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NEST SITES AND POPULATION DEMOGRAPHIES OF WHITE-BREASTED AND PIGMY NUTHATCHES IN COLORADO

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White-breasted (*Sitta carolinensis*) and Pigmy nuthatches (*S. pygmaea*), are sympatric throughout many of the mountainous regions of western North America (A.O.U. Check-list 1957). The White-breasted Nuthatch, occurring both in coniferous and deciduous forests, is widely distributed across temperate North America, while the Pigmy Nuthatch is restricted to coniferous forests of mountain regions in western North America. In north-central Colorado, these species breed principally in ponderosa pine (*Pinus ponderosa*) forests of the Transition Zone (Bailey and Niedrach 1965). Despite overall similarity in nesting habitat and breeding schedule, these species differ in nest site preferences and breeding population densities (Stallcup 1968).

Both of these nuthatches use (a) natural cavities, (b) cavities bored out by other species, (c) cavities excavated by conspecifics, and (d) modify pre-existing cavities, or (e) excavate their own cavities (Bent 1948, Norris 1958). Very little is known about the "historical" background of cavities used for nesting; however, Pigmy Nuthatches excavate cavities more frequently than White-breasted Nuthatches (Bent 1948). But, even in the case of Pigmy Nuthatches, new cavities are excavated rarely (Norris 1958). Breeding populations of cavity-nesting birds often are limited by the number of suitable and available nest sites (von Haartman 1971, Hogstad 1975). Consequently, population densities of birds within an area, although demonstrating within-year fluctuations due to recruitment, death, and dispersion, exhibit little between-year variation in breeding population densities (Lack 1966). Stallcup (1968) showed that Pigmy Nuthatches have higher breeding densities than White-breasted Nuthatches within a ponderosa pine habitat; however, both species' breeding populations exhibited little annual variation in the number of breeding pairs. I undertook analysis of the nest sites used by these species to see whether nest site availability was a factor associated with the differing levels of breeding populations.

Other life history phenomena, such as territorial behavior, also are important influences on breeding population levels (Wilson 1975). These two nuthatches have contrasting territorial behaviors. White-breasted Nuthatches are said to possess a year-long, type A territory (Nice 1941), while Pigmy Nuthatches defend only the nest tree (type C territory; Wilson 1975) and form gregarious flocks with conspecifics outside the breeding season (Bent 1948, Norris 1958, Bock 1969).

My report describes and compares nesting location and population dynamics for White-breasted and Pigmy nuthatches. This description yields knowledge of some proximate factors associated with the nesting biology of the birds which may be useful in management programs for cavity-nesting passerines.

STUDY AREA AND METHODS

The study site was approximately 72 km west of Fort Collins, Larimer Co., Colorado (40°37′N, 105°31′W). This site of 173 ha had an elevation ranging from 2,380 to 2,500 m. The terrain consisted of a relatively flat, east-west running basin surrounded by gentle slopes to the west and north and more precipitous hillsides to the south and east. Intermittent streams transversed the study area, eventually entering Little Beaver Creek to the south or Bennett Creek to the north.

The vegetation of the study area is ponderosa pine forest and parkland consisting of a relatively uniform stand of ponderosa pine trees interspersed with quaking aspen (*Populus tremuloides*) along stream bottoms and in the more mesic depressions. Northern slopes have Douglas-fir (*Pseudotsuga menziesii*) and Rocky Mountain juniper (*Juniperus scopulorum*) intermixed with the dominant ponderosa pines. At higher elevations lodgepole pine (*Pinus contorta*), Colorado blue spruce (*Picea pungens*), and Douglas-fir are more abundant. Open parks, areas devoid of trees or with widely scattered ponderosa pines, are common. I analyzed vegetation using the point-centered quarter method (Cottam and Curtis 1956).

Field data on nesting conditions were obtained from April through June in 1974 and 1975. The following information was recorded for each nest-cavity location: (a) species of nest tree, (b) condition of the tree (dead or alive), (c) tree height, (d) diameter of tree at breast height (dbh), (e) tree structure in which the nest cavity was situated, (f) height of the nest cavity above the ground, (g) location of nest in the study area, and (h) compass direction of the nest entrance.

The study site was censused for nuthatches every two weeks for 112 weeks (56 censuses), using a technique developed by Emlen (1971). During the reproductive months, densities of nuthatch breeding populations were determined by counting breeding pairs.

TABLE 1. Condition of the nest-cavity trees of White-breasted and Pigmy nuthatches during the 1974 and 1975 breeding seasons.

Year	Tree condition	Species: White-breasted Nuthatch	Species: Pigmy Nuthatch	Total
1974	Dead	0	11	14
	Alive	3	0	
1975	Dead	0	15	19
	Alive	4	0	

RESULTS

During the 1974 and 1975 breeding seasons I located a total of 33 nuthatch nesting cavities (7 White-breasted Nuthatch pairs and 26 Pigmy Nuthatch pairs). All of the nests were situated in cavities within trunks of ponderosa pine trees. Of the White-breasted Nuthatch nests, five of the cavities were natural—that is, not bored out by a bird but created by lightning, decay, or some other factor. These cavities had irregular entrances, often roughly triangular in shape. The remaining two cavities probably were made by other species, possibly woodpeckers, because the entrances were circular. A large limb was situated immediately below the entrance to the nest cavity in six of the seven White-breasted Nuthatch nest sites.

All Pigmy Nuthatch nest cavities appeared to be bored out by some avian species. I saw only one pair of these nuthatches excavating a nest cavity during the two breeding seasons. However, these birds reshaped the interior of existing cavities, a common activity during late April and early May. Like White-breasted Nuthatch nest sites, all Pigmy Nuthatch nest-cavities had limbs near the cavity opening; 23 cavities had limbs below the entrance and three cavities had limbs to the side of the entrance. The birds used the limbs for perching or alighting before entering the nest.

Table 1 summarizes the condition (dead or alive) of the trees used as nest sites. All White-breasted Nuthatch nests were in living pines, while all Pigmy Nuthatch nests were in dead pines. This difference was highly significant (Chi-square contingency test; $P < 0.001$). None of the ponderosa pine trees which happened to be sampled during vegetation analysis was dead. A total of 27 dead ponderosa pines (0.16 trees/ha) occurred within the study site, and of these 18 were used as nesting trees by Pigmy Nuthatches. Total tree density was estimated at 317 trees/ha and ponderosa pine density was estimated at 282 trees/ha.

Nest sites of the two species did not differ significantly in terms of tree height, dbh, or nest cavity height (Table 2: Student's t-test with heteroscedasticity, $P > 0.05$; Sokal and Rohlf 1969). However, the ranges for these characteristics were consistently larger for Pigmy Nuthatch nesting trees. The larger mean values, larger ranges, and unequal variances indicated a greater flexibility in nesting conditions among Pigmy Nuthatches. These data were analyzed by Taha's sum of squared ranks test (Mielke 1972), a test for differences in scale, to determine whether White-breasted Nuthatches were more restricted in their nesting. All three tests (on tree height, cavity height, and dbh) proved significant ($P < 0.02$).

The location of the nest trees within the study area is shown in Figure 1. The two species never nested simultaneously in the same tree, but I found them nesting near each other (as close as 6 m apart). Pigmy Nuthatches also nested within 10 m of conspecifics. Nest cavities used in 1974 were commonly re-used in 1975, with an 85% repetition frequency between the two breeding seasons for both species combined.

The majority of the nest cavity openings faced southward (70%), while none opened to the north, northwest, or west directions (Fig. 2). No significant differences occurred between species in the direction of the nest openings (Chi-square contingency test; $P >$

TABLE 2. Mensural data on ponderosa pine trees used as nesting sites for White-breasted and Pigmy nuthatches. Data are presented on mean ($\bar{x}$), standard error of the mean (SE), and range (in parentheses).

	Number of nests	Tree height (m) $\bar{x}$	Tree height (m) SE	Tree diameter (cm)[a] $\bar{x}$	Tree diameter (cm)[a] SE	Nest cavity height (m)[b] $\bar{x}$	Nest cavity height (m)[b] SE
White-breasted Nuthatch	7	16.66 (13.99–17.0)	0.37	53.77 (49.52–59.43)	1.56	8.99 (7.46–12.34)	0.61
Pigmy Nuthatch	26	16.15 (5.09–25.54)	1.01	57.93 (23.24–84.89)	3.65	10.79 (3.54–17.22)	0.73

[a] Diameter at breast height (dbh).
[b] Distance from ground to bottom of cavity entrance.

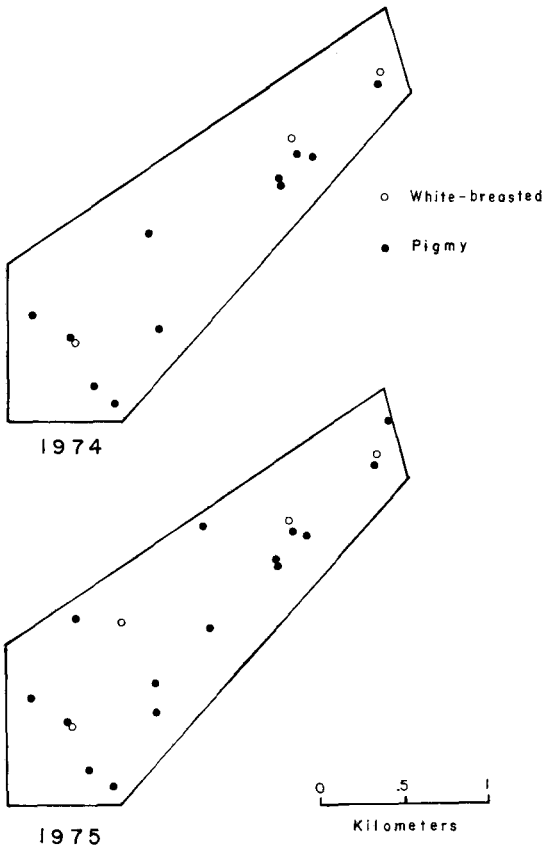

FIGURE 1. Nest tree locations occupied by White-breasted and Pigmy nuthatches during the 1974 and 1975 breeding seasons.

0.05). However, a highly significant difference occurred (Chi-square contingency test; $P < 0.001$) when the randomness of opening direction was tested. Since numerous cavities were found in all compass directions in all Pigmy Nuthatch nest trees, these data demonstrate that the birds selected nest cavities with openings facing south and east.

Pigmy Nuthatches were significantly more numerous than White-breasted Nuthatches ($P < 0.001$), while neither species differed significantly ($P > 0.05$) in population density between the two years of the study (Fig. 3).

DISCUSSION

Kendeigh (1961) demonstrated that at ambient temperatures below 25°C, roosting in cavities conserved energy in comparison to open roosting. The energy conservation increased curvilinearly as the temperature decreased. Because the prevailing winds, and therefore rains, in the region of my study come from the west and north and because nocturnal temperatures in May and early June below 0°C are not uncommon, the nuthatches' selection of cavities with entrances facing away from the prevailing wind probably conserved energy for both parents and offspring. Ricklefs and Hainsworth (1968) found that Cactus Wrens (*Campylorhynchus brunneicapillus*) used nests with entrances facing away from the cold winds, and Austin (1974) discovered that nest orientation was directly related to fledging success for this species. Reducing the amount of heat lost by forced convection could decrease daily incubation or brooding periods and thereby provide additional time to the parents for foraging.

Three factors were associated with the higher population density of Pigmy than White-breasted nuthatches. First, Pigmy Nuthatches nested in snags which, although not common, were far more abundant than the natural cavities in live trees used by White-breasted Nuthatches. Second, White-breasted Nuthatches excluded conspecifics from their territories, whereas Pigmy Nuthatches showed no intraspecific aggression in areas away from the immediate vicinity of their nest trees. Pigmy Nuthatches nested much closer together than White-breasted Nuthatch pairs (Fig. 1). Finally, Pigmy Nuthatches chose a greater variety of nest sites.

Although the between-year population fluctuations for both species were similar in form (both species showed little change in breeding densities between the two years), I found differences in the temporal pattern of population decline. White-breasted Nuthatches were most abundant immediately after breeding and declined to near breeding levels soon after the young fledged. Pigmy Nuthatches showed a similar post-breeding increase but remained at levels well above breeding density until spring, when the population declined rapidly. They were numerous in winter, while in flocks, and declined in numbers with the advent of the breeding season and the dispersal of flocks.

Pairs of White-breasted Nuthatches were dispersed before winter, thereby securing an adequate food supply and retaining a suitable nest site for the next breeding season. In contrast, Pigmy Nuthatches maintained high population levels throughout the winter and secured the advantages associated with flocking during this stressful period (Morse 1970, Cody 1971). Their flexibility in nesting location and defense of only the nesting tree allowed them to begin breeding activity rapidly.

The differences in nest location and pop-

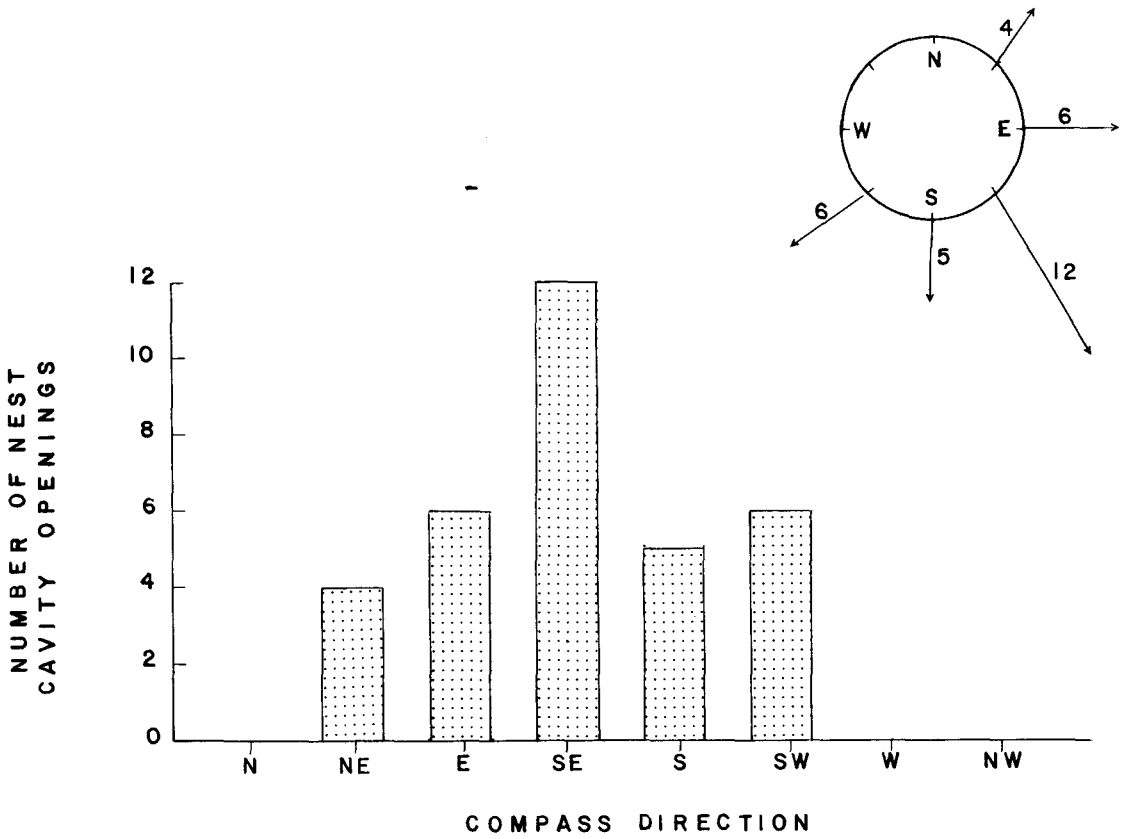

FIGURE 2. Direction of openings to nest cavities for both White-breasted and Pigmy nuthatches during two breeding seasons.

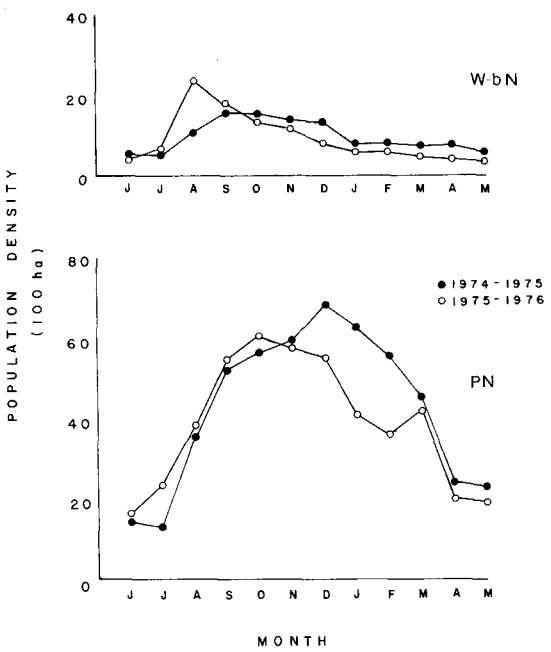

FIGURE 3. Monthly mean population density estimates of White-breasted (W-b N) and Pigmy nuthatches (PN) for the two field seasons (1974–1975; 1975–1976).

ulation demographic patterns complement differences between these species in foraging behavior and winter sociality (Stallcup 1968). In the Brewer's Blackbird (*Euphagus cyanocephalus*), nest dispersion is directly related to food distribution (Horn 1968). Uniform nesting distributions (territoriality) of blackbirds is associated with evenly distributed food items, while clumped nesting (coloniality) characterizes populations that harvest spatially or temporally non-uniformly distributed food supplies. The breeding dispersion and population demographies of nuthatches may reflect the distributions of the principal food items and represent adaptations toward the fullest exploitation of the food resources.

Pigmy Nuthatches depend upon dead, unmarketable trees for nesting, so removal of these trees would reduce the number of breeding pairs. Although little information has been published on the effects of removing dead trees, studies have suggested that this practice may harm avian populations (Allen and Nice 1952, Burns 1960). Stomach content analysis of White-breasted and Pigmy nuthatches in Oregon showed that these species fed principally on forest insects

(Anderson 1976). Koplin and Baldwin (1970) and Michael and Thornburgh (1971) presented data indicating that decreased bird populations could result in harmful increases in insect populations. The high abundance of Pigmy Nuthatches in my study indicates that they could be important in reducing insect numbers. The restricted nesting locations selected by the White-breasted Nuthatch indicate that management for this species would be difficult; however, their low population level also suggests that they exert less control on insect populations than Pigmy Nuthatches.

SUMMARY

In north-central Colorado, White-breasted Nuthatches nest in cavities in living ponderosa pines, while Pigmy Nuthatches use cavities in dead pines. Pigmy Nuthatches nest in a greater variety of sites than White-breasted Nuthatches. Both species avoid cavities with openings facing north or west.

Pigmy Nuthatches in this study had higher population densities than White-breasted Nuthatches, owing to a greater abundance of nest sites, more flexibility in nesting conditions, and smaller territories in the former species. Populations of the two species declined at different times of year, associated with territorial and winter flocking behaviors.

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