



Harris, J. P., L. M. Smith, and S. T. McMurry. 2020. A multiscale analysis of Gray Vireo (*Vireo vicinior*) nest-site selection in central New Mexico. *Avian Conservation and Ecology* 15(1):12. <https://doi.org/10.5751/ACE-01540-150112>  
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Research Paper

## A multiscale analysis of Gray Vireo (*Vireo vicinior*) nest-site selection in central New Mexico

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**ABSTRACT.** There are many gaps in our understanding of Gray Vireo (*Vireo vicinior*) life history especially as it relates to nesting ecology. Our objective was to determine habitat features selected by Gray Vireos for nesting to improve management strategies for breeding populations. We searched for Gray Vireo nests on Kirtland Air Force Base in Albuquerque, New Mexico from 2016 to 2017. We estimated Gray Vireo nest-site selection at the tree level, the surrounding vegetation, and at two broader scales corresponding to selection within territories. Nest-site selection was estimated for 99 Gray Vireo nests. For tree-level selection, we compared characteristics of nesting trees with mean characteristics from groups of six randomly selected one-seed junipers (*Juniperus monosperma*) within a 25-m radius. We also compared overall vegetation characteristics at the 25-m scale for nesting plots and 66 randomly selected plots. Broad-scale cover proportions of nest sites and random points were estimated at 50- and 100-m radius spatial scales using a geographic information system. 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 Gray Vireos nested 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); however, juniper proportions at nest sites consistently ranged from 15 to 30% of available cover. Gray Vireos also tended to select areas with less pinyon pine than what was randomly available at the 100-m radius scale. Future management strategies should provide large patches of old-growth juniper to optimize Gray Vireo nesting habitat.

## Analyse multiéchelle de la sélection du site de nidification du Viréo gris (*Vireo vicinior*) dans le centre du Nouveau-Mexique

**RÉSUMÉ.** Notre compréhension du cycle biologique du Viréo gris (*Vireo vicinior*) est incomplète, particulièrement en ce qui a trait à l'écologie de nidification. Notre objectif était de déterminer les caractéristiques d'habitat recherchées par les Viréos gris durant la nidification afin d'améliorer les stratégies d'aménagement destinées aux populations nicheuses. Nous avons cherché des nids de viréos sur la base des forces aériennes de Kirtland à Albuquerque, au Nouveau-Mexique, en 2016 et 2017. Nous avons évalué la sélection des sites de nidification des viréos à l'échelle de l'arbre, de la végétation environnante et à deux autres échelles plus grandes à l'intérieur des territoires des oiseaux. Nous avons analysé la sélection du site de 99 nids de Viréos gris. En matière de sélection à l'échelle de l'arbre, nous avons comparé les caractéristiques des arbres abritant un nid avec les caractéristiques moyennes de groupes de six genévriers monospermes (*Juniperus monosperma*) tirés aléatoirement dans un rayon de 25 m. Nous avons aussi comparé les caractéristiques de la végétation à l'échelle du 25 m des parcelles de nidification et de 66 parcelles tirées aléatoirement. La proportion de couvert à grande échelle aux sites de nidification et aux sites aléatoires a été calculée dans des rayons de 50 et 100 m, à l'aide d'un système d'information géographique. Les Viréos gris ont choisi des arbres de nidification qui étaient plus grands et plus gros que les genévriers adjacents. Les caractéristiques de la végétation voisinant le nid montraient une tendance similaire : les viréos ont niché dans des lieux où les genévriers étaient plus grands, plus gros et avaient une densité foliaire supérieure que ce qui était aléatoirement disponible. Les analyses à grandes échelles ont révélé que les viréos ont niché dans des endroits aux proportions plus élevées de genévriers à basse altitude (< 1954 m) et aux proportions plus faibles de genévriers à des altitudes plus élevées (> 1954 m); toutefois, la proportion de genévriers aux sites de nidification a toujours oscillé entre 15 et 30 % du couvert disponible. Les viréos avaient aussi tendance à choisir des endroits avec moins de pins pignons que ce qui était disponible aléatoirement à l'échelle du rayon de 100 m. Pour optimiser l'habitat de nidification du Viréo gris, nous recommandons que les futures stratégies d'aménagement visent à fournir de grands îlots de vieux genévriers.

**Key Words:** *Gray Vireo*; *nest-site selection*; *pinyon-juniper*; *Vireo vicinior*

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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 have 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 multiscale 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). 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 chaparral without junipers (Hargrove and Unitt 2017). 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 available (Johnson et al. 2012, Wickersham and Wickersham 2016). 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 (Johnson et al. 2012).

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 2007). Pinyon-juniper woodlands are anticipated to decline because of 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, in this region Gray Vireos may select areas with more trees and larger junipers than what is randomly available (Johnson et al. 2012). Therefore, we hypothesized that nesting trees would be larger (height and width) than randomly available trees and that the surrounding vegetation would consist of greater densities of junipers and shrubs, and 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), we predicted foliage density would be positively associated with nesting trees and nesting habitat. Additionally, we were interested in broader scale cover proportions surrounding nest sites that might be informative to habitat features of breeding territories.

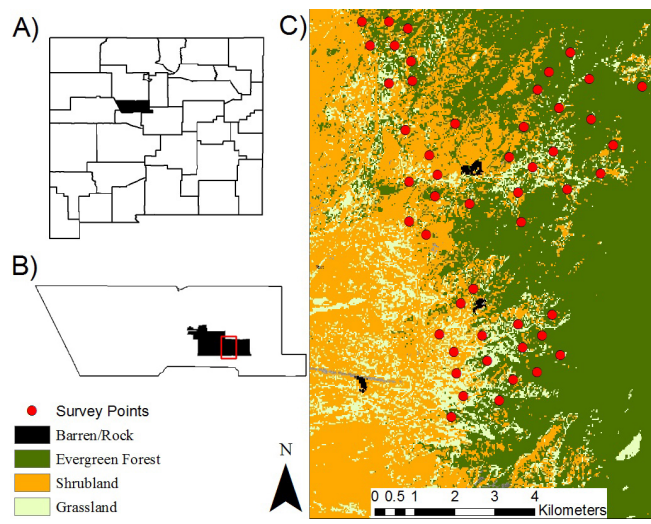
## METHODS

### Study site

Data were collected on Kirtland Air Force Base (KAFB), south of Albuquerque, NM (Fig. 1). Kirtland Air Force Base encompasses approximately 21,000 ha situated immediately adjacent to the Manzanita Mountains. Elevation on KAFB

ranges from 1600 to almost 2400 m (U.S. Air Force 2012). Previous vegetation surveys on base found four primary land cover types based on dominant vegetation: grasslands, pinyon-juniper woodlands, ponderosa pine woodlands, and wetlands/arroyos (U. S. Air Force 2012). All surveys were conducted in either pinyon-juniper woodlands or transitional regions between grasslands and pinyon-juniper woodlands because previous research suggested these areas to have the highest probability of Gray Vireo occurrence (Schlossberg 2006, Wickersham and Wickersham 2016). 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*), alder-leaf mountain mahogany (*Cercocarpus montanus*), scrub oak (*Quercus* spp.), one-seed juniper (*Juniperus monosperma*), and pinyon pine (U.S. Air Force 2012). Potential Gray Vireo nesting substrates on KAFB include one-seed juniper, mountain mahogany, and scrub oak.

**Fig. 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.



### Nest searching and monitoring

We conducted surveys for Gray Vireos at 50 random locations from 1 May to 15 June in 2016 and in 2017 (Fig. 1). Each random location was surveyed twice each year. Random points were located between 1823 and 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 (Johnson et al. 2013). At each point, we conducted 10-min call-back surveys, using a modified method used by Kubel and Yahner (2007), where a 1-min recording of a Gray Vireo song was played on an external speaker during the 5th-min. If a Gray Vireo was observed at that point we 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, we conducted 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.

### Nesting tree and local vegetation

Upon completion of a nest, i.e., depredated, abandoned, or fledged young, we conducted fine-scale vegetation surveys within a 25-m radius (196 ha) around each nesting tree. A 25-m radius was selected because of anecdotal behavioral observations, suggesting the relevance of this scale to territorial cues, i.e., alarm calling (Bates 1992). For each nest, we 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, we recorded 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, as a measure of canopy cover. For one-seed junipers, foliage width is often greater than the tree height. For each juniper within the plot, we also 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 we 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%). We 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, we 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 vegetation by comparing nest-site plots with random plots. We 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 cover proportions

We obtained 1x1 m resolution 2016 aerial imagery from KAFB. We 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 2300 m where Gray Vireos were present and thus were not included in statistical analyses. We 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 (Johnson et al. 2013). Thirty-nine out of 50 points were accurately classified (78%), which we deemed to be suitable for subsequent analyses (Myeong et al. 2001).

For each nest location and random point, we created two buffers: 50- and 100-m radius (0.79 ha and 3.14 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 broad-scale analyses, resulting in 58 random points used in broad-scale 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 (Wickersham and Wickersham 2016). However, multiscale 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, we 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

We developed generalized linear mixed-effect models (GLMM) for Gray Vireo nest-site selection as a function of tree characteristics (Table 1), surrounding vegetation characteristics (Table 2), and cover proportions at two broader 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 2020). 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. 2013).

We evaluated three groups of candidate models separately corresponding to our three levels of selection: tree-level, surrounding vegetation, and broad-scales. Models for tree-level selection incorporated combinations of juniper height, juniper width, and juniper foliage density, for a total of eight candidate

models. Models of the surrounding vegetation were based on a priori hypotheses related to juniper and shrub characteristics because those have been shown to be the most important cover types for Gray Vireos (Schlossberg 2006). We did not test shrub height because there was insufficient variance for analysis ( $= 1.3$  m,  $\sigma = 1.0$  m). This resulted in 11 candidate models for selection of the habitat surrounding nests. Because little work has been done at broad-spatial scales, we used a multistep, exploratory approach to develop a candidate set of models for broad-scale cover proportions. First, we determined the appropriate scale for each cover type by testing the performance of each scale for each cover type; 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, we determined the scale that best distinguished nests from random points for each cover type. Those subsequent scales were then used in a global model of all possible additive combinations of broad-scale variables. The global model was then dredged using the “MuMIn” package in RStudio (Bartoń 2019), to test all possible additive combinations of the variables (Doherty et al. 2010). All additive combinations with  $\Delta$ AICc less than 2 were included as 10 models for final analysis (Burnham and Anderson 2002). We also included four additional models with interactions post-hoc to account for varying selection of cover types 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 broad-scale selection (Table 2).

**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 | $\Delta$ AICc | $\omega_i$ | Deviance |
|----------------------------------|---|---------------|------------|----------|
| Height + Width <sup>†</sup>      | 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    |

<sup>†</sup>AICc value of 204.7.

## RESULTS

In 2016 and 2017, we 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 to 2047 m, with an average of  $1894 \pm 53.4$  m.

**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 | ω <sub>i</sub> | Deviance |
|---|---|-------|----------------|----------|
| Juniper Height + Width + Foliage Density <sup>†</sup> | 5 | 0     | 0.928          | 154.4    |
| Juniper Height + Foliage Density                      | 4 | 11.5  | 0.003          | 168      |
| Juniper Height * 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    |

<sup>†</sup>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).

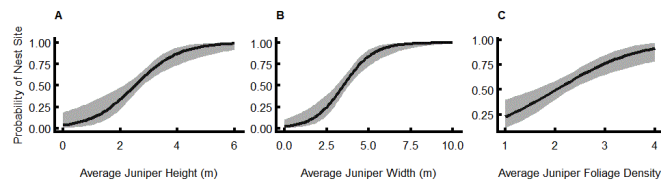
| Model  | K | ΔAICc | ω <sub>i</sub> | Deviance |
|--|---|-------|----------------|----------|
| Juniper50*Elevation <sup>†</sup>                         | 5 | 0     | 0.9920         | 174.8    |
| Juniper50+PinyonPine100+Elevation                        | 5 | 13.4  | 0.0012         | 188.2    |
| Juniper50+PinyonPine100                                  | 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    |

<sup>†</sup>AICc value of 184.8.

The top models for selection of the nesting tree and the surrounding vegetation included positive effects of juniper height and width (Tables 1 and 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, Fig. 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.

**Fig. 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.



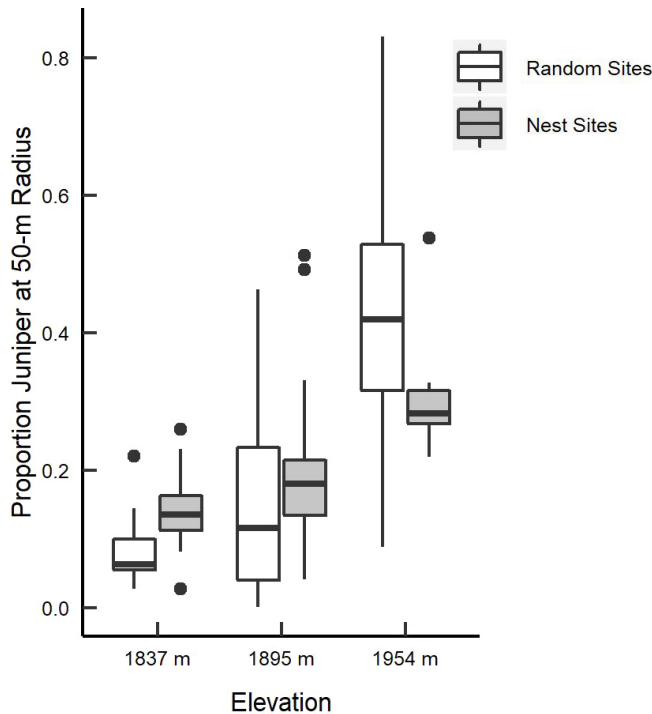
Our top model for broad-scale cover proportions at nest sites included juniper density at the 50-m scale, elevation, and their interaction (Table 3). The predicted probability of a nest occurring increased with increasing juniper density at a 50-m radius when the elevation was under 1950 m. Above 1950 m elevation, the predicted probability of a Gray Vireo nest occurring begins to decline as juniper density increases (Fig. 3). Overall juniper density at the 50-m radius scale ranged from approximately 15 to 30% of the total cover. The second most frequent cover type 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 vegetation characteristics within territories for nesting sites (Martin and Roper 1988, Bergin 1992). We 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. The vegetation surrounding Gray Vireo nest sites tended to have larger junipers with greater foliage density than what was randomly available (Fig. 2). Within this area, the nesting tree was often the largest juniper

**Fig. 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.



available. Larger trees may be selected because of 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 we lack 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. We 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, we found no difference in juniper or shrub densities at nest sites compared to random plots at this scale.

We predicted that broad-scale cover proportions at nest sites would consist of greater juniper and shrub cover than at random locations. We 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 to 30%, despite available juniper proportions of approximately 5 to 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. We 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. We 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 we 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 broad-scale 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 (U.S. Air Force 2012). 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.

Responses to this article can be read online at:  
<http://www.ace-eco.org/issues/responses.php/1540>

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### Acknowledgments:

We thank S. Young and J. Haughwout and for their help with data collection. We also thank D. H. Reynolds, A. R. Cuevas, M. B. Clark, and the Civil Engineering Division of Kirtland Air Force Base for their administrative and logistic support.

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