

Solitary Vireo, Chipping Sparrow, Hairy Woodpecker, and Steller's Jay), accounted for 55% of the total energy flow on the control plot. Four species (Common Flicker, Western Bluebird, Gray-headed Junco, and Steller's Jay) were members of the primary energy components on all the forested plots in 1974.

The primary energy components on all the forested plots in 1975 consisted of between five and seven species of birds. The lowest energy flux in terms of bird communities was on the clear cut plot, whereas the highest energy flux was on the silviculturally cut plot. On the severely thinned plot seven species (White-breasted Nuthatch, Gray-headed Junco, Robin, Mourning Dove, Common Flicker, Steller's Jay, and Acorn Woodpecker) accounted for 57% of the total energy flux. Seven species (White-breasted Nuthatch, Gray-headed Junco, Common Flicker, Steller's Jay, Western Bluebird, Robin, and Western Wood Pewee) accounted for 56% of the energy flow on the strip cut plot. On the control plot five species (Pygmy Nuthatch, Gray-headed Junco, Mourning Dove, Common Flicker, and Steller's Jay) accounted for 52% of the total energy flow and on the silviculturally cut plot the same five species plus the Grace's Warbler, Western Bluebird, and White-breasted Nuthatch comprised 60% of the energy flow. The Gray-headed Junco, Steller's Jay, and Common Flicker were members of the primary energy component on all plots with foliage.

#### BODY WEIGHT

Most of the species (23 of 28) clustered in the lower half of the weight range for each guild (Table 16). The pickers and gleaners and aerial feeders exhibited a fairly contracted body weight range. The pickers and gleaners ranged from 7.8 to 37.8 g, whereas the aerial feeders ranged from 3.5 to 51.2 g. On the other hand, hammerers and tearers and ground feeders have a very wide range of weight. The hammerers and tearers ranged from 18.4 g to 112.8 g, and the ground feeders from 12.6 to 122.8 g.

### DISCUSSION

#### COMMUNITY COMPOSITION

*Species numbers and densities.*—Comparisons of different bird communities in the ponderosa pine forest in Arizona are limited to those by Haldeman et al. (1973) who reported 27 species in similar areas of northern Arizona, and by Balda (1969) who recorded 31 species of breeding birds in the Chiricahua Mountains of southeastern Arizona. These numbers contrast with the high of 22 species in this study found on the strip cut plot in 1974, and an overall number of 28 breeding species. Balda (1969) recorded eight species in the Chiricahua Mountains found in the present study (Brown Creeper; Whip-poor Will, *Caprimulgus vociferus*; Virginia's Warbler, *Vermivora virginiae*; Band-tailed Pigeon, *Columba fasciata*; Coues' Flycatcher, *Contopus pertinax*; Mexican Junco, *Junco phaeonotus*; Olive Warbler, *Peucedramus taeniatus*; Mexican Chickadee, *Parus sclateri*; and Pygmy Owl, *Glaucidium gnoma*). The Mexican Junco and the Mexican Chickadee are replaced by ecological equivalents, the Gray-headed Junco and the Mountain Chickadee. The Brown Creeper, Virginia's Warbler, and Pygmy Owl are known to breed in the ponderosa pine forest of northern Arizona. The remaining species (Coues' Flycatcher, Olive Warbler, and Band-tailed Pigeon) are found only in the ponderosa pine forests of southern Arizona or in different habitats in northern

Arizona. Thus the species composition of the ponderosa pine forest in Arizona varies from area to area but remains fairly similar in overall species composition.

There are large differences in densities among the studies done by Snyder (1950), Balda (1969), Haldeman et al. (1973) and this study. Balda (1969) reported 336 prs/40 ha whereas Haldeman et al. (1973) reported 232 prs/40 ha. The breeding bird densities on our forested study plots ranged from 57.8 prs/40 ha on the severely thinned plot in 1973 to 162.8 prs/40 ha on the strip cut plot in 1974. On the control plot, the breeding bird densities ranged from 63.0 prs/40 ha in 1973 to 132.8 prs/40 ha in 1974. Snyder (1950) reported a density of 102.0 prs/40 ha in Colorado. These disparities can be attributed to certain species that had high densities in the studies by Balda and Haldeman et al., which were present in lower densities or not present at all in this study. In the Chiricahuas these species were Olive Warbler, Robin, Brown Creeper, Common Flicker, House Wren, Steller's Jay, Pygmy Nuthatch, and Mexican Junco. Haldeman et al. (1973) reported high densities of the Violet-green Swallow, Mountain Chickadee, Robin, Pine Siskin (*Carduelis pinus*), Hermit Thrush, and Brown Creeper. These differences in densities reflect the greater number of species found in the Chiricahuas plus possible differences in productivity between the study sites.

There are major differences in community composition between the breeding bird communities in eastern and western coniferous forests (Mengel 1970, Wiens 1975). Various warbler species are important constituents of many coniferous forests in eastern North America comprising more than half the individuals present in a stand. In contrast, warblers in most western coniferous forests account for less than 10% of the individuals (Wiens 1975). Only 7–20% of the total breeding bird densities on the silviculturally cut and control plots were contributed by the parulids. Thus both the relative and absolute densities of warblers are generally lower in western coniferous forests than in eastern coniferous forests.

However, the relative paucity of warblers in the West is only partially compensated for by a proportionate increase in other foliage foraging species in these western coniferous forests (Wiens 1975). Part of the difference is made up by other foliage gleaning species such as the Pygmy Nuthatch, Pine Siskin, Golden-crowned Kinglet (*Regulus satrapa*), and Ruby-crowned Kinglet (*Regulus calendula*) in various western coniferous forests, but rarely do more than two of these species occur with relatively high densities in any single forest. Wiens (1975) indicated that 49–61% of the total avian densities in eastern coniferous forests were made up of insectivorous foliage feeding species. In the west the insectivorous foliage feeders account for a much lower proportion of the total breeding bird densities. In the ponderosa pine forest (this study) 16–44% of the total breeding bird densities consisted of this same guild with the Pygmy Nuthatch on the silviculturally cut and control plots accounting for 10–21% of the breeding bird densities on these sites.

The possible reasons for the paucity of warbler species and the lack of a proportionate increase in other picking and gleaning species in the western coniferous forest are twofold. First, part of the reason for the relatively low numbers and densities of warbler species in the west may stem from biogeographic events and speciation processes (Mengel 1964, 1970). Second, the avian data suggest that there may be differences in the availability of prey resources in the different

forest regions (Wiens 1975). Insect densities and diversities in the ponderosa pine forest might be expected to be lower because it is a structurally simple plant community. The ponderosa pine forest is a monoculture with its tree foliage located in relatively distinct horizontal strata. Moreover, the ponderosa pine forest is one of the driest coniferous forests in North America (Kuchler 1967). Thus, the paucity of foliage foraging insectivores in the ponderosa pine forest may be due to a combination of biogeographic events as well as a depauperate insect fauna.

*Diversities.*—Bird species diversities ( $H'$ ) found on all forested sites varied from 2.23 on the control plot in 1973 to 2.89 on the strip cut plot in 1974. The 1974 diversities (2.67–2.89) are similar to those reported by Balda (1969) and Haldeman et al. (1973) in other ponderosa pine forests in Arizona (3.10 and 2.83, respectively).

The bird species diversities on the forested sites were relatively high because of the high degree of evenness ( $E$ ) found in these bird communities (.91–.97). Evenness was high probably because of the relatively simple structure of the ponderosa pine forest. Those species which were able to survive in the ponderosa pine forest did so in relatively low numbers. Certain species (Grace's Warbler, Pygmy Nuthatch, and Gray-headed Junco) did reach high densities on certain study plots, but the vast majority of species had densities between 2.0 and 9.0 prs/40 ha. The fairly equal densities of most species were probably brought about by the relatively few successful life styles available to the bird species in the ponderosa pine forest, with its limited number of microhabitats.

#### BIRD SPECIES DIVERSITY VS. VEGETATIONAL COMPLEXITY

The structure of avian communities and its relation to vegetational complexity has been studied by many investigators. Since birds are known actively to select their habitat on the basis of such proximate factors as features of the landscape, terrain, substrate, vegetative structure, or the arrangement of the vegetation (Hilden 1965, Wiens 1969), it is probable that foliage complexity is associated with structure of the avian community. Plant species composition is highly significant in regulating the composition of breeding bird communities in desert scrub habitats (Tomoff 1974). Bird species diversity (BSD) in deciduous forests has been correlated with foliage height diversity (MacArthur and MacArthur 1961, MacArthur et al. 1962, MacArthur et al. 1966, Recher 1969, Karr 1971, Karr and Roth 1971, Willson 1974). Other investigators have found little or no correlation between foliage height diversity and BSD (Balda 1969, Lovejoy 1972, Carothers et al. 1974, Pearson 1975). No correlation was evident between BSD and foliage height diversity, plant species diversity, or plant volume diversity in this study, except in 1974 when BSD was correlated ( $r = 0.95$ ) with plant volume diversity, and in 1975 when BSD was correlated ( $r = 0.95$ ) with plant species diversity. Willson (1974) showed that among forested areas no correlation of BSD with foliage height diversity was apparent. A significant correlation between BSD and a heterogeneity index (derived from the coefficient of variation of the distances between tree or shrubs and the central point of the point-quarter technique), was found in Texas, Illinois, and Delaware habitats (Roth 1976). There was no significant correlation between BSD and this parameter in the ponderosa pine forest. Perhaps such correlations are possible in dissimilar habitats because the between-

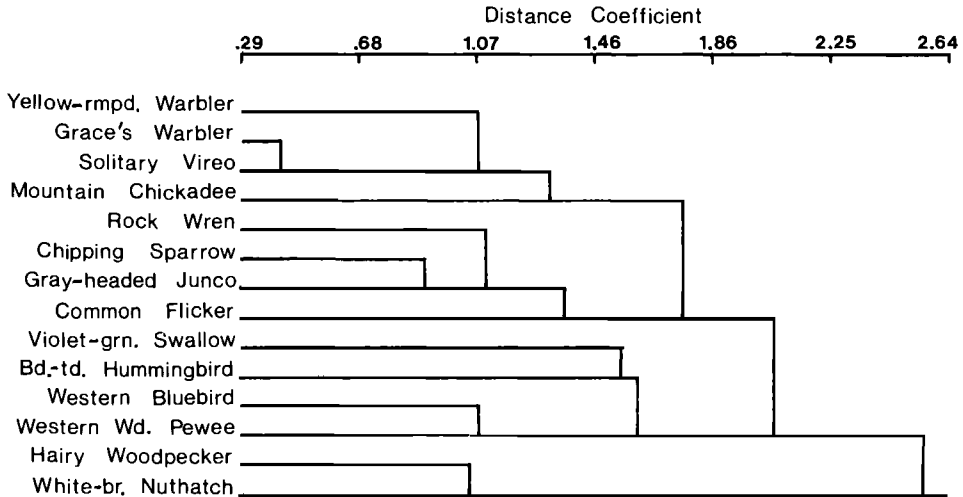


FIGURE 33. Dendrogram resulting from cluster analysis of the Euclidean distance matrix of composite behavior for the breeding birds of the severely thinned plot.

habitat effects are so great that differences in methodology and sample size are overshadowed. However, when comparing more homogeneous areas, the methodological differences are enough to influence the results. In this study, where all observations were made by a single observer, the methodological techniques were at least consistent. Moreover, BSD was very similar on all the forested plots in 1974 and 1975 (2.67–2.83) as were the heterogeneity indices (64.3–78.0). This similarity produced a fairly tight cluster of points which fit a little above the regression line presented by Roth (1976). In fact, his regression equation predicts that BSD in the ponderosa pine forest should range from 2.35 on the severely thinned plot to 2.61 on the control plot. We feel that significant correlations between BSD and habitat parameters in such similar habitats as we examined in the ponderosa pine forest are not possible because even after treatment the ponderosa pine forest is very homogeneous in plant species composition and in physiognomy. Needle bundles, twig configuration, bark pattern, and branch pattern are very similar from top to bottom of the foliage (Balda 1975). Thus factors such as intraspecific and interspecific competition rather than foliage configuration were probably of overriding importance in determining bird species diversity in the ponderosa pine forest.

#### RESOURCE PARTITIONING AND THE NICHE

Ecological isolation is particularly orderly and precise and especially noticeable in groups of ecologically related species (guilds) which commonly show non-overlapping ranges on a resource span (Cody 1974). However, the coexistence of guild members may be achieved by the evolution of some minimal degree of difference in resource use. It is clear that most guild members differ from other species in the same guild by differences along a number of resource spans. In fact, in this study shifts along resource spans are evident in activity patterns, foraging methods, tree species selection, trunk position, perch selection, stance selection and particularly along foliage height use spans.

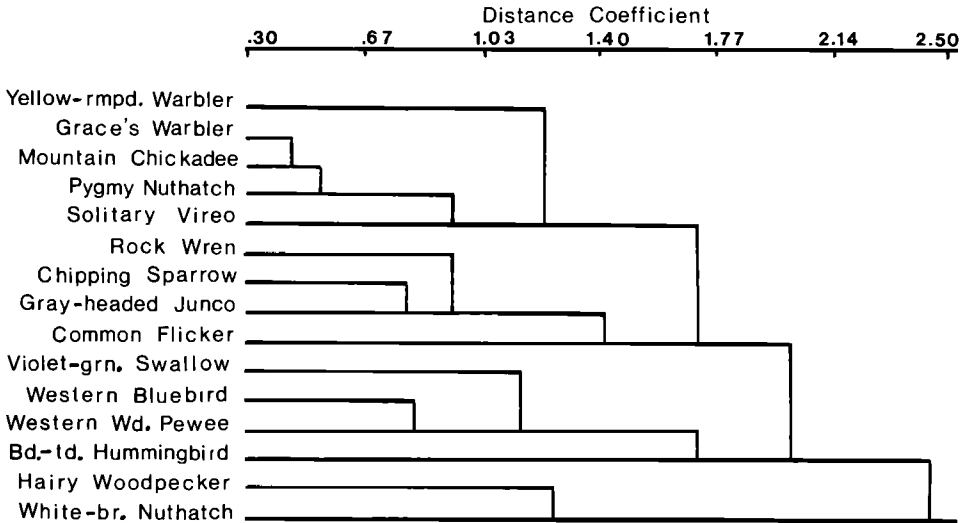


FIGURE 34. Dendrogram resulting from cluster analysis of the Euclidean distance matrix of composite behavior for the breeding birds of the strip cut plot.

*Composite cluster analyses.*—Before discussing differences between guild members it is necessary to verify that guild members are closer to each other than to members of other guilds. All seven factors (activities, foraging methods, tree species selection, horizontal tree positions, perch selection, stance, and foliage profile) are combined by taking the square root of the sum of the squares of the Euclidean distances of all the factors. The coefficient matrices are then subjected to cluster analysis in order to determine the actual ecological groupings present on the different study plots. Basically the bird species on all four study plots cluster into foraging guilds (Figs. 33–36). The only switch from one guild to another was that of the Common Flicker, which was a ground feeder on the severely thinned and strip cut plots but an exclusive hammerer and tearer on the silviculturally cut and control plots.

*Species segregation.*—Species that occur together in the habitat can most effectively separate their activities by the vertical segregation of foliage-use zones. Species which use different heights above the ground will come into competition only to the extent that these foliage-use zones overlap (Cody 1974). Competition in these zones of overlap will be reduced when there are differences in other resource dimensions. The number of coexisting species is greatly influenced by the vegetational diversity within a given area. Moreover, in a finite ecological space there is a presumed advantage in reducing the degree of overlap among species in resource use or habitat preference (MacArthur and Levins 1967).

Vertical stratification within avian communities has received much previous attention (Colquhoun and Morley 1943, Balda 1969, Pearson 1971, 1975). Species of woodland birds apparently occupy a definite vertical niche in the vegetation and this niche only partially overlaps that of its closest neighbor in the community (Colquhoun 1941). Three separate vertical communities exist in British oak woods (Colquhoun and Morley 1943). Pearson (1971) suggested that there is a limited vertical distribution of some species. MacArthur (1958), Morse (1971), and others

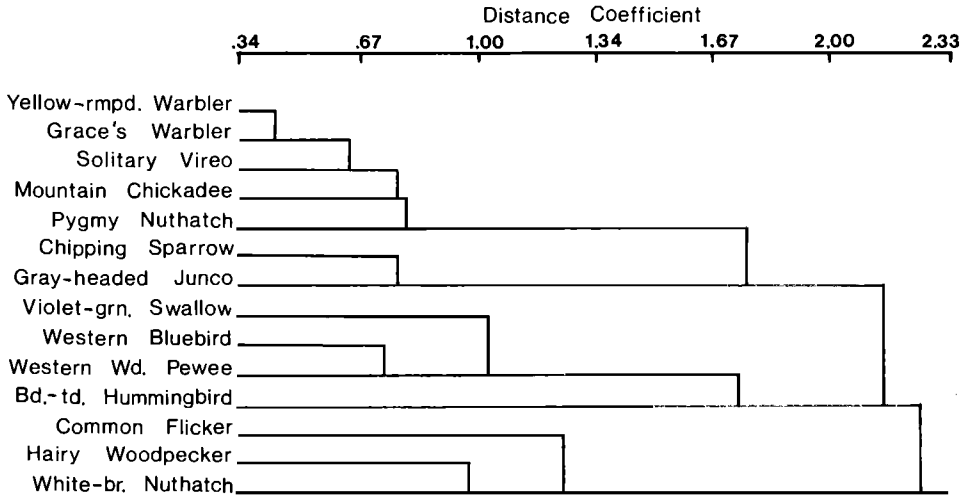


FIGURE 35. Dendrogram resulting from cluster analysis of the Euclidean distance matrix of composite behavior for the breeding birds of the silviculturally cut plot.

report that differences in foraging heights are important factors in the segregation of species' feeding activities in habitats other than grasslands. In a forest in New Guinea the foraging ranges of most bird species are vertically restricted with little overlap (Diamond 1970a). Thus, one way by which bird species reduce niche overlap between themselves and other species is by vertical segregation.

The pickers and gleaners exhibited vertical stratification by using different portions of the trees on all study plots. On the control plot the Solitary Vireo remained in the smaller shrub-like pines and lower reaches of the taller pines (mean height = 3.9 m), whereas the Mountain Chickadee was found at a mean height of 9.8 m. In contrast, Grace's Warbler utilized mainly the bulge region (mean height = 13.7 m) and the Pygmy Nuthatch was found at the tops of the trees

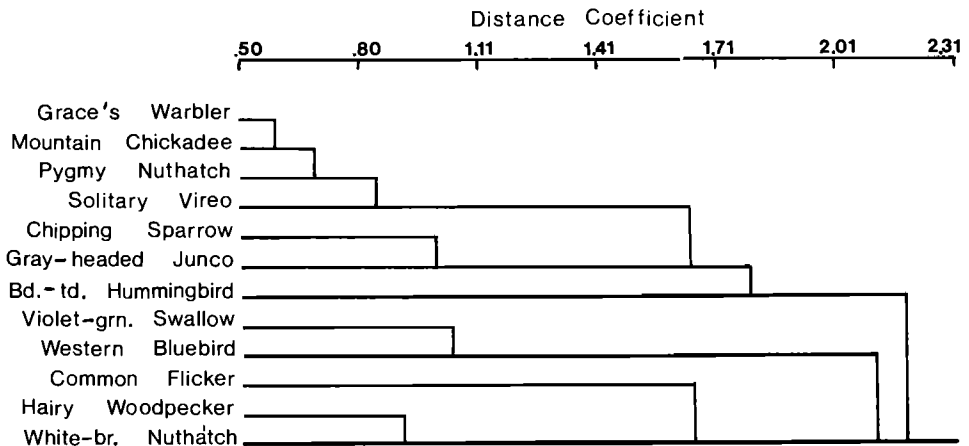


FIGURE 36. Dendrogram resulting from cluster analysis of the Euclidean distance matrix of composite behavior for the breeding birds of the control plot.

(mean height = 17.0 m). On the silviculturally cut plot the picker and gleaner species segregated by mean height in the following order: Yellow-rumped Warbler (6.8 m), Solitary Vireo (8.8 m), Mountain Chickadee (11.2 m), Pygmy Nuthatch (13.3 m), and Grace's Warbler (16.4 m). The same type of vertical separation occurred on the strip cut and severely thinned plots although the differences in mean height were somewhat smaller. Furthermore, there were shifts in distribution by the species, with the Solitary Vireo using the highest portions of the severely thinned plot but the lowest portions on the control plot. The Grace's Warbler and Pygmy Nuthatch reversed positions on the silviculturally cut and control plots. The Grace's Warbler and Yellow-rumped Warbler markedly segregated from one another on the basis of vertical segregation, with the latter utilizing the lower reaches and lower bulge and the former utilizing the upper bulge and spire on all study plots where they coexist. Diamond (1970b) showed that among southwest Pacific birds which were relieved of competition as a result of invading a species poor area, spatial expansion with change in foraging technique was often a prompt response requiring little or no evolutionary change in the genotype. Thus, on the control plot, where the Yellow-rumped Warbler was absent and only the Grace's Warbler was present, the latter made a shift downward into the lower portions of the trees.

In addition to vertical stratification, the pickers and gleaners segregated from each other along many other resource spans. The Yellow-rumped Warbler differed from Grace's Warbler by spending more time probing (4–32 vs. 0%) and in gambel oak (16–62 vs. 3–27%), but less time perched on twigs (45–86 vs. 89–90%). The Grace's Warbler differed from the Solitary Vireo by spending more time in the outer foliage (94–100 vs. 64–87%) and on twigs (85–90 vs. 53–78%), but spent less time on branches (1–6 vs. 20–46%). The Grace's Warbler differed from the Pygmy Nuthatch by spending less time hanging (2–7 vs. 13–23%) and perched in the needle clusters and buds (4–7 vs. 15–23%). The Grace's Warbler segregated from the Mountain Chickadee by spending less time perched on branches (1–6 vs. 7–18%) and in the ponderosa pine on severely thinned, strip cut, and control plots (72–88 vs. 91–100%), but more time in ponderosa pine on the silviculturally cut plot (97 vs. 63%). The Yellow-rumped Warbler separated from the Pygmy Nuthatch by spending less time hanging (4.5 vs. 13–20%) and in the needle clusters (6–11 vs. 15–20%). The Solitary Vireo differed from the Pygmy Nuthatch by spending less time hanging (1–6 vs. 13–23%) and in the needle clusters (1–2 vs. 15–23%), but more time in the inner trunk and branches (13–36 vs. 2–15%). The Solitary Vireo separated from the Mountain Chickadee by making greater use of the branches (20–46 vs. 7–18%) but lesser use of the needle clusters (1–2 vs. 4–33%) and hanging (1–6 vs. 7–18%). The Yellow-rumped Warbler segregated from the Solitary Vireo by probing more (4–32 vs. 0%), but using the pine (35–87 vs. 71–100%) and inner branch region (0–6 vs. 13–36%) less. The Mountain Chickadee differed from the Pygmy Nuthatch by spending less time hanging (7–11 vs. 13–23%) and perched on the trunk (0 vs. 2–9%). Thus pickers and gleaners segregated along a number of resource spans, but primarily on a vertical basis.

The situation is not as clear in the other foraging guilds. There was no vertical segregation by the ground feeders and the aerial feeders and only a slight vertical segregation on the part of the hammerers and tearers. In these cases where ver-

tical segregation was slight, the species segregated by differences in other niche dimensions.

Bird species that find themselves at the same point in space can segregate by using different food items (Cody 1974). Hesperheide (1971) showed that both body size and bill size of some insectivorous birds were well correlated with mean prey size, but in general the correlation was higher for body size. Other workers have suggested the possibility that body size is a more accurate predictor of prey size than is bill size in birds (Schoener 1965, Lack 1971, Cody 1974). An examination of the body sizes of these species may therefore further illustrate how species in the same guild can coexist in the same space.

The hammerers and tearers certainly separated on the basis of body size. Mean weight of the three species ranged from 113 g for the Common Flicker to 62 g for the Hairy Woodpecker and to 18 g for the White-breasted Nuthatch. Thus, these species were probably selecting greatly different prey sizes.

Hammerers and tearers also separated in many other niche dimensions. The Common Flicker differed from the Hairy Woodpecker by foraging less (20–46 vs. 55–100%), spending less time moving and foraging vertically upward (6–46 vs. 57–100%), but more time perching on the ground (31–46 vs. 0–2%) on the severely thinned and strip cut plots. This contrasts with Stallcup's (1968) findings in a ponderosa pine forest in Colorado where the Common Flicker was confined to the ground. In this study, the Common Flicker was observed on the ground only on the treated study plots. On the control plot the Common Flicker was confined to the trees. The Common Flicker and White-breasted Nuthatch differed in that the latter species spent more time picking and gleaning (1–16 vs. 0%), in gambel oak (15–33 vs. 0–10%), moving vertically down the trunk (23–44 vs. 0%), and perching on the trunk (71–97 vs. 14–46%) on all study plots. The White-breasted Nuthatch and Hairy Woodpecker differed in that the nuthatch spent more time in oak (15–33 vs. 0%), hanging (2–14 vs. 0%), and moving vertically downward (23–45 vs. 0%).

The three ground feeders segregated on the basis of body size as well as on other niche dimension differences. The Chipping Sparrow weighed 12.5 g whereas the Rock Wren weighed 16.9 g. The largest of these three ground feeders was the Gray-headed Junco at 20.1 g (Table 17). The Rock Wren differed from the other two species by foraging less and spending more time on the ground and in the slash piles. The Chipping Sparrow separated from the Gray-headed Junco by resting (7–28 vs. 0–13%) and singing (40–100 vs. 34–69%) more on all four study plots. The Chipping Sparrow also probed 100% of the time while foraging whereas the Gray-headed Junco picked and gleaned 10–28% of the time. The Common Flicker, which was a ground feeder on the severely thinned and strip cut plots, spent less time probing but more time on the trunk than any of the other ground feeders.

Segregation of the aerial feeders was more complicated. The Violet-green Swallow and Western Wood Pewee had the same body size (14.2 g). However, there was a significant vertical segregation between the two on the silviculturally cut plot (14.1 vs. 5.3 m). On the strip cut plot, where no vertical segregation existed between the two species, they separated on the basis of the Western Wood Pewee's greater use of oaks and of twigs of the outer foliage. The pewee was primarily a hawkler whereas the swallow was mainly an aerial feeder. The Broad-



tailed Hummingbird was the smallest bird in the study (3.5 g) whereas the Western Bluebird was the largest hawk (25.3 g). Cody (1974) suggested that the chief means of ecological segregation among flycatching species, at least in temperate areas, are body size differences (and hence prey size differences) and foraging height differences. This was exactly the case in this study.

Segregation in vertical height and prey size inferred from differences in body sizes were the most important factors in potentially reducing intraspecific and interspecific competition. Vertical segregation was more important in the pickers and gleaners where differences in body weights were less than those of the other guilds. The hammerers and tearers and the ground feeders separated primarily on a weight basis and thereby differences in prey size selection. These two guilds also segregated by differences in perch selection and foraging methods. The aerial feeders segregated primarily on a weight basis except for the Western Wood Pewee and Violet-green Swallow. These species separated on a vertical basis on the silviculturally cut plot and by differences in foraging methods (hawking vs. aerial feeding) on all study plots. Thus, in these groups of ecologically similar species there were various differences in several niche dimensions which allowed them to coexist.

#### FOLIAGE UTILIZATION

There was great variability in the foliage-use profiles of the individual species and of the entire bird communities from year to year as well as from study plot to study plot. The composite profiles of the avian communities on the treated study plots closely approximated the foliage profiles of these areas (Figs. 29–32). Use profiles of many species showed great yearly variation which averaged out on the composite profiles. These fluctuations may be in response to differences in yearly food abundance and distribution as suggested by Hartley (1953). Severe winter weather conditions may differentially affect the insects at different heights in the trees, thereby causing the birds to respond to areas of differential abundance. Heavy foraging in a particular zone one year may deplete the insect population for the following year. The cyclic patterns of foliage utilization may therefore be in response to a changing food supply. Such fluctuations were shown on a diurnal basis in tropical environments (Pearson 1971), whereas Hartley (1953) has reported them in titmice on a seasonal basis.

On the control plot, cyclic changes were also evident but the upper bulge region was consistently underutilized even on the three year composite profile (Fig. 32). This secondary upper bulge, which was not present on the treated study plots, may be characteristic of an aging forest. However, the secondary bulge may not be utilized fully simply because there is an overabundance of foliage on the control plot, whereas on the other study plots the community is forced to make better use of all the foliage because of its more limited availability.

The tendency for many species was to overutilize the lower reaches and lower bulge regions of the foliage profile on all plots. Some of this is undoubtedly due to sampling error, as the birds were more readily visible closer to the ground. The Western Wood Pewee, Western Bluebird, and Gray-headed Junco used primarily the lower portions of the trees as resting, foraging, and singing posts. These species overutilized the lower reaches because much of their food was obtained either on the ground or in the air space close to the ground. The White-

breasted Nuthatch heavily utilized the lower trunks on the severely thinned and control plots. The Yellow-rumped Warbler was commonly seen in the lower reaches and lower bulge on all plots, whereas the Grace's Warbler used the upper bulge and spires. In response to the denser foliage on the control plot, the Solitary Vireo greatly overutilized the lower reaches and shrubs. On the other plots the vireo overutilized the bulge region. This is in contrast to Balda's (1969) findings which showed that the Solitary Vireo had a better fit with the foliage profile than any other species in the ponderosa pine forest in southeastern Arizona. The vireo might be expected to respond differently on the control plot where there were 646 trees/ha than on the treated plots where tree densities ranged from 69 trees/ha on the severely thinned plot to 236 trees/ha on the silviculturally cut plot. Balda (1969) reported 242 trees/ha in southeastern Arizona. Therefore, even though tree densities were similar on the silviculturally cut plot and in southeastern Arizona, the Solitary Vireo has responded differently in northern Arizona than in southern Arizona.

Grace's Warbler and Pygmy Nuthatch, the two species that heavily utilized the upper bulge and spire were both foliage gleaners. Similarly, Balda (1969) showed that foliage inhabiting birds, such as the Grace's Warbler and Pygmy Nuthatch, showed a definite overuse of the upper portions of the trees.

Thus, the fluctuations in foliage utilization patterns by individual species and by the entire bird community seem to indicate that there is a cyclic pattern in bird use possibly resulting from fluctuations in food availability.

#### TERRITORY SIZE

Mean territory sizes of individual species varied from year to year (Table 16). One might expect territory size to exhibit an inverse relationship with density. However, this was not the case in the ponderosa pine forest. Territory was not predictable with changes in bird density, indicating that territory size is not defined by bird density in the ponderosa pine forest, and can expand and contract without regard for bird density. This is in direct contrast to Kendeigh's (1947) findings in the eastern spruce-fir forest where a direct relationship between territory size and density existed. This direct relationship between territory size and density in the eastern coniferous forest might reflect the abundance of warblers and other foliage gleaning species. The warblers are ecologically and systematically very similar to one another and there may therefore be a large amount of potential intraspecific and interspecific competition occurring among them in the eastern coniferous forest. The amount of interspecific competition is probably much lower in the west than in the east due to the paucity of warblers and a lack of proportionate increase in other insectivorous picker and gleaner species. Again, generalizations made in the eastern coniferous forest do not necessarily apply to the western coniferous forest and must be used with caution.

On the other hand, territory size in the ponderosa pine forest appears to be related to how the birds use the available foliage and the amount of utilized foliage volume per territory. In 19 cases from all forested plots, as territory size became larger, the fit with the available foliage decreased; that is, the birds became more selective of specific strata of foliage. In contrast, in 20 cases, as territory size decreased, the fit with the available foliage increased. It must be stressed that even though the changes in mean territory size were statistically significant in

TABLE 21  
RELATIONSHIP BETWEEN MEAN TERRITORY SIZE, USE OF THE BULGE, AND FIT WITH THE FOLIAGE PROFILE

Species	Plot	Years	Bulge use	Fit	Terr. size
Western Wood Pewee	Strip	73-74	I <sup>a</sup>	D	I
		74-75	I	I	D
Mountain Chickadee	Silv.	74-75	I	D	I
	Cntrl.	74-75	D	D	I
White-breasted Nuthatch	S. Thn.	73-74	I	I	D
		74-75	D	D	I
	Strip	73-74	I	I	D
		74-75	D	D	I
	Silv.	73-74	D	D	I
		74-75	D	D	I
Cntrl.	73-74	I	D	I	
	74-75	D	I	D	
Pygmy Nuthatch	Silv.	74-75	I	I	D
		73-74	D	D	I
	Cntrl.	74-75	I	I	D
Western Bluebird	S. Thn.	74-75	D	D	I
		73-74	I	I	D
	Strip	74-75	S	D	I
73-74		D	D	I	
Silv.	74-75	I	I	D	
	73-74	D	D	I	
Solitary Vireo	S. Thn.	74-75	D	D	I
		73-74	I	I	D
	Strip	74-75	S	D	I
		73-74	S	D	I
	Silv.	74-75	D	I	D
73-74		S	D	I	
Yellow-rumped Warbler	Silv.	74-75	D	D	I
		73-74	D	D	I
Grace's Warbler	S. Thn.	73-74	I	I	D
		74-75	D	I	D
	Strip	73-74	D	D	I
		74-75	I	I	D
	Silv.	73-74	D	I	D
		74-75	D	D	I
Cntrl.	73-74	D	D	I	
	74-75	I	I	D	
Gray-headed Junco	Silv.	73-74	I	D	I
		74-75	D	I	D
	Cntrl.	73-74	I	I	D
		74-75	D	D	I

<sup>a</sup> I = increased; D = decreased; S = stable.

only six cases ( $P \leq 0.05$ ), this trend between the foliage use index and territory size holds in all 39 cases. The changes in mean territory size were not significant probably because of the small sample sizes. Because the change in territory size can be predicted in all cases, the following model is suggested. A combination of bulge use and foliage fit and, thereby utilized foliage volume per territory, can be used to predict the direction of territory size change in all cases (Table 21). As

the foliage use index decreases (i.e., becomes smaller), the bird use profile better approximates the foliage profile. All species examined either increased or decreased foliage fit between years and, in conjunction, changed territory size. There are six options open to the birds in terms of changing territory size (percentages indicate the proportion of the 39 cases examined that used a particular option): 1) increase bulge use, increase fit with the available foliage, and decrease territory size (33%), 2) decrease bulge use, decrease fit, and increase territory size (33%), 3) decrease bulge use, increase fit, and decrease territory size (13%), 4) increase bulge use, decrease fit, and increase territory size (10%), 5) stable bulge use, decrease fit, and decrease territory size (8%), and 6) stable bulge use, increase fit, and decrease territory size (3%).

A bird can increase the amount of foliage volume it uses by increasing its use of the bulge, by increasing its fit with the foliage, by increasing its territory size or by any combination of these. Since foliage volume is probably directly related to the insect food supply, an increase in utilized foliage volume by a bird should indicate an increase in its resource base. In this manner, if a bird increases its resource base by more efficiently utilizing the foliage on its territory, it should not need as large a territory. In contrast, a bird should need a larger territory when it makes relatively inefficient use of the foliage on its territory. There were 13 samples of birds on a particular study plot increasing their bulge use and their foliage fit between years. These same species also reduced their territory size between years (option 1). In contrast, there were 13 samples of birds on a particular study plot decreasing their bulge use and foliage fit. These species also increased their territory sizes between years (option 2). A bird can still increase its resource base, even with decreased bulge use, as long as it uses the foliage more efficiently than it did the year before (option 3). There were five samples of birds decreasing territory size using option 3. In contrast, a bird can increase its bulge use but decrease its fit with the available foliage by becoming highly selective of specific strata of foliage. This stenotypic selection of foliage strata by a bird was coupled with an increase in territory size (option 4). The final two options revolve around increased or decreased fit with the foliage profile and stable bulge use. Only the Solitary Vireo on the control plot from 1974 to 1975 increased its fit with the foliage, had stable bulge use, and thereby decreased its territory size. The commoner option with stable bulge use was to become more selective of specific strata, thereby necessitating a larger territory. Thus, a bird can decrease its territory size by increasing its use of the bulge, using more total foliage volume and, most importantly, by more effectively using the foliage strata (Fig. 37).

#### ENERGY FLOW

The standing crop biomass of the bird communities on all the study areas was much lower than those reported by many previous workers. The standing crop varied from 67.0 to 218.6 g/ha on the forested areas (Table 17). Haldeman et al. (1973) reported 399.8 g/ha in similar areas of northern Arizona. Holmes and Sturges (1973) reported a standing crop of 653.8 g/ha in an eastern hardwood forest whereas Karr and Roth (1971) reported 335.3 g/ha in a coniferous forest in the Bahamas. On bare ground in Illinois the standing crop was 80.5 g/ha versus 782.1 g/ha in the early shrub layer (Karr 1971). Wiens and Nussbaum (1975)

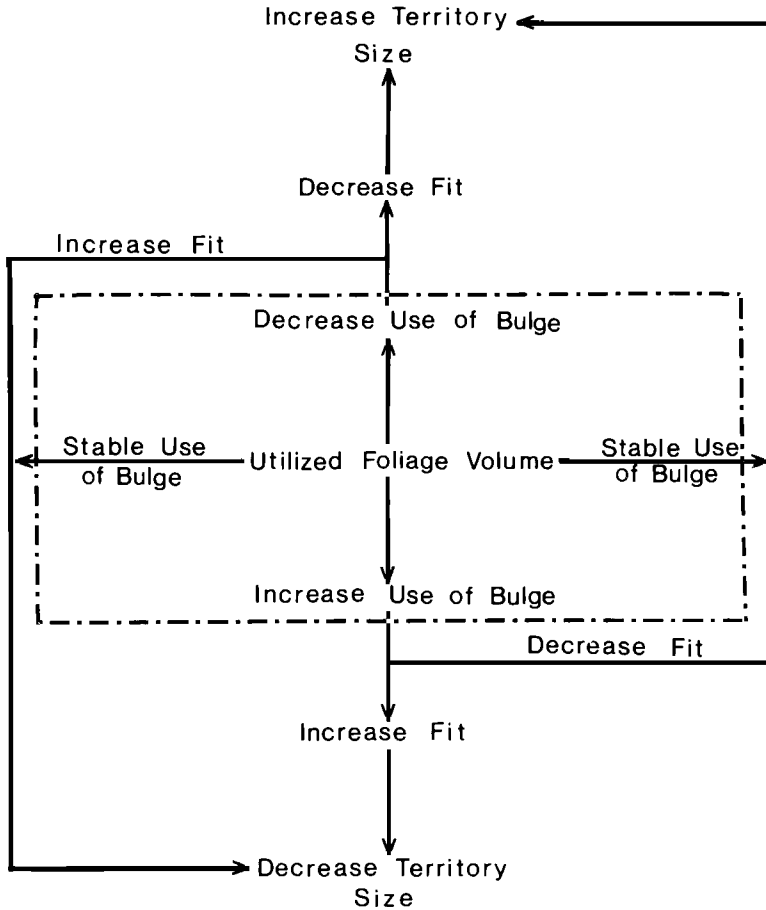


FIGURE 37. Relationship between mean territory size, utilized foliage volume, bulge use, and foliage fit.

reported standing crops of 223.3 to 526.1 g/ha in six coniferous forests in the Oregon Cascades. Thus, the standing crop biomass of the birds in the ponderosa pine forest is closer to that in an Illinois grassland than to that in any other forest.

Similarly, the consuming biomasses of the bird communities on all study areas were much lower than those reported in other forested areas by previous workers. The consuming biomass on the forested areas varied from 20.1 to 59.2 g/ha, whereas the consuming biomass in a similar area in northern Arizona was 95.9 g/ha (Haldeman et al. 1973), and in a coniferous forest in the Bahamas, 104.2 g/ha (Karr and Roth 1971). A consuming biomass of 18.0 g/ha was found on the bare ground area and 161.7 g/ha in the early shrub area in Illinois (Karr 1971). The consuming biomass of the bird community in a wet grazed grassland in Illinois was 30.0 g/ha (Karr 1971).

The low standing crops and consuming biomasses of the bird communities in this study were attributable to the low breeding bird densities. Higher values for standing crop and consuming biomass were found in other similar areas of north-

ern Arizona because of the higher densities of the Violet-green Swallow, Mountain Chickadee, Pine Siskin, and Brown Creeper (Haldeman et al. 1973). The higher values of standing crops and consuming biomasses in spruce-fir forests in Oregon (Wiens and Nussbaum 1975) were attributable to high densities of Chestnut-backed Chickadees (*Parus rufescens*), Brown Creeper, Golden-crowned Kinglets, and Hermit Warblers, (*Dendroica occidentalis*). Karr and Roth (1971) report that the breeding bird community in the Bahamas has a high proportion of warblers (42% on a density basis). The values of standing crop and consuming biomass in the Bahamas were greater than those reported in this study because of the lack in the ponderosa pine forest of proportionate compensation by other foliage feeding species for the paucity of warbler densities.

In terms of the primary energy component (based on existence energy), small birds (19-g body weight or less) only became important when their densities became very high. This contrasts with the finding of Wiens and Nussbaum (1975) that foliage gleaning bird species accounted for the greatest proportion of the energy intake in most stands of spruce-fir forest in Oregon. In their study, small species (10-g body weight or less) numerically dominated the bird communities at all stands. In this study, however, only five species weighed less than 10 g (Broad-tailed Hummingbird, Pygmy Nuthatch, Grace's Warbler, Red-faced Warbler, and House Wren). The species composition in this study was closer to that of shrub-steppe habitats in Oregon where 11–25-g species tended to predominate (Wiens 1974).

The total energy intake of the avian community was much lower than that reported by Weiner and Glowacinski (1975) and Karr (1971). The energy flow on the forested study plots varied from 39.7 to 112.8 kcal/ha-day (Tables 18–20). The total energy flow on bare ground in Illinois was 29.5 kcal/ha-day, whereas in the early shrub area it was 313.8 kcal/ha-day (Karr 1971). Weiner and Glowacinski (1975) reported a total energy flow of 232.9 kcal/ha-day in a deciduous forest in Poland, whereas Karr (1971) recorded a total energy flow of 411.3 kcal/ha-day in a mature bottomland deciduous forest in Illinois. The total energy flow of the wet grazed grassland in Illinois was 47.3 kcal/ha-day (Karr 1971). The energy flow in the ponderosa pine forest was similar to the energy flow of a bird community in a pine forest on Great Abaco Island, Bahamas (116.75 kcal/ha-day, Karr and Roth 1971).

The permanent residents were the primary energy component on all the forested areas (52–74%). Permanent residents accounted for 68–92% of the total energy flow in a coniferous forest in Oregon (Wiens and Nussbaum 1975). Thus, although the proportion of the total energy flow contributed by the permanent residents in the ponderosa pine forest was lower than that reported in an Oregon coniferous forest, the permanent residents were of great importance to the total energy flux in both communities.

Overall energy flow (in terms of existence energy) appears to be very low in the ponderosa pine forest bird community. The energy flux was higher on the strip cut and silviculturally cut plots than on the natural area, reflecting the higher densities on the former plots. The low energy flux of the bird community in the ponderosa pine forest reflects the low breeding bird densities. Other studies (Haldeman et al. 1973, Wiens and Nussbaum 1975) reported greater energy flows

because of the higher densities on their areas. In general, the energy flux through the avian community is small compared with the total system energy flow (Holmes and Sturges 1975), and it is highly probable that this generalization holds for the ponderosa pine forest. However, the avian community probably had a substantial effect on the overwintering insect population when its density was most likely at its low point, thereby affecting insect densities throughout the year.

#### SPECIES SUBSTITUTIONS

Potential competitive pressures were probably greatest in the closely clumped groups of species, on a weight basis, within each guild (Table 16). Interestingly, species substitutions (the replacement of a species on a natural or near natural area by another species) on the heavily treated areas occurred in these closely clustered groups of species. The Western Flycatcher, which prefers dense foliage and a nearly closed canopy, bred only on the control plot and some areas of the silviculturally cut plot, whereas the Western Wood Pewee, which prefers more open habitat, bred on the severely thinned and strip cut plots and in an open area on the silviculturally cut plot. Similarly, the Red-faced Warbler, which was only present on the control and silviculturally cut (before treatment) plots, was replaced on the treated areas by the Yellow-rumped Warbler.

The possibility exists that further niche exploitations could occur in those guilds with large gaps between bird sizes. Additional species probably could be accommodated between the following pairs of species: Solitary Vireo and Western Tanager, Broad-tailed Hummingbird and Common Nighthawk, Hermit Thrush and Robin, and White-breasted Nuthatch and Black-headed Grosbeak (Table 16). Haldeman et al. (1973) and Balda (1969) failed to find any intermediate species that could fill these gaps in their studies of bird communities in the ponderosa pine forest. The addition of potential competitors in the gaps between the larger species may be limited by food resources (Schoener 1971). The larger prey selected by the larger birds may be in short supply, whereas there may be large numbers of small prey species in the ponderosa pine forest. The commonest insect species in a lowland deciduous-conifer forest in Massachusetts are in the 2- to 4-mm class (Schoener and Janzen 1968). The majority of insects in temperate forests are between 2 and 8 mm in length (Schoener 1971). Since insect prey items are distributed log normally in size (a normal distribution on a log scale), large prey species are less abundant than are medium-sized prey species (Schoener and Janzen 1968, Price 1975). This suggests the possibility of greater specialization being possible on the smaller end of the weight spectrum. In the ponderosa pine forest, 23 of the 28 species examined were at the lower ends of the weight spectrums in their respective guilds.

#### SPECIES DOMINANCE

In conclusion, one might hypothesize on the basis of the bulk of the data of this study that those species able to alter their habitat requirements and niche dimensions in response to treatment should be the most dominant bird species in the ponderosa pine forest. As defined by McNaughton and Wolf (1970), generalists are able to maintain themselves over a broader environmental range than specialists. One hypothesis suggested by Järvinen and Väisänen (1976) is that behavioral flexibility with respect to habitat tolerance may account for the dif-

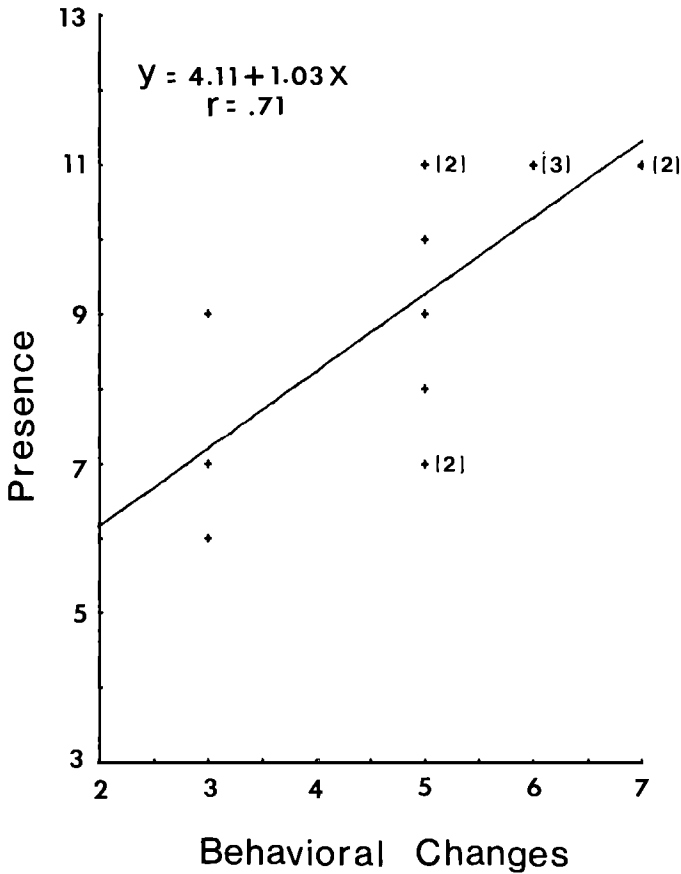


FIGURE 38. Relation between the number of behavioral changes (from Table 6) and overall presence. Overall presence is the sum of the number of times a species was present on the four forested study areas for the three-year period. The maximum value is 11 as the pre-treatment silviculturally cut plot was not used in the calculation.

ferences between successful (that is, a species which has occupied a large number of biotopes) and unsuccessful species. If this is the case, the most flexible species in the ponderosa pine forest should be present on more study plots during more years and with greater standing crops than relatively inflexible species. Behavioral plasticity was greatest in five species (Solitary Vireo, Gray-headed Junco, Western Bluebird, Common Flicker, and White-breasted Nuthatch). In response to habitat modification, these species significantly altered at least six of the seven behavioral characteristics examined (Table 6). If the suggested hypothesis is correct, then these five species should have been present on more study plots during more years and with greater standing crops than any other of the 15 species examined in detail. Indeed, these five species were present on all study plots in all years during the course of the study. The Grace's Warbler and Hairy Woodpecker were also present on all study plots in all years, and both species altered five behavioral characteristics in response to habitat alteration, indicating that they were also fairly resilient. Overall, there was a positive correlation ( $r = 0.71$ ,



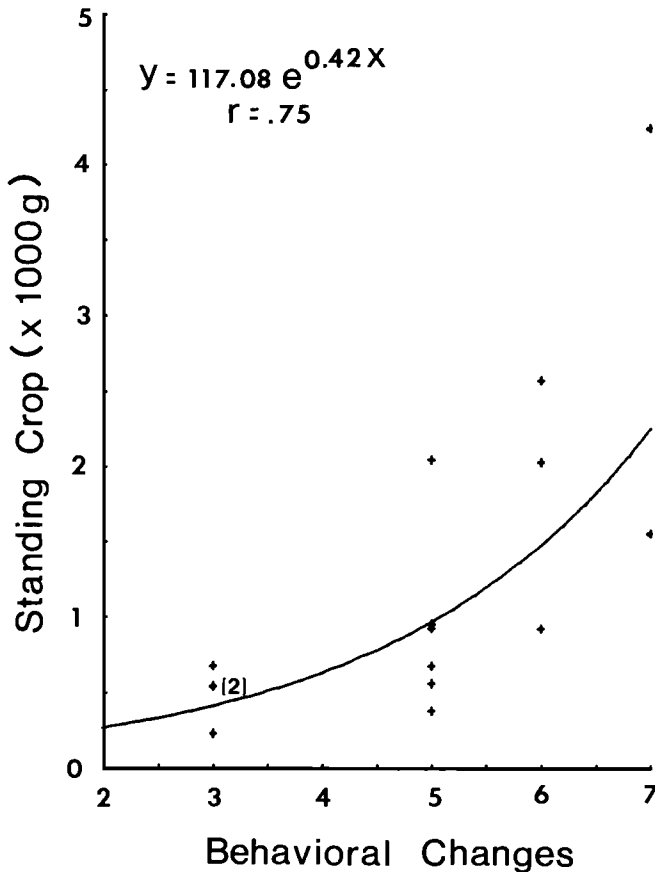


FIGURE 39. Relation between the number of behavioral changes (from Table 6) and overall standing crop. Overall standing crop is the sum of the total standing crop for a given species on the four forested study areas for the three-year period (exclusive of the pre-treatment silviculturally cut plot).

$P \leq 0.05$ ) between the number of behavioral changes and species presence over the three years on the study areas (Fig. 38).

In terms of standing crop (calculated for the overall study) the five most plastic species ranked first, second, fourth, fifth, and seventh out of the 15 breeding species examined in detail. The Hairy Woodpecker ranked third; Pygmy Nuthatch, sixth; and the Grace's Warbler, eighth. The Pygmy Nuthatch altered five behavioral characteristics and was important in terms of standing crop because of its high densities on the silviculturally cut and control plots. These high densities of Pygmy Nuthatches were due to the high availability of its typical habitat on these plots. There was a positive correlation ( $r = 0.75$ ,  $P \leq 0.05$ ) between the number of behavioral changes and standing crop of the bird species (Fig. 39). The most inflexible species (Violet-green Swallow, Rock Wren, and Broad-tailed Hummingbird) ranked ninth, thirteenth, and fifteenth in terms of standing crop and were not present on all study plots in all years. The Rock Wren was absent on the silviculturally cut and control plots whereas the Violet-green Swallow was

absent on the severely thinned plot. The Broad-tailed Hummingbird was a breeding species on all plots but was missing from most plots in 1973. Thus, those species which exhibited the greatest behavioral flexibility were also the most successful breeding species in the ponderosa pine forest.

An examination of how the most successful species related to the other species in their foraging guilds in terms of body weight may help explain why these species were able to be ecologically resilient. These five species (Solitary Vireo, Gray-headed Junco, Western Bluebird, Common Flicker, and White-breasted Nuthatch) plus the Grace's Warbler, Pygmy Nuthatch, and the Hairy Woodpecker, tended to be on the extremes of the weight ranges of each guild (Table 16). The Grace's Warbler was the smallest picker and gleaner, whereas the Solitary Vireo was the heaviest picker and gleaner except for the tanagers, which, besides being present in very low densities, were twice the size of the Solitary Vireo. The Western Bluebird was the largest aerial feeder except for the Common Nighthawk. However, not only was the nighthawk a crepuscular species, but it was twice the size of the Western Bluebird. The most successful hammerers and tearers were the Common Flicker and the White-breasted Nuthatch, which were the largest and smallest members of that guild. The Hairy Woodpecker, which was present all years and on all study plots, also faced potentially reduced competitor pressure by being three times as large as the White-breasted Nuthatch but half the size of the Common Flicker. The most successful ground feeder was the Gray-headed Junco. Its nearest potential competitors were the Rock Wren and Hermit Thrush. However, the Hermit Thrush was present only on the silviculturally cut and control plots in very low densities. The next heaviest species, the Robin, was four times the size of the junco. The Rock Wren, which was smaller than the junco, was present only on the severely thinned and strip cut plots. Competition between species of different size probably occurs only over a relatively narrow intermediate range of resource size classes (Ricklefs 1972). Indeed, Hespeneide (1971) showed that flycatchers exhibited a strong positive correlation of average prey size with body weight. Therefore, those species at the extremes or situated in the large gaps of the weight range of a particular guild probably have reduced competitive pressures when compared with those species of similar body weights in the same guild. Potential competition between species of different guilds is probably minimal as guild members use different foraging substrates. Broadening of habitat selection made possible by reduced competition has been observed in island situations (Crowell 1962, MacArthur and Wilson 1967, Williams 1969, Diamond 1970a). Thus, the behavioral plasticity observed in the five most successful species in the ponderosa pine forest was possible probably because of reduced competitive pressure. The Grace's Warbler and Hairy Woodpecker were successful for the same reason.

We conclude from this evidence that the most dominant species in the ponderosa pine forest community, when dominance is based on presence and standing crop biomass, are those species that have one or both of the following attributes: 1) behavioral plasticity, and 2) occupation of the extremes or occurrence in large gaps in the guild weight spectrum. One or both of these factors may be of prime concern in defining "niche dominance" in such a way that it will aid in understanding community composition. This is obviously an oversimplification of the constellation of factors that affects community organization but it does

account for a large proportion of the variability present in avian community organization in this study.

### SUMMARY

This study was undertaken to measure and evaluate 1) the effects of differing foliage volume, foliage patterns, and densities of trees on the diversity, density, and behavior patterns of the breeding birds of ponderosa pine forest, and 2) the standing crop biomass, consuming biomass, and existence energy requirements of the breeding birds on each plot. Five study plots were chosen in relatively homogeneous stands on ponderosa pine. Plots were selected in clear cut, strip cut, severely thinned, silviculturally cut, and natural areas. The trees on each study site were analyzed to determine the relative density, relative frequency, importance value, absolute density, and foliage volume in 2-m height classes for each tree species. Breeding bird behavior was examined in detail in seven different categories: activity pattern, foraging method, tree species selection, position from the trunk, perch selection, stance, and foliage use profile. The following major points were evident.

1. Breeding bird populations varied from a low of 12.5 prs/40 ha on the clear cut area in 1973 to a high of 162.8 prs/40 ha on the strip cut area in 1974. Bird densities on the natural area varied from a low of 63.0 prs/40 ha in 1973 to a high of 132.8 prs/40 ha in 1974. The number of nesting species was highest on the strip cut area where 22 species nested in 1974 and lowest on the clear cut area where three species nested in 1973.

2. When bird species diversity is related to plant species diversity, foliage height diversity, and plant volume diversity for the forested areas, it is evident that these factors are not significantly correlated with breeding bird diversity. Other factors such as territoriality, food supply, and the openness of the habitat or other foliage configurations are more important in determining breeding bird diversity than the above three factors.

3. The behavior patterns of most bird species were influenced by habitat alteration. Foraging method and stance were the two types of behavior least affected by habitat manipulation. Perch selection, tree species selection, and mean height were most affected by treatment.

4. Bird species in the ponderosa pine forest segregated primarily on a vertical basis by using different portions of the trees, or on a body weight basis. Pickers and gleaners separated primarily on a vertical basis, whereas the other three guilds (hammerers and tearers, ground feeders, and aerial feeders) segregated primarily by body weight. Species in the same guild also separated on the basis of differences in several other niche dimensions.

5. Comparisons between the foliage profiles and bird use profiles illustrated a cyclic pattern of bird use during the course of the study, perhaps in response to fluctuations in the resource base.

6. No correlation existed between territory size and breeding bird density for individual species or community densities. Territory size did vary directly with changes in the fit between the bird use profile and the foliage profile. Territory size decreased with (1) increased use of the foliage profile bulge, (2) increased utilized foliage volume per territory, and, most importantly, (3) an increased fit of the bird use profile and the foliage profile, or a combination of these.