

**ASSOCIATIONS AMONG BREEDING BIRDS AND CHARACTERISTICS OF  
GAMBEL OAK IN PONDEROSA PINE FORESTS**

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## ABSTRACT

Gambel oak in ponderosa pine forests is associated with increased bird abundance and diversity. Little is known, however, about specific structural characteristics of gambel oak trees, clumps, and stands that may be of importance to bird species in ponderosa pine-gambel oak forests. I examined associations among breeding birds and structural characteristics of gambel oak at a local scale (i.e. within areas similar in size to individual bird territories) in pine-oak forests in northern Arizona and New Mexico. I also characterized gambel oak trees and clumps used for nesting by cavity-nesting birds. Avian species richness as well as the presence of some bird species was associated with particular growth forms of gambel oak. The density of pole-sized gambel oak (7-15cm dbh) was positively associated with the presence of Virginia's warblers, red-faced warblers, and black-headed grosbeaks. Large gambel oak trees ( $\geq 23$ cm dbh) were positively associated with bird species richness and with the presence of some bird species. In addition, large oak trees provided nesting sites for three secondary cavity-nesting bird species and two primary cavity-nesting species. Cavity-nesting birds tended to select nests within oak clumps covering larger areas and having higher numbers of large diameter oak trees than available clumps. Because large oak trees are relatively scarce and their numbers are thought to be declining, efforts should be made to retain existing large oak trees where they are present and to promote the growth of additional oak in this size class. Maintaining a mosaic of forest openings will encourage gambel oak regeneration.

## INTRODUCTION

Gambel oak (*Quercus gambelii*) frequently occurs in association with ponderosa pine (*Pinus ponderosa*) forests throughout the southwestern United States at elevations ranging from 2,000-2,800 m (Hanks et al. 1983). Gambel oak occurs in multiple growth forms, including shrub-like plants, small trees, and large trees up to 90 cm in diameter (Clary and Tiedemann 1992, Kruse 1992). Because gambel oak reproduces both by seed and vegetatively, it can occur as scattered individuals or in dense clumps.

The presence of gambel oak in ponderosa pine forests is associated with increased bird abundance and diversity (Marshall 1957, Szaro et al. 1990, Rosenstock 1998). Numerous studies have found that coniferous forests with a deciduous component are associated with higher bird species richness than coniferous stands lacking this component (Dickson and Segelquist 1979, Rosenstock 1998, Mills et al. 2000, Griffis-Kyle and Beier 2003, Jansson and Andren 2003,). The addition of a deciduous tree species to a coniferous stand increases structural complexity and can provide additional foraging and nesting substrates for many songbirds (Dickson et al. 1995, Martin 1988). Several foliage-nesting species can nest in gambel oak trees and clumps (Cunningham et al. 1980, Paine and Martin 1994, Rosenstock 1998, Leidolf et al. 2000, Chambers 2002) and ground-nesting birds such as Virginia's (Vermivora virginiae) (Swanson et al. 2000) and red-faced warblers (*Pheucticus melanocephalus*) (Rosenstock 1998) nest in the understory of gambel oak. Foliage and bark gleaning species also forage extensively in gambel oak trees (Szaro and Balda 1979) and several species are known to eat the acorns and buds that gambel oak produces (Reynolds et al. 1970, Leidolf et al. 2000). Gambel

oak may also be an important nesting substrate for cavity-nesting birds, particularly when pine snags are uncommon (Ganey and Vojta 2004, Cunningham et al. 1980, Chambers 2002). Because the number of pine snags in many ponderosa pine forests has declined (Cunningham et al. 1980, Horton and Mannan 1988), and snag densities frequently fall below levels recommended for maintaining cavity-nesting bird populations (Ganey 1999), identifying gambel oak that provides cavity-nesting substrate may be especially important.

Identifying the attributes of oak that are important to bird communities is necessary from a management perspective because past and current silvicultural practices have affected the abundance and nature of gambel oak in managed forests (Leidolf et al. 2000). Some forms of gambel oak, particularly large trees, are thought to be in decline (Chambers 2002, Clary and Tiedmann 1992, Kruse 1992). Gambel oak grows slowly making large oak trees difficult to replace. Clary and Tiedeman (1992) found that it took 30 years for gambel oak to transition from shrub-like oak into trees and 100 years for an oak tree to reach a height of 9 meters. In addition, grazing of oak by cattle and ungulates can be detrimental to gambel oak growth and regeneration, and potentially can prevent the establishment of new trees (Harper et al. 1985). Kruse (1992) suggested that "old growth" gambel oak may be in danger of being lost completely.

Because different growth forms of gambel oak occur together within single ponderosa pine stands and even within single oak clumps, I chose to study the association between birds and gambel oak on a local scale, i.e. within areas similar in size to individual bird territories (Sherry and Holmes 1985). Of interest was whether specific gambel oak attributes could describe bird assemblages at a local scale more effectively

than general forest structure with no inclusion of floristic composition. The objectives of my study were to: 1) examine whether local gambel oak characteristics were related to local bird species richness after accounting for general forest structure, 2) identify characteristics of gambel oak trees and clumps associated with the presence of individual bird species, and 3) describe the characteristics of gambel oak trees, clumps and stands used for nesting by cavity-nesting birds.

## **METHODS**

### **Study area**

My research was conducted on study sites that were part of a larger research project coordinated by the USFS Rocky Mountain Research Station (RMRS) designed to examine the effects of prescribed fire on bird communities in ponderosa pine forests of the western United States. Study sites were located in ponderosa pine forests slated for prescribed burns meeting the RMRS's study criteria. I collected data on three study sites that were located within the expanse of ponderosa pine forest that begins west of Flagstaff, Arizona and runs along the Mogollon rim into New Mexico. Gambel oak cover at sites ranged between 15 and 20 percent. In Arizona, one study site was located on the Coconino National Forest approximately 60 km southeast of Flagstaff and a second site was located on the Apache-Sitgreaves National Forest about 8 km north of the community of Pinetop-Lakeside. A third site was located in New Mexico near the Arizona border on the Gila National Forest about 30 km southwest of Reserve, NM.

Two to three study units were established at each of the three study sites. The number and size of study units at a site was based upon proposed prescribed burn

boundaries established by Forest Service fire personnel and the extent of appropriate forest type. Total area contained within study units at each of the three locations ranged between 400 ha and 800 ha. Elevations on the units ranged from 2,070 m to 2,500 m. Ponderosa pine and gambel oak were the dominant tree species on all study units. Other tree species encountered include alligator bark juniper (*Juniperus deppeana*) and pinyon pine (*Pinus edulis*) at lower elevations and Douglas-fir (*Pseudotsuga menziesii*) at higher elevations. Perennial bunchgrass species including Arizona fescue (*Festuca arizonica*) and blue gramma (*Bouteloua gracilis*) occurred in scattered clumps throughout the understory. All study sites had a history of timber harvest and livestock grazing and were part of active grazing allotments.

### **Sampling Design**

I used a geographic information system (GIS; Arcview® 3.2a and ArcGIS 8.1; ESRI, Redlands, California, USA) to select and locate permanent avian and vegetation sampling points on all units. I placed a 125 m x 125 m grid over each unit and located sampling points at grid intersections ensuring each point was  $\geq 250$  m from any other point. Points were only located in ponderosa pine-gambel oak forest type. A total of 152 points were established: 47 points on the site in the Apache-Sitgreaves National Forest, 70 points on the site in the Coconino National Forest, and 35 on the site in the Gila National Forest.

I also established belt transects running between sampling points. Belt transects were used to conduct systematic nest searches on the study units. All belt centers were separated by 250 m and all permanent sampling points were on belt transect centers. Belt transects were arranged so that each unit was completely covered. I located the sampling

points on the ground using GPS coordinates obtained from the GIS. I permanently marked each station and belt transect with rebar and aluminum caps.

### **Avian sampling**

I used standard point count methodology (Ralph et al. 1993) to count birds in variable-radius circular plots centered at each sampling point. Counts were started just after sunrise and were completed no later than 4 hours after sunrise. Upon arriving at a point count station, I waited two to four minutes to allow birds to resume normal activities. All birds seen or heard within 5-minutes were recorded. Bird species, number of individuals, sex, mode of detection, distance and bearing to the bird were recorded for each detection. I also noted temperature and weather conditions before each count. Counts were not conducted during windy or rainy weather. Each point was visited four times between May 20<sup>th</sup> and July 1<sup>st</sup>.

From early May through July, I searched all study units for active cavity-nests. Nest searches were conducted by walking all belt transects on each unit. An area of 125 m on each side of the belt transect was surveyed so that each unit was searched uniformly. Once an active nest was located, a unique nest ID was assigned and the bird species, UTM coordinates, and a brief description of the nest recorded. Point counts and nest searches were conducted in 2002, 2003 and 2004 on the Gila National Forest study site and in 2003 and 2004 on the Apache-Sitgreaves and Coconino National Forest sites. In 2004 one study unit at each of the three study sites underwent prescribed burning. I did not include data collected on these three units in 2004 in my analyses.

## Vegetation sampling

I characterized forest composition and structure on the study units by measuring vegetation at each of the 152 point-count stations and at nest sites on each unit. At each point or nest, vegetation was measured along four transect lines all starting at the point or nest and extending 50 m in the cardinal directions. I recorded tree species, height, and diameter at breast height (dbh) for all live trees  $\geq 23$  cm dbh within 5 m on either side of the four transect lines. I recorded species, height, dbh, and decay class (see Bull et al. 1997) for all snags  $\geq 23$  cm dbh within 10 m of the transect lines. All trees and snags  $< 23$  cm dbh within 2 m of the transect lines were grouped into size classes (0 to  $< 2.5$  cm, 2.5 to  $< 8$  cm, 8 to  $< 15$  cm, and 15 to  $< 23$  cm) and tallied.

The size classes used for smaller trees were based on protocols for the Birds and Burns study. For trees  $\geq 23$  cm dbh, I grouped trees into two categories: 23-45.5 cm dbh and  $> 45.5$  cm dbh. These categories correspond loosely to VSS (vegetative structural stage) classes of ponderosa pine described by Moir and Dieterich (1988). Trees 23-45.5 cm dbh fall primarily within the VSS4 structural class and are considered characteristic of mid-aged stands. Trees  $> 45.5$  cm dbh correspond with the VSS5 structural stage. Trees in this size class are representative of mature ponderosa pine stands. I did not include the VSS6 structural stage (trees  $> 61$  cm dbh) associated with old growth pine because there were very few trees in this size class on my study units.

I characterized forest understory in three 5-m radius plots at each point or nest: one plot centered at the point or nest, one at the 50 m mark on the north transect, and one at the 50 m mark on the south transect. At each of these three plots, I used a point-intercept method to estimate percent grass, forb, and shrub cover. Readings were taken at

every 0.5 m interval (excluding the center point) along lines running out 5m in the cardinal directions.

Within a 30-m radius plot centered at each point count station and nest site, I characterized gambel oak abundance and structure in more detail. I defined an oak clump as  $\geq 2$  gambel oak trees having interlocking or adjacent crowns separated from neighboring crowns by  $\geq 1$  m. Because of the tendency of gambel oak to produce large numbers of clonal seedlings, I used this definition separately for the under- and over-story. Therefore, the canopy of one clump could overlap with the seedlings (oak  $< 1.4$  m tall) in the understory of another clump. The area of each oak clump was estimated by measuring the length through the longest section of the clump. Width was measured at the widest point of the clump at an angle perpendicular to length. I used formulas for the area and perimeter of an ellipse to calculate the area and perimeter of each oak clump. The structure of each oak clump was characterized by recording the number of trees per clump in each of three diameter size classes (0 cm to  $\leq 7$  cm, 7 cm to  $\leq 15$  cm, and 15 cm to  $\leq 23$  cm respectively). All gambel oak trees  $\geq 23$  cm in diameter, were measured at breast height, the number of cavities excavated by primary cavity-nesters counted, and a condition rating assigned (Brischler 2002). For small shrub-like oak seedlings that did not reach breast height, an estimate of the percent of the clump area covered by oak in this size class was recorded.

### **Data Set**

I defined avian species richness at a point as the total number of different bird species detected over all visits during the 2003 season. I used data from 2003 because this was the only year where data was collected on all study units at all sites. Detections

of adult birds <100 meters from the point were included. When I compared bird detections within 50 m to detections within 100 m, species richness counts were highly correlated ( $r = 0.74$ ) and associations with vegetation variables were consistent. I determined, therefore, that truncating detections at 50m was unnecessary. All flyover detections were excluded. Bird species with territories greater than 3 ha, according to the literature, were not included in richness counts in order to encourage independence between points. The species excluded were primarily raptors, corvids, and woodpeckers (Table 1).

I also selected 10 bird species for which I examined their **presence/absence** at points in relation to vegetation characteristics. I selected species considered to be associated with gambel oak (Chambers 2002, Leidolf 2000, Rosenstock 1998, Poole et al. 1995) and that were detected at >10 sampling points. All variables describing general forest structure used in data analyses were based upon vegetation data collected along the four 50-m transects (Table 2). All oak variables were derived from data collected in the 30-m radius plots.

### **Data Analysis**

I used multiple regression to identify vegetation factors associated with trends in bird species richness at point-count stations (Zar 1996). Before building models, I screened explanatory variables to ensure no variables were correlated ( $r \geq 0.70$ ). I also examined data for influential outliers and plotted residuals against richness counts to ensure that no data transformations were necessary (Gutzwiller and Anderson 1986). I used multiple logistic regression to identify vegetation factors associated with the

presence of selected bird species at points (Keating and Cherry 2004). I employed two different approaches to select regression models that best described the data.

Within the information-theoretic framework, I developed an *a priori* set of models and used Aikake's Information Criterion (AIC) to rank models (Burnham and Anderson 2002). I developed 22 candidate models containing different combinations of 14 vegetation variables measured at each point count station (Table 3). All models included a factor to account for variation between study sites. The models can be divided into subsets as follows: global models, general forest structure models containing no floristic information, models including both structural and floristic variables, floristic-only models, and models combining floristic and spatial variables. AICs were calculated for each model and adjusted for small sample sizes (AIC<sub>c</sub>). Models were ranked according to AIC<sub>c</sub> values and Aikake weights ( $w_i$ ) were calculated for each model. Models with AIC<sub>c</sub> values  $< 2.5$  were considered competitive for being the best approximating model (Burnham and Anderson 2002).

Within a hypothesis testing framework, I used either extra-sum-of-squares F-tests to compare nested multiple regression models or drop-in-deviance tests to compare nested logistic regression models (Ramsey and Schafer 2002). I used this hierarchical approach to test whether, after accounting for variation in bird response explained by general forest structure, adding oak variables to the model would provide significant additional explanatory power. This provided an alternative way to examine the importance of specific oak characteristics and allowed me to compare results obtained within different frameworks.

I began both the sum-of-squares F-tests and drop-in-deviance tests by creating a model containing only general forest structure variables. This model was then compared to a reduced model containing only the structural variables that showed a significant relationship to the response variable. Because this analysis **was** exploratory in nature, a variable was considered significant at the 0.10 level. If the P-value for **an** F or  $\chi^2$  statistic obtained **from** the sum-of-squares F or drop-in-deviance test was  $\leq 0.05$ , the reduced model with fewer variables was assumed inadequate and the **full** model retained. Oak variables were then added to the preferred forest structure model and a **drop-in-deviance** or sum-of-squares F-test performed to evaluate whether the model with oak variables accounted for significantly more variation. If appropriate, additional tests were performed to further refine which oak variables were included. Three additional factors were also examined to see if they added explanatory power to the model: 1) a spatial variable (the ratio of the **area/perimeter** of oak clumps); 2) the abundance of large pine trees; 3) an interaction term between abundance of large oak and large pine (see example in Table 4).

I used general descriptive statistics to describe nest trees where active cavity nests were located. I used logistic regression to compare oak clumps where nests were located to oak clumps available at study sites. I considered the oak clumps I characterized at point count stations to represent those available. I compared the number of oak trees in each size class comprising nest tree clumps to the numbers of trees per size class in available clumps. I also compared the percent cover of oak seedlings, the size of oak clumps (represented by the area which the oak clump covered), and the

structural complexity of oak clumps (described by the number of different size classes of oak contained within the clump).

## **RESULTS**

I first present results obtained from models selected as best predicting bird richness or presence within an information-theoretic framework. I present results from models derived from hierarchical comparisons within a hypothesis-testing framework in a separate section. In both sections, unless otherwise indicated, I discuss only the trends in bird response to habitat variables that reach a 0.05 level of significance within the selected models.

I detected a total of 43 bird species over all study units in 2003. Ten of these species were excluded in species richness counts due to large home-range size (Table 1). The following results are based upon the 33 remaining species. Species richness at sampling points ranged from 2 to 14 with a mean of 7.5 (95% C.I. 7.1 to 7.9) species detected per point. Average species richness per point was highest on the Gila National Forest site ( $\bar{x} = 9.2$ , 95% C.I. 8.3 to 10) and lowest on the Apache-Sitgreaves site ( $\bar{x} = 5.6$ , 95% C.I. 5.1 to 6.1).

### **Information-theory**

#### **Avian Species Richness**

The three models considered competitive (models with  $\Delta AIC_c < 2.5$ ) for best describing avian species richness suggested that the abundance of large oak and pine trees influenced species richness at points (Table 5). The two top ranking models also found associations between bird species richness and general forest structure.

Species richness associations with general forest structure included a negative association with the abundance of trees (of all species) 8-15 cm in diameter and a positive association with the number of trees 23-45.5 cm dbh. An increase of about 20 trees 8-15 cm dbh was associated with a one-unit decrease in species richness whereas an increase of 6 trees 23-45.5 cm dbh was associated with a one-unit increase in species richness (Table 6).

All competitive models suggested that interaction terms between the abundance of large oak ( $\geq 23$  cm dbh) and the two categories of large pine (pine 23-45.5 cm dbh and pine  $>45.5$  cm dbh) influenced bird species richness. There was also evidence that bird species richness was positively associated with ponderosa pine trees  $>45.5$  cm dbh ( $F=6.8$ ,  $df=1,143$ ,  $p\text{-value}=0.01$ ). An increase of approximately 4 pine trees in this size-class was associated with a one-unit increase in species richness (0.282, SE 0.108,  $p\text{-value}=0.0101$ ). To investigate the influence of the interaction between oak and pine, I compared the mean number of bird species detected at 3 levels of oak abundance over different densities of pine 23-45.5 cm dbh and at points with and without mature pine  $>45.5$  cm (Fig. 1). In both cases, when abundances of ponderosa pine trees were lower, a positive association existed between bird species richness and large oak. This association appeared to be weak or absent when the density of pine 23-45.5 cm dbh was high ( $>60$  trees/acre) and when mature pines were present. When pine trees in these two size classes were common, species richness averaged around 7 or 8 species per point over all levels of large oak abundance. When mature pine was absent or rare, species richness ranged from an average of 6.9 (95% C.I. from 6.1 to 7.6) at points where there were few or no large oak to an average of 9.4 (95% C.I. from 7.1 to 11.8) where they were

abundant. When the abundance of pine trees 23-45.5 cm dbh was low, average species richness ranged from 7 (95% C.I. from 6.3-7.8) at points with low large oak abundance to 10 (95% C.I. from 7-13) at points with high oak abundance.

### **Species presence/absence**

Black-headed grosbeaks were detected at 34 of 152 points and red-face warblers at 15 of 152 points. Each of the four best-fitting models (models with a AAIC, < 2.5) for the presence of black-headed grosbeaks contained "small oak" variables and all but one of six best-fitting models for the presence of red-faced warblers contained these variables (Table 7, models 1a-4a and 1e-6e). The model with the lowest AIC, for both bird species included only the variables "small oak" (Table 7, models 1a and 1e). Although none of the competing candidate models for these species can be discounted, the presence of "small oak" variables in nearly all of the top-ranking models suggested that the abundance of small oak influenced the presence of red-faced warblers and black-headed grosbeaks at points. An increase in abundance of pole-sized oak trees 7-15cm in diameter was associated with increased odds of detecting  $\geq 1$  black-headed grosbeak or red-faced warbler at a point (Table 8). The odds of detecting a black-headed grosbeak increased by approximately 2% and the odds of detecting a red-faced warbler increased by about 3% with the addition of each oak tree 7-15cm in diameter. Red-faced warblers were not detected at any point lacking oak trees in this size class.

Virginia's warblers were present at 22 of 152 point-count stations. Again, all top-ranking models (AAIC, < 2.5) included "small oak" variables (Table 6, models 1f-4f). The odds of  $\geq 1$  Virginia's warbler being present at a point increased by approximately 2% with each additional oak 7-15 and by 8% with each additional oak 15-23cm in

diameter (Table 8). Virginia's warblers were never detected at points lacking gambel oak trees 7-15cm in diameter ( $n = 14$ ), but were detected 50% of the time ( $n = 9$  of 18) at points with  $\geq 75$  oak trees in this size class. All top-ranking models produced comparable estimates of the magnitude of the positive association between the presence of Virginia's warbler and the abundance of oak in these two size classes.

Yellow-rumped warblers were detected at 80 of the 152 points sampled. All but one competitive model contained the variable large oak (Table 7, models 1h–4h and 6h). The odds of at least one yellow-rumped warbler being present at a point increased with the abundance of oak trees  $\geq 23$  cm in diameter. The odds of a yellow-rumped warbler occurring at a point increased by approximately 11% with an increase of one large oak tree (Table 8).

Grace's warblers were detected at 80 of 152 points. There were 9 plausible models for the presence of Grace's warblers (Table 7, models 1b-9b). The two top-ranking models contained only floristic variables and suggested that the abundance of large oak and pine influenced Grace's warbler presence (Table 7, models 1b-2b). The top model, which contained interaction terms between large oak and large pine, suggested that the influence of large oak on the probability of  $\geq 1$  Grace's warbler being at a point depended on the density of pine trees 23-45.5 cm in diameter. At points where pine trees 23-45.5cm dbh were abundant, Grace's warblers were detected at 63% of points with low large oak abundance versus at 43% of points where there were  $\geq 10$  large oak trees (Fig. 2). This suggests that the abundance of large oak was negatively associated with the presence of Grace's warblers when pine trees in this size class were abundant. This pattern was absent at lower levels of pine density. Four of the remaining seven plausible

models included only general forest structure (Table 7, models 3b-6b). Within these models, there was an indication that the probability of  $\geq 1$  Grace's warbler being detected at a point increased by about 20% with each percentage increase in shrub cover (0.19, SE = 0.09,  $\chi^2 = 4.17$ ,  $P = 0.0411$ ) and decreased by about 20 % with each additional pine snag (-0.23, SE = 0.12,  $\chi^2 = 3.86$ ,  $P = 0.0496$ ).

Plumbeous vireos were detected at 57 of the 152 points. The only candidate model considered plausible for predicting the presence of plumbeous vireos suggested that general tree abundance plus an interaction term between large oak and large pine abundance best described plumbeous vireo presence at points (Table 7, model 1d). Only the interaction terms showed a significant relationship to vireo presence (Table 8). The abundance of large gambel oak was positively associated with plumbeous vireo presence when the density of pine 23-45.5cm dbh was low (Fig. 3a). Plumbeous vireos were detected at 63% of points with low abundance of pines 23-45.5cm dbh in combination with high large oak abundance, but at only 29% of points having the same density of pine and low large oak abundance. The nature of the interaction between large oak and pine in mature stands was less clear (Figure 3b).

Western bluebirds were detected at 67 of the 152 points sampled. The one plausible model of western bluebird presence included only variables describing general forest structure. The odds of a western bluebird being at a point increased by about 16% with each meter increase in the height of the tallest tree and decreased by approximately 3% with the addition of each tree 2.5-8 cm in diameter (Table 8). No bluebirds were detected at points where there were >65 small trees. The odds of detecting a western

bluebird also decreased with increasing numbers of ponderosa pine snags  $\geq 23$  cm dbh (Table 8).

Hermit thrushes were detected at 21 of 152 points. Four of the five competitive candidate models contained only floristic variables (Table 7, models 1c-3c and 5c) and one contained only variables describing general forest structure (Table 7, model 4c). Within all of these models, no specific variables showed a significant (a 0.05) association with hermit thrush presence. For the remaining species I examined (mountain chickadees and cordilleran flycatchers), models did not adequately describe the data.

## **Hypothesis testing**

### **Avian Species Richness**

The model selected as best describing bird species richness at points through sum-of-squares F-test comparisons suggested that species richness was associated with both general forest structure and the floristic composition of vegetation at points (Table 4). After accounting for variation explained general forest structure, the addition of oak specific variables to the model did not provide enough additional explanatory power to justify their inclusion. The addition of large pine abundance (number of pine trees 23-45.5cm dbh and  $> 45.5$ cm dbh) as well as an interaction between these size classes of pine and large gambel oak ( $\geq 23$  cm dbh), however, were found to provide significant additional explanatory power (Table 4).

Species richness was positively associated with general forest structure described by the percent shrub cover and negatively associated with the abundance of all trees 8-15 cm dbh. The abundance of ponderosa pine trees  $>45.5$  cm dbh was positively associated with species richness. An increase of approximately 4 pine trees in this size-class was

associated with a one-unit increase in species richness and an increase of about 20 trees 8-15cm in diameter was associated with a one-unit decrease in species richness. Each additional 5% in shrub cover was associated with a one-unit increase in species richness (Table 6). The number of pine trees >45.5 cm dbh at a point ranged from 0 to 11 and shrub cover at points ranged from 0 to 14%. When the abundance of trees 23-45.5 cm dbh was low and when ponderosa pine trees >45.5 cm dbh were absent or scarce, a positive association existed between bird species richness and large oak (Fig. 1). This association appeared to be weak or absent when the density of pines in these two size classes were higher. When pine trees in these two classes were common, species richness averaged around 7 or 8 species per point over all levels of large oak abundance. When mature pine was absent or rare, species richness increased from an average of 6.9 (95% C.I. from 6.1-7.6) at points with few or no large oak to an average of 9.4 (95% C.I. from 7.1-11.8) where large oak trees were abundant. When the abundance of pine trees 23-45.5 cm dbh was low, average species richness ranged from 7 (95% C.I. from 6.3-7.8) at points with low large oak abundance to 10 (95% C.I. from 7-13) at points with high oak abundance.

### **Species presence/absence**

No forest structure variables in the initial general forest structure model were found to be significantly associated with the presence of either black-headed grosbeaks or red-faced warblers. For both of these species, the model selected as best through drop-in-deviance comparisons suggested that only the abundance of pole-sized gambel oak (7-15 cm dbh) significantly influenced the probability of these species being present at a point (Table 9). The odds of detecting  $\geq 1$  red-faced warbler or black-headed grosbeak

increased with abundance of pole-sized oak (Table 8). The odds of detecting a black-headed grosbeak increased by approximately 2% and the odds of detecting a red-faced warbler increased by about 3% with the addition of each oak tree 7-15cm in diameter. Red-faced warblers were not detected at any point lacking oak trees in this size class.

The abundance of pine snags was associated with the presence of Virginia's warblers. The odds of at least one Virginia's warbler being detected at a point increased by 25% (95% C.I. 1 to 55%) with each additional snag (Table 8). After accounting for variation in bird response explained by pine snag abundance, adding all oak variables explained significantly more variation ( $\chi^2 = 14.78$ , 4df,  $P = 0.005$ ) and the model containing both pine snag abundance and oak variables was selected. Although no oak variables within this model reached an 0.05 level of significance, all were positively associated with the presence of Virginia's warblers.

The abundance of gambel oak trees  $\geq 23$  cm in diameter was positively associated with the presence of yellow-rumped warblers after accounting for general forest structure described by height of the tallest tree and the abundance of trees 23-45.5cm dbh ( $\chi^2 = 4.5$ , 1df,  $P = 0.0339$ ) (Table 9). An increase in one large oak tree was associated with an 11% increase in the odds of at least one yellow-rumped warbler being present at a point. The odds of a yellow-rumped warbler being at a point decreased by about 4% with each additional tree 23-45.5 cm in diameter (Table 8).

Grace's warblers were associated with general forest structure characteristics (Table 9). Oak and oak spatial variables did not add significant explanatory power ( $\chi^2 = 1.85$ , 4df,  $P = 0.7631$  and  $\chi^2 = 0.01$ , 1df,  $P = 0.942$ ) to the model. The odds of detecting at least one Grace's warbler at a point increased by approximately 6% with each

percentage increase in shrub cover. The odds decreased by about 2% with each additional tree 2.5-8 cm in diameter and by 21% with each additional large pine snag at a point (Table 8).

General forest structure described by the abundance of trees 2.5-8 cm and 8-15cm in diameter was related to the presence of plumbeous vireos. Oak variables did not add enough additional explanatory power to justify their inclusion in the model ( $\chi^2 = 0.864$ , 4df,  $P = 0.9297$ ). However, interaction terms between large oak and pine 23-45.5 cm dbh and pine >45.5 cm dbh did provide additional explanatory power ( $\chi^2 = 15.4$ , 5df,  $P = 0.008$ ) (Table 9). The odds of a plumbeous vireo being present at a point increased with the abundance of trees 2.5-8 cm in diameter and decreased with increasing abundance of trees 8-15cm in diameter (Table 8). Large gambel oak abundance was positively associated with plumbeous vireo presence when the density of pine 23-45.5 cm dbh was low (Fig. 3a). Plumbeous vireos were detected at 63% of points with low abundance of pine in this size class in combination with high large oak abundance but only at 29% of points where the abundance of oak was low. The nature of the interaction between large oak and mature pine was less clear (Figure 3b).

The presence of western bluebirds was associated with general forest structure described by the height of the tallest tree and abundance of pine snags at a point. After accounting for the variation in the presence of bluebirds described by these two factors, the abundance of pole-sized gambel oak added significant explanatory power ( $\chi^2 = 4.33$ , 1df,  $P = 0.0361$ ) to the model and suggested that each additional pole-sized oak was associated with a 2% decrease in the odds of bluebird presence (Table 9). The odds of a western bluebird being at a point increased by about 16% with each meter increase in the

height of the tallest tree and decreased by approximately 26% with each additional pine snag (Table 8).

The presence of hermit thrushes was associated exclusively with general forest structure (Table 9). Adding oak factors, large pine, and an interaction term between large oak and pine did not describe enough additional variation in hermit thrush presence to warrant inclusion in the model ( $\chi^2 = 1.89$ , 4df,  $P = 0.755$ ;  $\chi^2 = 4.03$ , 2df,  $P = 0.133$ ; and  $\chi^2 = 6.19$ , 3df,  $P = 0.106$  respectively). The probability of detecting at least one hermit thrush at a point increased by approximately 19% with each additional tree 15-23cm in diameter and by 6% with each percentage increase in grass cover (Table 8).

For the remaining species I examined (mountain chickadees and cordilleran flycatchers), no general forest structure or floristic variables were found to influence the presence of these species at points.

### **Cavity nests**

I found active nests of seven cavity-nesting bird species: hairy woodpecker, mountain chickadee, northern flicker, pygmy nuthatch, violet-green-swallow, western bluebird, and white-breasted nuthatch. Pygmy nuthatches and violet-green swallows nested almost exclusively in ponderosa pine snags. The following results are based upon the remaining 5 species that frequently used gambel oak for nesting.

I found a total of 140 active cavity nests, 92 of which were in gambel oak. Nests used in multiple years by the same bird species were considered a single nest. I found more nests of secondary-cavity nesting birds in gambel oak trees than in ponderosa pine snags and the nests of primary-cavity excavators about equally in gambel oak and pine snags. White-breasted nuthatch nests were found exclusively in gambel oak trees.

The average diameter of gambel oak trees used for nesting among all species was 40.4 cm (Table 10). However, mountain chickadees selected oak trees smaller in diameter than this average and northern flickers selected larger diameter trees for nesting than average (Table 10, Fig. 5). All except 9 of the cavity nests found in gambel oak trees were found in live trees.

All oak clumps that contained an active nest had at least one large oak tree  $\geq 23$  cm dbh. When oak clumps containing a nest tree were compared to available oak clumps with at least one large oak tree, oak clumps selected for nesting by all species except white-breasted nuthatches had more large trees (Table 11). For all species except white-breasted nuthatches and northern flickers, the probability of an oak clump being used as a nest site increased with increasing area of the oak clump.

Northern flickers selected oak clumps with low structural complexity for nesting (Table 11) with 8 of 13 nests in oak clumps made up of one or two size classes of oak and no nests located in clumps made up of all four size classes of oak. Both northern flickers and western bluebirds selected oak clumps with low oak stem density per clump compared to those available, whereas white breasted nuthatches selected oak clumps with high stem densities (Table 11). Mountain chickadees were more likely to nest in clumps having high structural complexity (Fig. 6), high numbers of pole-sized oak, and a high percent seedling cover (Table 11). Western bluebirds selected clumps with a lower percentage of seedling cover compared to available oak clumps. Hairy woodpeckers were more likely to nest in oak clumps that had more small oak 0-7cm dbh than available clumps (Table 11).

## DISCUSSION

### Avian Species Richness

I found evidence that both general forest structure and floristic composition were associated with trends in avian species richness at a local scale in the pine-oak forests I examined. Trends between species richness and both floristic and non-floristic forest structure were consistent with previous research that suggested a majority of bird species in southwestern ponderosa pine forests prefer mature forest stands (Moir et al. 1997, Szaro and Balda 1982, Rosenstock 1996).

Mature ponderosa pine forests are characterized by loosely spaced, large pine trees (Covington and Moore 1994). Mature pine stands tend to have a multi-storied canopy, more understory vegetation, and higher numbers of large diameter snags than younger forest stands (Moir and Dieterich 1988). Many generalist bird species are found in higher abundances in mature stands and some species, such as brown creepers and western tanager, are strongly associated with mature pine stands (Mills et al. 2000). Many studies of bird associations with forest successional stages have also found that dense stands of young trees are associated with low bird diversity (Dickson and Segelquist 1979, Szaro and Balda 1982, Mill et al. 2000, Jasson and Andren 2003). The negative trend I saw between bird species richness and the density of trees 8-15 cm dbh suggested this trend also existed in the pine-oak forests I studied.

Floristic composition also appeared to be associated with avian species richness. Species richness increased not only with the number of ponderosa pine trees >45.5 cm dbh but also with the abundance of large oak trees in stands where mature pine were absent or scarce and in stands where the density of ponderosa pine 23-45.5cm dbh was <

60 trees/acre. This interaction between oak and pine could indicate either that some bird species selected areas with specific floristic combinations of oak and pine or that some bird species tended to selected territories with more abundant large trees regardless of species, thus richness was positively associated with oak only when there were not enough large pine present.

Although my analyses did not address this question directly, when I compared bird species richness at points with abundant large oak in combination with a low number of pine 23-45.5 cm dbh to bird species richness at points with higher numbers of pine in combination with low large oak abundance, there was some evidence ( $t = 1.938$ , 42df,  $p$ -value = 0.059) that points with the latter combination had a lower average species richness. This suggests that even when total numbers of trees were similar, more birds used stands with a higher proportion of oak and may therefore have been selecting for a specific oak/pine composition. When I conducted a similar comparison of large oak effects in mature pine stands, no significant difference in average bird species richness was found ( $t = 1.2$ , 34df,  $p = 0.239$ ).

Deciduous gambel oak canopy in pine stands may allow a larger number of bird species to co-exist by providing increased foraging and nesting substrates (Rosenstock 1998). It could be that mature pine stands already provide structural complexity and thus oak plays a more important role when mature pine trees are scarce or absent and large oak is the main source of structural complexity.

### **Species presence/absence**

Two size-classes of gambel oak, large oak (oak  $\geq 23$ cm dbh) and pole-sized oak (7-15cm dbh), were associated with the presence of a number of bird species at a local

scale. Pole-sized gambel oak appeared to be important to black-headed grosbeaks, red-faced warblers, and Virginia's warblers. These species were detected most often in areas with high densities of oak in this size class. This is consistent with the findings of Rosenstock (1996) who found that red-faced warblers were most abundant in forest stands where 50-60% of oak basal area was made up of trees <20.3 cm in diameter at root crown and with Ortega and Ortega (2003) who found that in gambel oak stands, black-headed grosbeak nests were found almost exclusively in small gambel oak trees (around 3 m tall), except in riparian areas where nests were found in willows and cottonwoods.

Rosenstock (1998) reported that red-faced warblers and Virginia's warblers were absent in ponderosa pine stands that lacked a gambel oak component. My results suggested that not only the presence of gambel oak, but the presence of pole-sized gambel oak is associated with the occurrence of Virginia's warblers and red-faced warblers in ponderosa pine-gambel oak stands. Pole-sized oak in my study sites typically occurred in dense clumps with smaller shrub-like oak in the understory. Dense leaf litter associated with oak clumps likely helped conceal the nests of these two ground-nesting warblers (Lesh 1999, Rosenstock 1998). Dense clumps could also provide cover as well as foraging opportunities near nests (Leidolf et al. 2000). Swanson et al (2000) found that Virginia's warblers in South Dakota were associated with dense shrub cover, often gambel oak, and mid-sized trees that were heavily used by singing males as perches. Neither red-faced or Virginia's warblers are exclusive to ponderosa pine-gambel oak forests, however, and both are found in other types of oak woodlands (Block et al. 1992).

Although drop-in-deviance comparisons suggested that the presence of Virginia's warblers was strongly associated with ponderosa pine snags, this association does not

seem biologically meaningful and could be due to the tendency of gambel oak to colonize areas where pine trees have died (Moir et al. 1997). Including snags in an earlier model likely masked the magnitude of the association between Virginia's warblers and oak. AIC, ranking supports this supposition since all competitive models contained only oak variables.

Large oak trees were positively associated with the presence of yellow-rumped warblers and under certain conditions with the presence of plumbeous vireos. The model selected for yellow-rumped warblers through drop-in-deviance testing suggested that in addition to being positively associated with the abundance of large oak, the presence of yellow-rumped warblers was negatively associated with the abundance of all trees 23–45.5cm in diameter. This suggests that yellow rumped-warblers were more likely to use stands with a specific combination of oak and pine.

In a similar trend, the presence of plumbeous vireos was positively associated with the abundance of large oak at points where the density of ponderosa pine 23-45.5 cm dbh was <60 trees/acre. I detected plumbeous vireos at over 60% of points having low densities of pine 23-45.5 cm dbh in combination with high oak abundance, but at less than 30% of points having low oak abundance in combination with high (>60trees/acre) pine abundance (Fig. 2). This suggests that when there were similar numbers of trees 23-45.5 cm, vireos used areas where a higher percentage of these trees were gambel oak.

My results are consistent with those of those of Szaro and Balda (1979) who found that yellow-rumped warblers used gambel oak foliage for foraging in greater proportion than available and Frazreb (1978) who found that yellow-rumped warblers frequently foraged in deciduous aspen foliage in mixed coniferous forests. Both Balda (1969) and

Lesh (1999) found that plumbeous vireos in Arizona favored open coniferous stands with a deciduous component and Lesh noted that plumbeous vireos frequently foraged in gambel oak.

The presence of large oak is not a requirement for yellow-rumped warblers and plumbeous vireos, however. I detected yellow-rumped warblers at 53% (N = 10 of 19) and plumbeous vireos at 32% (N = 6 of 19) of points having no large oak trees. Similarly, when Rosenstock (1998) compared bird assemblages in stands of pure ponderosa pine to bird assemblages in stands of pine with gambel oak, he found that both of these species occurred in both forest types.

Oaks tend to support a higher abundance of insect species than do coniferous trees (Southwood 1961) and in some eastern pine-oak forests, arthropod abundance in oak dominated stands peaks earlier in the breeding season than in pine dominated stands (Brush and Stiles 1986). Although there is no research comparing peak arthropod timing in gambel oak versus in ponderosa pine, Faeth and Rooney (1993) found that insect folivory was greatest on young gambel oak leaves early in the growing season. For foliage-gleaning insectivorous bird species, such as plumbeous vireos and yellow-rumped warblers, increased resources that may be provided by oaks earlier in the breeding season could make ponderosa pine stands with gambel oak canopy more attractive breeding territories than pine stands lacking this component.

The influence of gambel oak on the presence of Grace's warblers and hermit thrushes was unclear. Models selected by information theory suggested that the abundance of large oak and large pine were the most likely factors out of those considered to influence the probability of these species being present at a point.

However, the nature of these associations was unclear. There was some evidence that Grace's warblers were less likely to be present when large oak were abundant in stands with high numbers of pine 23-45.5 cm dbh. This contrasts with Szaro and Balda's (1979) finding that Grace's warblers used gambel oak for foraging in greater proportion than its availability in ponderosa pine forests. However, Grace's warblers also have been described as ponderosa pine specialists (Hall et al. 1997) who do not commonly feed elsewhere (Phillips et al 1964, Webster 1961).

Some competitive models for Grace's warblers and hermit thrushes suggested that general forest structure played a more prominent role in habitat use than did floristic composition. For both of these species, drop-in-deviance comparisons selected models with only general forest structure variables as best predicting their presence. Grace's warblers were less likely to be present with increasing numbers of pine snags and increasing numbers of small trees. Hermit thrush presence was positively associated with the density of trees 8-15 cm in diameter. Martin and Roper (1988) found that high densities of small white fir trees primarily distinguished hermit thrush nest sites from surrounding forest in northern Arizona. My results indicate that the density of small diameter trees, regardless of species, may be important to hermit thrushes. The lack of agreement between the models selected for Grace's warblers and hermit thrushes by the two statistical methods as well as the variation in factors included in the top-ranked models based on AIC, indicates that these models may be poor predictors of the presence of these species and that important factors affecting their breeding territory selection were not considered.

Western bluebirds did not appear to be associated with stands having particular oak characteristics. This is surprising since over half of the bluebird nests I located ( $n = 31$  of 51) were in large oak trees. Results from the information theoretic approach suggested a negative association between bluebird presence and abundance of small trees and drop-in-deviance comparisons suggested a negative association between bluebird presence and pole-sized oak. Bluebirds tend to prefer open forests (Rosenstock 1998, **Cunningham** et al. 1980) and simple vertical structure of vegetation around nests in pine-oak forests (Chambers 2002). Negative associations between bluebird presence and smaller trees could be indicative of these preferences. The counterintuitive negative association found between bluebird presence and pine snag abundance suggested by both statistical methods could be due to bluebird's avoidance of smaller oak and the tendency of oak to colonize areas where pines have died (Moir et al. 1997).

For the remaining species I examined (mountain chickadees and cordilleran flycatchers) no general forest structure or floristic variables were found to influence the presence of these species at points. Mountain chickadees are forest generalists (Behle 1956) and their lack of association with particular forest characteristics may be indicative of this. For cordilleran flycatchers, it could have been that I did not find association with forest structure due to a small sample size ( $n=18$ ).

### **Cavity Nests**

I found active hairy woodpecker and northern flicker nests in both gambel oak trees and ponderosa pine snags. For all secondary cavity-nesting species, I found more nests in gambel oak than in pine. White-breasted nuthatch nests were found exclusively in natural cavities (as opposed to excavated cavities) in gambel oak. Chambers (2002)

also found white-breasted nuthatch nests exclusively in natural cavities in large oak trees and Cunningham et al. (1980) found that white-breasted nuthatches used live oak for nesting in preference to ponderosa pine snags. Nests in gambel oak were primarily in large diameter trees ( $\geq 23$  cm dbh). These results match other descriptions of gambel oak trees used for nesting by these species (Chamber 2002, Cunningham et al. 1980).

I found evidence that birds selected nest sites in oak not just based upon nest tree characteristics but also based on the characteristics of the clump of oak within which the nest tree was located. Compared to available oak clumps on my sites, most cavity nesting birds nested in oak clumps that covered a larger area and that had more large oak trees per clump. Chambers (2002) found that western bluebirds and white-breasted nuthatches preferred to nest in oak clumps with simple vertical structure. I did not find this pattern on my study sites. However, I did find that bluebirds preferred clumps with low stem densities. Both of these patterns could be due to bluebirds' preference for open forests (Chambers 2002). Similar to Chambers, I found that chickadees tended to nest in oak clumps with high structural complexity.

Although white-breasted nuthatches nested exclusively in oak on my study sites, the only pattern seen in the oak clumps they selected for nesting was a preference for clumps with higher oak stem density. Chambers (2002) found that white-breasted nuthatches preferred clumps with simple structure but did not find a preference for high stem density in nest clumps.

Northern flickers nested in oak clumps with low stem density and used clumps with simple structure in higher proportion than available. Flickers also selected larger trees to nest in on average than the other bird species suggesting that flickers tended to

nest in oak clumps comprised primarily of large, loosely spaced oak trees. Some researchers have suggested that flickers prefer to use pine snags because they are unable to excavate the harder wood found in oak (Moore 1995). My results suggested that flickers were able either to excavate gambel oak effectively or modify pre-existing cavities. I observed northern flicker nests in what appeared to be enlarged naturally occurring cavities in oak trees.

Hairy woodpeckers, the other primary cavity nester found on my study sites, nested in oak clumps with higher numbers of large oak and higher numbers of small oak (0-7cm dbh) compared to clumps available. Because hairy woodpeckers and northern flickers provided nearly all excavated cavities available for secondary cavity nesters on my study sites, it is of interest that they selected oak clumps for nesting that had different characteristics. These differences should result in a wider range of oak structure associated with nest cavities available to secondary cavity nesters. These excavated cavities in live oak were likely of particular importance to western bluebirds, who at my study sites, nested most often in excavated cavities in live oak. Nearly all oak trees measured at point count stations had some areas of decay and potentially provided a source of nesting substrate for primary excavators however, only about 10% (N = 106 of 1060) of these trees had excavated cavities.

All species of cavity nesting birds seemed to select live rather than dead oak trees for nesting even though many dead oak had both natural and excavated cavities. All but 9 out of the 92 nests I found in gambel oak were in live trees. Hooge et al. (1999) found that cavities in the live limbs of trees tended to provide more favorable microclimates for cavity nests and experienced lower thermal variability than cavities in dead trees. If

cavities in live gambel oak provide a more favorable microclimate for nesting, gambel oak could potentially provide cavity-nesting birds in pine-oak forests with increased nesting opportunities by lessening restrictions on nest sites due to thermal restrictions (e.g. slope, aspect, cavity orientation, minimum nest tree diameter).

### **Management Implications**

Large gambel oak trees were associated with increased bird species richness and with the increased presence of some birds. In addition, large oak provided nesting sites for primary and secondary cavity-nesting bird species. Large oak trees are relatively uncommon and their numbers are thought to be declining (Chambers 2002). Because "old growth" gambel oak is slow to regenerate, efforts should be made to retain existing large oak trees where they are present and to promote the growth of additional oak in this size class. Moir et al (1997) stated that if large oak trees are desired, surrounding conifers must not overtop the oak trees until they have reached the desired diameter and height. The maintenance of canopy gaps in stands where mid-sized oak are approaching maturity may be desirable. Ganey and Vojta (2004) suggest that until natural fire regimes that maintain forest openings can be re-established, this could be accomplished through selective harvest. Trees selected for removal should be limited to those that specifically threaten the continued growth of selected oak trees that are close to attaining a desired size. Because ponderosa pine trees >45.5 cm dbh were associated with high bird species richness, ponderosa pine trees in this size class should not be among those trees removed.

Virginia's warblers and red-faced warblers are listed as species of special concern by the Arizona and New Mexico Partners in Flight (2004). Because Virginia's warblers,

red-faced warblers, and black-headed grosbeaks were strongly associated with pole-sized oak, efforts to encourage this growth form of gambel oak should benefit these species.

Gambel oak tends to **resprout** vigorously in areas that have been disturbed, especially by fire, and where overstory cover has been removed (Clary and Tiedeman 1992).

Maintaining a mosaic of forest openings in pine-oak forests, and especially using prescribed burns to do so, would stimulate oak regeneration and likely encourage the growth of pole-sized trees. Little is known, however, about the effects of prescribed burning on existing large or pole-sized oak trees, so care may need to be taken when prescribed burns are conducted to prevent mortality in existing oak.

In addition, regenerating oak may need protection from browsing by cattle and ungulates since repeated grazing can reduce regeneration and prevent shrub-like oak from developing into oak trees (Dahms and Geils 1997). This could be accomplished through selective closing of grazing allotments until regenerating oak are established. Exclusions to protect selected oak stands from cattle and ungulates could also be considered.

In addition to managing for particular growth forms of gambel oak trees for avian communities, the structure of oak clumps should be considered. Retaining oak clumps that cover large areas and contain large oak trees will benefit numerous cavity-nesting bird species. Oak clumps with a variety of structures should also be encouraged because different cavity nesting bird species preferred different structural complexities and composition of oak clumps for nesting.

### **Statistical Notes**

The purpose of this study was not to compare statistical methods. However, because I employed both information theory and traditional hypothesis testing to select

models, I am in a position to note some insights. Most importantly, both methods largely selected similar models for predicting both avian species richness and the presence of birds at points. An information theoretic approach enabled me to compare non-nested models which proved helpful for focusing attention on competing factors that were equally able to describe variation in the I data collected. However, successful use of information theory in model selection is dependent upon the development of adequate a priori models (Burnham and Anderson 1998). Creating models that are thoughtful yet contain all factors that may be of importance can be difficult and I argue that there are drawbacks to limiting results to those obtained through models created a priori, especially in an exploratory investigation. There are instances where even the most careful consideration of which variables to include will leave out an important association that is not obvious or simply has not occurred to the researcher. In fact, many breakthroughs in research have been made by the discovery of relationships that were unexpected.

Drop-in-deviance and sum-of-squares F-tests provided a **straight** forward and elegant approach to addressing the question of whether oak characteristics explained additional variation in bird response **after** accounting for general forest structure. However, the hierarchical nature of these tests may have masked important associations. For example, in this study, drop-in-deviance testing showed a strong correlation between ponderosa pine snag abundance and Virginia's warblers. This relationship seems almost certainly due oak colonizing areas where pine trees have died and created a forest opening. Thus results were not incorrect, but the relationship was indirect. By beginning with a model that does not contain the factors of interest, there is risk that an association

of interest may be masked in later models. However, if this conflict can be avoided through careful selection of variables, the technique can be powerful. This approach was also more flexible, especially in an exploratory setting such as this and allowed for inclusion of more specific factors within models.

A useful approach, especially in a setting where some information about a system is known, would be to develop and examine a set of *apriori* models within an information theoretic **framework**, and later conduct a more detailed inspection of the data using hypothesis testing. This would prevent data mining, but would allow for an *a postiri* examination of the data to see if important patterns making biological sense have been missed. In a setting where little is known about a system, hypothesis testing would likely be a better tool to investigate patterns that could be of important.

## **Conclusions**

Gambel oak is an important resource for birds in ponderosa pine forests. It provides additional nesting and foraging opportunities for numerous bird species. Large gambel oak trees that provide increased structural diversity within the forest canopy may be of particular importance to bird communities when large ponderosa pine trees are scarce and the multi-storied canopy associated with mature pine stands is absent. Virginia's warblers, red-faced warblers, and black-headed grosbeaks are strongly associated with abundant smaller oak trees and Virginia's and red-faced warblers may be dependent, at least within ponderosa pine systems, on the resources provided by gambel oak. Other bird species associated with certain types of gambel oak included yellow-rumped warblers and plumbeous vireos.

Large gambel oak trees also provide important resources for cavity-nesting birds in ponderosa pine forests. Gambel oak adds to the quantity, and possibly quality, of nesting substrate available to primary and secondary cavity-nesting birds. Gambel oak offers an alternative to nesting in ponderosa pine snags. This may be of particular importance in ponderosa pine stands where snags are scarce. In addition, for some bird species, cavities in live oak may provide a more favorable nesting microclimate than snags, and thus could be associated with higher nesting success.

Additional research focused on identifying the resources associated with pole-sized and large gambel oak is necessary to understand their importance to birds in ponderosa pine forests. Research should also be conducted to determine how forest management practices, especially prescribed burning, effect these growth forms of gambel oak and the bird species associated with them. Studies of the success of cavity nests in live oak versus in pine snags would provide important information for maintaining populations of cavity nesting birds, a group that comprises a large proportion of the breeding and wintering bird communities in ponderosa pine forests. The importance of large gambel oak trees within different successional stages of ponderosa pine forest should also be investigated.

**Table 1. Bird species detected in pine-oak forest, northern Arizona and New Mexico, 2003. The number of points at which each species was detected is listed by study site.**

<b>Species</b>	<b>Apache-Sitgreaves NF (47 points)</b>	<b>Coconino NF (70 points)</b>	<b>Gila NF (35 points)</b>
*northern goshawk ( <i>Accipiter gentilis</i> )	1	0	0
*wild turkey ( <i>Meleagris gallopavo</i> )	0	0	1
band-tailed pigeon ( <i>Columba fasciata</i> )	8	0	0
mourning dove ( <i>Zenaida macroura</i> )	12	5	3
broad-tailed hummingbird ( <i>Selasphorus platycercus</i> )	0	2	1
*northern flicker ( <i>Colaptes auratus</i> )	12	4	13
*hairy woodpecker ( <i>Picoides villosus</i> )	20	19	18
western wood pewee ( <i>Contopus sordidulus</i> )	3	18	4
gray flycatcher ( <i>Empidonax wrightii</i> )	3	21	0
**cordilleran flycatcher ( <i>Empidonax occidentalis</i> )	0	9	9
ash-throated flycatcher ( <i>Myiarchus cinerascens</i> )	0	0	5
<b>**plumbeous vireo (<i>Vireo plumbeus</i>)</b>	1	44	12
warbling vireo ( <i>Vireo gilvus</i> )	1	0	1
<b>*steller's jay (<i>Cyanocitta stelleri</i>)</b>	37	13	15
*western scrub jay ( <i>Aphelocoma californica</i> )	0	0	2
*pinyon jay ( <i>Gymnorhinus cyanocephalus</i> )	0	0	2
*common raven ( <i>Corvus corax</i> )	0	0	3
*violet-green swallow ( <i>Tachycineta thalassina</i> )	2	6	2
<b>**mountain chickadee (<i>Poecile gambeli</i>)</b>	37	31	21
bushtit ( <i>Psaltriparus minimus</i> )	0	5	14
brown creeper ( <i>Certhia americana</i> )	8	18	14
*white-breasted nuthatch ( <i>Sitta carolinensis</i> )	39	54	23
pygmy nuthatch ( <i>Sitta pygmaea</i> )	47	37	31
<b>**western bluebird (<i>Sialia mexicana</i>)</b>	7	42	18
mountain bluebird ( <i>Sialia currucoides</i> )	0	1	0
townsend's solitaire ( <i>Myadestes townsendi</i> )	3	2	7
<b>**hermit thrush (<i>Catharus guttatus</i>)</b>	12	2	19
american robin ( <i>Turdus migratorius</i> )	3	26	7
<b>**virginia's warbler (<i>Vermivora virginiae</i>)</b>	12	3	7
<b>**yellow-rumped warbler (<i>Dendroica coronata</i>)</b>	4	51	25
black-throated gray warbler ( <i>dendroica nigrescens</i> )	17	2	19
<b>**grace's warbler (<i>Dendroica graciae</i>)</b>	11	52	17
yellow warbler ( <i>Dendroica petechia</i> )	0	1	0
<b>**red-faced warbler (<i>Cardellina rubrifrons</i>)</b>	0	6	9
olive warbler ( <i>Peucedramus taeniatus</i> )	0	5	0
hepatic tanager ( <i>Piranga flava</i> )	1	6	0
western tanager ( <i>Piranga ludoviciana</i> )	28	41	25
spotted towhee ( <i>Pipilo maculatus</i> )	1	0	4
chipping sparrow ( <i>Spizella passerina</i> )	0	20	13
dark-eyed junco ( <i>Junco hyemalis</i> )	42	44	32
<b>**black-headed grosbeak (<i>Pheucticus melanocephalus</i>)</b>	14	14	6
brown-headed cowbird ( <i>Molothrus ater</i> )	0	15	1
lesser goldfinch ( <i>Carduelis psaltria</i> )	0	1	0

\* species excluded based on home-range size

\*\* species for which I examined presence/absence at points

**Table 2.** Vegetation variables considered in analyses of avian point count data collected in Arizona and New Mexico pine-oak forest, 2003. Individual variables and categories used to describe groups of variables are listed.

<b>Variable Categories</b>	<b>Variables</b>
<b><i>General forest structure</i></b>	
Tree counts	# trees 2.5-8cm dbh
	# trees 8-15cm dbh
	# trees 15-23cm dbh
	# trees 23-45.5cm dbh
	# trees >45.5cm dbh
Pine snags	# ponderosa pine snags >23cm dbh
Tallest tree	height of the tallest tree
Understory	% grass cover
	% forb cover
	% shrub cover
<b><i>Floristic structure</i></b>	
Small oak	# gambel oak 0-7cm dbh
	# gambel oak 7-15 cm dbh
	# gambel oak 15-23 cm dbh
Large pine	# ponderosa pine 23-45.5 cm dbh
	# ponderosa pine >45.5 cm dbh
Large oak	# gambel oak >23 cm dbh
<b><i>Oak spatial structure</i></b>	
Area/perimeter	ratio of area to perimeter of oak clumps

(Table 3 will be here in printed draft)

**Table 4. Summary** of sum-of-squares F-test comparisons used to select habitat models of avian species richness in pine-oak forest in Arizona and New Mexico, 2003. Variables within models that have P-values  $\leq 0.10$  are followed by the sign of the relationship inside parentheses. The model retained by the sum-of-squares F-test is listed in parentheses in bold print.

<i>Model</i>	<i>Extra SS F-test comparisons</i> (all models include unit effect)
Variables included in model	
<b>General forest structure</b>	NA
trees 2.5-8	
trees 8-15 (-)	
trees 15-23	
trees >23	
trees >45.5	
tallest tree	
pine snags	
grass	
forb	
shrub(+)	
<b>Structure with just significant variables</b>	<b>Structure vs. Significant structure</b>
trees 8-15 (-)	F=1.489 8,136df P=0.167 (sig. structure)
shrub (+)	
<b>Significant structure + oak variables</b>	<b>Significant structure vs. Significant structure + oak variables</b>
trees 8-15 (-)	F= 1.4315 4,142df P=0.227 (sig. structure)
shrub (+)	
oak 0-7	
oak 7-15	
oak 15-23	
oak >23	
<b>Significant structure + oak spatial</b>	<b>Significant structure vs. Significant structure + oak area/perimeter</b>
trees 8-15 (-)	F = 0.0152 1,145df P=0.902 (sig. structure)
shrub (+)	
oak area/perimeter	
<b>Significant structure + large pine</b>	<b>Significant structure vs. Significant structure + large oak and pine</b>
trees 8-15 (-)	F = 5.1682 3,141df P = 0.002 (sig. structure + large pine)
shrub (+)	
pine 23-45.5	
pine >45.5 (+)	
<b>Significant structure + large oak * pine interaction</b>	<b>Significant structure vs. significant structure + large oak * pine interaction</b>
trees 8-15 (-)	F= 4.44 3,143df P = 0.0052 (*sig. structure + large oak * pine interactions)
shrub (+)	
pine 23-45.5	
pine >45.5 (+)	
pine 23-45.5 * oak >23 (-)	
pine >45.5 * oak >23 (-)	

\* model retained as best

**Table 5.** Competitive models based on  $AIC_c$  for avian species richness at point-count stations, northern Arizona and New Mexico pine-oak forest, 2003.

<b>Candidate models ranked by <math>AIC_c</math></b>	<b>A <math>AIC_c</math></b>	<b><math>AIC_{wi}</math></b>
1. Forest structure with large oak, large pine, and large oak * large pine interaction	0.0000	0.4501
2. Forest structure with small oak, large oak, large pine, and large oak * pine interaction	0.6252	0.3292
3. Large oak, large pine, and large oak * large pine interaction	2.0963	0.1578

**Table 6.** Vegetation variables that explained variation in best-fitting models of avian species richness at point-count stations in pine-oak forest in northern Arizona and New Mexico, 2003. Parameter estimates and P-values are from multiple regression analysis. Estimates derived from models selected through sum-of-squares F-test comparisons are listed on the left and estimates from models selected through AIC<sub>c</sub> ranking are listed on the right.

Significant variables based on sum-of-squares F-tests				Significant variables based on AIC <sub>c</sub> ranking			
Variables	Parameter estimate	SE	P-value	Variables	Parameter estimate	SE	P-value
Abundance of trees 8-15cm dbh	-0.048	0.013	0.0003	Abundance of trees 8-15cm dbh	-0.049	0.016	0.0023
% shrub cover	0.184	0.075	0.0150	Abundance of trees 23-45.5 cm dbh	0.178	0.081	0.0304
Abundance of pine >45.5cm dbh	0.254	0.103	0.0150	Abundance of pine 23-45.5cm dbh	-0.160	0.082	0.0519
Large oak*pine 23-45.5cm interaction	-0.009	0.003	0.0038	Large oak*pine 23-45.5cm interaction	-0.010	0.003	0.0014
Large oak*pine >45.5cm interaction	-0.041	0.013	0.0024	Large oak*pine >45.5cm interaction	-0.033	0.014	0.0164

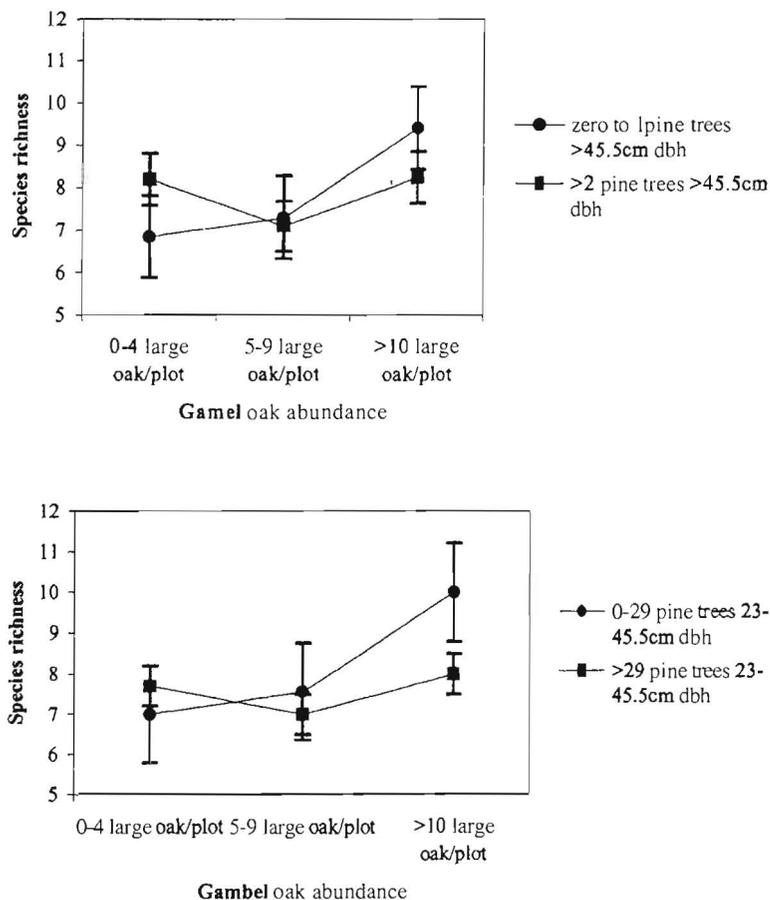


Figure 1. Avian species richness ( $\pm$  standard error) and abundance of large oak trees at different density levels of ponderosa pine 23-45.5cm dbh and ponderosa pine >45.5 cm at point count stations in pine-oak forest in Arizona and New Mexico, 2003.

Table 7. Multiple logistic regression models considered competitive ( $\Delta AIC_c < 2.5$ ) for being the best approximating models of bird species presence at points in pine-oak forest in northern Arizona and New Mexico, 2003.

	$\Delta AIC_c$	$AIC_{wi}$
<b>Black-headed grosbeak</b>		
1a. Small oak	0.0000	0.3238
2a. Small oak and oak spatial	0.4985	0.2524
3a. Small oak and large oak	1.1891	0.1787
4a. Small oak, large oak, and oak spatial	1.9853	0.1200
<b>Grace's warbler</b>		
1b. Large oak, large pine, and large oak*large pine interaction	0.0000	0.1683
2b. Large oak and large pine	0.8871	0.1080
3b. Forest structure including snags and tallest tree	0.9714	0.1035
4b. Forest structure including snags, tallest tree, and understory	1.3143	0.0872
5b. Forest structure and understory	1.4013	0.0835
6b. Forest structure	1.4950	0.0795
7b. Small oak	1.6781	0.0727
8b. Forest structure and large pine	2.3095	0.0530
9b. Forest structure and large oak	2.3416	0.0500
<b>Hermit thrush</b>		
1c. Small oak	0.0000	0.2296
2c. Large oak and large pine	1.3990	0.1141
3c. Small oak and large oak	1.4633	0.1105
4c. Forest structure including snags and tallest tree	2.0353	0.0830
5c. Small oak and oak spatial	2.1939	0.0767
<b>Plumbeous vireo</b>		
1d. Forest structure with large oak, large pine, and large oak*large pine interaction	0.0000	0.9908
<b>Red-faced warbler</b>		
1e. Small oak	0.0000	0.1837
2e. Small oak and large oak	0.1255	0.1726
3e. Small oak and oak spatial	0.2793	0.1598
4e. Small oak, large oak, large pine, and large oak*large pine interaction	0.9570	0.1139
5e. Small oak, large oak and oak spatial	1.1045	0.1058
6e. Large oak, large pine, and Large oak*large pine interaction	1.2503	0.0983
<b>Virginia's warbler</b>		
1f. Small oak and oak spatial	0.0000	0.3158
2f. Small oak, large oak, and oak spatial	0.3378	0.2667
3f. Small oak	0.7371	0.2185
4f. Small oak and large oak	2.1758	0.1064
<b>Western bluebirds</b>		
1g. Forest structure including snags and tallest tree	0.0000	0.3969
<b>Yellow-rumped warbler</b>		
1h. Large oak and large pine	0.0000	0.2468
2h. Large oak, large pine, and large oak*large pine interaction	1.2759	0.1304
3h. Small oak and large oak	1.2945	0.1292
4h. Forest structure with large oak and large pine	2.1139	0.0858
5h. Forest structure including snags and tallest tree	2.2915	0.0785
6h. Forest structure with large oak	2.4213	0.0735

(Table 8 will be here in printed draft)

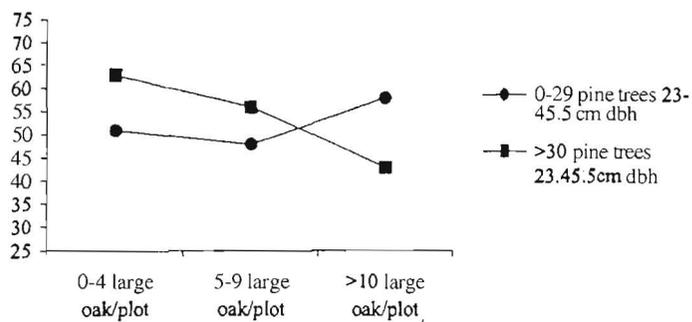
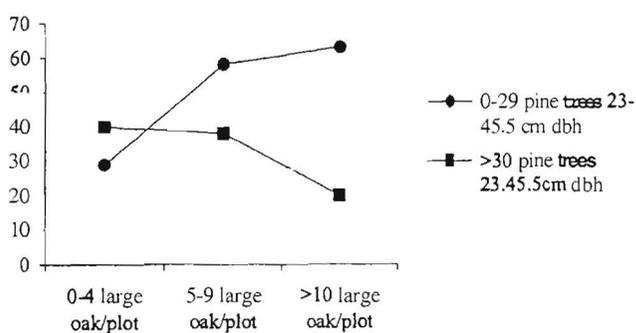


Figure 2. Presence of Grace's warblers and 3 levels of large oak abundance at points with low and moderate to high abundance of ponderosa pine trees 23-45.5cm in diameter, northern Arizona and New Mexico, 2003.

a)



b)

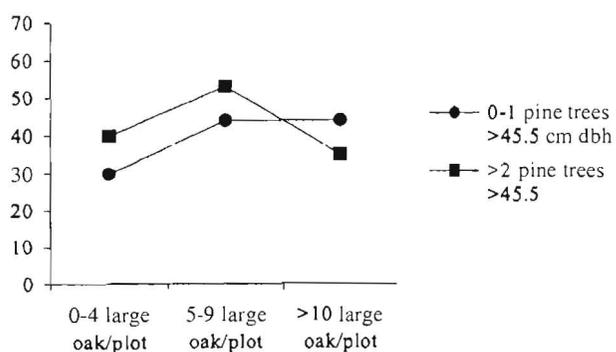
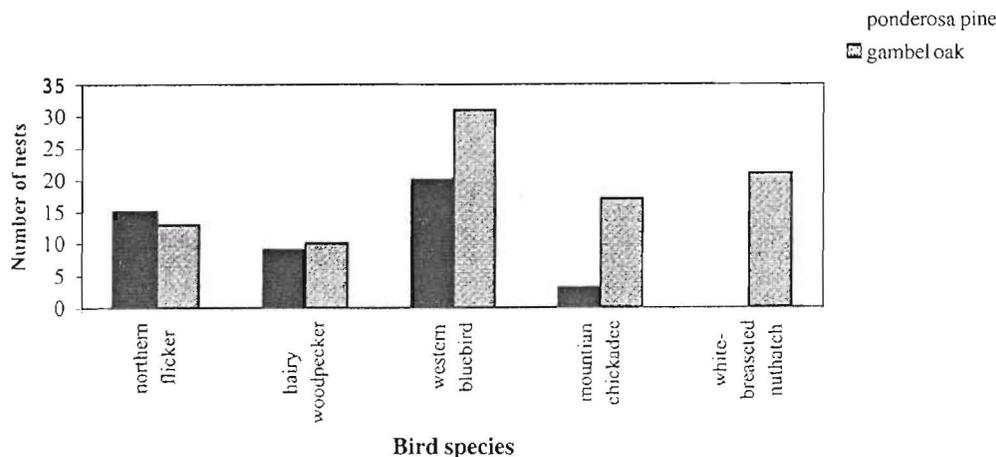


Figure 3. Presence of plumbeous vireos and 3 levels of large oak abundance at points with low and moderate to high abundance of ponderosa pine trees 23-45.5cm dbh and at points with low and moderate abundance of ponderosa pine trees >45.5cm dbh, northern Arizona and New Mexico, 2003.

**Table 9.** Variables included in logistic regression models selected through drop-in-deviance testing as best describing bird species presence at point count stations in pine-oak forest in northern Arizona and New Mexico, 2003. Variables found to be significant (P-value for  $\chi^2$  value < 0.05) are followed by the sign of the relationship.

<i>Species</i> Variables in best model	<i>Species</i> Variables in best model
<b>Black-headed grosbeak</b> oak 7-15 (+)	<b>Red-faced warbler</b> oak 7-15 (+)
<b>Grace's warbler</b> trees 2.5-8 (-) pine snags (-) shrubs (+)	<b>Virginia's warbler</b> pine snags (+) oak 0-7 oak 7-15 oak 15-23 oak >23
<b>Hermit thrush</b> trees 15-23 (+) % grass cover (+) trees > 45.5	<b>Western bluebird</b> trees 2.5-8 pine snags (-) tallest tree (+) oak 7-15 (-)
<b>Plumbeous vireo</b> trees 2.5-8 (+) trees 8-15 (-) pine >23 oak >23 oak >23 * pine 23 - 45.5 (-) oak >23 * pine > 45.5 (-)	<b>Yellow-rumped warbler</b> trees 23-45.5 (-) tallest tree (+) oak >23 (+)



**Figure 4.** Number of active cavity nests found in gambel oak compared to number of nests found in pine snags pine-oak forest, Arizona and New Mexico 2002-2004.

Table 10. Average and range of oak tree diameters and average nest height for cavities used for nesting by cavity nesting birds in pine-oak forest, northern Arizona and New Mexico, 2002-2004.

Species	n	Ave. nest tree		Range		Ave. nest	
		dbh (cm)	± SE	small	large	height (m)	± SE
mountain chickadee	17	28	4	16	44	3.1	0.38
hairy woodpecker	10	37	5.2	24	59	4.5	0.7
white-breasted nuthatch	21	43	3.6	22	91	3.6	0.47
western bluebird	31	43	3	22	110	4.3	0.41
northern flicker	13	47	4.6	29	68	4.5	0.48
All species	92	40	16.4	16	110	3.95	0.22

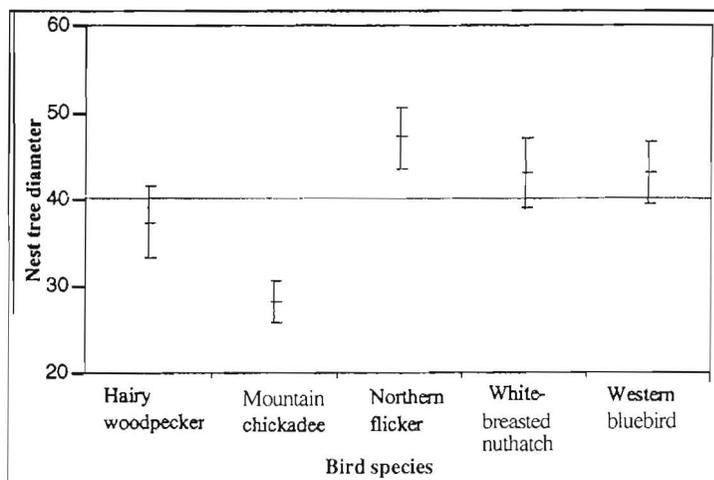
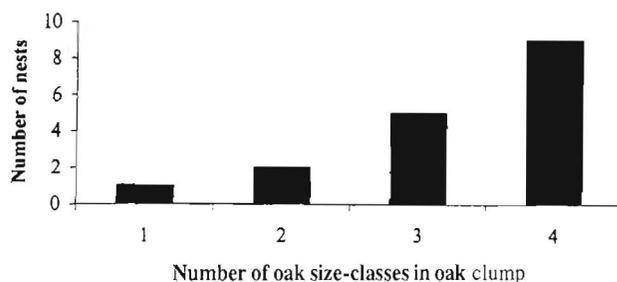


Figure 5. Average diameter (cm)  $\pm$  standard error for gambel oak trees used for nesting by cavity nesting birds in pine-oak forests, northern Arizona and New Mexico, 2002-2004.

**Table 11.** Characteristics of oak clumps used for nesting by cavity nesting birds compared to available oak clumps pine-oak forest, northern Arizona and New Mexico, 2002-2004.

<i>Species/variables</i>	p-value	parameter estimate ± SE	Odds	<u>Nest oak clumps</u>	<u>Available oak clumps</u>
				$\bar{X} \pm SE$	$\bar{X} \pm SE$
<b><i>Hairy woodpecker</i></b>					
number large oak/clump	0.0011	0.32 ± 0.10	1.38	4 ± 1.4	1.8 ± 0.06
number of oak 0-7cm dbh/clump	0.0444	0.02 ± 0.01	1.02	19.1 ± 16.3	7.1 ± 0.6
clump area	0.0008	0.004 ± 0.001	1.004	268 ± 123	79 ± 4
<b><i>Mountain chickadee</i></b>					
number large oak/clump	0.0092	0.25 ± 0.09	1.28	3.4 ± 1.3	1.8 ± 0.06
number of oak 15-23cm dbh/clump	0.0077	0.19 ± 0.07	1.21	0.25 ± 0.09	0.25 ± 0.09
clump area	0.0092	0.003 ± 0.001	1.00	180 ± 87	78 ± 42
% seedling cover/clump	0.0465	0.02 ± 0.01	1.02	37 ± 6	22 ± 1
number of size classes of oak in clump	0.0162	0.65 ± 0.27	1.92	3.3 ± 0.2	2.6 ± 0.05
<b><i>Northern flicker</i></b>					
number large oak/clump	0.0197	0.23 ± 0.1	1.26	3.5 ± 1	1.8 ± 0.06
number of size classes of oak in clump	0.0206	-0.68 ± 0.29	0.51	1.9 ± 0.27	2.6 ± 0.05
oak stem density/clump	0.0034	-18.34 ± 6.27	0.0001	0.06 ± 0.02	0.23 ± 0.01
<b><i>white-breasted nuthatch</i></b>					
oak stem density/clump	0.0437	-4.2 ± 2.1	0.015	0.13 ± 0.03	0.23 ± 0.01
<b><i>Western bluebird</i></b>					
number large oak/clump	0.0161	0.18 ± 0.08	1.2	2.9 ± 0.54	1.8 ± 0.06
clump area	0.0104	0.003 ± 0.001	1.003	146 ± 27.1	78 ± 42
oak stem density/clump	0.0007	-7.76 ± 2.3	0.0004	0.1 ± 0.02	0.23 ± 0.01
% seedling cover/clump	0.0381	-0.02 ± 0.01	0.082	17.2 ± 4.1	22.6 ± 0.89

**Figure 6.** Number of mountain chickadee nests found in gambel oak at study sites in northern Arizona and New Mexico, 2002-2004. Numbers of nests are shown at 4 levels of oak clump structural complexity represented by the number of size-classes of oak trees comprising the oak clump containing the nest.

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