

THE INFLUENCE OF TEMPERATURE ON BLACK-CAPPED VIREO NEST SITE
SELECTION

A Thesis

By

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ABSTRACT

For avian species in breeding habitats, reproductive success is highly influenced by nest site selection, and changes in the physical environment can drive small-scale changes in individual behavioral responses that influence the nest site selection process. Guthery's (1997) useable space hypothesis combines principles of habitat selection and habitat use, while considering habitat structures and environmental fluctuations, to evaluate the influence these changes have on avian behavior and reproductive success over time. From March to July of the 2013 and 2014 black-capped vireo-breeding seasons at Kerr Wildlife Management Area (KWMA) in Kerr County Texas, I examined the influence of temperature on vireo nest site selection to test Guthery's useable space hypothesis with relation to changes in nest sites and ambient temperature. I measured temperature in vireo breeding habitat at KWMA to determine the influence of vegetation characteristics on ambient temperature across sites. I compared vegetation measurements across the site to vegetation measured at nest sites specifically to determine differences in used versus available areas. I then investigated whether vireos change nest site characteristics over the course of the breeding season to finally evaluate if in fact temperature influenced vireo nest site selection. As expected, temperature increased over the course of the breeding season from April to July. In addition, vireos also chose nest sites with different vegetation characteristics in relation to time of season. As the useable space hypothesis is stated, changes in an organisms needs should be supported in the respective habitats. Vireos used areas of habitat with higher percent shrub cover at nest sites than at temperature data loggers site location measurements. Though I did not find

a difference in temperature within areas of different vegetation characteristics, I did not measure temperature at nest site locations; therefore, there could still be some thermal preferences for vireos at nest sites.

DEDICATION

I dedicate this work to the One that said; But seek ye first the Kingdom of God, and his righteousness; and all these thing shall be added unto you.

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NOMENCLATURE

USFWS	U.S. Fish and Wildlife Service
KWMA	Kerr Wildlife Management Area
cm	centimeter
ha	hectare
km	kilometer
m	meter
hr	hour
min	minute

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I. INTRODUCTION

Habitat is defined as the sum of species-specific resources present in an area that promote occupancy, survival, and reproductive success (Morrison et al. 1992). The collection of resources within an organism's habitat include but are not limited to, factors of microclimate, food availability, vegetation composition and structure (Krausman 1999). These resources, especially within breeding habitat, can influence the survival of adults, young and ultimately impact the propagation of the species (Black et al. 1991).

Changes in characteristics of the physical environment, such as ambient temperatures within a bird's habitat, can influence individual physiological and behavioral responses (Forrester et al. 1998, Bock et al. 2013, Visinoni et al. 2015). Changes in nest site selection and nest placement in response to variation in temperatures are also important aspects of habitat use (Wachob 1996, Tieleman et al. 2008). For avian species in breeding habitats, reproductive success is highly influenced by nest site selection, and changes in the physical environment can drive small-scale changes in individual behavioral responses that influence the nest site selection process. Thus, elevated temperatures can influence habitat use patterns (Martin et al. 2015), and recent local scale temperature studies in North America have focused on the influence of temperature increases on the habitat use and reproductive success of various avian species over time (Forrester et al. 1998, Gehlhausen et al. 2000, Goddard and Dawson 2009, Mathewson 2012).

Changes in nest site selection such as, the selection of vegetation structures that provide shelter from cold, heat or even slight shielding from the wind, may offer additional thermoregulatory benefits for avian species (Nelson and Martin 1999, Tieleman et al. 2008). By selecting nest orientations that optimize nest microclimate, species in cooler environments maximize the sun's warming potential during the early morning cold temperatures. For example, tree pipits (*Anthus trivialis*) orient their nests to maximize thermal conditions that promote hatching success (Burton 2006). Ardia et al. (2006) found that tree swallows (*Tachycineta bicolor*, hereafter swallows) also orient their nest according to more favorable temperature conditions. When temperatures were cooler, swallows built nests that created a warmer environment in the nesting box. Yet, as temperatures increased, swallows oriented nests to reduce internal nesting temperatures (Ardia et al. 2006). In contrast, the opposite may occur as temperatures increase, where birds prefer cooler temperatures for nest contents. For example, vesper sparrows (*Pooecetes gramineus*) that nested under more cover experienced less hours of high temperatures and improved nest success (Nelson and Martin 1999).

Because birds select specific habitat space during breeding periods (Amat and Masero 2004, Butler et al. 2009), the availability of suitable space may change over time. In this way, changes in temperature can act as an environmental constraint that can reduce the availability and quality of habitat space (Forrester et al. 1998, Tieleman et al. 2008), and the potential loss of habitat space is an important concept for the management of species of concern.

The interaction between a species thermal preferences and the desired structure of the habitat are important determinates for species occupancy in an area (Barnagaud et al. 2013). By linking information on habitat structure, nest placement, and temperature for bird species, we can better assess how temperatures influence habitat use and reproductive success in a species.

Guthery's (1997) useable space hypothesis combines principles of habitat selection and habitat use, while considering habitat structure and fluctuations in temperature, to determine the influence these factors have on avian behavior and reproductive success over time. Guthery defined useable space as an area designated by a single coordinate point location, that physically and physiologically supports the adaptations of a species (Guthery 1997). The useable space hypothesis suggests that the availability of habitat resources must be present on a time-unlimited basis in order for an area to be considered useable habitat space (Guthery 1997). This hypothesis also suggests that the use of space by an organisms may change over time due to environmental variation, but that this change in the use of space should be mitigated, especially in managed areas, by the availability of areas that will further support the new habitat requirements. Therefore, it is suggested that space in managed areas should be available to offset the change in habitat use so that environmental variation does not negatively influence an individual's ability to use the space. For example, Forrester et al. (1998) investigated northern bobwhites (*Colinus virginianus*, hereafter bobwhite) during bobwhite breeding, nesting and covey seasons in Texas. The evaluated bobwhite thermal preferences by using the average of two operative temperature measurements taken at; randomly selected

locations near bird sightings, the approximate location of a bird, and a location where a bird landed after being flushed, for each bobwhite they encountered. They found that temperatures where bobwhites flushed, and temperatures where bobwhites landed were significantly lower than temperatures taken at random locations, thus indicating a thermal preference and a final conclusion that temperature affects the operative temperatures of bobwhites and creates functional fragmentation of their habitat (Forrester et al. 1998). This concept, though important for all species of concern, is even more so important for actively managed endangered species, those with limited distributions and those with specific habitat requirements (Catry et al. 2011). Therefore, with evidence suggesting that temperature variation influences changes in reproductive success and may contribute to habitat fragmentation, it is imperative that we consider the influence of temperature on threatened and endangered bird species (Huntley et al. 2006).

The black-capped vireo (*Vireo atricapilla*, hereafter vireo) is a federally endangered neotropical migratory songbird threatened by habitat loss and other anthropogenic factors (Ratzlaff 1987). Population declines are attributed to habitat fragmentation and nest parasitism by brown-headed cowbirds (*Molothrus ater*)(Grzybowski 1995). Vireos breed in central Oklahoma, central and southwest Texas, and northeastern Mexico (Grzybowski 1995). The breeding range extends farther south than previously recorded, with no more traces of the bird found north of central Oklahoma.

In Texas, the vireo breeds from April through July in habitat that consists of shrubland vegetation, including deciduous and woody cover, comprised of live oak

(*Quercus virginiana*) and shin oak (*Quercus havardii*) mottes (Graber 1961). Vireos nest from 0.2 to 3.0 m (usually 0.5 to 2.0 m) above the ground (Graber 1961, Grzybowski 1995) with approximately 30 – 50% cover around the nest (Grzybowski 1995), although variation exists among different areas within the breeding range (Grzybowski et al. 1994, Wilkins et al. 2006, Pope et al. 2013b).

Previous research suggests that vireos may not select habitat for predator avoidance, as protective nest sites may be hard to locate due to the diversity in predator assemblage. Conkling et al. (2012) looked at the predictors of nest predation and found that nest survival was consistent across study sites though there was some variation in vegetation characteristics and predator assemblage. They found that nest height was consistent across the region and that concealment at the nest differed by substrate species, however vireos still selected nest sites with concealment percentages that fell within the known range. Thus, vireos seem to have a preference for a certain nest height (Grzybowski 1995), commit to a certain amount of concealment around the nest (Pope et al. 2013b) and do not experience major differences in predation rates based on these characteristics (Conkling et al. 2012). Therefore, if there are changes in vireo nest site characteristics, there must be other forces driving potential fine scale changes within the system. I propose that force is changes in temperature.

I examined the influence of temperature on vireo nest site selection from March to July of the 2013 and 2014 vireo-breeding season. The study objective was to test Guthery's useable space hypothesis with relation to changes in nest sites and ambient temperature. To accomplish this I measured temperature within characteristics of vireo

breeding habitat at KWMA to determine the influence of the vegetation characteristics on ambient temperature across sites. I compared vegetation measurements across the site to vegetation measured at nest sites specifically to determine differences in nest site vegetation and available habitat space. I then investigated whether vireos change nest site characteristics over the course of the breeding season to finally evaluate if in fact temperature influenced vireo nest site selection.

I expected to find a relationship between vegetation characteristics and ambient temperature, where ambient temperatures would decrease with increasing percent canopy cover, increased percent shrub cover and taller canopy height values. I predicted no difference between nest site characteristics and site vegetation as the areas were managed for vireo breeding habitat. Finally, I predicted vireos would build nests at sites with taller canopy and higher percent canopy cover and higher percent shrub cover as temperatures increased over the course of the breeding season.

II. METHODS

Study area

I conducted my study from March to July 2013 and 2014 at Kerr Wildlife Management Area (hereafter KWMA), a 2,628 ha publicly owned property managed by Texas Parks and Wildlife Department in Kerr County, Texas (Fig. 1). KWMA is located in the Edwards Plateau ecoregion of central Texas and consists of savanna grassland, oak shrubland, deciduous woodland, and oak-juniper woodland. Vegetation management at KWMA includes prescribed burning, slash and burn, dozing, understory thinning and occasional cattle grazing (Texas Parks & Wildlife Department 2015). The mean annual minimum temperature at KWMA is approximately 11°C, and the mean annual maximum temperature occurs in August and is approximately 24°C (NOAA 2015).



Figure 1. Kerr County, Texas.

Vireos at KWMA inhabit mid successional live oak and shin oak mottes, and oak-juniper woodlands of varying densities and heights (Pope et al. 2013b). Vegetation management activities at KWMA maintain suitable vegetation for vireos, and land managers conduct extensive brown-headed cowbird trapping efforts across the area to minimize the negative effect of brood parasitism on nesting vireos and other breeding birds.

Study site selection

I chose study sites at KWMA based on known occurrence of vireos and variation in vegetation height, canopy cover, and shrub cover (Graber 1961, Pope et al. 2013b). In 2013, I selected a 59 ha study site on the west side of KWMA that was last burned in 1999. Personal observations prior to data collection indicated that vegetation on the

study site was variable, but that overall, shrubs were taller and canopy cover was higher when compared to other areas of known vireo occupancy at KWMA. In 2014, I selected one 22 ha study site last burned in 2007 and one 60 ha study site last burned in 2011 to demonstrate the varying vegetation structures vireos occupy at KWMA. The 2014 60 ha study site consisted of shorter vegetation than the 2013 59 ha study site but the 22 ha and had considerably more woodland and less grassland. The 60 ha site was more representative of the savanna-oak grassland and shrubland than the 22 ha with very little oak-juniper woodland. The vegetation at all three sites was representative of vireo breeding habitat in this region of its breeding range (Graber 1961, Grzybowski et al. 1994, Conkling et al. 2012).

Data collection

Ambient temperature — To obtain site scale ambient temperatures, I recorded temperature using Lascar EL-USB temperature data loggers. The temperature data loggers were approximately 10 cm in length and were fitted with a ½ AA 3.6V lithium battery. The data loggers had a temperature measurement range of -35 – 80 °C (Lascar Electronics 2015). I created a grid network of points using ArcGIS at 200 m spacing between grid points where I systematically placed the temperature data loggers at each grid point along the 200 m grid. I attached the data loggers to 1 m wooden stakes, between 0 – 1 m, with duct tape. I covered the data loggers with green plastic cups in order to protect the loggers from direct sunlight. I placed data loggers along grid points in woody vegetation representative of vireo breeding habitat. If a point location along the grid was bare ground or only covered in a herbaceous ground layer, I placed the data

logger in a random position within the nearest clump of vegetation to better represent vireo nesting and foraging substrates and to avoid temperature spikes from direct sunlight. I took a GPS point at the new location and removed the old point. Random point locations were no more than 10 m away from the original location. The data loggers recorded temperature in degrees Celsius (°C) every hour between late March to late July during the 2013 and 2014 vireo breeding seasons.

Site vegetation — I measured vegetation across each site once during the vireo-breeding season to identify site-wide vireo breeding habitat vegetation characteristics using the grid network of points created for temperature data logger placement. At each grid point, and at four points located 5 m from the grid point in each cardinal direction, I recorded canopy cover to the nearest 10% using a tubular densitometer. In addition, I used a 3 m range pole to measure height of the vegetation at each of these five points. I established a 5 m radius circle around the center point and divided the circle into four quadrants based on the four cardinal directions. Within each quadrant, I visually estimated the percent woody shrub cover to the nearest tenth percent for shrubs under 2 m.

Territory establishment and monitoring — To locate vireos on each study site I conducted transect surveys along a grid network of points with 200 by 200 m spacing. I walked at a 1 km/hr pace from point to point from sunrise to 13:00 to detect singing male vireos and marked their locations with a Garmin Rino GPS unit. I surveyed each transect three times between early March and late April and used the GPS point locations of vireo detections to relocate birds for subsequent monitoring. I revisited each

location at 3 – 5 day intervals to map territories. I considered males territorial if I detected them within a specific location for ≥ 4 weeks.

Nest searching and monitoring — I conducted nest searching within established vireo territories from late March to late July in 2013 and 2014. I used behavioral cues of the birds (e.g., alarm calls, food carries, territorial behavior) to locate nest sites. I placed a flag ≥ 10 m away from each nest to aid in relocation. I monitored nests every 2 – 3 days and determined nest fate (i.e., nest failed or fledged). During nest checks, I remained at the nest no longer than 1 min to minimize disturbance to the adults and nest sites. After a nest failed or fledged, I continued to monitor and search the territory, every 3 – 5 days, looking for subsequent nesting attempts.

Nest vegetation — To identify vegetation characteristics of each active nest, I recorded measurements at all nests within monitored territories in which I found at least one vireo or cowbird egg or young. I recorded nest height, canopy height, percent shrub cover, and percent canopy cover only after all nests had fledged or failed at the end of the season. Nest vegetation measurement methods followed the procedures used for the above-mentioned temperature data logger vegetation measurements.

Data analysis

Ambient temperature — To address the first objective, I calculated the mean temperature, maximum temperature (i.e., highest temperature value recorded at each data logger point location), and the average maximum temperature (i.e., mean of daily maximum temperatures on each data logger), for all temperatures recorded at site vegetation locations for each temperature data logger.

Vegetation — I obtained average values for the vegetation metrics measurements of; percent canopy cover, percent canopy cover and percent shrub cover in vireo breeding vegetation across all sites at each temperature data logger location. I took a mean of the five measurements taken for each vegetation metric at each temperature data logger grid point location. I also took the mean canopy height, percent canopy cover and percent shrub cover at nest sites. I ran an analysis of variances (ANOVA; $\alpha=0.05$) to determine mean differences in vegetation at the sites between the 2013 and 2014 vireo breeding season sites. Lastly, I ran a one-way ANOVA for all vegetation metrics collected at the temperature data logger points and at nest sites to assess differences between site vegetation at temperature data logger locations and nest site vegetation during each year.

Relationship of vegetation and ambient temperature — To further investigate the first objective, I used linear regression analyses to evaluate relationships among temperature at temperature data logger locations and the associated vegetation measurements at temperature data logger locations for each site during the 2013 and 2014 vireo-breeding season. I used each of the calculated temperature variables; mean temperature, maximum temperature and average maximum temperature, as a means to determine how vegetation characteristics influenced these values within certain canopy height, canopy over percentages and shrub cover percentages.

Temporal changes in nest characteristics — I ran linear regression for each nest characteristic to determine relationship of change in reference to time of season. All nest site characteristics were analyzed from nest start date. Nest start date was defined as the day the first egg was laid. If a nest was located with more than one egg or at the nestling

stage, I obtained the nest start date based on known vireo nesting parameters. Vireos usually lay one egg per day after the first egg is laid. Vireos will incubate eggs for approximately 15 – 17 days before hatching. After hatching nestling will remain in the nest for 10 – 12 days before fledging (Graber 1961). For the purpose of this study and to address the final objective I calculated nest start date for all nests.

I performed all analyses using version 2.15.3 of the R statistical software program (R Development Core Team, 2015).

III. RESULTS

Temperature

From 15 April to 1 August 2013, I deployed 18 temperature data loggers that resulted in 44,723 hourly temperature readings. In 2014, I deployed 21 temperature data loggers that resulted in 54,408 temperature readings from 10 April to 31 July 2014. In 2013, temperatures ranged from $-1.5 - 45$ °C ($\bar{x} = 24.2$, $SD = 6.9$) and from $-3 - 48$ °C ($\bar{x} = 24.3$, $SD = 7.28$) in 2014. The mean difference between years was 0.1 m, where 2014 had a higher mean temperature. The increase in mean temperature during the season was 7 °C. I combined temperature data across years.

Average temperature and vegetation — I conducted a linear regression and found no relationship between average canopy cover and average temperature at temperature data logger locations ($F_{1,37} = 0.200$, $P = 0.67$). Similarly, I conducted a linear regression and found no linear relationship between average canopy height and average temperature at temperature data logger locations ($F_{1,37} = 1.130$, $P = 0.30$). Finally, I conducted a linear regression and found no relationship between average shrub cover and average temperature at temperature data logger locations ($F_{1,37} = 0.310$, $P = 0.58$) (Fig. 2).

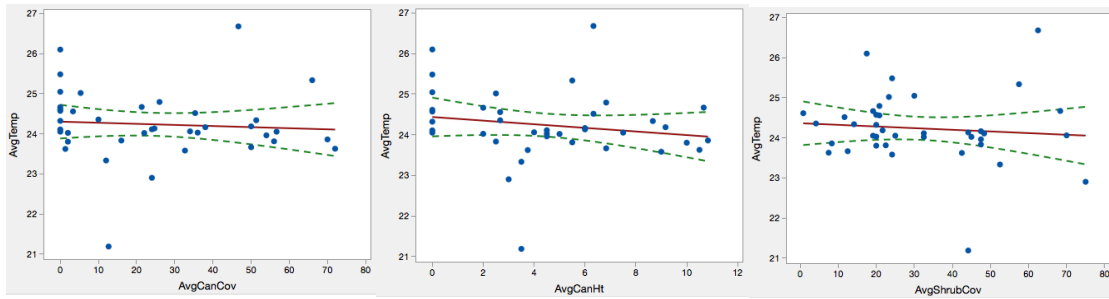


Figure 2. Linear model of average temperature and average canopy cover, average canopy height, and average shrub cover measurements at temperature data logger locations at three sites at Kerr Wildlife Management Area, Kerr County, Texas during the 2013 and 2014 black-capped vireo (*Vireo atricapilla*) breeding season.

Maximum temperature and vegetation —I conducted a linear regression and found no relationship between average canopy cover and maximum temperature at temperature data logger locations ($F_{1,37} = 2.480$, $P = 0.12$). Similarly, I conducted a linear regression and found no relationship between average canopy height and maximum temperature at temperature data logger locations ($F_{1,37} = 1.590$, $P = 0.22$). Finally, I conducted a linear regression and found no relationship between average shrub cover and maximum temperature at temperature data logger locations ($F_{1,37} = 0.130$, $P = 0.72$) (Fig. 3).

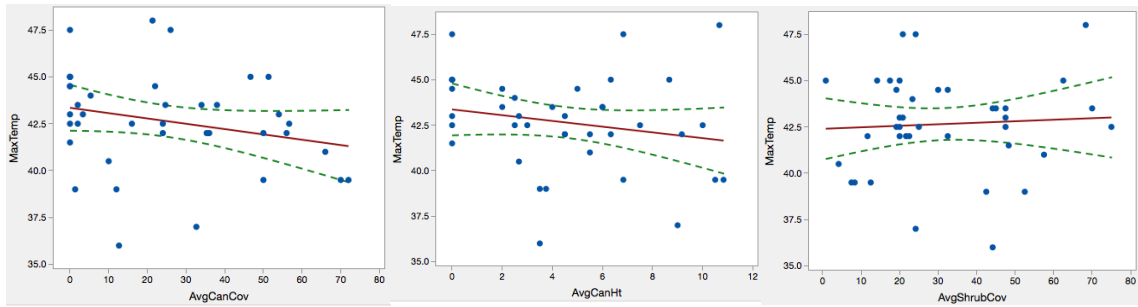


Figure 3. Linear model of maximum temperature and average canopy cover, average canopy height, and average shrub cover measurements at temperature data logger locations at three sites at Kerr Wildlife Management Area, Kerr County, Texas during the 2013 and 2014 black-capped vireo (*Vireo atricapilla*) breeding season.

Average maximum temperature and vegetation —I conducted a linear regression and found no relationship between average canopy cover and average maximum temperature at temperature data logger locations ($F_{1,37} = 1.530$, $P = 0.22$). Similarly, I conducted a linear regression and found no relationship between average canopy height and average maximum temperature at temperature data logger locations ($F_{1,37} = 0.450$, $P = 0.51$). Finally, I conducted a linear regression and found no relationship between average shrub cover and average maximum temperature at temperature data logger locations ($F_{1,37} = 0.090$, $P = 0.76$) (Fig. 4).

Due to the insignificant relationships between the vegetation metrics and the temperature measurements, I conducted a general linear model in addition to Tukey's HSD post hoc analysis of each vegetation characteristics together to determine if there was interaction between them. There was a significant interaction between shrub cover and canopy cover with relation to ambient temperature ($t_{38} = 3.555$, $P \leq 0.01$).

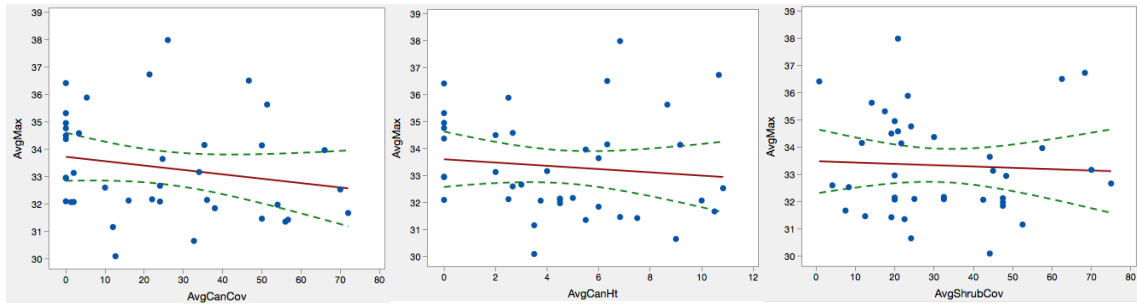


Figure 4. Linear model of average maximum temperature and average canopy cover, average canopy height, and average shrub cover measurements at data logger location taken at three sites at Kerr Wildlife Management Area, Kerr County, Texas during the 2013 and 2014 black-capped vireo (*Vireo atricapilla*) breeding season.

Vegetation

I measured vegetation at 39 temperature data logger locations at KWMA during the 2013 and 2014 vireo breeding season (n = 18 in 2013, n = 21 in 2014). Mean, minimum, maximum and standard deviation values for each vegetation metric for all 39 locations is found in Table 1.

Table 1. Mean, minimum, maximum, standard deviation and sample sizes for site vegetation metrics at temperature data logger locations at three sites at Kerr Wildlife Management Area, Kerr County, Texas during the 2013 and 2014 black-capped vireo (*Vireo atricapilla*) breeding season.

Vegetation variable (units)	2013 (n = 18)				2014 (n = 21)			
	Mean	Min	Max	SD	Mean	Min	Max	SD
Canopy Cover (%)	21.0	0.0	66.0	21.79	27.0	0.0	72.0	24.53
Shrub Cover (%)	38.0	17.5	75.0	18.07	26.0	0.0	68.0	18.74
Canopy Height (m)	3.0	0.0	10.0	2.73	5.5	0.0	11.0	3.61

I conducted an ANOVA to compare means of each vegetation metric between years. I found that shrub cover percentages and canopy height were significantly different at temperature data logger locations in 2013 than at both sites for 2014 ($F_{1,37} = 4.162$, $P = 0.04$ and $F_{1,37} = 4.291$, $P = 0.04$ respectively). Shrub cover was higher at the 2013 site than at both sites for 2014 and canopy height was lower at the 2013 site than at both of the 2014 sites. However, this was not the case for canopy cover percentages, as the results of the ANOVA show that mean values were statistically similar between years ($F_{1,37} = 0.573$, $P = 0.45$).

I measured vegetation at 181 vireo nest sites at KWMA during the 2013 and 2014 vireo breeding season (n = 55 in 2013, n = 126 in 2014) (Table 2). Nest height ranged

from 0.2 – 4.0 m, with the mean of 1.0 m, which is within the average nest height range for the species (Table 2). Results of an ANOVA showed nest height did not differ between years ($F_{1,179} = 1.525, P = 0.22$). Mean shrub cover was 47% across years, with results of an ANOVA showed no individual differences in shrub cover means between years ($F_{1,179} = 3.291, P = 0.07$). Mean percent canopy cover at nest sites was ~ 24% (SD = 17.7) across years. An ANOVA showed that canopy cover percentages were significantly different between years due to differences in vegetation at sites ($F_{1,179} = 4.129, P = 0.04$). In 2013, mean percent canopy cover was higher at nest sites than in 2014 ($\bar{x} = 28.04, SD = 20.90$ in 2013, $\bar{x} = 22.22, SD = 16.13$ in 2014). Mean canopy height above nests was 4.0 m (SD = 2.3; Table 2) and the results of the ANOVA showed this was similar between years ($F_{1,179} = 0.428, P = 0.51$).

Table 2. Mean, minimum, maximum, and standard deviation for nest vegetation metrics at vireo nest site locations at Kerr Wildlife Management Area, Kerr County, Texas during the 2013 and 2014 black-capped vireo (*Vireo atricapilla*) breeding seasons.

Nest vegetation variable (units)	2013 (n = 55)				2014 (n = 126)			
	Mean	Min	Max	SD	Mean	Min	Max	SD
Nest Height (m)	1.0	0.3	2.6	0.6	1.1	0.2	4.3	0.6
Canopy Cover (%)	28.0	0.0	92.0	20.9	22.0	0.0	72.0	16.1
Shrub Cover (%)	50.0	10.0	90.0	20.0	45.0	0.0	97.5	18.1
Canopy Height (m)	4.0	0.0	11.0	1.9	4.5	0.0	12	2.4

When considering differences between site vegetation and nest site vegetation, I conducted an ANOVA and found that average nest canopy cover and average site canopy cover did not differ ($F_{1,218} = 0.020$, $P = 0.89$), nor did average nest canopy height and average site canopy height did not differ ($F_{1,218} = 0.160$, $P = 0.69$). However, results of an ANOVA showed that average nest shrub cover percentage and average site shrub cover percentages were significantly different ($F_{1,218} = 21.410$, $P < 0.01$), where the mean difference was about ~15 % (Fig. 2).

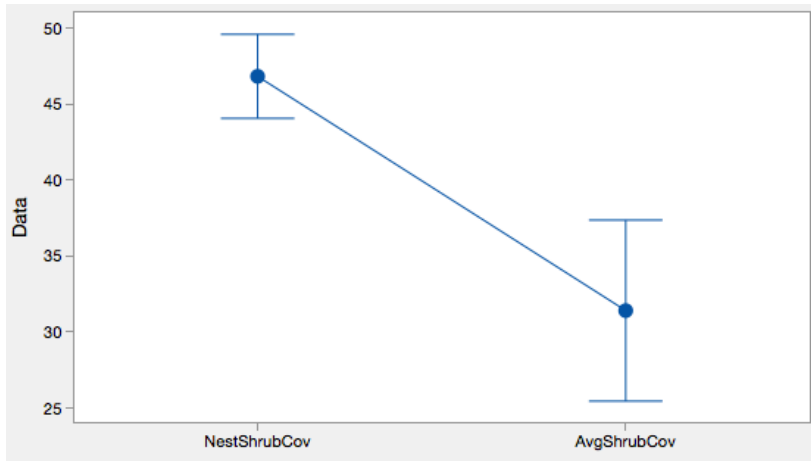


Figure 5. Average nest shrub cover and average site shrub cover across three sites at Kerr Wildlife Management Area, Kerr County, Texas during the 2013 and 2014 black-capped vireo (*Vireo atricapilla*) breeding season.

Temporal changes in nest characteristics

Over both years of the vireo breeding season, the results of the linear regression showed no significant change in mean nest height as the season progressed ($F_{1,179} = 3.890$, $P = 0.05$). However, the results of the linear regression showed that mean canopy cover at nest sites decreased by approximately 10 % over time ($F_{1,179} = 5.160$, $P = 0.02$). Similarly, the results of the linear regression showed that the approximate 10 % increase in percent shrub cover over the breeding season was also significant ($F_{1,179} = 9.400$, $P < 0.01$). In addition, the results of the linear regression showed that canopy height above nests decreased by an average of 1.5 m over the course of the breeding season ($F_{1,179} = 8.530$, $P < 0.01$) (Fig. 6).

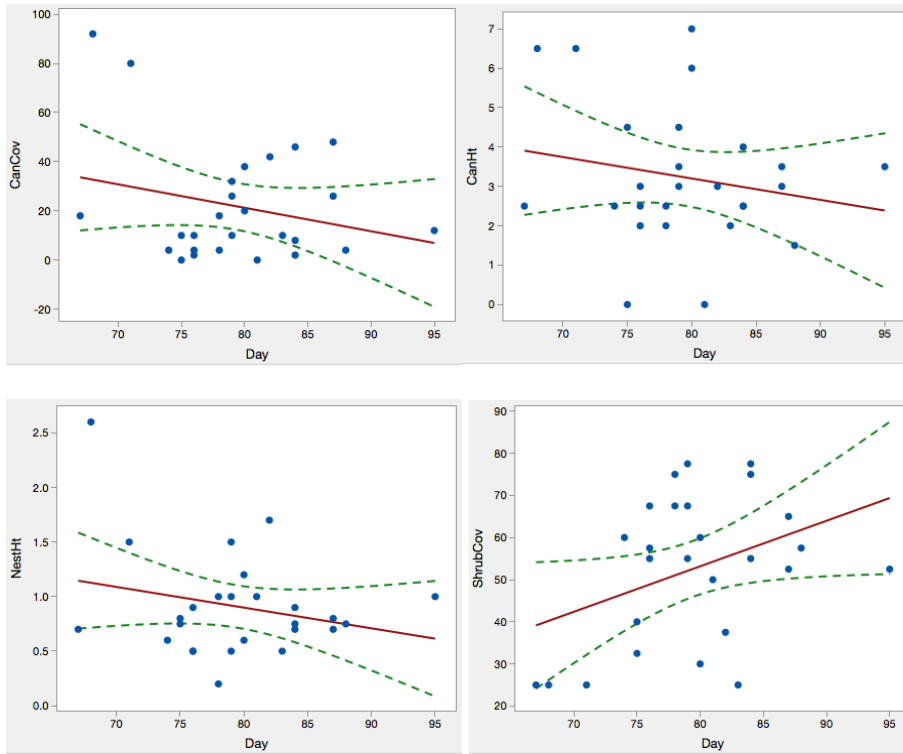


Figure 6. Linear model of canopy cover, canopy height, nest height, and shrub cover over time at nest sites across three sites at Kerr Wildlife Management Area, Kerr County, Texas during the 2013 and 2014 black-capped vireo (*Vireo atricapilla*) breeding season.

IV. DISCUSSION, CONCLUSION AND MANAGEMENT IMPLICATIONS

While my study did not conclude that temperature was a limiting factor for black-capped vireo breeding useable habitat space at Kerr Wildlife Management Area, I did find that, as expected, temperature increased over the course of the breeding season from April to July. In addition, vireos nested in areas with different vegetation characteristics in relation to time of season. As the useable space hypothesis is stated, changes in an organisms needs should be supported in respective habitat space. Vireos did use areas of habitat with higher amounts of shrub cover at nest sites than at temperature data loggers site location measurements. Though, I did not find a difference in temperature within areas of different vegetation characteristics, there could still be some thermal preferences for vireos at nest sites, as I did not measure temperature at nest site locations to avoid disturbing nesting birds (and to comply with permit restrictions).

Temperature

As expected, temperature increased over time during the 2013 and 2014 vireo-breeding seasons. While only a small difference was found in temperatures between both years, the 2014 breeding season had a higher maximum temperature and lower average minimum temperature. This difference in measured temperatures between both years may be due to differences in site vegetation in addition to annual variation. In this study maximum ambient temperatures did exceed 40 °C. In addition, the majority of data loggers placed across sites experienced readings over 40 °C in both years. In previous studies temperature increases as low as 2 – 3 degrees during bird breeding seasons resulted in changes in reproductive success (Cox et al. 2013b). Most temperature loggers

have a warning threshold set at 40°C (Case and Robel 1974, Spiers et al 1983), and while I did not test for operative temperatures for vireo, evidence of temperature studies show that operative temperatures above 40°C can be harmful for various bird species (Forrester et al. 1998, Cox et al. 2013b).

Vegetation

Although vireo habitat is managed with similar techniques across the sites at KWMA, differences in time since last management treatment has resulted in varied vegetation characteristics across sites. The vegetation measured at the 2013 site had higher percentages of canopy cover but lower canopy heights. However, site vegetation and nest site vegetation was very similar, though, there was a difference between nest site shrub cover and site vegetation shrub cover percentages. Vireos nested and used vegetation that was more dense than surrounding areas within the site, supporting previous claims that vireos on the Edwards plateau avoid more open areas (Grzybowski et al. 1994). This observation could lead to further conclusions about foraging preferences, predator avoidance and thermal needs of the species.

Temperature and vegetation

The evaluation of temperatures across sites and the associated measurements of the surrounding point location vegetation did not yield any predictive properties for any one vegetation characteristic and ambient temperature therein. Ultimately, in each of the three vegetation metrics, average temperature showed slight trends though they were not strong enough to be true predictors of ambient temperature. However, the interaction between shrub cover and canopy cover percentages creates an interesting condition. As

percent shrub cover changed, the relationship between temperature, canopy cover, and canopy height also changed. In areas of high percent canopy cover, temperature was low until shrub cover percentages increased. This may be explained by the lack of airflow through the trees, though I did not measure airflow. Wind speed reduces ambient temperatures and the taller the vegetation, the more wind it receives, but in areas closer to larger stands of trees or woodlands, there is less airflow, and densely packed vegetation of the woodland can cause a still and warm thermal environment (Adams and Adams 2010). This occurrence is seen even more when dense shrubs, that also have heat trapping properties due to high stem density (Adams and Adams 2010), block the flow of air beneath the canopy. Thus, the increase in temperature under higher percentages of canopy cover may be due to an increased amount of shrub or ground cover under the trees.

Nest site characteristics

As the season progressed, vireos placed nests lower to the ground in 2014. In 2014, the average temperature during the vireo-breeding season was higher than the previous year. However, this is unlikely to be related to the decrease in nest height, as ambient temperatures are often higher closer to the ground (Adams and Adams 2010). An alternative explanation may be the avoidance of the brown-headed cowbird, as I observed an increase in cowbird parasitism during that year. This increase in parasitism may be correlated to cattle grazing at KWMA during the 2014 vireo-breeding season (unpublished data). Although this study did not identify predation rates or predator assemblage, we know that cowbirds also contribute to decent levels of predation

(Conkling et al. 2012), and previous studies on avian nest predators have found that avian predation risk decreases with decreasing nest height (Piper and Catterall 2004). However, this contradicts evidence found at vireo nests in central Texas where Conkling et al. (2012) found no correlation between nest height and avian predation. While solid evidence of these results has yet to be found in vireos, evidence does support that vireos may select nest sites for reasons other than predator avoidance. While vireos in my study area placed nests lower over time, nest height remained within the known range (Graber 1961, Grzybowski 1995, Conkling et al. 2012). Such a small difference may be biologically negligible with reference to temperature especially considering the lack of relationship found between vegetation characteristics and temperature. Furthermore, the tradeoff between avoiding predation and a preferable thermal refuge may also change during breeding seasons, where predator avoidance may prevail in the early portion of the breeding season, but needs for thermal refuge prevails towards the end of the breeding season when temperatures begin to increase (Tieleman et al. 2008). Thus, we must also consider individual variation. The variation amongst individuals adds additional factors to the study of predation risk versus thermal refuge preferences as body conditions and learned actions may cause individuals to alter behaviors accordingly (Amat and Masero 2004).

As predicted, vireos used areas with increased percent shrub cover at nest sites over time. Increased shrub cover at nest sites could provide thermal cover for vireos and nestlings as ambient temperatures increase over the course of the season. Increased cover may also provide more protection from predators that use visual cues for locating nests

(Pope et al. 2013a). However, vireos did not select nest sites with higher percent canopy cover over time, which countered initial predictions. Over both years, vireos used areas of reduced canopy cover at nest sites. I made my initial predictions based on the idea that shade from canopy would decrease the amount of heat at the surface level but the observed decrease in percent canopy cover could rather be the result of changes in ambient temperature based on airflow. In areas closer to larger stands of trees of woodlands, there is less airflow (Adams and Adams 2010). Where trees are sparse, air is able to flow through and ultimately decrease ambient temperature, but because I did not measure airflow, I cannot confirm this explanation.

In conclusion, I was unable to find any direct relationship between ambient temperature and vegetation characteristics, and for this reason I cannot confirm any evidence of temperatures influencing vireo habitat use and nest site selection. However, I did find that vegetation characteristics were interacting with one another causing different fluctuations in temperatures. The complexity of vegetation structures in vireo habitat may require more aspects of the microclimate in addition to temperature. Though the temperature results did not match my predictions, I can conclude that vireos altered nest site characteristics over time. This change in nest site selection may influence the amount of useable space vireos have access to across sites at KWMA, and though I have not found the driving factor to be temperature, future research should look to identify stimulus moving the system. The disparity of site shrub cover versus shrub cover used at the nest should prompt some concern for land managers as this difference may require altered management strategies.

Management implications

Guthery's useable space hypothesis suggests that the availability of food resources, appropriate vegetation structure, composition and microclimatic factors must be present on a time-unlimited basis in order for an area to be considered useable habitat space (Guthery 1997). Adapting management strategies within black-capped vireo breeding habitat, based on the threat of expected environmental variation, might be critical for future success of the breeding population in south central Texas. Although we do not fully understand how expected climatic variation will change the vireos environment, we must consider the observed trends and adapt management strategies accordingly.

Seasonal changes influence the ambient temperature under vegetation in vireo breeding habitat in south central Texas (this study). As the vireo-breeding season goes on from April to July, average ambient temperatures increase. Areas of scarce vegetation exhibit the warmest temperatures and lack the cover options needed for thermal refuge for the vireo. Shrublands with higher percent shrub cover may provide the necessary cover options and appropriate thermal refuge for vireo as seasonal temperatures increase. The results of this study suggest that vireos may need shrub cover options that are higher than previously recorded percentages (30 – 50%) (Grzybowski et al. 1994), as temperatures increase over the course of the vireo breeding season. The availability of woodland vegetation may also provide thermal cover in the absence of shrub cover, but an excess of the two should not be intermixed. The results of the study also suggest management for more cover options in the form of woody deciduous vegetation at approximately 2 m in height. This suggestion corresponds with previous studies that

report vireo breeding habitat needs (Graber 1961, Grzybowski et al. 1994, Wilkins et al. 2006). With all of these recommendations comes the caveat that further research should be conducted to provide a better understanding of the different biological interactions influencing vireo habitat conditions.

In addition to management suggested based on the results of this study, previously suggested and implemented management strategies that complement these are also recommended for vireo in this portion of its breeding range. Managers should continue to focus on creating habitat space for successful foraging for adults and young, such as cowbird management and prescribed burning (Pope et al. 2013b). In areas where more recent prescribed burns have occurred, allowing a longer growth period before the next burn may allow a higher occupancy of birds as the vegetation becomes taller and more dense (Grzybowski et al. 1994, Wilkins et al. 2006, Conkling et al. 2012, Pope et al. 2013b). Conkling et al. (2012) suggested steady management that supported the needs for vireo breeding habitat characteristics as opposed to managing for habitat structures that reduce predation. Similar to this study, where results showed that a great deal of variation occurs in the thermal environment, Conkling et al. (2012) found that the variability in predator assemblage was far too great to appropriately manage habitat for each predator type (Conkling et al. 2012). However, the removal of grazing or more active cowbird trapping may decrease levels of parasitism (Locatelli 2014). Until further research is conducted, we must continue to consider all hypotheses for vireo nest site selection and nest characteristics.

Future research

Evidence suggests that birds select nest sites for thermoregulatory purposes in addition to factors involving predator avoidance and food availability (Forrester et al. 1998, Nelson and Martin 1999, Tieleman et al. 2008, Morgan 2012, Cox et al. 2013b, Cox et al. 2013a). Increases in temperatures may be influencing vireos nest site selection, as they may need more thermal refuge later in the season. Increasing temperatures may also effect the predator assemblage and the rate of predation (Cox et al. 2013b), causing vireos change nest site characters for increases chance of success (Conkling et al. 2012). Because the black-capped vireo is a habitat specialist, with a very limited distribution, any change in its environment and or habitat structure may have detrimental effects on individuals and overall population status (Graber 1961). The change in nest site characteristics for the black-capped vireo over the course of it's breeding season gives further evidence to the case that habitat should be managed based on a gradient of heights and densities to ensure useable space for seasonal changes in breeding habitat in the central portion of Texas. Because these changes have been recorded in this portion of the breeding area, it is important that the remainder of the breeding range be considered for similar studies as these differences may be more or less important across the breeding range (Grzybowski et al. 1994).

Because Kerr County Texas is considered the center and most representative area of the vireo breeding range in Texas (Graber 1961), changes in temperature and the resulting changes in behavior may be harder to tease out. Similar studies, conducted at

the edges of the species range where temperatures can be very high and where population sizes begin to taper off, may yield results that are more conclusive.

If the observed pattern seen in this study on vireo nest site selection and the influence of temperature is biologically significant, future studies should focus on behavioral aspects of vireos during the breeding season. Although we cannot apply evidence found in a study between different species, we can use models of previous studies and to test the applications validity for other species (Primack et al. 2009).

Future research focused on nest microclimates using temperature data loggers at nest sites would also provide a more accurate evaluation of the microclimate at the nest. Researchers should also investigate the thermal microclimate within the nest as studies show that incubation temperatures vary greatly from the ambient temperature surrounding the nest (Wiebe and Swift 2001, Ardia et al. 2006, Butler et al. 2009).

Future research should also look in to changes in predator assemblage over time to see if vireo is changing based on predation risk (Forstmeier and Weiss 2004). Nest design and location of the nest are decided based on cues formed through natural selection to minimize predation risks (Mainwaring et al. 2014), although it is still unclear if birds can actually assess predation risk. Selection of appropriate nest sites may be more related to other factors like food availability, trial and error or maybe thermal properties (Forstmeier and Weiss 2004).

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