The Condor 100:485–492

INFLUENCE OF GAMBEL OAK ON BREEDING BIRDS IN PONDEROSA PINE FORESTS OF NORTHERN ARIZONA[1]

STEVEN S. ROSENSTOCK
Arizona Game and Fish Department, Research Branch - WMRS, 2221 W. Greenway Rd., Phoenix, AZ 85023, e-mail: ssr@usgs.nau.edu

Abstract. Gambel oak (*Quercus gambelii*) is widely distributed in the Southwestern United States, where it frequently occurs in association with ponderosa pine (*Pinus ponderosa*). Fire suppression and fuelwood harvest likely have reduced oak abundance within the pine-oak type. Gambel oak occurs in multiple age-related growth forms, from small shrubs to large, old trees, and may provide important foraging and nesting habitat for breeding birds. I compared attributes of breeding bird communities in 16 northern Arizona ponderosa pine stands from 1993–1995, that were structurally similar except for the presence or absence of Gambel oak. Overlap in bird species composition was high; pine and pine-oak stands had a mean Jaccard similarity value of 0.67. Five species were unique to pine stands, whereas 10 species were largely restricted to or only found in pine-oak stands. Overall bird diversity was significantly higher in pine-oak stands, which also had more species of Neotropical migrants, ground nesters, primary cavity excavators, and secondary cavity users than did pine stands. Pine and pine-oak stands had similar species evenness and similar rates of annual species turnover. Total bird abundance did not differ between cover types; however, primary cavity excavators were more abundant in pine-oak stands. Because of the apparent positive influence of oak on breeding birds, forest managers are encouraged to use treatments that retain and enhance the various growth forms of Gambel oak found in pine-oak stands.

Key words: breeding birds, community structure, forest management, Gambel oak, Pinus ponderosa, *ponderosa pine,* Quercus gambelii.

INTRODUCTION

Gambel oak (*Quercus gambelii*) is widely distributed in lower transition zone vegetation types of Southwestern North America, primarily in Colorado, Utah, Arizona, and New Mexico (Harper et al. 1985). At elevations of 2,000–2,800 m, Gambel oak frequently is associated with ponderosa pine (*Pinus ponderosa*) (Hanks et al. 1983). In central and northern Arizona, pure ponderosa pine stands have relatively simple physiognomy, consisting of various-aged ponderosa pine trees and an open herbaceous understory (Hanks et al. 1983). Where Gambel oak is present, it dramatically changes the structure of the stand. Gambel oak occurs in multiple age-related growth forms, including shrub-like young plants, saplings, and trees up to 90 cm in diameter. In some pine-oak stands, Gambel oak may comprise up to 30% of total tree basal area (Reynolds et al. 1970).

For many years, Gambel oak was considered a "pest" species and considerable effort was devoted to oak control (Engle et al. 1983, Lauver et al. 1989). Because of its high heat content and availability near human population centers, Gambel oak is a popular source of fuelwood (Wagstaff 1984). However, Reynolds et al. (1970) suggested that timber harvest and other management practices could negatively impact wildlife associated with pine-oak stands. Recently, the management of Gambel oak in Southwestern forests has become an important issue. Loss of oaks, particularly large, old trees, may have negative impacts on passerine birds, raptors, and other wildlife (U.S. Fish and Wildlife Service 1995, Block and Finch 1997). Fire suppression has dramatically increased the density of Southwestern ponderosa pine stands (Harrington and Sackett 1992, Covington and Moore 1994), which also may have contributed to oak declines in the pine-oak type (Moir et al. 1997).

Birds have evolved a high degree of habitat selectivity, using habitat features that increase survival and reproductive output (Cody 1985). An important consequence of this selectivity is the strong influence of habitat composition and physiognomy on avian populations and communities (Robinson and Holmes 1984, Wiens

[1] Received 27 October 1997. Accepted 14 April 1998.

TABLE 1. Habitat characteristics of 16 ponderosa pine and ponderosa pine-Gambel oak stands in northern Arizona, 1993–1995 (Rosenstock 1996). Values are medians for (n = 8) stands representing each cover type. All Z-values are nonsignificant (Mann-Whitney U-test, $P > 0.05$).

Habitat variable	Pine	Pine-oak	Z-value
Tree density (trees ha^{-1})			
Ponderosa pine	769.7	521.6	−1.36
Gambel oak	0.0	168.2	
Canopy cover (%)			
Ponderosa pine	45.9	38.1	−1.09
Gambel oak	0.0	7.4	
Quadratic mean diameter (cm)			
Ponderosa pine	26.7	23.4	−0.61
Gambel oak	—	18.8	
Basal area (m^2 ha^{-1})			
Ponderosa pine	26.3	18.1	−1.02
Gambel oak	0.0	3.8	
Snag density (no. ha^{-1})	3.7	3.7	−0.03

1989). Studies in other North American forests have found that the presence and physiognomy of deciduous trees in a conifer stand affect breeding bird abundance and community composition (Morrison and Meslow 1984, Dickson et al. 1995). Brawn and Balda (1988b) and O'Brien (1990) suggested that Gambel oak might similarly influence breeding bird communities in ponderosa pine forests of northern Arizona.

This study was initiated in 1993 as part of a larger project examining habitat relationships of breeding passerine birds in ponderosa pine forests of northern Arizona (Rosenstock 1996). My objective in the present study was to quantify the influence of Gambel oak on breeding bird communities. I predicted that the presence of Gambel oak would alter the composition of the breeding avifauna, and that it also would increase avian abundance and diversity. My null hypothesis was that there were no significant differences in bird community variables between ponderosa pine stands that were structurally similar except for the presence or absence of Gambel oak.

METHODS

STUDY AREA

Research was conducted on the Coconino National Forest and Camp Navajo, an Arizona Army National Guard facility. Both study areas were within a 60-km radius of Flagstaff, Arizona. The study areas have a long history of commercial sawtimber harvest, beginning in the late 1800s (Scurlock and Finch 1997). Common silvicultural treatments have included single-tree selection, shelterwood, group selection, patch cuts, and pre-commercial thinning (Schubert 1974). Non-sawtimber products (pulp, fuelwood, poles, and Christmas trees) have comprised a large proportion of wood fiber harvest in recent years (Raish et al. 1997). Wildfires on the study areas have been actively suppressed since the late 1800s. Prescribed fire was used in some areas, primarily for removal of woody debris resulting from timber harvest and thinning activities. The study areas have been grazed in summer by domestic livestock (primarily cattle) since the 1800s.

Data were collected from 1993–1995 in 16 stands representing two naturally occurring forest cover types: ponderosa pine and ponderosa pine-Gambel oak. Both cover types had an herbaceous understory dominated by grasses, primarily Arizona fescue (*Festuca arizonica*) or blue grama (*Bouteloua gracilis*). Eight stands were located within the pine cover type, and eight were in the pine-oak type. Stands were defined as contiguous areas of structurally similar forest ≥ 20 ha in size. Study stands in both cover types occurred on similar aspects and topographic positions, and on sites of comparable growth potential (site index). The two groups of stands were not significantly different with respect to the density of ponderosa pine, pine canopy cover, pine diameter, pine basal area, and density of snags (Table 1). These habitat variables were correlated with many breeding bird community attributes across a larger set of study stands (Rosenstock 1996). Stands in the pine-

TABLE 2. Density of Gambel oaks by growth form in ponderosa pine-Gambel oak stands in northern Arizona, 1993–1995. Values are medians for eight stands representing this cover type.

Growth form	Diameter at root collar (cm)	Stems ha^{-1}
Shrub-like	<2.5	230.8
Small tree	2.5–20.0	95.3
Mature tree	20.0–38.0	76.3
Large, old tree	>38.0	7.6

oak cover type had a well-developed Gambel oak component that included shrub-like and tree growth forms (Table 2). Gambel oak was absent from all stands in the pine cover type. To minimize potential confounding by recent habitat disturbance, I selected study stands that had no fire, commercial sawtimber harvest, or other silvicultural activity for ≥ 5 years prior to, and throughout the duration of the study.

AVIAN SAMPLING

Within each stand, I established eight bird sampling stations originating at a random location. This sample size yielded stable estimates of abundance and diversity in other western montane forests, including ponderosa pine (Morrison et al. 1981). Stations were spaced 200 m apart along two parallel transect lines, also spaced 200 m apart. Breeding birds were sampled using 100-m radius point counts (Ralph et al. 1995). Observers counted all birds seen or heard, and estimated their distance to the nearest 5 m, using marked trees at known distances as a reference. Each stand was visited three times during the peak breeding season (June 1–July 10), once by each of three observers. Counts were 8 min long and conducted within the 3-hr period beginning 30 min after sunrise. Counts were not done during periods of wind (> 15 km hr^{-1}) or rain, that could alter avian activity or detectability. To reduce interobserver variability, field personnel received extensive training in bird identification and point count methodology (Kepler and Scott 1981).

For many species, frequency distributions of observation distances violated assumptions of commonly used density estimators (Buckland et al. 1993). Therefore, I used total counts (Verner and Ritter 1985, Raphael 1987) to derive an index of avian density. To minimize repeat counts of individual birds from adjacent stations, I removed all detections beyond 75 m from the data set. "Flyover" observations and birds identified as juveniles also were excluded from analysis. Density index values were calculated as the mean number of individuals observed in each stand across the three annual census visits, divided by the total area sampled.

DATA ANALYSIS

Similarity in bird species composition between stands in pine and pine-oak cover types was measured with Jaccard's Index (*J*) (Ludwig and Reynolds 1988). Total density was calculated as summed density index values for all species present within a stand. Metrics describing diversity, evenness, and species turnover were used to quantify community structure. I used Hill's diversity number N1 as a measure of species diversity. N1 represents the number of "abundant" species in a given sample, and is more directly interpretable than dimensionless diversity indices (Ludwig and Reynolds 1988). The modified Hill's ratio E5 was used as a measure of evenness among species' relative abundances. E5 approaches zero as a single species becomes numerically dominant, and unlike other commonly-used evenness indices, is relatively insensitive to differences in species richness (Ludwig and Reynolds 1988). Percent annual turnover in overall species composition was calculated following Diamond (1969).

I divided breeding avifauna into two classes based upon migration patterns. Classes were: (1) species that occur year-round in the study area or migrate short distances to wintering habitats within the continental U.S. (hereafter referred to as residents), and (2) species that migrate into Mexico and Central America (Neotropical migrants). I also classified the breeding avifauna with respect to nest location (ground, foliage, or tree cavity). Cavity nesters were further divided into species that excavate their own nest cavities (cavity excavators) and species that use previously excavated cavities (secondary cavity users). Finally, I examined the subset of breeding species that forage primarily by gleaning insects from tree and shrub foliage (foliage gleaners). Guild assignments were based upon Szaro and Balda (1979), Ehrlich et al. (1988), Corman (1996), and observational data collected during this study.

I used repeated measures analysis of variance (Neter et al. 1990) to compare bird assemblage variables between pine and pine-oak cover types, using stands as replicates, cover type as the main effect, and year as the repeated measures factor. Interactions were tested with the multivariate Wilk's Lambda statistic. Main effects and interactions were considered significant at $P \leq 0.05$.

RESULTS

SPECIES COMPOSITION

I observed 42 breeding bird species during point counts (Table 3); of these, 25 were resident species and 17 were Neotropical migrants. Seven species were ground nesters, 20 were foliage nesters, 5 were cavity excavators, 9 were secondary cavity users, and 1 parasitized ground and foliage nests of other species (Table 3).

A total of 36 breeding bird species was found in the pine cover type, and 37 species in pine-oak. Overlap in species composition between cover types was high, mean ($\pm$ SE) similarity between pine and pine-oak stands was $J = 0.67 \pm 0.01$. Nineteen species were present in nearly all stands in both cover types (Broad-tailed Hummingbird, Northern Flicker, Hairy Woodpecker, Western Wood-pewee, Violet-green Swallow, Steller's Jay, Mountain Chickadee, White-breasted Nuthatch, Pygmy Nuthatch, Western Bluebird, American Robin, Plumbeous Vireo, Yellow-rumped Warbler, Grace's Warbler, Dark-eyed Junco, Brown-headed Cowbird, Western Tanager, Pine Siskin, and Red Crossbill [scientific names are given in Table 3]).

Pine-oak stands had more distinct species composition than did pine stands. Ten species occurred more frequently in, or were restricted to, pine-oak stands (Acorn Woodpecker, Downy Woodpecker, Cordilleran Flycatcher, House Wren, Rock Wren, Ruby-crowned Kinglet, Warbling Vireo, Virginia's Warbler, Red-faced Warbler, and Black-headed Grosbeak). In contrast, five species (Williamson's Sapsucker, Clark's Nutcracker, Red-breasted Nuthatch, Hepatic Tanager, and Cassin's Finch) were detected only in pine stands (Table 3).

DIVERSITY

Breeding bird diversity was higher ($F_{1,14} = 16.7$, $P < 0.001$) in pine-oak compared to pine stands (Table 4). Pine-oak stands also had more species of Neotropical migrants ($F_{1,14} = 12.1$, $P < 0.01$), ground nesters ($F_{1,14} = 5.4$, $P < 0.05$), cavity excavators ($F_{1,14} = 4.5$, $P < 0.05$), and secondary cavity users ($F_{1,14} = 9.0$, $P < 0.01$) than did pine stands. Species richness of residents varied among years ($F_{2,28} = 12.1$, $P < 0.01$). Species richness did not differ between cover types for resident species ($F_{1,14} = 2.5$, $P > 0.05$), foliage gleaners ($F_{1,14} = 3.8$, $P > 0.05$), and foliage nesters ($F_{1,14} = 1.5$). Pine and pine-oak stands also were not significantly different with respect to evenness ($F_{1,14} = 0.6$) and annual species turnover ($F_{1,14} = 0.1$). All year x cover type interactions for the above response variables were nonsignificant ($P > 0.05$).

DENSITY

The most abundant birds in both cover types were resident species (Table 4). Cavity excavators were significantly more abundant in pine-oak stands ($F_{1,14} = 4.4$, $P < 0.05$). Total bird density did not differ between the two cover types ($F_{1,14} = 0.5$), but varied among years ($F_{2,28} = 6.3$, $P < 0.01$). Pine and pine-oak stands also did not differ with respect to density index values for resident species ($F_{1,14} = 0.8$), Neotropical migrants ($F_{1,14} = 0.1$), ground nesters ($F_{1,14} = 1.1$), foliage nesters ($F_{1,14} = 0.3$), secondary cavity users ($F_{1,14} = 0.01$), and foliage gleaners ($F_{1,14} = 0.8$). Density index values varied among years for resident species ($F_{2,28} = 11.0$, $P < 0.001$), ground nesters ($F_{2,28} = 6.7$, $P < 0.01$), and foliage gleaners ($F_{2,28} = 4.7$, $P < 0.05$). Year x cover type interactions were nonsignificant ($P > 0.05$) for all bird density variables.

DISCUSSION

My results suggest that although ponderosa pine and ponderosa pine-Gambel oak forest stands in northern Arizona support similar breeding bird assemblages, they differ with respect to species composition and diversity. Previous studies in northern Arizona forests have reported apparent correlations between bird abundance and Gambel oak. O'Brien (1990) reported that three secondary cavity nesters (Pygmy Nuthatch, White-breasted Nuthatch, and Mountain Chickadee) were more abundant in a study area that had a more well-developed Gambel oak component, compared to another site with fewer oaks. Brawn and Balda (1988b) found that insectivorous bird species were more abundant on a study plot with higher Gambel oak density, compared to another plot that had fewer oaks, but similar numbers of live pines and snags.

Unmeasured habitat characteristics or abiotic

TABLE 3. Migratory pattern, nest location, and occurrence (number of stands) of 42 breeding bird species found in northern Arizona ponderosa pine (n = 8) and ponderosa pine-Gambel oak (n = 8) stands, 1993–1995. Species classified as foliage gleaners are followed by (f).

Common name	Species	Mig.[a]	Nest[b]	Occurrence	
				Pine	Pine-oak
Band-tailed Pigeon	*Columba fasciata*	N	F	2	2
Mourning Dove	*Zenaida macroura*	R	G	5	8
Broad-tailed Hummingbird	*Selasphorus platycercus*	N	F	8	8
Northern Flicker	*Colaptes auratus*	R	PC	8	8
Acorn Woodpecker	*Melanerpes formicivorus*	R	PC	2	6
Williamson's Sapsucker	*Sphyrapicus thyroideus*	R	PC	2	0
Downy Woodpecker	*Picoides pubescens*	R	PC	0	3
Hairy Woodpecker	*Picoides villosus*	R	PC	7	8
Olive-sided Flycatcher	*Contopus borealis*	N	F	3	1
Western Wood-pewee	*Contopus sordidulus*	N	F	6	7
Cordilleran Flycatcher	*Empidonax occidentalis*	N	SC	4	8
Violet-green Swallow	*Tachycineta thalassina*	N	SC	6	8
Steller's Jay	*Cyanocitta stelleri*	R	F	8	8
Clark's Nutcracker	*Nucifraga columbiana*	R	F	4	0
Mountain Chickadee (f)	*Parus gambeli*	R	SC	8	8
Brown Creeper	*Certhia americana*	R	SC[c]	5	8
White-breasted Nuthatch	*Sitta carolinensis*	R	SC	8	8
Red-breasted Nuthatch	*Sitta canadensis*	R	SC	1	0
Pygmy Nuthatch (f)	*Sitta pygmaea*	R	SC	8	8
House Wren (f)	*Troglodytes aedon*	N	SC	0	4
Rock Wren	*Salpinctes obsoletus*	R	G	0	1
Ruby-crowned Kinglet (f)	*Regulus calendula*	R	F	0	1
Western Bluebird	*Sialia mexicana*	R	SC	8	8
Townsend's Solitaire	*Myadestes townsendi*	R	G	4	5
Hermit Thrush	*Catharus guttatus*	R	G	4	6
American Robin	*Turdus migratorius*	R	F	8	8
Plumbeous Vireo (f)	*Vireo solitarius*	N	F	8	8
Warbling Vireo (f)	*Vireo gilvus*	N	F	0	1
Virginia's Warbler (f)	*Vermivora virginiae*	N	G	0	4
Yellow-rumped Warbler (f)	*Dendroica coronata*	R	F	8	8
Grace's Warbler (f)	*Dendroica graciae*	N	F	8	7
Red-faced Warbler (f)	*Cardellina rubrifrons*	N	G	0	5
Olive Warbler (f)	*Peucedramus taeniatus*	N	F	2	3
Black-headed Grosbeak	*Pheucticus melanocephalus*	N	F	2	7
Chipping Sparrow	*Spizella passerina*	N	F	3	5
Dark-eyed Junco	*Junco hyemalis*	R	G	8	8
Brown-headed Cowbird	*Molothrus ater*	R	—[d]	8	8
Western Tanager (f)	*Piranga ludoviciana*	N	F	8	8
Hepatic Tanager (f)	*Piranga flava*	N	F	1	0
Pine Siskin (f)	*Carduelis pinus*	R	F	7	7
Red Crossbill	*Loxia curvirostra*	R	F	8	8
Cassin's Finch	*Carpodacus cassinii*	R	F	2	0

[a] Migratory pattern: N = Neotropical migrant, R = resident.
[b] Nest location: F = foliage, G = ground, PC = cavity excavator, SC = secondary cavity user.
[c] Uses naturally-occurring cavities under loose bark.
[d] Nest parasite, places its eggs in nests of other species, usually in foliage or on the ground.

factors may have influenced apparent differences in breeding bird assemblages between pine and pine-oak stands. Although not statistically significant, the two groups of stands differed in the density and basal area of ponderosa pine, which may have affected habitat suitability for some species. However, stands were quite similar with respect to pine canopy cover, pine diameter, and snag density; habitat characteristics that were correlated with many breeding bird community attributes across a larger set of study areas (Rosenstock 1996). Therefore, the observed differences were due at least in part to the presence or absence of Gambel oak.

The influence of Gambel oak on breeding birds likely is due to the additional nesting and

TABLE 4. Means (± SE) of variables describing breeding bird communities in ponderosa pine (n = 8) and ponderosa pine-Gambel oak (n = 8) stands in northern Arizona, 1993–1995.

Variable	Pine	Pine-oak
Diversity[a]	13.64 ± 0.37	17.00 ± 0.50
Evenness[b]	0.84 ± 0.03	0.88 ± 0.03
Species turnover (%)[c]	17.67 ± 1.44	16.81 ± 1.33
Density index (birds ha^{-1})		
All birds	4.90 ± 0.26	5.29 ± 0.25
Residents	3.50 ± 0.17	3.78 ± 0.18
Neotropical migrants	1.39 ± 0.12	1.51 ± 0.12
Ground nesters	0.60 ± 0.04	0.69 ± 0.06
Foliage nesters	1.16 ± 0.09	1.27 ± 0.10
Cavity excavators	0.25 ± 0.03	0.34 ± 0.04
Secondary cavity users	2.02 ± 0.19	1.94 ± 0.11
Foliage gleaners	2.38 ± 0.13	2.63 ± 0.16
Species richness		
Residents	13.38 ± 0.48	14.42 ± 0.41
Neotropical migrants	6.23 ± 0.29	8.58 ± 0.39
Ground nesters	1.90 ± 0.14	2.67 ± 0.21
Foliage nesters	10.38 ± 0.35	11.13 ± 0.31
Cavity excavators	1.75 ± 0.20	2.46 ± 0.15
Secondary cavity users	4.33 ± 0.18	5.08 ± 0.12
Foliage gleaners	6.29 ± 1.25	7.33 ± 0.30

[a] Hill's N1, an index reflecting the number of abundant species (Ludwig and Reynolds 1988).
[b] Hill's E5, an index of equitability among species. E5 approaches zero as one species becomes numerically dominant (Ludwig and Reynolds 1988).
[c] Percent change in total species composition from year to year (Diamond 1969).

foraging substrates that oaks provide for ground, foliage, and canopy nesting species. Ground nesting species, such as Virginia's Warbler (Zyskowski 1993) and Red-faced Warbler (pers. observ.) commonly place their nests under small, shrub-like oaks. Although we did not conduct nest searches, oaks likely were used by foliage nesting species found in the pine-oak cover type. The multiple layers of deciduous foliage provided by Gambel oak increase potential nest sites, and may thereby increase species diversity (Martin 1988).

Gambel oak also is used by cavity excavators and secondary cavity users. Compared to ponderosa pine, smaller oak trees provide usable substrates for cavity nesters. Mean diameters of oaks and pines used by cavity nesters in northern Arizona were 38 and 71 cm, respectively (Cunningham et al. 1980). Live oaks often contain nest cavities, which are comparatively uncommon in live ponderosa pines (Rosenstock 1996). In ponderosa pine forests of northern Arizona, nest sites apparently are limiting for some cavity nesting species (Brawn and Balda 1988a), which have been adversely affected by historical management practices that reduced the abundance of snags (Brawn and Balda 1988b). The presence of an alternate cavity substrate in Gambel oak may increase the diversity and abundance of cavity nesting species. Gambel oak may be particularly important to cavity nesters in areas where pine snags are uncommon (Cunningham et al. 1980).

Gambel oaks also provide foraging substrates for foliage and bark gleaning birds. Oaks on the study areas were used as foraging substrates by numerous species, including Red-faced Warbler, Mountain Chickadee, Pygmy Nuthatch, White-breasted Nuthatch, Plumbeous Vireo, Virginia's Warbler, Grace's Warbler, Yellow-rumped Warbler, and Western Tanager (pers. observ.). Szaro and Balda (1979) found that 15 breeding bird species generally used Gambel oak foliage in greater proportion than its availability. Because oak foliage supports more insect species (Southwood 1961) and greater insect biomass than does pine (Clary 1978), Gambel oak may be a preferred or higher quality foraging substrate for foliage gleaning birds. Studies elsewhere have found that the presence of a deciduous tree foraging substrate affects avian community structure and species diversity (Robinson and Holmes 1984).

Results of this study have implications for future research and management in Southwestern ponderosa pine forests. The differences I found may be limited to the season and geographic area encompassed by my research. Therefore, studies of bird communities need to be undertaken during migration and winter periods, as well as in other forest types that have a Gambel oak component. Because Gambel oak appears to be an important habitat component, studies are needed to quantify specific resources provided by oaks, and their use by nesting and foraging birds.

Compared to pure ponderosa pine stands, pine-oak stands had higher breeding bird diversity and more species of Neotropical migrants, ground nesters, primary cavity excavators, and secondary cavity users. Five Neotropical migrants that were considerably more common in, or restricted to the pine-oak cover type are species of special management concern in Arizona and New Mexico (Cordilleran Flycatcher, Warbling Vireo, Virginia's Warbler, Red-faced Warbler, and Black-headed Grosbeak; Hall et al. 1997). Because of their apparent value to breeding birds, pine-oak stands should be given special consideration in management planning. I recommend that managers provide a mix of Gambel oak growth forms, by (1) retaining and recruiting mature and old-growth oaks wherever possible, and (2) using prescribed fire and other treatments that enhance regeneration and recruitment of younger growth forms of oak.

ACKNOWLEDGMENTS

This study was undertaken with funds from the Federal Aid in Wildlife Restoration Act, Project W-78-R, of the Arizona Game and Fish Department, and a grant from the Arizona Game and Fish Department Heritage Fund. Project cooperators with the USDA Forest Service and Arizona Army National Guard (Greg Goodwin, Heather Green, Don Hack, Sandy Nagiller, Dick Tinus, Mark Whitney, and Mark Wirtanen) provided valuable help selecting study areas. Terry Frederick, Tricia Hurley, Tammi Lesh, Amparo Rifa, and Diana Wotherspoon assisted with collection of point count and habitat data. Warren Ballard, Bill Block, Carol Chambers, Susi MacVean, and two anonymous reviewers provided constructive reviews of the draft manuscript.

LITERATURE CITED

BLOCK, W. M., AND D. M. FINCH [eds.]. 1997. Songbird ecology in southwestern ponderosa pine forests: a literature review. USDA For. Serv. Gen. Tech. Rep. RM-292, Fort Collins, CO.

BRAWN, J. D., AND R. P. BALDA. 1988a. Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities? Condor 90:61–71.

BRAWN, J. D., AND R. P. BALDA. 1988b. The influence of silvicultural activity on ponderosa pine forest bird communities in the southwestern United States, p. 3–21. *In* J. A. Jackson [ed.], Bird conservation 3. Univ. Wisconsin Press, Madison, WI.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, AND J. L. LAAKE. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, New York.

CLARY, W. P. 1978. Producer-consumer biomass in Arizona ponderosa pine. USDA For. Serv. Gen. Tech. Rep. RM-56, Fort Collins, CO.

CODY, M. L. 1985. An introduction to habitat selection in birds, p. 4–46. *In* M. L. Cody [ed.], Habitat selection in birds. Academic Press, San Diego, CA.

CORMAN, T. E. 1996. Neotropical migratory birds of Arizona (revised). Unpubl. Rep. Arizona Game and Fish Dept., Nongame Branch, Phoenix, AZ.

COVINGTON, W. W., AND M. M. MOORE. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. J. Forestry 92:39–47.

CUNNINGHAM, J. B., R. P. BALDA, AND W. S. GAUD. 1980. Selection and use of snags by cavity-nesting birds of the ponderosa pine forest. USDA For. Serv. Res. Pap. RM-222, Fort Collins, CO.

DIAMOND, J. M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proc. Natl. Acad. Sci. 69:3199–3203.

DICKSON, J. G., F. R. THOMPSON III, R. N. CONNER, AND K. E. FRANZREB. 1995. Silviculture in central and southeastern oak-pine forests, p. 245–266. *In* T. E. Martin and D. M. Finch [eds.], Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford Univ. Press, New York.

EHRLICH, P. A., D. S. DOBKIN, AND D. WHEYE. 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon and Schuster, New York.

ENGLE, D. M., C. D. BONHAM, AND L. E. BARTEL. 1983. Ecological characteristics and control of Gambel oak. J. Range Manage. 36:363–365.

HALL, L. S., M. L. MORRISON, AND W. M. BLOCK. 1997. Songbird status and roles, p. 69–88. *In* W. M. Block, and D. M. Finch [eds.], Songbird ecology in southwestern ponderosa pine forests: a literature review. USDA For. Serv. Gen. Tech. Rep. RM-292, Fort Collins, CO.

HANKS, J. P., E. L. FITZHUGH, AND S. R. HANKS. 1983. A habitat type classification for ponderosa pine forests of northern Arizona. USDA For. Serv. Gen. Tech. Rep. RM-97, Fort Collins, CO.

HARPER, K. T., F. J. WAGSTAFF, AND L. M. KUNZLER. 1985. Biology and management of the Gambel oak vegetative type: a literature review. USDA For. Serv. Gen. Tech. Rep. INT-179, Ogden, UT.

HARRINGTON, M. G., AND S. G. SACKETT. 1992. Past and present fire influences on southwestern ponderosa pine old growth, p. 44–50. *In* W. R. Kaufman, W. H. Moir, and R. L. Bassett [tech. coordinators], Old-growth forests in the Southwest and Rocky Mountain regions; proceedings of a workshop. USDA For. Serv. Gen. Tech. Rep. RM-213, Fort Collins, CO.

KEPLER, C. B., AND J. M. SCOTT. 1981. Reducing count variability by training observers. Stud. Avian Biol. 6:366–371.

LAUVER, C. L., D. A. JAMESON, AND L. R. RITTENHOUSE. 1989. Management strategies for Gambel oak communities. Rangelands 11:213–216.

LUDWIG, J. A., AND J. F. REYNOLDS. 1988. Statistical ecology: a primer on methods and computing. John Wiley and Sons, New York.

MARTIN, T. E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? Ecology 69:74–84.

MOIR, W. H., B. GEILS, M. A. BENOIT, AND D. SCURLOCK. 1997. Ecology of southwestern ponderosa pine forests, p. 3–27. *In* W. M. Block, and D. M. Finch [eds.], Songbird ecology in southwestern ponderosa pine forests: a literature review. USDA For. Serv. Gen. Tech. Rep. RM-292, Fort Collins, CO.

MORRISON, M. L., R. W. MANNAN, AND G. L. DORSEY. 1981. Effects of number of circular plots on estimates of avian density and species richness. Stud. Avian Biol. 6:405–408.

MORRISON, M. L., AND E. C. MESLOW. 1984. Response of avian communities to herbicide-induced vegetation changes. J. Wildl. Manage. 48:14–22.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied linear statistical models. 3rd ed. Irwin, Boston.

O'BRIEN, R. A. 1990. Assessment of nongame bird habitat using forest survey data. USDA For. Serv. Res. Pap. INT-431, Ogden, UT.

RAISH, C., W. YONG, AND J. MARZLUFF. 1997. Contemporary human use of southwestern ponderosa pine forests, p. 28–42. *In* W. M. Block, and D. M. Finch [eds.], Songbird ecology in southwestern ponderosa pine forests: a literature review. USDA For. Serv. Gen. Tech. Rep. RM-292, Fort Collins, CO.

RALPH, C. J., S. DROEGE, AND J. R. SAUER. 1995. Managing and monitoring birds using point counts: standards and applications, p. 161–168. *In* C. J. Ralph, S. Droege, and J. R. Sauer [eds.], Monitoring bird populations by point counts. USDA For. Serv. Gen. Tech Rep. PSW-149, Albany, CA.

RAPHAEL, M. G. 1987. Estimating relative abundance of forest birds: simple versus adjusted counts. Wilson Bull. 99:125–131.

REYNOLDS, H. G., W. P. CLARY, AND P. F. FFOLLIOTT. 1970. Gambel oak for Southwestern wildlife. J. Forestry 68:545-547.

ROBINSON, S. K., AND R. T. HOLMES. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101:672–684.

ROSENSTOCK, S. S. 1996. Habitat relationships of breeding birds in northern Arizona ponderosa pine and pine-oak forests. Arizona Game and Fish Dept. Tech. Rep. 23, Phoenix, AZ.

SCHUBERT, G. H. 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. USDA For. Serv. Res. Pap. RM-123, Fort Collins, CO.

SCURLOCK, D., AND D. M. FINCH. 1997. A historical perspective, p. 43–68. *In* W. M. Block, and D. M. Finch [eds.], Songbird ecology in southwestern ponderosa pine forests: a literature review. USDA For. Serv. Gen. Tech. Rep. RM-292, Fort Collins, CO.

SOUTHWOOD, T. R. E. 1961. The number of insect species associated with various trees. J. Anim. Ecol. 30:1–8.

SZARO, R. C., AND R. P. BALDA. 1979. Bird community dynamics in a ponderosa pine forest. Stud. Avian Biol. 3:1–66.

U.S. FISH AND WILDLIFE SERVICE. 1995. Recovery plan for the Mexican Spotted Owl. Vol. I. Albuquerque, NM.

VERNER, J., AND L. V. RITTER. 1985. A comparison of transects and point counts in oak-pine woodlands of California. Condor 87:47–68.

WAGSTAFF, F. J. 1984. Economic considerations in use and management of Gambel oak for fuelwood. USDA For. Serv. Gen. Tech. Rep. INT-165, Ogden, UT.

WIENS, J. A. 1989. The ecology of bird communities. Vol. I: Foundations and patterns. Cambridge Univ. Press, New York.

ZYSKOWSKI, K. 1993. Nest-site placement in Orange-crowned and Virginia's Warblers in high-elevation forests of the Mogollon Rim (Arizona): variation in nest placement, phenology, and microclimate. M.Sc. thesis, Univ. Arkansas, Fayetteville, AR.