EXPLORING GRADIENTS OF HABITAT

SUITABILITY, HABITAT QUALITY, AND

MICROCLIMATE: IMPLICATIONS FOR GRAY VIREO

NESTING ECOLOGY AND MANAGEMENT


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Abstract: Gray Vireos are one of the most understudied songbirds in North America and are considered a species of conservation concern for multiple state and federal agencies. I sought to address some of the gaps in our understanding of the species' habitat requirements and ecology, using a novel approach of spatially quantifying an index of habitat quality, and by evaluating their nesting strategy as an evolutionary mechanism to control microclimate.

i)      I studied Gray Vireo nest-site selection at three spatial scales: the nesting tree, the vegetation surrounding nests, and within territories. Gray Vireos selected nesting trees that were taller and wider than other adjacent junipers. Selection of vegetation characteristics surrounding nests showed a similar pattern, where nests were in areas where junipers were taller, wider, and had greater foliage density than was randomly available. Broad-scale analyses suggested that Gray Vireos selected nest sites in areas with higher proportions of junipers at low elevations (< 1954 m), and lower proportions of junipers in higher elevations (> 1954 m).

ii)     Daily nest survival probabilities were estimated as a function of nest placement and fine-scale vegetation characteristics. Nest survival was high, with daily and overall nest survival probability of 0.98 and 0.44, respectively. Our top models included positive effects of nest-tree foliage density and nest distance from the edge of the nesting tree.

iii)    I sought to quantify the proportion of selected habitat that has a high probability of contributing to population growth. Gray Vireos tended to nest in locations where they had the highest probability of nest survival. Approximately 85% of the area selected by Gray Vireos for nesting habitat had a high probability of contributing to population growth through nest survival.

iv)     The microclimate of Gray Vireo nests was monitored to evaluate the thermal benefits of nesting on the periphery of a nesting substrate through orientation. Nests were on average 3 ℃ cooler than the opposite orientation of the nesting tree at the hottest times of the day (1700–1830). Nests also received significantly less light exposure throughout the day than the opposite orientation of the nesting tree.

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CHAPTER I

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INTRODUCTION

An understanding of the habitat preferences for species of conservation concern is one of the most fundamental goals of ecological research (Southwood 1977). For migratory birds, nest-site selection patterns are arguably the most important life-history consideration for habitat management, as nest sites can influence reproductive success and population growth for migratory breeding birds (Schmidt 2004, Kus and Whitfield 2005). Nest-site selection studies can be used to create and enhance management prescriptions for breeding birds (Manly et al. 2002).

Nest-site selection is continuously influenced by evolutionary forces, such as predation (Martin 1993), brood parasitism (Forsman and Martin 2009), and microclimate (DuRant et al. 2013). These selection pressures can interact, resulting in perceived trade-offs to maximize reproductive output and offspring survival (Rauter et al. 2002, Tieleman et al. 2008). These trade-offs in nest placement has been demonstrated in Water Pipits (*Anthus spinoletta*) (Rauter et al. 2002) and Hoopoe Larks (*Alaemon alaudipes*) (Tieleman et al. 2008), where predation risk is higher in locations with optimal microclimate, resulting in nest locations that minimize the negative effects of both conditions. These interactions can be difficult to quantify in nest-site selection studies but they are important to consider when managing nesting habitat for species of conservation concern.

The nesting ecology of many species within the Vireonidae family is not well understood. Specifically, several species with breeding ranges in the Southwestern United States are of conservation concern, yet we lack detailed data on their nesting requirements (Bent 1965). Information about vireo nest-site selection is generally vague site characteristics and varies greatly by species and region. For example, the federally endangered Black-capped Vireo (*Vireo atricapilla*), favors higher proportions of woody cover at multiple spatial scales and greater proportions of edge habitat (Bailey and Thompson 2007). Similarly, Bell's Vireo (*Vireo belli*) in Nevada, Arizona, and New Mexico tend to nest in areas with higher vegetation density and more canopy cover than what is randomly available (Parody and Parker 2002). For Plumbeous Vireos (*Vireo plumbeus*), we lack multi-scale assessments of nest sites. However, nests in pinyon pine (*Pinus edulis*)/ponderosa pine (*Pinus ponderosa*) woodlands are generally located in pinyon pines, junipers, alder-leaf mountain mahoganies (*Cercocarpus montanus*), or other shrubs (Goguen and Curson 2012).

Similarly to other southwestern vireos, Gray Vireos (*Vireo vicinior*) are understudied in many aspects of their life-history (Barlow et al. 1999, Schlossberg 2006). Gray Vireos are migratory with a breeding range that includes New Mexico, Colorado, Arizona, Utah, and small populations in California, Nevada, and Texas (Barlow et al. 1999). Throughout the majority of their range, Gray Vireos are likely breeding habitat specialists that rely on high densities of juniper (*Juniperus spp.*) in pinyon-juniper woodlands (Barlow et al. 1999, Schlossberg 2006). In Colorado, Gray Vireos tended to occupy areas with higher densities of junipers than pinyon pines, and with higher densities of sagebrush (*Artemisia tridentata*) (Schlossberg 2006). Unpublished observations of Gray Vireo behavior (Barlow et al. 1999) suggest that shrub cover is an important substrate for foraging of insects, while junipers seem to be the primary nesting substrate for Gray Vireos in this region. The importance of juniper density has also been demonstrated in Utah, where populations were completely extirpated following juniper thinning (Crow and van Riper 2010). However, small populations in California can be found in arid chapparal without junipers (Hargrove and Unitt 2017).

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Nests in this part of their range were located in chamise (*Adenostoma fasciculatum*), desert ceanothus (*Ceanothus greggii*), and mountain mahogany (*Cercocarpus betuloides*) (Hargrove and Unitt 2017). Nest success in this region was low, with an average probability of nest survival of 0.08 (Hargrove and Unitt 2017). Additional work on the nesting ecology of Gray Vireos has been limited to federal and state reports. In New Mexico, Gray Vireos have been studied extensively on military lands over the last 10 years. These reports suggest that Gray Vireos in central New Mexico nest almost exclusively in junipers and nested in taller trees than what was randomly availably (K. Johnson et al., unpublished report; L. E. Wickersham and J. L. Wickersham, unpublished report). Additionally, selection for nest sites at fine scales (0.04 ha) was predominately driven by the presence of more trees than what was randomly available (K. Johnson et al., unpublished report).

Gray Vireos are considered a species of conservation concern by the U.S. Fish and Wildlife Service, New Mexico Partners in Flight, and a threatened species by the New Mexico Department of Game and Fish (NMDGF). The conservation concerns largely stem from a limited breeding range (Barlow et al. 1999), low population densities (Schlossberg 2006), and susceptibility to habitat loss (Pierce, L. S. J., unpublished report). Pinyon-juniper woodlands are anticipated to decline due to climate change-induced drought in the future (Clifford et al. 2011). Consequently, various populations have been considered vulnerable under future climate change projections (Gardali et al. 2012).

Given the conservation concerns and our minimal understanding of their life-history, our goal was to identify Gray Vireo habitat requirements for breeding populations in central New Mexico. Specifically, our objective was to analyze Gray Vireo nest-site selection at multiple spatial scales to describe second and third-order selection (Johnson 1980). Schlossberg (2006) suggested that breeding populations select sites with high juniper densities at multiple scales and areas where sagebrush is prevalent. Additionally, unpublished data in this region suggests that Gray Vireos may select areas with more trees and larger junipers than what is randomly available (K. Johnson et al., unpublished

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report). Therefore, I hypothesized that nesting trees would be larger (height and width) than randomly available trees and that habitat selection would be driven by greater densities of junipers and shrubs, and areas with larger junipers. Foliage density has not been tested in other Gray Vireo studies. However, given the importance of vegetation density for Bell's Vireo (Parody and Parker 2002) and Black-capped Vireo ((Bailey and Thompson 2007), I predicted foliage density would be positively associated with nesting trees and nesting habitat. Given the lack of previous work at broader spatial scales, I performed exploratory data analyses for landscape-level selection.

## METHODS

**Study site**

Data were collected on Kirtland Air Force Base (KAFB), south of Albuquerque, NM (Figure 1). Kirtland Air Force Base encompasses approximately 21,000 ha situated immediately adjacent to the Manzanita Mountains. Elevation on KAFB ranges from 1,600 to almost 2,400 m (Department of Defense, unpublished report). Previous vegetation surveys on base found four primary landcover types based on dominant vegetation: grasslands, pinyon-juniper woodlands, ponderosa pine woodlands, and wetlands/arroyos (Department of Defense, unpublished report). All surveys were conducted in either pinyon-juniper woodlands or transitional regions between grasslands and pinyon-juniper woodlands, as previous research suggested these areas to have the highest probability of Gray Vireo occurrence (Schlossberg 2006, Wickersham, L. E. and J. L. Wickersham, unpublished report). Dominant plant species within these areas include blue grama (*Bouteloua gracilis*), side-oats grama (*B. curtipendula*), four-winged saltbush (*Atriplex canescens*), sand sagebrush (*Artemisia filifolia*), broom snakeweed (*Gutierrezia sarothrae*), rubber rabbitbrush (*Ericameria nauseosa*), threadleaf groundsel (*Senecio flaccidus*), apache plume (*Fallugia paradoxa*), alderleaf mountain mahogany (*Cercocarpus montanus*), scrub oak (*Quercus spp.*), one-seed juniper (*Juniperus monosperma*), and

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pinyon pine (Department of Defense, unpublished report). Potential Gray Vireo nesting substrates on KAFB include one-seed juniper, mountain mahogany, and scrub oak.

**Nest searching and monitoring**

I conducted surveys for Gray Vireos at 50 random locations from May 1 to June 15 in 2016 and in 2017 (Figure 1). Each random location was surveyed twice each year. Random points were located between 1823-2148 m.a.s.l. in pinyon-juniper woodlands or juniper savannahs, and separated by at least 500 m. Elevation restrictions were due to the availability of junipers, and the categorization of pinyon-juniper woodlands and juniper savannahs was based on previous vegetation surveys performed by KAFB contractors (K. Johnson et al., unpublished report). At each point, I conducted 10-min call-back surveys, using a modified method used by Albrecht-Mallinger and Bulluck (2016), where a 1-min recording of a Gray Vireo song was played on an external speaker during the $5^{th}$-min. If a Gray Vireo was observed at the point I recorded its distance and bearing to approximate the actual location of the individual. Additional breeding territories were found opportunistically in pinyon-juniper woodlands. Once a breeding territory had been identified, Iconducted nest searching by observing nesting behaviors (e.g., carrying nesting material, males singing from nests, etc.). Nests were monitored once per week until completion to determine fate.

**Tree and habitat-level selection**

Upon completion of a nest (i.e. depredated, abandoned, or fledged young), I conducted fine-scale habitat surveys within a 25-m radius (196 ha) around each nesting tree. A 25-m radius was selected due to anecdotal behavioral observations, suggesting the relevance of this scale to territorial cues (i.e., alarm calling) (Bates 1992). For each nest, I recorded height from the ground, distance from the edge of the nesting tree, and the bearing that the nest was facing relative to the center of the nesting tree (Smith et al. 2005). In addition, Irecorded height and width of each tree, shrub, or cactus that was at least 1 m in height within the plot. Vegetation width was estimated as the width of foliage

cover at its widest point. For each juniper within the plot, Ialso recorded the approximate foliage density at four cardinal directions around the juniper. Foliage density was estimated using a modified Braun-Blanquet method (Wikum and Shanholtzer 1978), where I estimated percentage of limbs and trunks that were obscured by foliage and assigned a categorical value: 1 (0–25%), 2 (26–50%), 3 (51–75%), or 4 (76–100%). I then averaged foliage density at each cardinal direction around the juniper to get one estimate of foliage density for each juniper in the plot. To determine tree-level selection within the 25-m radius scale, I randomly selected six junipers within each nesting plot and averaged their height, width, and foliage density (Anderson and LaMontagne 2016). Mean vegetation characteristics from random trees were paired with nesting trees for analyses. Averaging a group of randomly selected trees as opposed to a single paired tree, allows for a comparison that is more reflective of the available habitat (Anderson and LaMontagne 2016).

Data from the 25-m radius scale were also used to estimate selection of the surrounding habitat by comparing nest-site plots with random plots. I located 66 random points in areas designated as pinyon-juniper woodlands or juniper savannah by KAFB personnel (the 50 used for Gray Vireo surveys plus an additional 16). Although the 50 points used in surveys helped to identify territories, none of the points had nests located within a 25-m radius buffer. All random points had junipers ($\bar{x} = 12 \pm 10$ SD), suggesting they were potentially usable as nesting habitat. Sixty-six random points were the maximum number of points that could be created within the designated habitat types while being at least 500 m apart. Vegetation characteristics at random plots were compared to nesting plots to estimate second-order selection.

**Broad-scale landscape assessment**

I obtained 1x1 m resolution 2016 aerial imagery from KAFB. I used ArcGIS (v. 10.2.2) to perform an Iso Cluster Unsupervised Classification, where similar pixels are grouped into 20 categories of cover type. The resulting raster was then resampled into a 2x2 m resolution to decrease

classification error, and reclassified into the seven most common cover types distinguishable by aerial imagery: bare ground, grass, shrub, shrub/cholla mix, juniper, pinyon pine, and ponderosa pine. Based on our surveys, ponderosa pines rarely occurred at elevations less than 2,300 m where Gray Vireos were present and thus were not included in statistical analyses. I estimated classification accuracy of the cover type raster at 50 random points by determining the proportions of points accurately identified by the cover type classification raster. Random points were generated in ArcGIS and were restricted to pinyon-juniper woodlands and juniper savannahs as outlined by KAFB (K. Johnson et al., unpublished report). Thirty-nine out of 50 points were accurately classified (78%), which I deemed to be suitable for subsequent analyses (Myeong et al. 2001).

For each nest location and random point, I created two buffers: 50- and 100-m radius (790 ha and 3,140 ha, respectively). Eight out of the 66 random points used for fine-scale habitat comparisons had 100-m radius buffers that overlapped with nest-site buffers and were subsequently excluded from landscape-level analyses, resulting in 58 random points used in landscape analyses. The two spatial scales were chosen to represent selection of nesting locations within territories, where mean territory size has been shown to be 4.5 ha on KAFB (L. E. Wickersham and J. L. Wickersham, unpublished report). However, multi-scale analyses of Gray Vireo nest-site selection have not been done previously, so these specific scales were chosen somewhat arbitrarily in hopes of identifying the primary scale at which selection occurs. For each spatial scale, I recorded proportions of all cover type within each buffer by counting the total number of pixels for each cover type and dividing by the total number of pixels. Elevation was recorded at each point using a digital elevation model (DEM) obtained from the Earth Data Analysis Center at the University of New Mexico.

**Statistical analyses**

I developed generalized linear mixed-effect models (GLMM) for Gray Vireo nest-site selection as a function of tree characteristics (Table 1), surrounding habitat characteristics (Table 2),

and landscape composition at two spatial scales (Table 3). GLMMs were developed using the "lme4"

package in RStudio (2019, v. 1.2.1) (Bates et al. 2015, R Core Team 2016) and evaluated using

Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002)

using the "bbmle" package in RStudio (Bolker and R Development Core Team 2017). All models

incorporated a random effect of "year" and had a binomial error distribution with a logit-link

function. Independent variables with pairwise correlation coefficients ($|r|$) > 0.7 were not included

within the same model (Dormann et al. 2012).

I evaluated three groups of candidate models separately: tree-level selection, habitat-level

selection, and landscape composition at multiple scales. Models for tree-level selection incorporated

combinations of juniper height, juniper width, and juniper foliage density, for a total of eight

candidate models. Habitat-level models were based on *a priori* hypotheses related to juniper and

shrub characteristics, as those have been shown to be the most important cover types for Gray Vireos

(Schlossberg 2006). I did not test shrub height, as there was insufficient variance for analysis ($\tilde{x}$=1.3

m, $\sigma$=1.0 m). This resulted in 11 candidate models for selection of the habitat surrounding nests.

However, because little work has previously been conducted at broad spatial scales, I used a multi-

step, exploratory approach to develop a candidate set of models for landscape composition. First, I

determined the appropriate scale for each landscape variable (except for elevation, which was a point

estimate) by testing the performance of each scale for each landscape variable; this was done by

forming two univariate models for each variable at each scale and comparing their relative AICc

values (Lockyer et al. 2015). In this way, I determined the scale that best determined nests from

random points for each landscape variable. Those subsequent scales were then used in a global model

of all possible additive combinations of landscape-level variables. The global model was then

dredged using the "MuMIn" package in RStudio (Barton 2019), to test all possible additive

combinations of the variables (Doherty et al. 2010). All additive combinations with ΔAICc less than 2

were included as 10 landscape-level models for final analysis (Burnham and Anderson 2002). I also

included four additional models with interactions post-hoc to account for varying selection of landscape features across elevation gradients and to determine if selection of junipers and shrubs interacted, where one cover type may supplement the other. This resulted in a final set of 15 candidate models (14 plus one null model) for landscape-level selection (Table 2).

## RESULTS

In 2016 and 2017, I found 99 Gray Vireo nests. All nests were located in one-seed junipers with an average height of $3.6 \pm 1.1$ m and an average width of $5.6 \pm 2.2$ m. Nests were on average $2.4 \pm 0.7$ m off the ground, $0.72 \pm 0.57$ m from the periphery of the nesting tree, and were most frequently found on the north side of nesting trees ($n = 33$, 33%), but were distributed across all cardinal directions (south: 29%, east: 20%, west: 18%). Elevation of Gray Vireo nests ranged from 1792–2047 m, with an average of $1894 \pm 53.4$ m.

The top models for tree and habitat-level selection included positive effects of juniper height and width (Table 1, Table 2). Gray Vireos frequently nested in the largest juniper within a 25-m radius plot (Table 1). All nests were located in junipers greater than 2.0 m tall and 1.7 m wide. The junipers surrounding nests were also taller, wider, and had greater foliage density than junipers at random plots (Table 2, Figure 2). Average juniper height and width within a 25-m radius around nest sites was $3.0 \pm 1.2$ m and $4.1 \pm 2.4$ m, respectively, compared to $2.4 \pm 1.0$ m and $3.2 \pm 1.5$ m at random plots. Foliage density scores for junipers in nesting plots were $2.5 \pm 0.9$, compared to an average foliage density score of $1.8 \pm 0.9$ at random plots. An average foliage density score of 2.5 translates into approximately 50% of the woody stems of junipers being obstructed by foliage, while a score of 1.8 is approximately 25% obstruction.

Our top model for broad-scale landscape composition at nest sites included juniper density at the 50-m scale, elevation, and their interaction (Table 3). The predicted probability of a nest occurring increased with increasing juniper density at a 50 m radius when the elevation was under 1950 m.

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Above 1950 m elevation, the predicted probability of a Gray Vireo nest occurring begins to decline as juniper density increases (Figure 3). Overall juniper density at the 50-m radius scale ranged from approximately 15–30% of the total cover. The second most frequent vegetation variable in the top models was the proportion of pinyon pine, which was negatively associated with nest-site selection at the 100-m radius scale.

## DISCUSSION

For many passerines, nest-site selection has been shown to be a hierarchical process, where species will select broad-scale landscape features for breeding territories, followed by fine-scale habitat features within territories for nesting sites (Martin and Roper 1988, Bergin 1992). I found that Gray Vireo nest-site selection followed such a hierarchical process, where breeding territories were characterized by optimum proportions of juniper cover at lower elevation, and potential nesting habitat was driven by characteristics of junipers at finer scales.

Juniper height and width seem to be important characteristics of potential nesting substrates for Gray Vireos. At the habitat level, Gray Vireos selected areas with larger junipers that had greater foliage density than what was randomly available (Figure 2). Within this area, the nesting tree was often the largest juniper available. Larger trees may also be selected due to greater within-tree availability of nest sites, as there is greater surface area for potential nest locations, or an indirect preference for older growth pinyon-juniper woodlands. Selection for junipers of larger size may also contribute to predator avoidance via a presumed increase in concealment (Wilson and Cooper 1998) and a better vantage point for predator surveillance. In California populations, California Scrub Jays (*Aphelocoma californica*) were the most frequent nest predator of Gray Vireos. At our study site, Woodhouse's Scrub Jays (*Aphelocoma woodhouseii*) are abundant and although I lacked direct observations of predation events, are considered probable nest predators (Barlow et al. 1999). Consequently, nest placement may aim to minimize predation from such aerial predators. Nest sites

were located in areas where the average juniper foliage density was greater than random sites. Selection for junipers with greater foliage density at the nesting tree and the adjacent trees is likely related to increased concealment (Martin and Roper 1988); however, nest concealment was not directly measured in our study. Greater foliage density may also provide a beneficial microclimate at nests (Carroll et al. 2015). In general, fine-scale selection of vegetation was characterized by physical characteristics of potential nesting trees, as opposed to density of nesting substrates or foraging cover. I had predicted that at fine scales, juniper and shrub count would be higher at nest sites than what was randomly available based on Schlossberg (2006). However, I found no difference in juniper or shrub densities at nest sites compared to random plots at the habitat level.

I predicted that broad-scale landscape composition at nest sites would have higher proportions of juniper and shrub cover than at random locations. I found that at elevations less than 1954 m, the probability of nest-sites increased with higher proportions of juniper cover at the 50-m radius scale. The importance of junipers is self-evident, as junipers were the exclusive nesting substrate at our study site and juniper bark is the primary material used in nest construction (Barlow et al. 1999). Consequently, there is likely a minimum threshold of juniper necessary for the occupancy of breeding territories in pinyon-juniper woodlands. Further evidence to the importance of junipers is that the second most frequent variable in our top models was pinyon pine at the 100-m scale, which was negatively associated with nest-site selection. Schlossberg (2006) found a similar result, where Gray Vireo density positively correlated with increasing proportions of junipers and decreasing proportions of pinyon pines.

At higher elevations, junipers were selected at lower proportions than what was randomly available. One possible explanation for this relationship is that the average and variance of juniper proportion was greater at higher elevation, with junipers at some points exceeding approximately 80% of available cover. Gray Vireos did not generally nest in areas with juniper proportions greater than 30%, suggesting an optimum proportion of juniper cover for Gray Vireos at the 50-m radius

scale. Indeed, Gray Vireos consistently nested in areas with juniper proportions ranging from approximately 15–30%, despite available juniper proportions of approximately 5–80%. It is unclear what the ecological mechanism is that limits the upper bounds of juniper proportions as nesting habitat. One possible explanation is that high densities of juniper may restrict surveillance of predators while incubating nests. Gray Vireos nest on the periphery of their substrate (Barlow et al. 1999), often with no vegetation adjacent to the nesting tree.

Additionally, one of the primary constraints of Gray Vireo nest-site occurrence at our study site was elevation. I graphically determined a threshold of approximately 1960 m in elevation in which nests are unlikely to occur, despite junipers being prevalent up to approximately 2200 m in elevation. I surveyed 14 random points at elevations greater than 1960 m but only found four nests within this region, with a maximum nest-site elevation of 2047 m. Conversely, at elevations less than 1960 m I surveyed 52 random points and found the remaining 95 nests. Upper elevation restrictions may be due to greater weather extremes, such as high winds or colder temperatures, or decreased arthropod abundances. Shepherd (et al. 2002) found decreased arthropod diversity in higher elevations of the pinyon-juniper woodlands adjacent to our study site. Our finding of an upper elevation limit of Gray Vireo occupancy is similar to that of Schlossberg (2006), who found that Gray Vireo density dropped significantly at an elevation greater than 1900 m. However, optimal elevations for Gray Vireos are likely to vary by geographic region.

Surprisingly, the top three models did not incorporate shrub cover. Shrub cover at the 100-m scale was incorporated in a landscape-level model that was significantly better than the null model (14.1 $\Delta$AICc); however, the second best performing variable was pinyon pine at the 100-m radius scale. Schlossberg (2006) noted that Gray Vireo population density in Colorado increased with shrub density in pinyon-juniper woodlands, and this relationship was primarily influenced by sagebrush occurrence. It is presumed that shrub cover is primarily used as a foraging substrate for invertebrates. In the pinyon-juniper woodlands of KAFB, sagebrush was not common (Department of Defense,

unpublished report). Insect community composition in sagebrush found in Colorado may differ considerably from the common shrub species on KAFB (e.g., four-winged saltbush, apache plume). Consequently, a difference in forage availability may contribute to our different findings. More behavioral observations are needed to determine the primary foraging substrate at our study site and how foraging behavior may vary throughout the species' range. The importance of shrub cover as a foraging substrate may vary geographically.

## MANAGEMENT IMPLICATIONS

The most important cover type at all spatial scales for nest-site selection was juniper. Gray Vireos selected higher densities of junipers at lower elevations and strongly selected specific juniper characteristics at fine-spatial scales. Vireos selected junipers that were larger, wider, and had greater foliage density than what was available, suggesting a preference for old-growth juniper woodland; the benefits of which may include greater forage availability, nesting resources, or nest concealment. In dense juniper woodlands, some thinning may be appropriate given that Gray Vireo nests rarely nested in areas with proportions of juniper cover exceeding 30%. Although Crow and van Riper (2010) found that Gray Vireos were extirpated post mechanical thinning, in their study system they removed an average of 92% of live trees. Care should be taken to ensure that live junipers represent 15–30% of the available cover for optimal nesting habitat. However, further experimental manipulation of juniper density through thinning would be helpful in verifying optimal nesting habitat for Gray Vireos across elevation gradients.

To improve nesting density, management practices should protect large patches of old-growth juniper to increase the prevalence of junipers that are taller, wider, and have greater foliage density than new-growth junipers. In this region, optimizing habitat characteristics and cover proportions should be focused in pinyon-juniper woodlands at elevations less than 1950 m.

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Table 1. Generalized linear mixed-effect models of Gray Vireo (*Vireo vicinior*) nest-site selection at the tree scale. Nesting trees were compared with a subset of six possible nesting trees within a 25-m radius. Models were formed from 99 nests found in 2016 and 2017 on Kirtland Air Force Base in Albuquerque, NM. Relative model performance was evaluated using Akaike Information Criteria corrected for small sample sizes (AICc).

| Model | K | ΔAICc | $\omega_i$ | Deviance |
|---|---|---|---|---|
| Height + Width[†] | 4 | 0 | 0.595 | 196.7 |
| Height + Width + Foliage Density | 5 | 1.77 | 0.245 | 196.3 |
| Width | 3 | 4.37 | 0.067 | 203.1 |
| Height | 3 | 4.98 | 0.049 | 203.7 |
| Width + Foliage Density | 4 | 6.4 | 0.024 | 203.1 |
| Height + Foliage Density | 4 | 6.8 | 0.02 | 203.5 |
| Null Model | 2 | 42.79 | 0 | 243.6 |
| Foliage Density | 3 | 44.82 | 0 | 243.6 |

[†]AICc value of 204.7

Table 2. Generalized linear mixed-effect models of Gray Vireo (*Vireo vicinior*) nest-site selection at a 25-m radius spatial scale. Models were formed from 99 nests and 66 random points found in 2016 and 2017 on Kirtland Air Force Base in Albuquerque, NM. Relative model performance was evaluated using Akaike Information Criteria corrected for small sample sizes (AICc).

| Model | *K* | ΔAICc | $\omega_i$ | Deviance |
|---|---|---|---|---|
| Juniper Height + Juniper Width + Foliage Density[†] | 5 | 0 | 0.928 | 154.4 |
| Juniper Height + Foliage Density | 4 | 11.5 | 0.003 | 168 |
| Juniper Height * Juniper Width | 5 | 16.8 | 0.016 | 175.5 |
| Juniper Height | 3 | 19.6 | <0.001 | 174 |
| Juniper Height + Juniper Count | 4 | 28.1 | <0.001 | 186.8 |
| Foliage Density | 3 | 32.9 | <0.001 | 191.6 |
| Shrub Count | 3 | 40.8 | <0.001 | 199.5 |
| Null | 2 | 41.6 | <0.001 | 202.4 |
| Shrub Count * Juniper Count | 5 | 42.1 | <0.001 | 196.5 |
| Shrub Width | 3 | 43.6 | <0.001 | 202.3 |
| Juniper Count | 3 | 43.7 | <0.001 | 202.3 |

[†]AICc value of 164.4

Table 3. Generalized linear mixed-effect models of Gray Vireo (*Vireo vicinior*) nest-site selection at 50- and 100-m radius spatial scales. The spatial scale of each parameter is included in the parameter name. Models were formed from 99 nests and 58 random points found in 2016 and 2017 on Kirtland Air Force Base in Albuquerque, NM. Relative model performance was evaluated using Akaike Information Criteria corrected for small sample sizes (AICc).

| Model | $K$ | $\Delta$AICc | $\omega_i$ | Deviance |
|---|---|---|---|---|
| Juniper50*Elevation[†] | 5 | 0 | 0.9920 | 174.8 |
| Juniper50+PinyonPine100+Elevation | 5 | 13.4 | 0.0012 | 188.2 |
| Juniper50+PinyonPine100 | 4 | 13.4 | 0.0012 | 190.3 |
| Juniper50+PinyonPine100+Shrub100 | 5 | 13.9 | <0.001 | 188.6 |
| Juniper50+PinyonPine100+Shrub100+ Elevation | 6 | 14.1 | <0.001 | 186.7 |
| Juniper50+PinyonPine100+Shrub100+ChollaMix100 +Elevation | 7 | 14.1 | <0.001 | 184.6 |
| Juniper50+PinyonPine100+Shrub100+ChollaMix100 | 6 | 15.0 | <0.001 | 187.6 |
| Juniper50+PinyonPine100+ChollaMix100+Elevation | 6 | 15.2 | <0.001 | 187.8 |
| Juniper50+PinyonPine100+Grass50 | 5 | 15.2 | <0.001 | 190.0 |
| Shrub50+PinyonPine100+Juniper50+Bareground50 | 6 | 15.3 | <0.001 | 187.9 |
| Juniper50+PinyonPine100+ Grass50+Elevation | 6 | 15.3 | <0.001 | 188.0 |
| PinyonPine100*Elevation | 5 | 15.8 | <0.001 | 190.6 |
| Null Model | 2 | 28.0 | <0.001 | 209.1 |
| Juniper50*Shrub100 | 5 | 29.2 | <0.001 | 204.0 |
| Shrub100*Elevation | 5 | 33.0 | <0.001 | 207.8 |

[†]AICc value of 184.8
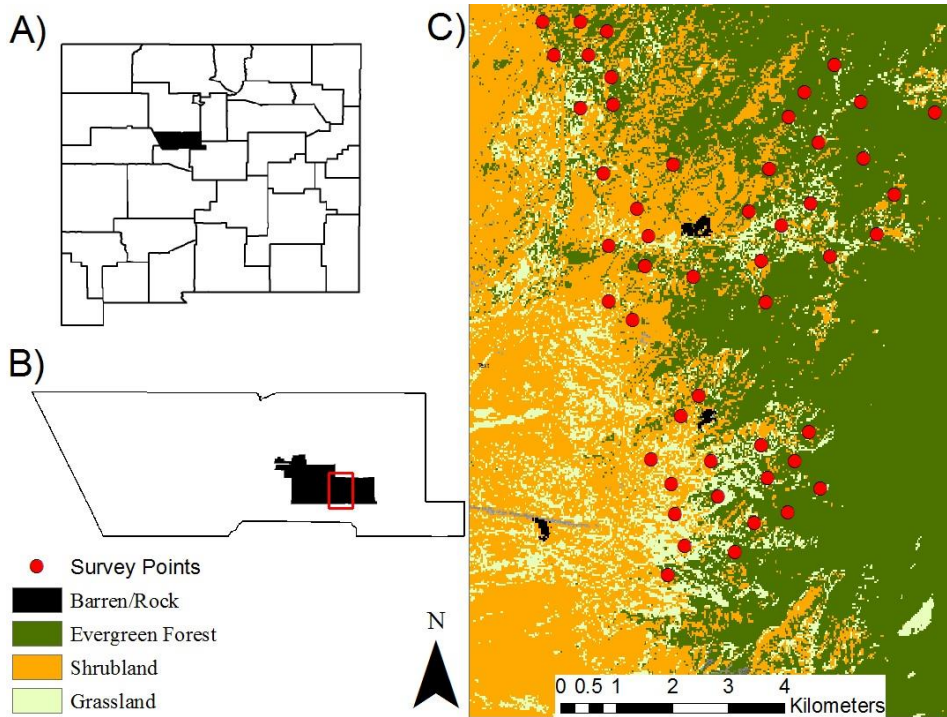
Figure 1. (A) The location of Bernalillo County in New Mexico is shaded in black. (B) Within Bernalillo County, the area constituting Kirtland Air Force Base is shaded in black. The red rectangle represents the approximately region of our study location seen in C. (C) Our study location on Kirtland Air Force Base, where red dots represent Gray Vireo survey points. Four cover classifications (Barren, Evergreen Forest, Shrubland, and Grassland) were available within our study location.
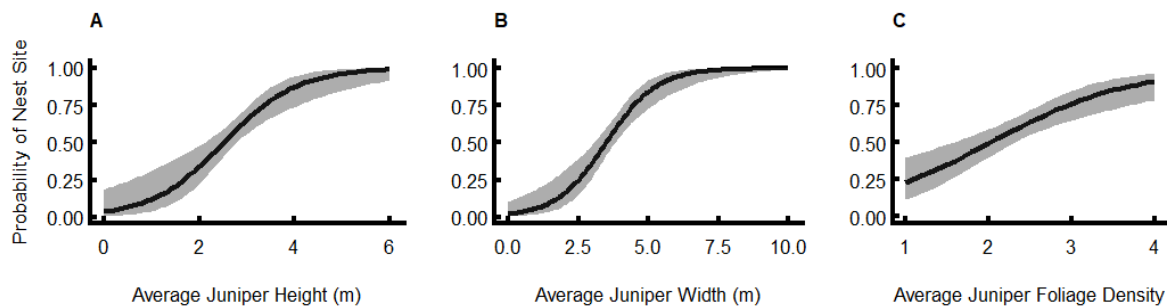


Figure 2. Predicted probability of Gray Vireo (*Vireo vicinior*) nest occurrence as a function of (A) average juniper height, (B) average juniper width, and (C) average juniper foliage density within a 25-m radius sampling plot. Foliage density was measured at four sides of each juniper within a plot, where each side was assigned a foliage density category: 1 (0–25%), 2 (26–50%), 3 (51–75%), 4 (76–100%). Gray Vireos selected nesting areas with taller, wider, and more densely foliated junipers than what was randomly available. The shaded gray region represents a 95% confidence interval.
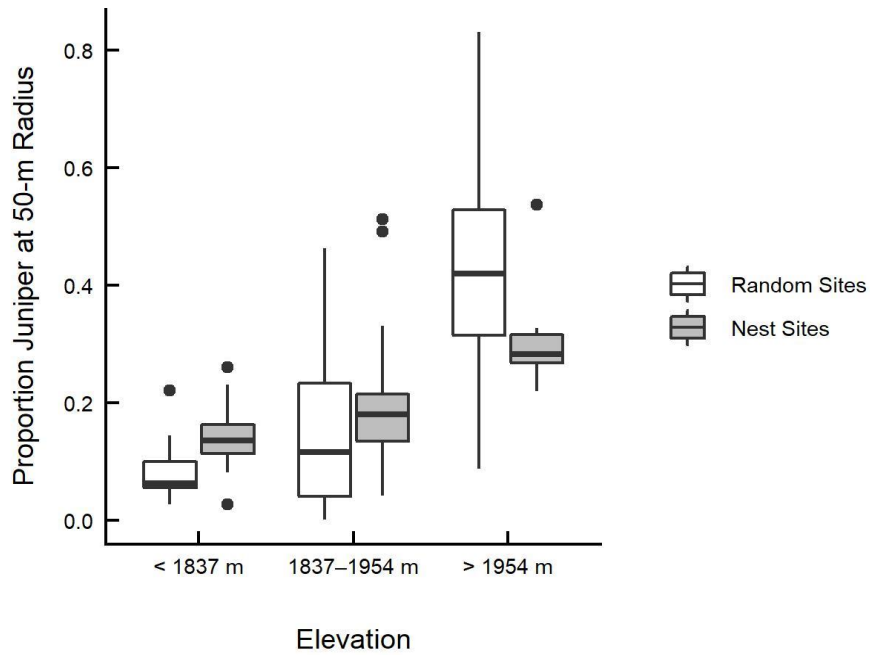
Figure 3. The average percentage of juniper cover at the 50-m scale for nesting plots (gray) and random plots (white). Percent juniper cover at random points and nesting points varies across three elevations: 1 SD below the mean (1837 m), the mean (1895 m), and 1 SD above the mean (1954 m). Outliers are represented as black circles.

CHAPTER II


HOW VARIATION IN QUALITY OF PINYON-JUNIPER WOODLANDS EFFECTS GRAY

VIREO (*VIREO VICINIOR*) NEST SURVIVAL IN CENTRAL NEW MEXICO

INTRODUCTION

Pinyon (*Pinus spp*.) and juniper (*Juniperus spp*.) woodlands are the most abundant forest

type in the American southwest (Shaw et al. 2005) and are the third largest cover type in the

continental United States (West 1984). Despite this, pinyon-juniper woodlands are among the

most poorly studied North American forest types and many questions related to management

strategies still exist (Gottfried et al. 1995). Recently, these woodlands have experienced large-

scale die-off due to drought (Shaw et al. 2005, Clifford et al. 2011). Additionally, the distribution

and connectivity of these woodlands under various climate change scenarios remains uncertain

(Copeland et al. 2018), given that climate projections for the southwestern United States suggest

an increase in the frequency of drought and overall levels of aridity (Seager et al. 2007). These

forest communities represent critical habitat for a variety of species of conservation concern

(Francis et al. 2011), which makes the development of conservation and management strategies a

priority for the future.

Gray Vireos are an example of a species of conservation concern at state and federal

levels (U.S. Fish and Wildlife Service 2008, NM Department of Game and Fish 2018) that is an

obligate of pinyon-juniper woodlands throughout the majority of the species' range (Barlow et al.

2020). Gray Vireos rely on junipers as a nesting substrate (Harris et al. 2020) and are more

frequently found in areas with high densities of juniper (Schlossberg 2006). Consequently, Gray Vireo demography is likely dependent on the availability and quality of pinyon-juniper woodlands. Although data from the breeding bird survey suggests that overall population size has remained stable (Pardieck et al. 2018), the species may be susceptible to declines due to a limited breeding range (Barlow et al. 1999), low population densities (Schlossberg 2006), and susceptibility to habitat loss (Pierce 2007). Additionally, population stability varies considerably by state. For example, populations in California have declined by about 75–95% (Hargove and Unitt 2014), while populations in New Mexico have increased (Sauer et al. 2017, Pardieck et al. 2018). It has been suggested that the population declines in California may be due to Brown-headed brood parasitism (Remsen 1978), however there is little evidence to support this assertion.

Nest success for species in the Vireonidae family is highly dependent on Brown-headed Cowbird parasitism rates, typically resulting in relatively low reproductive output compared to other passerines (Barber and Martin 1997, Woodworth 1997, Smith et al. 2005, Hargrove and Unitt 2017). Brown-headed Cowbird parasitism has been shown to occur at 43–93% of Black-capped Vireos nests (Graber 1961, Grzybowski 1991), 43–75% of Warbling Vireo nests (Gardali and Ballard 2000), and 49% of White-eyed Vireo nests (Hopp et al. 1995). One possible explanation for high parasitism rates across the Vireonidae family is that most species of vireos will nest on the periphery of the nest substrate, often on a terminal fork (Bent 1950). This may increase their visibility and consequently their susceptibility to brood parasitism and predation from avian predators (Liebezeit and George 2002).

Only one study exists on Gray Vireo nest survival probabilities (Hargrove and Unitt 2017). Conducted in arid chaparral of San Diego County, California, vireos nested exclusively in shrubs such as chamise (*Adenostoma fasciculatum*), desert ceanothus (*Ceanothus greggii*), and mountain mahogany (*Cercocarpus betuloides*). Nest success was poor, with a model-averaged probability of nest survival of only 8%, and nest failure most commonly caused by predation

(83% of failures). Nest survival probabilities were best explained by a negative effect of surrounding shrub height and a positive effect of nest height. The most common nest predator was California Scrub Jays (*Aphelocoma californica*), which accounted for 67% of predation events. Parasitism by Brown-headed Cowbirds accounted for only 13% of failures. Contrary to this study in California, unpublished reports on Gray Vireos in pinyon-juniper woodlands has found apparent nest success range from 40–60% (Frei and Finley 2008, Wickersham and Wickersham 2015). Throughout the majority of their range, Gray Vireos breed in pinyon-juniper woodlands and are dependent on high juniper densities (Schlossberg 2006, Crow and van Riper 2010). However, more data are needed to confirm estimates of reproductive success in these more stable populations (Sauer et al. 2017, Pardieck et al. 2018) and to identify potential drivers of Gray Vireo nest failures in pinyon-juniper woodlands.

I estimated Gray Vireo reproductive success in a location with high densities of breeding territories and stable local populations. Specifically, our objectives were to estimate nest survival probabilities (probability that a nest fledge ≥1 young) and identify factors that influence survival at the scales of the nest and surrounding vegetation. Based on results from Hargrove and Unitt (2017), I hypothesized that nest survival would be driven by nest height and the height of the surrounding vegetation. I also expected nest survival to be negatively related to tree density, as woodland habitat may be more suitable for nest predators, such as Woodhouse's Scrub Jay (*Aphelocoma woodhouseii*) (Curry et al. 2017).

METHODS

**Study Site**

All nests were found on Kirtland Air Force Base (KAFB), located south of Albuquerque, NM. Elevation on KAFB ranges from 1,600 to almost 2,400 m and encompasses four primary landcover types: grasslands, pinyon-juniper woodlands, ponderosa pine (*Pinus ponderosa*)

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woodlands, and wetlands/arroyos (Department of Defense 2012). Kirtland Air Force Base is approximately 21,000 ha predominantly consisting of large swaths of one-seed juniper (*Juniperus monosperma*) forests and savannah, intermixed with four-winged saltbush (Atriplex canescens), sand sagebrush (*Artemisia filifolia*), and rubber rabbitbrush (*Ericameria nauseosa*) (Department of Defense 2012).

**Nest Searching and Monitoring**

To identify the locations of breeding territories, I conducted two rounds of call-back surveys for Gray Vireos at 50 random locations from May 1 to June 15 in 2016, 2017, and 2018. Random points were situated in pinyon-juniper woodlands or juniper savannahs, as categorized by KAFB personnel (Department of Defense 2012), with elevations ranging from 1823–2148 m. At each point, I conducted 10-min call-back surveys, where a 1-min recording of a Gray Vireo song was played on an external speaker during the 5th-min (Albrecht-Mallinger and Bulluck 2016). I also located additional territories opportunistically when traveling between points. Once a breeding territory had been identified, I searched for nests by following individuals exhibiting nesting behaviors (e.g., carrying nesting material, males singing from nests, etc.). Nests were monitored once per week until completion to determine survival. I categorized the status of the nest at each visit as active, fledged, depredated, parasitized, or abandoned. When possible, I determined the status of nests using binoculars from 5–10 m away to minimize the impact of monitoring on nest outcome.

**Nest Placement and Vegetation Surveys**

I was interested in how daily nest survival probability was affected by nest placement, characteristics of the nesting tree, and characteristics of the surrounding habitat. In this way, I collected data at three scales: the nest, the nesting tree, and a 25-m radius around the nesting tree. For nest placement, I measured height from the ground, distance from the periphery of the nest

tree, and orientation of the nest from the central trunk (Smith et al. 2005). For the nesting tree and

all trees within a 25-m radius around the nest, I measured height (m ± 1 cm), width of foliage (m

± 1 cm) measured at its widest point, and an estimation of foliage density for junipers. Foliage

density was only considered for junipers because Gray Vireos only nested in junipers at our study

site. Foliage density has been used as a proxy for nest concealment in other studies (Banks and

Martin 2001, Borgmann and Conway 2015). To estimate foliage density for many trees

expediently, I used a modified Braun-Blanquet method (Wikum and Shanholtzer 1978), where I

estimated percentage of limbs and trunks that were obscured by foliage at four cardinal directions

around each tree. At each direction I assigned a categorical value: 1 (0–25%), 2 (26–50%), 3 (51–

75%), or 4 (76–100%). Categorical values were then averaged at each cardinal direction to get

one estimate of foliage density for each tree in the plot. For measurements at the 25-m radius

scale, I averaged tree height, width, and foliage density for trees within the plot. I also considered

total juniper count within this scale.

**Statistical Analyses**

I estimated the probability that a nest would survive one day (daily nest survival) and

overall nest survival using Mayfield's methods (Mayfield 1975). I used logistic exposure models

(LEMs) to estimate Gray Vireo nest survival as a function of nest placement and characteristics

of surrounding vegetation (Shaffer 2004). LEMs are equivalent to generalized linear mixed-effect

models, except they incorporate exposure time in the exponent of a logit-link function (Shaffer

2004). The dependent variable for all LEMs was a binary variable of "Nest Survival" for each

nest check and all models used a random effect of "Year". All analyses were conducted using the

"lme4" package in Program R (v. 1.1.4) and evaluated using Akaike Information Criterion

corrected for small sample size (AICc) (Burnham and Anderson 2002). Independent variables

with pairwise correlation coefficients ($|r|$) > 0.7 were not included within the same model

(Dormann et al. 2012). I developed a global model with all additive combinations of variables.

Tree heights were highly correlated with tree widths so only tree heights were incorporated in the global model, for a total of seven independent variables. I then dredged the global model using the "MuMIn" package (v. 1.43.6), which produces an AICc value for every possible additive combination of variables (Doherty et al. 2012). Additive combinations with a $\Delta$AICc $\leq$ 2.0 (Burnham and Anderson 2002) were included in the final model selection subset. In addition, I also included three models that contained interactions of interest and a null model for a total set of 13 models. Models were considered competitive if they had an AICc $\leq$ 2.0 compared to the null model.

## RESULTS

Gray Vireos were first observed on KAFB as early as April 19th in 2017. Population densities at our study site were high, with an average of 60% of random points occupied by $\geq$ 1 Gray Vireo and an average of 57 breeding territories found each year. The earliest nest was found on May 9th in 2017, with an average start date of May 12th. Many of the nests found in early to mid-May could be considered "bachelor nests", where males without mates built nests to present to perspective females. These nests were not included in analyses. All nests were located in one-seed juniper despite additional nesting substrates available in the area (pinyon pine, mountain mahogany). Nests were on average 2.4 $\pm$ 0.7 m off the ground and 0.72 $\pm$ 0.57 m from the periphery of the nesting substrate. While most studies have found Gray Vireos preferably nest on the south-facing side of the nesting substrate (Barlow et al. 1999, Hargrove et al. 2017), I did not see a strong pattern in nest-site aspect (north: 33%, south: 29%, east: 20%, west: 18%).

I monitored 101 Gray Vireo nests from 2016–2018. Fifty-six nests successfully fledged $\geq$ 1 young (Table 1). Daily nest survival for all nests was 0.98 and overall nest survival probability was 0.44. The most common cause of nest failure was predation, which accounted for 56% of nest failures (n=25). Brood parasitism by Brown-headed Cowbirds accounted for 24% of failures

(n=11) and the remainder of nests were abandoned (n=9) (Table 1). All parasitised nests were subsequently abandoned.

Dredging a global model for every additive combination of variables produced 9 additive and univariate competitive models ($\Delta$AICc $\leq$ 2.0) that were included in the final set of candidate models (Table 2). Three models were considered competitive relative to the null, all of which include foliage density of the nest tree (Table 2). Two models had a $\Delta$AICc of zero: a negative interaction of foliage density and the distance from the edge of the nesting tree, and an additive combination of the same variables (Table 2). Daily nest survival probabilities increased with foliage density for all models (Figure 1), and increased with distance from the edge of the nesting tree when foliage density was low (Figure 2). Because foliage density was found in all of the top models, all other parameters tested, with the exception of "Distance to Edge", would be considered uninformative parameters (Arnold 2010).

## DISCUSSION

Nest survival probabilities of Gray Vireos at our study site were higher than what has previously been observed. Hargrove and Unitt (2017) found that daily nest survival and overall nest survival in arid chaparral habitat of California was 0.91 and 0.08, respectively. Conversely, I found daily nest survival was 0.98 and overall nest survival was 0.44 at our study site. Gray Vireo populations throughout California occur in low densities, with small, isolated patches of suitable habitat (Hargrove and Unitt 2014). The relatively low reproductive success in these regions is likely a contributing factor to low population densities (Hargrove and Unitt 2017). Populations at our study site occurred in large swaths of continuous pinyon-juniper woodland. Unpublished reports suggest that Gray Vireos in pinyon-juniper woodlands tend to have higher reproductive success than what was shown in chaparral (Barlow et al. 1999, Wickersham and Wickersham 2015); however, our observed survival probabilities are the highest that I have found in

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unpublished reports in pinyon-juniper woodlands. It remains unclear why pinyon-juniper

woodland habitat may have higher probabilities of reproductive success than chaparral or if this

trend is consistent across the species' range. However, local population stability, as seen in New

Mexico, is likely related to the high reproductive success and high site fidelity.

Based on Hargrove and Unitt (2017), I hypothesized that daily nest survival would be

positively related to nest height, and negatively related to the height and density of the

surrounding vegetation. They hypothesized that this was due to decreased Scrub Jay use in areas

where vegetation was shorter. I tested this finding by incorporating a model with an interaction

between "nest tree height" and "average tree height"; however, this was our worst performing

model. At our study site, Gray Vireos nested in juniper savannah and pinyon-juniper woodlands,

where Scrub Jay occurrence was seemingly ubiquitous relative to vegetation height. However,

Scrub Jay habitat use was not directly measured. Nest survival at our study site was mostly driven

by foliage density of the nesting tree and by nest placement. Nests were more likely to survive if

they were located closer to the interior of the nesting tree when the nesting tree was sparsely

foliated, or if they were located nearer to the outer tree edge when foliage density was high. This

result is in consonance with previous studies on passerine nest survival, where concealment is the

best predictor of survival (Davis 2005). Visual concealment of nests has been shown to be

particularly important to reduce predation by other avian species (Colombelli-Negrel and

Kleindorfer 2009). This is compared to mammalian and ground-dwelling predators that primarily

use olfactory cues to locate nests (Colombelli-Negrel and Kleindorfer 2009).

Nest concealment may be more critical for species in the Vireonidae family, as vireos are

often prone to avian predation and brood parasitism. This is likely a consequence of nesting on

the periphery of their nesting substrate. In our study, the distance of Gray Vireo nests to the outer

tree edge ($0.72 \pm 0.57$ m) was greater on average than what was seen in previous unpublished

studies (0.4 m, Wickersham and Wickersham 2015), which may account for our relatively high

daily nest survival probabilities. Nesting closer to the interior of the nesting tree would likely increase concealment from avian predators, but may increase risk from ground-dwelling predators. It is unclear what the most common nest predator was at our study site. However, Woodhouse's Scrub Jays were abundant and frequently observed in Gray Vireo territories and California Scrub Jays were the most common nest predator of Gray Vireos in California.

Brown-headed Cowbird parasitism at our study site accounted for higher proportions of failed nests (24%) than what was observed in California (13%, Hargrove and Unitt 2017). Brown-headed Cowbirds range throughout the United States and can be found in many habitat types (Lowther 1993); however, breeding habitat is often characterized by woodland-field transition zones (Gates and Gysel 1978). In our study, Gray Vireos often nested in juniper savannahs instead of dense pinyon-juniper woodlands. Nest sites were located in areas where juniper density was 15–30% at a 25-m radius scale, despite denser juniper cover at higher elevations. This transition zone between pinyon-juniper woodland and desert grassland may represent more suitable habitat for Brown-headed Cowbirds, and may result in more spatial overlap and parasitism risk. Brown-headed Cowbirds are edge specialists that are more likely to parasitize nests that occur adjacent to human edges or grasslands (Howell et al. 2007). However, throughout their range Gray Vireos seem less susceptible to brood parasitism than other species in Vireonidae, such as Black-capped Vireos and Least Bell's Vireo. This is likely because Gray Vireos seem to be capable of identifying Brown-headed Cowbird eggs (Barlow et al. 1999). All of the parasitized Gray Vireo nests observed in our study were subsequently abandoned, which is consistent with other observations (Barlow et al. 1999).

## MANAGEMENT IMPLICATIONS

In New Mexico, habitat management recommendations for Gray Vireos have been based almost entirely on various reports and unpublished data (Pierce 2007). The current paradigm has

been to simply maintain high densities of juniper and shrub cover. Although this strategy may allow for sustained habitat availability, current management practices may not be adequately considering habitat quality and productivity. This could potentially result in large swaths of ecological traps if quality is poor.

One of the best indicators of Gray Vireo nest success was juniper foliage density, as it was consistently included in the top models for Gray Vireo daily nest survival probabilities. Greater foliage density for nesting trees provides greater visual obscurity for nests, particularly from avian predators and brood parasites. This is a particularly important consideration when nests are located in juniper savannahs, where there may be greater Brown-headed Cowbird parasitism than in other parts of Gray Vireo breeding range due to habitat selection overlap. Habitat management efforts in these areas may seek to maintain junipers with high foliage density during thinning and overall juniper health should be monitored for longer-term planning.

Juniper health is dependent primarily on climate (Meager 1943). Drought in the southwestern United States has been shown to cause mortality to 70% of the juniper population in grassland systems (Gitlin et al. 2006). In these systems, competition with understory vegetation increases water stress and stymies seedling growth (Teague et al. 2001, Gitlin et al. 2006). At our study site, Gray Vireos predominantly nested in juniper savannahs, where juniper cover represents 15–30% of the available cover and grasses represent the remaining majority. This nesting habitat would be at risk of juniper die-off when drought conditions are severe. Juniper foliage density should be monitored during drought conditions, particularly in areas where junipers are competing directly with understory vegetation for water. Under future climate projections, drought conditions are expected to intensify, with temperate drylands potentially contracting by 33% (Schlaepfer et al. 2017). Gray Vireos may require additional conservation protections given these future threats to habitat quantity and quality.

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Table 1. Summaries of Gray Vireo nest outcomes on Kirtland Air Force Base in Albuquerque, New Mexico from 2016–2018. Nests found in 2018 were minimal due to base closure for fire danger restrictions.

|  | 2016 | | 2017 | | 2018 | | Total | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Nest Outcome | N | % | N | % | N | % | N | % |
| Fledged ≥ 1 | 27 | 0.53 | 26 | 0.59 | 3 | 0.50 | 56 | 0.55 |
| Depredated | 9 | 0.18 | 13 | 0.30 | 2 | 0.33 | 24 | 0.24 |
| Parasitized | 7 | 0.14 | 4 | 0.09 | 1 | 0.17 | 12 | 0.12 |
| Abandoned[*] | 8 | 0.16 | 1 | 0.02 | 0 | 0 | 9 | 0.09 |
| Total | 51 | | 44 | | 6 | | 101 | |

[*]Abandoned nests are not including parasitized nests that were subsequently abandoned.

Table 2. Logistic Exposure Models of Gray Vireo daily nest survival probabilities. Models were formed from 101 nests found from 2016–2018 on Kirtland Air Force Base in Albuquerque, NM. Relative model performance was evaluated using Akaike Information Criterion corrected for small sample sizes (AICc).

| Model | ΔAICc | k | weight |
| --- | --- | --- | --- |
| FoliageDensity * EdgeDistance | 0 | 5 | 0.15 |
| FoliageDensity + EdgeDistance | 0 | 4 | 0.15 |
| Foliage Density | 0.2 | 3 | 0.138 |
| Foliage Density + Nest Height | 0.8 | 4 | 0.102 |
| FoliageDensity + EdgeDistance + AvgFoliageDensity | 1.5 | 5 | 0.07 |
| FoliageDensity + EdgeDistance + NestHeight | 1.6 | 5 | 0.066 |
| FoliageDensity + AvgFoliageDensity | 1.7 | 4 | 0.065 |
| FoliageDensity + AvgTreeHeight | 1.8 | 4 | 0.06 |
| FoliageDensity + AvgTreeHeight + EdgeDistance | 1.9 | 5 | 0.058 |

| | | | |
|---|---|---|---|
| FoliageDensity + EdgeDistance + JuniperCount | 2 | 5 | 0.055 |
| FoliageDensity * Nest Height | 2.5 | 5 | 0.043 |
| Null Model | 2.7 | 2 | 0.039 |
| NestTreeHeight * AvgTreeHeight | 6.1 | 5 | 0.007 |

[a]AICc value of 210.5
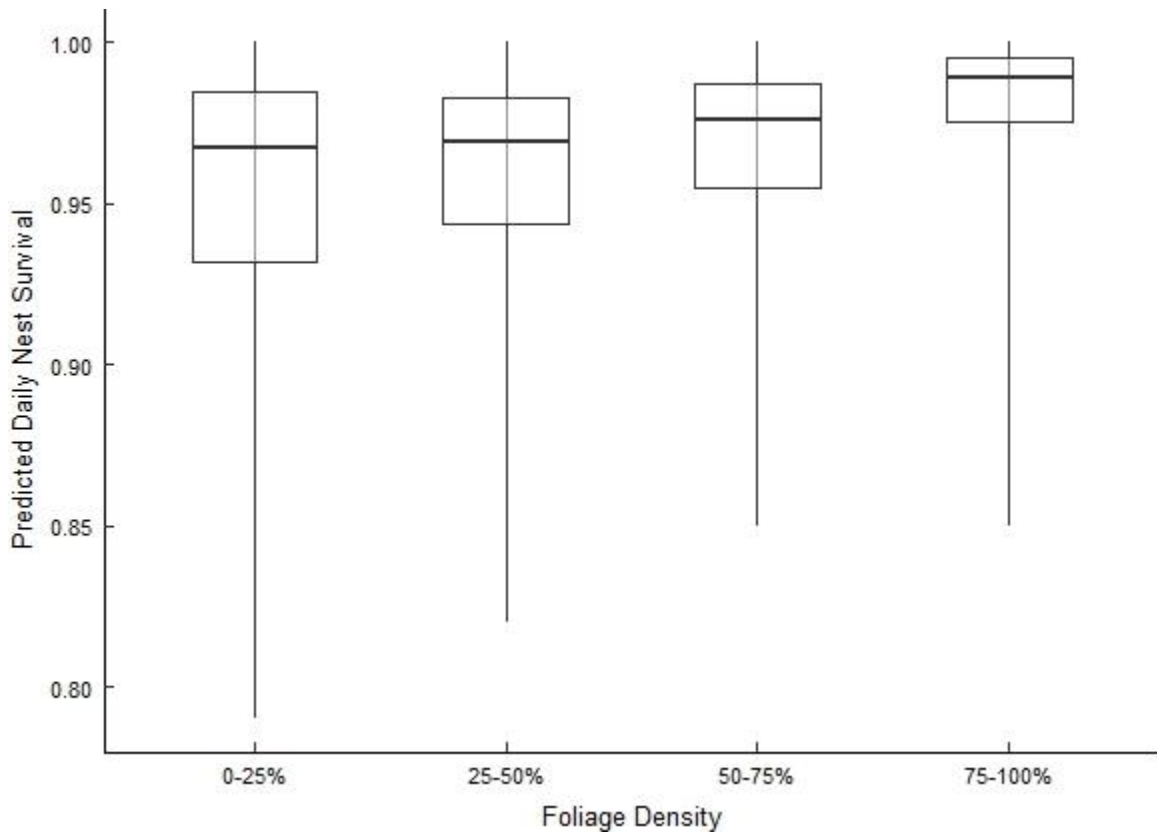


Figure 1. Box and whisker plots showing the daily nest survival ($\geq$ 1 nestling survives one day) for Gray Vireo nests as a function of juniper foliage density for nesting trees. Foliage density was measured as the percentage of woody stems obscured by foliage at four angles of each nesting tree. Boxes represent the mean, 1st quartile, and 3rd quartile, while vertical lines represent outliers. Data are based on 101 Gray Vireo nests found on Kirtland Air Force Base in Albuquerque, New Mexico from 2016–2018.
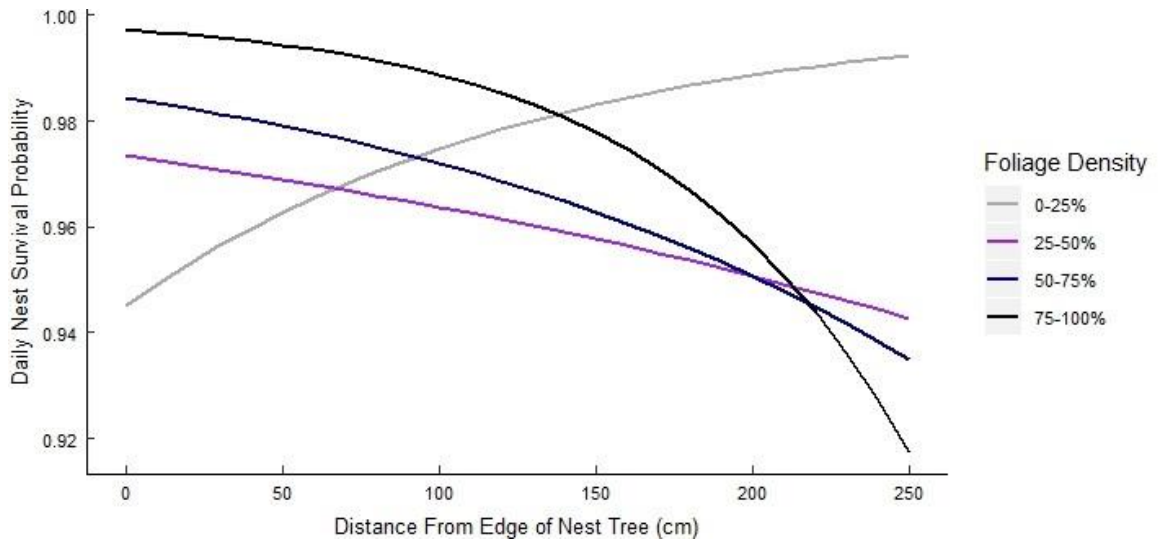
Figure 2. Predicted daily nest survival (≥ 1 nestling survives one day) probability for Gray Vireo nests as a function of a negative interaction between juniper foliage density and the distance of nests from the edge of the nesting tree. Foliage density was measured as the percentage of woody stems obscured by foliage at four angles of each nesting tree. Data are based on 101 Gray Vireo nests found on Kirtland Air Force Base in Albuquerque, New Mexico from 2016–2018.

CHAPTER III

INTERACTIONS OF HABITAT SELECTION AND NEST-SURVIVAL PROBABILITIES:

SPATIAL ESTIMATIONS OF A HABITAT QUALITY RATIO

INTRODUCTION

Since Van Horne (1983), many ecologists have recognized that density should not be the sole indicator of habitat quality (Hall et al. 1997, Johnson 2007). Consequently, there has been an increased effort to use multiple demographic indicators of population growth, including density, reproduction, and survival (Paradis 1995, Hall et al. 1997, Johnson 2007). A literature review habitat quality studies found that when multiple indicators of population demographics were used, a broader understanding of habitat quality was obtained (Johnson 2007). However, perhaps the only standardized approach to estimate habitat quality is the habitat suitability index (HSI), which only rely on species-habitat relationships (US Fish and Wildlife Service 1981).

Habitat quality is generally quantified for discrete patches of habitat (Moilanen and Hanski 1998, Visconti and Elkin 2009, Mortelliti et al. 2010). Indeed, this is a primary assumption for foundational ecological theory, such as Levin's patch model (Levin 1970), island biogeography theory (MacArthur and Wilson 1967) and metapopulation dynamics (Hanski 1998), where discrete patches are evaluated by their propensity for population growth, and are thus designated as "sources" or "sinks" within the metapopulation framework. However, discrete patches are often difficult to delineate in nature or may not exist at the resolution of the study (Freckleton and Watkinson 2002). Additionally, delineating patches of habitat as "high quality"

or "low quality" within a study area not only requires subjectively identifying spatial boundaries across environmental gradients (i.e., patch versus continuous), but also introduces subjective thresholds of quality (Alexander et al. 2011). Plant ecologists have long recognized these limitations, resulting in extensive discussion about the usefulness of metapopulation theory to plant ecology (Freckleton and Watkinson 2002, Ehrlen and Ericksson 2003, Freckleton and Watkinson 2003). Consequently, plant community ecologists more commonly view species-habitat relationships as gradients instead of a network of discrete patches (Choler et al. 2001, Cornwell and Ackerly 2009, Elmendorf et al. 2015). Moreover, although metapopulation theory has resulted in several advancements in ecological (Howell et al. 2018), a shift in the scale of inference to within-patch gradients of habitat quality may result in more detailed information for habitat management. However, the necessity of such a shift is dependent on conservation goals.

Habitat selection and survival can interact in positive and negative ways (DeCasare et al. 2013). Positive interactions can occur when habitats with abundant resources are selected by individuals, which consequently increases reproductive activity and output or survival (DeCasare et al. 2013). Negative interactions could also be considered ecological traps, which are commonly viewed as a disconnect between habitat cues and habitat quality (Schlaepfer et al. 2002). This concept can be visualized graphically (Figure 1), where the area of environmental conditions under a habitat selection coenocline that does not overlap with a habitat quality coenocline would be where ecological traps may occur (Figure 1). The underlying mechanisms that can cause ecological traps may include increased predation rates due to high prey density, increased intraspecific competition, or disturbances (Dwernychuk and Boag 1972).

There have been few attempts in the ecological literature to spatially quantify the interactions of habitat selection and habitat quality. Most of these studies attempt to estimate predation risk of large herbivores in areas of frequently selected habitat. For example, DeCasare et al. (2013) created spatial estimates of the interaction between habitat selection and survival of

Woodland Caribou (*Rangifer tarandus caribou*), which resulted in a map of survival probabilities in areas that caribou frequently selected. Similarly, Hebblewhite et al. (2005) estimated both the encounter and predation probabilities of Elk (*Cervis elaphus*) and Gray Wolves (*Canis lupus*) using resource selection functions. These approaches can be extended to locate areas where all possible interactions occur (positive and negative). Additionally, the focus of these studies has only been on negative interactions of selection and survival instead of spatially estimating all possible interactions. Spatial estimations of these interactions would provide us with a percentage of highly selected habitat that has a high probability of contributing to population growth, which I call a Habitat Quality Ratio (HQR), as this is likely a useful indicator of habitat quality. In addition, by identifying locations where selected habitats are not contributing to population growth (ecological traps), management efforts could be more precise and detailed for species of conservation concern.

Gray Vireos (*Vireo vicinior*) are a species of conservation concern according to the US Fish and Wildlife Service (2008), New Mexico Avian Conservation Partners (2016), and the New Mexico Department of Game and Fish (2018). Gray Vireos generally occur in low densities (Schlossberg 2006) and have a breeding range that is limited to pinyon-juniper woodlands of the southwestern US (Barlow et al. 1999). As with other species of vireos (Kus and Whitfield 2005, Kostecke et al. 2005), one of the primary limiting factors for Gray Vireo population growth is likely nest success (Hargrove and Unitt 2017). However, there has been only one study on Gray Vireo survival (Hargrove and Unitt 2017) and one study on Gray Vireo nesting habitat (Harris et al. 2020). Hargrove and Unitt (2017) found that populations breeding in arid chapparal of California experienced unsustainably low reproductive success, predominately due to high rates of predation from California Scrub Jays (*Aphelocoma californica*) and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). In New Mexico, unpublished reports suggest that breeding territories are almost exclusively in pinyon-juniper woodlands and juniper savannahs,

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and that the primary nesting substrate is one-seed juniper (*Juniperus monosperma*) (Wickersham and Wickersham, unpublished report). It remains unclear if these trends in nesting habitat and nest survival are consistent throughout the species' range.

The primary limiting factor to habitat selection for migratory birds during the breeding season is likely nesting locations. Several studies have shown birds will change their habitat requirements during the breeding season to maximize the number of nesting sites (Rodewald and Brittingham 2004, Keller and Yahner 2007). Consequently, to determine the approximate amount and location of habitat during the breeding season, I analyzed nest-site selection at multiple spatial scales. Similarly, to determine the relative habitat quality during the breeding season, I calculated the percentage of selected habitat that had a high probability of nesting success. Modeling of passerine population growth has shown that nest success is the most important life-history stage in determining the magnitude of population growth (Clark and Martin 2007).

My goals were to estimate within-patch gradients of habitat selection and survival, and to spatially display their interaction to create a HQR for a species of conservation concern. Specifically, I wanted to locate and map areas where Gray Vireo nesting habitat was i) low selection and low survival, ii) low selection and high survival, iii) high selection and low survival (ecological traps), and iv) high selection and high survival.

## METHODS

**Study Site**

Data were collected on Kirtland Air Force Base (KAFB) in Albuquerque, NM in 2016–2019. KAFB is approximately 21,000 ha consisting of four primary cover types: arid grasslands (including sagebrush steppe, juniper savannah), pinyon-juniper woodlands, ponderosa pine (*Pinus ponderosa*) woodlands, and riparian/wetlands (Department of Defense, unpublished report).

Cover types are oriented along an elevation gradient that ranges from approximately 1,600–2,000 m.a.s.l. (Department of Defense, unpublished report).

**Nest Searching and Monitoring**

I searched for Gray Vireo nests from May–July using stratified random sampling locations and opportunistic searching. For detailed methods on my Gray Vireo surveys see Harris et al. (2020). Briefly, at 50 random points I used a portable speaker to perform 10-min call-back surveys, where a 1-min recording of a Gray Vireo song was played during the 5th-min (Kubel and Yahner 2007). Once a breeding territory was identified, nest searching was conducted via behavioral observations (e.g., individuals carrying nesting materials, males consistently singing from the same tree, etc.) until a nest was located. Nests were observed once per week from a distance of ~10 m using binoculars to verify its activity status with minimal disturbance. If nests appeared inactive from a distance, I would examine the nest contents to determine if it had been depredated, abandoned, or parasitized.

**Extracting Data From GIS**

I used ArcGIS (v. 10.2.2) to extract land cover proportions at nesting locations and 58 random points. Random points were generated in ArcGIS and were located in either pinyon-juniper woodland or juniper savannah suggesting they were usable as nesting habitat. All nest sites were ≥ 200 m away from random points so that buffers to extract land cover proportions did not overlap.

KAFB personnel provided a GIS layer of coarse polygons representing broad cover types on KAFB (grassland, juniper savannah, pinyon-juniper woodland, etc.). I used this layer to define boundaries of analyses, where I would only extract data and project findings within areas designated as juniper savannah or pinyon-juniper woodland. Juniper savannah and pinyon-juniper woodlands were considered as "available habitat". To project our model results onto a GIS, I

required cover-type data at a finer resolution. I created a cover-type raster using 1x1 m resolution aerial imagery obtained from KAFB personnel. I used ArcMap to perform an Iso-Cluster Unsupervised Classification, which grouped similar pixels into 20 discrete categories. Each category was reclassified into seven relevant categories: bare ground/buildings, grass, shrub, shrub/cholla mix, juniper, pinyon pine, and ponderosa pine. Ponderosa pine was not included in subsequent analyses because it occurred at elevations exceeding those where Gray Vireos were surveyed (< 2,300 m.a.s.l.). The resulting raster was then resampled into a 2x2 m resolution cover type raster to decrease classification error. Classification error was estimated by ground-truthing 50 random locations and determining the proportions of points that were correctly classified. Thirty-nine out of 50 random points were accurately classified (78%). Seven out of the 11 inaccurate classifications were due to hill shade effects, when random points were located on hill slopes. However, none of our Gray Vireo nests were located in these areas so I assumed classification accuracy to be adequate.

**Estimating Habitat Selection**

A detailed description of methodology used to quantify nest-site selection can be found in Harris et al. (2020). Briefly, nest-site selection was analyzed by comparing land-cover proportions at nest sites with random points. Land-cover proportions were extracted at two scales: 50-m radius (0.79 ha) and 100-m radius (3.14 ha). These scales were chosen to represent nest-site selection within territories, where mean territory size on KAFB has been shown to be 4.5 ha (Wickersham and Wickersham, unpublished report). The largest Gray Vireo territory on KAFB was estimated as 23.7 ha (Wickersham and Wickersham, unpublished report); however, this was calculated using minimum convex polygons, which have been shown to consistently overestimate territory size (Barg et al. 2004). For each spatial scale, I extracted the cover types of all pixels and determined the proportion of each cover type within each buffer.

Statistical analyses were performed in RStudio (2019, v. 1.2.1). I used the "lme4" package (Bates et al. 2015, R Core Team 2016) to create generalized linear mixed effect models (GLMM) and the "bbmle" package (Bolker and R Development Core Team 2017) to perform model selection using Akaike Information Critera corrected for small sample size (AICc) (Burnham and Anderson 2002). Given the limited amount of data on Gray Vireo habitat selection, our statistical techniques followed a step-wise, exploratory approach. First, I determined the most appropriate scale for each land cover type by creating three univariate GLMMs (one for each scale) for each land cover type. The random effect was "Territory ID" and all models had a binomial error distribution. For each land cover type, I compared the relative AICc values of each scale to determine the appropriate scale for each land cover type (Lockyer et al. 2015) (Appendix 1). The best scale for each land cover type was then incorporated into a global model of nest-site selection that was subsequently dredged using the "MuMIn" package (Barton 2019), which tests all possible additive combinations of the variables (Doherty et al. 2010). In addition, I incorporated post-hoc interactions with elevation, to determine how habitat selection varies across changes in elevation. I retained all models with a ΔAICc value < 2.0 and then removed all models with uninformative parameters (Arnold 2010).

**Estimating Daily Nest Survival**

I estimated Gray Vireo daily nest survival probabilities as a function of land cover proportions at three spatial scales: 25-m radius (0.20 ha), 50-m radius (0.79 ha), and 100-m radius (3.14 ha). Land cover proportions were extracted for all nest sites using the same cover classification raster and method outlined in nest-site selection section. The 25-m radius scale was chosen because preliminary analyses suggested that average foliage densities at this scale may influence nest survival probabilities. The 50-m and 100-m radii scales were chosen to account for broader-scale effects of predator and Brown-headed Cowbird habitat selection overlap with Gray Vireo territories. In addition to cover proportions, I was also interested in how the proximity to

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adjacent territories affected daily nest survival probabilities. For each nest, I used ArcGIS to calculate the distance to the nearest nest of adjacent territories.

I used Logistic Exposure Models (LEMs) to estimate Gray Vireo daily nest survival probabilities (Shaffer 2004). LEMs were formed using a GLMM model structure with a customized log-link function that incorporates exposure time. Exposure time was defined as the number of days between nest checks. I used the same multi-step, exploratory approach that was used to estimate nest-site selection probabilities, where I first identified the scale with the best explanatory power for each variable. Each subsequent scale was then incorporated into a global model that was dredged for all possible additive combinations and ranked using AICc.

Because previous work has identified California Scrub Jay predation and Brown-headed Cowbird parasitism as primary causes of Gray Vireo nest failure (Hargrove and Unitt 2017), I was interested in determining if habitat selection of Woodhouse's Scrub Jay (*Aphelocoma woodhouseii*) and Brown-headed Cowbirds corresponded to areas of low habitat quality; this would provide some evidence that these species may restrict the amount of available habitat for Gray Vireos. To estimate habitat selection, I used abundance data from our point count surveys and land cover proportions extracted at the 50-m, 100-m, and 200-m scales to perform a partial Canonical Correspondence Analysis (pCCA). CCAs are a constrained, unimodal ordination that allow for the inclusion of covariates, which account for variation explained by uninteresting parameters (ter Braak and Verdonschot 1995). Cover proportions and their corresponding scales were included in the pCCA using forward-selection based on their percentage of variation explained and degree of correlation with other environmental gradients (i.e., highly correlated variables were excluded). I predicted that Woodhouse's Scrub Jays would occur at higher elevations with greater proportions of juniper and pinyon pine cover than Gray Vireos (Curry et al. 2017). Additionally, I predicted that Brown-headed Cowbirds would be more in abundant at lower elevations with greater proportions of grass and bare ground cover (Lowther 2020).

**Estimating a Habitat Quality Ratio**

To create spatial gradients of nest-site selection and daily nest survival, I incorporated our top into a GIS. I integrated the coefficients from each top model into the cover type raster using the Raster Calculator tool in ArcMap, which produced two rasters illustrating the relative, continuous probabilities of nest-site selection and daily nest survival.

For each raster, I established binary thresholds (i.e., high selection/low selection, high survival/low survival). The threshold for nest-site selection raster was defined as the average predicted probability of nest occurrence at each nest location (Liu et al. 2005). In other words, I extracted the predicted relative probability from the habitat selection raster at each nest location, and averaged that value. Similarly, the threshold for the habitat quality raster was defined as the average predicted daily nest survival probability at each successful nest. I reclassified the binary rasters as described by York et al. (2011), where locations with low selection habitat were reclassified as 1 and locations with high selection were reclassified as 2. Similarly, the nest survival raster was reclassified as 3 for areas below the threshold (low daily nest survival) and 4 for areas above the threshold (high daily nest survival). I then multiplied the two reclassified rasters to produce a map with four classifications: areas with i) low selection and low survival, ii) low selection and high survival, iii) high selection and low survival, and iv) high selection and high survival. I determined the total area of each classification by counting the number of pixels of each raster. A HQR was calculated using

$$HQR = \frac{Area\ of\ Classification\ IV}{Area\ of\ Classification\ IV + Area\ of\ Classification\ III}$$

.

RESULTS

50

I found 173 Gray Vireo nests from 2016–2019. All nests were used in nest-site selection analyses. However, in 2018 KAFB was closed for the majority of the breeding season, which prevented us from monitoring a majority of nests that year. Additionally, "bachelor nests" (Barlow et al. 2020) that never contained eggs were not included in survival analyses. This resulted in a total of 121 nests used for nest survival analyses.

**Habitat Selection and Survival**

Gray Vireos only nested in one-seed junipers. The best performing spatial scale for Gray Vireo nest-site selection varied by cover type. For proportions of grass, bare ground, and juniper the best performing scale was at a 50-m radius. For proportions of shrubs, and pinyon pines, the best performing scale was at a 100-m radius scale. The top model for Gray Vireo nest-site selection was a negative interaction of proportion of juniper cover at the 50-m radius scale and elevation (Table 1). The probability of nest occurrence increased with proportions of juniper cover at low elevations (< 1950 m.a.s.l.), and decreased with proportions of juniper cover at high elevations (> 1950 m.a.s.l.). Consequently, Gray Vireo breeding habitat was almost exclusively in areas where juniper cover represented 15–30% of the available cover, at elevations ranging from 1800–1950 m.a.s.l. (Figure 2).

Daily nest survival was 0.98 and overall nest survival probability of 0.44. Seventy nests fledged ≥ 1 young (58%) and 51 failed (42%). Of the failed nests, 27 were caused by predation (53%), 12 by Brown-headed Cowbird parasitism (23%), 10 by abandonment (20%), and 2 by severe weather (4%). All parasitized nests were abandoned. Clutch size for Gray Vireo was either three or four eggs, with an average of 3.4; the number of fledglings ranged from 1–4 individuals. The best performing model to predict daily nest survival probabilities included a negative response to proportions of juniper cover at the 50-m radius scale and a positive response to proportions of shrub cover at the 25-m radius scale (Table 2).

To understand habitats that may be more prone to predation from Woodhouse's Scrub Jays and parasitism from Brown-headed Cowbirds, I performed a pCCA to test their relative abundances across environmental gradients. The pCCA explained 29.2% of the variation in relative abundances of Gray Vireos, Woodhouse's Scrub Jays, and Brown-headed Cowbirds. The forward selection resulted in eight variables, with juniper at the 100-m radius scale contributing the most to variation explained (8%). The primary environmental gradient represents a transition from grass and bare ground cover at lower elevations to higher proportions of juniper cover at higher elevations (Figure 3). A secondary gradient is one of increasing proportions of pinyon pine cover. Woodhouse's Scrub Jays were more abundant in locations of higher proportions of juniper cover and at higher elevations than Gray Vireos (Figure 3). Brown-headed Cowbirds occurred in areas with greater proportions of pinyon pine than Gray Vireos (Figure 3). Gray Vireos were generally found at lower elevations, with lower proportions of juniper cover and pinyon pine than Woodhouse's Scrub Jays and Brown-headed Cowbirds (Figure 3).

**Estimating a Habitat Quality Ratio**

Using the cover-type polygons provided to us by KAFB, I determined the spatial extent of our projections to be 28,242 $m^2$ of available habitat (juniper savannah or pinyon-juniper woodlands). The model coefficients from each of our top models (nest-site selection and daily nest survival) were projected onto this extent (Figure 4). Our binary raster of nest-site selection estimated that 45% of available habitat (28,242 $m^2$) would be suitable nesting habitat (12,580 $m^2$) (Figure 4). This area represents optimums of juniper cover proportions (15–30%) and elevation (1800–1960 m.a.sl.).

The nest-site survival raster was patchier than the nest-site selection raster (Figure 4). In total, areas designated as high quality represented 63% (17,906 $m^2$) of the available habitat

(28,242 m$^2$). The majority of this region was characterized by high proportions of juniper cover on the eastern half of our study extent, which was rarely selected as nesting habitat.

I calculated a HQR as

$$\frac{10{,}730\ m^2}{10{,}730\ m^2 + 1{,}850\ m^2} = 0.85$$

where 10,730 m$^2$ is the total area of high selection, high survival habitat, and 1,850 m$^2$ is the total area of high suitable, low quality habitat (Figure 5). An HQR of 0.85 suggests that approximately 85% of the highly selected habitat had a high probability of contributing to Gray Vireo population growth. Gray Vireos tended to select nesting habitat that had the highest probability of nest success (Figure 5). Specifically, these locations had enough juniper cover to provide variation in nesting substrates, while avoiding areas of high juniper density that may have higher concentrations of nest predators and brood parasites.

## DISCUSSION

Spatial projections of habitat selection and survival allowed me to determine the ratio of highly selected habitat that has a high probability of contributing to population growth, which is a useful indicator of habitat quality. I found that densities of Gray Vireos on KAFB were high, with much of KAFB having a high probability of being nesting habitat. Gray Vireos selected areas where juniper cover only represented 15–30% of the available cover, despite juniper being the only nesting substrate used. At higher proportions of juniper cover, daily nest survival probabilities decreased; however Gray Vireos rarely nested in these locations, resulting in a high HQR of 0.85. Approximately 85% of the area of highly selected Gray Vireo nesting habitat had a high probability of increasing population growth.

Gray Vireos tended to select nesting habitat that had a high probability of nest survival and avoided locations with greater predation and parasitism risk. Despite juniper being the only

nesting substrate used on KAFB, Gray Vireos predominately selected nesting locations where 15–30% of the available cover was juniper. These areas were mainly juniper savannahs, where sparse densities of junipers were mixed with grass and shrub cover. Locations with higher densities of juniper had higher probabilities of nest failure. Higher densities of juniper were also correlated with higher abundances of Woodhouse's Scrub Jays and Brown-headed Cowbirds. I expected Gray Vireo nesting habitat to be positively related to juniper densities because that would equate to an increase in available nesting habitat. However, Gray Vireos on KAFB have an upper threshold of juniper density corresponding to greater risk of nest failure. This suggests that Woodhouse's Scrub Jay and Brown-headed Cowbird may be limiting the amount of available breeding habitat for Gray Vireos. If so, this would be an example of fundamental versus realized niche (Hutchinson 1958), where higher densities of juniper cover would normally be suitable habitat for Gray Vireos if not for the higher risk of predation and brood parasitism. However, additional limitations to higher densities of juniper cover may be related to colder or windier microclimates at higher elevations, different arthropod communities, or another unknown ecological effect. To actually determine that Woodhouse's Scrub Jays and Brown-headed Cowbirds are limiting the available Gray Vireo habitat, more data would be needed to directly identify Woodhouse's Scrub Jays as nest predators and to more directly link their predation risk with gradients of juniper density.

In general, the interaction of habitat selection and survival was consistently positive throughout KAFB, resulting in few locations of potential ecological traps. Given that there was little within-patch variation in this interaction, KAFB might be a "source" patch where the high reproductive output is supplementing poorer quality habitats in other locations. However, more data would be needed to determine if the high probability of nesting success is actually contributing to population growth and if the resulting growth is contributing individuals to sink patches. In California, reproductive success for Gray Vireo populations was low, which is

believed to be contributing to population declines in the state (Hargrove and Unitt 2017). Population modeling of Puerto Rican Vireos (*Vireo latimeri*) suggested that brood parasitism and nest predation were critical parameters to population growth rate, despite a wide range of adult and juvenile survival rates (Woodworth 1999). The high rates of nest failure were due introduction of the invasive Shiny Cowbird (*Molothrus bonariensis*) and various mammalian predators, which resulted in the Guánica Forest becoming a "sink" for Puerto Rican Vireos (Woodworth 1999). Consequently, the high reproductive output on KAFB is likely aiding in local population growth. However, Gray Vireos tend to have high site fidelity (Barlow et al. 1999), which may minimize the effects of population growth on surrounding habitats. If KAFB reaches some theoretical carrying capacity, I would expect surplus individuals to begin to occupy sites of lower quality.

I wanted to estimate the ratio of highly selected habitat that also has a high probability of contributing to population growth as an indicator of habitat quality. To do so, I spatially projected probabilities of nest-site selection and daily nest survival probabilities, and determined the percentage of overlap. The potential benefits of this approach are two-fold. First, a HQR provides a continuous estimate for the propensity of a habitat to contribute to population growth, instead of binary distinctions in the source-sink model. This is beneficial because binary thresholds are obviously coarser and tend to be arbitrarily defined. Secondly, spatial projections used to produce a HQR allow for approximate locations of ecological traps where management efforts can be focused. Additionally, these methods can be extended to other fauna and other indicators of population growth. For breeding birds, nest success has been shown to be the best predictor of the magnitude of population growth (Clark and Martin 2007). However, additional indicators of habitat quality could be modeled and projected, such as offspring or adult survival.

Gray Vireos are considered a species of conservation concern throughout the species' range due to limited habitat (Barlow et al. 1999), low breeding densities (Schlossberg), and

concerns about poor reproductive success (Hargrove and Unitt 2017). For poorly studied species, such as Gray Vireos, management efforts can be difficult without information on potential drivers of habitat quality. In pinyon-juniper woodlands, the importance of junipers as a nesting substrate seems self-evident given that all of our nests were located in junipers. However, optimum densities of juniper cover may drive habitat selection so as to maximize reproductive success. This suggests that optimum juniper density may be dependent on nest predator community composition and the presence of Brown-headed Cowbirds. In our study system, care should be taken to maximize the area of juniper savannah cover, as habitat quality was high in these areas.

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Table 1. Results from nest-site selection analysis from Harris et al. (2020). Models were formed used generalized linear mixed-effect structure, with territory as a random effect. The top model illustrates a negative interaction between the proportion of juniper cover at the 50-m radius scale and elevation.

| Model | K | ΔAICc | $\omega_i$ | Deviance |
|---|---|---|---|---|
| Juniper50*Elevation | 5 | 0 | 0.9920 | 174.8 |
| Juniper50+PinyonPine100+Elevation | 5 | 13.4 | 0.0012 | 188.2 |
| Juniper50+PinyonPine100 | 4 | 13.4 | 0.0012 | 190.3 |
| Juniper50+PinyonPine100+Shrub100 | 5 | 13.9 | <0.001 | 188.6 |
| Juniper50+PinyonPine100+Shrub100+ Elevation | 6 | 14.1 | <0.001 | 186.7 |
| Juniper50+PinyonPine100+Shrub100+ChollaMix100 +Elevation | 7 | 14.1 | <0.001 | 184.6 |
| Juniper50+PinyonPine100+Shrub100+ChollaMix100 | 6 | 15.0 | <0.001 | 187.6 |
| Juniper50+PinyonPine100+ChollaMix100+Elevation | 6 | 15.2 | <0.001 | 187.8 |
| Juniper50+PinyonPine100+Grass50 | 5 | 15.2 | <0.001 | 190.0 |
| Shrub50+PinyonPine100+Juniper50+Bareground50 | 6 | 15.3 | <0.001 | 187.9 |
| Juniper50+PinyonPine100+ Grass50+Elevation | 6 | 15.3 | <0.001 | 188.0 |
| PinyonPine100*Elevation | 5 | 15.8 | <0.001 | 190.6 |
| Null Model | 2 | 28.0 | <0.001 | 209.1 |
| Juniper50*Shrub100 | 5 | 29.2 | <0.001 | 204.0 |
| Shrub100*Elevation | 5 | 33.0 | <0.001 | 207.8 |

Table 2. Top eight Logistic Exposure Models (LEMs) from dredging a global model predicting daily nest survival probabilities. Models with uninformative parameters (Arnold 2010) were excluded. The top model suggests that daily nest survival was negatively related to the proportion of juniper cover at the 50-m radius scale and positively related to the proportion of shrub cover at the 25-m radius scale.

| Model | K | ΔAICc | $\omega_i$ | Deviance |
|---|---|---|---|---|
| Juniper50+Shrub25 | 4 | 0 | 0.283 | 280.4 |
| Juniper50 | 3 | 0.3 | 0.238 | 282.8 |
| Juniper50+PinyonPine25 | 4 | 2.1 | 0.098 | 282.5 |
| Juniper50+Bareground50 | 4 | 2.2 | 0.094 | 282.6 |
| Juniper50+Grass25 | 4 | 2.3 | 0.091 | 282.7 |
| Null Model | 2 | 2.4 | 0.087 | 286.8 |
| Shrub25 | 3 | 3.2 | 0.058 | 285.6 |
| PinyonPine25 | 3 | 3.5 | 0.05 | 285.9 |
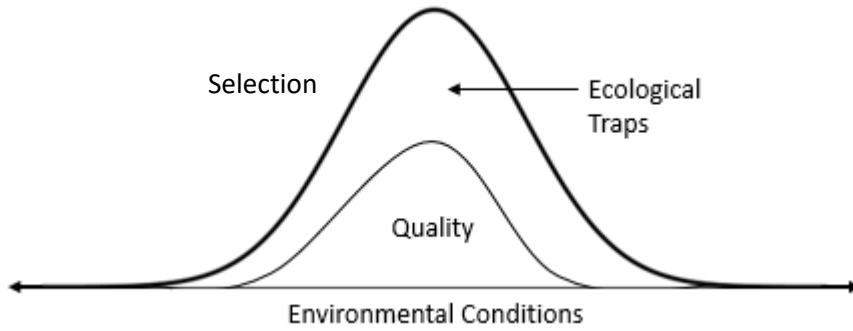
Figure 1. A coenocline illustrating optimums for habitat selection and survival across environmental gradients, and the environmental space in which ecological traps occur.
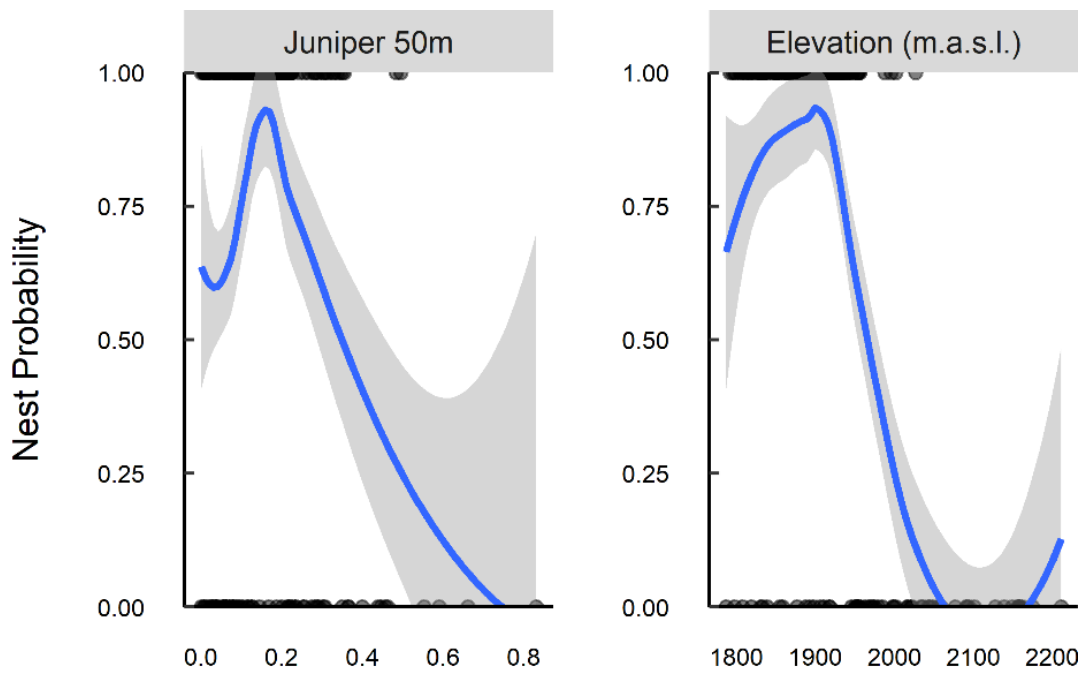


Figure 2. Optimum proportions of juniper cover at the 50-m radius scale and elevation for Gray Vireo nesting probabilities. Best-fit lines were generated using Locally Weighted Smoothing (LOESS). Black dots represent nest locations (y-value = 1) and random points (y-value = 0). Gray area represents a 95% confidence interval.
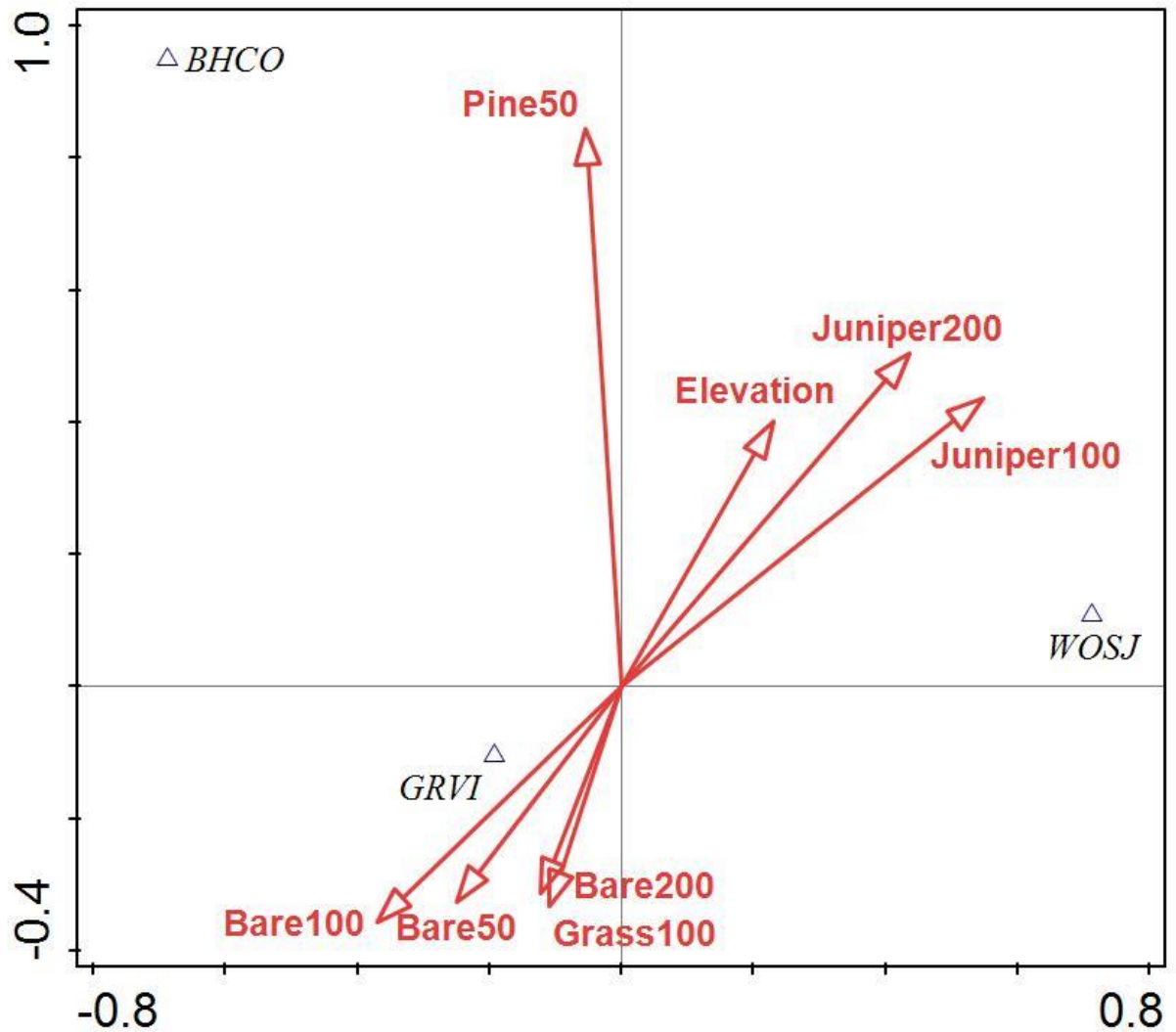
Figure 3. Biplot from a partial Canonical Correspondence Analysis (pCCA). Results suggest that the variance in relative abundances for our three species (Gray Vireo, Woodhouse's Scrub Jay, and Brown-headed Cowbird) is best explained by gradients of bare ground, juniper, elevation, and pinyon pine. Woodhouse's Scrub Jays and Brown-headed Cowbirds were more abundant in areas of higher juniper and pine cover, at higher elevations, relative to Gray Vireos.
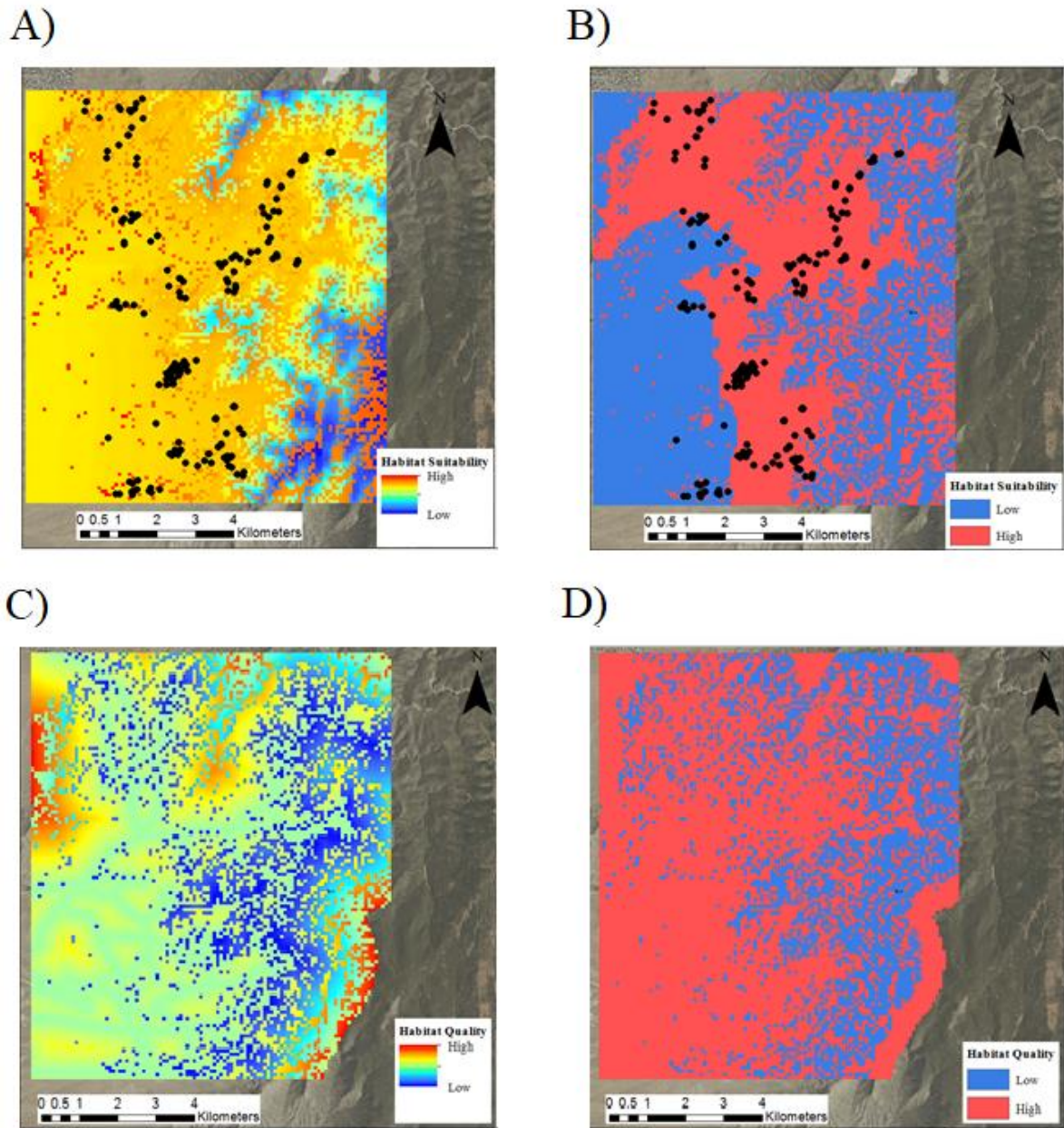
Figure 4. Spatial projections of Gray Vireo nest-site selection (A and B) and daily nest survival probabilities (C and D) based on our top models. Gradients of nest-site selection (A) nest survival (C) were converted into binary outputs (B and D). Warmer colors represent areas of higher selection and survival, colder colors represent poor selection and survival. Black dots on A and B represent Gray Vireo nest locations from 2016–2019.
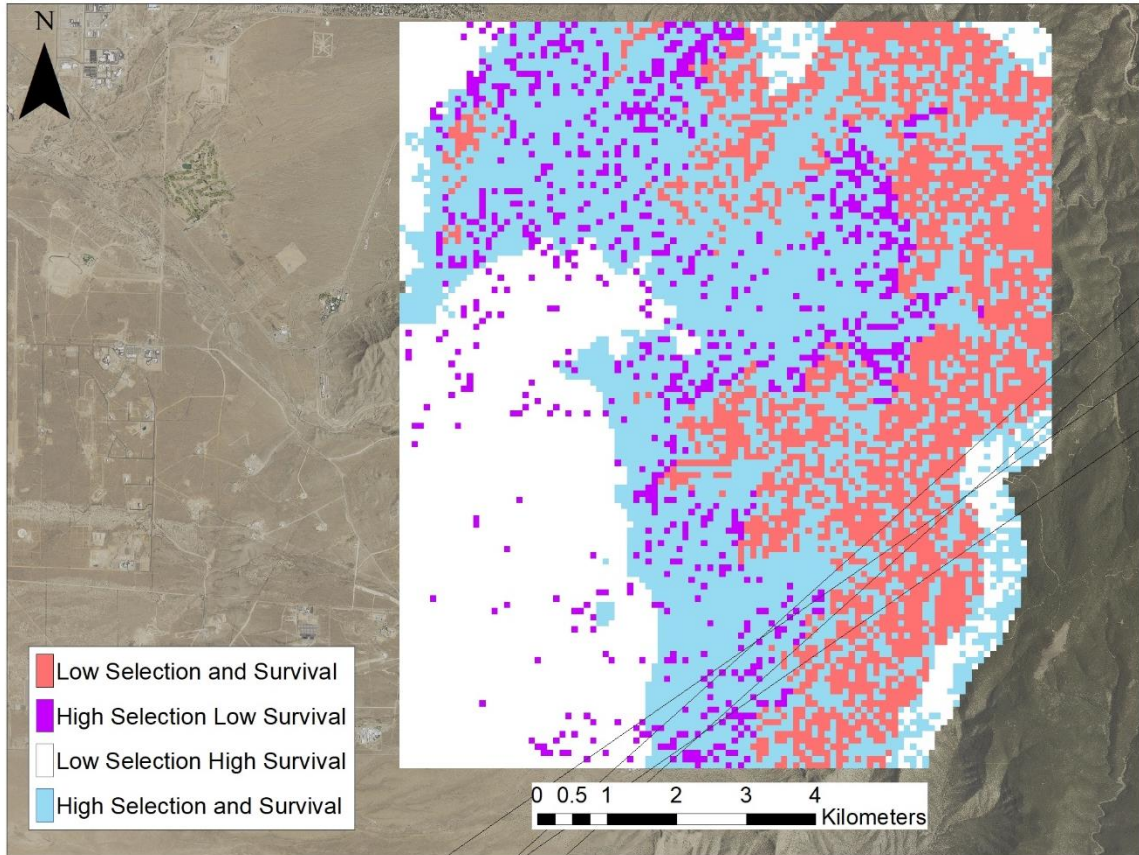
Figure 5. A spatial projection of the interaction between habitat selection and survival. Light blue represents a positive interaction (high selection and survival), purple represents a negative interaction (high selection but low survival), red represents low selection and quality, and white represents low selection but high survival. An HQR was quantified by dividing the total area of light blue by the total area of light blue plus purple.

CHAPTER IV


GRAY VIREOS (*VIREO VICINIOR*) UTILIZE NEST ORIENTATION TO OPTIMIZE NEST

MICROCLIMATE

INTRODUCTION

The thermal landscape is an environmental dimension that species have to account for in their life-history and ecology (Peterson et al. 2011). At broader scales, species' distributions are likely constrained by the climatic conditions for which they are physiologically adapted (Somero 2005); while at finer scales, the thermal landscape can directly affect population dynamics through survival, fitness, and reproductive success (Olsson and Uller 2003, Dawson et al. 2005). Despite this, ecologists more commonly focus on biotic relationships (Hovick et al. 2014) and rarely consider the thermal environment when establishing management actions for species of conservation concern (Elmore et al. 2017) or when considering behavioral evolution.

Behavioral adaptations to thermal stressors are common in arid environments (Cloudsley-Thompson 1993). For birds, such behavioral adaptations include selection of cooler microhabitats during foraging (Cunningham et al. 2015), roosting (Barrows 1981), and nesting (Hartman and Oring 2003, Tieleman et al. 2008, Carroll et al. 2015). The importance of microclimate to nest-site selection in arid environments has been demonstrated for a variety of species and nesting strategies, where cooler microclimates in arid environments have been linked to increased

survival probabilities (Carroll et al. 2015, Grisham et al. 2016) and normal rates of embryo

development (Webb 1987). Consequently, species-specific nesting strategies in arid environments

tend to minimize thermal variances and lower maximum temperatures (Hartman and Oring 2003,

Tieleman et al. 2008, Carroll et al. 2015). For example, some ground-nesting species will select

nest sites with greater proportions of woody and grass cover to increase visual obstruction for

shade (Carroll et al. 2015), while cup-nesting species may increase the height of their nests as

temperatures increases to decrease conductive warming (Tieleman et al. 2008) or utilize

orientation to increase shade (Hartman and Oring 2003).

The majority of species in the Vireonidae family have pensile nests placed on the edge of

the nesting substrate (Bent 1965). This is particularly true for species which breed in arid

environments, such as Bell's Vireo (*Vireo belli*) (Kus et al. 2020), Plumbeous Vireo (*Vireo*

*plumbeus*) (Goguen and Curson 2020), Black-capped Vireo (*Vireo atricapilla*) (Grzybowski

2020), and Gray Vireo (*Vireo vicinior*) (Harris et al. 2020), compared to vireos that breed in

cooler climates with pensile nests closer to the interior of their nesting substrate, such as Blue-

headed Vireos (*Vireo solitaris*) (Morton and James 2020), Yellow-throated Vireos (*Vireo*

*flavifrons*) (James 1976), and White-eyed Vireos (Peake and Ritchison 1998). Nesting at the edge

of the nesting substrate may be beneficial in arid environments because nest orientation can be

used to maximize shade during the hottest parts of the day (Hartman and Oring 2003) and

increase solar radiation in cooler mornings.

The Gray Vireo is a short-distance migrant that predominantly breeds in the southwestern

United States (Barlow et al. 2020) from May–August. Breeding habitat is generally in pine (*Pinus*

*spp.*) and juniper (*Juniperus spp.*) woodlands that have higher densities of juniper than pine

(Schlossberg 2006, Harris et al. 2020). In pinyon-juniper woodlands, Gray Vireos will almost

exclusively nest in junipers (Harris et al. 2020) and nests are commonly located on the periphery

of the juniper (Barlow et al. 2020, Harris et al. 2020). Orientation of nests relative to the center of the nesting tree varies. Hargrove and Unitt (2017) found that Gray Vireo nests in California tended to be located on the south side of nesting shrubs, however nests in other regions can be north or west facing (Barlow et al. 2020).

Our objective was to determine the thermal and radiative benefits of nesting on the periphery of a tree in an arid environment. Specifically, I hypothesized that Gray Vireos would choose an orientation (i.e., cardinal direction relative to the center of the tree) that would be warmer in the colder mornings and cooler in the hotter afternoons than at the opposite orientation of the nesting tree. Additionally, because Gray Vireos may also utilize foliage to increase shade at nest sites, wanted to measure microclimate as a function of vegetation structure. To do so, I measured temperature and solar radiation at i) Gray Vireo nests, ii) the opposite orientation of nests within the nesting tree, and iii) the same orientation as nests but in adjacent trees.

## METHODS

**Study Site**

I monitored microclimate at Gray Vireo nests on Kirtland Air Force Base (KAFB) in 2016, 2017, and 2019. KAFB is located south of Albuquerque, New Mexico, and consists of approximately 108 ha of pinyon-juniper woodlands and juniper savannah (U.S. Air Force 2012). The area is immediately west of the Manzanita mountains, with elevation ranging from 1600–2400 m (U.S. Air Force 2012). During June 1–August 1 of 2016–2019, the mean precipitation totals for each summer were 88.0 mm (range: 57.4–118.9 mm) (New Mexico Climate Center). The mean high and low temperatures from June 1–August 1 in 2016–2019 were 33.7°C (± 2.8°C SD) and 23.7°C (± 4.3°C SD), respectively (New Mexico Climate Center). There was a maximum ambient temperature of 39.4°C and a minimum ambient temperature of 2.8°C (Figure 1) (New Mexico Climate Center, https://weather.nmsu.edu/coop/request/station/290234/data/).

**Locating Nests**

I located Gray Vireo territories using call-back surveys at 50 random points in pinyon-juniper woodlands and juniper savannahs (U.S. Air Force 2012). For detailed methods on Gray Vireo nest searching, see Harris et al. (2020). Briefly, I surveyed for Gray Vireos using methods from Kubel and Yahner (2007). When Gray Vireos were observed at a point I recorded a distance and direction to determine the approximate location of the territory. Once a breeding territory had been identified, I searched for nests using behavioral cues, such as carrying nesting material, males singing from nests, or following females. Nests were monitored once a week until completion (i.e. fledged, depredated, abandoned).

**Microclimate Monitoring**

Within one week after a nest had completed, I recorded air temperature ($T_N$) and solar radiation ($L_N$) at the nest site, at the opposite orientation of the nest ($T_O$, $L_O$) within the nesting tree, and at the same orientation of the nest but in an adjacent tree to account for variation in vegetation structure ($T_S$, $L_S$) (Figure 2). $T_N$ and $L_N$ were measured with a temperature/light data logger (HOBO pendant, Onset Computer Corporation, Bourne, MA) within the nest, yet situated so that the light sensor was above the rim of the nest. For destroyed nests, data loggers were hung in the tree at the location of the nest prior to destruction. $T_O$ and $L_O$ were measured by placing a data logger at the opposite orientation of the nest within the nesting tree, yet at the same relative location as the nest (i.e., same nest height and distance from the edge of the tree). Similarly, data loggers used to measure $T_S$ and $L_S$ were placed in the nearest adjacent tree of the same species, with the same orientation, nest height, and distance from the edge of the tree (Figure 2). For example, if a nest was located on the east side of a tree (90°), I placed data loggers at the nest site, at the west side of the nesting tree (270°), and at the east side of an adjacent tree (90°). Data were recorded every 30 minutes from 0700–1900 hr (approximate hours of sunlight) and were

averaged across five consecutive days. Five days were chosen somewhat arbitrarily but allowed us to avoid single-day weather extremes in analysis.

**Statistical Analyses**

To test the hypothesis that Gray Vireos select nest orientations that increase temperatures during early mornings and decrease temperatures during hot afternoons, I compared $T_N$, $T_O$ and $T_S$ throughout the day. I compared temperature/light exposure $T_N$, $T_O$ and $T_S$ using linear mixed effect models via the "nlme" package in Rstudio (2019, v. 1.2.1; Pinheiro et al. 2020, R Core Team 2016). I also used the same model structure to compare temperature/light exposure differences between nest sites as a function of cardinal direction (north, south, east, west). I used the "lme" function to assign an autocorrelation structure to our model, to account for temporal autocorrelation among 30-minute temperature/light readings. I used a first-order autoregressive process as autocorrelation structure, with "Time of Day" as time variable. Temperature (°C) and light (lm) were dependent variables with "Sample Location" (Nest, Opposite Orientation, or Adjacent Tree) and "Time of Day" as independent variables. Both models incorporated an interaction between "Sample Placement" and "Time of Day" to account for changing effects of sample locations during hotter or cooler times of the day. As a post-hoc analysis, I used the "emmeans" package (Lenth et al. 2020) to calculate estimated marginal means (or least squares means) with a Bonferroni correction and a Tukey-adjusted pairwise comparison. I used an alpha value of 0.05 to determine differences in temperature and light at various combinations of sample locations and times.

## RESULTS

Gray Vireos initiated nesting on KAFB as early as 24 April (2019) and as late as 03 August (2017). I monitored temperature of 71 nests, with a subset of 37 nests for light exposure. The distribution of nest orientations was similar among cardinal directions (north: 19, east: 17,

south: 19, west: 16). The range of temperatures were 10.1°C–47.0°C. Both extremes were recorded on $T_O$ samples, while the range of $T_N$ was 10.5°C–45.6°C. Nests began cooling at approximately 1600 hr, compared to $T_O$, which began cooling at approximately 1730 hr (Figure 3). Additionally, the rate of cooling for $T_N$ was faster than for $T_O$ in the afternoon (Figure 3). From 1600–1800 hr, $T_N$ decreased at a rate of 3.1°C/hr, while $T_O$ decreased at a rate of 1.5°C/hr.

Both "Sample Placement" (nest, opposite orientation, or adjacent tree) and "Time of Day" significantly influenced differences in average temperature, however their interaction was not significant (Table 1). While average $T_N$ was less than average $T_O$ and $T_S$ at all times of the day (except at 0700 hr), differences only occurred between 1700–1830 hr (Figure 3). During these times $T_N$ was cooler than $T_O$ (Table 2, Figure 3), where nests were 3.0 °C ($\pm$ 0.4 °C) cooler. $T_N$ was also slightly cooler in the mornings (0830–0900 hr) than $T_O$, however this relationship was not significant (0830 hr: P = 0.06, 0900 hr: P = 0.07) (Figure 3).$T_N$ was only significantly cooler than $T_S$ at 1800 hr. Differences in $T_N$ at different orientations were minimal. North-facing nests were cooler than nests at other orientations from 0900–0930 hr (Figure 4). Generally, north and east-facing nests had the most variability in temperature throughout the day, while south-facing nests tended to have lower variation (Figure 4). However, I found little evidence that any one orientation was optimal for nest microclimate (i.e., less thermal variation and/or lower overall temperatures).

Light exposure was different between "Sample Placement" and at different times (Table 1). Nests received less light on average than $L_O$ and $L_S$, where the average $L_N$ was 6,569 lm ($\pm$ 4,153 lm) less than the average $L_O$ and 9,780 lm ($\pm$ 9,624 lm) less than $L_S$ throughout the day (Figure 5). The degree of difference changed by time (P = <0.001). Differences between $L_N$ and $L_S$ occurred between 1000–1200 hr and 1300–1400 hr (Table 3). Similarly, differences between $L_N$ and $L_O$ occurred between 0930–1030 hr and then sporadically in the afternoon (Table 3,

Figure 5). However, the overall variance of light exposure was greater than temperature across all samples and all orientations. Variation in $L_N$ was less throughout the day ($\sigma$ = 35,439 lm) than $L_O$ ($\sigma$ = 39,413 lm) and $L_S$ ($\sigma$ = 40,702 lm). Additionally, variance of light exposure within time periods was also less for $L_N$ than $L_O$ and $L_S$ (Figure 5) I did not find a link between nest orientation and light exposure with time of day (Figure 6).

## DISCUSSION

Gray Vireo nests were cooler than the nesting tree's opposite orientation at all times, with the greatest difference occurring from 1700–1830 hr. In Albuquerque during the summer months (May–August), the highest ambient temperature occurs between 1600–2000 hr (Albuquerque International Airport, https://weatherspark.com/y/3318/Average-weather-in-Albuquerque-New-Mexico-United-States-Year-Round). These findings suggest that the nests had a cooler microclimate during the hottest times of the day, with an average temperature difference of 3 ℃ cooler than the opposite orientation of the nesting tree. Nests also had a smaller range of temperatures throughout the day and began cooling in the evenings faster than the opposite orientation.

Although thermal extremes in our study would not likely induce direct mortality of embryos (Webb 1987), minimizing thermal stress and variability could be important to other aspects of reproductive success and embryonic development. Grenõ et al. (2008) found a negative correlation between nest temperatures and fledgling survival probabilities. Additionally, several studies have shown that nest temperatures greater than 34 ℃ can negatively affect nestling physiology for a variety of songbirds (Ardia 2013, Cunningham et al. 2013, Rodriguez and Barba 2016). Specifically, nestlings can experience higher hematocrit (proportion of blood volume composed of red blood cells) levels (Ardia 2013), stunted growth (Rodriguez and Barba 2016), and delayed fledging (Cunningham et al. 2013). The threshold of 34 ℃ was reached by 65 of our

Gray Vireo nests (92%) and 68 of the opposite orientation samples (96%). Temperatures I measured could have even greater adverse effects on nestling physiology, considering I measured ambient temperature as opposed to operative temperature, which may be higher when accounting for relative humidity (Yahav et al. 1995) and solar radiation (Dzialowski 2005).

Although Gray Vireos seem to choose the cooler orientation of their nesting tree, I did not find a pattern in certain cardinal directions being more commonly selected or having cooler microclimates. Some cavity nesting species, such as Tree Swallow (*Tachycineta bicolor*), utilize the orientation of nest openings to maximize wind exposure (Ricklefs and Hainsworths 1969) and to increase solar exposure during colder mornings (Ardia et al. 2006). Conversely, Horned Larks (*Eremophila alpestris*) have been shown to disproportionately nest on the north-facing side of their substrate to increase the amount of shade the nest experiences throughout the day (Hartman and Oring 2003). Some studies have found that Gray Vireos more commonly nest on the south side of the nesting tree (Hargrove and Unitt 2017, Barlow et al. 2020), however I did not see this trend. At our study site, the south side of nesting trees was significantly warmer than the north side of nesting trees between 0900–0930 hr. But generally, there was no clear relationship between the four cardinal directions and temperature at almost any time of day. Similarly, I did not find a clear pattern between light exposure and cardinal direction. The high variance in temperature and light exposure at any given orientation may be because of the topographic variation at our study site (U.S. Air Force 2012). Nest sites were almost always situated in valleys with slopes immediately to the north, east, or south. Such topographic variation could result in shade effects that vary light exposure considerably. Additionally, unlike the Hargrove and Unitt (2017) study, our nests were located in wooded areas, where nesting trees were likely to receive shade from taller adjacent vegetation. These factors may lead to inconsistency in light exposure

and temperature by orientation, resulting in Gray Vireos using all nesting orientations. Consequently, the cues that Gray Vireos use to determine optimal nest placement remain unclear.

Although differences between $L_N$ and $L_O$ were observed, almost all differences occurred in morning, when there were not temperature differences. Seemingly, relative differences observed in light exposure did not translate into differences in temperatures. Part of this may be accounted for by latency effects, where locations exposed to more light in the mornings maintain greater heat throughout the day. However, this may also be due differences between ambient and operative temperatures. I measured ambient temperature instead of operative temperature because I was more interested in relative comparisons of thermal conditions than modeling thermal stress an animal experiences. Operative temperature directly accounts for solar radiation and convective heat transfer (Campbell and Norman 1998). Another possible explanation for why light exposure did not translate into differences in temperature, is that variation between light readings was high, particularly in $L_O$ and $L_S$. Light exposure was measured instantaneously every 30-minutes, which could result in high variation between readings. Our study site frequently had high winds and tall, adjacent vegetation which may have resulted in inconsistent shade when collecting instantaneous samples.

The biggest differences in light exposure were between $L_N$ and $L_S$. This finding suggests that Gray Vireos utilize vegetation structure (more so than orientation) to increase shade and minimize variance in light exposure at nests. The utilization of vegetation to increase visual obstruction and shade has been documented for a wide variety of species, most commonly with ground-nesting species (Flaspohler et al. 2000, Hubbard et al. 2006, Carroll et al. 2015). Although I did not measure visual obstruction directly, the relative lower light exposure in the late mornings suggests that Gray Vireos utilize overhead vegetation cover, particularly in the south-easterly direction. However, this did not translate to differences in temperature between $T_N$ and

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$T_S$. Consequently, the use of overhead vegetation cover may be more attributable to increased visual obstruction from aerial predators. Hargove and Unitt (2017) found that the most common nest predator of Gray Vireos was the California Scrub Jay (*Aphelocoma californica*), which accounted for 67% of all predation events. At our study site, Woodhouse's Scrub Jays (*Aphelocoma woodhouseii*) were common and are a likely nest predator of Gray Vireos (Barlow et al. 2020). Additionally, Brown-headed Cowbirds (*Molothrus ater*) are a common cause of Gray Vireo nest failure (Hargrove and Unitt 2017).

The distance that a nest placed from the center of a tree varies among species in the Vireondae family (Bent 1965). This seemingly corresponds to differences in latitudinal gradients, where northern species of vireos tend to nest closer to the center of a tree and southern species tend to nest near the edge of a tree. Intraspecific variation in nest orientation across latitudinal gradients has been shown for eight species of passerines, where species with nests in lower latitudes tended to have more northerly orientations than in higher latitudes (Burton 2007). However, thermal evidence for this pattern has been missing.

In arid environments, minimizing thermal variation and decreasing maximum temperatures at nest sites is critical to reproductive success and survival (Carroll et al. 2015, Grisham et al. 2016). I found evidence that Gray Vireos were able to do this by selecting orientations of nest sites that are cooler than the opposite orientation of the nesting tree, particularly at the hottest times of the day. Conversely, temperatures of samples located at the same orientation, but with different vegetation structures, were not different from nests, suggesting that microclimate slection had more to do with nest orientation than the vegetation surrounding nests. This provides some evidence that nesting on the periphery of a nesting substrate does play a role in maintaining microclimates at nesting sites. However, it remains unclear if the advantages of this behavior are the result of behavioral plasticity or are adaptive

(i.e., selected for). Further information on the microclimates and nest placements of other species across latitudinal gradients is needed to effectively demonstrate that this behavior is evolutionary in nature.

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Table 1. Results from linear mixed-effect models testing differences in temperature and light exposure as functions of sample placement, orientation, and time. Data are based on 71 Gray Vireo nests found on Kirtland Air Force Base, Albuquerque, NM in 2016–2017 and 2019.

| Dependent Variable | Intercept | Independent Variable P-value | | | Pseudo $R^2$ |
|---|---|---|---|---|---|
| | | Placement | Time | Placement*Time | |
| Temperature | 16.7 | <0.001 | <0.001 | 0.999 | 0.31 |
| | | Orientation | Time | Orientation*Time | |
| | 16.3 | 0.133 | <0.001 | 0.39 | 0.41 |
| | | Placement | Time | Placement*Time | |
| Light Exposure | 302.7 | <0.001 | <0.001 | <0.001 | 0.428 |
| | | Orientation | Time | Orientation*Time | |
| | 200.8 | 0.11 | <0.001 | 0.763 | 0.434 |
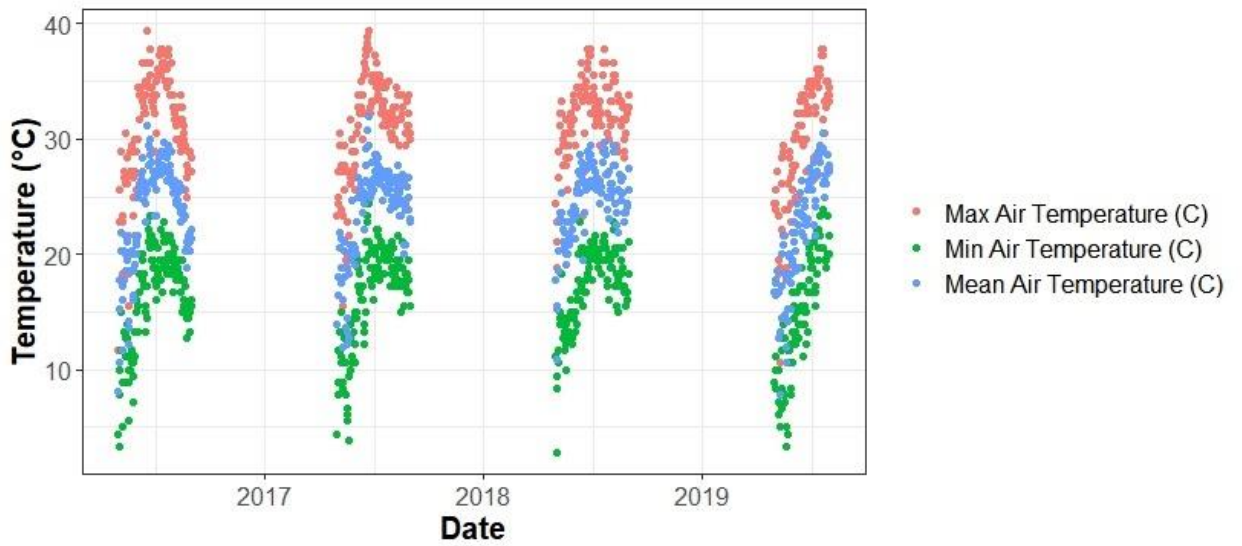
Figure 1. The recorded ambient temperature at Albuquerque International Sunport from June 1–August 1 in 2016–2019. Data are available at the New Mexico Climate Center.
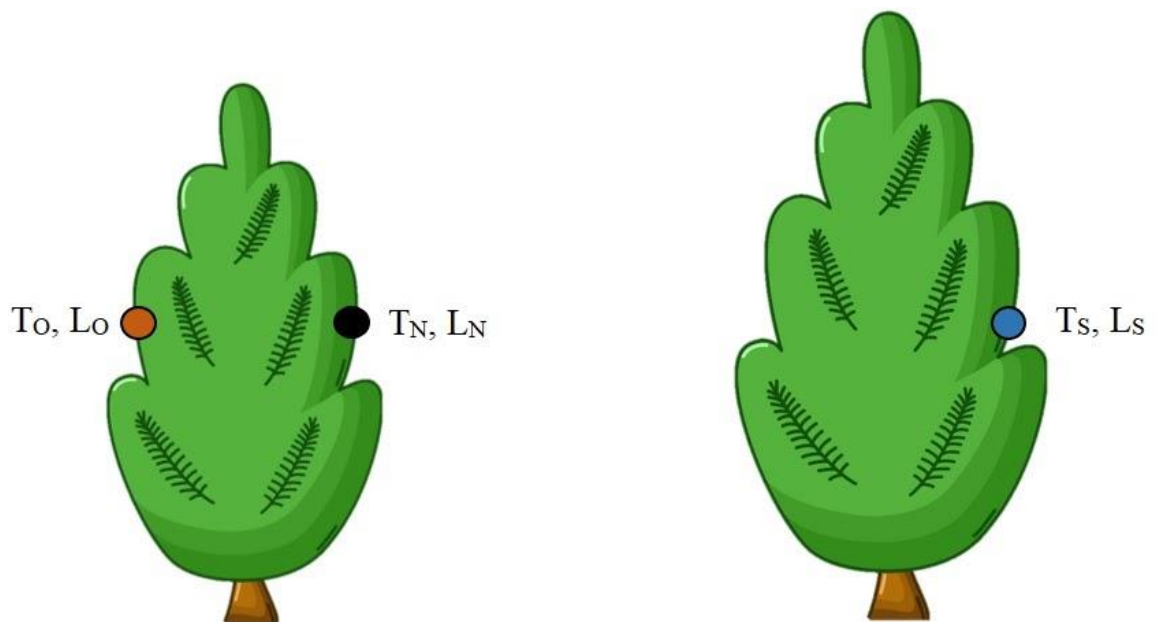


Figure 2. An illustration of the experimental design with the three sample locations. The black dot represents the location of a Gray Vireo nests (location of $T_N$ and $L_N$ samples). The orange dot

represents the opposite orientation of the Gray Vireo nest but at the same relative position ($T_O$ and $L_O$). And the blue dot represents the same orientation of the Gray Vireo nest in an adjacent tree to compare differences in vegetation structure ($T_S$ and $L_S$).
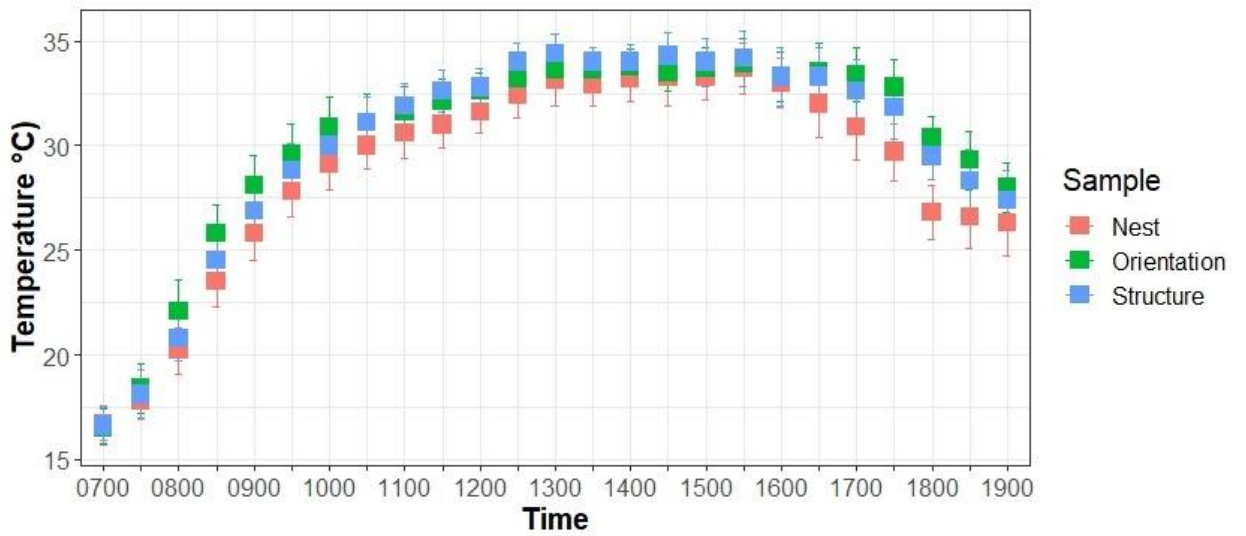


Figure 3. Average temperatures at Gray Vireo nest sites ($T_N$), the opposite orientation ($T_O$), and in different vegetation structures ($T_S$) with 95% confidence intervals. Significant differences between $T_N$ and $T_O$ occurred between 1700–1830 hr.
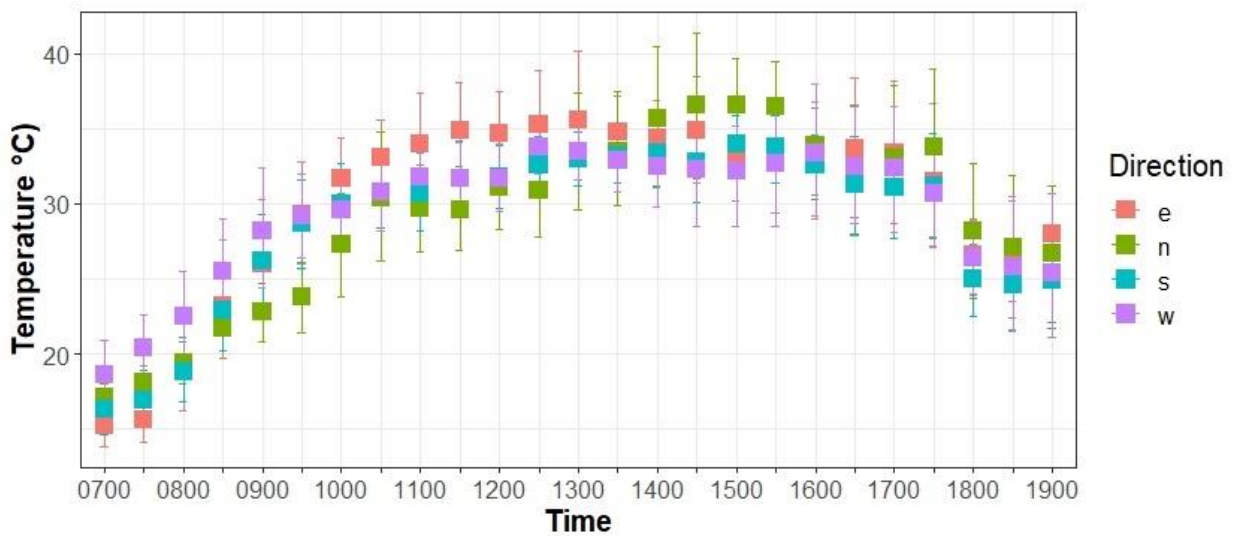
Figure 4. Average temperatures at Gray Vireo nest sites (*n*=71) in each cardinal direction with 95% confidence intervals. North-facing nests were significantly cooler than other orientations from 0900–0930 hr.
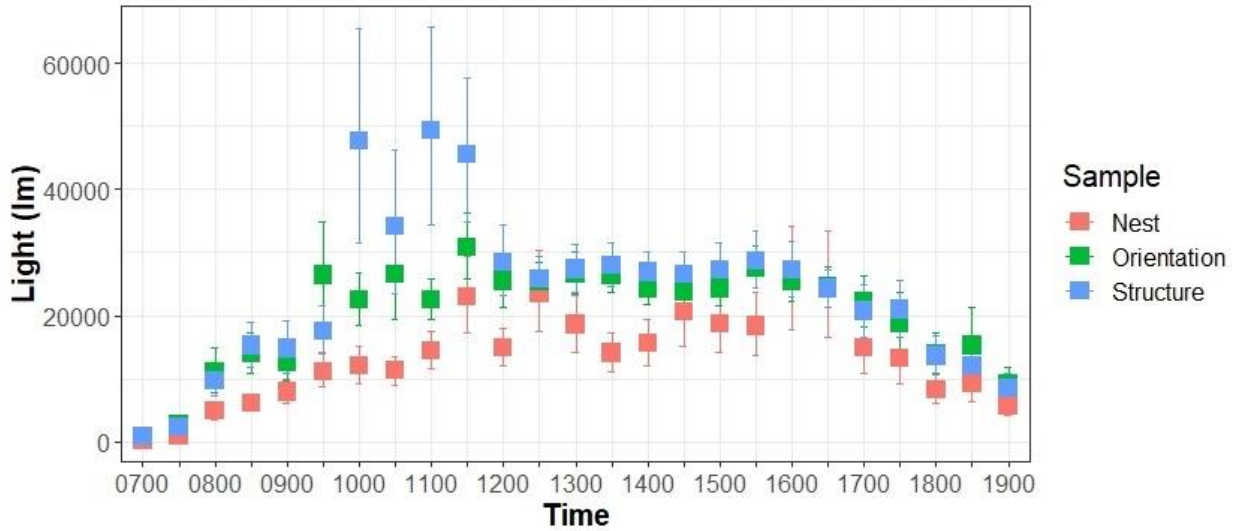


Figure 5. Average light exposure at Gray Vireo nest sites ($L_N$), the opposite orientation ($L_O$), and in different vegetation structures ($L_S$) with 95% confidence intervals. Significant differences were generally greatest between $L_N$ and $L_S$, with largest differences occurring between 1000–1130 hr.
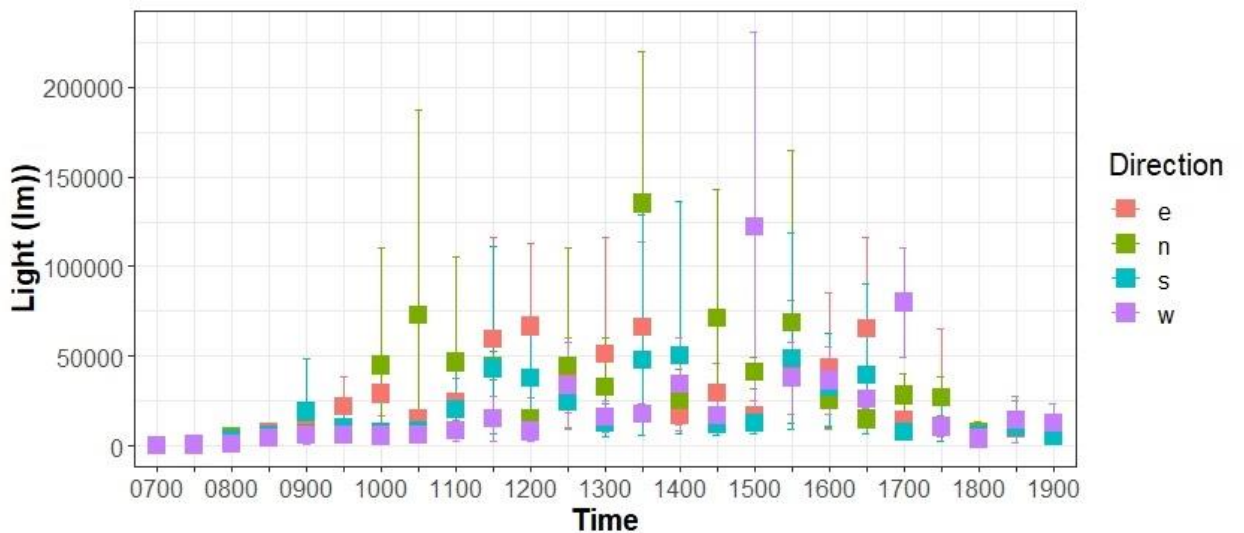


Figure 6. Average light exposure at Gray Vireo nest sites (*n*=37) in each cardinal direction with 95% confidence intervals. There were no clear differences in light exposure between orientations except for western orientations receiving more light at 1500 and 1700 hrs than other orientations.

Appendix 1. Pairwise P-value matrices for temperature and light exposure, showing post-hoc comparisons between nests ($T_N$, $L_N$), the opposite orientation ($T_O$, $L_O$), and the same orientation with different vegetation structure ($T_S$, $L_S$). The bracketed diagonals are the sample means, the upper triangle shows P-values, and the lower triangle shows pairwise differences. P-values representing significant differences from nests are highlighted in bold in the upper triangle.

|  | Temperature | | | Light | | |
|---|---|---|---|---|---|---|

**Time = 0700**

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [16.7] | 0.9919 | 0.9982 | [303] | 0.9892 | 0.9876 |
| Orientation | 0.1328 | [16.5] | 0.9978 | -531.5 | [834] | 1 |
| Structure | 0.0624 | -0.074 | [16.6] | -564.6 | -33.1 | [867] |

**Time = 0730**

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [17.7] | 0.8218 | 0.9291 | [ 885] | 0.8914 | 0.9221 |
| Orientation | -0.651 | [18.4] | 0.972 | -1796 | [2681] | 0.997 |

| Structure | -0.401 | 0.25 | [18.1] | -1506 | 290 | [2392] |

Time = 0800

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [20.1] | 0.1356 | 0.7751 | [ 4990] | 0.2399 | 0.4208 |
| Orientation | -2.087 | [22.2] | 0.4444 | -6092 | [11082] | 0.9162 |
| Structure | -0.747 | 1.34 | [20.8] | -4602 | 1490 | [ 9592] |

Time = 0830

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [23.4] | **0.0566** | 0.595 | [ 6331] | 0.1152 | 0.0416 |
| Orientation | -2.51 | [25.9] | 0.3925 | -7626 | [13956] | 0.9356 |
| Structure | -1.07 | 1.44 | [24.5] | -8934 | -1308 | [15265] |

Time = 0900

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [25.7] | 0.0684 | 0.559 | [ 7890] | 0.426 | 0.152 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Orientation | -2.42 | [28.2] | 0.4704 | -4806 | [12696] | 0.8545 |
| Structure | -1.13 | 1.29 | [26.9] | -6908 | -2102 | [14798] |

Time = 0930

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [27.7] | 0.1833 | 0.5902 | [11232] | **0.0002** | 0.2269 |
| Orientation | -1.921 | [29.7] | 0.7232 | -15192 | [26424] | 0.057 |
| Structure | -1.076 | 0.846 | [28.8] | -6281 | 8911 | [17513] |

Time = 1000

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [29.1] | 0.2051 | 0.7233 | [12500] | **0.0461** | **<.0001** |
| Orientation | -1.856 | [31.0] | 0.6282 | -9400 | [21900] | <.0001 |
| Structure | -0.843 | 1.014 | [29.9] | -35159 | -25759 | [47659] |

Time = 1030

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [30.0] | 0.498 | 0.5764 | [11280] | **0.0002** | **<.0001** |
| Orientation | -1.23 | [31.2] | 0.9924 | -15209 | [26489] | 0.1195 |
| Structure | -1.1 | 0.13 | [31.1] | -22727 | -7518 | [34007] |

Time = 1100

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [30.5] | 0.544 | 0.4782 | [14355] | 0.0909 | **<.0001** |
| Orientation | -1.148 | [31.7] | 0.993 | -8208 | [22564] | <.0001 |
| Structure | -1.273 | -0.125 | [31.8] | -35015 | -26807 | [49370] |

Time = 1130

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [31.0] | 0.4856 | 0.3644 | [22979] | 0.1 | **<.0001** |
| Orientation | -1.251 | [32.2] | 0.9745 | -7703 | [30682] | 0.0001 |
| Structure | -1.49 | -0.239 | [32.5] | -22663 | -14961 | [45643] |

Time = 1200

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
| --- | --- | --- | --- | --- | --- | --- |
| Nest | [31.6] | 0.5766 | 0.5049 | [15018] | **0.0182** | **0.0016** |
| Orientation | -1.092 | [32.7] | 0.992 | -10437 | [25455] | 0.7178 |
| Structure | -1.225 | -0.133 | [32.8] | -13394 | -2957 | [28412] |

Time = 1230

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
| --- | --- | --- | --- | --- | --- | --- |
| Nest | [32.4] | 0.7191 | 0.3105 | [23630] | 0.8601 | 0.8382 |
| Orientation | -0.844 | [33.2] | 0.77 | -1992 | [25622] | 0.999 |
| Structure | -1.604 | -0.76 | [34.0] | -2159 | -167 | [25789] |

Time = 1300

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
| --- | --- | --- | --- | --- | --- | --- |
| Nest | [33.0] | 0.8336 | 0.4509 | [18548] | 0.0785 | **0.0505** |
| Orientation | -0.627 | [33.7] | 0.8033 | -8173 | [26721] | 0.9865 |
| Structure | -1.323 | -0.695 | [34.4] | -8772 | -599 | [27320] |

Time = 1330

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [32.9] | 0.7793 | 0.5522 | [14139] | **0.0044** | **0.0009** |
| Orientation | -0.734 | [33.6] | 0.9275 | -12279 | [26418] | 0.8968 |
| Structure | -1.142 | -0.407 | [34.0] | -13887 | -1608 | [28026] |

Time = 1400

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [33.2] | 0.8338 | 0.7638 | [15660] | **0.0586** | **0.0065** |
| Orientation | -0.627 | [33.8] | 0.991 | -8562 | [24222] | 0.7552 |
| Structure | -0.768 | -0.141 | [34.0] | -11263 | -2701 | [26923] |

Time = 1430

|  | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [33.3] | 0.9638 | 0.6715 | [20529] | 0.6502 | 0.2566 |
| Orientation | -0.282 | [33.6] | 0.8246 | -3370 | [23899] | 0.7786 |
| Structure | -0.934 | -0.652 | [34.2] | -5942 | -2572 | [26471] |

Time = 1500

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [33.3] | 0.9258 | 0.8389 | [18745] | 0.3018 | 0.0649 |
| Orientation | -0.408 | [33.7] | 0.9798 | -5479 | [24225] | 0.7153 |
| Structure | -0.62 | -0.212 | [33.9] | -8408 | -2929 | [27154] |

Time = 1530

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [33.7] | 0.9684 | 0.9264 | [18382] | **0.0407** | **0.0196** |
| Orientation | -0.263 | [34.0] | 0.9904 | -9263 | [27645] | 0.9658 |
| Structure | -0.409 | -0.146 | [34.1] | -10202 | -939 | [28584] |

Time = 1600

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [33.0] | 0.953 | 0.9695 | [25468] | 0.999 | 0.8835 |
| Orientation | -0.3225 | [33.3] | 0.9982 | 158 | [25310] | 0.8633 |

| Structure | -0.2604 | 0.0621 | [33.3] | -1778 | -1936 | [27246] |

**Time = 1630**

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [32.0] | 0.3375 | 0.5065 | [24359] | 0.9948 | 0.9998 |
| Orientation | -1.535 | [33.6] | 0.9564 | -370 | [24729] | 0.9926 |
| Structure | -1.222 | 0.313 | [33.2] | 70 | 440 | [24289] |

**Time = 1700**

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [30.9] | **0.0584** | 0.2756 | [14955] | 0.1254 | 0.2735 |
| Orientation | -2.492 | [33.4] | 0.7441 | -7240 | [22195] | 0.916 |
| Structure | -1.684 | 0.808 | [32.6] | -5769 | 1471 | [20724] |

**Time = 1730**

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [29.7] | **0.0147** | 0.1537 | [13211] | 0.3112 | 0.0869 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Orientation | -3.08 | [32.8] | 0.622 | -5517 | [18728] | 0.8137 |
| Structure | -2.05 | 1.02 | [31.8] | -7814 | -2298 | [21025] |

Time = 1800

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [26.8] | **0.0041** | **0.0413** | [ 8362] | 0.2791 | 0.3302 |
| Orientation | -3.52 | [30.4] | 0.7307 | -5634 | [13996] | 0.9926 |
| Structure | -2.687 | 0.832 | [29.5] | -5212 | 422 | [13574] |

Time = 1830

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|
| Nest | [26.6] | **0.0445** | 0.2771 | [ 9327] | 0.2231 | 0.7323 |
| Orientation | -2.64 | [29.3] | 0.6705 | -5963 | [15290] | 0.6406 |
| Structure | -1.7 | 0.94 | [28.3] | -2691 | 3272 | [12018] |

Time = 1900

| | Nest | Orientation | Structure | Nest | Orientation | Structure |
|---|---|---|---|---|---|---|

| | | | | | | |
|---|---|---|---|---|---|---|
| Nest | [26.3] | 0.2829 | 0.5679 | [5656] | 0.5966 | 0.7029 |
| Orientation | -1.685 | [28.0] | 0.8704 | -3547 | [9203] | 0.9844 |
| Structure | -1.13 | 0.555 | [27.4] | -2928 | 619 | [8584] |

VITA

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Candidate for the Degree of

Doctor of Philosophy

Dissertation:   EXPLORING GRADIENTS OF HABITAT SUITABILITY, HABITAT QUALITY, AND MICROCLIMATE: IMPLICATIONS FOR GRAY VIREO NESTING ECOLOGY AND MANAGEMENT


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