

Associations Among Breeding Birds and Gambel Oak in Southwestern Ponderosa Pine Forests

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ABSTRACT Ponderosa pine (*Pinus ponderosa*) forests with Gambel oak (*Quercus gambelii*) are associated with higher bird abundance and diversity than are ponderosa pine forests lacking Gambel oak. Little is known, however, about specific structural characteristics of Gambel oak trees, clumps, and stands that may be important to birds in ponderosa pine–Gambel oak (hereafter pine–oak) forests. We examined associations among breeding birds and structural characteristics of Gambel oak at a scale similar in size to individual bird territories in pine–oak forests in northern Arizona and western New Mexico, USA. Avian species richness and occurrence of some bird species were associated with specific growth forms of Gambel oak. Estimated probability of Virginia’s warblers (*Vermivora virginiae*), black-headed grosbeaks (*Pheucticus melanocephalus*), and red-faced warblers (*Cardellina rubrifrons*) occurring at points increased with increasing density of pole-sized Gambel oak 7–15 cm in diameter at breast height. We also found evidence that large Gambel oak trees (≥ 23 cm dbh) were associated with increased occurrence of yellow-rumped warblers (*Dendroica coronata*) at points. Some avian associations with oak were influenced by characteristics of ponderosa pines. For example, bird species richness was positively associated with the abundance of large Gambel oak when density of large pine trees ≥ 23 cm in diameter at breast height was low. Because large oak trees are rare and their numbers are thought to be declining, efforts should be made to retain and promote growth of additional oaks in this size class. Forest management practices that maintain forest openings, such as prescribed burning, could promote growth of pole-sized Gambel oak, which appears important to some bird species in pine–oak forests. (JOURNAL OF WILDLIFE MANAGEMENT 72(4):994–1000; 2008)

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Gambel oak (*Quercus gambelii*) 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 sprouting, it occurs as both scattered individuals and dense clumps (Leidolf et al. 2000). In the southwestern United States, Gambel oak is often found in association with ponderosa pine (*Pinus ponderosa*) at elevations of 2,000–2,800 m (Hanks et al. 1983). Presence of Gambel oak in ponderosa pine forests is associated with increased bird abundance and diversity (Marshall 1957, Szaro et al. 1990, Rosenstock 1998). Little is known, however, about how specific growth forms of Gambel oak contribute to occurrence of specific breeding bird species and to patterns in avian species richness in ponderosa pine–Gambel oak (pine–oak) forests of the Southwest.

Southwestern ponderosa pine forests have become the focus of management practices that aim to reduce risk of stand-replacing wildfire and to restore forest structure to conditions similar to those that occurred historically (Fulé et al. 2005). Because these practices can be implemented on a large scale and can also influence abundance and structure of Gambel oak (Leidolf et al. 2000), identifying attributes of Gambel oak that are important to birds in pine–oak forests would be a valuable conservation measure. In addition, past forest management practices that aimed to reduce Gambel oak in ponderosa pine forests, increased

ponderosa pine density due to fire suppression, and lack of recruitment of mature oak trees have resulted in declining numbers of large oak trees (Clary and Tiedeman 1992, Kruse 1992, Chambers 2002, Ryniker et al. 2006). Bird species that may be affected by the loss of large oak should be identified.

We aimed to examine whether Gambel oak was related to bird species richness or with presence versus absence (hereafter, occurrence) of individual bird species at a local scale (i.e., within areas similar in size to individual bird territories; Sherry and Holmes 1985). Our specific objectives were to 1) test whether characteristics of Gambel oak or ponderosa pine were associated with patterns in bird species richness and species occurrence after accounting for associations with general forest structure and 2) describe characteristics of Gambel oak associated with patterns in bird species richness and with occurrence of particular bird species.

STUDY AREA

Our study area was in pine–oak forests in Arizona and New Mexico, USA, on sites that were part of a larger research project coordinated by the United States Department of Agriculture Forest Service Rocky Mountain Research Station designed to examine effects of prescribed fire on bird communities in ponderosa pine forests. Study sites were located in pine–oak forests that were slated for prescribed burns. Three study sites were located within the expanse of

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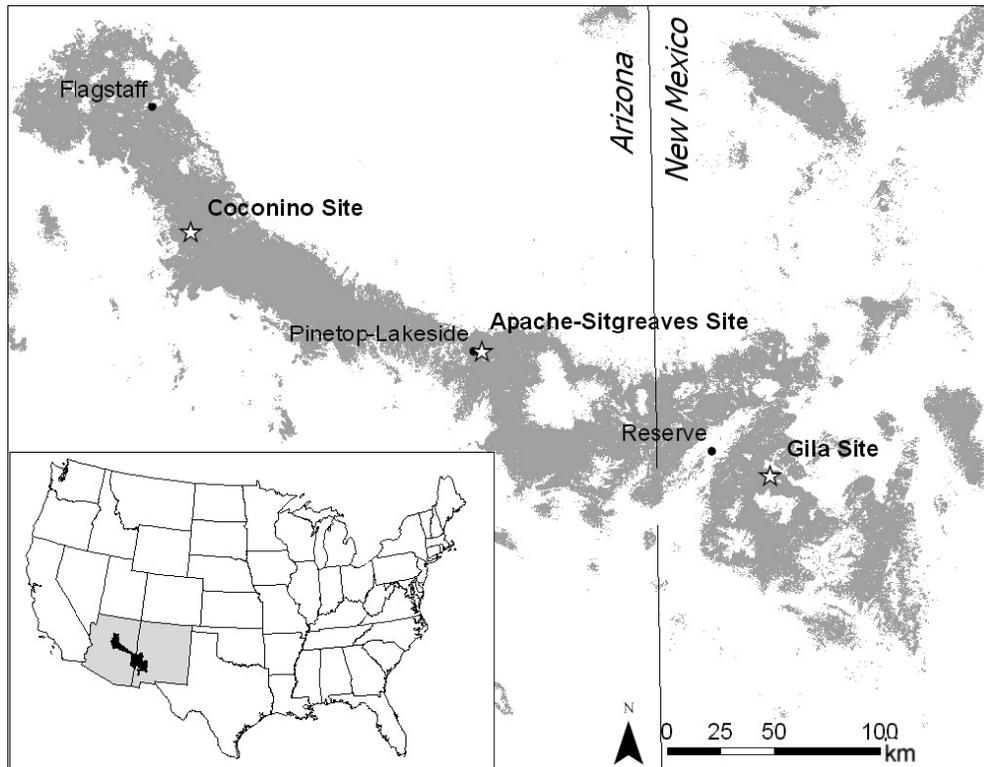


Figure 1. Location of 3 study sites used to examine associations between breeding birds and Gambel oak in pine–oak forests in northern Arizona and New Mexico, USA, 2003. Study sites were located on Apache-Sitgreaves National Forest, Coconino National Forest, and Gila National Forest. Dark shading indicates areas of ponderosa pine-dominated forest.

ponderosa pine forest that begins west of Flagstaff, Arizona and runs along the Mogollon Rim into New Mexico (Fig. 1). In Arizona, one study site was located on the Mogollon Rim Ranger District of the Coconino National Forest approximately 60 km southeast of Flagstaff and a second site was located on the Lakeside Ranger District of the Apache-Sitgreaves National Forest about 8 km from the community of Pinetop-Lakeside. A third site was located in New Mexico on the Reserve District of the Gila National Forest about 30 km southeast of Reserve, New Mexico. Elevations on study sites ranged from 2,122 m to 2,412 m. Ponderosa pine and Gambel oak were the most common tree species at all study sites. Other tree species encountered included alligatorbark 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 grama (*Bouteloua gracilis*) occurred in scattered clumps throughout the understory. All sites had a history of timber harvest and livestock grazing. We collected data on study sites in 2003 prior to implementation of prescribed burning. Precipitation and temperature measurements for 2003 did not differ dramatically from long-term averages. Total precipitation for 2003 (1 Oct 2002–30 Sep 2003) was 32.5 cm (88% of average) on the Arizona study sites and 25.5 cm (77% of average) on the New Mexico study site (Western Regional Climate Center 2007).

METHODS

Avian and Vegetation Sampling

At each of the 3 study sites, we sampled an area that ranged between 400 ha and 800 ha. We used a Geographic Information System (GIS) to locate avian and vegetation sampling points (hereafter, points) at each study site. Within the GIS, we placed a lattice of 125 × 125-m cells over each site and randomized placement of the first cell location. We located points at lattice intersections so each point was ≥ 250 m from any other point. We used Universal Transverse Mercator coordinates identified in the GIS to locate and permanently mark points on the ground using a Global Positioning System. In total, we established 152 points in pine–oak forest: 47 points in the Apache-Sitgreaves National Forest, 70 points in the Coconino National Forest, and 35 in the Gila National Forest.

We used standard point-count methodology to count birds detected in 100-m fixed-radius circular plots centered at each point (Ralph et al. 1993). We started counts just after sunrise and completed them no later than 4 hours after sunrise. Upon arriving at a point, we waited 2–4 minutes to allow birds to resume normal activities. We recorded all birds seen or heard within 5 minutes. For each detection, we recorded bird species, number of individuals, mode of detection, distance, and bearing to the bird. Before each count we noted temperature and weather conditions. We did not conduct counts during windy or rainy weather. We visited each point 4 times between 20 May and 1 July 2003.

Table 1. Categories and groups of vegetation variables measured at sampling points and included in analysis of avian point count data in pine-oak forests in Arizona and New Mexico, USA, 2003.

Category, groups, and variables	
General forest structure	Floristic structure
Tree counts	Oak variables
No. trees 2.5–8-cm dbh	Small oak
No. trees 8–15-cm dbh	No. Gambel oak 0–7-cm dbh
No. trees 15–23-cm dbh	No. Gambel oak 7–15-cm dbh
No. trees ≥23-cm dbh	No. Gambel oak 15–23-cm dbh
Pine snags	Large oak
No. ponderosa pine snags ≥23-cm dbh	No. Gambel oak ≥23-cm dbh
Tallest tree	Oak spatial
Ht of tallest tree	Ratio area:perimeter of oak clumps
Understory	Ponderosa pine variables
% grass cover	Large pine
% forb cover	No. ponderosa pine 23–45.5-cm dbh
% shrub cover	No. ponderosa pine >45.5-cm dbh

At each of the 152 points we measured vegetation along 4 transect lines that extended 50 m in each cardinal direction. Transect lines running east and west started 10 m out from points to avoid overlap with north and south transects (Saab et al. 2006). We tallied all trees ≥23 cm in diameter breast height occurring within 5 m of the transect lines by species. We further grouped large ponderosa pine trees (≥23 cm dbh) into 2 size classes. We considered pine trees with 23–45.5-cm diameter at breast height characteristic of mid-aged ponderosa pine and trees with >45.5-cm diameter at breast height characteristic of mature ponderosa pine (Moir and Dieterich 1988). We used a clinometer to measure height of the tallest tree within the transect lines to the nearest 0.1 m. We assigned stems <23 cm in diameter at breast height that reached breast height and occurred within 2 m of the transect line to 1 of 3 diameter classes (Table 1). We tallied all pine snags ≥23 cm in diameter at breast height occurring within 10 m of the transect lines.

We characterized understory vegetation in 3 plots at each point: one plot centered at the point, one at the 50-m mark on the north transect, and one at the 50-m mark on the south transect. We used a point-intercept method at 0.5-m intervals (excluding the center point) along transect lines that extended 5 m in each cardinal direction to estimate percent grass, forb, and shrub cover. We considered tree seedlings and shrub-like Gambel oak that did not reach breast height (1.4 m) shrubs.

Within a 30-m radius (0.3 ha) plot centered at each point we characterized Gambel oak abundance, structure, and spatial arrangement. We recorded number of large oak trees (≥23 cm dbh) and number of small oak trees in each of 3 diameter classes (Table 1). We defined an oak clump as ≥1 Gambel oak trees with interlocking crowns that were separated from neighboring oak crowns by ≥1 m. Because of the tendency of Gambel oak to produce large numbers of clonal seedlings, we used this definition separately for understory and overstory. Thus, the canopy of one clump could overlap with seedlings or shrub-like oak (<1.4 m tall) in the understory of another clump. We measured length of

each oak clump through the longest axis of the clump. We measured width at an angle perpendicular to length at the widest point of the clump. We estimated area and perimeter of each oak clump using formulas for area and perimeter of an ellipse. For all oak clumps within a plot, we summed the area and perimeter and calculated an area-to-perimeter ratio for the plot. We considered the area-to-perimeter ratio to be representative of the spatial arrangement of oak within the plot (i.e., a measure of the extent that oak occurred in large clumps vs. smaller clumps or as individual trees).

Data Analysis

We considered avian species richness to be total number of different bird species detected over all 4 visits to a point. We included detections of birds <100 m from the point. We excluded all flyover detections. For our initial analysis of avian species richness, we excluded 10 bird species with territories typically >3 ha, according to the literature, so that we could use statistical tests that assumed independence among points. Species excluded were primarily raptors, woodpeckers, and corvids. Following our initial analysis, we repeated the analysis with all species encountered. We focused our analysis of bird species occurrence on 10 species considered to be associated with Gambel oak that we detected at >10 points (Poole et al. 1995, Rosenstock 1998, Leidolf et al. 2000, Chambers 2002). These species included cordilleran flycatcher (*Empidonax occidentalis*), plumbeous vireo (*Vireo plumbeus*), mountain chickadee (*Poecile gambeli*), western bluebird (*Sialia mexicana*), hermit thrush (*Catharus guttatus*), Virginia's warbler (*Vermivora virginiae*), yellow-rumped warbler (*Dendroica coronata*), Grace's warbler (*Dendroica graciae*), red-faced warbler (*Cardellina rubrifrons*), and black-headed grosbeak (*Pheucticus melanocephalus*). We considered a species to be present at a point if we detected it within 100 m of the point on ≥1 visit.

We used multiple linear regression to identify vegetation features associated with trends in bird species richness at points (Zar 1996). We used multiple logistic regression to identify vegetation features associated with occurrence of selected bird species at points (Keating and Cherry 2004). We conducted all analyses with JMP IN statistical software (Sall et al. 2001). We examined data for influential outliers and plotted residuals against estimates of species richness to ensure that no data transformations were necessary (Gutzwiller and Anderson 1986).

We used extra-sum-of-squares *F*-tests to compare nested multiple-regression models and drop-in-deviance tests to compare nested logistic regression models (Ramsey and Schafer 2002). We considered *F* statistics (from sum-of-squares *F*-test comparisons) or chi-square statistics (from drop-in-deviance comparisons) with *P*-values ≥0.05 as indicating that additional variables included in the more complex model did not provide significant additional explanatory power.

We began our comparison of nested models by comparing a model containing all general forest structure variables measured at points to a model containing only general forest structure variables that showed a relationship to the response

Table 2. Parameter estimates and standard errors for major effects calculated from multiple linear regression model of avian species richness at sampling points in pine–oak forests in northern Arizona and New Mexico, USA, 2003.

Variables	Parameter estimate	SE	P-value
Abundance of trees 8–15 cm dbh	−0.06	0.015	<0.001
% shrub cover	0.21	0.089	0.019
Abundance of pine >45.5 cm dbh	0.36	0.122	0.004
Large oak × pine 23–45.5 cm interaction	−0.01	0.004	0.052
Large oak × pine >45.5 cm interaction	−0.05	0.015	0.001

variable significant at a 0.10 alpha level. We chose a 0.10 alpha level due to the exploratory nature of our study. We used the general forest structure model selected through this comparison as a basis for tests to determine whether addition of oak- and pine-specific variables would provide significant additional explanatory power. To the general forest structure model we added 1) all oak-specific variables, 2) all pine-specific variables, and 3) 2 interaction terms: one between large oak and large pine 23–45.5 cm in diameter at breast height and one between large oak and large pine >45.5 cm in diameter at breast height. In each case we retained the set of additional variables in the model when a chi-square or F statistic was significant at the 0.05 alpha level. Between each step we also conducted a test to assess whether we should retain nonsignificant variables. All models included a variable for study site location to account for variation explained due to differences among the 3 study sites.

RESULTS

Avian Species Richness

We detected 43 bird species over all study sites in 2003. Species richness at points ranged from 2 to 19 with a mean of 9.6 (95% CI = 9.2–10.1) species detected per point. Average species richness per point was highest on the Gila National Forest site (11.5, 95% CI = 10.4–12.6), slightly lower on the Coconino National Forest site (9.7, 95% CI = 9.0–10.4), and lowest on the Apache-Sitgreaves National Forest site (8.2, 95% CI = 7.7–8.7). Relationships between avian species richness and vegetation characteristics as well as estimates of effect size were consistent between models of truncated versus full estimates of species richness. The following results, therefore, are based on estimates of full species richness at points.

Elements of general forest structure, as well as abundance of large oak and pine trees, were associated with avian species richness at points (Table 2). Within general forest structure, bird species richness was positively associated with percentage shrub cover and negatively associated with the abundance of trees (all species) 8–15 cm in diameter at breast height. We estimated one more bird species with every 5% increase in shrub cover and one less bird species with an increase of about 17 trees in the 8–15 cm in diameter at breast height size-class.

Ponderosa pine variables added explanatory power ($F_{2,143} = 3.61$, $P = 0.030$). Bird species richness was positively associated with abundance of mature ponderosa pine trees

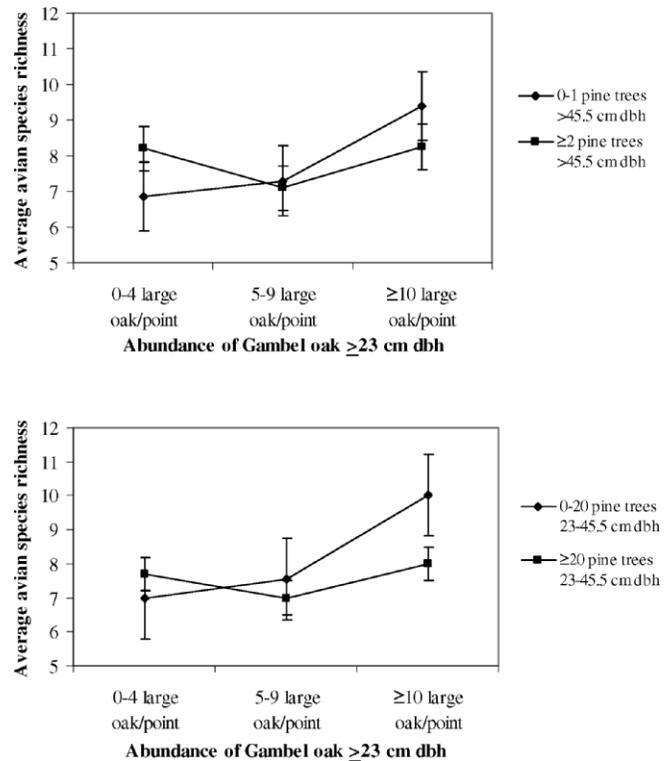


Figure 2. Average number of bird species detected (with 95% CI) and 3 levels of large Gambel oak abundance at different densities of ponderosa pine 23–45.5 cm in diameter at breast height and ponderosa pine >45.5 cm in diameter at breast height at sampling points in pine–oak forest in Arizona and New Mexico, USA, 2003.

>45.5 cm in diameter at breast height with a predicted increase of one bird species with addition of about 3 pine trees in this size class (Table 2). Gambel oak variables were not significantly associated with bird species richness ($F_{5,143} = 1.31$, $P = 0.264$); however, interaction terms between abundance of large oaks and the 2 categories of large pine were ($F_{4,143} = 4.57$, $P = 0.002$; Table 2). To investigate these interactions, we compared mean number of bird species detected at 3 levels of large oak abundance over different densities of pine 23–45.5 cm in diameter at breast height (hereafter, mid-aged pine) and at points with and without pine trees >45.5 cm in diameter at breast height (hereafter, mature pine; Fig. 2). In both cases, when abundance of ponderosa pine was lower, a positive association existed between bird species richness and large oak abundance, which appeared to be weak or absent when density of mid-aged pine was high (>20 trees/point) and when ≥ 2 mature pine trees were present.

Species Occurrence

Virginia's warblers occurred at 22 of 152 points. Within general forest structure, Virginia's warblers were positively associated with abundance of ponderosa pine snags ≥ 23 cm in diameter at breast height (Table 3). The addition of each snag was associated with about a 30% increase in estimated odds of ≥ 1 Virginia's warbler occurring at a point. Virginia's warblers were also associated with Gambel oak variables ($\chi^2_5 = 17.5$, $P = 0.004$). Occurrence of Virginia's warblers at

Table 3. Parameter estimates and standard errors for variables found to be significantly related ($\alpha = 0.05$) to bird species occurrence at points in pine-oak forests in northern Arizona and New Mexico, USA, 2003. We calculated estimates from multiple logistic regression models.

Species and variables	Parameter estimate	SE	P-value
Plumbeous vireo			
Trees 2.5–8 cm dbh	0.044	0.016	0.007
Trees 8–15 cm dbh	-0.064	0.021	0.003
Large oak × pine 23–45.5 cm dbh	-0.019	0.005	<0.001
Large oak × pine >45.5 cm dbh	-0.054	0.02	0.007
Western bluebird			
Ht of tallest tree	0.147	0.053	0.006
Pine snags	-0.295	0.137	0.032
Trees 2.5–8 cm dbh	-0.030	0.011	0.006
Hermit thrush			
% grass	0.061	0.03	0.045
Trees 15–23 cm dbh	0.169	0.065	0.009
Virginia's warbler			
Pine snags	0.259	0.108	0.017
Oak 7–15 cm dbh	0.024	0.009	0.005
Yellow-rumped warbler			
Ht of tallest tree	0.132	0.063	0.038
Trees ≥23 cm dbh	-0.050	0.021	0.016
Large oak	0.103	0.049	0.034
Grace's warbler			
Pine snags	-0.243	0.115	0.035
% shrub cover	0.173	0.089	0.045
Trees 2.5–8 cm dbh	-0.019	0.010	0.050
Red-faced warbler			
Oak 7–15 cm dbh	0.021	0.001	0.020
Black-headed grosbeak			
Oak 7–15 cm dbh	0.020	0.001	0.003

points was positively associated with abundance of pole-sized Gambel oak (7–15 cm dbh) with estimated odds of a Virginia's warbler occurring at a point increasing by approximately 2% with each additional pole-sized oak tree (Table 3). We did not detect Virginia's warblers at any point lacking pole-sized Gambel oak.

Black-headed grosbeaks occurred at 34 of 152 points. No general forest structure variables or ponderosa pine specific variables were associated with their occurrence at points. Occurrence of black-headed grosbeaks at points was associated with Gambel oak characteristics ($\chi^2_5 = 12.6$, $P = 0.027$). The addition of each pole-sized oak tree (7–15 cm dbh) was associated with approximately a 2% increase in estimated odds of ≥1 black-headed grosbeak occurring at a point (Table 3). Similarly, red-faced warblers, which occurred at 15 of 152 points, were not associated with general forest structure or ponderosa pine specific variables. Although adding all oak variables did not provide significant explanatory power ($\chi^2_5 = 9.95$, $P = 0.090$), pole-sized oak showed a positive relationship to red-faced warbler occurrence at points (Table 3). In addition, we did not detect red-faced warblers at any point lacking oak trees in this size class.

Plumbeous vireos occurred at 57 of 152 points. Within general forest structure, estimated odds of a plumbeous vireo occurring at a point increased with abundance of trees 2.5–8 cm in diameter and decreased with increasing abundance of trees 8–15 cm in diameter (Table 3). Interaction terms

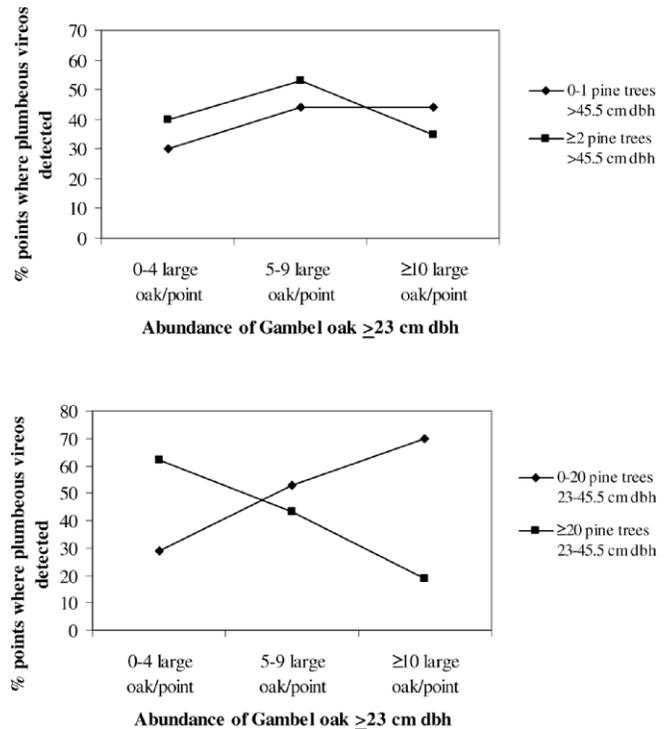


Figure 3. Percentage of points where plumbeous vireos occurred and 3 levels of large Gambel oak abundance over different densities of ponderosa pine 23–45.5 cm in diameter at breast height and ponderosa pine >45.5 cm in diameter at breast height at sampling points in pine-oak forest in Arizona and New Mexico, USA, 2003.

between large oak and pine 23–45.5 cm in diameter at breast height and pine >45.5 cm in diameter at breast height provided additional explanatory power ($\chi^2_5 = 15.4$, $P = 0.008$). Abundance of large Gambel oak appeared to be positively associated with occurrence of plumbeous vireos when density of mid-aged pine was low (Fig. 3). The nature of the interaction between large oak and mature pine was unclear.

Yellow-rumped warblers occurred at 80 of 152 points. Within general forest structure, yellow-rumped warblers were positively associated with height of the tallest tree and negatively associated with number of trees (all species) ≥23 cm in diameter at breast height (Table 3). Although adding all oak-specific variables did not provide significant additional explanatory power ($\chi^2_5 = 7.66$, $P = 0.176$), abundance of large oak trees ≥23 cm in diameter at breast height was positively associated with yellow-rumped warbler occurrence (Table 3). Estimated odds of a yellow-rumped warbler occurring at a point increased by approximately 11% with each additional large oak tree.

Occurrence of 3 species: western bluebirds, hermit thrushes, and Grace's warblers, were associated only with general forest structure characteristics (Table 3). For the remaining species we examined (mountain chickadees and cordilleran flycatchers) no variables showed a significant association with occurrence of these birds at points.

DISCUSSION

Both physiognomic vegetation structure and floristics can influence composition and diversity of bird communities

(MacArthur and MacArthur 1961, Rotenberry 1985). Our findings suggest that in the pine–oak forests we studied, aspects of general forest physiognomic structure as well as oak- and pine-specific floristic characteristics were associated with patterns in avian species richness and occurrence at a local scale. We did not find evidence that spatial arrangement of Gambel oak (i.e., degree to which it occurred in large vs. small clumps) was associated with either bird species richness or species occurrence. However, this finding could be indicative of shortcomings in our methods for characterizing spatial arrangement of oak.

The trends we found between avian species richness and general forest structure (i.e., a positive association between richness and percent shrub cover and a negative association between richness and the density of all trees 8–15 cm dbh) are consistent with results of other studies (Dickson and Segelquist 1979, Szaro and Balda 1982, Rosenstock 1996). Although we considered shrub cover an element of general forest structure, shrub-like Gambel oak was the primary shrub component on our study sites. Therefore, our results could suggest that shrub-like oak in the understory of ponderosa pine forests is associated with increased avian species richness.

The positive association we found between bird species richness and abundance of mature ponderosa pine trees is similar to other studies that suggest a majority of bird species in southwestern ponderosa pine forests prefer mature forest stands (Szaro and Balda 1982, Rosenstock 1996, Moir et al. 1997). In addition, our results suggest that avian species richness increased not only with abundance of mature ponderosa pine trees, but also with abundance of large oak trees in stands where mature pines were absent or scarce and in stands where density of mid-aged ponderosa pine was low. Deciduous Gambel oak canopy in pine stands may allow a larger number of bird species to coexist by providing increased structural complexity (Rosenstock 1998). Structural complexity added by Gambel oak may be particularly important in lower density ponderosa pine stands where pine canopy may be less complex.

Two size-classes of Gambel oak trees, pole-sized oak and large oak, were associated with increased occurrence of some bird species at a local scale. Pole-sized oak was positively associated with occurrence of black-headed grosbeaks, Virginia's warblers, and red-faced warblers at points. We detected each of these species most often in areas with high densities of oak in this size class. Rosenstock (1998) reported that Virginia's warblers and red-faced warblers were absent in ponderosa pine stands that lacked a Gambel oak component. We did not detect red-faced or Virginia's warblers at points lacking pole-sized oak, suggesting that in ponderosa pine-dominated forests, occurrence of these species may be tied not only to Gambel oak, but to pole-sized oak trees.

Swanson et al. (2000) found that Virginia's warblers in South Dakota were associated with dense shrub cover, often Gambel oak, and that mid-sized trees were heavily used by singing males as perches. At our study sites, pole-sized oak

typically occurred in dense clumps with smaller shrub-like oak in the understory. Dense leaf litter associated with these oak clumps could conceal nests of these ground-nesting warblers and pole-sized oak could provide cover, foraging opportunities, and singing perches near nest sites. The positive association we found between Virginia's warblers and ponderosa pine snags could be due to the tendency of Gambel oak to colonize areas where pine trees have died (Moir et al. 1997).

We found some evidence that 2 bird species were associated with abundance of large Gambel oak. Where density of mid-aged pine was low, occurrence of plumbeous vireos appeared to be positively associated with abundance of large Gambel oak. We also found evidence that yellow-rumped warblers were positively associated with abundance of large oak trees. Other studies (e.g., Szaro and Balda 1979, Lesh 1999) have suggested that plumbeous vireos and yellow-rumped warblers were associated with Gambel oak. Occurrence of these 2 species was not contingent upon presence of large oak, however, and both species occurred at points with 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.

Although we did not measure insect abundance, oak trees tend to support a higher abundance of insects than do coniferous tree species, and in some eastern pine–oak forests, arthropod abundance in oak-dominated stands will peak earlier in the breeding season than in pine-dominated stands (Southwood 1961, Brush and Stiles 1986). Although we are unaware of research comparing timing of peak arthropod abundance in Gambel oak versus 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 food resources occurring on oaks earlier in the breeding season could provide more attractive breeding territories.

MANAGEMENT IMPLICATIONS

Maintaining a mosaic of forest openings in pine–oak forests, especially by using prescribed burns, would stimulate Gambel oak regeneration and could encourage growth of pole-sized oak trees that our results suggest are important to some bird species (Clary and Tiedemann 1992). Little is known, however, about effects of prescribed burning on existing oak trees and regenerating oak can fail to grow into trees if plants are repeatedly browsed or grazed (Harper et al. 1985, Ryniker et al. 2006). Because large oak trees appear to contribute structural complexity important to some birds, particularly when large pine trees are absent or scarce, maintenance of canopy gaps in stands where mid-sized oak are approaching maturity may be desirable. Until natural fire regimes that maintain forest openings can be reestablished, gaps could be created through selective harvest (Ganey and Vojta 2004). Trees selected for removal should be limited to

those that threaten continued growth of oak trees close to attaining a desired size. Because ponderosa pine trees >45.5 cm in diameter at breast height were associated with high bird species richness, ponderosa pine trees in this size class should not be removed.

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