FORAGING RELATIONSHIPS OF MOUNTAIN CHICKADEES AND PYGMY NUTHATCHES

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The Pygmy Nuthatch *(Sitta pygmaea)* and Mountain Chickadee *(Parus gambeli)* are two of the most abundant resident birds in yellow pine *(Pinus ponderosa, P. jeffreyi)* forests of western North America. Although nuthatches and chickadees usually forage in different ways, *pygmaea* has been characterized as "remarkably titlike in many of its foraging actions" (Norris 1958). In yellow pine woods, these two birds occupy what Sturman (1968) has called the "titmouse niche," which might be more appropriately referred to as the titmouse "guild" *(sensu* Root 1967). This guild has been intensively studied in many parts of the northern hemisphere, primarily because its members are common, conspicuous and potentially important insect predators in temperate zone woodlands (Sturman 1968). In this paper, I focus on resource use patterns in relation to environmental structure, seasonal changes in resource distribution and interspecific flocking of the Pygmy Nuthatch and Mountain Chickadee.

STUDY AREA AND METHODS

The foraging habits and intra- and interspecific associations of *pygmaea* and *gambeli* were studied during June and July 1973 and January and February 1974 on 42 ha of Jeffrey Pine *(Pinus jeffreyi)* and Western Juniper *(Juniperus occidentalis)* woodland, including the field station of California State University, Chico, and adjoining private land, along the western shore of Eagle Lake, Lassen County, California. Roughly the western third of the plot is flat and dominated by *J. occidentalis*, with scattered clumps of *P. jeffreyi* and mountain-mahogany *(Cercocarpus ledifolius)*. Sagebrush *(Artemisia tridentata)* and rabbitbrush *(Chrysothamnus nauseosus)* are common shrubs. The eastern two-thirds of the plot rises on a slope from north to south, being higher than the western third and separated from it by a lava dike. The predominant tree in this area is *P. jeffreyi*. This area contains a number of large (1-5 ha) piles of jumbled volcanic rocks, barren of vegetation except for lichens and bordered by thickets of *C. ledifolius, Ribes* spp. and Desert Sweet *(Chamaebatiaria millefolium)*. The private section has been logged within the last half century. Except in open areas of the woods, brush is largely absent.

Foraging height data were obtained by noting the heights at which foraging birds were first seen. Foraging site data were gathered by recording, on cassette tapes, foraging time spent on different sites for birds encountered on random walks through the plot at various times of day. Foraging sites were divided into the following five classes: trunk, large branches (greater than 3 cm diameter), small branches (less than 3 cm diameter), needle clusters and ground (including objects on the ground). These site classes correspond roughly to similar categories defined by Ligon (1973) and Bock (1969) in their studies of birds foraging in yellow pines, and hopefully, with the categories defined by the birds themselves. Foraging overlap was determined by calculating percent overlap values, i.e., adding percent values shared between two species for all foraging height or site categories (Holmes and Pitelka 1968).

Vegetational analysis followed the methods of Balda (1969). The point-quarter method was used to sample trees on the plot, with each tree's foliage volume considered either a cone or a cylinder, and its dimensions measured with the aid of a 2 m stick and compass. A computer program calculated the percent of the total sample volume in any desired height interval. Only pine foliage was considered, as virtually all foraging data were collected in pines.

Foraging height observations for each species in each season were sorted into 3 m intervals from the ground up, the number of observations within each interval was plotted as a percent of the total number of sightings, and these foraging height profiles were compared to the profile of foliage volume (Figure 1). Three meter intervals were chosen because of the small sample sizes, and because of the chance of error in estimation, particularly at higher levels. Percent overlap values were determined for the foraging height profile of one species versus the other, for the foraging profiles of each species versus the foliage volume profile and for the overlap of time spent foraging on different sites by the two species (Figure 2) in both seasons (Table 2).

Population sizes in summer were estimated by combining knowledge of some nest sites, the foraging ranges of birds that were either color-banded or observed carrying food to a particular nest, and the distribution of family groups after the young had fledged. Winter population sizes were estimated from seven morning censuses during the period 17-26 January. These censuses involved plotting observations of all species on grid maps of the study area.

RESULTS

More individuals of both species appear to have been present in winter than in summer (Table 1). Summer estimates are of breeding adults present before young had fledged. The structures of the populations were also different in the two seasons. In summer, pairs of both species occupied foraging areas that did not appear to overlap intraspecifically, but exhibited considerable interspecific overlap. Adults of the two species were often observed foraging in the same or nearby trees, but interspecific aggression was never noted. In winter, both species exhibited a tendency to forage in flocks (Table 1).

Although the extremely close fit of the summer foraging height data for *pygmaea* to the foliage profile (Figure 1) must be viewed, in part, as an artifact of the graphical methods employed, it agrees with the observation that Pygmy Nuthatches foraged most of the time on small branches and needle clusters in summer (Figure 2). There was a slight increase in foraging height overlap between the two species in the winter versus summer (Table 2). The greater overlap appears to be the result of 1) increases in the ranges of foraging heights of the chickadee and the nuthatch in winter and 2) the tendency of both species to forage at nearby heights in mixed flocks. These two factors may be interdependent. The order of values for the percent overlap of foraging height with the foliage profile for the two species is the reverse, in winter, of the summer order (Table 2). The chickadee foraged almost exclusively on small branches and needle clusters in winter, whereas the nuthatch spent about half of its time on these substrates in that season (Figure 2). The seasonal change in overlap values for feeding sites is almost directly proportional to the seasonal differences in the time spent foraging on small branches and needle clusters by Pygmy Nuthatches.

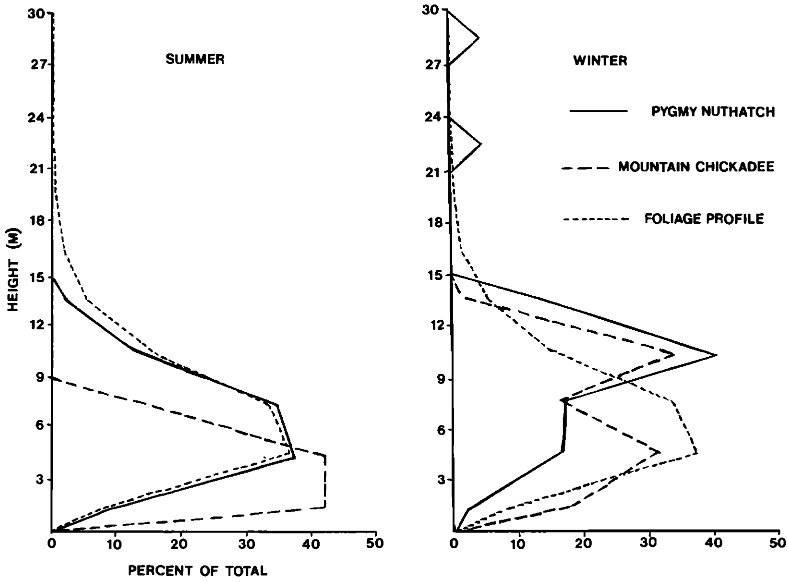

Figure 1. Foraging height profiles for Mountain Chickadee and Pygmy Nuthatch in winter and summer and the foliage volume profile for Jeffrey Pine on the Eagle Lake study plot. Sample sizes equal 29 winter and 31 summer observations of nuthatches, 45 winter and 28 summer observations of chickadees and 125 pine trees. The vertical axis is divided into discrete 3 m intervals.

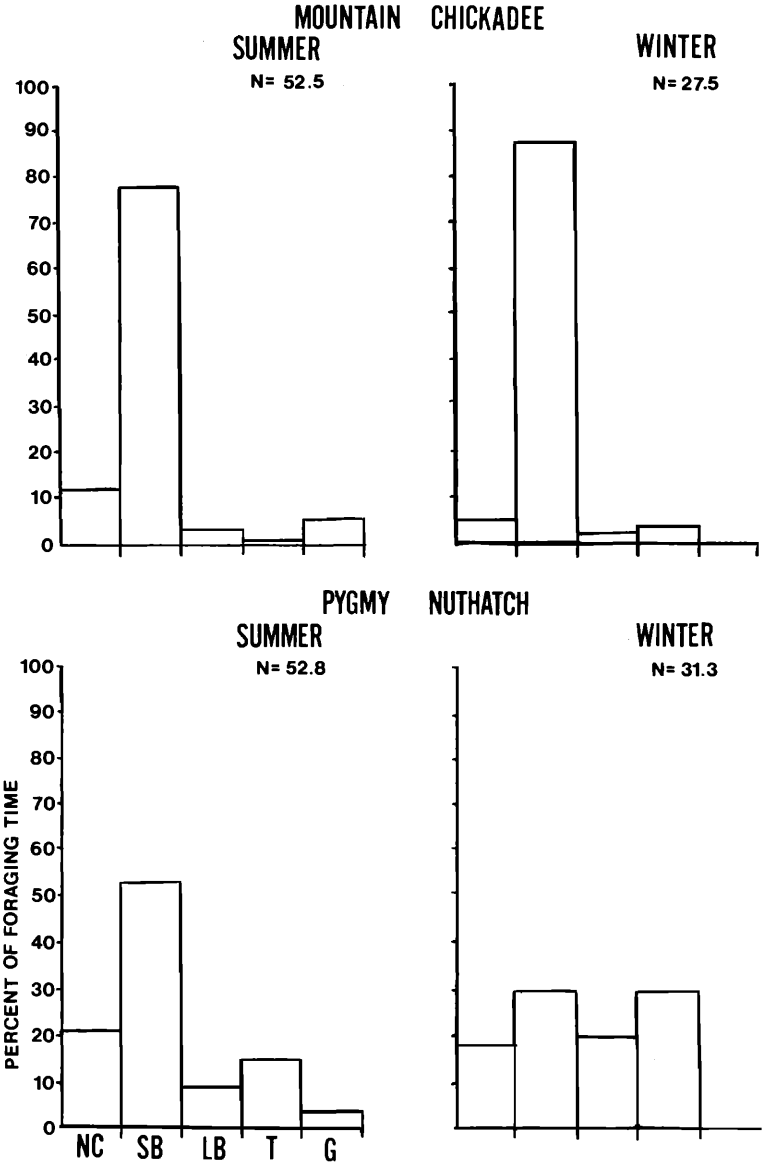

Figure 2. Percent of time spent foraging by Mountain Chickadees and Pygmy Nuthatches in five different habitat zones in winter and summer. Zones include: NC=needle clusters; SB=small branches; LB=large branches; T=trunk; G=ground. Total sample sizes (N) are in minutes of taped time.

Table 1. Estimated population sizes in winter and summer and the numbers of different types of associations, observed in winter, of Mountain Chickadees and Pygmy Nuthatches on the 42 ha Eagle Lake study plot.

SPECIES	POPULATION SIZE		NO. OBSERVATIONS IN WINTER		
	Summer	Winter	Alone	In conspecific groups	In mixed flocks
Mountain Chickadee	12-14	15†(32*)	10	6	21
Pygmy Nuthatch	10	21†(32*)	11	22	21

† Average of seven censuses
* Highest single census tally

DISCUSSION

A current approach to the study of resource utilization patterns of organisms in general (Schoener 1971) and insectivorous birds in particular (Morse 1971) has been to view them as adaptive strategies designed by natural selection to use available resources most efficiently. This perspective can provide a framework in which observed patterns of resource exploitation may take shape as well-integrated systems. It is in this context that the foraging patterns of the species studied are discussed.

Qualitative sampling of pine branches in the summer study revealed an abundance of surface arthropods. Anderson (1976) found that three species of nuthatches *(Sitta pygmaea, S. canadensis* and *S. carolinensis)* in Ponderosa Pine woods in Oregon overlapped considerably in the kinds of foods taken in summer, the bulk of their diets being insects associated with the twigs and foliage. Ligon (1973) noted that the "flush" of insects in Ponderosa Pine foliage in summer, coupled perhaps with the structural simplicity of pine forests, may make intersexual habitat partitioning by White-headed Woodpeckers *(Picoides albolarvatus)* at that season unnecessary. That the foraging overlap of Pygmy Nuthatches and Mountain Chickadees was greatest in summer, and primarily involved intensive use of the foliage and twigs by both species, may reflect a similar phenomenon. The close association of foraging by *pygmaea* to the foliage volume in summer (Figure 1) supports Balda's (1969) impression that foliage distribution in Arizona pine forests seemed to be an important determinant of foraging for Pygmy Nuthatches. The poorer fit of the chickadee's summer foraging height profile to the foliage profile possibly reflects its preference for foraging on small branches, including dead twigs below the needle-bearing branches included in our sampling of foliage volume. Laudenslayer and Balda (1976) found a similar relationship between the foraging height profile of Mountain Chickadees and the foliage profile of pine-juniper woodland in Arizona, and suggested that the requirements of breeding birds may be met by resources available in the lower foliage layers.

Table 2. Matrix of percent overlap values for Mountain Chickadee and Pygmy Nuthatch foraging data and Jeffrey Pine foliage volume. Percent overlap equals sum of percent values shared for all categories for the two species compared (Holmes and Pitelka 1968).

	Foliage Profile	Mountain Chickadee Foraging Height Profile		Mountain Chickadee Foraging Site Use	
		Winter	Summer	Winter	Summer
Foliage Profile	–	71.6	59.5	–	–
Pygmy Nuthatch Foraging Height Profile					
Winter	53.2	69.7	–	–	–
Summer	94.8	–	62.7	–	–
Pygmy Nuthatch Foraging Site Use					
Winter	–	–	–	42.7	–
Summer	–	–	–	–	72.7

There are other ways these two species might be avoiding consumption of identical resources in summer. The different foraging tactics of the chickadee and nuthatch (see discussion of tactics below), which seemed to hold in all seasons, may expose them to different items in winter, but it is hard to see how the surface prey upon which they both seemed to concentrate in the summer should be more obvious from any particular angle versus another; however, such may be the case. The longer-billed nuthatch may take insects at the bases of needle clusters and fascicles more effectively than the chickadee, thereby reducing apparent foraging overlap.

Fretwell (1972) hypothesized that species with seasonal shifts in feeding patterns might show the greatest degree of correlation between morphological adaptations for foraging and preferred foraging zones during the season of greatest stress (i.e., winter for resident temperate zone birds). The chickadee and nuthatch appear to occupy winter roles as small branch forager and trunk, large branch and needle cluster forager, respectively. The locomotor aspects of morphology of each species seem best adapted to their preferred winter substrates and integrally related to their different tactics used when "attacking" a pine tree for insects (Richardson 1942). Chickadees typically spiral around a tree, hopping from branch to branch, while nuthatches usually hitch their way in or out along a branch, often moving across the trunk from branch to branch. These different foraging patterns no doubt provide each species with a different perspective on the same objects, and may result in different foods being taken. In addition, their bills seem best adapted to their winter roles, the longer bill of the nuthatch enabling it to probe deep fissures in the bark, whereas the shorter bill of the chickadee is probably more efficient at chipping bark from the small branches.

Morse (1967, 1970) and Austin and Smith (1972) presented evidence that the different species in mixed flocks accomodate each other's presence by foraging in different zones of the habitat. Morse (1971) felt that such flocks might provide the most efficient means for each individual to exploit the resources present with a minimal degree of interspecific contact. Hartley (1953), Morse (1967) and Bock (1969) all observed an increase in the number of aggressive interactions between species in mixed groups when food became abundant in a particular part of the environment (e.g., feeders and good cone crops). During this study, only one aggressive encounter between a chickadee and a nuthatch was observed in the winter, despite their constant association in mixed flocks. Unless food is made readily available in a small part of the total habitat, the structure of such flocks may be important in reducing the potential for aggressive encounters which offer no advantage to either party.

Krebs (1973), in experiments with mixed-species flocks of chickadees, found that differences in learned foraging height preferences of two species *(Parus atricapillus* and *P. rufescens)* tended to disappear in mixed groups, and that individuals of one species would alter their foraging patterns (i.e., search the site of discovery) in response to food-finding by an individual of the other species. He hypothesized that if food was clumped in the environment, each species could effectively increase its range of exploitable feeding sites by feeding in groups of species adapted for foraging in a variety of sites. This theory is particularly attractive, at least in reference to the chickadee-nuthatch-creeper-kinglet flocks observed in the northern hemisphere, in that it simultaneously provides a reason for the formation of these flocks while it explains the integration of foraging patterns of species within them, such as observed in this study. Additional species observed flocking with *pygmaea* and *gambeli* in winter were Bushtit *(Psaltriparus minimus),* Golden-crowned Kinglet *(Regulus satrapa),* Brown Creeper *(Certhia familiaris)* and White-breasted Nuthatch *(Sitta carolinensis),* but for these species, insufficient data were obtained to discuss their impact on flock structure.

SUMMARY

Seasonal changes in foraging habits of Mountain Chickadees and Pygmy Nuthatches are discussed in relationship to the different time and energy demands they face in different seasons. Both species foraged extensively on foliage and small branches in summer, but at different heights. Nuthatches foraged higher than chickadees in both seasons. Both species commonly occurred in mixed-species flocks in winter, and the observed differences in preferred foraging zones in winter may serve to reduce the number of undesirable interactions between species and/or to increase the range of foraging sites exploited by the flock as a whole.

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