

THE EFFECTS OF TIMBER HARVESTING ON BREEDING BIRDS IN A MIXED-CONIFEROUS FOREST

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Logging represents a habitat alteration which may appreciably affect avian populations. In a study on the effects of clear-cutting areas of Douglas-fir in northwestern California, Hagar (1960) found a marked change in avian species composition after logging. The total number of birds declined at first but recovered within a year and in three years the numbers of both species and individuals had increased.

The purpose of our investigation was to determine differences in individual avian species densities, species occurrence, and diversity values in a virgin mixed-coniferous forest and in a recently harvested forest. In the logged portion of the study area most of the trees forming the forest canopy were removed. We wanted to determine whether selective harvesting retained avian diversity and to assess how birds were affected by logging.

DESCRIPTION OF THE STUDY AREA

The Willow Creek study area is approximately 80 km S of Springerville in the Apache-Sitgreaves National Forest, Greenlee Co., White Mountains, Arizona. It is a U.S. Forest Service experimental watershed ranging in elevation from 2,682 to 2,805 m.

Climatological data were furnished by the Rocky Mountain Forest and Range Experiment Station, U.S. Forest Service, Tempe, Arizona. Precipitation data were from Willow Creek, but temperature data were from Castle Creek, 8.1 km from Willow Creek and at an elevation of 2,592 m.

Annual precipitation in the Willow Creek watershed averaged 76.3 cm during the last 15 years. Total yearly precipitation was 108.1 cm in 1973 and 54.2 cm in 1974. The winter of 1973 was extremely wet, with 40.4 cm of precipitation. The long-term mean precipitation value for 1 January to 31 May was 17.1 cm and was most closely approximated during the winter of 1974 (21.1 cm).

During the breeding season (May–August) the mean daily maximum temperature was 23.1°C with a minimum of 2.8°C and a mean daily temperature of 13.1°C. Of these months, May had the lowest average minimum temperature (−3.6°C).

The Willow Creek watershed is a mixed-coniferous forest with Douglas-fir and ponderosa pine being the dominant tree species. The harvested area of Willow Creek consisted of 201.6 ha; the unmodified portion comprised 131.2 ha. In most of the area, the natural understory vegetation was sparse; however, sprouts of quaking aspen were found in sections of the logged area.

MATERIALS AND METHODS

VEGETATION

Timber harvesting by a logging company began in May 1972 and was completed in September 1972. The reductions in overall tree density, as well as tree species density, frequency, dominance, and importance values (importance value = relative density of the tree species + relative frequency + relative dominance) were determined with the plotless point-quarter vegetation sampling method (Cottam and Curtis 1956) in the summer of 1973 for trees with dbh (diameter at breast height) ≥ 7.6 cm. One-hundred stations (400 trees) were sampled in a 15.5-ha unharvested and 15.5-ha logged study plot. For the tree in each quadrat closest to the center stake, we recorded its species, height, dbh, and distance from the center of the trunk to the stake.

Quaking aspen and snags (dead trees) were not removed when part of the watershed was logged in the summer of 1972. However, some aspen and a number of snags were blown down during a severe storm in late 1972. The category "snag" may contain representatives of any tree species and is considered as one vegetation type.

Degree of heterogeneity of each plot was calculated using the diversity formula of Shannon (1948). All diversity values are to the base e . Computations derived from relative tree species densities resulted in tree species diversity (TSD) for each plot. Species richness indicates the number of species. Evenness (J') is H'/H'_{\max} , where H' is the diversity value and H'_{\max} represents the maximum diversity value possible (Pielou 1975).

FOLIAGE VOLUME

The volume of live foliage was analyzed by calculating the amount of foliage for each tree species and the foliage volume in each 3-m height interval measured from the ground in the modified and unlogged habitats. Data for these analyses were collected at the same time as the point-quarter measurements. Species, tree height, height to the first live branch, radius of the longest branch, and distance from the center of the trunk to the first live foliage on the longest branch were recorded for each tree sampled.

The amount of live foliage present for a given tree species was determined by calculating the total space occupied by the foliage and then subtracting from this the core space that lacked live needles or leaves. To obtain volume in terms of m^3/ha for a particular species, we divided the live volume for each species by the number of trees of the given species sampled. Next, we multiplied this by the absolute density of the species sampled. Spruces, firs, and Douglas-fir were regarded as being conical in shape, pines as being cylindrical, and aspen as being spherical. The actual formulae used to determine volumes for a given tree were:

1. Live foliage volume for spruces, firs, and Douglas-fir = $\pi/3(r_0^2h_0 - r_1^2h_1)$ where $h_1 = h_0 - (r_0 - r_1)$.
2. Live foliage volume for pines = $\pi(r_0^2h_0 - r_1^2h_1)$ where $h_1 = h_0 - (r_0 - r_1)$.
3. Live foliage volume for quaking aspen = $4/3\pi(r_0^3 - r_1^3)$.

In all cases, r_0 represents the length of the longest branch and r_1 is the distance from the center of the trunk to the beginning of the live vegetation on the longest branch; h_0 represents the height of the tree's live vegetation (i.e., total tree height-height to first branch); h_1 is the height of the portion of the tree containing branches which have dead foliage, minus the height to the first branch. Our calculations for foliage volume represent approximations because we assumed vegetation density to be constant within a given tree and for all tree species.

From these data, tree volume diversity (TVD) was derived by using the total foliage volume present for each tree species. In addition foliage height diversity (FHD) was calculated by using the total amount of foliage present in each of the respective 3-m height intervals.

AVIAN SPECIES COMPOSITION AND DENSITIES

The study was begun mid-May 1973 and continued through August 1974. Composition and density of avian species were measured during the summers of 1973 and 1974.

Species densities were determined using the spot-map method (Williams 1936). Two 15.5-ha plots with similar slope and aspect were established 0.6 km apart, one in the logged area and the other in the unmodified area. We put plastic flags at 25-m intervals along nine parallel lines, each 390 m long and 50 m apart. Each flag was labelled with a number corresponding to the transect line and a letter corresponding to the distance traveled from the beginning of the line.

Censusing was conducted 4 June–9 August 1973 and 1 June–9 August 1974. Each study plot was censused six times monthly for a total of 18 censuses. Results represent the mean of the monthly values; for most species, this was the mean for June and July, since breeding was completed before August. Sampling began one-half hour after sunrise when birds were most active and continued up to three hours.

Data were analyzed using two-way analysis of variance to determine if statistically significant ($P < 0.05$) differences occurred in individual species densities or in the total population between the two study plots. Analyses also were conducted on the various foraging and nesting guilds. Analysis of variance was done using density values for June and

July. The two avifaunas were compared using the index of similarity (Sørensen 1948). To determine if statistically significant differences in diversity values existed for TSD, TVD, FHD, and BSD (bird species diversity) between the unlogged and harvested plots, a t-test was used (Hutcheson 1970). Significant values are defined as having $P < 0.05$.

RESULTS

VEGETATION

Plotless point-quarter analyses indicate that total tree density was 626.2 trees per ha in the unlogged plot versus 167.7 trees per ha in the modified plot (Table 1). In the unmodified plot, Douglas-fir had the highest density as well as the highest importance value, followed in importance by ponderosa pine. In the logged plot, Douglas-fir also showed the highest importance value; however, snags and quaking aspen were more likely to be used were next in importance. Both snags and quaking aspen were more likely to be used in the modified habitat because they represented a larger proportion of the available vertical substrate, although a smaller absolute value with respect to density.

U.S. Forest Service pre-treatment and post-treatment data (Gottfried and Jones 1975) for Willow Creek indicate that before logging, tree (dbh ≥ 17.8 cm) density was 362.5 trees/ha. After logging, it decreased to 108.4 trees/ha. Basal area was reduced from 41.20 m^2/ha to 6.74 m^2/ha . This represents a 70% reduction in tree density and an 84% decrease in basal area.

Diversity values derived from tree density results in Table 1 indicate that the unlogged plot had significantly less diversity of trees ($P < 0.05$) than the logged plot.

Calculations of foliage volume (Table 2) indicate that the total volume available was approximately 7.5 times greater in the unharvested plot than in the logged plot. However, foliage height diversity (FHD) did not differ significantly between the two plots.

Most of the foliage in the unmodified plot was ponderosa pine and southwestern white pine, whereas in the lumbered plot most of it was quaking aspen (Table 3). Tree volume diversity (TVD) was not significantly different between the two plots.

AVIFAUNA

Overall, birds were significantly more abundant in the unlogged plot than in the modified plot for each summer (Table 4). The percent of similarity between the plots was 0.76 for 1973 and 0.80 for 1974. This was based on the

TABLE 1. Composition of unlogged and logged mixed-coniferous forests, White Mountains, Arizona.

Species	Density ^a (dbh \geq 7.6 cm)	Relative ^b density	Relative ^c dominance	Relative ^d frequency	Importance ^e value
UNLOGGED AREA					
Ponderosa pine (<i>Pinus ponderosa</i>)	112.7	18.0	30.5	19.3	67.8
Southwestern white pine (<i>Pinus strobiformis</i>)	109.6	17.5	10.6	18.6	46.7
Douglas-fir (<i>Pseudotsuga menziesii</i>)	194.1	31.0	35.2	26.1	92.3
Alpine fir (<i>Abies lasiocarpa</i>)	3.1	0.5	0.3	0.7	1.5
White fir (<i>Abies concolor</i>)	51.7	8.3	7.6	8.6	24.5
Blue spruce (<i>Picea pungens</i>)	12.5	2.0	0.7	2.5	5.2
Englemann spruce (<i>Picea engelmanni</i>)	31.3	5.0	2.7	5.4	13.0
Quaking aspen (<i>Populus tremuloides</i>)	50.1	8.0	4.1	8.2	20.3
Snag	61.1	9.8	8.3	10.7	28.7
Total	626.2	100.0	100.0	100.0	300.0
Tree species diversity (TSD)	1.87				
Species richness	9.0				
Evenness (E)	0.85				
LOGGED AREA					
Ponderosa pine	4.6	2.8	9.6	4.0	16.3
Southwestern white pine	8.8	5.3	3.1	6.1	14.5
Douglas-fir	42.3	25.3	16.1	22.7	64.0
Alpine fir	13.0	7.8	4.4	8.7	20.8
White fir	19.7	11.8	6.5	12.3	30.5
Blue spruce	9.6	5.8	2.0	6.1	13.9
Englemann spruce	19.3	11.5	7.6	11.9	31.0
Quaking aspen	29.3	17.5	18.5	15.2	51.2
Snag	21.0	12.5	32.2	13.0	57.8
Total	167.7	100.0	100.0	100.0	300.0
Tree species diversity (TSD)	2.03				
Species richness	9.0				
Evenness (E)	0.92				

^a Absolute number of trees per hectare.

^b $\frac{\text{Number of individuals of the species}}{\text{Number of individuals of all species}} \times 100$.

^c $\frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \times 100$.

^d $\frac{\text{Number of points of occurrence of the species}}{\text{Number of points of occurrence of all species}} \times 100$.

^e Importance value = b + c + d.

number of species common to both plots and it indicates the degree of overlap in species composition. Although for both summers bird species were slightly more diverse in the unharvested than in the logged plot, the differences were not significant.

The number of breeding bird species and population size differed between years much more than between plots (Table 4). This indicates that the effect of year was more in-

fluent in creating changes than was the effect of habitat treatment.

Using 1973 as the base year, both the number of species and densities in the unlogged plot varied approximately the same degree as did those in the logged plot (Table 5). The harvested plot had three more new species and three additional lost species compared to the unharvested plot.

Birds that forage by searching in tree foliage

TABLE 2. Foliage volume (m³/ha) profile of unlogged and logged mixed-coniferous forests, White Mountains, Arizona.

Height class (m)	Unlogged plot	Logged plot
0-3	5,993.9	1,090.3
3-6	15,638.0	2,149.4
6-9	16,949.6	2,116.5
9-12	16,790.3	2,550.7
12-15	14,871.2	2,627.5
15-18	13,729.1	2,321.7
18-21	11,285.8	1,374.2
21-24	9,408.7	619.9
24-27	6,102.8	194.5
27-30	2,119.3	76.7
30-33	567.9	64.2
33-36	240.5	54.0
36-39	182.8	29.1
39-42	104.1	1.1
Total	113,984.0	15,269.8
Foliage height diversity (FHD)	2.24	2.11

or gleaning in timber appeared to be the most adversely affected by logging; they were significantly more numerous in the virgin forest (Table 6). Ground or slash (logging debris) foragers were substantially more numerous in the harvested plot. Species that drill in timber differed significantly in abundance, resulting from the effect of years rather than the effect of logging.

All timber-gleaning species were significantly more numerous in the unlogged than logged plot (Table 7). Of the foliage-searchers, 61.5% and 15.4% of the species differed significantly in density between plots and between years, respectively. Five of eight tree foliage searching species with significant density differences had higher densities in the unaltered plot in both years.

Species that construct cup nests were significantly more dense and represented a larger

proportion of the avifauna in the unlogged than logged plots (Table 8). Although hole nesters were more numerous and comprised a higher percentage of the population in the harvested plot than unlogged plot, the difference in density was not significant.

Comparing the plots, 35% of both hole and cup nesting species and 40% of ground nesters differed significantly in abundance (Table 9). Logging apparently affected birds with like nesting habits similarly with respect to number of species with significant differences in density. Based on nesting requirements, 35.4% of all species were significantly affected by logging and 16.7% by years.

DISCUSSION

Habitat conditions that may influence bird species occurrence and abundance include food availability and quality, cover, nest sites, foliage volume, amount of open ground, tree density, amount of canopy, and climate. In addition, species can respond to many foliage-related characteristics with respect to habitat selection including, but not limited to, the life-form of the vegetation (Pitelka 1941), the height of the vegetation (Lack 1933, Cody 1969, and Wiens 1969), the presence of certain vegetative strata (MacArthur and MacArthur 1961, MacArthur 1964, Roth 1971), and the amount of foliage present (Balda 1969, Verner 1975). Despite the proximity of our plots to each other, they differed with regard to several of the above features. Even though aspens were not removed, the logged area had a lower density of aspen and yet a higher foliage volume than in the unharvested plot, because aspen in the logged plot were larger and more mature.

Snags were less numerous in the harvested plot, partly due to unintentional loss during the logging operation and a severe winter

TABLE 3. Foliage volume (m³/ha) of tree species in unlogged and logged mixed-coniferous forests, White Mountains, Arizona.

Tree species	Unlogged plot		Logged plot	
	m ³ /ha	%	m ³ /ha	%
Ponderosa pine	40,910.4	35.9	1,070.2	7.0
Southwestern white pine	40,253.4	35.3	1,921.8	12.6
Douglas-fir	20,001.0	17.6	1,679.2	11.0
Alpine fir	181.7	0.2	497.0	3.3
White fir	4,305.8	3.8	544.9	3.6
Blue spruce	552.6	0.5	421.0	2.8
Englemann spruce	2,213.2	2.0	1,030.1	6.8
Quaking aspen	5,565.9	5.0	8,105.6	53.1
Total	113,984.0	100.0	15,269.8	100.0
Tree volume diversity (TVD)	1.43		1.54	

TABLE 4. Avian species occurrence, breeding density (no./40 ha), and diversity in unlogged and logged mixed-coniferous forests, White Mountains, Arizona.

Species	Foraging method ^a	Nest type ^b	1973		1974		Density variation ^c
			Unlogged	Logged	Unlogged	Logged	
Turkey Vulture (<i>Cathartes aura</i>)			P		P	P	
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	P	C		P		5.1	
American Kestrel (<i>Falco sparverius</i>)	P	H			P	10.2	
Band-tailed Pigeon (<i>Columba fasciata</i>)					P	P	
Mourning Dove (<i>Zenaida macroura</i>)						P	
Flammulated Owl (<i>Otus flammeolus</i>)	P	H	10.6		10.2		
Great Horned Owl (<i>Bubo virginianus</i>)	P	C	5.3	5.3	5.1	10.2	
Pygmy Owl (<i>Glaucidium gnoma</i>)	P	H		5.3			
Saw-whet Owl (<i>Aegolius acadicus</i>)	P	H		5.3		5.1	
Broad-tailed Hummingbird (<i>Selasphorus platycercus</i>)	N	C	5.3	5.3	30.8	20.5	**
Common Flicker (<i>Colaptes auratus</i>)	GS	H	10.6	13.2	25.6	20.5	
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	TD	H	10.6	15.8	10.2	20.5	
Williamson's Sapsucker (<i>Sphyrapicus thyroideus</i>)	TD	H	2.7	2.7	5.1	5.1	
Hairy Woodpecker (<i>Picoides villosus</i>)	TD	H	11.8	10.5	10.2	10.2	
Downy Woodpecker (<i>Picoides pubescens</i>)	TD	H	5.3	7.9	10.2	7.7	
Northern Three-toed Woodpecker (<i>Picoides tridactylus</i>)	TD	H	2.7	1.4	15.4	15.4	**
Dusky Flycatcher (<i>Empidonax oberholseri</i>)	F	C	2.6	5.3			
Western Flycatcher (<i>Empidonax difficilis</i>)	F	C	47.4	2.6	48.7	15.4	*
Coues' Flycatcher (<i>Contopus pertinax</i>)	F	C		2.7			
Olive-sided Flycatcher (<i>Nuttallornis borealis</i>)	F	C			5.1	12.8	**
Violet-green Swallow (<i>Tachycineta thalassina</i>)	A	H	2.6	15.8	10.2	51.3	**
Purple Martin (<i>Progne subis</i>)	A	H		1.4		2.6	
Steller's Jay (<i>Cyanocitta stelleri</i>)	TFS	C	15.8	13.2	25.6	28.2	
Common Raven (<i>Corvus corax</i>)	P	C		2.6	5.1	P	
Clark's Nutcracker (<i>Nucifraga columbiana</i>)	C	C	P	P	5.1	5.1	
Mountain Chickadee (<i>Parus gambeli</i>)	TFS	H	44.7	11.8	58.9	30.8	*
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	TG	H	2.6		15.4		*
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	TG	H	2.6		25.6	10.2	**
Pygmy Nuthatch (<i>Sitta pygmaea</i>)	TG	H	2.6		25.6	10.2	**

TABLE 4. Continued.

Species	Foraging method ^a	Nest type ^b	1973		1974		Density variation ^c
			Unlogged	Logged	Unlogged	Logged	
Brown Creeper (<i>Certhia familiaris</i>)	TG	H	39.5		51.3	P	*
House Wren (<i>Troglodytes aedon</i>)	GS	H	26.3	79.0	7.7	79.5	*
American Robin (<i>Turdus migratorius</i>)	GS	C		5.3	5.1	12.8	
Hermit Thrush (<i>Catharus guttatus</i>)	GS	C	71.0	36.8	76.9	43.6	*
Western Bluebird (<i>Sialia mexicana</i>)	F	H		2.7		5.1	
Mountain Bluebird (<i>Sialia currucoides</i>)	F	H				5.1	
Townsend's Solitaire (<i>Myadestes townsendi</i>)	GS	G			5.1		
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	TFS	C	26.3	5.3	30.8	5.1	*
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	TFS	C	71.0	42.1	74.4	23.1	*
Warbling Vireo (<i>Vireo gilvus</i>)	TFS	C	21.0	47.4	25.6	35.9	*
Orange-crowned Warbler (<i>Vermivora celata</i>)	TFS	G	2.6				
Virginia's Warbler (<i>Vermivora virginiae</i>)	TFS	C				5.1	
Olive Warbler (<i>Peucedramus taeniatus</i>)					P		
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	TFS	C	131.6	100.0	89.8	76.9	*
Grace's Warbler (<i>Dendroica graciae</i>)	TFS	C			25.6		***
Red-faced Warbler (<i>Cardellina rubrifrons</i>)	TFS	G	10.6	2.6	25.6		*
Western Tanager (<i>Piranga ludoviciana</i>)	TFS	C	7.7	15.8	12.8	15.4	*
Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	TFS	C			5.1		
Pine Siskin (<i>Carduelis pinus</i>)	TFS	C	7.9	2.6	25.6	23.1	**
Red Crossbill (<i>Loxia curvirostra</i>)	C	C				P	
Green-tailed Towhee (<i>Pipilo chlorurus</i>)	GS	C				5.1	
Gray-headed Junco (<i>Junco caniceps</i>)	GS	G	31.6	76.3	51.3	74.4	*
Chipping Sparrow (<i>Spizella passerina</i>)	GS	C			5.1	5.1	
Total			632.9	544.0	865.9	712.4	**
Bird species diversity (BSD)			2.75	2.70	3.19	3.14	
Species richness			29.0	30.0	35.0	35.0	
Evenness			0.82	0.79	0.90	0.88	

^a Foraging method: A = Aerial forager, F = flycatcher, GS = ground or slash forager, N = nectar feeder, P = predator on vertebrates, C = cone forager, TD = timber driller, TFS = timber-foliage searcher, TG = timber gleaner.

^b Nest type: H = hole, C = cup (non-ground), G = ground.

^c Significant ($P < 0.05$) difference in density between the unlogged and logged plots is indicated by *, ** indicates a significant difference between years; *** indicates a significant ($P < 0.05$) interaction between plots and years.

P = Present.

Transients: Rufous Hummingbird (*Selasphorus rufus*), Yellow Warbler (*Dendroica petechia*), Cassin's Finch (*Carpodacus cassinii*), Dark-eyed Junco (*Junco hyemalis*), and White-crowned Sparrow (*Zonotrichia leucophrys*).

TABLE 5. Comparison of changes in number of breeding bird species and densities between years and plots.*

	1973	Same as 1973	During 1974		1974 Total
			New	Lost	
<u>Unlogged plot</u>					
No. species	29	27	7	2	35
No. breeding birds/40 ha	632.9	809.7	56.2		865.9
<u>Logged plot</u>					
No. species	30	27	10	5	35
No. breeding birds/40 ha	544.0	638.4	74.0		712.4

* Using 1973 as the base year.

storm prior to vegetation sampling. There may have been other, more subtle differences between the plots before logging. Our results should therefore be viewed as a comparison of the avifaunas in logged and unlogged areas, and not as a before-and-after study.

In assessing the total avifauna we found that on a yearly basis both plots varied in approximately the same way, each losing and gaining several species. Population differences between the plots were mostly the result of changes in species that were present both years. Logging did not result in either the appearance or disappearance of substantially more species from one summer to the next.

The annual variation in species composition and densities may reflect the climatic conditions of the preceding winter and/or spring. Fretwell (1969, 1972) and Willson (1974) described how breeding populations may be influenced by certain events of the non-breeding season. A long, wet winter and spring in 1973 was hypothesized as being responsible for keeping many birds from migrating to their preferred montane habitats (Monson 1973). In Willow Creek, snow persisted on more

sheltered areas in mid-May and the quaking aspen did not begin to leaf out until the second week in June 1973. Such conditions may adversely affect food supplies (Holmes and Sturges 1975). Both permanent and summer residents were less abundant in 1973 than 1974, which may have resulted from the adverse weather. This emphasizes the necessity of using paired plots rather than plots sampled before and after timber harvesting.

Densities of birds according to their manner of foraging and nesting indicate how the habitat is being used. Nest site selection in terms of number of sites available as well as quality is important in determining which species will utilize an area and the density which the habitat can support (von Haartman 1957). Food availability, quantity, and accessibility coupled with foraging habits (Sturman 1968) and preferences for certain tree species (Hartley 1953, Balda 1969) or preferred tree heights (Jackson 1970) may also influence species distribution and densities. Nest site preferences and foraging habits affect species densities and occurrence in altered habitats (Bock and Lynch 1970).

TABLE 6. Distribution of breeding bird densities^a (no./40 ha) according to method of foraging in the unlogged and logged plots.

Code	Method of foraging	Number of individuals and percent distribution			
		Unlogged		Logged	
		No.	%	No.	%
A	Aerial forager	12.8	0.9	71.1	5.7
F	Flycatcher	103.8	6.9	51.7	4.1
GS	Ground or slash	316.3	21.1	451.6	35.9
N	Nectar feeder	36.1	2.4	25.8	2.1
P	Predator	36.3	2.4	49.1	3.9
C	Cone forager	5.1	0.4	5.1	0.4
TD	Timber-driller ^c	84.2	5.6	97.2	7.7
TFS	Tree foliage-searcher ^b	739.0	49.3	484.4	38.6
TG	Timber gleaner ^b	165.2	11.0	20.4	1.6
	Total	1,498.8	100.0	1,256.4	100.0

^a Data for 1973 and 1974 combined for purposes of this table. Data for 2-way analysis of variance considered separately.

^b Significant difference in density ($P < 0.05$) between the unlogged and logged plots.

^c Significant difference in density ($P < 0.05$) between 1973 and 1974.

TABLE 7. Comparison of foraging guilds with respect to number of species with significant density differences between plots and years.

Code	Foraging guild	No. species in guild	No. of species with significant density differences and percent			No. species with sig. higher density in unlogged plot
			Unlogged vs. logged	1973 vs. 1974		
A	Aerial forager	2	1 (50%)	1 (50%)	—	
F	Flycatcher	6	1 (16.7%)	1 (16.7%)	1	
GS	Ground or slash	8	3 (37.5%)	0	2	
N	Nectar feeder	1	0	1 (100%)	—	
P	Predator	7	0	0	—	
C	Cone forager	2	0	0	—	
TD	Timber-driller ^b	5	0	1 (20%)	—	
TFS	Tree foliage-searcher ^a	13	8 (61.5%)	2 (15.4%)	5	
TG	Timber-gleaner ^a	4	4 (100%)	2 (50.0%)	4	
	Total	48	17 (35.4%)	8 (16.7%)	12	

^a Significant difference ($P < 0.05$) in density between the unlogged and logged plots both years.

^b Significant difference in guild density ($P < 0.05$) between 1973 and 1974.

We found that species which were more abundant in the unharvested area were mainly bark-searching (Pigmy Nuthatch and Brown Creeper) and foliage insect-gleaning forms (Mountain Chickadee, Golden-crowned Kinglet, Ruby-crowned Kinglet and Yellow-rumped Warbler). Foliage-searching species also were more prevalent in the unharvested plot, where substantially more foliage was available. The greater area of leaf surface presumably accommodated more insects but we have no data on this.

Aerial foragers such as the Violet-green Swallow and most flycatching species were more abundant in the logged plot. Investigators have speculated that such birds have difficulty when maneuvering in dense foliage and show a negative or no correlation between foliage volume and avian densities (Karr and Roth 1971, Willson 1974, Szaro and Balda, unpubl. report to U.S. Forest Service, 1976). The Willow Creek hawkers and aerial foragers may have benefited from

TABLE 8. Distribution of breeding bird densities^a (no./40 ha) by type of nest in the unlogged and logged plots.

Code	Type of nest	Number of individuals and percent distribution			
		Unlogged		Logged	
		No.	%	No.	%
H	Hole	126.8	8.4	158.4	12.6
C	Cup ^b	915.2	61.1	635.7	50.6
G	Ground	456.8	30.5	462.3	36.8
	Total	1,498.8	100.0	1,256.4	100.0

^a Data for 1973 and 1974 combined for purposes of the table. Data for analysis of variance considered separately.

^b Statistically significant ($P < 0.05$) difference in guild densities between the unlogged and logged plots.

logging because the lack of overstory facilitated maneuvering while foraging.

Species that foraged on the ground or in slash benefited substantially from timber harvesting. House Wrens and Gray-headed Juncos were much more abundant in the modified plot. This was especially true in 1973 when an abundance of loose slash and slash piles provided foraging surface, observation posts, and in the case of the junco, protection for nest sites. Densities of House Wrens as well as those of Gray-headed Juncos were similar in 1973 and 1974. Overall densities increased in the logged area from 1973 to 1974. A commensurate increase might have also been noted for both species if the slash piles had not been burned in late July 1973. In a study comparing clear-cut areas to Douglas-fir forest (Hagar 1960), the Dark-eyed Junco was the most numerous of all birds in the cutover forest. Hagar concluded that "removal of logging debris constitutes a good control measure for juncos" (p. 121). In our study, junco numbers declined after slash was burned, supporting Hagar's finding.

According to nesting habit, only cup-nesting species were significantly more abundant in the virgin forest. The proportion of these birds was higher and the number of individuals was greater in the unlogged than the logged plot, presumably because more nest sites were available there. Many cup-nesters were also foliage-gleaners, hence the unmodified plot was additionally attractive to them.

Snags provided cavity nest sites for Violet-green Swallows, Mountain Chickadees, House Wrens, and other species. Competition for such cavities was evident (Franzreb 1976).

TABLE 9. Comparison of nesting guilds with respect to number of species with significant density differences between plots and years.

Code	Nesting guild	No. species in guild	No. of species with significant density differences and percent		No. species with sig. higher density in unlogged plot
			Unlogged vs. logged	1973 vs. 1974	
H	Hole nester	20	7 (35.0%)	4 (20.0%)	5
C	Cup nester*	23	8 (34.8%)	4 (17.4%)	6
G	Ground nester	5	2 (40.0%)	0	1
	Total	48	17 (35.4%)	8 (16.7%)	12

* Significant difference ($P < 0.05$) in density between the unlogged and logged plots both years.

Hole-nesters were not significantly affected by logging, yet 35% of those species differed significantly in abundance between the plots. Gains in some species were apparently balanced by losses in others. Cavity-nesting species that were adversely affected by logging, such as the Mountain Chickadee, Pigmy Nuthatch, and Red-breasted Nuthatch, spent much of their foraging time on live trees, gleaning insects from the foliage and bark.

To examine the influence of foliage volume, tree species composition, and tree species densities on the avifaunas in the two plots, we used diversity indices. Basically, a diversity value reflects the number of categories—in the case of birds, species—and the distribution of data in those categories (species). This index can be useful in understanding community relationships.

In analyzing the effects of lumbering on ponderosa pine habitat, Szaro and Balda (1976) found no correlation between breeding bird diversity and plant species diversity (PSD), foliage height diversity, or plant volume diversity (PVD). They concluded that the amount of food, territoriality, openness of habitat and/or configuration of foliage more strongly influenced diversity in bird species (BSD) than did diversity of foliage height, plant species, or plant volume. In the present study we found no significant differences in BSD, FHD, and tree volume diversity (TVD) in the harvested and unmodified plots. Only the difference in tree species diversity was statistically significant.

The amount of foliage provided by a habitat can also substantially influence the composition, densities, and diversity of avian species (Balda 1969, 1970, this study). Foliage volume may limit the abundance of certain birds (MacArthur 1958, Morse 1967).

Foliage not only provides places for nesting and foraging but it may also furnish pro-

tection against predators and inclement weather. Birds that glean or nest in foliage appeared to be less numerous in the harvested plot. The abundance of these species was apparently determined by the volume of foliage rather than the diversity of foliage height or tree volume.

In order to predict or assess the effects of timber harvesting on birdlife, it is best to consider the available volume and configuration of foliage rather than rely upon TSD, FHD, or TVD. Our results show that FHD and TVD can be similar in two plant communities, and yet the total avian population density, and to a lesser extent the species composition, can be different. Although the two plots had fairly similar avifaunas, several species were restricted to only one or the other.

Nearby populations of certain species, such as the Purple Martin, Coues' Flycatcher and Olive-sided Flycatcher, may have enabled these birds to quickly invade the modified area when conditions were suitable for them. Such influxes constitute readjustments in a local population—made possible by the high degree of mobility of birds—rather than changes in the composition of the avifauna. Although the logged plot sustained nearly the same diversity of birds as the unlogged plot, it had a smaller avian population.

The greater capacity of the unmodified plot undoubtedly was the result of more habitat being available to birds. The larger amount of foliage made this plot more suitable for foliage-searching and timber-gleaning foragers as well as for foliage-nesting species.

SUMMARY

Avian species composition and densities in a mixed-coniferous virgin forest and in a similar area that sustained a moderately heavy overstory removal form of timber harvesting were examined in the White Mountains in

Arizona during the summers of 1973 and 1974. The unlogged plot supported significantly ($P < 0.05$) more individuals than did the logged plot (88.9 birds/40 ha more in 1973; 153.5 birds/40 ha more in 1974).

The harvested plot supported far fewer tree-foliage searching species. Timber-gleaning species and those that nest in foliage were significantly denser in the unlogged plot. The effect on cavity nesters depended largely on their foraging behavior. Mountain Chickadees, which usually nest in snag cavities and forage mainly on live vegetation and bark, were significantly less abundant in the logged plot, whereas woodpeckers which forage on both live and dead trees were equally abundant in both plots. Aerial foragers as well as birds that used slash, benefited by the lumbering.

This selective logging led to an increase in tree species diversity, and no appreciable change in diversity of foliage height, tree volume, or bird species. Nevertheless, the modified plot, while containing approximately the same number of avian species, supported a far smaller total population.

The amount of foliage available undoubtedly exerts a strong influence on avian species composition and densities because it furnishes nesting sites and foraging substrate. The virgin forest provided substantially more foliage (113,984.0 m³/ha vs. 15,269.8 m³/ha) than did the logged plot. Along with foliage volume and configuration, presence of suitable numbers of snags and significant amounts of slash also were important.

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LITERATURE CITED

- BALDA, R. P. 1969. Foliage use by birds of the oak-juniper woodland and ponderosa pine forest in southeastern Arizona. *Condor* 71: 399-412.
- BALDA, R. P. 1970. Effects of spring leaf-fall on composition and density of breeding birds in two southern Arizona woodlands. *Condor* 72:325-331.
- 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.
- CODY, M. L. 1969. Convergent characteristics in sympatric populations: A possible relation to interspecific territoriality. *Condor* 71:222-239.
- COTTAM, G., AND J. CURTIS. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451-460.
- FRANZREB, K. E. 1976. Nest site competition between Mountain Chickadees (*Parus gambeli*) and Violet-green Swallows (*Tachycineta thalassina*). *Auk* 93:836-837.
- FRETWELL, S. D. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). *Bird-Banding* 40:1-25.
- FRETWELL, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey.
- GOTTFRIED, G., AND J. JONES. 1975. Logging damage to advance regeneration on an Arizona mixed conifer watershed. USDA For. Serv. Res. Pap. RM-147.
- HAGAR, D. C. 1960. The interrelationships of logging, birds and timber regeneration in the Douglas-fir region of northwestern California. *Ecology* 41:116-125.
- HARTLEY, P. H. T. 1953. An ecological study of the feeding habits of the English titmouse. *J. Anim. Ecol.* 22:261-288.
- HOLMES, R. T., AND F. W. STURGES. 1975. Bird community dynamics and energetics in a northern hardwoods ecosystem. *J. Anim. Ecol.* 45:175-200.
- HUTCHESON, K. 1970. A test for comparing diversities based on the Shannon formula. *J. Theor. Biol.* 29:151-154.
- JACKSON, J. A. 1970. A quantitative study of the foraging ecology of Downy Woodpeckers. *Ecology* 51:318-323.
- KARR, J. R., AND R. R. ROTH. 1971. Vegetation structure and avian densities in several New World areas. *Am. Nat.* 105:423-435.
- LACK, D. 1933. Habitat selection in birds with special reference to the effects of afforestation on the Breckland avifauna. *J. Anim. Ecol.* 2:239-262.
- MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599-619.
- MACARTHUR, R. H. 1964. Environmental factors affecting bird species diversity. *Am. Nat.* 98: 387-397.
- MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology* 42:594-598.
- MONSON, G. 1973. The spring migration. Southwest region. *Am. Birds* 27:803-809.
- MORSE, D. H. 1967. The contents of songs in Black-throated Green and Blackburnian warblers. *Wilson Bull.* 79:64-74.
- PIELOU, E. C. 1975. *Ecological diversity*. John Wiley and Sons, New York.
- PITELKA, F. A. 1941. Distribution of birds in relation to major biotic communities. *Am. Midl. Nat.* 25:113-137.
- ROTH, R. R. 1971. Ecological features of bird communities in south Texas brush-grasslands. Ph.D. diss., Univ. Illinois, Urbana.
- SHANNON, C. E. 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27:379-423; 623-656.
- SØRENSEN, T. 1948. A method of establishing groups of equal amplitude in plant society based on similarity of species content. *K. Dan. Vidensk. Selsk.* 5:1-34.
- STURMAN, W. A. 1968. The foraging ecology of

- Parus atricapillus* and *P. rufescens* in the breeding season, with comparisons with other species of *Parus*. *Condor* 70:309-322.
- VERNER, J. 1975. Avian behavior and habitat management. U.S. Forest Service Gen. Tech. Rep. WO-1:39-58.
- VON HAARTMAN, L. 1957. Adaptation in hole-nesting birds. *Evolution* 11:339-347.
- WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithol. Monogr.* No. 8.
- WILLIAMS, A. B. 1936. The composition and dynamics of a beech-maple climax community. *Ecol. Monogr.* 6:317-408.
- WILLSON, M. F. 1974. Avian community organization and habitat structure. *Ecology* 55:1017-1029.
- Endangered Species Office, U.S. Fish and Wildlife Service, 2800 Cottage Way, Sacramento, CA 95825. Address of second author: Department of Zoology, Arizona State University, Tempe, AZ 85281. Accepted for publication 25 April 1978.*