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YEARLY VARIATION IN RESOURCE-USE BEHAVIOR BY PONDEROSA PINE FOREST BIRDS

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Abstract. Foraging patterns of breeding birds in a ponderosa pine (*Pinus ponderosa*) forest of northern Arizona were studied from 1973 to 1975. Significant yearly differences occurred for many bird species in activity patterns, foraging mode, tree species selection, substrate use, foraging posture, horizontal tree positioning, and vertical tree positioning. Relationships determined over a single year or using data pooled across years can lead to misinterpretations about community organization, competitive interactions, and foraging ecology of single species, guilds, or entire communities.

Key Words: Foraging ecology; annual variation; ponderosa pine.

Foraging patterns and resource partitioning are popular areas of investigation by avian ecologists. Many studies emphasize differences in foraging technique (Airola and Barrett 1985), food selection (Kuban and Neill 1980), substrate or vegetation preferences (Holmes and Robinson 1981; Parker 1986b; Morrison et al. 1986, 1987b), vegetation structure (Maurer and Whitmore 1981, Robinson and Holmes 1984, Morrison and With 1987), search tactics (Robinson and Holmes 1982, Holmes and Recher 1986a), resource availability (E. P. Smith 1982), foraging efficiency (Pulliam 1985, Rogers 1985), foraging height (Szaro and Balda 1979, Alatalo 1981), and feeding posture or position (Alatalo 1982, Saether 1982) when investigating foraging relationships in bird communities. Yet, few studies examine annual variation in resource use and foraging (Grant and Grant 1980; Saether 1982; Ford et al., this volume; Hejl and Verner, this volume).

Most studies have not attempted to examine annual changes in foraging behavior even when substantial differences in bird density, species composition, and weather patterns could affect the availability of food items and/or territory selection and establishment (Grubb 1975, 1977, 1978; K. G. Smith 1982; Szaro and Balda 1986; Szaro 1986). This paper examines annual changes in foraging patterns and resource use by birds in ponderosa pine (*Pinus ponderosa*) forests during three breeding seasons, in Arizona.

STUDY AREAS AND METHODS

Four 15-ha plots within a 21-km radius in the Coconino National Forest, 43–63 km southeast of Flagstaff, Arizona were studied from 1973 to 1975. Ponderosa pine, gambel oak (*Quercus gambelii*), and alligator juniper (*Juniperus deppeana*) were the only tree species present, with ponderosa pine dominant on all sites. A wide spectrum of silvicultural treatments were represented by four study plots (Brown et al. 1974). Large trees (>25 cm diameter at breast height) and small dense thickets were selectively removed from the lightly cut area, resulting in a density of 263 trees/ha and a crown volume of 1.70×10^3 m^3/ha. The moderately cut area was thinned in a pattern of strips of trees 36 m wide alternating with cleared areas 18 m wide, resulting in a density of 181 trees/ha and a crown volume of 0.65×10^3 m^3/ha. The heavily cut plot was severely thinned to 69 trees/ha and a crown volume of 0.40×10^3 m^3/ha, with slash piled in windrows spaced at regular intervals. The uncut area had 646 trees/ha and a crown volume of 1.94×10^3 m^3/ha. Yearly precipitation, mostly in the form of snow, was 135 cm in 1973, 40 cm in 1974, and 64 cm in 1975. Annual mean temperature was 4.8°C in 1973, 6.7°C in 1974, and 4.9°C in 1975. For a more complete description of the study sites, see Szaro and Balda (1979).

The spot-mapping method (Robbins 1970) was used to estimate breeding bird densities. Eight visits were made annually to each plot between May and July from 1973 to 1975. Counts began within 15 min after sunrise and continued for 3 hours. Starting points differed for each count to minimize temporal bias. Sampling was done beyond plot boundaries where bird territories extended beyond the study area to provide a better estimation of territory size. All field data were collected by the senior author in all years.

Plots were systematically traversed and data were recorded for the first observation of each bird encountered. Data recorded at each sighting included bird species, activity pattern (singing, foraging, or resting), foraging mode (pick and glean, hover and hawk, tear and peck, or ground probing), substrate (trunk, branch, twig, foliage, ground, or air), posture (upright, hanging, head up, or head down), tree species (ponderosa pine, gambel oak, or alligator juniper), horizontal position in tree (outer foliage-twigs or inner trunks-branches), and height of bird. All bird species were recorded and observed but only those species in each foraging guild with the greatest number of observations were used in further analyses: pick and glean—Grace's Warbler (*Dendroica graciae*), Pygmy Nuthatch (*Sitta pygmaea*), Solitary Vireo (*Vireo solitarius*); hover and hawk—Western Bluebird (*Siala mexicana*), Western Wood-Pewee (*Contopus sordidulus*); tear and peck—Northern Flicker (*Colaptes auratus*), White-breasted Nuthatch (*Sitta carolinensis*); and ground probing and walking—Dark-eyed Junco (*Junco hyemalis*) and Chipping Sparrow (*Spizella passerina*). Observations on the ground were excluded from analyses of horizontal tree position and tree species selection. We compared vertical tree

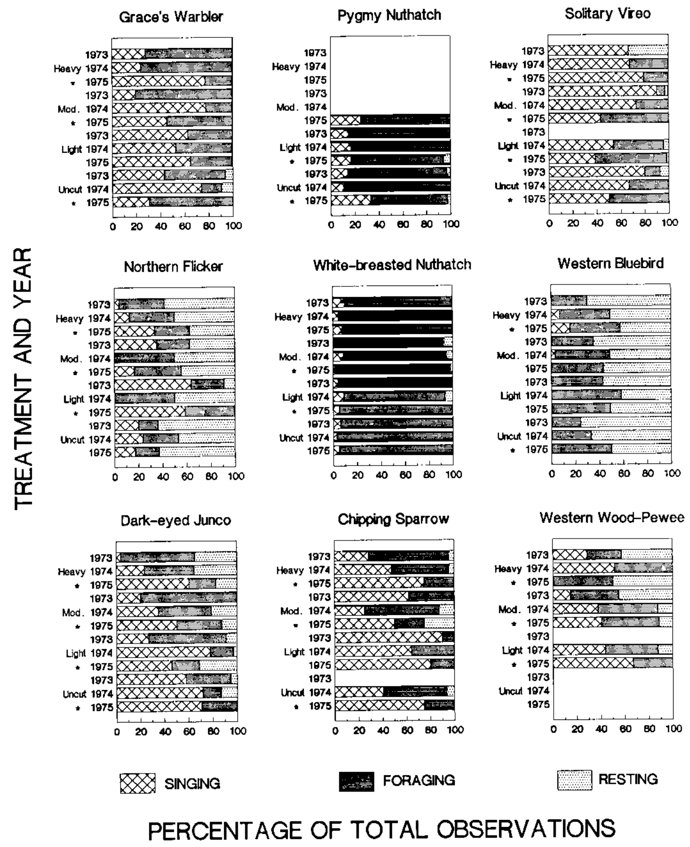

FIGURE 1. Activity patterns of nine ponderosa pine forest bird species by treatment and year. An asterisk under treatment indicates that the association among activity pattern and years was significant (*G*-test, $P \leq 0.05$).

profiles for Grace's Warblers and Yellow-rumped Warblers (*Dendroica coronata*), because this was the only observed occurrence of one species potentially responding to the presence of another in the same guild. Yellow-rumped Warblers were not used in other analyses of resource-use behaviors; yearly comparisons were not possible because these warblers were not observed on any site for all 3 years.

Analysis of frequencies for each behavioral attribute was initially attempted with three-way tables (i.e., treatment by year by behavioral attribute) using log-linear models (Sokal and Rohlf 1981:747). The occurrence of significant interaction terms in all cases precluded fits to any simpler models. All further analyses were based on separate two-way tests of independence within each level of treatment (i.e., we examined the association between a behavioral attribute and years). We specifically asked the question, "Are activity, foraging method, substrate use, posture, tree species use, or position in the tree independent of year?" All significant yearly differences in proportions of a given behavior were determined with a goodness-of-fit test (*G*-test) at $P \leq 0.05$ (Sokal and Rohlf 1981).

RESULTS

On an individual species basis, significant yearly differences in resource-use behaviors occurred for Pygmy Nuthatches in 92% (N = 12) of all cases, as contrasted with only 42% (N = 24) for Chipping Sparrows. The changes were basically conservative, however, and none would result in classifying a species in different guilds in different years. No marked yearly differences were noted between treatments, as 69%, 63%, 52%, and 63% of resource-use behaviors by all species on the heavily cut, moderately cut, lightly cut, and uncut plots, respectively, were significant.

Examination of yearly differences for each behavioral attribute (33 possible comparisons) revealed that activity patterns varied significantly among years for all species on at least one treatment (79% of all cases; Fig. 1). For most species, shifts were from singing-calling to foraging or

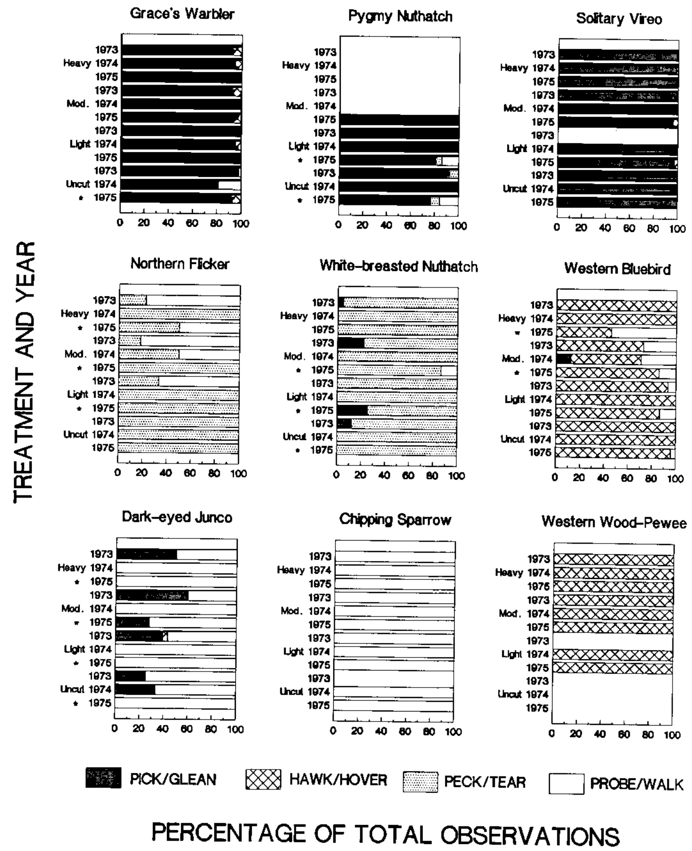

FIGURE 2. Foraging modes of nine ponderosa pine forest bird species by treatment and year. An asterisk under treatment indicates that the association among foraging mode and years was significant (*G*-test, $P \leq 0.05$).

vice versa. But for aerial feeders such as the Western Bluebird and Western Wood-Pewee the shifts in activity pattern occurred between foraging and resting/preening. Significant yearly differences for all treatments were found only for Pygmy Nuthatches, Solitary Vireos, Dark-eyed Juncos, and Western Wood-Pewees.

Significant differences in foraging mode occurred on at least one treatment for six of the nine species (Grace's Warbler, Pygmy Nuthatch, Northern Flicker, White-breasted Nuthatch, Western Bluebird, and Dark-eyed Junco; Fig. 2). Overall, foraging mode varied significantly between years in 46% of the cases ($N = 15$). The Dark-eyed Junco was the only species whose foraging mode varied significantly between years on all plots. No changes were found for Solitary Vireos, Chipping Sparrows, and Western Wood-Pewees.

Substrate selection by individual species varied significantly on at least one plot among years for all species and in most cases (82%; Fig. 3). Substrate selection by four species—Northern Flicker, White-breasted Nuthatch, Western Bluebird, and Dark-eyed Junco—varied significantly between years on all plots. In contrast, substrate selection by the Solitary Vireo differed between years only on the uncut plot, where it was observed on branches 47% of the time in 1973, but only 16% and 21% of the time in 1974 and 1975, respectively.

Posture significantly differed between years in only 30% of all cases (Fig. 4). In fact, postures of only Pygmy Nuthatches, Northern Flickers, and White-breasted Nuthatches differed significantly between years on more than one plot. Pygmy Nuthatches significantly decreased their use of hanging, head up, and head down postures in 1975, compared to either 1973 or 1974. The shift in upright posture by White-breasted Nuthatches from 23% and 26% of all observations in 1973 and 1974 to 7% in 1975, to a greater proportion

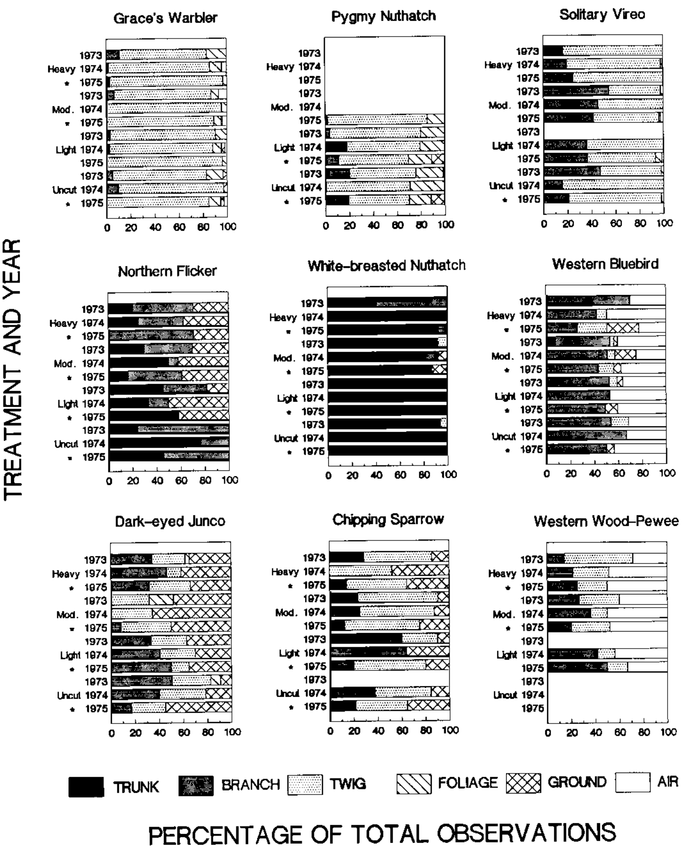

FIGURE 3. Substrate use of nine ponderosa pine forest bird species by treatment and year. An asterisk under treatment indicates that the association among substrate use and years was significant (*G*-test, $P \leq 0.05$).

of time in the head up or down positions, corresponded with an increase in the use of the trunk as a substrate.

Horizontal tree position varied significantly between years on at least two plots for all species (Fig. 5). Similar to the situation for substrate use, 82% of the comparisons for horizontal tree position varied significantly between years. For most species, the amount of time spent in the inner tree (i.e., inner trunk and branch area not associated with foliage) increased from 1973 to 1974. For example, the Solitary Vireo increased its use of the inner trunks and branches from 0–11% in 1973 to 14–52% in 1974.

Tree species selection varied significantly between years in 17 of 33 cases (51%; Fig. 6). However, no bird species' use of tree species was significantly different between years on all four plots. Solitary Vireos and White-breasted Nuthatches had most significant differences between years (3 of 4), whereas Pygmy Nuthatches, Western Bluebirds, and Chipping Sparrows had the fewest.

Significant annual differences ($P \leq 0.05$) in vertical tree positions were observed for all species (see Szaro [1976] and Szaro and Balda [1979] for foliage-use profiles by year and treatment). We found only one case, between Grace's and Yellow-rumped warblers, of an apparent interspecific interaction (Fig. 7). When Yellow-rumped Warblers were absent on the heavily cut, lightly cut, and control plots, Grace's Warblers were observed from 6 to 14, 6 to 14, and 0 to 18 m in 1973, and from 6 to 14 m on the heavily cut plot in 1974, and from 0 to 26 m on the untreated plot in 1975. In contrast, when Yellow-rumped Warblers were present and using foliage <18 m, Grace's Warblers shifted higher in the foliage, ranging from 0 to 34 and 0 to 30 m on the lightly cut plot in 1974 and 1975, and from 0 to 28 m on the untreated plot in 1974. The differences in

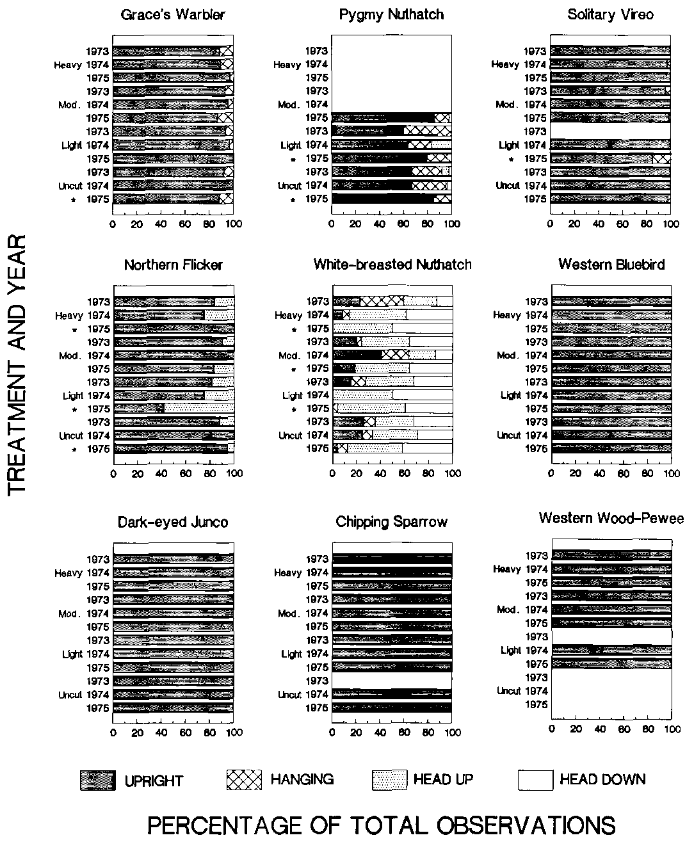

FIGURE 4. Postures of nine ponderosa pine forest bird species by treatment and year. An asterisk under treatment indicates that the association among postures and years was significant (*G*-test, $P \leq 0.05$).

the amount of shifting higher in the trees might be related to differences in densities of the two species on the two plots. There were 15 and 9 breeding pairs/40 ha of Yellow-rumped Warblers on the lightly cut plot in 1974 and 1975, respectively, but only 3 breeding pairs/40 ha on the untreated plot in 1974 and none in 1975. At the same time, 18.7 and 19.5 breeding pairs/40 ha of Grace's Warblers were on the lightly cut plot in 1974 and 1975, respectively, and only 12 and 6 breeding pairs/40 ha in 1974 and 1975, respectively, were on the untreated plot.

DISCUSSION

Avian foraging studies frequently examine seasonal, intersexual, and overall variation in resource and habitat use, and foraging behavior. Our review of more than 150 papers that dealt with attributes of avian foraging behavior over the past 10 years found that only seven examined yearly differences. This seems peculiar, especially because so much has been written about the necessity of long-term studies for determining relationships between population densities and habitat (Wiens 1984, Raphael et al. 1987). The same reasoning should apply to annual variation in foraging behavior. Wiens et at. (1987b) made a strong case for multiple-year studies to determine the dynamics of variation in behavior.

Modifications in foraging patterns by bird species in response to changing environmental conditions and resource availability should be expected. Inter- and intraspecific foraging patterns between years are not static. Resource-use behavior tends to be plastic and varies considerably among years and study sites, particularly in our case, in which alterations in habitat physiognomy resulted in 73% of all behavioral attributes varying significantly with treatment (Szaro and Balda 1979). Moreover, in 62% of all cases (N = 198), the six behavioral attributes examined varied significantly between years.

Annual variation in resource-use behaviors is considerable, since birds tend to be opportunistic

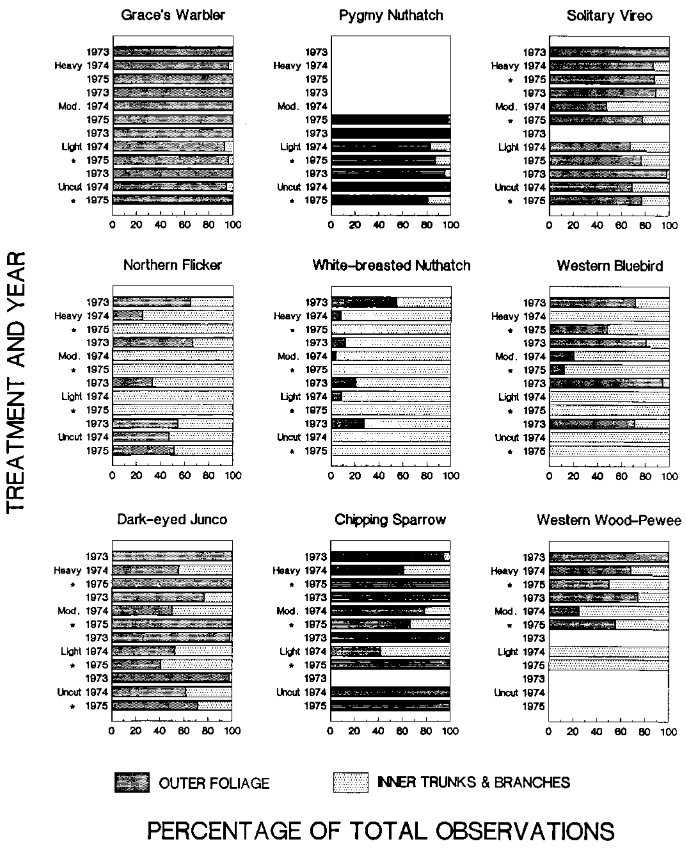

FIGURE 5. Horizontal tree position of nine ponderosa pine forest bird species by treatment and year. An asterisk under treatment indicates that the association among horizontal tree position and years was significant (*G*-test, $P \leq 0.05$).

foragers and often make ready use of superabundant food resources. For example, substantial changes were noted in the percent of total foraging on seeds and other foods by two species of Galapagos finches (*Geospiza fortis* and *G. scandens*) from foraging primarily on soft seeds in March 1976 to *Opuntia* buds, flowers, and nectar in March 1977 and to insects in March 1978 (Boag and Grant 1984). Ford et al. (this volume) observed significant annual differences in bark versus flower foraging by Fuscous Honeyeaters (*Lichenostomus fuscus*) and ground foraging versus leaf-gleaning by Buff-rumped Thornbills (*Acanthiza reguloides*). Robinson (1981) concluded that if he had studied Red-eyed Vireos (*Vireo olivaceous*) and Philadelphia Vireos (*V. philadelphicus*) in 1978 alone, he would have found no interaction between the two species. Yet, the frequency and intensity of aggressive encounters between them varied considerably between years and seasons as a function of changes in spatial overlap while foraging. In this study, the significant shifts along several niche dimensions for all species among years emphasize the need for both longer-term studies and the examination of annual variation in any foraging study. Moreover, the most biologically meaningful annual changes may be those in which the potential for differences in prey density and dispersion should have the most impact. More species showed differences in substrate use and horizontal tree position than in foraging mode.

Inter- and intraspecific shifts in resource-use patterns in response to changing densities are hard to document without experimentation to separate confounding factors such as changes in food availability and weather conditions. We were unable to discern any density related patterns in resource-use behaviors. Significant differences in resource-use behaviors were just as likely by Northern Flickers, which had almost equal densities on all study sites and years, as by White-

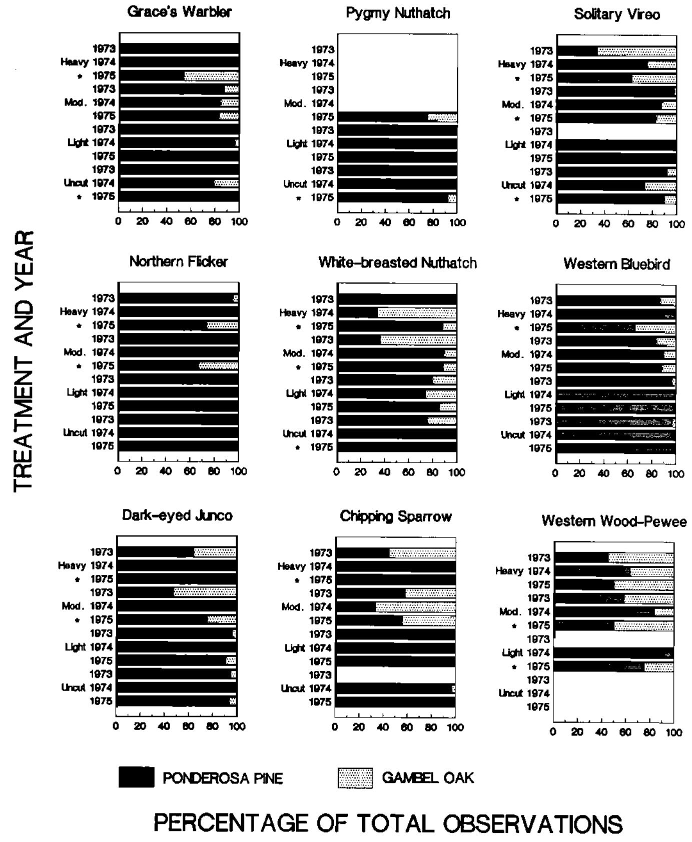

FIGURE 6. Tree species selection of nine ponderosa pine forest bird species by treatment and year. An asterisk under treatment indicates that the association among tree species selection and years was significant (*G*-test, P ≤ 0.05).

breasted Nuthatches, which had the most variable density patterns (Table 1). Although, Grace's Warblers apparently foraged higher on plots and during years when Yellow-rumped Warblers were present than on plots and during years when they were absent. At the Hubbard Brook Experimental Forest in New Hampshire, Philadelphia Vireos were observed foraging in the upper canopy and Red-eyed Vireos in the lower canopy, but Robinson (1981) was unable to determine if the Philadelphia Vireos were displaced by the Red-eyed Vireos or merely preadapted to foraging conditions of the upper strata. Relative population densities of both species, the stage of the nesting cycle, and food abundance may affect whether these two vireos segregate vertically, horizontally, or at all. Moreover, Wiens (1977) suggested that little parallelism may exist between increasing niche overlap and intensified competition, and that overlap may be greatest when competition is least, particularly when resources are superabundant and ecological overlap carries no selective penalties.

Brawn et al. (1987) found the variation in bird species densities in picking-gleaning and aerial feeding guilds in ponderosa pine forests was independent of changes in densities of other species within the guild over an 8-yr period, on the same heavily cut and lightly cut plots used in this study. They were unable to demostrate any indication of competitive interactions even with controlled manipulation experiments to increase bird densities. This implies that competition for food is unimportant to the structure of breeding bird communities in ponderosa pine forests of north-central Arizona.

Year-to-year changes in foraging may be either simply the consequence of incomplete sampling of the population or may result from the idiosyncracies of the birds that happen to end up in

TABLE 1. DENSITY, NUMBER OF RESOURCE-USE OBSERVATIONS, NUMBER OF POSSIBLE COMPARISONS (BASED ON SIX RESOURCE-USE BEHAVIORS), AND NUMBER OF SIGNIFICANT COMPARISONS BETWEEN RESOURCE-USE BEHAVIORS AND YEARS

Species Study site Year	Density (pairs/40 ha)	N	Possible annual comparisons	Significant annual comparisons[a]
Grace's Warbler			24	12 (50.0%)
Heavily cut				
1973	3.8	36		
1974	6.0	50		
1975	7.5	97		
Lightly cut				
1973	7.5	47		
1974	18.7	72		
1975	9.8	84		
Moderately cut				
1973	11.2	92		
1974	18.7	111		
1975	19.5	82		
Uncut				
1973	7.5	143		
1974	12.0	96		
1975	6.0	92		
Pygmy Nuthatch			12	11 (91.7%)
Moderately cut				
1973	7.5	50		
1974	15.0	72		
1975	18.0	72		
Uncut				
1973	13.5	122		
1974	15.0	156		
1975	13.5	120		
Solitary Vireo			24	12 (50.0%)
Heavily cut				
1973	3.8	48		
1974	6.0	143		
1975	6.0	72		
Lightly cut				
1973	6.0	44		
1974	12.0	132		
1975	6.0	84		
Moderately cut				
1973				
1974	6.0	89		
1975	6.0	60		
Uncut				
1973	1.5	127		
1974	3.0	73		
1975	3.0	80		
Northern Flicker			24	18 (75.0%)
Heavily cut				
1973	3.0	48		
1974	3.0	32		
1975	3.0	48		

TABLE 1. CONTINUED

Species Study site Year	Density (pairs/40 ha)	N	Possible annual comparisons	Significant annual comparisons[a]
Lightly cut				
1973	2.3	40		
1974	3.8	36		
1975	3.0	48		
Moderately cut				
1973	3.0	33		
1974	3.0	36		
1975	3.0	36		
Uncut				
1973	3.0	31		
1974	3.0	34		
1975	3.0	35		
White-breasted Nuthatch			24	19 (79.2%)
Heavily cut				
1973	5.2	22		
1974	9.0	36		
1975	6.0	24		
Lightly cut				
1973	4.5	25		
1974	9.0	118		
1975	12.0	53		
Moderately cut				
1973	3.0	25		
1974	7.5	46		
1975	15.0	48		
Uncut				
1973	3.0	39		
1974	10.5	37		
1975	3.0	37		
Western Bluebird			24	13 (54.2%)
Heavily cut				
1973	6.0	30		
1974	8.3	85		
1975	3.0	57		
Lightly cut				
1973	6.7	62		
1974	12.0	96		
1975	15.0	48		
Moderately cut				
1973	5.2	88		
1974	8.3	36		
1975	7.5	59		
Uncut				
1973	4.5	41		
1974	6.0	48		
1975	3.0	48		
Dark-eyed Junco			24	18 (75.0%)
Heavily cut				
1973	9.8	26		
1974	6.7	60		
1975	6.0	53		

TABLE 1. CONTINUED

Species Study site Year	Density (pairs/40 ha)	N	Possible annual comparisons	Significant annual comparisons[a]
Lightly cut				
1973	6.0	25		
1974	10.5	52		
1975	12.0	48		
Moderately cut				
1973	12.7	78		
1974	22.5	130		
1975	15.0	48		
Uncut				
1973	9.0	97		
1974	18.0	60		
1975	12.0	102		
Chipping Sparrow			24	10 (41.7%)
Heavily cut				
1973	6.0	21		
1974	6.0	23		
1975	3.0	24		
Lightly cut				
1973	4.5	21		
1974	12.0	48		
1975	6.0	24		
Moderately cut				
1973	3.0	20		
1974	7.5	36		
1975	4.5	30		
Uncut				
1973				
1974	1.5	32		
1975	3.0	24		
Western Wood-Pewee			18	9 (50.0%)
Heavily cut				
1973	3.0	28		
1974	3.0	37		
1975	3.0	24		
Lightly cut				
1973	8.2	80		
1974	9.0	124		
1975	9.0	104		
Moderately cut				
1973	2.3	0		
1974	3.0	48		
1975	1.5	24		
Total			198	122 (61.6%)

[a] Goodness-of-fit test (G-statistic) at $P \leq 0.05$.

the areas studied. While observed differences could be due to sampling errors or biases resulting from small sample sizes for some species in this study, the substanial proportion of resource-use behaviors (62%) that varied significantly between years strongly indicates the potential for significant annual variation in resource-use behavior. Thus, studies attempting to determine the presence or absence of competition between bird species by examining shifts in

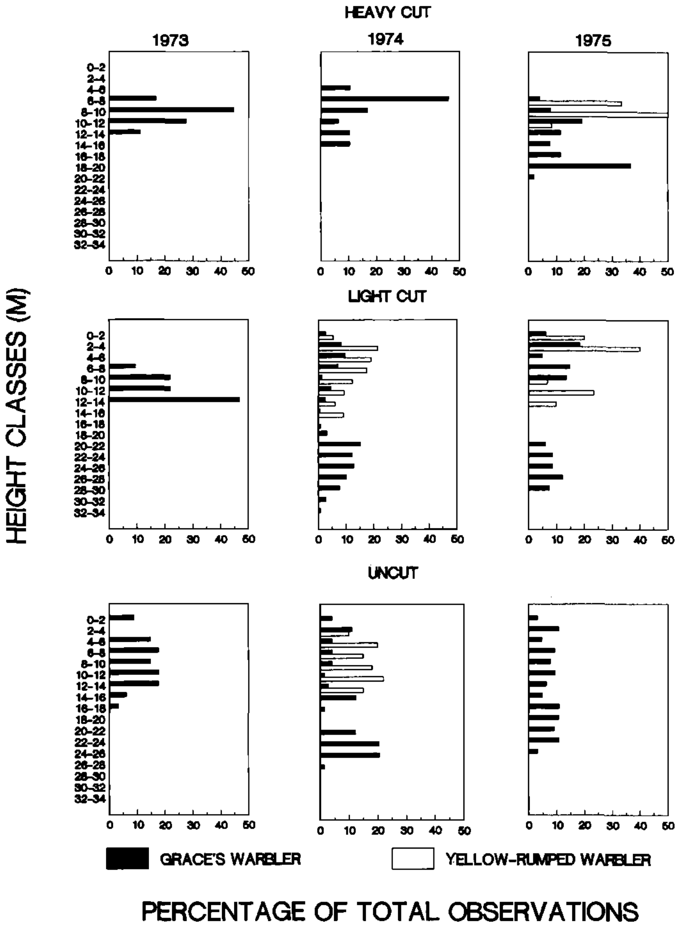

FIGURE 7. Vertical tree profiles of Yellow-rumped and Grace's warblers on the heavily cut, lightly cut, and uncut plots for 1973 to 1975 in a ponderosa pine forest of northern Arizona.

niche dimensions should be done over several years and seasons, and obtain information on resource conditions, to adequately determine patterns in species overlap. Relationships determined over a single year or pooling data across years are insufficient. The ideal study would be based on marked individuals followed from year to year. Studies should be specifically designed to identify the proximate mechanisms that "drive" this variation in foraging behavior. Some possibilities are resource availability, weather, predation, and phenology.

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