WA) sites at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 30

Figure 5. Observed mean distance (m) and associated 95% confidence intervals between young, intermediate, and old black-capped vireo fledgling locations and woodland cover at low, medium, and high woodland availability sites at the Balcones Canyonlands National Wildlife Refuge area, US, 2013–2014...31

Figure 6. Predicted black-capped vireo post-fledging woodland use over the post-fledging season and associated 95% confidence intervals at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 32

Figure 7. Mean predicted post-fledging woodland use for young, intermediate, and old black-capped vireo fledglings and associated 95% confidence intervals at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 34

LIST OF TABLES

Page

Table 1. Number of total black-capped vireo fledgling locations, fledgling locations in woodland cover, and proportion of locations in woodland cover during the early, middle, and late post-fledging period at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 32

Table 2. Number of total black-capped vireo fledgling locations, fledgling locations in woodland cover, and proportion of locations in woodland cover for each post-fledging age class at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 33

Table 3. Comparison of vegetation metrics (mean ± SD) of study site-wide sampling points in non-woodland cover between low, medium, and high woodland availability (WA) sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 48

Table 4. Comparison of vegetation metrics (mean ± SD) between fledgling locations in non-woodland cover at low, medium, and high woodland availability (WA) sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 49

Table 5. Comparison of vegetation characteristics (mean ± SD, minimum, and maximum) between locations of black-capped vireo fledgling detection points and study site-wide sampling points in non-woodland cover on study sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 50

Table 6. Comparison of vegetation metrics (mean ± SD) between study site-wide sampling points in woodland cover at low, medium, and high woodland availability (WA) sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 52

Table 7. Comparison of vegetation metrics (mean ± SD) between fledgling locations in woodland cover at low, medium, and high woodland availability (WA) sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 53

Table 8. Comparison of vegetation metrics (mean ± SD, minimum, and maximum) between locations of black-capped vireo fledgling detection points and study site-wide sampling points occurring in woodland cover study sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 54

Table 9. Comparison of vegetation metrics (mean ± SD, minimum, and maximum) between locations of black-capped vireo fledgling detection points and nest sampling points occurring in non-woodland cover on study sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 57

Table 10. Comparison of vegetation metrics (mean ± SD, minimum, and maximum) between locations of black-capped vireo fledgling detection points and nest sampling points in woodland cover on study sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014. 58

CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Landscape-scale Habitat

The habitat needs of migratory birds are a growing concern due to declining population trends (Sauer et al. 2003) and increasing anthropogenic disturbance of breeding, wintering, and migratory stopover habitats (Martin and Finch 1995). Habitat in the context of wildlife is defined as an area that supports the survival and reproduction of a species, or population, through the provision of appropriate and sufficient resources and conditions (Morrison et al. 2006). A “high quality” habitat allows long-term success of survival and reproduction compared to other areas based on their performance. Therefore, assessing habitat quality is vital for maintaining stable populations of migratory birds by enhancing productivity, particularly for endangered species that face threats from habitat loss and fragmentation, and parasitism.

One such endangered species in the black-capped vireo (*Vireo atricapilla*; hereafter vireo). The vireo is a migratory songbird that was listed as an endangered species in 1987 by USFWS due to habitat loss and nest predation by the brown-headed cowbird, (*Molothrus ater*; Ratzlaff 1987). Its breeding range historically included Kansas, Oklahoma, Texas and central Coahuila, Mexico (Shull 1986) but the vireo currently breeds only in central and southwest Texas, and in parts of Oklahoma and Northern Mexico (Grzybowski 1995, Wilkins et al. 2006).

Vireo breeding habitat consists of low, scrubby shrubs and trees that are usually of irregular height (Graber 1961). Vireo territories have high densities of deciduous growth with heights less than 2 m, and in Texas and Oklahoma habitats had 30% to 45% deciduous cover and 36% to 55% woody cover, including junipers (*Juniperus* spp.; Grzybowski 1995). Across the vireo's range, breeding habitat varies regionally due to differences in soil composition, land management practices, recent fire history, topography, and climate, particularly between east and west Texas where these components have a pronounced effect on the low understory structure (Wilkins et al. 2006, McFarland et al. 2012). In some parts of their range vireos occupy and reproduce successfully in deciduous and oak-juniper woodlands (*Quercus* spp.; M. Martinez, pers. obs., Pope 2013), which were previously considered as marginal or lower-quality habitats compared to shrublands.

The loss of typical vireo breeding habitat has been attributed to several factors. Vireos generally occur in early to mid-successional vegetation that historically relied on disturbances like fire to maintain suitable breeding habitat (Graber 1961, Benson and Benson 1990, USFWS 1991). Repeated burning was a common feature of rangelands prior to European settlement and was a major factor in the formation of an oak-dominated plant community within the vireo breeding range (Smeins 1980, Fonteyn et al. 1988, Diamond et al. 1995). However, the absence of fire allowed vegetation successional phases to advance, resulting in unfavorable changes to the structural characteristics of the native rangelands and woodlands for the vireo (Wilkins et al. 2006). Vegetation succession occurs from an increase in canopy cover and stature of woody vegetation and was considered a factor of habitat reduction in the federal listing of the species (Ratzlaff 1987). Fire suppression coupled with over-browsing reduces the suitability of nesting habitat for vireos by converting a mixed-oak savannah into an Ashe juniper-dominated (*J. ashei*) woodland with dense understory (Fonteyn et al. 1988, Marshall et al. 1985). Thus, fire suppression is regarded as an indirect threat to the vireo as a cause of loss of breeding habitat (Grzybowski 1995, Gehlbach 1988, Smeins and Merrill 1988).

As the pressures for land use conversion and private land fragmentation increases across the vireo's breeding range, efficient land management strategies to sustain vireo populations are of increasing demand. Much of the breeding habitat restoration efforts include coordinated brush control, prescribed burning, grazing management, and cowbird trapping to improve reproductive success (USFWS 1991, Wilkins et al. 2006). Though reproductive success is a critical component of population persistence, the exclusive use of nest success as a measure of seasonal productivity ignores the fundamental relationship between juvenile survival and population growth and can yield misleading results (Streby and Andersen 2011). Studies have shown that fluctuations in juvenile survival can significantly influence the growth rate and viability of a population (Arcese et al. 1992, Gaillard et al. 1998, Finkelstein et al. 2010) and that juvenile survival is more affected by environmental variation such as weather, habitat structure and population density (Albon et al. 2000, Powell et al. 2000, Robinson et al. 2007). Despite the importance of post-fledging ecology, current vireo management fails to consider this life-stage due to a lack of research.

Compared to the adult life-stage, knowledge of the juvenile life-stage, particularly the post-fledging period between fledging and migration, is limited in the vireo and among Neo-tropical migratory songbirds in general (Anders et al. 1998, Streby and Andersen 2011). This shortcoming is due to limitations in detection of young that behave more secretively after fledging or, that disperse long distances away from their natal area (Anders et al. 1998). During the post-fledging period, young must transition from parental care to self-sufficiency and cope with novel demands in their environment such as acquiring foraging skills and avoiding predators. Additionally, fledglings must learn to forage sufficiently to accumulate fat reserves for migration (Moore et al. 1993). The numerous ecological pressures on fledglings accentuate the importance of appropriate habitat during this vulnerable period.

Recognizing habitat requirements are necessary to implement effective species management practices. Additionally, it is important to consider how these requirements may change as wildlife-habitat associations shift over space and time. Animals typically respond to their environments at two spatial scales; the landscape or macrohabitat, which identifies general environmental factors, vegetation types, and seral stages; and the local or microhabitat, which emphasizes specific environmental conditions such as vegetation structure and composition (Morrison 2009). Although one scale may be better predictor of a response, a multi-scale spatial approach in avian habitat use studies may uncover different patterns than a single-scale approach (Block and Brennan 1993). For instance, yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) selected nest sites in marshes with high odonate abundance, their primary food source during the nesting period (Gordon and Wittenberger 1991). However, at the microhabitat scale, nest location correlated with vegetation density and not local odonate abundance. While features at the local scale can promote the understanding of the mechanisms driving landscape-scale patterns, data collected from these two scales are complementary and are needed to implement comprehensive habitat management plans.

Habitat associations also shift between seasons or years due changes in regional weather patterns, food abundance, predators-prey interactions, and population dynamics (Block and Brennan 1993). For example, biomass, abundance, and order richness of arthropods, the primary forage of vireos, vary by tree species and timing during the breeding seasons in central Texas (Morgan 2012). Habitat associations also change over an animal's lifetime where particular abilities (e.g., mating and vocalizing) and tasks (e.g., rearing young and establishing territories) vary with developments in age, physiology, or status. For instance, during the post-fledging stage, young must develop the ability to fly, forage, and seek cover from predators. Within the first two weeks of fledging, vireo young are largely dependent on adults for food (Graber 1961), but as they age, they become more independent and may leave the territory (Grzybowski 1995). These behavioral shifts during the post-fledging stage have not yet been linked to changes in habitat associations over spatial or temporal scales in the vireo.

Local-scale Habitat

Comprehensive studies on fledgling habitat use and movement patterns have been conducted for only a few Neo-tropical songbird species. In several of these studies, young used vegetation types different from their typical nesting habitats. For instance, juvenile wood thrushes (*Hylocichla mustelina*) in Missouri (Anders et al. 1998) and Virginia (Vega Rivera et al. 1998) dispersed from their nesting areas, consisting of mature oak-hickory (*Carya* spp.) forest, and moved into early-successional vegetation with greater vertical structure, denser understory, and thicker cover. Other studies found migratory songbirds that nested in late successional woodland used regenerating clearcuts during the post-fledging period (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2007).

King et al. (2006) reported that fledgling ovenbirds (*Seiurus aurocapilla*) selected areas with greater vegetation structure and fewer trees than the nesting sites, and usage of these habitats increased their survival. Ovenbird fledgling survival was influenced by the distance of the nest to various non-nesting cover types and the subsequent selection among those cover types, but that the influence of non-nesting cover types varied depending on the availability of dense understory vegetation in mature forest (Streby and Andersen 2011). These studies confirm that vegetation characteristics of the post-fledging habitat differ from those of the nesting habitat for several songbird species and that these differences may have consequences on survivorship.

Although post-fledging habitat use and movement patterns have not been studied extensively in the Vireonidae family, there are several accounts of fledgling black-capped vireos using habitat different than typical nesting habitat. Graber (1961) observed family groups move from typical nesting habitat into shaded ravines with water, and from hillsides into heavily wooded, dry streambeds, respectively. Fledglings in Travis, Burnet, and Kerr Counties, Texas were observed moving from their nests in shrubby vegetation to more heavily wooded areas and foraging in juniper woodland along canyon ridges and slopes, one woodland cluster being >4 m in average height (Houston 2008).

Dittmar et al. (2014) found that independent fledglings at Fort Hood Military Reservation in Texas selected riparian areas over other vegetation types and used areas characterized by greater canopy cover, denser foliage, and higher arthropod abundance. Such findings verify that fledglings use areas atypical of nesting habitat and may prefer patches of greater vertical variation more than low-growing shrub habitat. However, research that assesses the intensity of use and selection of these areas by fledglings is lacking. Knowing where fledglings occur and the vegetation components that characterize post-fledging habitat would not only uncover important aspects of post-fledging ecology, but would assist landowners in managing habitat that enhances productivity for all life stages of the vireo.

Several hypotheses have been proposed to explain post-fledging habitat use patterns of migratory birds. Four hypotheses pertinent to the vireo are breeding site selection, food search, socialization, and predator-avoidance. The breeding site selection hypothesis states that fledglings explore habitat prior to migration to prospect for future breeding sites (Morton et al. 1991). So they spend a portion of time outside of their natal territories visiting potential breeding habitat, and then return to those visited sites the subsequent year to establish a territory. The food search hypothesis states that fledglings disperse from their natal areas to look for available food resources and familiarize themselves with feeding sites to use in future nesting seasons (Eden 1987), so their foraging time increases with increasing availability of a food-rich habitat type (Fig. 1A).

The predator-avoidance hypothesis states that fledglings select habitat with greater vegetation complexity that offers protection from predators (King et al. 2006), so they select for areas with a specific range of a vegetation feature (e.g., cover) and selection of those areas increases their survival (Fig 1B). The socialization hypothesis proposes that fledglings disperse from their natal areas to flock with conspecifics to socialize and migrate with, as well as to locate patchy food resources and protect from predators (Hamilton 1971, Powell 1974). So fledgling density increases with increasing measures of a vegetation feature (e.g., cover) that provides protection from predators, food resources, or ideal microclimatic conditions (Fig. 1C).

These hypotheses reinforce the importance of vegetation in an animal's habitat, by explaining how vegetative variation can influence the local conditions and overall quality of the habitat (Morrison et al. 2006). Therefore it is essential that land managers understand the vegetative conditions, succession, and associations of the land and the factors that affect them. It is this increased knowledge of wildlife-habitat relationships that promotes efficient and sustainable management actions.

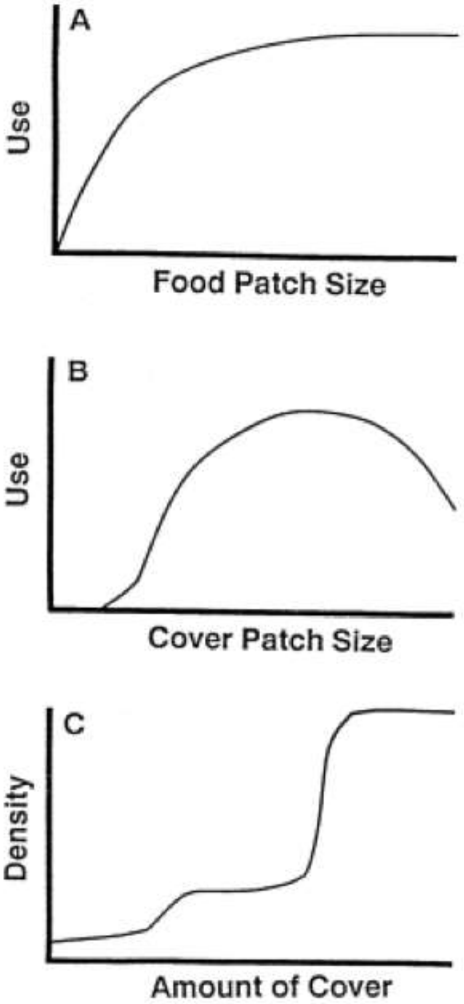


Figure 1. Hypothetical relationships demonstrating three possible drivers of post-fledging habitat (adapted from Garshelis 2000). In Fig. 1A, food resources drives fledglings to increase their foraging with increasing availability of a food-rich habitat type. In Fig. 1B, predator avoidance drives fledglings to select for areas with greater vegetation cover and the selection of those areas increase their survival. In Fig. 1C, socialization drives fledgling density to increase with increasing cover, which provides protection from predators, food resources, and ideal microclimatic conditions.

Research Objectives

The overall research objectives of this research study are 1) use a multi-scale approach to evaluate post-fledging habitat and 2) identify temporal changes in post-fledging habitat use and characteristics. In Chapter II, first I address landscape-scale use versus availability of woodland cover of post-fledging habitat. I predict fledglings use woodland cover greater than its availability in the study area. Second, I identify changes in woodland use over the post-fledging season and with post-fledging age. I predict post-fledging use of woodland increases over both temporal scales. Third, I quantify fledgling movements towards woodland cover over time. I predict fledglings move closer to woodland cover over both temporal scales.

In Chapter III, I assess local-scale characteristics of post-fledging habitat. I predict that in non-woodland cover, fledglings use areas with greater cover and higher compositions of key species than what is typical of the study area. In woodland cover, fledglings use areas similar in vegetation structure and composition to the study area. Second, I identify changes in local-scale characteristics of post-fledging habitat over the post-fledging season and with post-fledging age. I predict cover and compositions of key species of areas used by fledglings increase over both temporal scales. Third, I compare local-scale characteristics between post-fledging and nesting habitats. I predict in non-woodland cover, fledglings use areas with greater cover and compositions of key species than at nest sites. In woodland cover, fledglings use areas with similar vegetation structure and composition as the nest sites. In Chapter IV, I present conclusions and management implications of my results from Chapters II and III.

CHAPTER II

LANDSCAPE-SCALE POST-FLEDGING HABITAT USE

Introduction

The habitat needs of migratory birds are a growing concern due to declining population trends (Sauer et al. 2003) and increasing anthropogenic disturbance of breeding, wintering, and migratory stopover habitats (Martin and Finch 1995). Habitat in the context of wildlife is defined as an area that supports the survival and reproduction of a species, or population, through the provision of appropriate and sufficient resources and conditions (Morrison et al. 2006). A "high quality" habitat allows long-term success of survival and reproduction compared to other areas based on their performance. Therefore, assessing habitat quality is vital for maintaining stable populations of migratory birds by enhancing productivity, particularly for endangered species that face threats from habitat loss and fragmentation, and parasitism.

One such endangered species in the black-capped vireo (*Vireo atricapilla*; hereafter vireo). The vireo is a migratory songbird that was listed as an endangered species in 1987 by USFWS due to habitat loss and nest predation by the brown-headed cowbird, (*Molothrus ater*; Ratzlaff 1987). Its breeding range historically included Kansas, Oklahoma, Texas and central Coahuila, Mexico (Shull 1986) but the vireo currently breeds only in central and southwest Texas, and in parts of Oklahoma and Northern Mexico (Grzybowski 1995, Wilkins et al. 2006).

Vireo breeding habitat consists of low, scrubby shrubs and trees that are usually of irregular height (Graber 1961). Vireo territories have high densities of deciduous growth with heights less than 2 m, and in Texas and Oklahoma habitats had 30% to 45% deciduous cover and 36% to 55% woody cover, including junipers (*Juniperus* spp.; Grzybowski 1995). Across the vireo's range, breeding habitat varies regionally due to differences in soil composition, land management practices, recent fire history, topography, and climate, particularly between east and west Texas where these components have a pronounced effect on the low understory structure (Wilkins et al. 2006, McFarland et al. 2012). In some parts of their range vireos occupy and reproduce successfully in deciduous and oak-juniper woodlands (*Quercus* spp.; M. Martinez, pers. obs., Pope 2013), which were previously considered as marginal or lower-quality habitats compared to shrublands.

The loss of typical vireo breeding habitat has been attributed to several factors. Vireos generally occur in early to mid-successional vegetation that historically relied on disturbances like fire to maintain suitable breeding habitat (Graber 1961, Benson and Benson 1990, USFWS 1991). Repeated burning was a common feature of rangelands prior to European settlement and was a major factor in the formation of an oak-dominated plant community within the vireo breeding range (Smeins 1980, Fonteyn et al. 1988, Diamond et al. 1995). However, the absence of fire allowed vegetation successional phases to advance, resulting in unfavorable changes to the structural characteristics of the native rangelands and woodlands for the vireo (Wilkins et al. 2006). Vegetation succession occurs from an increase in canopy cover and stature of woody vegetation and was considered a factor of habitat reduction in the federal listing of the species (Ratzlaff 1987). Fire suppression coupled with over-browsing reduces the suitability of nesting habitat for vireos by converting a mixed-oak savannah into an Ashe juniper-dominated (*J. ashei*) woodland with dense understory (Fonteyn et al. 1988, Marshall et al. 1985). Thus, fire suppression is regarded as an indirect threat to the vireo as a cause of loss of breeding habitat (Grzybowski 1995, Gehlbach 1988, Smeins and Merrill 1988).

As the pressures for land use conversion and private land fragmentation increases across the vireo's breeding range, efficient land management strategies to sustain vireo populations are of increasing demand. Much of the breeding habitat restoration efforts include coordinated brush control, prescribed burning, grazing management, and cowbird trapping to improve reproductive success (USFWS 1991, Wilkins et al. 2006). Though reproductive success is a critical component of population persistence, the exclusive use of nest success as a measure of seasonal productivity ignores the fundamental relationship between juvenile survival and population growth and can yield misleading results (Streby and Andersen 2011). Studies have shown that fluctuations in juvenile survival can significantly influence the growth rate and viability of a population (Arcese et al. 1992, Gaillard et al. 1998, Finkelstein et al. 2010) and that juvenile survival is more affected by environmental variation such as weather, habitat structure and population density (Albon et al. 2000, Powell et al. 2000, Robinson et al. 2007). Despite the importance of post-fledging ecology, current vireo management fails to consider this life-stage due to a lack of research.

Compared to the adult life-stage, knowledge of the juvenile life-stage, particularly the post-fledging period between fledging and migration, is limited in the vireo and among Neo-tropical migratory songbirds in general (Anders et al. 1998, Streby and Andersen 2011). This shortcoming is due to limitations in detection of young that behave more secretively after fledging or, that disperse long distances away from their natal area (Anders et al. 1998). During the post-fledging period, young must transition from parental care to self-sufficiency and cope with novel demands in their environment such as acquiring foraging skills and avoiding predators. Additionally, fledglings must learn to forage sufficiently to accumulate fat reserves for migration (Moore et al. 1993). The numerous ecological pressures on fledglings accentuate the importance of appropriate habitat during this vulnerable period.

Recognizing habitat requirements are necessary to implement effective species management practices. Additionally, it is important to consider how these requirements may change as wildlife-habitat associations shift over space and time. Animals typically respond to their environments at two spatial scales; the landscape or macrohabitat, which identifies general environmental factors, vegetation types, and seral stages; and the local or microhabitat, which emphasizes specific environmental conditions such as vegetation structure and composition (Morrison 2009). Although one scale may be better predictor of a response, a multi-scale spatial approach in avian habitat use studies may uncover different patterns than a single-scale approach (Block and Brennan 1993). For instance, yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) selected nest sites in marshes with high odonate abundance, their primary food source during the nesting period (Gordon and Wittenberger 1991). However, at the microhabitat scale, nest location correlated with vegetation density and not local odonate abundance. While features at the local scale can promote the understanding of the mechanisms driving landscape-scale patterns, data collected from these two scales are complementary and are needed to implement comprehensive habitat management plans.

Habitat associations also shift between seasons or years due changes in regional weather patterns, food abundance, predators-prey interactions, and population dynamics (Block and Brennan 1993). For example, biomass, abundance, and order richness of arthropods, the primary forage of vireos, vary by tree species and timing during the breeding seasons in central Texas (Morgan 2012). Habitat associations also change over an animal’s lifetime where particular abilities (e.g., mating and vocalizing) and tasks (e.g., rearing young and establishing territories) vary with developments in age, physiology, or status. For instance, during the post-fledging stage, young must develop the ability to fly, forage, and seek cover from predators. Within the first two weeks of fledging, vireo young are largely dependent on adults for food (Graber 1961), but as they age, they become more independent and may leave the territory (Grzybowski 1995). These behavioral shifts during the post-fledging stage have not yet been linked to changes in habitat associations over spatial or temporal scales in the vireo.

Study Objectives

The specific study objectives were to (a) evaluate post-fledging habitat use versus availability, (b) assess temporal changes in post-fledging habitat use, and (c) quantify post-fledging movements towards woodland cover. Vireo adults and fledglings are known to use woodland in addition to shrubland (Pope 2013, Dittmar et al. 2014). Woodland areas may provide more canopy cover for avoiding predators (M. Martinez, pers. obs.) and additional food resources than non-woodland areas due to differences in vegetation and arthropod species (Morgan 2012). Therefore, I predicted fledglings would use woodland greater than its availability in the study area. To account for site variability, I assessed patterns in post-fledging habitat use based on differences in woodland availability. I predicted fledglings would use woodland similarly at sites with low, medium, and high woodland availabilities.

As temperature increases and food availability decreases over the post-fledging season, woodland may provide more shade and abundant food resources than shrubland due to greater canopy cover and different tree species composition, respectively (Morgan 2012). Additionally, during the first week post-fledging young tend to conceal themselves, remain near the nest, and depend on parents for food (M. Martinez, pers. obs.) and after four weeks, young can fly farther distances and forage independently (Graber 1961, Dittmar et al. 2014). Therefore, I predicted post-fledging use of woodland increases over post-fledging season and with post-fledging age and fledglings will move closer to the woodland cover over both temporal scales.

Study Area

I established my study area in the Edwards Plateau ecoregion of central Texas, consisting of areas within BCNWR and several private properties. The Ecological Systems Classification and Mapping Project classifies the ecosystem of the area as Edwards Plateau Limestone Savanna and Woodland (Texas Parks & Wildlife Department). The dominant landcover types are shrubland, limestone woodland, dry-mesic slope woodland, riparian forest, and grassland. Steep canyons characterize the topography of the area with broad plateaus primarily composed of limestone bedrock (Sellards 1933). The woody vegetation is predominantly composed of the evergreen Ashe juniper with sub-dominant species of broad-leafed hardwood such as Texas red oak (*Quercus buckleyi*), plateau live oak (*Q. virginiana var. fusiformis*), post oak (*Q. stellata*), shin oak (*Q. havardii*), and escarpment black cherry (*Prunus serotina var. exima*; Diamond 1997, Gehlbach 1988). The study area is classified as sub-humid, having mean annual precipitation of 60 cm, with an accumulation of approximately 39.5 cm between March and July during the vireo's breeding season. The accumulation of precipitation from March–July was average in 2013 at 39.5 cm and below average in 2014 at 21.6 cm and had Palmer Drought Severity Index (PDSI) values of -3.16 and -2.61, respectively. Mean annual temperature in this region is 18.5°C, with an average of 22.4°C from March–July. Mean temperatures were average during these months in 2013 and 2014 at 22.9 °C and 22.7 °C, respectively (NCDC 2014).

I included BCNWR in my study sites for its known breeding vireo populations (Sexton 2002, 2005), suitable breeding habitat, and vegetative heterogeneity resulting from a prescribed burning program. The BCNWR lies along the eastern edge of the Edwards Plateau region in central Texas and was acquired in 1992 under the Endangered Species Act of 1973 to preserve breeding habitat for the endangered golden-cheeked warbler (*Dendroica chyrsoparia*) and vireo (USFWS 2001). BCNWR currently contains 53 noncontiguous tracts of land covering over 8,100 ha (USFWS 2001). To obtain adequate variation at the landscape scale, I systematically chose tracts that represented high, medium, and low woodland coverage. Within each category, I specifically selected tracts with a minimum area of 75 ha, located >3 km from other tracts, and had known breeding vireos. This is because vireo territories range from 1 ha (Graber 1961) to 10 ha (Tazik 1991) and first year males can disperse several kilometers to establish new territories. Therefore, this design increased the likelihood that each study site would host >7 territories and that males would not establish territories at 2 different study sites. In addition, I selected 2 tracts where a pilot study on vireo post-breeding habitat use was conducted by Texas A&M University in 2012 providing useful preliminary data.

In 2013, the study sites were the North Rodgers (188 ha), Rodgers East (132 ha), southwest Eckhardt and Heine (270 ha), and Simons (275 ha) tracts on BCNWR, which included a 200 m buffer around the perimeter of each tract to account for within-season dispersal. The buffer overlapped with portions of 3 private properties in Williams, Travis, and Burnet Counties. In 2014 the study sites were 4 private properties that ranged from 78–240 ha. The 200 m buffer overlapped with 4 tracts on BCNWR. The total area studied in 2013 and 2014 covered approximately 733 ha and 559 ha, respectively, across Travis, Burnet, and Williamson Counties (Fig. 2).

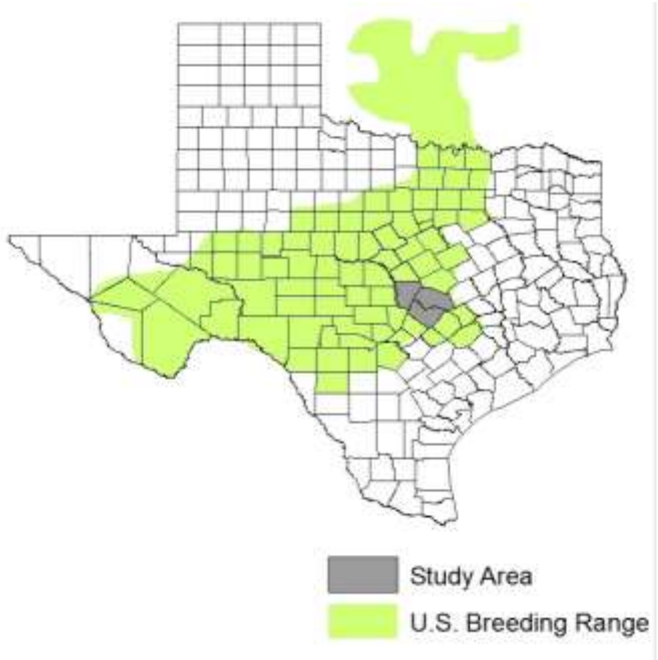


Figure 2. Map of the study area (2013–2014) within the black-capped vireo's breeding range in the U.S.

Methods

Data Collection

Early Breeding Transect Surveys

I conducted early breeding transect to determine vireo occupancies. I created a grid network of points with 200 by 200 m spacing, originating from a random starting point, across the entirety of each study site. I walked from point to point at a 1 km/hr pace from sunrise to 13:00 to detect singing male vireos and marked their locations with a Garmin GPS unit. I conducted early breeding transect surveys at each study site 2–3 times per week for 1–2 weeks.

Territory Mapping

After conducting early breeding transect surveys, I visited the locations of each singing male vireo every 3–5 days to delineate the spatial extent of each vireo territory. I used the locations of individual male vireos to estimate fixed kernel density utilization distributions (UDs) or minimum convex polygons (MCPs) for each monitored territory (Seaman et al. 1996, 1999) using ArcGIS 10.1 (ESRI Inc., Redlands, CA). To obtain points for UDs or MCPs, I used a GPS unit to mark vireo locations every 2 min, recording up to 30 points in 1 hr (Barg et al. 2005). This method is referred to as burst sampling and the constructed UDs represent the relative frequency distribution of a bird's location over a specified period (Van Winkle 1975). I only constructed UDs using male points within the 2-min sampling range for territories with >30 points at the end of the breeding. When there was insufficient data to construct UDs, I created MCPs for all territorial males with >15 points but <30 points. MCPs included all male points, regardless of time interval between point location records. For vegetation measurement purposes, I defined the spatial extent of each territory by the 50% UD polygon or MCP.

I assumed that each territory represented an individual male. If a singing male was present for over 4 weeks in an area, I defined that area as an established territory. I ceased territory mapping in a territory when adults were no longer exhibiting breeding activity. While territory mapping, I monitored the reproductive status vireos to estimate productivity. Using a ranking system, I determined mating status (e.g., paired, breeding) by the presence or absence of females within territories and territory success by the presence of ≥1 fledged young (Vickery et al. 1992).

Nest Searching and Monitoring

When a female was located in a monitored territory, I focused attention on her behavior. Using behavioral cues that signify breeding of adults (e.g., alarm calls, carrying nest material, carrying food, males singing on the nest) and a search image, I searched the monitored vireo territories for nests every 3–5 days, spending no longer than 1 hr in a territory per visit as stipulated by the federal permit. Once I located a nest, I checked the status of the nest every 2–3 days until the nest failed or fledged young. I used a nest mirror, binoculars, or direct observation to determine the contents of nests, choosing the method that caused the least disturbance to the nest and nearby vegetation. To reduce the risk of force-fledging young, I conducted nest checks with binoculars after day 8 of the nestling period and rechecked the nest within 48 hr of the estimated day of fledge. When a nest failed, I monitored the territory for another nesting attempt. If the nest fledged, I began post-fledging habitat monitoring in that territory (see Post-fledging Monitoring).

Banding and Resighting

I banded nestlings 6–8 days old when they are of adequate size to receive the bands but too young to fledge prematurely. I marked nestlings with one numbered USGS anodized aluminum band colored red to identify birds banded by Texas A&M University, and a unique combination of plastic color bands. After banding, I rechecked nest within 1 hr to observe whether parents resumed normal parental behavior (e.g., feeding, shading, shradding). I relied on color band resighting for fledgling identification. In addition, I used targeted mist-netting when possible to band adult vireos to assist in family group identification. Texas A&M University, USFWS, or other research institutions banded several adult vireos in previous years.

Post-fledging Monitoring

Territory Visits: I conducted post-fledging monitoring at a territory when ≥1 host young successfully fledged. I approached the nest area and searched for fledglings using visual or audio cues from the parent (e.g., food carries, calling) or young (e.g., begging calls). Upon detection of a fledgling, I conducted a post-fledging survey (see Post-fledging). I visited territories every 3–5 days to relocate fledglings by approaching the area of the last detection. If I detected adults but not fledglings between 30 min and 1 hr of searching the territory, I returned within the next 2 days to attempt to locate fledglings. If I detected neither adults nor fledglings, I expanded my search <200 m outwards from the territory for 30 min to 1 hr. If I did not find any members of the family group after 3 consecutive visits, I ceased visits at that territory and relied on transect visits to relocate fledglings (see Post-fledging Monitoring: Transect Visits). If I did not detect fledglings after 3 consecutive visits and they were at >4 weeks post-fledging, I assumed that the fledglings dispersed out of the territory (Grzybowski 1995) or have died, ceased territory visits, and relied on transect visits to locate fledglings.

Transect Visits: I conducted transect visits across the study site by walking the same transects used during the early breeding transect surveys. I conducted transect visits to detect fledglings that moved out of a territory with a family group, dispersed independently, or fledged from undetected nests (and were therefore not banded). I began transect visits at a study site approximately 3 weeks from the day the first nest fledged at that site. I walked transects every 3–5 days at a 1 km/hr pace from sunrise to 13:00 looking and listening for vireos. If I detected an adult, I followed it for 10 min to search for fledglings. Upon detection of a fledgling I conducted a post-fledging survey (see Post-fledging Survey) and returned to the point. To minimize time of day effects I varied the temporal order in which I visited transects. Additionally, I began surveying at opposite ends of a transect with each visit to minimize spatial bias that may arise from flushing birds ahead of me in the same direction during each survey. I alternated between transect visits and territory visits at each site so that I visited the site about every 2 days. I ceased transect visits at a study site when there were consistently zero fledgling detections.

Post-fledging Survey

I conducted post-fledging surveys to record vegetation use and key behavioral information associated with a focal fledgling at a specific location at a point in time. Upon detection of a fledgling, I took an initial GPS point of its location and then 1 GPS point of its location every 2 min for 10 min for a total of 5 GPS points. Every 2 min I also recorded the species of the substrate the focal fledgling was in and the behavior it displayed for the majority of the 2-min interval. I used behavioral observations to assist in ageing (see Ageing of Fledglings). After the 10-min survey, I spent up to 30 min to determine if the focal fledgling was banded and resight its color band combinations. I also resighted all conspecifics that were present during the survey. After 30 min passed, I recorded a GPS point of the location where I last detected the focal fledgling.

I remained at a distance of >10 m from the bird, making sure not to approach too closely or aggressively to avoid influencing the behavior or movement of the fledgling or nearby birds. If I influenced the behavior of any birds (e.g., birds began shradding, fledglings ceased begging calls), I left the area and returned after 5 min to determine if birds have resumed normal activity to minimize bias. If birds resumed normal activity, I began the survey and recorded the start time.

Ageing of Fledglings

While conducting post-fledging surveys I used behavioral and physiological cues to categorize the focal fledgling's age class as young (<2 weeks post-fledging), intermediate (2–4 weeks post-fledging), or old (>4 weeks post-fledging). Young fledglings tend to be completely dependent on parents for food and remain near the nest (<20 m) and concealed in the vegetation (Graber 1961, Grzybowski 1995, Pope 2013). Intermediate fledglings become more adept at flying and move about the territory and forage, but typically remain with the family group (Graber 1961, M. Martinez pers. obs.). Old fledglings begin to forage and travel outside of the territory alone and eventually reach independence at this age. (Graber 1961, Grzybowski 1995, Dittmar et al. 2014). I determined the age class for banded fledglings by calculating the number of days since fledging based on known or estimated fledging date. In addition, I calibrated ages of non-banded fledglings based on the plumage and tail lengths of banded birds with known ages. I characterized non-banded fledglings with similar physical characteristics of a banded fledgling as the same age class.

Data Analysis

Landcover Map

To assess the landscape of my study area, I produced a landcover map that delineated woodland and non-woodland cover at each study site. Using ArcGIS, I created a 300-m buffer around the minimum convex polygon (MCP) of all fledgling GPS points because 300 m is the mean distance juvenile vireos move between consecutive locations (Dittmar et al. 2014). I used 2012 National Agriculture Imagery Program (NAIP, 1 m resolution) and ecological site descriptions collected by the Natural Resources Conservation Service (U.S. Department of Agriculture) as base layers. The years when these images and classifications were collected did not need to overlap the years of this study since the study area did not undergo considerable landcover change from what I was able to detect via NAIP imagery and on-the-ground observations.

Using my on-the-ground knowledge of the vegetation communities at each study sites, I used visual analysis to identify areas as either woodland or non-woodland cover. I defined woodland cover as contiguous vegetation of oak-juniper and deciduous forest (excluding oak mottes within a non-woodland area). I defined non-woodland as contiguous vegetation of shrub cover (including oak mottes within a non-woodland area), herbaceous cover, and bare ground. To calculate the percentage of available woodland cover, I divided the area of woodland cover by the total area of woodland and non-woodland cover. I categorized each study site as low, medium, or high woodland availability (WA) if there was <30%, 30–60 %, or >60% woodland availability at the study site, respectively.

Post-fledging Habitat Use

I used a chi-square test of goodness of fit to test the null hypothesis that fledglings used woodland in proportion to its occurrence within the study area (Neu et al. 1974, Cherry 1996). Since this technique requires that the animal's location be independent, I used the initial GPS point of each post-fledging survey for analyses since these locations were temporally independent. I projected the GPS points onto the landcover map and assigned each point to woodland or non-woodland cover. I calculated woodland use by dividing the total number of GPS points assigned to woodland cover by the total number of GPS points obtained at that site. I compared woodland use by WA class using a chi-square goodness of fit test to determine if woodland availability influenced post-fledging habitat use. I performed all analyses described in this Chapter using R statistical software (R Development Core Team, 2013).

Post-fledging Movements

For each initial fledgling GPS point, I measured the distance to the edge of the nearest woodland cover using Geospatial Modelling Environment 7.3.0 software (Spatial Ecology, LLC). I calculated mean distances for low, medium, and high WA sites separately because the maximum distance was negatively correlated with woodland availability ($R^2 = 0.355$) and conducted a one-way analysis of variance (ANOVA) to test for differences between WA classes. Twenty-nine fledgling locations were removed from the analysis because they belonged to birds that fledged from nests located in woodland cover. I conducted a factorial ANOVA to test the effects of season and age on fledglings' distance to woodland cover for each WA class.

Evaluating Temporal Trends

I used post-fledging season and post-fledging age to identify temporal trends in habitat use at the landscape scale. I averaged the dates the first nest fledged at each site in 2013 and 2014 to determine the start day of the post-fledging season. The season ended on the date of the last post-fledging survey. I categorized the post-fledging season into three periods based on the number of weeks from the start date of the season: early (<4 weeks), middle (4–8 weeks), and late (>8 weeks). I categorized post-fledging age into three classes based on estimated the number of weeks since the bird's fledge date; <2 weeks, 2–4 weeks, and >4 weeks. I was only able to calculate the exact number of weeks post-fledging for birds I banded.

Based on these criteria, I assigned each post-fledging survey a post-fledging period, post-fledging period in days, post-fledging age class, and post-fledging age in days (if the bird was banded). I used a chi-square test of goodness of fit to test the null hypothesis that fledglings during each period, and fledglings of each age class use woodland cover in proportion to its occurrence within the study area. I used a general linear model (GLM) to predict post-fledging woodland use based on the day of post-fledging season and post-fledging age class.

Results

Landscape-scale Habitat Use

Woodland availability of the study area ranged from 5.9% to 80.9% with a mean percent availability (± SD) of 46.3% (± 26.8%, $n = 9$). The area of woodland cover ranged from 6.92–146.61 ha ($\bar{x} = 60.09$, SD = 40.65). At low WA sites, woodland availability ranged from 5.9–16.6% with a mean percent availability was 11.6% (± 5.4%, $n = 3$). Woodland cover was distributed as a single area or as two distinct areas ranging from 3.88–28.06 ha, and the total area covered 6.92–39.38 ha ($\bar{x} = 20.92$, SD = 13.62) of the study sites. At medium WA sites, woodland availability ranged from 46.0–46.7% with a mean availability of 46.4% (± 0.4%, $n = 2$). Woodland cover was either distributed as a single area of 44.15 ha or as two distinct areas of approximately 73.30 ha each, and the total area covered 44.15–146.61 ha ($\bar{x} = 95.38$, SD = 51.23) of the study sites. At high WA sites, woodland availability ranged from 68.0–80.9% with a mean availability of 72.3% (± 5.8%, $n = 4$). Woodland cover was distributed as a single area that enclosed non-woodland cover, and the total area covered 52.83–100.92 ha ($\bar{x} = 71.82$, SD = 18.84) of the study sites.

I conducted 279 post-fledging surveys in 2013 and 238 surveys in 2014. In 2013, 146 of the surveys occurred on two low WA sites and 119 on three high WA sites. There were no medium WA sites in 2013. In 2014, 60 of the surveys occurred on one low WA site, 73 occurred on two medium WA sites, and 63 occurred on two high WA sites. Over both years, I conducted 438 surveys during territory visits and 79 surveys during transect visits. Of the 517 initial fledgling mapping points acquired from post-fledging surveys, 16.2% occurred in woodland cover, which was less than expected based on the mean woodland availability of all sites ($\chi_1^2 = 186.830$, $P < 0.001$). Out of the 85 locations in woodland cover, 82.4% occurred on high WA sites 12.9% occurred on low WA sites, and 4.7% occurred on medium WA sites.

At low, medium, and high WA sites 5.3% ($\chi_1^2 = 8.119$, $P < 0.01$), 4.3% ($\chi_1^2 = 66.126$, $P < 0.001$), and 32.4% ($\chi_1^2 = 175.475$, $P < 0.001$) of the locations occurred in woodland cover, which was less than expected based on the mean woodland availability for each WA class (Fig. 3). Woodland use differed by woodland availability ($\chi_2^2 = 68.890$, $P < 0.001$).

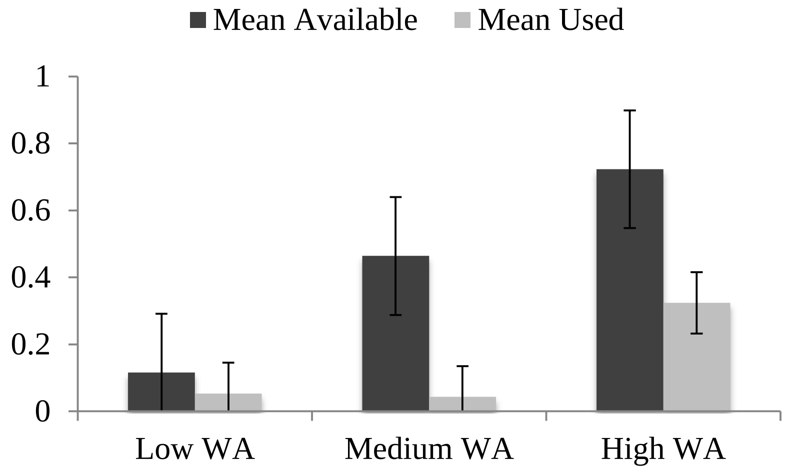


Figure 3. Mean proportions of available woodland and woodland and associated standard error bars at low, medium, and high woodland availability (WA) sites at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Post-fledging Movements

The maximum distance between fledgling location and woodland cover for low, medium, and high WA sites was 483.26 m, 288.44 m, and 119.35 m, respectively. Mean distance between fledgling locations and woodland cover at low WA sites ($\bar{x} = 189.48$, SE = 9.23, n =199), medium WA sites ($\bar{x} = 130.72$, SE = 8.85, n = 93), and high WA sites ($\bar{x}$ = 31.64, SE = 2.25, n = 198) were different from each other ($F_{3,490}$ = 186.64, $P <$ 0.001). On average, fledglings at high WA sites were located 157.25 m and 98.49 m closer to the woodland than fledglings at low and medium WA sites, respectively.

At low, medium, and high WA sites, mean distance to woodland did not change over the season ($F_{1,199}$ = 2.47, P = 0.118; $F_{1,93}$ = 3.04, P = 0.085; $F_{1,196}$ = 0.001, P = 0.975; $F_{2,190}$ = 2.36, P = 0.097; Fig. 4) or with fledgling age ($F_{2,196}$ = 0.16, P = 0.854; $F_{2,92}$ = 0.619, P = 0.541; Fig. 5).

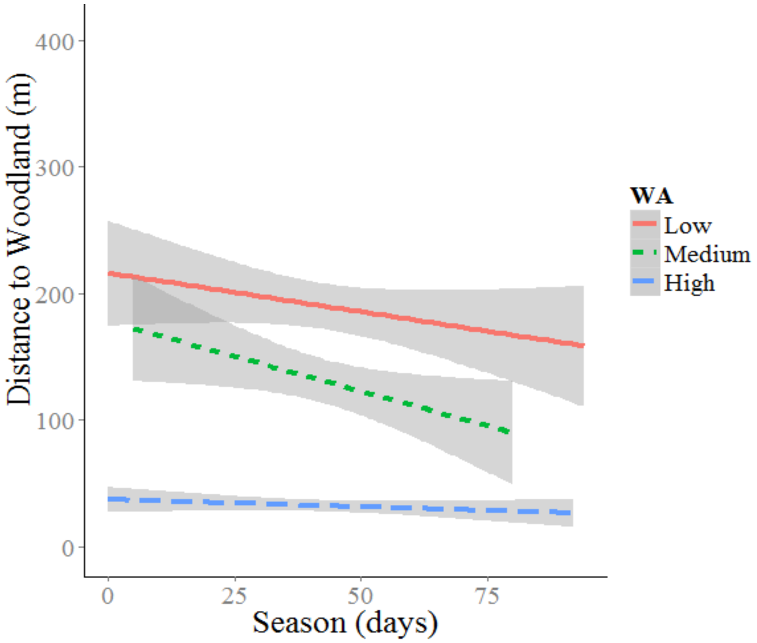


Figure 4. Observed distance (m) and associated 95% confidence intervals between black-capped vireo fledgling locations and woodland cover over the post-fledging season and at low, medium, and high woodland availability (WA) sites at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

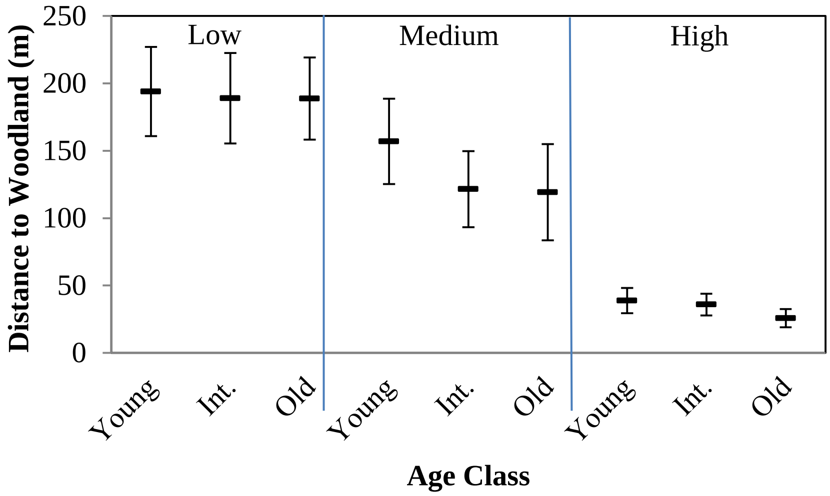


Figure 5. Observed mean distance (m) and associated 95% confidence intervals between young, intermediate, and old black-capped vireo fledgling locations and woodland cover at low, medium, and high woodland availability sites at the Balcones Canyonlands National Wildlife Refuge area, US, 2013–2014.

Temporal Trends in Landscape Scale Habitat Use

Post-fledging Season

The early period of the post-fledging season was 11 May–7 June in 2013 and 17 May–13 June in 2014. The middle period was 8 June–6 July in 2013 and 14 June–12 July in 2014. The late period was 7 July–9 August in 2013 and 13 July–9 August in 2014. During each period, I obtained a lower proportion of fledgling locations in the woodland cover than in the non-woodland cover (early: $\chi_1^2 = 67.047$, $P < 0.001$; middle: $\chi_1^2 = 107.584$, $P < 0.001$; late: $\chi_1^2 = 61.340$, $P < 0.001$). Even though I obtained the majority of fledgling locations during the middle period, the proportion of fledgling locations in woodland cover was not different between periods ($\chi_2^2 = 0.784$, $P = 0.676$; Table 1). The post-fledging season did not have an effect on the probability of woodland use ($z = 0.786$, $P = 0.432$). On day 0 of the post-fledging season, the predicted probability of woodland use is 0.139 (CI, $0.085 \leq x \leq 0.219$) and increased to 0.197 (CI, $0.119 \leq x \leq 0.309$) by day 94 (Fig. 6).

Table 1. Number of total black-capped vireo fledgling locations, fledgling locations in woodland cover, and proportion of locations in woodland cover during the early, middle, and late post-fledging period at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Period	**Total Locations**	**Locations in Woodland**	**Proportion in Woodland**
Early	129	18	0.139
Middle	247	43	0.174
Late	141	24	0.170

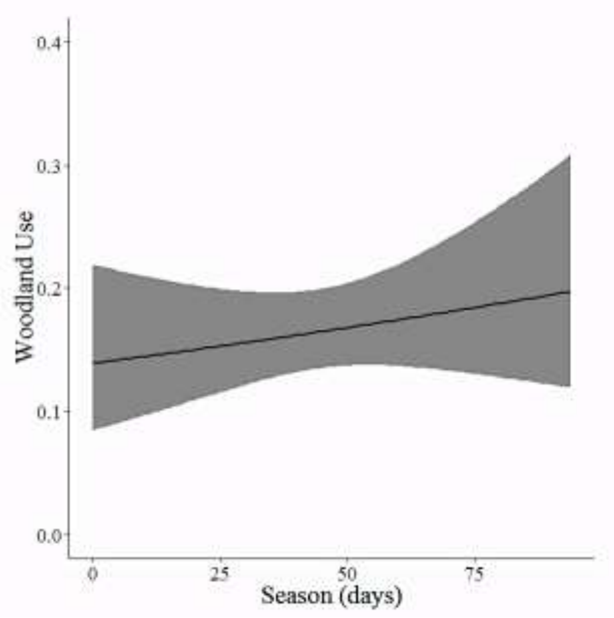


Figure 6. Predicted black-capped vireo post-fledging woodland use over the post-fledging season and associated 95% confidence intervals at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Post-fledging Age

For each age class, I obtained a lower proportion of fledgling locations in woodland cover than in non-woodland cover (young: $\chi_1^2 = 78.192$, $P < 0.001$; intermediate: $\chi_1^2 = 85.383$, $P < 0.001$; old: $\chi_1^2 = 67.328$, $P < 0.001$). Although, I found proportionally more fledglings in woodland cover as age increased, the proportions were not statistically different between age classes ($\chi_2^2 = 2.832$, $P = 0.243$; Table 2). The probability of woodland use was similar amongst young (0.128), intermediate (0.158), and old fledglings (0.197), and age did not have an effect on predicting post-fledging woodland use ($\chi_2^2 = 2.8$ $P = 0.250$; Fig. 7).

Table 2. Number of total black-capped vireo fledgling locations, fledgling locations in woodland cover, and proportion of locations in woodland cover for each post-fledging age class at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Age Class	Total Locations	Locations in Woodland	Proportion in Woodland
Young	141	19	0.135
Intermediate	183	28	0.153
Old	141	28	0.197
NA	10	----	----

Figure 7. Mean predicted post-fledging woodland use for young, intermediate, and old black-capped vireo fledglings and associated 95% confidence intervals at the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Discussion

Landscape Scale Habitat Use and Post-fledging Movements

Fledglings used woodland less than its availability in the study area. Though fledglings will occupy areas of late successional vegetation if it is available, fledglings used non-woodland areas considerably more than woodland areas. This finding supports Dittmar et al.'s (2014) results of fledglings selecting shrub vegetation over other vegetation types. Of the individuals that she captured in the shrubland, many remained in there or moved to riparian habitats, while a few moved between shrub and vegetation or moved into the forest. Post-fledging use of non-woodland areas indicate that these areas provide important resources that may not differ than those used by adults during the breeding season, such as protective cover and food availability. Dittmar et al. (2014) found that arthropod abundance did not significantly differ between vegetation types, though it was lower at forest than shrub. The canopy and shrub layers of the non-woodland areas were primarily comprised of Ashe juniper, shin oak, or live oak, which are common vireo foraging substrates (Houston 2008, Morgan 2012). The non-woodland areas may have provided sufficient food resources for fledglings, thus encouraging continual use of non-woodland areas.

Fledglings were six times more likely to occupy woodland cover at high WA sites than fledglings at low or medium WA sites. At low WA sites, this result was likely due to woodland availability being six times lower than high WA sites. However at medium WA sites, woodland availability was just 1.5 times lower than high WA sites. The average distance between fledgling locations and woodland cover was four times greater at medium WA sites than at low sites. The greater distance between fledglings and the woodland areas coupled with the lower availabilities of those areas could explain why the probability of woodland use was lower than expected at medium WA sites.

Temporal Trends in Landscape Scale Habitat Use

Fledglings used non-woodland areas significantly more than woodland areas regardless of the period of the post-fledging season or their post-fledging age. Over the post-fledging season I obtained the highest number of fledgling locations during the middle period since this was the peak of fledgling activity. During this period, I detected birds that fledged during the early period (which were located within or near their natal areas) as well as recently fledged birds. As a result, the majority of the woodland locations across all periods occurred during the middle period. But when comparing the proportion of woodland locations between the periods, the late period had the highest value indicating that fledglings used the woodland cover the most during the latest part of the post-fledging season, from July to August. Although the trend was not significant, I also observed fledglings moving closer to the woodland over the season. Fledglings may have been located closer towards the woodland and entered the woodland more towards the end of the post-fledging season in search of thermal refuge provided by the greater canopy and shrub cover typical of woodland areas. DeWoskin (1980) found that foraging white-crowned sparrows (*Zonotrichia leucophrys*) could decrease their metabolic rate up to 20% due to the thermal environment of dense understory. Further information on microclimate of post-fledging habitat is needed to support this hypothesis.

Out of the three age classes, I obtained the least number of locations for young fledglings. This may have been due to their guarded behavior, such as cessation of calling and moving when observers or predators were nearby, which made it more difficult to detect them than intermediate and older fledglings that shradded frequently (M. Martinez, pers. obs.). I obtained the majority of woodland locations for old fledglings, which resulted in this age class having the highest proportion of woodland points. I located more fledglings near the woodland as they aged. Fledglings may have moved closer to the woodland and entered the woodland more frequently as they age since they were able to fly farther to reach the woodland areas thus making these areas more accessible to them.

Although post-fledging woodland use varied by period and age class, the differences were not statistically significant. In addition, season and age did not have a significant effect on the probability of woodland use. Studies have shown that arthropod abundance fluctuates over the season (Quinn 2000, Marshall et al. 2013). Despite these fluctuations, non-woodland areas may provide sufficient food resources for fledglings throughout the post-fledging season. This may be because fledglings use a wide spectrum of vegetation to take advantage of various food sources that come with a heterogeneous matrix of vegetation composition and structure.

CHAPTER III

LOCAL-SCALE POST-FLEDGING HABITAT USE

Introduction

Comprehensive studies on fledgling habitat use and movement patterns have been conducted for only a few Neo-tropical songbird species. In several of these studies, young used vegetation types different from their typical nesting habitats. For instance, juvenile wood thrushes (*Hylocichla mustelina*) in Missouri (Anders et al. 1998) and Virginia (Vega Rivera et al. 1998) dispersed from their nesting areas, consisting of mature oak-hickory (*Carya* spp.) forest, and moved into early-successional vegetation with greater vertical structure, denser understory, and thicker cover. Other studies found migratory songbirds that nested in late successional woodland used regenerating clearcuts during the post-fledging period (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2007).

King et al. (2006) reported that fledgling ovenbirds (*Seiurus aurocapilla*) selected areas with greater vegetation structure and fewer trees than the nesting sites, and usage of these habitats increased their survival. Ovenbird fledgling survival was influenced by the distance of the nest to various non-nesting cover types and the subsequent selection among those cover types, but that the influence of non-nesting cover types varied depending on the availability of dense understory vegetation in mature forest (Streby and Andersen 2011). These studies confirm that vegetation characteristics of the post-fledging habitat differ from those of the nesting habitat for several songbird species and that these differences may have consequences on survivorship.

Although post-fledging habitat use and movement patterns have not been studied extensively in the Vireonidae family, there are several accounts of fledgling black-capped vireos using habitat different than typical nesting habitat. Graber (1961) observed family groups move from typical nesting habitat into shaded ravines with water, and from hillsides into heavily wooded, dry streambeds, respectively. Fledglings in Travis, Burnet, and Kerr Counties, Texas were observed moving from their nests in shrubby vegetation to more heavily wooded areas and foraging in juniper woodland along canyon ridges and slopes, one woodland cluster being >4 m in average height (Houston 2008).

Dittmar et al. (2014) found that independent fledglings at Fort Hood Military Reservation in Texas selected riparian areas over other vegetation types and used areas characterized by greater canopy cover, denser foliage, and higher arthropod abundance. Such findings verify that fledglings use areas atypical of nesting habitat and may prefer patches of greater vertical variation more than low-growing shrub habitat. However, research that assesses the intensity of use and selection of these areas by fledglings is lacking. Knowing where fledglings occur and the vegetation components that characterize post-fledging habitat would not only uncover important aspects of post-fledging ecology, but would assist landowners in managing habitat that enhances productivity for all life stages of the vireo.

Several hypotheses have been proposed to explain post-fledging habitat use patterns of migratory birds. Four hypotheses pertinent to the vireo are breeding site selection, food search, socialization, and predator-avoidance. The breeding site selection hypothesis states that fledglings explore habitat prior to migration to prospect for future breeding sites (Morton et al. 1991). So they spend a portion of time outside of their natal territories visiting potential breeding habitat, and then return to those visited sites the subsequent year to establish a territory. The food search hypothesis states that fledglings disperse from their natal areas to look for available food resources and familiarize themselves with feeding sites to use in future nesting seasons (Eden 1987), so their foraging time increases with increasing availability of a food-rich habitat type (Fig. 1A).

The predator-avoidance hypothesis states that fledglings select habitat with greater vegetation complexity that offers protection from predators (King et al. 2006), so they select for areas with a specific range of a vegetation feature (e.g., cover) and selection of those areas increases their survival (Fig 1B). The socialization hypothesis proposes that fledglings disperse from their natal areas to flock with conspecifics to socialize and migrate with, as well as to locate patchy food resources and protect from predators (Hamilton 1971, Powell 1974). So fledgling density increases with increasing measurement of a vegetation feature (e.g., cover) that provides protection from predators, food resources, or ideal microclimatic conditions (Fig. 1C).

These hypotheses reinforce the importance of vegetation in an animal’s habitat, by explaining how vegetative variation can influence the local conditions and overall quality of the habitat (Morrison et al. 2006). Therefore it is essential that land managers

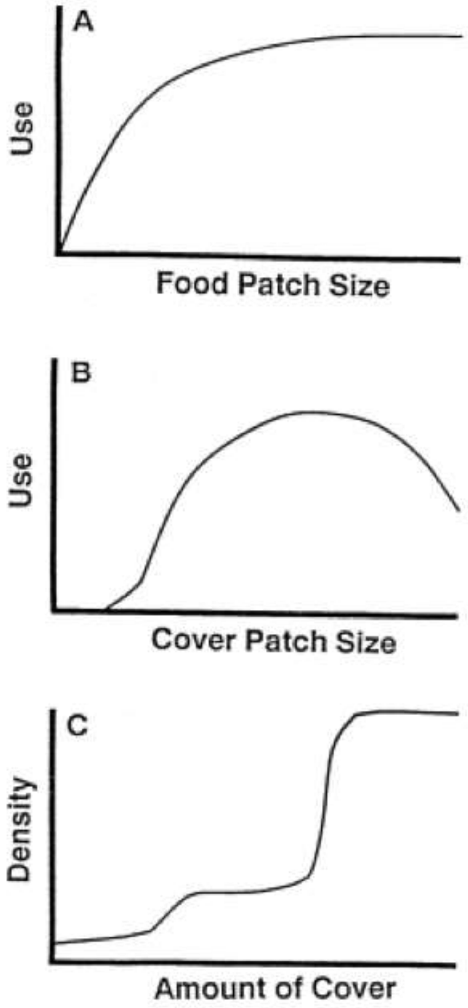


Figure 1. Hypothetical relationships demonstrating three possible drivers of post-fledging habitat (adapted from Garshelis 2000). In Fig. 1A, food resources drives fledglings to increase their foraging with increasing availability of a food-rich habitat type. In Fig. 1B, predator avoidance drives fledglings to select for areas with greater vegetation cover and the selection of those areas increase their survival. In Fig. 1C, socialization drives fledgling density to increase with increasing cover, which provides protection from predators, food resources, and ideal microclimatic conditions.

understand the vegetative conditions, succession, and associations of the land and the factors that affect them. It is this increased knowledge of wildlife-habitat relationships that promotes efficient and sustainable management actions.

Study Objectives

The specific study objectives were to (a) assess local-scale characteristics of post-fledging habitat, (b) identify temporal changes of local-scale habitat, and (c) compare local characteristics of post-fledging and nesting habitat. I assessed vegetation characteristics of site, fledgling, and nest locations within a 0.04 ha circular plot. I predicted fledglings in non-woodland cover use areas with greater cover and compositions of key species that what is typical of the study area, and fledglings in non-woodland cover use areas with vegetation structure and composition similar to what is typical of the study area. To account for site variability, I assessed local-scale characteristics by woodland availability at the site. I predicted vegetation structure and composition of site locations would be similar across low, medium, and high woodland availability (WA) sites, whereas nest and fledgling locations would vary by WA site.

Additionally, I predicted fledglings use areas with increasing cover and compositions of key species over the post-fledging season and with post-fledging age. Lastly, I predicted in non-woodland cover, fledglings use areas with greater cover and compositions of key species than at nest sites, and in woodland cover, fledglings use areas with similar vegetation structure and composition as the nest sites.

Study Area

I established study sites across Travis, Burnet, and Williamson Counties. I included BCNWR in my study sites for its known breeding vireo populations (Sexton 2002, 2005), suitable breeding habitat, and vegetative heterogeneity resulting from a prescribed burning program. The BCNWR lies along the eastern edge of the Edwards Plateau region in central Texas and was acquired in 1992 under the Endangered Species Act of 1973 to preserve breeding habitat for the endangered golden-cheeked warbler (*Dendroica chyrsoparia*) and vireo (USFWS 2001). BCNWR currently contains 53 noncontiguous tracts of land covering over 8,100 ha (USFWS 2001). The woody vegetation of the study area is predominantly composed of the evergreen Ashe juniper (*J. ashei*), with sub-dominant species of broad-leafed hardwood such as Texas red oak (*Quercus buckleyi*), plateau live oak (*Q. virginiana var. fusiformis*), post oak (*Q. stellata*), shin oak (*Q. havardii*), and escarpment black cherry (*Prunus serotina var. exima*; Diamond 1997, Gehlbach 1988).

Methods

Data Collection

Avian-related Monitoring

Please refer to the Methods section in Chapter II.

Vegetation Sampling

I conducted vegetation surveys to determine the typical vegetation structure and composition at the site. To pre-determine the survey locations, I overlaid GIS map layers with a grid network of points at 200 by 200 m spacing across the study area from a random start point. I used the point-centered quarter method (Martin et al. 1997, Mitchell 2007) to measure characteristics of vegetation within 0.04-ha circular plot. I established a 5-m radius circle around each grid point and divided the circle into 4 quadrants based on the four cardinal directions. Standing at the center point, I estimated the percent shrub, herbaceous, and cactus cover in each quadrant. I recorded the species, distance, and DBH of the nearest tree in each quadrant <11 m away to estimate tree density. At the center point and at a point at each cardinal direction 5 m away, I recorded percent canopy cover, height, and diameter breast height (DBH; at 1.5 m) of the 3 dominant tree species present >3 m tall. At all 5 points I estimated percent visual obstruction of understory vegetation at 3 height classes (0–1 m, 1–2 m, and 2–3 m) and recorded the maximum height of the vegetation in each category.

To identify vegetation characteristics of the nest sites, I conducted surveys in the same manner as at the study site but used the nest location as the center point. I only recorded vegetation measurements for active nests in which I observed at least one host egg or nestling. I recorded additional measurements including nest height, nest substrate species, height of the nest substrate and DBH of nest substrate >1.5 m tall. I conducted vegetation surveys when the nest was no longer active (i.e. the nest failed or fledged young).

I conducted vegetation surveys to identify local scale characteristics of post-fledging habitat. I conducted surveys in the same manner as at the study site but centered the sampling point on the first GPS point acquired from the post-fledging survey (see Methods section in Chapter II).

Data Analysis

Calculating Vegetation Metrics

I evaluated 13 vegetation metrics obtained from vegetation surveys. Ashe juniper, live oak, and shin oak were the key species because they are the top three common vireo foraging substrates at BCNWR (Morgan 2012), common vireo nesting substrates (Grzybowski 1995), and occur abundantly across the study area. I used the landcover map from Chapter II to assign each site, nest, and fledgling location to woodland or non-woodland cover, and then evaluated the locations separately by landcover type since I expected the vegetative structure and composition of woodland and non-woodland cover to differ considerably. I conducted a one-way ANOVA analyses for site, nest, and fledglings locations separately to test for differences in vegetation metrics between low, medium, and high WA sites.

To compare the post-fledging habitat to the study area and to the nesting habitat, I compared the means of each vegetation metric between fledgling and site-wide locations and between fledgling and nest locations using Student's t-test, respectively. I performed all analyses described in this Chapter using R statistical software (R Development Core Team, 2013).

Evaluating Temporal Trends

I used post-fledging season and post-fledging age to identify temporal trends in local-scale characteristics of post-fledging habitat. To determine the start dates of the season used the date the first nest fledged in 2013 and 2014. The end dates of the season occurred on the date of the last post-fledging survey in 2013 and 2014. I divided the post-fledging season into three periods based on weeks from the start date; early (<4 weeks), middle (4–8 weeks), and late (>8 weeks). I categorized post-fledging age into three classes based on the estimated weeks from the bird's fledge date; <2 weeks, 2–4 weeks, and >4 weeks. To assess how vegetation characteristics of post-fledging habitat changed with time, I conducted a factorial linear model with post-fledging period and age class as explanatory variables. I only selected vegetation metrics that were not correlated with one another ($R^2 < 0.10$) as dependent variables in the model.

Results

Nesting Ecology

I monitored 78 nests from 11 April–19 July in 2013; 18, 14, and 5 nests fledged young during the early, middle, and late periods, respectively. Of the remaining 41 nests that did not fledge young, 40 failed and 1 nest fate was unknown. I monitored 74 nests from 9 April– 21 July in 2014; 14, 8, and 4 nests fledged during the early, middle, and late periods, respectively. Of the remaining 48 nests that did not fledge young, all of them failed. Apparent nest success was 48.1% (*n* = 77) in 2013 and 35.1% (*n* = 74) in 2014, and did not vary statistically between the two years ($\chi_1^2 = 2.09$, P = 0.1487). Of the 151 monitored nests with known fates, I located 69 (45.7%) in low WA sites, 20 (13.2%) in medium WA sites, and 61 (40.4%) in high WA sites. I located 13 of the 151 nests (8.6%) in woodland cover, 8 of which were from two high WA sites, and 5 of which were from one low WA site. I conducted 124 surveys on a fledgling that fledged from a monitored nest on the study site.

Local-scale Habitat

Non-woodland Cover

Vegetation metrics across the study site-wide locations were similar, except for canopy height (which was highest at low WA sites) and Ashe juniper canopy cover (which was greatest at medium WA sites; Table 3). At low WA sites, the canopy was primarily composed of Ashe juniper and live oak with an understory of Ashe juniper, cactus, and shin oak. At medium WA sites the canopy was primarily comprised of Ashe juniper with an understory of mixed species including Ashe juniper, cactus, elbow bush, and shin oak. At high WA sites the canopy was comprised of Ashe juniper or elbow bush with an understory of Ashe juniper, cactus, and shin oak.

Vegetation characteristics across the post-fledging locations varied by woodland availability. Canopy cover, Ashe juniper canopy cover, live oak canopy cover and live oak shrub cover were two to six times lower at high WA sites while shrub cover was approximately two times lower, and shin oak shrub cover was six to nine times lower at medium WA sites (Table 4). Across all sites, vegetation characteristics at fledgling locations differed from site-wide locations (Table 5). Canopy cover, shrub cover, vertical cover, tree density, and compositions of Ashe juniper (canopy only), live oak, and shin oak were two to three times higher at fledgling locations. The ranges for shin oak canopy cover, vertical cover, and Ashe juniper shrub cover were two to four times wider at fledgling locations than site-wide locations.

Table 3. Comparison of vegetation metrics (mean ± SD) of study site-wide sampling points in non-woodland cover between low, medium, and high woodland availability (WA) sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Vegetation Metric	**Low WA** (*n* = 102)	**Medium WA** (*n* = 31)	**High WA** (*n* = 22)	F_2	***P***
Canopy Cover (%)	8.75 ± 14.85	10.58 ± 11.86	7.18 ± 10.36	1.452	0.239
Canopy Height (m) ^	4.62 ± 1.75	3.42 ± 1.15	3.14 ± 0.80	7.039	< 0.01*
Ashe Juniper Canopy Cover	2.08 ± 6.04	6.77 ± 9.24	3.00 ± 6.61	5.562	< 0.01*
Live Oak Canopy Cover (%)	3.76 ± 10.03	0.97 ± 3.65	0.00 ± 0.00	2.653	0.074
Shin Oak Canopy Cover (%)	0.37 ± 2.04	0.19 ± 0.79	0.00 ± 0.00	0.488	0.615
Vertical Cover 0–1 m (%)	6.49 ± 11.11	4.13 ± 5.95	8.64 ± 13.61	1.178	0.311
Vertical Cover 1–2 m (%)	2.12 ± 4.24	3.16 ± 5.08	4.00 ± 7.98	1.484	0.230
Vertical Cover 2–3 m (%)	1.55 ± 3.79	3.23 ± 4.52	1.82 ± 5.31	1.924	0.150
Shrub Cover (%)	18.97 ± 21.12	15.48 ± 15.82	23.75 ± 23.09	1.048	0.353
Ashe Juniper Shrub Cover (%)	0.84 ± 2.29	0.48 ± 1.50	2.07 ± 4.30	2.722	0.069
Live Oak Shrub Cover (%)	1.67 ± 7.31	0.08 ± 0.45	0.34 ± 1.17	1.077	0.343
Shin Oak Shrub Cover (%)	4.67 ± 13.19	3.87 ± 10.43	5.23 ± 14.74	0.078	0.926
Tree Density (trees/ha)	795.49 ± 2634.85	731.05 ± 1549.08	1922.03 ± 3302.36	1.873	0.157

* Significance ($P < 0.05$)

^ *n* = 61, 20, and 10 for low, medium, and high WA sites, respectively

Table 4. Comparison of vegetation metrics (mean ± SD) between fledgling locations in non-woodland cover at low, medium, and high woodland availability (WA) sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Vegetation Metric	**Low WA** (*n* = 197)	**Medium WA** (*n* = 89)	**High WA** (*n* = 146)	***F***	***P***
% Canopy Cover	24.11± 20.65	23.17 ± 12.99	12.04 ± 15.49	21.68	< 0.001*
Canopy Height (m)^	4.48 ± 1.92	4.02 ± 1.02	3.54 ± 1.16	10.34	< 0.001*
% Ashe Juniper Canopy Cover	5.46 ± 11.05	11.84 ± 12.89	2.49 ± 7.85	22.00	< 0.001*
% Live Oak Canopy Cover	8.47 ± 15.06	6.09 ± 11.29	1.34 ± 5.69	15.23	< 0.001 *
% Shin Oak Canopy Cover	4.48 ± 12.12	3.24 ± 8.19	2.96 ± 10.02	0.95	0.387
% Vertical Cover (0–1 m)	19.68 ± 18.37	6.61 ± 6.56	22.59 ± 18.10	27.27	< 0.001*
% Vertical Cover (1–2 m)	10.25 ± 11.12	7.21 ± 7.23	10.21 ± 9.28	3.344	< 0.05 *
% Vertical Cover (2–3 m)	4.76 ± 6.74	9.17 ± 8.16	2.55 ± 4.44	29.63	< 0.001 *
% Shrub Cover	47.22 ± 26.54	29.47 ± 16.21	55.72 ± 19.75	37.76	< 0.001*
% Ashe Juniper Shrub Cover	1.69 ± 6.22	0.65 ± 1.79	2.00 ± 4.16	1.812	0.165
% Live Oak Shrub Cover	4.07 ± 10.96	2.22 ± 6.91	0.77 ± 4.16	6.588	< 0.05*
% Shin Oak Shrub Cover	20.81 ± 27.93	3.43 ± 9.02	27.45 ± 24.85	27.98	< 0.001*
Tree Density (stems/ha)	8619.58 ± 49991.52	9647.29 ± 67792.21	2048.63 ± 4895.04	1.112	0.330

* Significance (*P* < 0.05)

^ *n* = 171, 85, 83 for low, medium, and high WA sites, respectively

Table 5. Comparison of vegetation characteristics (mean ± SD, minimum, and maximum) between locations of black-capped vireo fledgling detection points and study site-wide sampling points in non-woodland cover on study sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Vegetation Metric	**Fledgling Locations** (*n* = 432)		**Site-wide Locations** (*n* = 155)		***t***	***P***
% Canopy Cover	19.84 ±18.45	0–96	8.89 ± 13.70	0–78	7.742	< 0.001
Canopy Height (m)^	4.14 ± 1.62	2–12.6	4.19 ±1.66	2–11.0	-0. 295	0.769
% Ashe Juniper Canopy Cover	5.77 ± 11.02	0–64	3.15 ± 7.07	0–42	3.390	< 0.001
% Live Oak Canopy Cover	5.57 ± 12.25	0–86	2.67 ± 8.43	0–62	3.229	< 0.05*
% Shin Oak Canopy Cover	3.71 ± 10.71	0–86	0.28 ± 1.70	0–18	6.422	< 0.001
% Vertical Cover (0–1 m)	17.97 ± 17.54	0–100	6.32 ± 10.72	0–60	9.660	< 0.001
% Vertical Cover (1–2 m)	9.61 ± 9.87	0–86	2.59 ± 5.10	0–28	11.192	< 0.001
% Vertical Cover (2–3 m)	4.92 ± 6.82	0–42	1.92 ± 4.20	0–24	6.371	< 0.001
% Shrub Cover	46.44 ± 24.38	0–100	18.95 ± 20.49	0–90	13.600	< 0.001
% Ashe Juniper Shrub Cover	1.58 ± 5.42	0–45	0.95 ± 2.58	0–18	1.906	0.057
% Live Oak Shrub Cover	2.58 ± 8.51	0–67.5	1.16 ± 5.98	0–45	2.340	< 0.05*
% Shin Oak Shrub Cover	19.47 ± 25.59	0–100	5.49 ± 12.85	0–72.5	9.267	< 0.001
Tree Density (stems/ha)	6610.57 ± 4757.14	0–640000	942.40 ± 2582.27	0–25600	2.563	<0.05*

* Significance ($P < 0.05$)
^ n = 339 and 91 for fledgling and site-wide locations, respectively

Woodland Cover

Vegetation characteristics were similar across all sites except Ashe juniper shrub cover, which was highest at low WA sites (Table 6). At low WA sites the canopy was primarily comprised of Ashe juniper and live oak canopy with an understory of Ashe juniper, cactus, live oak, and shin oak shrubs. At medium WA sites the canopy was primarily comprised of Ashe juniper and Texas oak with an understory of Ashe juniper, cactus, and shin oak. At high WA sites the canopy was primarily comprised of Ashe juniper, Texas oak, shin oak, and live oak with a mixed-species understory including Ashe juniper, cactus, and shin oak. A few of the vegetation characteristics across fledgling locations varied by woodland availability. Ashe juniper canopy cover was almost three times lower at low WA sites while shrub cover was almost two times greater and live oak shrub cover was nine times greater at low WA sites (Table 7).

Table 6. Comparison of vegetation metrics (mean ± SD) between study site-wide sampling points in woodland cover at low, medium, and high woodland availability (WA) sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Vegetation Metric	**Low WA** (*n* = 16)	**Medium WA** (*n* = 33)	**High WA** (*n* = 57)	F_2	***P***
Canopy Cover (%)	30.00 ± 22.79	41.88 ± 22.94	39.91 ± 24.18	1.452	0.239
Canopy Height (m) ^	4.08 ± 1.46	4.943 ± 2.24	4.55 ± 1.22	1.344	0.266
Ashe Juniper Canopy Cover (%)	12.25 ± 17.57	19.70 ± 17.74	22.28 ± 18.65	1.900	0.155
Live Oak Canopy Cover (%)	5.25 ± 13.18	0.97 ± 3.88	3.26 ± 10.51	1.214	0.301
Shin Oak Canopy Cover (%)	2.378 ± 6.50	1.58 ± 5.40	1.193 ± 3.54	0.404	0.669
Vertical Cover 0–1 m (%)	4.75 ± 6.527	5.27 ± 7.36	4.56 ± 7.77	0.095	0.909
Vertical Cover 1–2 m (%)	3.50 ± 4.29	5.76 ± 7.05	4.88 ± 6.72	0.650	0.524
Vertical Cover 2–3 m (%)	4.25 ± 4.55	8.36 ± 11.68	4.737 ± 5.81	2.507	0.087
Shrub Cover (%)	23.75 ± 25.00	17.01 ± 17.41	17.15 ± 5.98	0.929	0.398
Ashe Juniper Shrub Cover (%)	6.50 ± 11.21	0.98 ± 1.87	2.97 ± 5.83	4.34	< 0.05*
Live Oak Shrub Cover (%)	0.156 ± 0.63	0.00 ± 0.00	0.61 ± 3.00	0.871	0.422
Shin Oak Shrub Cover (%)	5.31 ± 10.12	2.05 ± 5.095	6.62 ± 13.62	1.775	0.175
Tree Density (trees/ha)	2373.97 ± 3068.00	1980.75 ± 2348.04	3574.32 ± 4042.26	2.433	0.093

*Significance ($P < 0.05$)

^ n = 13, 31, 51 for low, medium, and high WA sites, respectively

Table 7. Comparison of vegetation metrics (mean ± SD) between fledgling locations in woodland cover at low, medium, and high woodland availability (WA) sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Vegetation Metric	**Low WA** (n = 11)	**Medium WA** (n = 4)	**High WA** (n = 70)	F_2	P
% Canopy Cover	28.91 ± 21.15	38.00 ± 10.46	39.11 ± 17.48	1.568	0.215
Canopy Height (m)	4.54 ± 1.58	4.11 ± 0.75	4.12 ± 0.82	0.966	0.385
% Ashe Juniper Canopy Cover	9.27 ± 15.56	28.50 ± 15.09	25.97 ±16.33	5.433	< 0.01*
% Live Oak Canopy Cover	9.27 ± 15.86	7.00 ± 14.00	2.46 ± 8.53	2.677	0.075
% Shin Oak Canopy Cover	3.09 ± 5.47	0.00 ± 0.00	4.91 ± 8.53	0.883	0.417
% Vertical Cover (0–1 m)	13.10 ± 11.57	8.50 ± 5.26	5.77 ± 7.81	3.790	< 0.05*
% Vertical Cover (1–2 m)	5.09 ± 4.76	7.50 ± 5.26	4.40 ± 5.58	0.762	0.470
% Vertical Cover (2–3 m)	4.00 ± 5.29	11.00 ± 6.22	4.75 ± 5.58	2.571	0.083
% Shrub Cover	43.86 ± 26.01	25.63 ± 15.33	28.00 ± 17.34	3.59	< 0.05*
% Ashe Juniper Shrub Cover	2.27 ± 5.18	5.00 ± 5.77	2.93 ± 6.73	0.257	0.774
% Live Oak Shrub Cover	9.55 ± 22.27	0.00 ± 0.00	0.11 ± 0.66	7.017	< 0.05*
% Shin Oak Shrub Cover	6.59 ± 13.10	0.00 ± 0.00	14.93 ± 14.58	3.471	< 0.05*
Tree Density (stems/ha)	10651.63 ± 15248.32	5117.97 ± 8457.31	3937.63 ± 8851.66	2.213	0.116

* Significance ($P < 0.05$)

Table 8. Comparison of vegetation metrics (mean ± SD, minimum, and maximum) between locations of black-capped vireo fledgling detection points and study site-wide sampling points occurring in woodland cover study sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Vegetation Metric	**Fledgling Locations** (*n*= 85)		**Site-wide Locations** (*n* = 106)		***t***	***P***
% Canopy Cover	37.74 ±17.89	4–66	39.03 ± 23.70	0–84	-0.423	0.670
Canopy Height (m)^	4.18 ± 0.94	2.75–7.33	4.61 ±1.64	2.5–11.3	-0. 248	< 0.05*
% Ashe Juniper Canopy Cover	23.93 ± 16.69	0–66	19.96 ± 18.37	0–68	1.561	0.120
% Live Oak Canopy Cover	3.55 ± 9.77	0–46	2.85 ± 9.51	0–52	0.501	0.617
% Shin Oak Canopy Cover	4.45 ± 8.04	0–34	1.49 ± .467	0–26	3.007	< 0.01*
% Vertical Cover (0–1 m)	6.85 ± 8.56	0–40	4.81 ± 7.41	0–42	1.733	0.085
% Vertical Cover (1–2 m)	4.64 ± 5.04	0–22	4.94 ± 6.51	0–38	-3.869	0.713
% Vertical Cover (2–3 m)	4.94 ± 5.67	0–20	5.79 ± 8.10	0–44	-0.853	0.395
% Shrub Cover	29.94 ± 19.11	0–77.5	18.10 ± 17.99	0–80	4.367	< 0.001*
% Ashe Juniper Shrub Cover	2.94 ± 6.47	0–32.5	2.89 ± 6.35	0–35	0.058	0.954
% Live Oak Shrub Cover	1.32 ± 8.34	0–67.5	0.35 ± 2.22	0–20	1.043	0.300
% Shin Oak Shrub Cover	13.15 ± 14.54	0–52.5	5.00 ± 11.21	0–67.5	4.250	< 0.001*
Tree Density (stems/ha)	4862.05 ± 9984.96	278–71111	2897.02 ± 3506.29	0–17778	1.731	0.087

* Significance ($P < 0.05$)

^ n = 98 for site-wide locations

Across all sites some of the vegetation characteristics at fledgling locations differed from site-wide locations. Shin oak canopy cover was approximately four times greater, shrub cover was approximately two times greater, and shin oak shrub cover was approximately three times greater higher at fledgling locations than site-wide locations. The ranges of the values were similar between fledgling and site-wide locations, except for live oak shrub cover, which was over three times greater at fledgling locations (Table 8).

Temporal Trends in Local-scale Post-fledging Habitat Characteristics

I evaluated changes in canopy cover, vertical cover, shrub cover, Ashe juniper shrub cover, and live oak shrub cover over post-fledging season and post-fledging age. I chose these metrics since they were not correlated with one another ($R^2 < 0.10$). Mean percent canopy cover of fledgling locations ($\bar{x} = 22.781$, SE = 0.858, $n = 517$) did not change over the season ($F_{1,517} = 3.251$, $P = 0.072$) or with fledgling age ($F_{2,507} = 0.7635$, $P = 0.467$). Mean percent vertical cover of vegetation 0–1 m ($\bar{x} = 16.139$, SE = 0.744, $n = 517$), 1–2 m ($\bar{x} = 8.793$, SE = 0.415, $n = 517$), and 2–3 m ($\bar{x} = 4.925$, SE = 0.292, $n = 517$) did not change over the season (0–1 m: $F_{1,517} = 1.692$, $P = 0.194$; 1–2 m: $F_{1,517} = 0.015$, $P = 0.903$; 2–3 m: $F_{1,517} = 0.001$, $P = 0.971$) or with fledgling age (0–1 m: $F_{2,507} = 1.703$, $P = 0.183$; 1–2 m: $F_{2,507} = 0.475$, $P = 0.622$; 2–3 m: $F_{2,507} = 0.204$, $P = 0.816$).

Mean percent shrub cover ($\bar{x} = 43.723$, SE = 1.071, $n = 517$) did not change over the season ($F_{1,517} = 0.607$, $P = 0.436$) but it changed with fledgling age ($\mathrm{F}_{2,507} = 3.655$, $P < 0.05$). Mean percent shrub cover was 10% lower at locations of old fledglings ($\bar{x} = 38.757$, SE = 1.741, $n = 183$) than at locations of young fledglings ($\bar{x} = 47.181$, SE =

1.955, $n = 141$). Mean percent Ashe juniper shrub cover ($\bar{x} = 1.804$, SE = 0.247, $n = 517$) did not change over the season ($F_{1,517} = 0.761$, $P = 0.383$) or with age ($F_{2,507} = 1.560$, $P = 0.211$). Mean percent live oak shrub cover ($\bar{x} = 2.370$, SE = 0.373, $n = 517$) did not change over the season ($F_{1,517} = 0.896$, $P = 0.344$) or with age ($F_{2,507} = 1.501$, $P = 0.224$).

Post-fledging Habitat Versus Nesting Habitat

A few vegetation characteristics differed between fledging and nest locations across all sites. In non-woodland cover shrub cover and shin oak shrub cover at nest locations exceeded fledgling locations by ~10% (Table 9). Although the Ashe juniper shrub cover was not different between fledgling and nest locations, the range for fledgling locations was more than double than nest locations. In woodland cover, shrub cover at nest locations exceeded fledgling locations by ~20% (Table 10). Although mean percent Ashe juniper shrub cover and mean percent live oak shrub cover were not different between fledgling and nest locations, the ranges were approximate three to four time wider at fledgling locations.

Table 9. Comparison of vegetation metrics (mean ± SD, minimum, and maximum) between locations of black-capped vireo fledgling detection points and nest sampling points occurring in non-woodland cover on study sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Vegetation Metric	**Fledgling Locations** (*n* = 432)		**Nest Locations** (*n* = 137)		***t***	***P***
% Canopy Cover	19.84 ±18.45	0–96	26.91 ± 18.45	0–100	-3.325	<0.05*
Canopy Height (m)^	4.14 ± 1.62	2–12.6	3.48 ±1.38	1.5–9.0	4.190	<0.0001*
% Ashe Juniper Canopy Cover	5.77 ± 11.02	0–64	4.18 ± 9.68	0–48	1.627	0.105
% Live Oak Canopy Cover	5.57 ± 12.25	0–86	5.87 ± 14.78	0–78	-0.215	0.830
% Shin Oak Canopy Cover	3.71 ± 10.71	0–86	5.91 ± 10.09	0–44	-2.194	<0.05*
% Vertical Cover (0–1 m)	17.97 ± 17.54	0–100	16.77 ± 13.18	0–88	0.751	0.453
% Vertical Cover (1–2 m)	9.61 ± 9.87	0–86	10.41 ± 13.18	0–88	-0.653	0.515
% Vertical Cover (2–3 m)	4.92 ± 6.82	0–42	4.99 ± 6.38	0–38	-0.112	0.911
% Shrub Cover	46.44 ± 24.38	0–100	55.94 ± 24.31	0–100	-3.983	<0.0001*
% Ashe Juniper Shrub Cover	1.58 ± 5.42	0–45	1.02 ± 3.82	0–20	1.336	0.183
% Live Oak Shrub Cover	2.58 ± 8.51	0–67.5	1.79 ± 6.66	0–45	1.123	0.262
% Shin Oak Shrub Cover	19.47 ± 25.59	0–100	28.39 ± 28.88	0–97.5	-3.236	<0.05*

* Significance ($P < 0.05$)
^ n = 339 and 114 for fledgling and nest locations, respectively

Table 10. Comparison of vegetation metrics (mean ± SD, minimum, and maximum) between locations of black-capped vireo fledgling detection points and nest sampling points in woodland cover on study sites in the Balcones Canyonlands National Wildlife Refuge area, USA, 2013–2014.

Vegetation Metric	**Fledgling Locations**		**Nest Locations**		***t***	***P***
	(*n* = 85)		(*n* = 13)			
% Canopy Cover	37.74 ±17.89	4–66	43.69 ± 17.98	14–80	-1.113	0.282
Canopy Height (m)	4.18 ± 0.94	2.75–7.33	4.45 ±1.10	2.81–6.25	-0. 849	0.409
% Ashe Juniper Canopy Cover	23.93 ± 16.69	0–66	19.38 ± 19.50	0–50	0.767	0.438
% Live Oak Canopy Cover	3.55 ± 9.77	0–46	2.31 ± 8.32	0–30	0.490	0.630
% Shin Oak Canopy Cover	4.45 ± 8.04	0–34	6.31 ± 8.56	0–28	-0.736	0.473
% Vertical Cover (0–1 m)	6.85 ± 8.56	0–40	13.38 ± 14.17	0–54	-.1.618	0.129
% Vertical Cover (1–2 m)	4.64 ± 5.04	0–22	8.00 ± 7.70	0–22	-1.526	0.150
% Vertical Cover (2–3 m)	4.94 ± 5.67	0–20	4.62 ± 5.25	0–14	0.206	0.839
% Shrub Cover	29.94 ± 19.11	0–77.5	50.00 ± 27.84	0–100	-2.509	< 0.05*
% Ashe Juniper Shrub Cover	2.94 ± 6.47	0–32.5	2.12 ± 5.39	0–17.5	0.500	0.623
% Live Oak Shrub Cover	1.32 ± 8.34	0–67.5	0 ± 0	0–20	1.463	0.147
% Shin Oak Shrub Cover	13.15 ± 14.54	0–52.5	27.88 ± 25.39	0–80	-2.042	0.06

* Significance ($P < 0.05$)

Discussion

Local-scale Post-fledging Habitat Characteristics

The vegetation composition and structure of post-fledging habitat differed from the average vegetation composition and structure across the study sites. In non-woodland areas, fledglings used areas with greater vertical cover of vegetation between 0–3 m tall. This finding is consistent with the results of other studies. Anders et al. (1998) proposed that juvenile wood thrushes selected sites with denser understory than random sites because dense cover may decreases predation risks, particularly by avian predators. Cohen and Lindell (2004) speculated that higher mortality of fledgling white-throated was attributed to the minimal vegetative structure in coffee plantations. Similarly, King et al. (2006) found that fledgling ovenbirds selected habitat with thick understory and their survival rates were positively related to habitat structure.

Vireos and their nests are predated by avian species such as western scrub jay (*Aphelocoma californica*), hawks spp., and brown-head cowbird. Conkling et al. (2012) found that avian predators were the most frequent predator class of vireo nests at Kerr Wildlife Management Area and Devils River area. There is no information on avian predators of vireo fledglings, but avian predators are believed to use visual cues to locate prey (Robinson and Robinson 2001, Hughes 2011) and depredate nests that are less concealed (Liebezeit and George 2002). In non-woodland areas where canopy cover was lower, fledglings may have used areas with denser understory as protective cover from avian predators, particularly while foraging since they primarily forage in shrubs <3 m tall (Houston 2008).

In non-woodland areas, fledglings used areas of greater canopy and shrub cover with higher compositions of Ashe juniper, live oak, and shin oak than what was average at the site. In woodland areas, fledglings used areas with greater shrub cover and greater shin oak composition. These findings are consistent with our knowledge of vireo breeding habitat and foraging ecology in central Texas. Graber (1961) recorded live oak and Ashe juniper as predominant tree species in their central Texas habitat. The latter is not typically considered a key species of vireo breeding habitat and several studies have observed vireos occupying areas with less Ashe juniper cover (Tazik et al. 1993, Grzybowski et al. 1994). However, Ashe juniper was documented as a common foraging substrate for adult vireos (Houston 2008, Morgan 2012). In the non-woodland areas of my study sites, Ashe juniper shrubs were mostly found mixed with other deciduous vegetation, or as the understory of larger trees. In woodland areas, Ashe juniper was usually the most common tree and shrub species, and occurred in uniformly across the area.

Live oak and shin oak are the principal oak species found in vireo territories across the Edwards Plateau (USFWS 1991, Grzybowski et al. 1994) and are common nesting (Graber 1961, Grzybowski 1995) and foraging substrates (Houston 2008, Morgan 2012). Houston (2008) identified shin oak and live oak as the primary foraging substrates for fledglings, followed by Texas red oak, Ashe juniper, cedar elm, Texas persimmon and Western soapberry. Ashe juniper, live oak, and shin oak provide a variety of arthropod prey, which is the bulk of fledglings' diet (Dittmar et al. 2014). Areas with higher canopy and shrub cover provide more foliage to forage on, which is the primary surface substrate for fledglings (Houston 2008), and could explain why fledglings were found in areas with greater cover. Dittmar et al. (2014) found vireo fledglings in areas with greater canopy cover and foliage density than random locations.

The large ranges and high standard deviations of vegetation metrics at fledgling locations may indicate that fledglings are not constrained by the composition and structure of their surroundings. Robinson and Holmes (1982) found that wider range of vegetation layers provided increased foraging opportunities and food resources for birds. Morgan (2010) and Houston (2008) also reported adult and fledgling vireos foraging at wide range of vegetation heights. Fledglings may use a high variation of vegetation cover to acquire maximum foraging opportunities.

Lastly, vegetation characteristics of the post-fledging habitat differed significantly between low, medium, and high WA sites. In non-woodland areas, I unexpectedly found that canopy cover and canopy height were significantly lower at high WA sites. The result for canopy height could be explained by the result that study site-wide locations at high WA sites had the lowest mean canopy height. Eight other variables for locations in the non-woodland areas and four other variables for locations in woodland areas could not be explained by within-site differences. These findings suggest that post-fledging habitat is highly variable across the landscape, which reflects findings of other studies where the composition of wood thrush post-fledging habitat varied across the study area (Anders et al. 1998) and varying fledgling survival estimates may have been attributed to differences in geographic location and habitat types (Rush and Stutchbury 2008).

Temporal Trends in Local Scale Habitat Use

Besides shrub cover, vegetation characteristics of post-fledging habitat did not change significantly over time. The wide range of values for most metrics precluded detection of any clear trend for either temporal scale. Post-fledging season and age exhibited similar trends, which I expected since they were correlated. Fledglings did not exhibit a drastic temporal shift in vegetation characteristics because they may not be pressured to. The areas they used may have provided such a wide range of vegetative cover, complexity, and composition that it provided sufficient resources throughout the post-fledging season and post-fledging stage.

Although seasonal fluctuations in weather and inter- and intraspecific interactions influence seasonal arthropod abundance (Quinn 2000, Marshal 2011), which can drive post-fledging habitat shifts (Anders et al. 1998, Vega Rivera et al. 1998, Cohen and Lindell 2004, King et al. 2006), the vegetation composition of vireo post-fledging habitat may have provided sufficient arthropod abundance throughout the season. Morgan (2010) reported no seasonal change in arthropod abundance in Ashe juniper, live oak, and shin oak species, and Dittmar et al. (2014) reported no seasonal change in arthropod abundance in forest and shrub vegetation. Food availability becomes increasingly critical as fledglings age since they must ultimately learn to forage independently. Starvation was a primary cause of mortality for independent yellow-eyed junco fledglings (Sullivan 1989). However, the pattern of local-scale habitat use was consistent over both temporal scales indicating no significant change in habitat characteristics associated with fluctuating food abundance.

Shrub cover was the only vegetation variable that changed significantly with age. Young fledglings tended to use areas with 10% more shrub cover than old fledglings. Shrub cover, like vertical cover, provides protective shelter from predators, which is especially important for young fledglings that are highly susceptible to predation due to their limited mobility and flying ability (Sullivan 1989, Anders et al. 1998, Vega Rivera et al. 1998). As fledglings age, they become more adept at flying and may not rely on understory cover for protection as much as when they were younger.

The change in shrub cover with age may also be attributed to the vegetation characteristics at the nest site. Shrub cover at nest locations was about 10% higher than at fledgling locations. Shrub cover provides concealment for nests, which can decrease predation risk due reduced visual and olfactory cues (Martin 1992). Vireos tend to build their nest in dense vegetative areas (USFWS 1991) where percent nest concealment is high around 75% (Conkling et al. 2012). Young fledglings tended to be located within 20 m of their nest and then moved further away as they aged (pers. obs. M. Martinez). The close proximity to the nest during this age could explain why young fledglings were located in areas with higher shrub cover.

In addition to shrub cover, canopy cover and shin oak composition were higher at the nest locations than at fledgling locations in the non-woodland areas. Canopy cover is an important characteristic at the nest site because it provides additional concealment from avian predators (Martin 1992, Conkling et al. 2012). Additionally, shin oak is a common vireo nesting substrate since it is dominant species in vireo territories and grows to heights where vireos tend to place their nests (USFWS 1991).

CHAPTER IV

CONCLUSION AND MANAGEMENT RECOMMENDATIONS

The USFWS Recovery Plan for the vireo specifies one of the research and information needs as determining habitat use throughout the range and prioritizes habitat management as a measure to maintain and assure viable populations (USFWS 1991). However, the Plan makes no mention of the post-fledging life-stage or habitat. An effective habitat management plan should implement a holistic approach and address the entire life cycle of the species. Knowing the habitat requirements for a species throughout its life cycle can uncover differences resulting from the physiological, social, or reproductive development the species undergoes. It can also improve existing management strategies by directing management actions to fundamental landscape or local-scale habitat characteristics required by overlapping life-stages. Lastly, it can promote the stabilization and persistence of viable populations by maintaining high quality habitat that supports the survivorship and reproductive success of the species.

The post-fledging is arguably the least-known life stage in avian species, yet the most vulnerable to mortality (Streby and Andersen 2011). Fledglings are exposed to numerous ecological pressures, such as predation, starvation, and exposure within an abbreviated time period to learn and adapt to their surroundings. Therefore, understanding and managing the habitat used during this stage is integral to ensuring a successful graduation for the fledgling to the adult stage.

The black-capped vireo habitat in the BCNWR and surrounding area where I conducted my research was composed primarily of irregular patches of mixed deciduous and evergreen vegetation, varied in structure, and with dense understory. The composition of the vegetation mainly consisted of shin oak and live oak mixed with Ashe juniper and other woody species, such as Texas red oak (*Quercus buckleyi*), Texas persimmon (*Diospyros texana*), yaupon (*Ilex vomitoria*), netleaf hackberry (*Celtis laevigata*), gum bumelia (*Sideroxylon lanuginosum*), Texas redbud (*Cercis canadensis*), cedar elm (*Ulmus crassifolia*), escarpment black cherry (*Prunus serotina*), and flameleaf sumac (*Rhus lanceolata*; USFWS 2001, M. Martinez, pers. obs.). Management activities on the Refuge and surrounding private land include cattle grazing, prescribed burning, mechanical treatments (e.g., flat cut, dozer, masticator, and shaded fuel break), deer management, feral hog trapping, and cowbird trapping. The most recent prescribed burns on BCNWR occurred between 2009 and 2014.

I found that post-fledging habitat mainly consisted of shrubland areas, already documented as vireo breeding habitat, but the vegetation characteristics were significantly different than what was average at the study site. The average canopy cover of post-fledging habitat was 20% and average shrub cover was 46% but fledglings used areas with canopy and shrub covers of up to 100%. Ashe juniper, live oak, and shin oak made up the majority of the canopy and the understory, with shin oak being the leading species for shrub cover at 20%. Vertical cover was highest at height 0–1 m tall at 18% but fledglings used areas up to 100% cover. Vertical cover decreased with height up to 3 m tall. These areas likely provide sufficient resources for fledglings to survive such as protective cover from predators and arthropod availability, which would explain the absence of drastic trends in vegetation characteristics or landcover type over the post-fledging season and with post-fledging age.

I would recommend creating or maintaining heterogeneity in the vegetation structure and composition making sure shrub cover is at the recommended percentage of 30–60% extending 2 m or more in height (USFWS 1991), and that Ashe juniper, live oak, and shin is abundant and available. A diversity of woody species at a variation of heights should promote foraging opportunities within and between seasons, while providing protective cover from predators. I would not recommend implementing any extensive vegetative manipulation that would modify or remove vegetation in shrubland areas, such as prescribed burning, understory thinning, or grazing, until after the post-fledging season ends. The season may vary from year-to-year but fledglings have been sighted through the end of August.

I also documented fledglings using woodland areas where average vegetation characteristics were similar to what was average at the site. The average canopy cover of post-fledging habitat was 38%, 24% Ashe juniper canopy cover, vertical cover <10%, 30% shrub cover, and 13% shin oak shrub cover. Live oak composition was less at woodland areas than non-woodland areas. Older fledglings typically used woodland areas and fledglings moved closer to the woodland towards the end of the post-fledging season. Land managers should be aware of woodland areas and edges and recognize them as suitable habitat for fledglings. These areas may include mature oak-juniper woodlands, which the endangered golden-cheeked warbler (*Dendroica chrysoparia*) inhabits and occasionally overlaps with vireos (Pulich 1976).

Additionally, I would suggest further research on post-fledging habitat use across the vireo’s range where the landscape and local characteristics differ from that of the Edwards Plateau in central Texas. Assessing foraging behavior, vegetation sampling, and microclimate data would be helpful to discriminate between the hypotheses of post-fledging habitat use and improve our understanding of this critical life-stage.

REFERENCES

Albon, S. D., T. N. Coulson, D. Brown, F. E. Guinness, J. M. Pemberton, and T. H. Clutton-Brock. 2000. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. Journal of Animal Ecology 69:1099-1110.

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

Arcese, P., J. N. Smith, W. M. Hochachka, C. M. Rogers, and D. Ludwig. 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. Ecological Society of America 73:805-822.

Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: Suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139-149.

Benson, R. H., and K. L. P. Benson. 1990. Estimated size of black-capped vireo population in northern Coahuila, Mexico. Condor 92:777-779.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: theory and applications. Current Ornithology 11:35-91.

Cherry, S. 1996. A comparison of confidence interval methods for habitat use-availability studies. The Journal of Wildlife Management 60:653-658.

Cohen, E. B., and C. A. Lindell. 2004. Survival, habitat use, and movement of fledgling white-throated robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. The Auk 121:404-414.

Conkling, T. J., T. L. Pope, K. N. Smith, H. A. Mathewson, M. L. Morrison, N. W. Wilkins, and J. W. Cain III. 2012. Black-capped vireo nest predator assemblage and predictors for nest predation. The Journal of Wildlife Management 76:141-1411.

DeWoskin, R. 1980. Heat exchange influence on foraging behavior in Zonotrichia flocks. Ecology 61:30-36.

Diamond, D. D., G. A. Rowell, and D. P. Keddy-Hector. 1995. Conservation of Ashe juniper (*Juniperus ashei Buchholz*) woodlands of the central Texas hill country. Natural Area Journal 15:189-197.

Diamond, D. D. 1997. An old-growth definition for western juniper woodlands: Texas ash juniper dominated or codominated communities. U.S. Department of Agriculture, Forest Service, Southern Research Station, Report, SRS-15, Asheville, North Carolina, USA.

Dittmar, E. M., D. A. Cimprich, J. H. Sperry, and P. J. Weatherhead. 2014. Habitat selection by juvenile black-capped vireos following independence from parental care. Journal of Wildlife Management 78:1005-1011.

Eden, D. F. 1987. Natal philopatry of the magpie pica pica. Ibis 129:477-90.

Finkelstein, M. E., D. F. Doak, M. Nakagawa, P. R. Sievert, and J. Klavitter. 2010. Assessment of demographic risk factors and management priorities: impacts on juveniles substantially affect population viability of a long-lived seabird. Animal Conservation 13:148-156.

Fonteyn, P. J., M. W. Stone, M. A. Yancy, J. T. Baccus, and N. M. Nadkarni. 1988. Determination of community structure by fire. Pages 79-90 in B.B. Amos and F.R. Gehlbach, editors. Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor University Press, Waco, USA.

Gaillard, J. M., R. Andersen, D. Delorme, and J. D. C. Linnell. 1998. Family effects on growth and survival of juvenile roe deer. Ecology 79:2878-2889.

Garshelis, D.L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111-164 in Boitani, L., and T. K. Fuller, editors. Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York, USA.

Gehlbach, F. R. 1988. Forests and woodlands of the northeastern Balcones escarpment. Pages 57-77 in B.B. Amos and F.R. Gehlbach, editors Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor University Press, Waco, USA.

Gordon, H. O., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. The American Naturalist 137:S29-S49.

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

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

Grzybowski, J. A. 1995. Black-capped vireo (*Vireo atricapilla*). In A. Poole and F. Gill, editors. The birds of North America, No. 181. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists Union, Washington, D. C., USA.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295-311.

Houston, D. R. 2008. Foraging behavior of the black-capped vireo in central Texas. Thesis, Texas State University, San Marcos, USA.

Hughes, J. M. 2011. Greater roadrunner (*Geococcyx californianus*). Account 244 in A. Poole, editor. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American, Ornithologists' Union, Washington, D.C., USA.

King, D. I., R. M. Degraaf, M.L. Smith, and J. P. Buonaccors. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). Journal of Zoology 269:414-421.

Liebezeit, J. R., and T. L. George. 2002. Nest predators, nest-site selection, and nesting success of the dusky flycatcher in a managed ponderosa pine forest. Condor 104:507-517.

Marshall, J. T., R. B. Clapp, and J. A. Grzybowski. 1985. Status Report: *Vireo atricapillus*. Prepared for U.S. Fish and Wildlife Service, Office of Endangered Species, Albuquerque, New Mexico, USA.

Marshall, M. R., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper. 2003. Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. Forest Ecology and Management 183:127-135.

Marshall, M., M. L. Morrison, and N. R. Wilkins. 2013. Tree species composition and food availability affect productivity of an endangered species: the golden-cheeked warbler. The Condor 115:882-892.

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

Martin, T. E., and D. M. Finch, editors. 1995. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York, USA.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, USA.

McFarland, T. M., H. A. Mathewson, M. L. Morrison, R. T. Snelgrove, J. E. Groce, K. Skow, B. A. Collier, and R. N. Wilkins. 2012. Estimating the distribution and abundance of the black-capped vireo in Texas. Texas A&M Institute of Renewable Natural Resources, College Station, Texas, USA.

Mitchell, K. 2007. Quantitative analysis by the point-centered quarter method. Hobart and William Smith Colleges. < arXiv:1010.3303v1>. Accessed 11 February 2013.

Moore, F. R., S. A. Gauthreaux, Jr., P. Kerlinger, and T. R. Simons. 1993. Stopover habitat: Management implications and guidelines. Pages 58-69 in D. M. Finch and P. W. Stangel, editors. Status and management of Neotropical migratory birds. U.S. Forest Service General Technical Report RM-229, Fort Collins, Colorado, USA.

Morgan, D. 2012. Foraging ecology and forage availability for the black-capped vireo (*Vireo atricapilla*). Dissertation, Texas State University, San Marcos, USA.

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

Morrison, M. L., editor. 2009. Restoring wildlife: ecological concepts and practical applications. Second edition. Island Press, Washington D.C., USA.

Morton, M. L., M. W. Wakamatsu, M. E. Pereyra, and G. A. Morton. 1991. Postfledging dispersal, habitat imprinting, and philopatry in a montane, migratory sparrow. Ornis Scandinavia 22:98-106.

NCDC. 2014. Climate at a glance, National Climate Data Center, National Oceanic and Atmospheric Administration, Asheville, North Carolina, USA.<http://www.ncdc.noaa.gov/ cag/>.

Neu, C. W., C. R. Byers, J. M. Peek, and V. Boy. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541-545.

Pagen, R. W., F. R. Thompson III, and D. E. Burhans. 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. Condor 102:738-747.

Pope, T. L., T. J. Conkling, K. N. Smith, M. R. Colon, M. L. Morrison, and R. N. Wilkins. 2013. Woodlands as quality breeding habitat for black-capped vireos. The Journal of Wildlife Management 77(5):994-1001.

Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. Animal Behaviour 22:501-505.

Powell, L. A., D. L. Jason, M. J. Conroy, and D. G. Krementz. 2000. Effects of forest management on density, survival, and population growth of wood thrushes. The Journal of Wildlife Management 64:11-23.

Pulich, W. M. 1976. The golden-cheeked warbler: a bioecological study. Texas Parks and Wildlife Department, Austin, USA.

Quinn, M. A. 2000. Abundance and distribution of potential arthropod prey species in a typical golden-cheeked warbler habitat. Thesis, Texas A&M University, College Station, USA.

R Core Development Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Robinson, R. A., S. R. Baillie, and H. Q. P. Crick. 2007. Weather-dependent survival: implications of climate change for passerine population processes. Ibis 149:357-364.

Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918-1931.

Robinson, W. D., and T. R. Robinson. 2001. Is host activity necessary to elicit brood parasitism by cowbirds? Ethology, Ecology & Evolution 13:161-171.

Rush, S. A., and B. J. M. Stutchbury. 2008. Survival of fledgling hooded warblers (*Wilsonia citrina*) in small and large forest fragments. The Auk 125:183-191.

Sauer, J. R., J. E. Fallon, and R. Johnson. 2003. Use of North American breeding bird survey data to estimate population change for bird conservation regions. The Journal of Wildlife Management 67:372-389.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management. 63:739-747.

Sellards, E. H., 1933. The geology of Texas. The University of Texas Bulletin, 3232.

Sexton, C. W. 2002. List of black-capped vireo populations on Balcones Canyonlands NWR. Unpublished manuscript. U.S. Fish and Wildlife Service, Marble Falls, Texas, USA.

Sexton, C. W. 2005. Black-capped vireo populations on Balcones Canyonlands National Wildlife Refuge. Unpublished data. U.S. Fish and Wildlife Service, Marble Falls, Texas, USA.

Shull, A. M. 1986. Endangered and threatened wildlife and plants: proposal to determine the black-capped vireo to be an endangered species. Federal Register 51:44808-44812.

Smeins, F. E. 1980. Natural role of fire on the Edwards Plateau. Pages 4-16 in L. D. White, editor. Prescribed burning of the Edwards Plateau of Texas. Texas Agricultural Extension Service, College Station, Texas, USA.

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

Streby, H. M., and D. E. Andersen. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. Ecosphere 2:art78. http://dx.doi.org/10.1890/ES10-00187.1.

Sullivan, K. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). Journal of Animal Ecology 58:275-286.

Tazik, D. J. 1991. Proactive management of an endangered species on Army lands: The black-capped vireo on the lands of Fort Hood, Texas. Dissertation. University of Illinois, Urbana-Champagne, USA.

Tazik, D. J., and J.D. Cornelius. 1993. Status of the black-capped vireo at Fort Hood, Texas. Vol. 3, Population and nesting ecology. U.S. Army Construction Engineering Research Laboratories Technical Report EN-94/01/ADA 277544, Champaign, Illinois, USA.

U.S. Fish and Wildlife Service. 1991. Black-capped vireo (*Vireo atricapillus*) recovery plan. Austin, Texas, USA.

U.S. Fish and Wildlife Service. 2001. Balcones Canyonlands National Wildlife Refuge: Comprehensive Conservation Plan 2001–2016. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.

Van Winkle, W. 1975. Comparison of several probabilistic home-range models. The Journal of Wildlife Management 39:118-123.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100:69-78.

Vickery, P. D., M. L. Hunter, Jr., and J. V. Wells. 1992. Use of reproductive index to evaluate relationships between habitat quality and breeding success. Auk 109:697-705.

Vitz, A. C., and A. D. Rodewald. 2007. Vegetative and fruit resources as determinants of habitat use by mature-forest birds during the postbreeding period. The Auk 124:494-507.

Wilkins, N., R. A. Powell, A. A. T. Conkey, and A. G. Snelgrove. 2006. Population status and threat analysis for the black-capped vireo. Texas A&M Institute of Renewable Natural Resources, College Station, Texas, USA.

APPENDIX A

A1. Descriptions and codes used to categorize fledgling black-capped vireo behaviors observed during post-fledging surveys at Balcones Canyonlands National Wildlife Refuge, USA, 2013–2014.

Behavior	*Description*
Begging	Vocalization: begging call for food
Feeding from adult	Receiving a food carry from adult
Foraging	Attempting to catch prey (scanning) or seen with food in beak
Perched/Inactive	Not moving or vocalizing
Shradding	Vocalization: shradding
Singing	Vocalization: singing
Territorial	Interaction between same species (e.g., chasing)
Unknown	Activity unknown

A2. Descriptions of physical and behavioral traits used to age fledgling black-capped vireo detected during post-fledging surveys at Balcones Canyonlands National Wildlife Refuge, USA, 2013–2014.

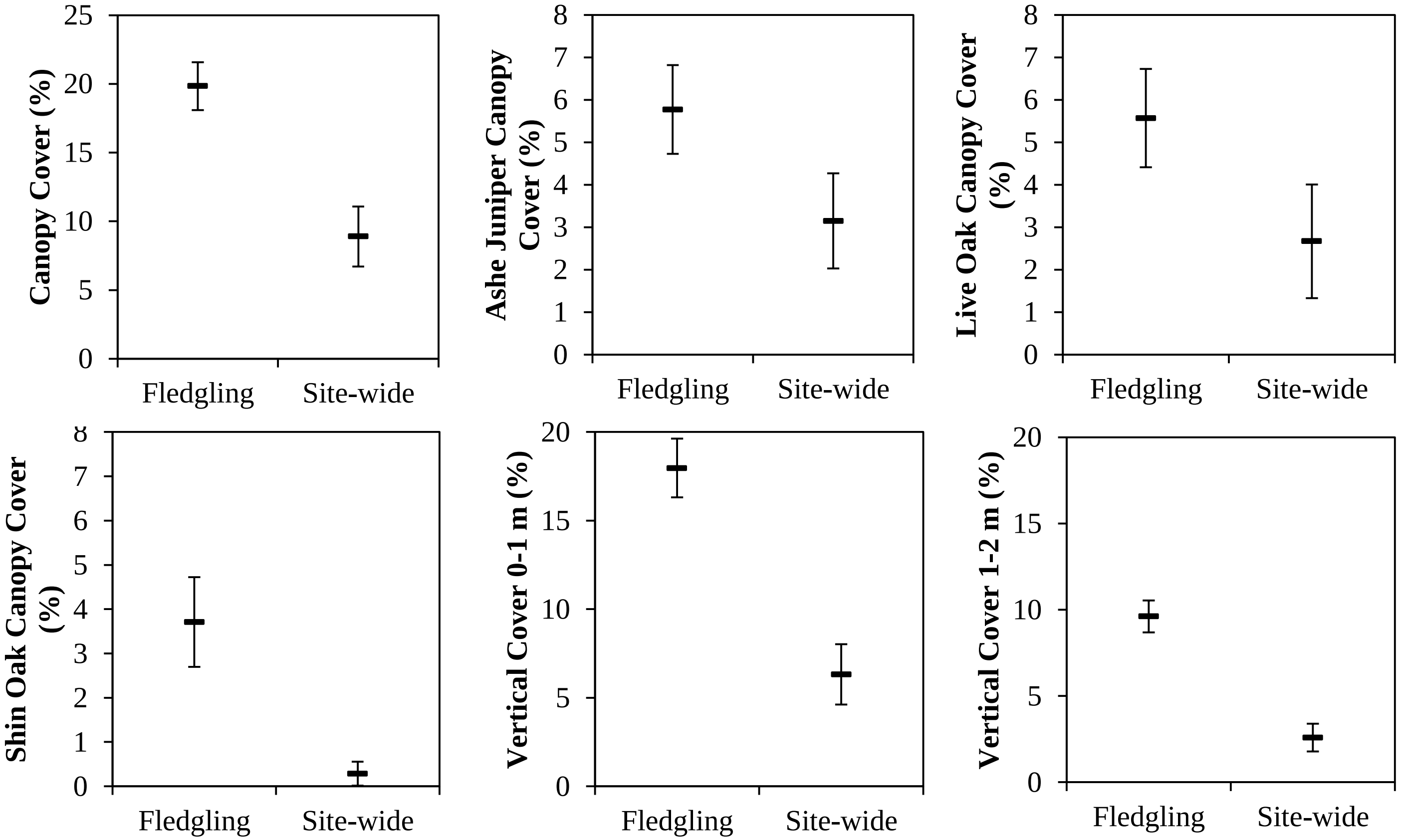
Age Class (number of weeks post-fledging)	*Description*[a]
Young (<2)	Primaries unsheathed, greenish feathers in mid-dorsum, auriculars molting, downy feathers on breast, tail length 6–12 mm at 0–1 week, thick yellow gape flange at base of beak. High-pitched, soft begging calls. Able to preen at around 12 days. No delimited cap, down feathers still growing in.
Intermediate (2–4)	Pale gray head, pale olive-gray back and shoulders, distinct whitish wing-bars, less obvious gape flange. At 2–3 weeks molt on nape and occiput, incoming feathers darker, greenish first winter plumage "V" across back, bright yellow axillaries, tips of buffy feathers on breast, lores and eye ring molting (whitish), tail length is approximately ½ to ⅓ of body length. At 3–4 weeks buffy first winter feathers form inverted "V" from mid-line, feathers on thighs, medium and greater coverts visible against medium dark gray feathers, tail length is closer to ⅓ body length. Louder begging calls, able to shrad, preen efficiently, forage independently, and increased mobility.

A2. Continued.

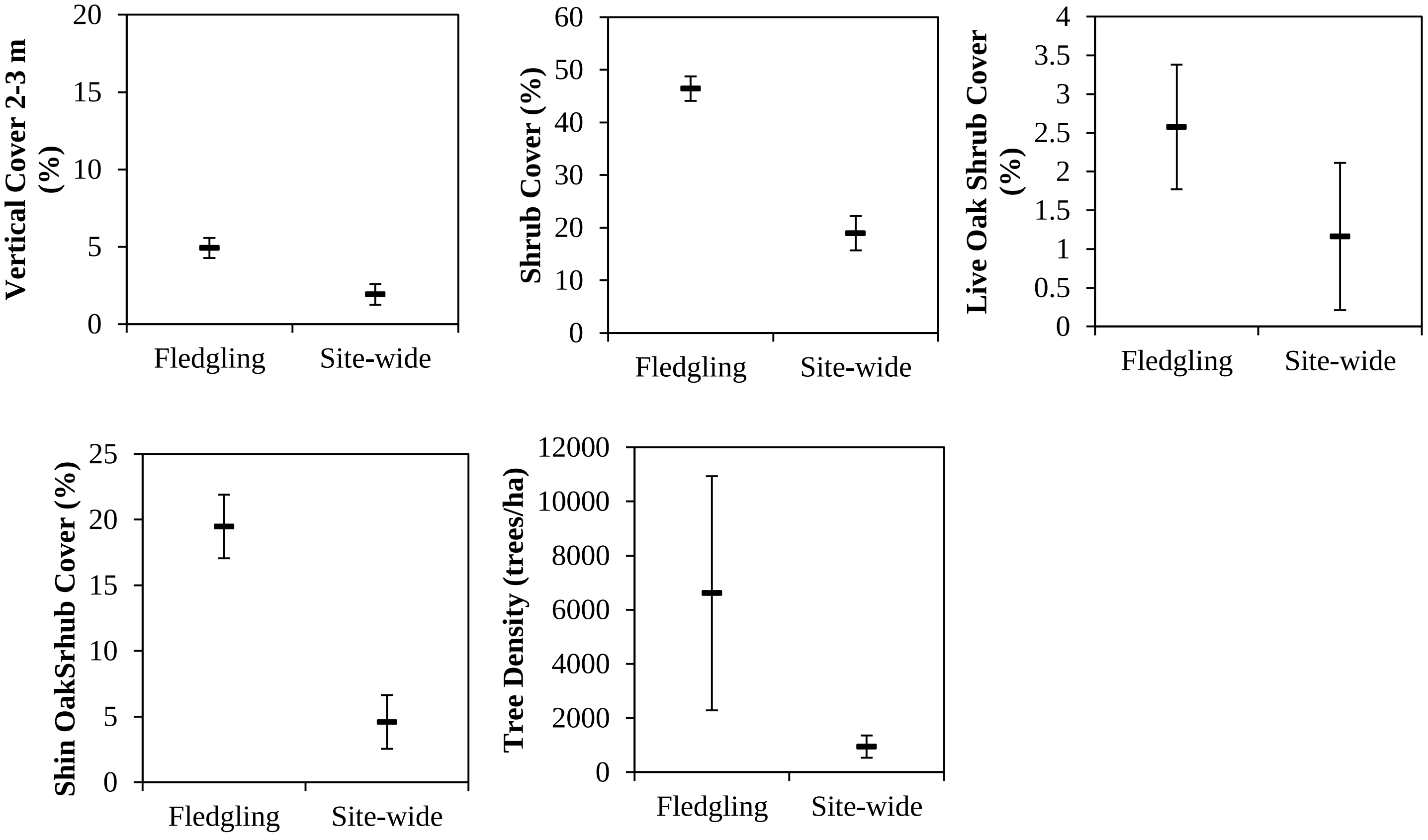
Old (>4)	Plumage similar to adult female but paler, more whitish underneath, less clearly delimited cap and spectacles, and dark brown eyes instead of red. Tail is close to full length of 42 mm. Males have whiter throat, breast and spectacles and more distinctive gray cap than females, which have pale buff to buff spectacles and underparts, and indistinctly gray cap with green feathering. Males begin to sing, clarity of song varies from garbled notes to full song.

[a] Graber 1961, Grzybowski 1991

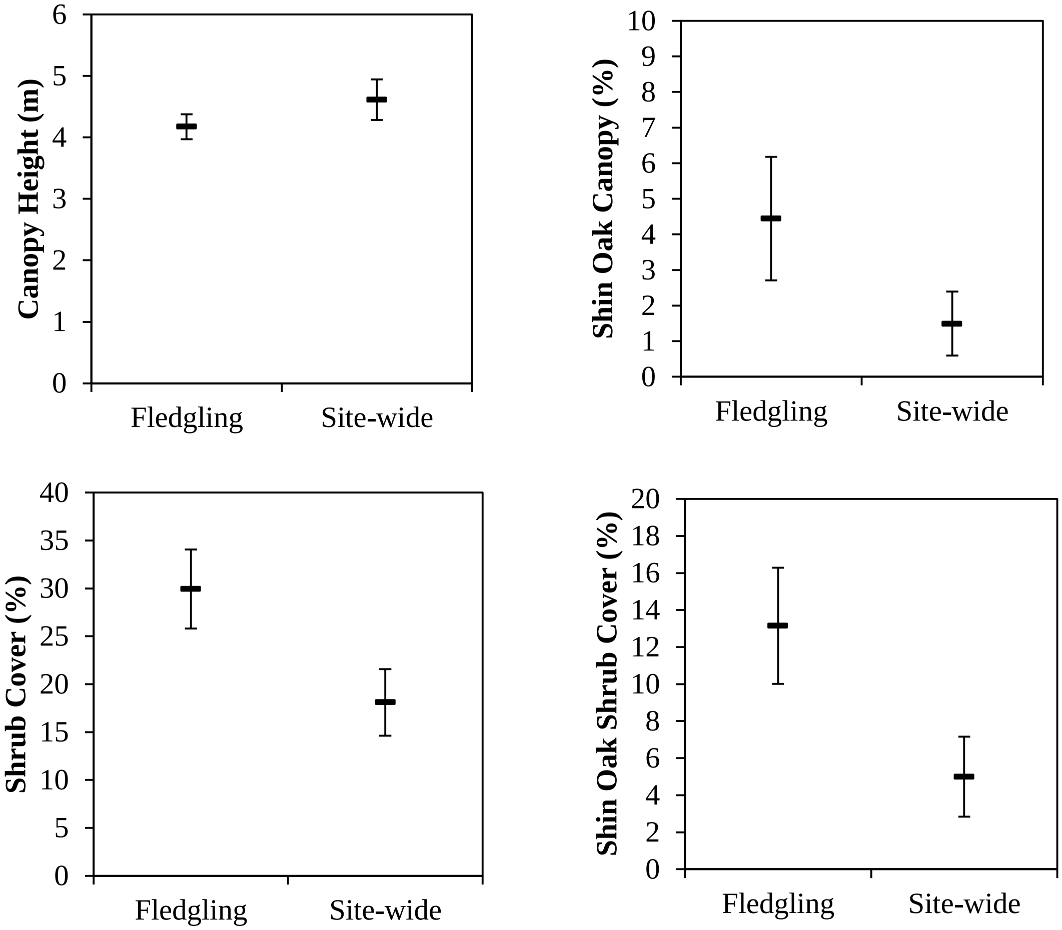
APPENDIX B



B1. Eleven vegetation metrics significantly different between black-capped vireo fledgling detection points and study site-wide sampling points in non-woodland cover at the Balcones Canyonlands National Wildlife area, USA, 2013–2014.



B1. Continued.



B2. Four vegetation metrics significantly different between fledgling locations and study site-wide locations in woodland cover at the Balcones Canyonlands National Wildlife area, USA, 2013–2014.