

A COMPARISON OF AVIAN FORAGING BEHAVIOR IN UNLOGGED AND LOGGED MIXED-CONIFEROUS FOREST

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Numerous studies have examined foraging behavior in birds (Hartley 1953; MacArthur 1958; Morse 1967a, 1967b; Jackson 1970; Grubb 1975; others). However, little work has been done on determining differences in avian habitat use in modified vs natural environments. To what extent are birds capable of behaviorally compensating for habitat changes? Are some species less affected by habitat alteration than others? The purpose of this investigation was to examine foraging behavior of five avian species in a virgin, mixed-coniferous forest and a recently logged site in the White Mountains, Arizona.

DESCRIPTION OF STUDY AREA

The Willow Creek watershed (131 ha unlogged, 202 ha logged) is located approximately 80 km south 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 2682–2805 m. The watershed is covered by a mixed-coniferous forest in which Douglas-fir, ponderosa pine, and southwestern white pine are the dominant tree species. A portion of the watershed was logged in 1972 by the selective overstory removal method. Quaking aspen and snags (dead trees) were not removed during timber harvesting. One logged study plot and one unlogged plot, each 15.5 ha and each having approximately the same slope and aspect, were located within 0.6 km of each other. The two plots were selected so that the vegetational components (i.e., tree species composition and densities, and understory vegetation) of the unlogged plot approximated the original vegetation of the logged plot.

MATERIALS AND METHODS

Vegetation analysis.—Within each study plot, vegetation was sampled using the plotless point-quarter method (Cottam and Curtis 1956). The basal area of each tree species was determined using measurements from 400 mature (dbh ≥ 7.6 cm) trees. The volume of live foliage available was determined using integration of standard volume formulas for conical (Douglas-fir, spruces [*Picea* spp.], and firs [*Abies* spp.]), cylindrical (pines), and spherical (aspen) tree forms. Specific details on volume determinations may be found in Franzreb (1978). Tree heights were also estimated using a clinometer and then segregated into 3-m height intervals.

Foraging behavior.—Daily foraging observations were collected from mid-May through August 1973 and 1974 while I systematically traversed parallel transect lines. Observations were taken under skies that were clear or less than 30% overcast and wind conditions varied from no wind to light wind (Beaufort scale 0–2). Although data were collected throughout the day, the majority of observations were taken during morning hours (06:00–10:00).

Observations were recorded and analyzed for five species: the Yellow-bellied Sapsucker (*Sphyrapicus varius*), Mountain Chickadee (*Parus gambeli*), Ruby-crowned Kinglet (*Regulus*

calendula), Yellow-rumped Warbler (*Dendroica coronata*), and Gray-headed (=Dark-eyed) Junco (*Junco hyemalis caniceps*). These species were selected because they represent hole, open-cup, and ground nesting species and because they were sufficiently abundant in both study plots to permit vigorous analysis of the data. Data on both sexes were combined since I was primarily interested in species differences between the two habitats and because determination of sex in the field for three of these five species is difficult.

Foraging data were collected for seven niche dimensions: method of prey procurement, substrate character of the foraging surface, perch diameter, distance from branch tip to the perch site, tree species preferred, tree height used, and foraging distance from the ground. One observation (obtained when the bird was first observed) per bird per sighting, was taken to reduce sampling bias.

A Chi-square goodness of fit test was used to compare tree species use to relative frequency of tree species in both plots. The G-statistic (Zar 1974) was used to determine differences in tree species selection between unlogged and logged plots. For this and all other statistical tests, the significance level was defined as $P \leq 0.05$.

For each observation I recorded the height of the tree in which the bird foraged and the foraging distance from the ground. Data were then segregated into 3-m height intervals. Mean values for tree height and foraging height were calculated. The G-statistic was used to compare tree height selection to actual tree height frequency for both plots. A G-test was also used to compare foraging heights in the unlogged and logged areas.

Chi-square contingency tables were developed for plot vs four of the foraging variables (method, substrate, distance from tip, perch diameter) to test for significant differences between the unlogged and logged stands.

Foraging behavior diversity (H') was calculated using Shannon's (1948) formula. A higher diversity value indicates a species that is more of a generalist with regard to that particular foraging trait. The range in variability in the diversity values was calculated for 95% confidence intervals. Diversity values were tested to determine significant differences ($P \leq 0.05$) using a t -test as described by Hutcheson (1970).

An indication of niche breadth and degree of specialization was estimated by calculating the proportional similarity index (PSI) (Feinsinger et al. 1981) whereby

$$PSI = 1 - \frac{1}{2} \sum |p_i - q_i|$$

Here p_i is the proportion of resource items in state i of all the items used by members of the species and q_i is the proportion of i items in the resource base available to the birds. This index has an advantage over H' because it relates use to availability and gives a more accurate reflection of the degree of niche specialization. Values range from 0–1 with higher values indicating more generalized behavior in that foraging variable. The PSI was calculated separately for each species and was only determined for those foraging variables for which it was possible to quantify resource availability (tree species, tree height, and foraging height).

Niche overlap was estimated from

$$O_{xy} = 1 - \frac{1}{2} \sum |P_{xi} - P_{yi}|$$

where P_{xi} is the proportion of time spent in resource state i by species X (Schoener 1968); O_{xy} represents the extent of niche overlap between species x and y with total overlap along a dimension yielding a value of 1. Comparisons were made among the three primarily foliage-bark gleaning species (Mountain Chickadee, Ruby-crowned Kinglet, and Yellow-rumped Warbler) as it was anticipated that the greatest degree of potential competition existed among them. Overlap results were then tested using the Wilcoxon paired-sample test (Zar 1974) to determine if there were significant differences between the unlogged and logged plots.

TABLE 1
VEGETATION ANALYSIS OF UNLOGGED AND LOGGED MIXED-CONIFEROUS FOREST

Tree species	Tree density (N/ha)		Basal area ^a (m ² /ha)		Foliage vol. (m ³ /ha)		Relative freq. (%)	
	unlog.	log.	unlog.	log.	unlog.	log.	unlog.	log.
Ponderosa pine (<i>Pinus ponderosa</i>)	112.7	4.6	16.32	0.81	35.9%	7.0%	19.3	4.0
Southwestern white pine (<i>P. strobiformis</i>)	109.6	8.8	4.98	0.24	35.3	12.6	18.6	6.1
Douglas-fir (<i>Pseudotsuga menziesii</i>)	194.1	42.3	17.04	2.29	17.6	11.0	26.1	22.7
Alpine fir (<i>Abies lasiocarpa</i>)	3.1	13.0	0.15	0.35	0.2	3.3	0.7	8.7
White fir (<i>A. concolor</i>)	51.7	19.7	4.87	0.52	3.8	3.6	8.6	12.3
Blue spruce (<i>Picea pungens</i>)	12.5	9.6	0.33	0.16	0.5	2.8	2.5	6.1
Engelmann spruce (<i>P. engelmanni</i>)	31.3	19.3	1.20	0.61	2.0	6.8	5.4	11.9
Quaking aspen (<i>Populus tremuloides</i>)	50.1	29.3	1.96	1.96	5.0	53.1	8.2	15.2
Snag (dead tree)	61.1	21.0	4.02	2.52	—	—	10.7	13.0
Total	626.2	167.7	50.88	9.47	100.0	100.0	100.0	100.0

^a Trees with dbh (diameter at breast height) ≥ 7.6 cm.

RESULTS

Vegetation analysis.—The logged area had sustained a moderately heavy overstory removal; most of the canopy was eliminated and the original basal area was reduced 83.7% (Gottfried and Jones 1975). Basal area was 50.88 m²/ha in the unlogged area vs 9.47 m²/ha in the logged plot (Table 1). The logged study area had an overall tree density of 167.7 trees/ha including snags vs 626.2 trees/ha for the unharvested plot (Table 1). Basal area and foliage volume (113,984 m³/ha unlogged, 15,270 m³/ha logged) indicated the logged habitat provided a far more open canopy situation with substantially less foliage volume in which to forage in comparison to the unlogged plot. Mean height of live trees was 18.9 m in the unlogged and 12.8 m in the logged plot (Table 2). Additional information on the vegetation is provided in Franzreb (1978) and Franzreb and Ohmart (1978).

Foraging behavior.—The foraging method of the Yellow-bellied Sapsucker was not significantly different in the study areas (Fig. 1). There was a significant difference ($\chi^2 = 13.43$, $df = 2$, $P < 0.005$) in selection

TABLE 2
MEAN TREE HEIGHT, MEAN FORAGING HEIGHT, COMPARISON OF TREE HEIGHT SELECTION TO HEIGHT AVAILABILITY, PROPORTIONAL SIMILARITY INDICES, AND COMPARISON OF FORAGING HEIGHT DISTRIBUTION BETWEEN FORAGING BIRDS IN UNLOGGED AND LOGGED FORESTS

Species ^a	Mean tree height (m)		Tree height use vs avail. ^b		Tree height use in log. vs unlog. ^c		PSI ^d tree height		Mean foraging height (m)		P value ^e	PSI ^d foraging height	
	unlog.	log.	unlog.	log.	unlog.	log.	unlog.	log.	unlog.	log.		unlog.	log.
YBS	23.4	19.6	**	***	***	***	0.55	0.62	7.4	8.0	NS	0.79	0.84
MC	18.9	16.2	***	***	***	***	0.75	0.76	9.5	9.5	***	0.92	0.88
RCK	20.5	18.1	***	***	***	***	0.70	0.64	10.9	10.6	<0.005	0.90	0.89
YRW	24.8	18.1	***	***	***	***	0.53	0.69	15.5	11.0	***	0.61	0.85
GHJ	16.8	11.6	***	***	***	***	0.73	0.71	6.1	5.7	***	0.75	0.71
Mean tree height ^f	16.4 m 14.4 m												
Mean live tree height	18.9 m 12.8 m												

** $P < 0.01$; *** $P < 0.001$.

^a Species acronyms: YBS—Yellow-bellied Sapsucker, MC—Mountain Chickadee, RCK—Ruby-crowned Kinglet, YRW—Yellow-rumped Warbler, GHJ—Gray-headed (=Dark-eyed) Junco.

^b G-statistic comparing tree use data to tree height frequency in unlogged and logged plots; all G values ≥ 64 , df = 12, all P values < 0.001 .

^c G-statistic comparing use of tree heights in unlogged to use in logged plots; all G values ≥ 43.5 , df = 12, all P values < 0.001 .

^d PSI = Proportional similarity index (see text for details).

^e P value from G-statistic for comparison of foraging height in unlogged vs logged plots; all G values ≥ 30.9 except for YBS.

^f Including snags.

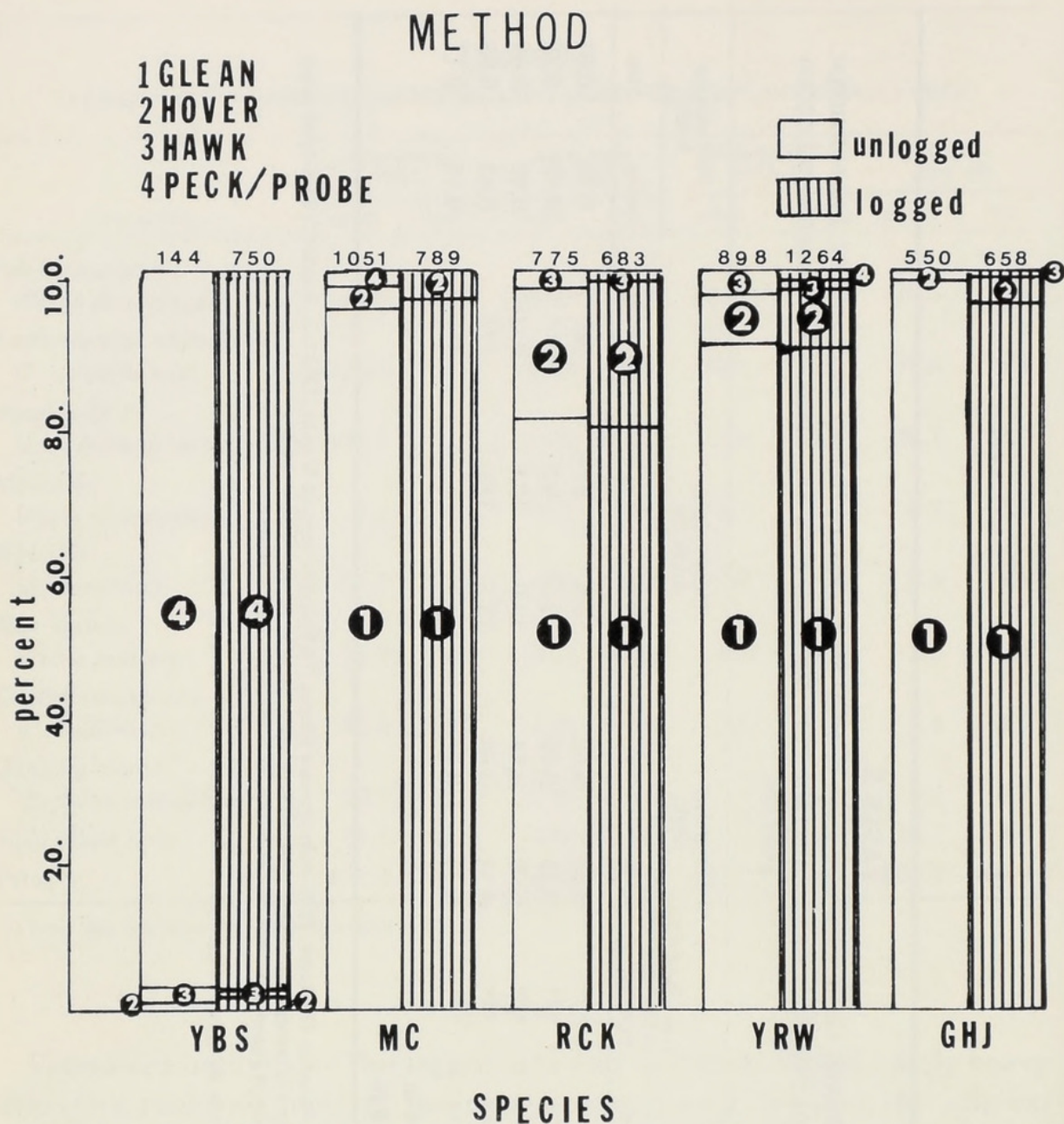


FIG. 1. Method used during foraging behavior. Open bar represents frequency of class observations in the unlogged area while hatched bar represents those in the logged area. Number at top of each bar is sample size. Bird species are: YBS—Yellow-bellied Sapsucker, MC—Mountain Chickadee, RCK—Ruby-crowned Kinglet, YRW—Yellow-rumped Warbler, GHJ—Gray-headed (=Dark-eyed) Junco. Values less than 1% are not graphed. Chi-square values: YBS ($\chi^2 = 0.61$, $df = 3$, NS), MC ($\chi^2 = 12.39$, $df = 3$, $P < 0.01$), RCK ($\chi^2 = 5.94$, $df = 3$, NS), YRW ($\chi^2 = 3.98$, $df = 3$, NS), GHJ ($\chi^2 = 9.03$, $df = 2$, $P < 0.025$).

of foraging substrate between the unlogged and logged plots; the trunk was used more frequently in the unharvested site (Fig. 2). No significant difference was observed in diameter of branches used; larger-diameter branches were selected more often than smaller ones in both study plots

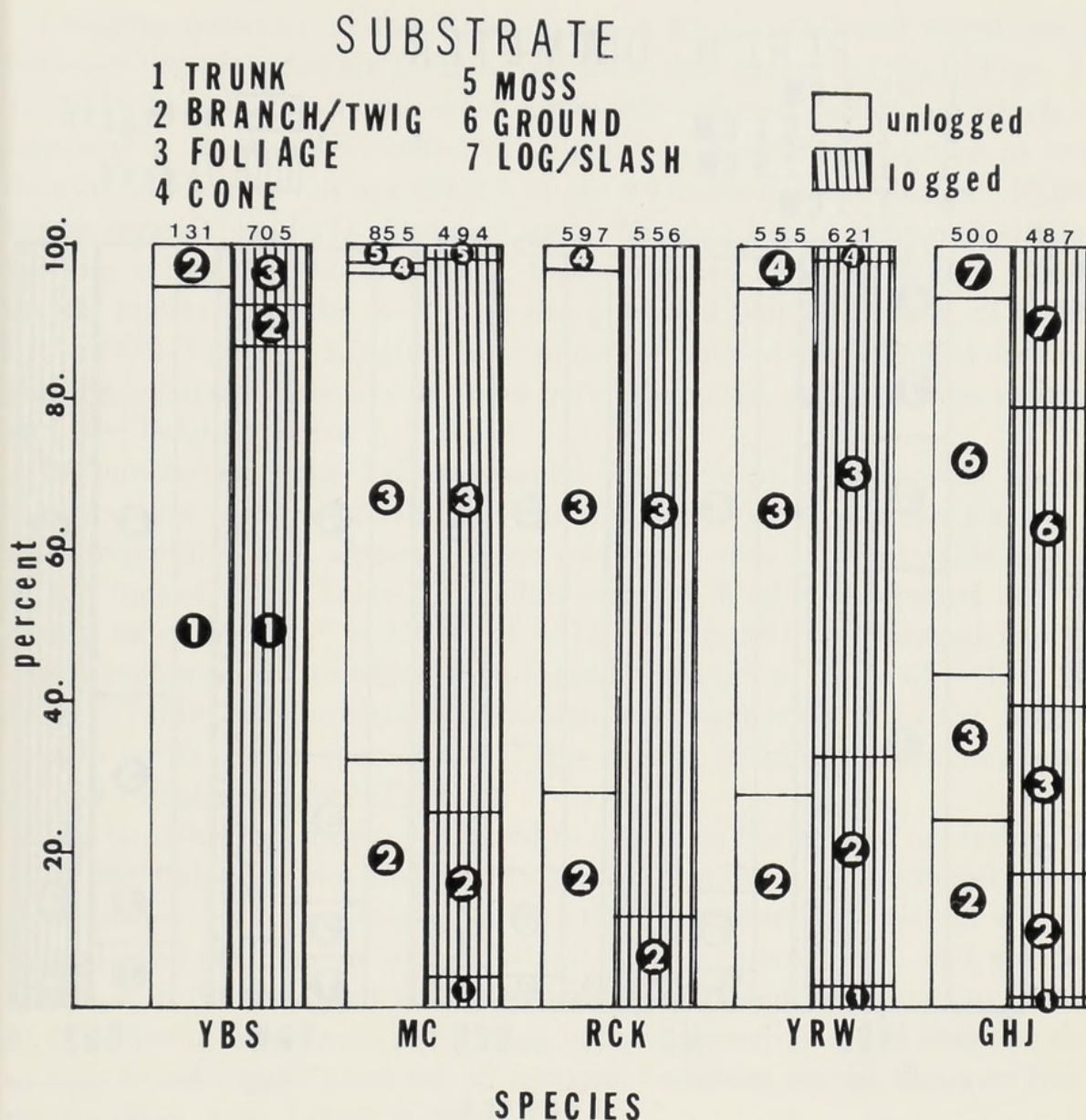


FIG. 2. The foraging substrate from which the bird foraged. Legend follows Fig. 1. Chi-square values: YBS ($\chi^2 = 13.43$, $df = 2$, $P < 0.005$), MC ($\chi^2 = 47.3$, $df = 4$, $P < 0.001$), RCK ($\chi^2 = 53.9$, $df = 3$, $P < 0.001$), YRW ($\chi^2 = 19.7$, $df = 4$, $P < 0.001$), GHJ ($\chi^2 = 52.5$, $df = 5$, $P < 0.001$).

(Fig. 3). Sapsuckers did not randomly select tree species but were significantly different in tree species use when compared to availability in both study plots (Table 3, unlogged $\chi^2 = 304.4$, $df = 8$, $P < 0.001$; logged $\chi^2 = 164.4$, $df = 8$, $P < 0.001$). Sapsuckers preferentially selected tall trees in both areas although foraging height from the ground was not significantly different (Table 2). For this species foraging differed significantly in the two study sites for substrate, tree species preferences ($G = 75.8$, $df = 8$, $P < 0.001$), and tree height use ($G = 315.1$, $df = 12$, $P < 0.001$).

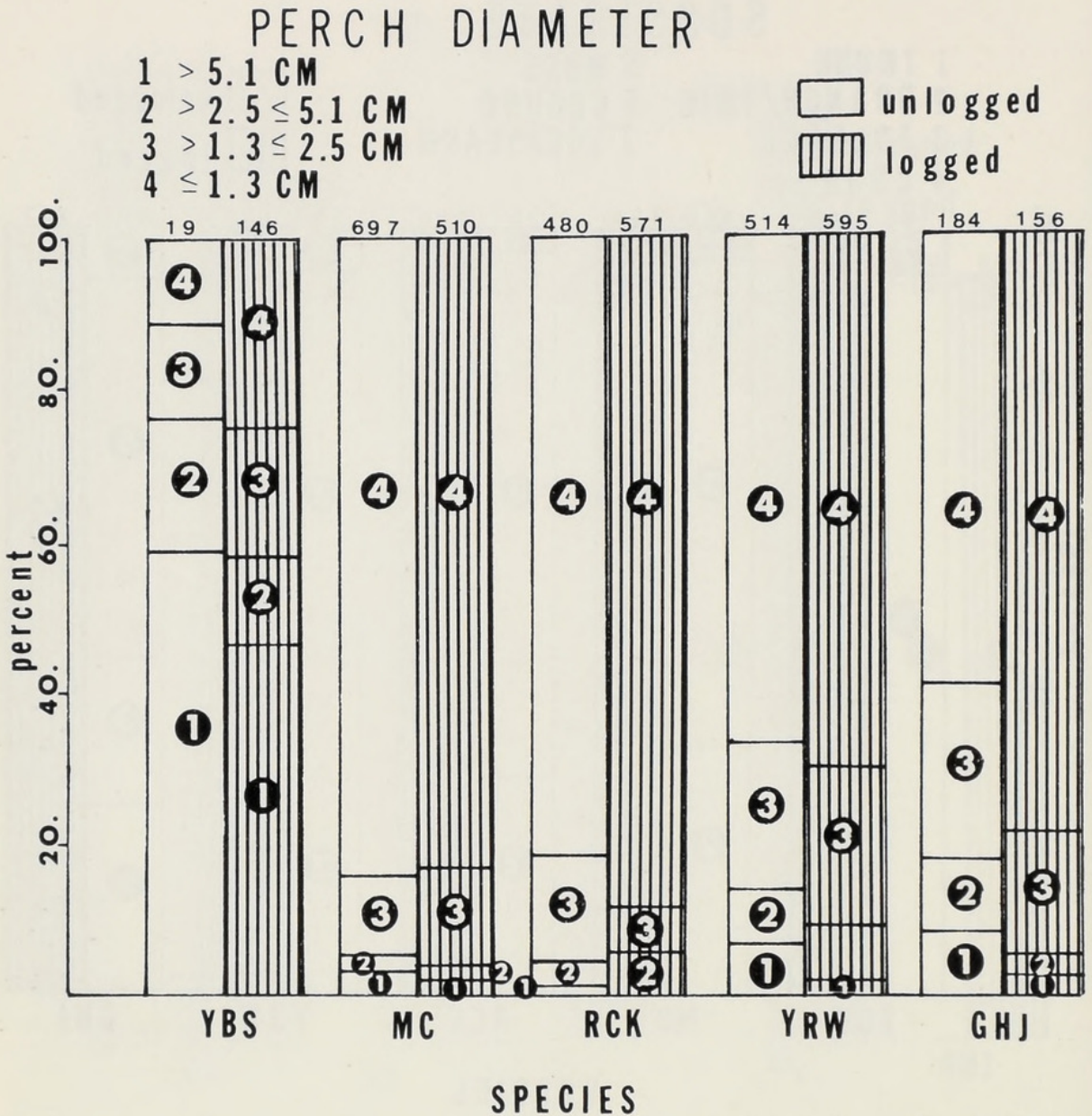


FIG. 3. Perch diameter selected during foraging. Legend follows Fig. 1. Chi-square values: YBS ($\chi^2 = 2.51$, $df = 3$, NS), MC ($\chi^2 = 9.38$, $df = 3$, $P < 0.025$), RCK ($\chi^2 = 30.9$, $df = 3$, $P < 0.001$), YRW ($\chi^2 = 11.7$, $df = 3$, $P < 0.01$), GHJ ($\chi^2 = 16.1$, $df = 3$, $P < 0.005$).

(Table 2). The PSI based on use vs resource availability indicated that sapsuckers were considerably more generalized in tree species selection (Table 3) and tree height use (Table 2) in the logged area.

Significant differences in foraging behavior of Mountain Chickadees were observed for all but the perch diameter variable (Figs. 1–4). Chickadees foraged significantly more frequently near the tips of branches in the unlogged area (Fig. 4) ($\chi^2 = 33.8$, $df = 2$, $P < 0.01$). Greater specialization with respect to tree species selection was evident in the unlogged area (PSI = 0.63 unlogged, 0.77 logged) (Table 3).

Foraging behavior of the Ruby-crowned Kinglet differed significantly between the plots for six foraging variables (all except method) (Figs. 1–4, Table 2). Foliage was the most commonly selected surface on which to forage (Fig. 2). Kinglets relied principally on Engelmann spruce as evidenced by its frequent use (39.2% of observations in the unlogged, 40.8% in the logged) (Table 3). Although mean foraging height appeared similar (10.9 m unlogged, 10.6 m logged), Ruby-crowned Kinglets foraged significantly higher from the ground in the unlogged plot ($G = 30.8$, $df = 12$, $P < 0.005$) (Table 2). Kinglets were more specialized in the logged area regarding substrate, tree species use, perch diameter, distance from the tip, and tree height (Tables 2, 3, 4).

In both habitats the Yellow-rumped Warblers principally used Engelmann spruce and Douglas-fir. In the unlogged site ponderosa pine was also frequently used, whereas aspen was selected to a considerable extent in the logged area (Table 3). Yellow-rumped Warblers selected significantly taller trees ($\chi^2 = 152.2$, $df = 12$, $P < 0.001$) and foraged significantly higher in the unlogged than logged areas ($\chi^2 = 117.5$, $df = 11$, $P < 0.001$) (Table 2). Warblers were much more generalized in the logged area in terms of tree species use (Table 3), tree height preferences (Table 2), and foraging heights (Table 2).

The Gray-headed Junco preferred to forage on the ground or slash (Fig. 2). In the unlogged plot Engelmann spruce was the most frequently used tree species, whereas Douglas-fir was the most commonly visited species in the logged site. Juncos were substantially less generalized in tree species selection in the unlogged area ($PSI = 0.60$ unlogged, 0.74 logged) (Table 3). Significant differences in foraging behavior were observed between the unlogged and logged plots for all foraging variables except distance from the tip (Figs. 1–4; Tables 2, 3).

Foraging niche overlap was significantly lower in the timber harvested than unlogged plot for the Mountain Chickadee/Ruby-crowned Kinglet (Wilcoxon paired-sample test, $P(T = 0) < 0.02$) (Table 5). Differences between the plots were particularly notable in distance from the tip (Ruby-crowned Kinglet/Yellow-rumped Warbler), foraging substrate (Ruby-crowned Kinglet/Yellow-rumped Warbler), tree species preferences (Mountain Chickadee/Yellow-rumped Warbler), and foraging height (Mountain Chickadee/Yellow-rumped Warbler and Ruby-crowned Kinglet/Yellow-rumped Warbler).

DISCUSSION

For many species foraging behavior does not appear to be highly stereotyped or inflexible, and therefore permits a certain degree of accommodation to environmental change. Studies have shown that birds may

TABLE 3
COMPARISON OF TREE SPECIES SELECTION BY FORAGING BIRDS IN UNLOGGED AND LOGGED FORESTS BASED ON TREE SPECIES
AVAILABILITY^a, COMPARISON OF TREE USE IN UNLOGGED VS LOGGED PLOTS, AND PROPORTIONAL SIMILARITY INDICES FOR
TREE SPECIES USE

Tree species	UNLOGGED PLOT Bird Species ^b									
	YBS		MC		RCK		YRW		GHJ	
	N	%	N	%	N	%	N	%	N	%
Ponderosa pine	22	15.5	53	4.7	41	4.9	238	26.0	3	1.1
Southwestern white pine	—	—	94	8.3	53	6.3	128	14.0	28	10.1
Douglas-fir	30	21.1	474	42.1	243	28.9	212	23.2	76	27.4
Alpine fir	16	11.3	35	3.1	20	2.4	26	2.8	2	0.7
White fir	6	4.2	152	13.4	58	6.8	74	8.1	24	8.7
Blue spruce	7	4.9	46	4.1	61	7.2	31	3.4	26	9.4
Engelmann spruce	25	17.6	194	17.3	330	39.1	162	17.7	103	37.2
Quaking aspen	10	7.1	66	5.9	34	4.0	34	3.7	9	3.2
Snag	26	18.3	12	1.1	3	0.4	10	1.1	6	2.2
Total	142	100.0	1126	100.0	843	100.0	915	100.0	277	100.0
χ^2 value ^a , df	304.4, 8		825.8, 8		2142.2, 8		466.2, 8		653.5, 8	
P level ^c	$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$	
PSI ^d	0.67		0.63		0.57		0.78		0.60	

TABLE 3
CONTINUED

Tree species	LOGGED PLOT Bird species ^b											
	YBS		MC		RCK		YRW		GHJ			
	N	%	N	%	N	%	N	%	N	%	N	%
Ponderosa pine	18	2.7	1	0.1	2	0.3	30	2.6	5	1.9		
Southwestern white pine	22	3.3	6	0.8	16	2.2	53	4.5	22	8.1		
Douglas-fir	120	18.0	235	30.5	33	39.6	277	23.8	79	28.9		
Alpine fir	141	21.1	50	6.5	289	4.5	103	8.9	21	7.8		
White fir	77	11.5	153	19.9	39	5.3	139	12.0	52	18.9		
Blue spruce	13	2.0	58	7.5	31	4.3	87	7.5	31	11.5		
Engelmann spruce	39	5.8	142	18.4	298	40.8	227	19.5	47	17.4		
Quaking aspen	107	16.0	108	14.0	20	2.7	219	18.8	9	3.3		
Snag	132	19.8	18	2.3	2	0.3	28	2.4	6	2.2		
Total	668	100.0	771	100.0	730	100.0	1163	100.0	272	100.0		
χ^2 value ^a , df	142.2, 8		223.1, 8		860.6, 8		180.8, 8		85.8, 8			
P level ^c for χ^2	$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$			
PSI ^d	0.83		0.77		0.54		0.86		0.74			
G-statistic ^e	75.8		197.0		79.8		462.0		58.1			
P level ^c for G	$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$			

^a Based on tree species relative frequency values.^b Species abbreviations follow Table 2.^c Significance level for Chi-square and G-statistic tests $P \leq 0.05$.^d PSI = Proportional similarity index (see text for details).^e G-statistic comparing tree species use in unlogged vs logged plots.

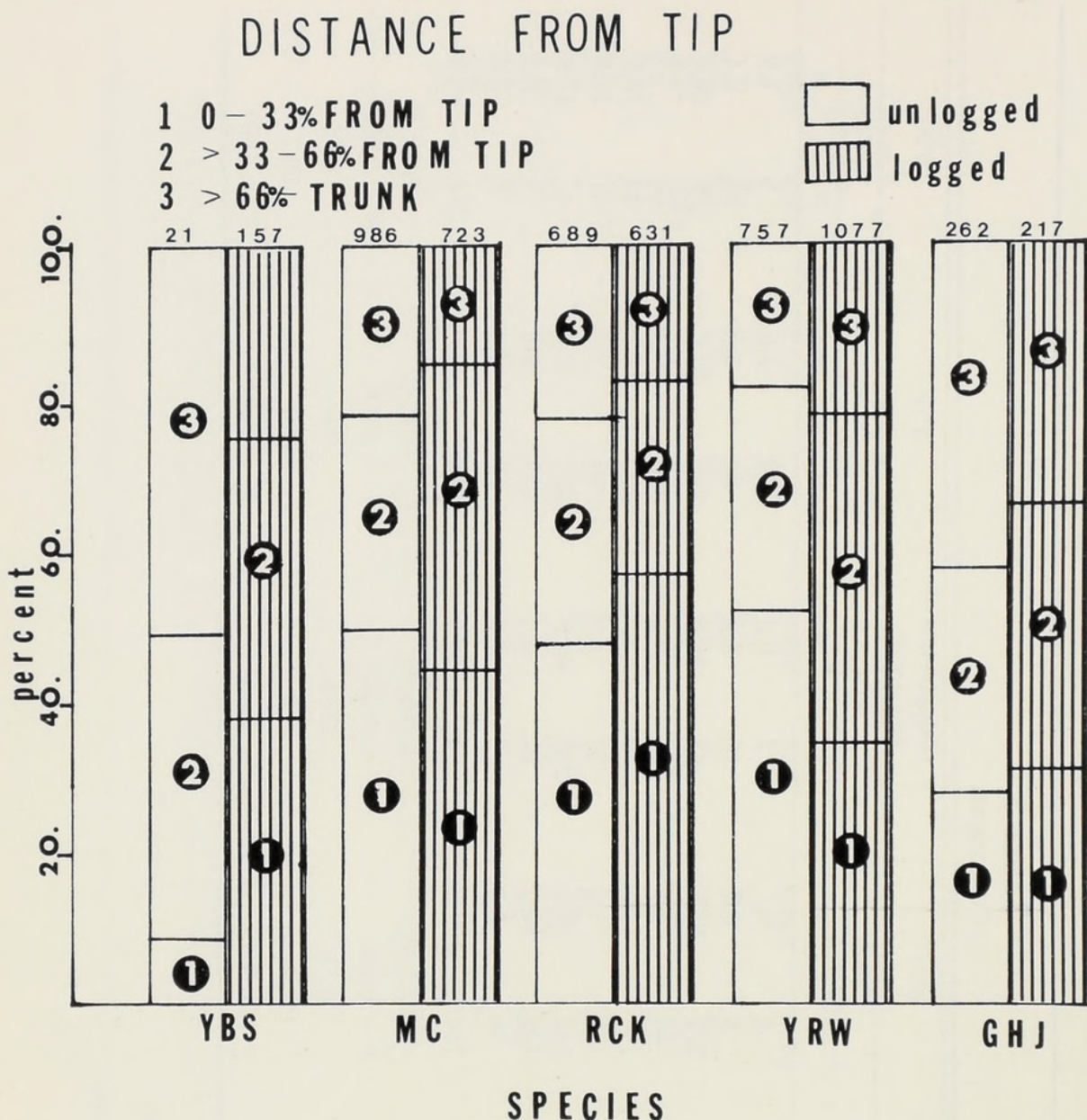


FIG. 4. Distance from the branch tip to the perch site during foraging. Legend follows Fig. 1. Chi-square values: YBS ($\chi^2 = 10.9$, $df = 2$, $P < 0.01$), MC ($\chi^2 = 33.8$, $df = 2$, $P < 0.001$), RCK ($\chi^2 = 13.0$, $df = 2$, $P < 0.005$), YRW ($\chi^2 = 58.5$, $df = 2$, $P < 0.001$), GHJ ($\chi^2 = 2.9$, $df = 2$, NS).

modify foraging behavior in response to a number of factors such as changes in the structure of the habitat (Grubb 1979) or vegetation composition (Sturman 1968). Szaro and Balda (1980) found that timber harvesting in ponderosa pine forest influenced the behavior pattern of most avian species especially with regard to perch type and tree species selection.

The unlogged habitat presented a vegetation profile of taller trees, with a closed canopy in many places, and a poorly developed understory. Timber harvesting reduced the amount of foraging substrate available for tree

TABLE 4
DIVERSITY (H'), 95% CONFIDENCE INTERVALS, AND SIGNIFICANCE LEVELS FOR FORAGING
VARIABLES IN UNLOGGED AND LOGGED FORESTS

Species ^a	Foraging variable		Perch diameter	Distance from tip
	Method	Substrate		
YBS	unlogged	0.12 ± 0.13	0.21 ± 0.13	1.13 ± 0.14
	logged	0.14 ± 0.14	0.47 ± 0.17	1.25 ± 0.09
	SD ^b	NS	$t = 2.3, P < 0.02$	NS
MC	unlogged	0.19 ± 0.16	0.82 ± 0.16	0.61 ± 0.19
	logged	0.14 ± 0.12	0.75 ± 0.17	0.56 ± 0.18
	SD	NS	NS	NS
RCK	unlogged	0.55 ± 0.15	0.72 ± 0.13	0.66 ± 0.19
	logged	0.55 ± 0.13	0.41 ± 0.15	0.44 ± 0.18
	SD	NS	$t = 3.0, P < 0.01$	NS
YRW	unlogged	0.39 ± 0.17	0.79 ± 0.14	0.96 ± 0.17
	logged	0.39 ± 0.18	0.76 ± 0.14	0.87 ± 0.17
	SD	NS	NS	NS
GHJ	unlogged	0.05 ± 0.09	1.21 ± 0.13	1.09 ± 0.14
	logged	0.17 ± 0.13	1.36 ± 0.09	0.69 ± 0.17
	SD	NS	NS	$t = 3.5, P < 0.01$

^a Species abbreviations follow Table 2.

^b t -test as described by Hutcheson (1970).

foragers by drastically decreasing tree density and by removing a substantial proportion of the larger trees (thereby reducing much of the foliage volume and limbs upon which to forage). Reductions along several resource dimensions were apparent in the logged plot including substrate availability, foliage volume, mean tree height, and possibly, food accessibility, quantity, and quality. In addition, there was also an increase in canopy openness as well as an increase in slash and possibly appurtenant changes in insect distributions and densities.

The Yellow-bellied Sapsucker was more generalized in the logged plot in a number of categories such as foraging substrate which may be accounted for by their increased use of branches and foliage. If the logged site was less suitable with regard to nesting and/or foraging either because of reductions in foliage volume or tree densities, one might predict a lower density of sapsuckers there than in the unlogged site. Such was not the case for this species since densities were not significantly different in the two plots during either 1973 or 1974 (Franzreb and Ohmart 1978). The more open habitat (and possibly increased accessibility to prey) and pres-

TABLE 5
COMPARISON OF NICHE OVERLAP^a BETWEEN SPECIES IN UNLOGGED AND LOGGED FORESTS

Foraging variable	Species compared ^b					
	MC/RCK		MC/YRW		RCK/YRW	
	unlog.	log.	unlog.	log.	unlog.	log.
Method	0.83	0.82	0.94	0.93	0.89	0.88
Substrate	0.94	0.86	0.95	0.90	0.97	0.80
Perch diameter	0.97	0.92	0.84	0.86	0.86	0.81
Distance from tip	0.97	0.86	0.96	0.90	0.96	0.77
Tree species	0.75	0.67	0.73	0.85	0.69	0.63
Tree height	0.81	0.72	0.72	0.80	0.75	0.83
Foraging height	0.86	0.82	0.56	0.85	0.65	0.85
Mean overlap	0.88	0.81	0.81	0.87	0.82	0.80
Standard deviation	0.086	0.087	0.150	0.002	0.129	0.081
Difference in mean	0.07		0.06		0.02	
<i>P</i> value ^c	<i>P</i> (<i>T</i> = 0) < 0.02		<i>P</i> (<i>T</i> = 7), NS		<i>P</i> (<i>T</i> = 11), NS	

^a Overlap = $O_{xy} = 1 - \frac{1}{2} \sum |P_{xi} - P_{yi}|$.

^b Species abbreviations follow Table 2.

^c Wilcoxon paired-sample test; significance level $P < 0.05$.

ence of larger, more mature aspen in the logged plot (in which the sapsucker constructed its nests) may have been important determinants of its density. Even though densities were similar, there were still a number of significant differences in foraging behavioral categories. These presumably reflect the foraging adaptability of this species, and may have been instrumental in permitting the sapsucker to successfully use the modified habitat.

In the logged plot the Mountain Chickadee shifted its foraging location downward and used shorter trees, thus apparently accommodating to a shift in the overall vegetation structure including the distribution and volume of foliage. In the logged area the chickadee doubled its use of aspen, perhaps reflecting the large amount of aspen foliage available (53.1%) and also its increased relative frequency. Even with this flexibility, the harvested plot supported significantly ($P < 0.05$) fewer Mountain Chickadees than did the unlogged habitat (44.7 birds/40 ha unlogged vs 11.8/40 ha logged in 1973, 58.9/40 ha unlogged vs 30.8/40 ha logged in 1974) (Franzreb and Ohmart 1978).

The Ruby-crowned Kinglet's relatively high degree of specialization in a number of foraging variables presumably allowed for more efficient exploitation of certain aspects of the logged environment. Kinglets preferred to forage in portions of the trees replete with dense foliage and spent considerable time in the upper portions of trees where the vegetation was

the most dense; this tendency was particularly pronounced in the logged plot. The unaltered habitat provided dense cover in many of the even shorter trees because of the high tree density. Kinglets were most active in Engelmann spruce and Douglas-fir, two of the tree species with the most dense vegetation. Tree species with more open needle/leaf configurations such as ponderosa pine, southwestern white pine, and quaking aspen were even less frequently used in the logged than unlogged habitat. The unlogged plot supported significantly ($P < 0.05$) more Ruby-crowned Kinglets than did the logged plot (71.0/40 ha vs 42.1/40 ha in 1973, 74.4/40 ha vs 23.1/40 ha in 1974) (Franzreb and Ohmart 1978). Even though the kinglet markedly altered its foraging strategy by specializing more with respect to all foraging variables (except method), the logged plot still did not support as high a density. The changes in behavior may have been related to a change in structure of the vegetation profile, particularly to the reduction in tree density and mean tree height, and a decline in both foliage density and volume.

In the logged plot the Yellow-rumped Warbler was much more generalized; the extent of the increase in generalization for specific foraging variables was more obvious than for any other species. This warbler frequently forages in open, less dense foliage, so was not as restricted in its location with respect to needle/leaf density as was, for example, the Ruby-crowned Kinglet; hence, more levels of the vegetation profile were acceptable. This may account for the shift to lower foraging sites in the logged area. Although it still preferred to forage in Engelmann spruce and Douglas-fir, the Yellow-rumped Warbler increased its use of quaking aspen in the logged plot and was more generalized in its overall use of the various tree species. Apparently the warbler was quite behaviorally plastic as indicated by its substantially more generalized behavior in the logged area for a number of foraging variables (tree species, tree height, foraging level) and achieved the highest density of any species in the logged plot. Even so, it had significantly ($P < 0.05$) higher densities in the unlogged than logged plot (131.6/40 ha unlogged vs 100.0/40 ha logged in 1973, 89.8/40 ha vs 76.9/40 ha in 1974) (Franzreb and Ohmart 1978).

Gray-headed Junco densities were significantly ($P < 0.05$) higher in the logged plot (76.3/40 ha logged vs 31.6/40 ha unlogged in 1973, 74.4/40 ha vs 51.3/40 ha in 1974) (Franzreb and Ohmart 1978). This may have resulted from the ground-foraging junco's use of logs and slash that were far more abundant in the timber harvested area, its more generalized use of tree species, and because it is a ground nester.

Although it is difficult to substantiate competition using overlap values (Colwell and Futuyma 1971), such values are indicative of resource dimensions along which competition may take place (Williams and Batzli

1979). Even if species exhibit little overlap in one dimension, substantial competition may still occur. Potential competition may have modified foraging behavior for several species in this study; however, it is difficult to distinguish the direct effects of logging and concomitant reductions in resource availability from either the release from, or initiation of, competitive influences.

Kinglets were quite specialized in tree species use—over 80% of the observations were in Douglas-fir and Engelmann spruce in the logged plot—and partitioned the habitat primarily in this regard with respect to the Yellow-rumped Warbler. In comparing the Ruby-crowned Kinglet and Mountain Chickadee, it was evident that there was less overlap in all variables in the logged area, mainly because the kinglets became significantly ($P < 0.05$) less diverse in a number of foraging variables.

With the removal of the mid- to large-sized trees, the vegetation profile was shifted downward in the logged area; hence, the increased degree of overlap in foraging level and tree height use was predicted. Birds may also have responded in the logged site to the shift in tree species frequencies, reduction in foliage densities, openness of the habitat (Yellow-bellied Sapsucker), and enhanced ground slash abundance (Gray-headed Junco). Reductions in foliage volume and densities of preferred tree species could not be compensated for totally by shifts to more abundant plant resources subsequent to logging. Preferences for certain tree species may reflect variation in insect fauna, abundance or accessibility (Orians 1977) and may occur, in part, because different tree species provide varying amounts and densities of foliage.

In studying foraging behavior in 22 insectivorous birds in a northern hardwood forest, Holmes et al. (1979) suggested that the ability to obtain food may vary with distance from the ground and is influenced by certain physical and chemical characteristics of the plant species, principally those related to foraging substrates, food-seeking methods, and food abundances. They noted that the birds partitioned the habitat by tree species use, foraging substrate, and method. Maurer and Whitmore (1981) in comparing an immature to mature deciduous forest, suggested that differences in foraging were related to altered distribution of resources arising from differences in plant species composition and structure.

This study provides further evidence to suggest that these species partition the habitat by selecting different tree species, substrates, tree heights, and foraging heights, and that the vertical distribution of the vegetation, the foliage density, and the relative frequencies of tree species are of major importance in predicting the response of birds to a logged environment. These factors may influence the distribution and availability of resources

such as food, cover, and nesting substrate, and hence, the number of birds a modified habitat can support. Further work is needed on refining the complex interplay of these factors and the resulting responses of the avifauna.

SUMMARY

Foraging behavior of five avian species (Yellow-bellied Sapsucker, Mountain Chickadee, Ruby-crowned Kinglet, Yellow-rumped Warbler, and Gray-headed [=Dark-eyed] Junco) was compared in a recently logged mixed-coniferous forest (selective overstory removal) and a natural forest. The structure and profile of the vegetation in the two forest types differed, with the logged area possessing a different tree-species, foliage-volume distribution, far more open canopy cover, and a greater ground surface complexity resulting from abundant slash (logging debris). In the timber harvested plot, foliage volume, mean tree height, and overall tree density were substantially reduced.

In the logged plot some species responded by reducing foraging heights and using shorter trees. Tree species selection varied significantly ($P < 0.05$) for all avian species when comparing tree species use to tree species availability based on relative frequencies and also when contrasting use in unlogged vs logged areas. The distribution of foliage volume by tree species was considerably different in the two plots. Aspen comprised over 53.1% of the total foliage volume in the logged area vs 5.0% in the unlogged. Use of aspen in the logged plot increased at least twofold for the Yellow-bellied Sapsucker, Mountain Chickadee, and Yellow-rumped Warbler.

In the logged area the increase in degree of generalization for the Yellow-rumped Warbler was more pronounced than for any other species. In contrast, the Ruby-crowned Kinglet was quite stereotyped in its foraging and even more so in the harvested area; this coupled with substantially greater specialization in the warbler, was reflected in a reduction in niche overlap between the kinglet and both the chickadee and Yellow-rumped Warbler in the logged site. The results of this study suggest that changes in foraging behavior such as those observed for tree species selection, foraging substrate, tree height use, and foraging height, reflect a shift in vegetation structure and distribution and/or availability of resources.

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