The Condor 89:614–626

BREEDING BIRD POPULATIONS DURING TWENTY-FIVE YEARS OF POSTFIRE SUCCESSION IN THE SIERRA NEVADA[1]

MARTIN G. RAPHAEL
Rocky Mountain Forest and Range Experiment Station, 222 South 22nd Street, Laramie, WY 82070

MICHAEL L. MORRISON AND MICHAEL P. YODER-WILLIAMS[2]
Department of Forestry and Resource Management, University of California, Berkeley, CA 94720

Abstract. We summarized breeding bird censuses done from 1966 to 1985 on two Sierra Nevada forest plots, one that was burned in 1960 and an adjacent, unburned control. Our objective was to examine yearly trends in bird abundance in relation to changing vegetation structure and composition and in relation to yearly weather variation. From 1969 to 1983 shrub cover on the burned plot increased from about 22% to over 43%, and density of overstory trees increased by about 50%. Herb and grass cover decreased during this period, as did density of snags originally resulting from the fire. During this period of rapid postfire succession, total density of birds was nearly equal on the two plots but species richness increased on the burned plot compared with the unburned plot. Ground- and brush-foraging birds were more numerous on the burned plot, and their population size increased significantly from 1966 to 1985. Foliage-searching birds were more numerous on the unburned plot, and their populations were stable over time relative to the burned plot. In contrast, numbers of foliage-searching birds increased significantly on the burned plot. Bark-gleaning birds declined on the burned plot, probably in response to loss of snags used for nesting by most of these species. Variations in weather, as indicated by measures of temperature and precipitation, did not explain yearly variations in bird populations. Rather, changing vegetation structure resulted in predictable trends related to the foraging and nesting habits of the birds we studied.

Key words: Bird community structure; conifer forest; fire; foraging guild; nesting guild; Sierra Nevada; vegetation succession.

INTRODUCTION

Changes in species composition and abundance (and, thus, diversity) of bird communities have been related to successional processes of plant communities (e.g., Johnston and Odum 1956; Haapanen 1965, 1966; Shugart and James 1973). Such bird-vegetation relationships can be influenced, however, by variation in environmental conditions, especially weather. Weather conditions in winter and early spring are known to impact population numbers during the breeding season (e.g., Kricher 1975; Graber and Graber 1979, 1983; Smith 1982; Faaborg et al. 1984; Järvinen and Väisänen 1984). In addition, extended snowpack can delay the onset of nest construction (Morton 1978), thus influencing breeding success. Therefore, analyses of bird communities are complicated and require long-term studies to identify the factors that influence bird populations (Wiens 1984).

In 1960 a fire consumed about 18,000 ha of pine-fir forest of the eastern Sierra Nevada near Truckee, California. In 1965, two permanent study plots were established, one in the burn and one in the adjacent unburned vegetation. Breeding birds were compared on these plots from 1966 to 1968 (Bock and Lynch 1970) and in 1975 (Bock et al. 1978a). Subsequent counts have been done every year except 1980. During the 25 years since the fire, vegetation on the burn has undergone dramatic changes. Most notably, dense shrub cover developed, regenerating trees became taller with larger crowns, and numbers of standing dead trees declined. The purpose of this study was to determine the possible influence of vegetation changes and weather conditions on species composition and abundance of birds during this period of rapid postfire succession.

STUDY AREAS

The burned and unburned study plots are located at the University of California Sagehen Creek

[1] Received 1 October 1986. Final acceptance 28 January 1987.
[2] Present address: Department of Botany KB-15, University of Washington, Seattle, WA 98195.

Field Station, in the eastern Sierra Nevada, 13 km north of Truckee, California (latitude 39°N, longitude 120°W). The plots are situated on a broad ridgetop at an elevation of about 2,100 m within a 39-km^2 basin dominated by second-growth mixed forest of yellow pine (complex of *Pinus jeffreyi, P. ponderosa, P. washoensis,* and their intermediates [see Haller 1961]) and white fir (*Abies concolor*). Meadows and stands of lodgepole pine (*Pinus contorta* var. *murrayana*) and aspen (*Populus tremuloides*) occur elsewhere in the basin near springs and streams, and stands of red fir (*Abies magnifica*) and mountain hemlock (*Tsuga mertensiana*) occur at higher elevations. Additional descriptions are provided by Bock and Lynch (1970) and by Raphael and White (1984).

Two 8.5-ha (21-acre) study plots, measuring 214 × 397 m (700 × 1300 ft) were established in 1965. Each was marked at 30.5 m (100 ft) intervals with permanent metal stakes. Vegetation on the unburned plot consisted of second-growth yellow pine and white fir in association with lesser numbers of sugar pine (*Pinus lambertiana*), lodgepole pine, red fir, and incense cedar (*Calocedrus decurrens*). Following regrowth from the harvest of selected mature trees from 1890 to 1920, this plot has been essentially undisturbed.

The Donner Ridge fire occurred in 1960 and burned about 18,000 ha. The burned plot was within this area, separated from the unburned plot by about 400 m. The plot included a few scattered mature pines and firs that survived the fire, but was otherwise dominated by brush (primarily *Ceanothus velutinus*) and by regenerating conifers.

METHODS

VEGETATION

The line-point intercept technique was used to sample understory vegetation cover in August 1969 (Burk, unpubl.), 1975 (Bock et al. 1978a), and 1983 (Yoder-Williams, unpubl.). In 1969, presence of vegetation or other cover was recorded at 2,035 points located at 1.5-m intervals along alternate 30.5-m grid intervals. A steel tape was suspended 1.5 m above the ground, and items located below the tape were recorded. The 1975 and 1983 samples each consisted of 1,170 points. For these samples, points were located at 1-m intervals along three transects running the entire length of each plot along grid lines. We sampled vegetation above and below the transect line. Canopy stem densities and basal areas were determined in 1975 and 1983 by a point-centered quarter method (Mueller-Dombois and Ellenburg 1974). Points were located at 30.5-m intervals at 192 grid points per plot in 1975 and at 220 (burned) and 224 (unburned) points in 1983.

Changes in density of standing dead trees (snags) were estimated by Raphael and White (1984) from 1960 through 1979. All snags on each plot were resurveyed in 1983 (Raphael and Morrison, in press) to estimate losses of existing snags and numbers of new snags resulting from live-tree mortality.

BIRD POPULATIONS

Birds were surveyed by means of the spot-mapping method (following Bock and Lynch 1970). Most yearly counts summarized in this paper appeared previously: from 1966 to 1968 (Bock and Lynch 1970), 1975 to 1979 (Bock et al. 1978a, b; Raphael and White 1984; Raphael, unpubl. data), and 1981 to 1985 (Harris and Raphael 1982a, b; Yoder-Williams 1983a, b; Yoder-Williams and With 1984a, b; Yoder-Williams et al. 1985a, b; With and Morrison 1986a, b). Numbers of visits to each plot varied from eight to 23 and generally extended from mid-May to early July. Duration of each visit varied from 1 to 3 hr. Numbers of territories were estimated to the nearest quarter within the boundary of each plot. Birds that were detected at least three times on a plot, and that were known to nest in the vicinity, were recorded as breeders and, when less than a quarter of their territory was within the plot, were assigned an arbitrary value of 0.05 for analysis (following Bock and Lynch 1970). Birds that were observed only once or twice were recorded as visitors and were not included in our analyses.

Following Bock and Lynch (1970), we assigned each bird species to one of five feeding categories: flycatching, tree foliage-searching, bark-gleaning, timber drilling, and ground-brush foraging. Because these groupings did not distinguish between carnivory and herbivory, they were not necessarily the best set of categories, but they were useful for comparing results of later censuses to results reported by Bock and Lynch (1970).

We used Ruzicka's Index (RI) to compute the

TABLE 1. Weather data used in analyses of yearly variation of bird populations Sagehen Creek, California, 1966 to 1985.

Description	Correlation with principal component[a] I	II	III
Mean January minimum temperature	−0.70	0.24	0.50
Range of January minimum temperatures	0.31	−0.25	0.65
Number of days when minimum fell below freezing (0°C)	−0.53	−0.76	−0.06
Number of days when minimum fell below −12.2°C			
Mean July maximum temperature	−0.34	0.84	0.07
Range of July maximum temperatures	−0.01	−0.19	−0.87
Number of days when maximum temperature was >0°C			
Number of days when maximum temperature was >26.7°C	0.18	0.81	−0.00
Number of days when maximum temperature was >32.2°C			
Total annual precipitation, 1 July to 30 June	0.65	0.26	0.34
Precipitation from 1 April to 30 September			
Precipitation from 1 October to 31 March			
Number of days with >3 cm snow cover (1 July to 30 June)	0.86	0.07	0.20
Total amount of snow, 1 July to 30 June			
Mean April minimum temperature			
Mean May minimum temperature			
Range of minimum temperatures in April			
Range of minimum temperatures in May			

[a] Variables for which no values are recorded (blanks) were not included in the principal components analysis.

similarity of avifaunas between plots and among years (Pielou 1984:44):

$$RI = \sum^{s} [\min(i, j)/\max(i, j)]$$

where i and j were the numbers of territories of each species for any pair of plots or years, and s was the total number of species in the two plots.

WEATHER

Because earlier studies (Raphael and White 1984) implicated weather as an important contributor to yearly variation in bird numbers, we defined 18 variables describing weather variation for the years covered by this study (Table 1). A yearly value for each weather variable was extracted from daily weather records recorded by the field station manager (methods of Finklin 1983) at a permanent facility located within 2 km of each plot. We computed Pearson's correlation coefficients between each of the 18 weather variables and the abundances of the more common bird species as well as the combined abundances of all species classified as residents or migrants. More general trends were examined using a principal components analysis. A subset of eight variables, selected for lack of redundancy among all possible pairs (correlation coefficient <0.60), was included in this analysis using the program FACTOR of the SPSS/PC+ package (Norusis 1986). Significant factors (eigenvalues >1.0) were then used as independent variables in Pearson's correlations with abundance of the more abundant bird species or species-groups. For each correlation analysis, the sample size was 13 years.

RESULTS

VEGETATION

The major differences between the burned and unburned plots for equivalent years were the greater densities of tree species on the unburned plot (Table 2) and the greater cover of shrubs

TABLE 2. Canopy stem density (stems/ha)[a] and basal area (m^2/ha) on the burned and unburned plots in 1975 and 1983, Sagehen Creek, California.

Species		Burned 1975	Burned 1983	Unburned 1975	Unburned 1983
Yellow pine complex[b]	DE[c]	97.4	143.9	335.5	316.3
	BA	3.1	4.4	24.2	30.1
Abies concolor	DE	3.9	9.2	415.2	381.3
	BA	1.5	4.2	13.7	23.3
Abies magnifica	DE	0.6	0.9	33.6	19.7
	BA	0.2	0.3	1.4	0.7
Pinus contorta var. *murrayana*	DE	21.2	29.1	0.0	0.0
	BA	0.1	0.2	0.0	0.0
Pinus lambertiana	DE	0.0	0.0	8.4	13.2
	BA	0.0	0.0	0.3	1.0

[a] Stems >2 m tall were included.
[b] Yellow pine complex includes *Pinus jeffreyi, P. ponderosa, P. washoensis,* and their intermediates.
[c] DE = Density; BA = basal area.

TABLE 3. Understory cover (%)[a] on the burned and unburned study plots, Sagehen Creek, California.

Category	Burned			Unburned[b]	
	1969	1975	1983	1975	1983
Shrub species					
Arctostaphylos patula	0.8	3.8	6.0	0.0	0.3
Chrysolepis sempervirens	0.4	0.2	0.0	1.5	2.1
Ceanothus prostratus	9.4	17.4	7.5	11.8	10.9
C. velutinus	8.3	18.5	26.2	2.6	0.9
Haplopappus bloomeri	1.9	1.8	0.8	0.0	0.0
Ribes cereum	1.2	1.5	3.3	0.0	0.0
Total shrubs	22.0	43.2	43.8	15.9	14.2
Herbaceous species	34.5	16.3	4.2	4.5	3.6
Graminoids	23.8	25.8	8.8	0.0	0.2
Logs, stumps, dead brush	3.9	23.3	4.9	6.2	3.7
Bare ground, rocks, and litter	15.8	20.3	38.3	73.4	78.3

[a] Except for 1969, totals add to >100% because more than one vegetation layer was recorded if present at any sample point.
[b] No data available for unburned plot in 1969.

(especially *C. velutinus*), herbs, grasses, and downed wood on the burned plot (Table 3). The most obvious changes over time on the burned plot (Fig. 1) included an increase in density and basal area of pines in the overstory (Table 2), an increase in shrub cover from about 22% in 1969 to over 43% in 1983, and a decrease in herb and graminoid cover (Table 3). Stem density in the canopy (individuals >2 m tall) was still five times greater and basal area was seven times greater on the unburned compared to the burned plot (Table 2).

FIGURE 1. Photographs of the burned study plot in 1966 (above) and 1985 (below).

Density of all snags declined by 90% from 1968 to 1983 on the burned plot; density of snags >38 cm dbh (sizes known to be suitable for nesting by cavity-nesting birds [Raphael and White 1984]) declined by 82% (Table 4). Densities of large snags were similar on the burned and unburned plots in 1975, but numbers of snags had increased by 36% on the unburned plot by 1983 and large snags were 2.5 times more abundant than on the burned plot (Table 4). We have no data on snag density for the unburned plot prior to 1975.

BIRD COMMUNITY COMPOSITION

We recorded 45 bird species that bred on or near either of the two plots (Table 5). Thirty-two species bred on the unburned plot and 38 bred on the burned plot; 25 species were known breeders on both plots. More breeding species were

TABLE 4. Estimated density (stems/ha) of snags (standing dead trees) on the burned and unburned plots during three time periods, Sagehen Creek, California.[a]

	Burned			Unburned	
	1968	1975	1983	1975	1983
All snags	153.0	46.5	17.0	14.2	44.3
Snags >38 cm dbh	26.0	8.7	4.8	8.8	12.0

[a] Data for 1968 and 1975 from Raphael and White (1984). 1983 data from Raphael and Morrison (in press).

TABLE 5. Mean numbers of territories/plot/year of bird species breeding during three time periods on the burned and unburned study plots, Sagehen Creek, California.

Species	Life form[a]	Burned			Unburned		
		1966–1968	1975–1979	1981–1985	1966–1968	1975–1979	1981–1985
Cooper's Hawk *Accipiter cooperii*	CA–GB	0	0	0	0	+[b]	0
American Kestrel *Falco sparverius*	SC–GB	0	0	+	0	0	0
Blue Grouse *Dendragapus obscurus*	GR–GB	0	0	0	0	+	0
Mountain Quail *Oreortyx pictus*	GR–GB	0	0	0.4	0	0	0
Mourning Dove *Zenaida macroura*	CA–GB	0	+	+	0	0	0
Lewis' Woodpecker *Melanerpes lewis*	CA–GB	0	0	0	0	+	0
Common Nighthawk *Chordeiles minor*	GR–FL	0	0.1	0.7	0	0	0
Calliope Hummingbird *Stellula calliope*	BR–GB	0	0.9	0.4	0	0.6	+
Red-breasted Sapsucker *Sphyrapicus ruber*	PC–TD	0.1	0	0	0.3	0.1	0
Williamson's Sapsucker *Sphyrapicus thyroideus*	PC–TD	0.2	0.1	0.1	0	0.3	0.3
Hairy Woodpecker *Picoides villosus*	PC–TD	0.3	0.4	0.3	0.1	0.1	0.1
White-headed Woodpecker *Picoides albolarvatus*	PC–TD	0.1	0.1	+	+	+	0
Black-backed Woodpecker *Picoides arcticus*	PC–TD	0.7	0	0	0.1	+	+
Northern Flicker *Colaptes auratus*	PC–GB	0.7	0.7	0.2	0.1	+	0.2
Olive-sided Flycatcher *Contopus borealis*	CA–FL	0.2	0.6	0.7	0	0	0
Western Wood-Pewee *Contopus sordidulus*	CA–FL	0.6	+	0.4	0.1	+	0
Dusky Flycatcher *Empidonax oberholseri*	BR–FL	1.0	2.1	3.1	1.8	3.0	2.4
Steller's Jay *Cyanocitta stelleri*	CA–FS	0	+	+	0.1	0.1	0.5
Mountain Chickadee *Parus gambeli*	SC–FS	1.1	3.2	2.9	3.3	3.0	2.6
Red-breasted Nuthatch *Sitta canadensis*	PC–BG	0	0	0	1.1	1.7	2.1
White-breasted Nuthatch *Sitta carolinensis*	SC–BG	0.5	0.5	0.1	0.1	0.3	+
Pygmy Nuthatch *Sitta pygmaea*	PC–BG	0.8	1.1	0.2	0	0	0
Brown Creeper *Certhia americana*	SC–BG	0.4	0	0	0.8	1.2	1.5
House Wren *Troglodytes aedon*	SC–GB	0.6	0.5	0	0	0	0
Golden-crowned Kinglet *Regulus satrapa*	CA–FS	0	0	0	3.7	2.7	2.6
Mountain Bluebird *Sialia currucoides*	SC–GB	3.2	1.8	1.0	0	0	0
Townsend's Solitaire *Myadestes townsendii*	GR–GB	0.3	+	+	0.4	0.6	1.0
Hermit Thrush *Catharus guttatus*	GR–GB	0	0	0	0.5	1.9	1.6
American Robin *Turdus migratorius*	CA–GB	0.8	0.4	1.1	0.1	0.1	1.1

TABLE 5. Continued.

Species	Life form[a]	Burned 1966–1968	Burned 1975–1979	Burned 1981–1985	Unburned 1966–1968	Unburned 1975–1979	Unburned 1981–1985
Solitary Vireo *Vireo solitarius*	CA–FS	0	0	0	0.1	0	0
Nashville Warbler *Vermivora ruficapilla*	GR–FS	0	0	0.6	0.4	0.3	1.0
Yellow Warbler *Dendroica petechia*	BR–FS	0	0.9	2.5	0	0	0
Yellow-rumped Warbler *Dendroica coronata*	CA–FS	0.4	0.3	0.4	0.5	1.5	2.0
Western Tanager *Piranga ludoviciana*	CA–FS	0.2	0	0.2	1.2	1.3	1.7
Lazuli Bunting *Passerina amoena*	BR–GB	+	0	+	0	0	0
Green-tailed Towhee *Pipilo chlorurus*	BR–GB	0.2	1.8	2.1	0	0	0
Chipping Sparrow *Spizella passerina*	CA–GB	1.2	0.4	0.5	0	0.2	0
Brewer's Sparrow *Spizella breweri*	BR–GB	0.8	0.7	0	0	0	0
Fox Sparrow *Passerella iliaca*	BR–GB	0.3	6.8	6.4	0.2	+	0
Dark-eyed Junco *Junco hyemalis*	GR–GB	3.8	2.0	1.9	3.7	2.9	3.1
Brown-headed Cowbird *Molothrus ater*	BR–GB	0	0.2	0.9	0	0	0
Cassin's Finch *Carpodacus cassinii*	CA–GB	0.9	1.1	0.9	0.7	0.6	0.6
Red Crossbill *Loxia curvirostra*	CA–FS	0	0	+	0	0.1	0.5
Pine Siskin *Carduelis pinus*	CA–FS	0	+	0.7	0	0.3	0.7
Evening Grosbeak *Coccothraustes vespertinus*	CA–FS	0	0	0.1	0	0	0.8
Totals		19.0	26.2	28.1	19.1	22.2	26.0

[a] Life form (Haapanen 1965) indicates a species' generalized primary nesting (first two letters) and feeding (last two letters) habitat. Abbreviations for nesting habitat are: GR = ground; BR = brush; CA = canopy; PC = cavities excavated by species; and SC = cavities not excavated by species. Abbreviations for foraging habitat are: GB = ground or brush; FS = foliage searching; BG = bark gleaning, including trunk and branches; TD = timber drilling; and FL = flycatching.
[b] + <0.1 territory.

observed on the burned plot only (13) than on the unburned plot only (seven). Over all years, the burned plot supported a slightly richer avifauna than the unburned plot.

As indicated earlier, numbers of visits to each plot varied from year to year. Verner (1985:264) displayed the theoretical relationship between number of territories recognized with spot mapping and number of visits on a plot. According to this model, numbers of territories increased with census effort. We examined this relationship for our study and found no significant correlation (Fig. 2). Similarly, species richness was not correlated with census effort (Fig. 2).

The average abundance of birds over the 13 census years was similar on the burned and unburned plots (25.2 vs. 23.0 pairs/plot). Density of territories remained stable on the unburned plot relative to the burned plot as evidenced by a lower variance among years ($s^2 = 19.8$ vs. 29.0). Density on both plots increased since 1966, especially from 1966 to 1968 (Fig. 3). Species richness remained fairly constant on the unburned plot (Fig. 4). Richness was slightly greater on the burned plot compared to the unburned plot from 1966 to 1968, and from 1981 to 1985.

Community similarity was low (23 to 29%) between the two plots in each time interval (Table 6). The avifauna on the burned plot in 1966 to 1968 was much less similar to that in either later time period (26 to 36%) than the two later periods compared (63%). In contrast, similarities among time periods were consistently high on the unburned plot (52 to 69%, Table 6).

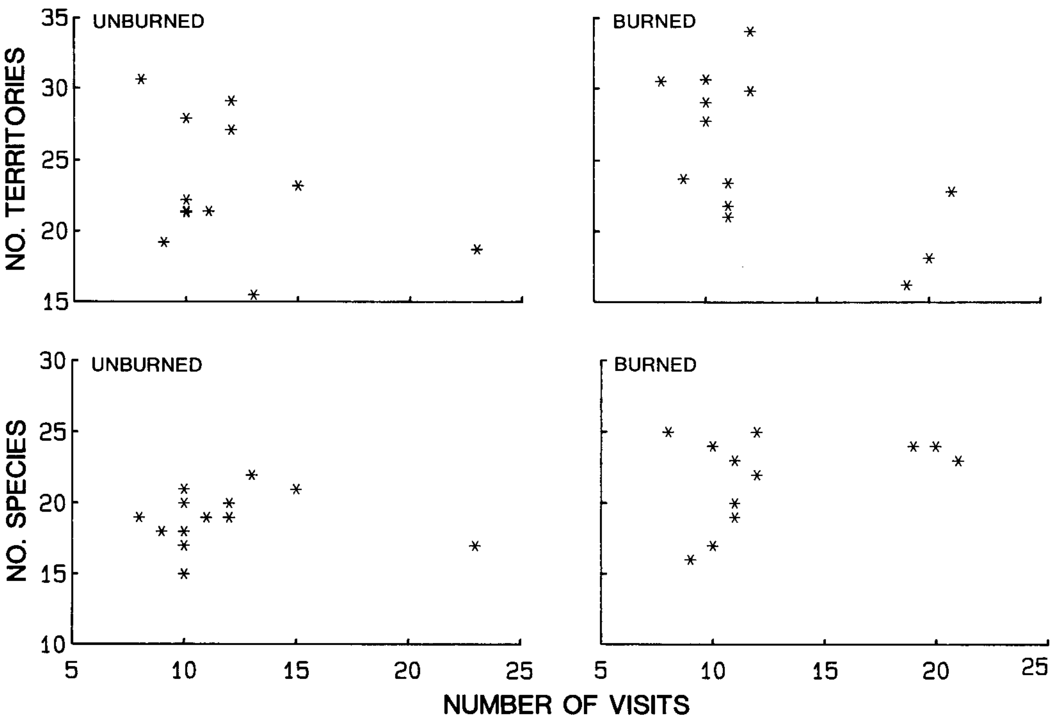

FIGURE 2. Relationships between yearly census effort (number of visits), species richness, and number of territories recorded on the burned and unburned study plots, Sagehen Creek, California.

SPECIES AND SPECIES-GROUPS

Foraging groups. The burned plot consistently supported a significantly higher number of ground-brush foragers than the unburned plot (Fig. 5). Overall, the proportion of total birds in this category varied from 57 to 67% on the burned plot compared with 29 to 32% on the unburned. Numbers of ground-brush foragers have increased since the early period on both plots (Table 7), but the increase seemed to stabilize from 1975 to 1985 on the burned plot. Foliage-searching birds were much more abundant on the unburned plot, varying from 41 to 48% of the total vs. 9 to 25% on the burned plot. However, foliage-searchers increased dramatically on the burned plot whereas they increased less consistently on the unburned plot (Table 7). Bark-gleaning species also were more abundant on the unburned plot, and their numbers have increased since the early period. In contrast, their numbers declined significantly on the burned plot (Table 7, Fig. 5). Timber-drilling species were more abundant on the burned plot than on the unburned plot in the 1966 to 1968 period, but since then they have declined to numbers equivalent to the unburned plot, where their numbers have remained consistently low (Fig. 5). Average abundance of flycatching birds was about equal on the two plots (Fig. 5), but abundance has increased significantly on the burned plot (Table 7).

Nesting groups. Ground-nesting species have averaged 5.8 territories on the unburned plot compared to 2.8 territories on the burned plot. Ground nesters were nearly equally abundant on the two plots during 1966 to 1968, but have since declined (although not significantly) on the burned plot while significantly increasing on the unburned plot (Fig. 6, Table 7). Brush nesters were much more abundant on the burned plot than the unburned plot (13.7 vs. 2.7 territories/year) and numbers have increased significantly on the burned plot (Table 7). Over all years, canopy nesters were about twice as abundant on the unburned compared with the burned plot. Numbers were greater in the 1981 to 1985 counts compared with the earlier periods on the unburned plot; numbers on the burned plot did not change

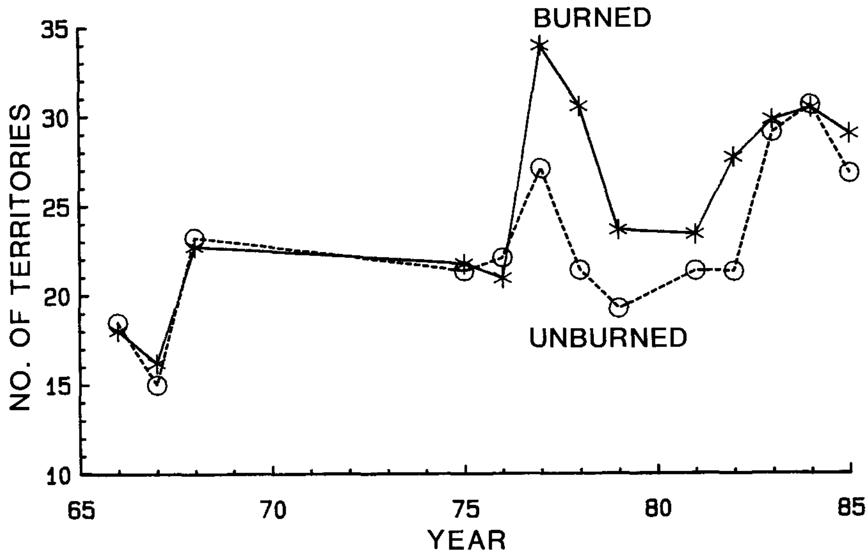

FIGURE 3. Yearly estimates of total abundance of breeding birds on the burned and unburned study plots, Sagehen Creek, California.

consistently between periods. Primary cavity nesters (hole excavators) have averaged equal abundance on the plots (Fig. 6) but numbers have declined significantly in the burned plot while increasing on the unburned plot (Table 7). Secondary cavity nesters have also averaged equal numbers on the two plots (Fig. 6), but their numbers have not changed significantly over time (Table 7).

Nesting-foraging combinations. Changes in abundance of nesting groups are not independent of changes in foraging groups because the same species are represented in each analysis; they are simply grouped differently. Among the combi-

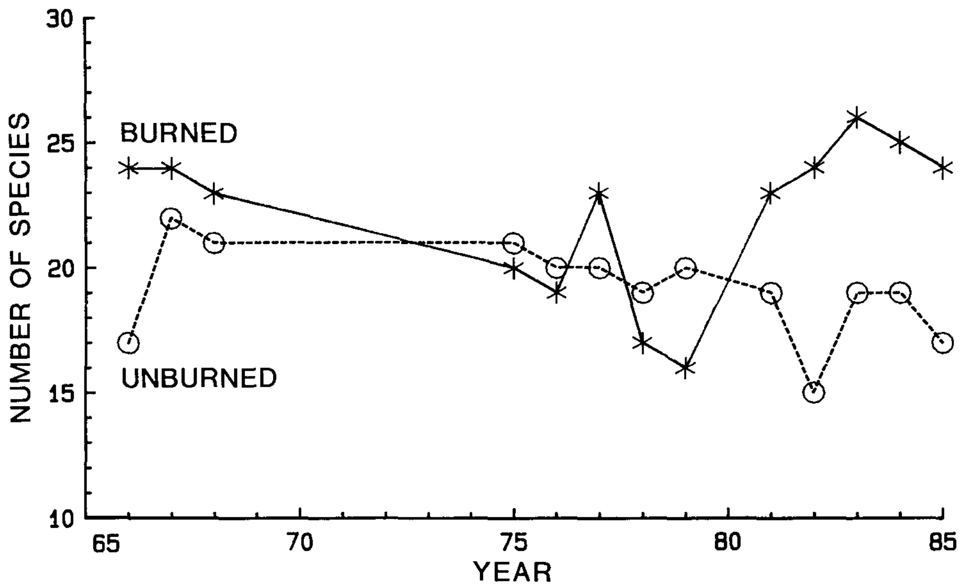

FIGURE 4. Numbers of breeding bird species recorded on the burned and unburned study plots, Sagehen Creek, California.

TABLE 6. Percent similarity[a] of breeding bird communities among time periods and between burned and unburned study plots, Sagehen Creek, California.

	Burned		Unburned		
Plot and years	1975–1979	1981–1985	1966–1968	1975–1979	1981–1985
Burned					
1966–1968	36.2	26.2	28.8	23.0	20.8
1975–1979		63.0	23.0	22.8	19.3
1981–1985			23.4	26.1	25.2
Unburned					
1966–1968				64.2	51.6
1975–1979					68.6

[a] Similarity (%) based on data in Table 5, calculated using Ruzicka's Index (Pielou 1984).

nations of nesting and feeding categories on the two plots (Fig. 7), the predominant group on the burned plot was composed of species that nest in brush and feed on the ground or in brush. In contrast, the unburned plot was dominated by species that nest and feed in the tree canopy. As shown in Figure 7, the burned plot supported a more even distribution of birds among the 15 categories. Equitability (J′) among these categories was 0.83 on the burned plot vs. 0.72 on the unburned plot.

Annual variation in relation to weather. Total abundance of birds varied from year to year and was highly correlated between the two plots. This correlation suggested that some common factor, unrelated to vegetation changes, may have been influencing population sizes. One obvious possibility was that fluctuation in yearly weather affected populations in some way. However, our data did not convincingly support this explanation. Of 432 correlations between abundance of

TABLE 7. Trends in abundance of birds grouped into foraging and nesting categories from 1966 to 1985, Sagehen Creek, California.[a]

Group	Burned	Unburned
Foraging category		
Ground-brush	0.54*	0.67**
Flycatching	0.78***	0.24
Timber-drilling	−0.68**	−0.18
Tree-foliage searching	0.88***	0.50*
Bark-gleaning	−0.51*	0.73***
Nesting category		
Ground	−0.41	0.56**
Brush	0.89***	0.21
Canopy	0.22	0.61**
Primary cavity	−0.61**	0.61**
Secondary cavity	−0.46	−0.03

[a] Trends calculated using Pearson's correlation of territories with year ($n = 13$ years). *$P < 0.10$, **$P < 0.05$, ***$P < 0.01$.

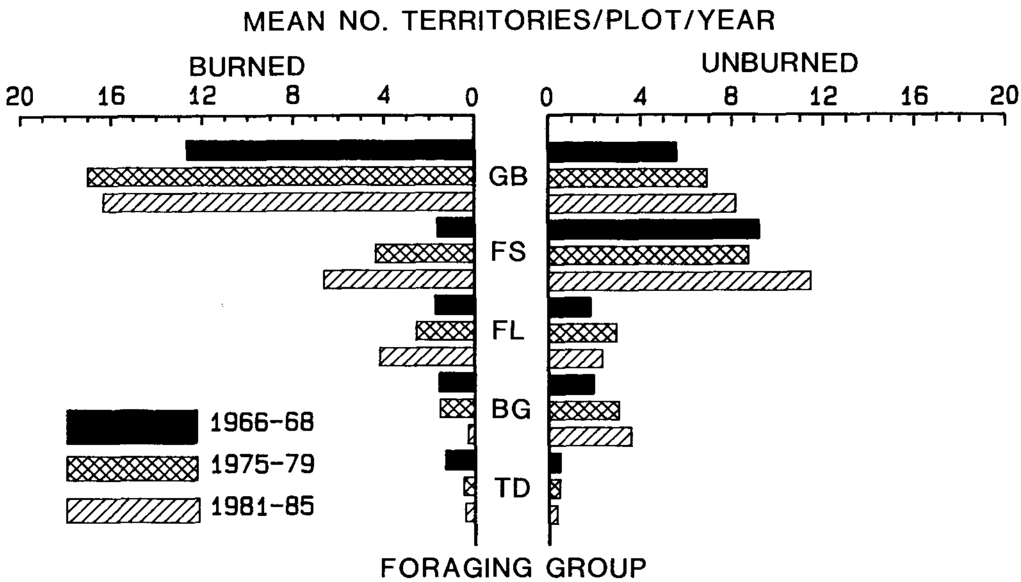

FIGURE 5. Mean abundance of breeding birds among foraging groups during three time intervals on the burned and unburned study plots, Sagehen Creek, California. GB = ground brush, FS = foliage searching, FL = flycatching, BG = bark gleaning, and TD = timber drilling.

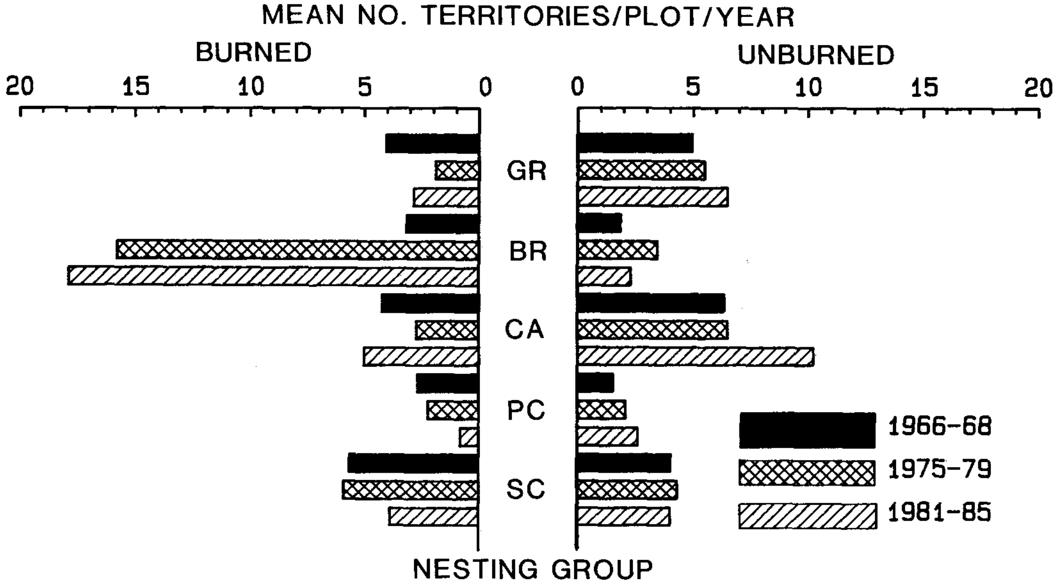

FIGURE 6. Mean abundance of breeding birds among nesting groups during three time intervals on the burned and unburned study plots, Sagehen Creek, California. GR = ground nesting, BR = brush nesting, CA = canopy nesting, PC = primary cavity nesting (hole excavators), and SC = secondary cavity nesting (nonexcavators).

the 24 most common bird species and the 18 weather variables, 27 were significant at $P < 0.10$ and 12 were significant at $P < 0.05$ (unpubl. data). At the 10% and 5% levels of significance, one would expect 43 and 22 significant correlations, respectively, by chance alone. Similarly, numbers of correlations between residents, migrants, and weather were fewer than expected. Therefore, although some of these correlations may have biological significance, we cannot con-

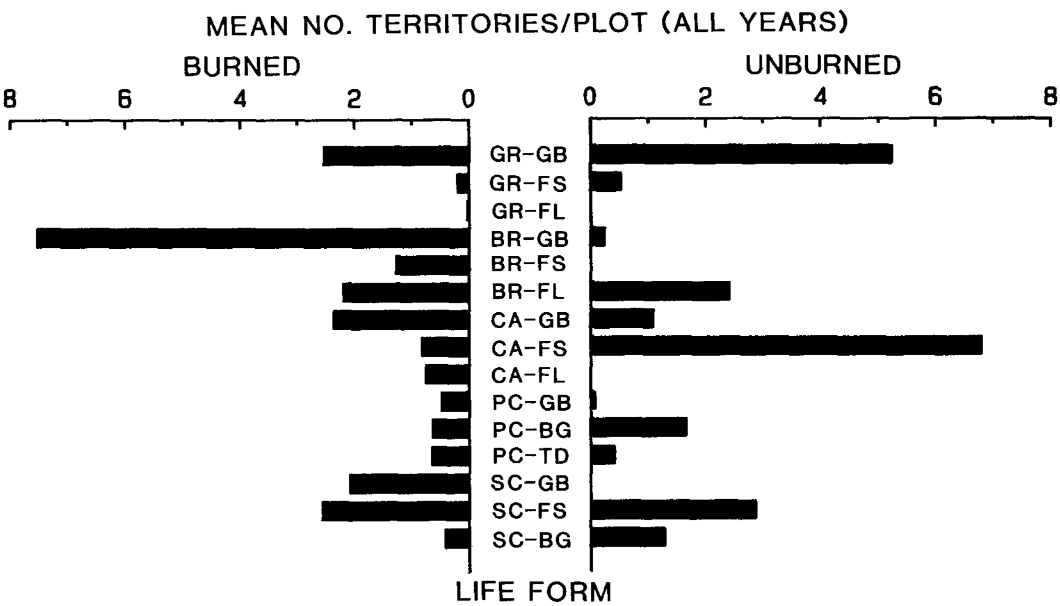

FIGURE 7. Mean abundance of birds among foraging and nesting guild combinations (see Table 5 for codes) on the burned and unburned plots, 1966 to 1985.

clude that yearly bird population sizes were significantly related to weather changes.

The principal components analysis, based on eight weather variables, resulted in three components accounting for 74% of the total variance contributed by the original variables (Table 1). Component I was associated with snow cover, precipitation, and winter cold; we interpret this component as a measure of winter wetness and coldness. Component II was associated with warm conditions (fewer days below freezing, greater July maxima, and greater number of days above 26.7°C). We interpreted Component III as a measure of weather variability; it was most strongly correlated with the ranges of January temperature minima and July maxima (Table 1). None of the simple regressions of these three factors with the combined abundance of birds in the various foraging and nesting categories resulted in significant ($P < 0.05$) relationships.

DISCUSSION

Because this study is based on results from single burned and unburned plots, we do not feel justified in extending our results to a general discussion of the impact of fire on bird communities of the Sierra Nevada. However, the unusually long-term nature of the study permits discussion of overall predictability of changes in bird populations in response to habitat change on this study area. Bird numbers on the burned plot have changed over the 20-year period of this study while remaining relatively more stable on the unburned plot. Concomitant with this changing avifauna on the burned plot, two major changes in vegetation structure have been observed: (1) standing dead trees, which served as important foraging substrates for timber-gleaning and timber-drilling birds and as nesting substrates for cavity-nesting birds (Raphael and White 1984), have declined in density from about 26/ha in 1966 to <5/ha in 1985, and (2) shrub cover has increased from about 20% to over 43%, and birds that nest and feed in shrubs have increased in number by over 500%.

The decline in snag density on the burned plot was likely a cause of the significant decline in numbers of primary cavity-nesting (PCN) birds. Because the study plots were small relative to the size of woodpecker home ranges, our data were subject to large random error. Nonetheless, these trends are in the expected direction, as predicted in an earlier study (Raphael 1983). This decline could be due to loss of foraging or nesting substrate supplied by standing snags. As Table 5 shows, most of the decline in PCN bird density was attributed to the Northern Flicker (*Colaptes auratus*) and Pygmy Nuthatch (*Sitta pygmaea*). Flickers nest in snags but feed on the ground, and nuthatches nest in snags but feed most often from the bark of live trees rather than snags (Raphael and White 1984). Because these two species do not rely on snags for foraging, loss of nesting habitat was probably the more important cause of the decline in PCN bird density.

Why then did secondary cavity-nesting (SCN) birds decline on the burned plot to a lesser degree? One possibility is that the number of cavities available on the plot has not declined to limiting levels. Using a simulation model, Raphael (1983) predicted that the yearly accumulation of cavities abandoned by PCN should exceed requirements of SCN until about 25 years following fire. For the sum of all SCN, our results fit this prediction. However, results for the individual species are less clear. Of the five SCN species breeding on the burned plot, four declined and one (Mountain Chickadee, *Parus gambeli*) increased. The Mountain Chickadee is not totally dependent upon abandoned woodpecker cavities for nesting. Raphael and White (1984) found 43% of 116 chickadee nests in crevices or other natural sites. For this species, which often nests in logs or stumps, nest sites remained plentiful and the increased size of growing trees apparently resulted in increased foraging substrate.

The increase of PCN on the unburned plot was likely due to increased foraging habitat through live-tree mortality. Most of this increase was due to the Red-breasted Nuthatch, *Sitta canadensis* (Table 5), which forages by gleaning insects from the bark of both live and dead trees. Most of the recently killed snags on the unburned plot were Jeffrey pines killed by bark beetles. Among available trees, Jeffrey pine was preferred for foraging by Red-breasted Nuthatches (Raphael and White 1984). Insect outbreaks are known to attract cavity-nesting birds (Koplin 1969), especially for the first few years following tree death.

We observed increasing numbers of birds on the burned plot that nest and feed in canopy foliage, and we attribute this to increasing canopy volume associated with maturing trees. An even stronger trend toward increases occurred on the unburned plot, where foliage volume has probably remained constant. However, different species were involved on that plot. Most of the increase was due to Yellow-rumped Warbler (*Dendroica coronata*), Nashville Warbler (*Vermivora ruficapilla*), and Western Tanager (*Piranga ludoviciana*), all of which were rare on the burned plot. It is possible that the increase on the burned plot may be attributed to sampling error, influences on the wintering grounds, or other causes extrinsic to the burn itself.

We found insufficient evidence to conclude that bird numbers varied in a fashion predictable by weather. Using a subset of the data analyzed herein (1966 to 1979), Raphael and White (1984) found that precipitation explained the majority of temporal variation in total cavity-nesting bird density in the Sagehen Creek Basin. They found no correlation between precipitation and non-cavity-nesting bird density, however. Over the full 13 census years of this study, we found no correlation between precipitation and cavity-nesting bird density. Even if weather variation was a significant cause of bird population fluctuations on a large geographic scale, the small area we sampled may not be sufficient to detect a correlation. For example, if our plots were in high quality habitat for a species, then birds may establish territories in them prior to doing so in adjacent areas of marginal habitat (Fretwell and Lucas 1969, Van Horne 1983) and it may be that weather effects would be more apparent in these marginal habitats. High habitat quality could thus mask fluctuations in bird numbers caused by weather factors. Also, variation in observer error among years would further complicate identification of fine-scale changes in bird numbers over time.

The overriding trend evident from our long-term analyses indicates, however, that changes in bird numbers were related primarily to the successional pattern of vegetation development on the plots. Yearly variation was such that a word of caution is necessary to workers seeking to develop models of bird-habitat relationships: patterns apparent over the short term (e.g., 3 to 5 years) may be biased (in a positive or negative fashion) by short-term factors that could render application of results—temporally or spatially—invalid.

ACKNOWLEDGMENTS

This study was supported in part by the University of California Agriculture Experiment Station Projects 3501 MS and 4274 MS. We thank the late A. Starker Leopold, Marshall White, Don Erman, and Reginald H. Barrett for making the station available during the course of this study, and Kimberly A. With and Marc C. Liverman for assisting in the field. We also thank Carl E. Bock, Robert C. Szaro, and Jared Verner for their comments on earlier drafts.

LITERATURE CITED

BOCK, C. E., AND J. F. LYNCH. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72:182–189.

BOCK, C. E., M. RAPHAEL, AND J. H. BOCK. 1978a. Changing avian community structure during early post-fire succession in the Sierra Nevada. Wilson Bull. 90:119–123.

BOCK, J. H., M. RAPHAEL, AND C. E. BOCK. 1978b. A comparison of planting and natural succession after a forest fire in the northern Sierra Nevada. J. Applied Ecol. 15:597–602.

FAABORG, J., W. J. ARENDT, AND M. S. KAISER. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: a nine year study. Wilson Bull. 96:575–593.

FINKLIN, A. I. 1983. Summarizing weather and climatic data—a guide for wildland managers. U.S. Dep. Agric. For. Serv. Gen. Tech. Rept. INT-148. Intermountain Forest and Range Experiment Station, Ogden, UT.

FRETWELL, S. D., AND H. L. LUCAS, JR. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical Development. Acta Biotheor. 19:16–36.

GRABER, J. W., AND R. R. GRABER. 1979. Severe winter weather and bird populations in southern Illinois. Wilson Bull. 91:88–103.

GRABER, J. W., AND R. R. GRABER. 1983. Expectable decline of forest bird populations in severe and mild winters. Wilson Bull. 95:682–690.

HAAPANEN, A. 1965. Bird fauna of the Finnish forests in relation to forest succession. I. Ann. Zool. Fenn. 3:153–196.

HAAPANEN, A. 1966. Bird fauna of the Finnish forests in relation to forest succession. II. Ann. Zool. Fenn. 3:176–200.

HALLER, J. R. 1961. Some recent observations on ponderosa, Jeffrey and Washoe pines in northeastern California. Madroño 16:126–132.

HARRIS, R. D., AND M. G. RAPHAEL. 1982a. Burned pine-fir forest. Am. Birds 36:88.

HARRIS, R. D., AND M. G. RAPHAEL. 1982b. Mature pine-fir forest. Am. Birds 36:88–89.

JÄRVINEN, A., AND R. A. VÄISÄNEN. 1984. Reproduction of Pied Flycatchers (*Ficedula hypoleuca*) in good and bad breeding seasons in a northern marginal area. Auk 101:439–450.

JOHNSTON, D. W., AND E. P. ODUM. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology 37:50–62.

KOPLIN, J. R. 1969. The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. Condor 71:436–438.

KRICHER, J. C. 1975. Diversity in two wintering bird communities: possible weather effects. Auk 92:766–777.

MORTON, M. L. 1978. Snow conditions and the onset of breeding in the mountain White-crowned Sparrow. Condor 80:285–289.

MUELLER-DOMBOIS, D., AND H. ELLENBURG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

NORUSIS, M. J. 1986. Advanced statistics, SPSS/PC+. SPSS, Chicago.

PIELOU, E. C. 1984. The interpretation of ecological data. John Wiley & Sons, New York.

RAPHAEL, M. G. 1983. Cavity-nesting bird response to declining snags on a burned forest: a simulation model, p. 211–215. *In* J. W. Davis, G. A. Goodwin, and R. A. Ockenfels [tech. coords.]. Snag habitat management: proceedings of the symposium. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-99.

RAPHAEL, M. G., AND M. L. MORRISON. In press. Decay and dynamics of snags in the Sierra Nevada. Forest Science.

RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags of cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. 86:1–66.

SHUGART, H. H., JR., AND D. JAMES. 1973. Ecological succession of breeding bird populations in northwestern Arkansas. Auk 90:62–77.

SMITH, K. G. 1982. Drought-induced changes in avian community structure along a montane sere. Ecology 63:952–961.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47: 893–901.

VERNER, J. 1985. Assessment of counting techniques, p. 247–302. *In* R. F. Johnston [ed.], Current ornithology. Vol. 2. Plenum Press, New York.

WIENS, J. A. 1984. The place of long-term studies in ornithology. Auk 101:202–203.

WITH, K., AND M. L. MORRISON. 1986a. Burned pine-fir forest. Am. Birds 40:71.

WITH, K., AND M. L. MORRISON. 1986b. Mature pine-fir forest. Am. Birds 40:71.

YODER-WILLIAMS, M. P. 1983a. Burned pine-fir forest. Am. Birds 37:89.

YODER-WILLIAMS, M. P. 1983b. Mature pine-fir forest. Am. Birds 37:89.

YODER-WILLIAMS, M. P., AND K. WITH. 1984a. Burned pine-fir forest. Am. Birds 38:108.

YODER-WILLIAMS, M. P., AND K. WITH. 1984b. Mature pine-fir forest. Am. Birds 38:108–109.

YODER-WILLIAMS, M. P., M. LIVERMAN, AND K. WITH. 1985a. Burned pine-fir forest. Am. Birds 39:114.

YODER-WILLIAMS, M. P., M. LIVERMAN, AND K. WITH. 1985b. Mature pine-fir forest. Am. Birds 39:114.