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FORAGING RELATIONSHIPS OF BROWN-HEADED NUTHATCHES AND PINE WARBLERS

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Abstract. Foraging behavior and interactions between Brown-headed Nuthatches (*Sitta pusilla*) and Pine Warblers (*Dendroica pinus*) were studied in longleaf pine lands of Louisiana during the fall and winter of 1963-64 and 1964-65. Both species frequently were members of flocks that formed around Carolina Chickadees (*Parus carolinensis*) and Tufted Titmice (*P. bicolor*). Most contact between the former two species occurred in these flocks. While in flocks, Brown-headed Nuthatches foraged most heavily on the distal parts of limbs and on twigs, Pine Warblers on proximal parts of limbs. When alone, Brown-headed Nuthatches foraged more heavily on trunks and proximal parts of limbs than they did when with Pine Warblers. When pine seeds were abundant, Brown-headed Nuthatches fed upon them heavily and regularly ventured to large limbs and trunks to crack seeds, causing increased hostilities with Pine Warblers. Attempts to crack seeds where bark was not sufficiently rough to permit adequate anchoring met with little success. Pine Warblers fed upon pine seeds much less frequently than did Brown-headed Nuthatches. During the height of seed abundance, Brown-headed Nuthatches lingered behind mixed flocks and often became separated from them. More competition for food apparently exists between Brown-headed Nuthatches and Pine Warblers than between either of these species and others. The noticeably different foraging distribution

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of the two species when together and apart is probably largely the result of the presence or absence of the other. Dividing the habitat in each other's presence avoids fighting over a similar foraging station. Abundant food sources may cause this system to break down.

Introduction

A number of studies have recently dealt with the subject of competition between closely related species of animals for some item in short supply, both in the field and under laboratory conditions. Following Crombie (1947), competition will be considered the demand at the same time by more than one organism for the same resources of the environment in excess of immediate supply.

Much of the basic understanding of competitive interactions between species is the result of laboratory studies such as those of Gause (1934, 1935), Park (1954, 1957), and many others on yeasts and invertebrate animals. As pertinent information of this nature is much more difficult to obtain in the field, the problem there has received less attention in the past, though a number of important contributions to the understanding of this problem have been recently made from the field, both in studies of vertebrates and invertebrates (e.g. Hairston 1951; Connell 1961). Most studies of interspecific interactions of this nature among birds have been based upon field work conducted during the breeding season, but those of Lack (1946), Hartley (1953), and Gibb (1954, 1960) are concerned with the problem at other times of the year.

The study of foraging relationships between members of taxonomic groups as widely divergent as families has been limited. Following Darwin (1859), competition between closely related species has usually been considered more intense than between distantly related ones. However, where convergence in foraging behavior has taken place, competition may also be strong. This possibility sometimes has been obscured from consideration by the more prevalent situation existing between closely related species, though Gilbert, Reynoldson, and Hobart (1952) point out that a close taxonomic relationship is not necessarily involved in a concept of ecological similarity.

The present study was undertaken to investigate the foraging of species from two different families, Brown-headed Nuthatches (*Sitta pusilla*) and Pine Warblers (*Dendroica pinus*), and their effect upon each other in an area where they come into regular contact. Brown-headed Nuthatches and Pine Warblers are common winter residents in longleaf pine (*Pinus australis*) forests, both regularly participating in mixed species flocks that form around Carolina Chickadees (*Parus carolinensis*) and Tufted Titmice (*P. bicolor*), several nuthatches and warblers usually being found in such a flock. Brown-headed Nuthatches and Pine Warblers most frequently come into intimate contact in these flocks.

This study was conducted during the fall and winter of 1963-64 and 1964-65 in the extensive even-aged longleaf pine forests directly west of Fluker, Tangipahoa Parish, Louisiana. These trees reach a maximum height of approximately 16 m. The only others are scattered black jack oaks (*Quercus marilandica*), ranging up to 7.5 m, and occasional yaupons (*Ilex vomitoria*). Periodic burning controls other species except in occasional small stream bottoms. The land is gently rolling, and the ground cover consists of various grasses and blackberry (*Rubus* sp.).

Supplementary observations on Pine Warblers were made in a mixed pine-deciduous forest directly northeast of Satsuma, Livingston Parish, Louisiana. Principal species here include loblolly pine (*Pinus taeda*), spruce pine (*Pinus glabra*), water-oak (*Quercus nigra*), and American hornbeam (*Carpinus caroliniana*). Though tree species are somewhat clumped, the forest is approximately 50% pine and 50% deciduous.

The two species are widely sympatric, the Brown-headed Nuthatch being a permanent resident over much of the southeastern United States (see Norris 1958), and the Pine Warbler being found throughout the year in most of this area (see Bent 1953). Although neither species is exclusively confined to pine forests, both are characteristically birds of these trees, where they are often common.

The Brown-headed Nuthatch in the manner of its congeners possesses the ability to move about with considerable agility on both horizontal and vertical surfaces, and it maneuvers easily on the undersides of limbs. However, individuals of this species spend much of their time foraging in the small branches and foliage, where their long pointed bill may be of considerable assistance when probing in the large needle clusters of the longleaf pine.

Pine Warblers are surprisingly nuthatchlike in many of their foraging movements, being able to move rapidly along large horizontal limbs, and even venturing regularly onto trunks, upon which they hang, sometimes even hitching about rather clumsily. However, the birds that I observed did not maneuver on this part of the tree as adeptly as did those described by Bent (1953). Otherwise

my observations on foraging in this species and in the Brown-headed Nuthatch agree with those found in the literature. Pine Warblers also work regularly in the small branches and needle clusters, though less frequently than Brown-headed Nuthatches.

The two species frequently chip the flaky bark scales off longleaf pines with their beaks in search of hidden prey, and both hawk for insects in favorable weather. In these habitats they both confine their foraging almost entirely to pines.

Methods

Extensive notes were taken on the flocks in the field. Data were obtained in a manner rather similar to that of Gibb (1954, 1960). As far as possible each observation contained information on the bird's activities, its height and position in the vegetation, food obtained and the method used in procuring it. Further observations were made on the numbers of individuals of different species in mixed flocks and the frequency of the species concerned away from such flocks. Locations where seeds were cracked were also tallied, since both species were dependent upon rough surfaces for this task. Because of the manner in which the birds foraged and the rather simple habitat being studied, foraging observations were separated into six basic categories; ground and herb, deciduous growth, pine branch (distal), cone, pine branch (proximal), and pine trunk. The data obtained appeared consistent with a great number of incidental observations that I made while pursuing other studies of mixed flocks concurrently.

Results

Foraging in mixed flocks out of the pine seed season

Most direct contact between the two species occurred in mixed flocks, whose other most characteristic members, in addition to Carolina Chickadees and Tufted Titmice, were Downy Woodpeckers (*Dendrocopos pubescens*), Brown Creepers (*Certhia familiaris*), Golden-crowned Kinglets (*Regulus satrapa*), and Ruby-crowned Kinglets (*R. calendula*). A great majority of the flocks whose participants were counted contained both Brown-headed Nuthatches and Pine Warblers (Table I). Usually these two species occurred in nearly equal numbers and were the most abundant species in the flocks, commonly numbering four to eight individuals apiece.

A strong tendency existed for the nonterritorial species, which included both Brown-headed Nuthatches and Pine Warblers, to move into different flocks when the territorial leaders (Carolina Chickadees and Tufted Titmice) reached their boundaries. However, the constancy in numbers of the nuthatches and warblers in the study area, in addition to their strong tendency to remain within a limited range when followed for considerable periods of time, suggested that these species occupied a definite home range (see Fitch 1958) at this season. While some overlap was noted along the edges of these ranges, there was no indication that this overlap was extensive. Each Brown-headed Nuthatch or Pine Warbler probably regularly foraged over an area that encompassed two to five chickadee and titmouse territories. Brown-headed Nuthatches showed a much higher tendency than Pine Warblers to occur away from mixed chickadee and titmouse flocks; however, this difference may be slightly exaggerated because of the extreme conspicuousness of the noisy Brown-headed Nuthatches and the almost complete silence of Pine Warblers outside the breeding season.

Table I. Occurrence of birds in mixed flocks in longleaf pines

Species	Mixed flocks		Groups of individuals	
	No. observed	Percentage containing species	No. observed	Percentage occurring in mixed flocks
Brown-headed Nuthatch....	57	98.2	141	39.7
Pine Warbler.....	57	91.2	65	80.0

Brown-headed Nuthatches in mixed flocks spent a large percentage of their foraging time on the distal parts of limbs and on twigs. Pine Warblers spent a large part of their time on the proximal parts of the limbs and regularly ventured onto the trunks (Table II).

Foraging away from mixed flocks out of the pine seed season

Though Brown-headed Nuthatches spent some of their time foraging on large limbs and trunks when in mixed flocks, they occurred a substantially greater part of the time on large limbs and trunks when in pure flocks (Table II). The difference in foraging at these two times is highly significant ($P < .001$). This P-value and those found elsewhere in the paper were obtained by applying chi-square tests to the enumerated data. The tendency to forage on large limbs and trunks appeared stronger in flocks that contained only one or two Pine Warblers than where more occurred, and in the very few instances that I saw Pine Warblers and Brown-headed Nuthatches in groups composed of approximately equal num-

TABLE II. Percentage frequency of foraging positions

Foraging position	Brown-headed Nuthatch		Pine Warbler	
	Mixed flock longleaf pine	Pure flock longleaf pine	Mixed flock longleaf pine	Mixed flock pine-deciduous
Ground	1.0	0.3	1.4	0.0
Deciduous	1.9	0.0	1.0	0.0
Pine branch				
distal half	55.1	29.4	22.0	51.9
proximal half	13.5	32.1	63.0	36.6
Pine cone	22.1	10.8	1.6	0.0
Pine trunk	6.4	27.4	11.0	11.5
Total no. observations	312	599	509	52

TABLE III. Percentage frequency of foraging positions in longleaf pines before and during a heavy cone crop[a]

Foraging position	Brown-headed Nuthatch				Pine Warbler	
	Mixed flock		Pure flock		Mixed flock	
	Before	During	Before	During	Before	During
Ground	0.0	1.7	0.0	0.6	0.0	2.0
Deciduous	1.5	2.2	0.0	0.0	1.9	0.6
Pine branch						
distal half	71.0	43.6	28.5	30.2	19.1	23.3
proximal half	16.0	11.6	40.2	25.2	67.9	60.8
Pine cone	6.9	33.2	0.3	19.7	0.0	2.3
Pine trunk	4.6	7.7	31.0	24.3	11.1	11.0
Total no. observations	131	181	274	325	162	347

[a]This table is a further breakdown of the data presented in Table II.

bers of the two species alone, the behavior of both seemed similar to that of mixed flocks containing more species.

Since Pine Warblers were seldom seen away from mixed flocks during the fall and winter seasons, and since almost no mixed flocks were found in the study area that did not contain Brown-headed Nuthatches, I was unable to obtain adequate data on Pine Warblers under reciprocal conditions. However, in a mixed pine-deciduous forest 45 km away, where the nuthatches were rare, Pine Warblers spent proportionately more time on the distal parts of the limbs (Table II) than they did in the longleaf pine forest. Pine Warblers were not particularly common in the mixed forest, and my data are consequently limited. However, the difference in foraging in the two areas is highly significant ($P < .001$). The few observations of Pine Warblers that I obtained away from mixed flocks in the longleaf pines fit the mixed forest distribution very closely.

Foraging during an abundant seed crop

Seed production of longleaf pines is sporadic; an abundant crop is produced every 5 to 7 yr and a complete failure occurs as frequently. Smaller crops are produced in other years (Wahlenberg 1946). The cones grow on the distal parts of the limbs and are more abundant in the top 5 m of the trees than at lower heights. Usually birds must venture into the foliage to reach the cones, but occasionally they can be reached from large branches. Though cones with exposed seeds may be found most of the fall and winter except during the seasons in which the cone crop fails completely, an abundance of available seeds was found only from late November 1964, to mid-January 1965. During this period birds sometimes foraged heavily upon as many as 8 to 10 cones in a single tree. A single tree might contain 25 to 30 or more cones, though they usually did not all ripen simultaneously.

During an abundant cone crop, the foraging of Brown-headed Nuthatches changed from the condition existing earlier in the season and in years of poor cone crops (Table III). Pine seeds were then utilized heavily, with the result that the foraging of the species in and out of mixed flocks became more similar than it was before this time. The change in foraging distribution of pure flocks at this time was highly significant ($P < .01$). Brown-headed Nuthatches fed more heavily upon these seeds than did Pine Warblers (Table IV), and although a slight change was noted in the Pine Warbler foraging distribution (Table III), it was not statistically significant.

All species that procured seeds from cones did so in a rather similar manner. They either perched upon or hung from the cones, or stretched to reach the cone from adjacent foliage or limbs. Longleaf pine seeds are very loosely attached to the cones when they ripen. Since the spaces between cone scales of this species are so large, even such short-billed birds as Carolina Chickadees and Tufted Titmice could readily reach between these scales and pull out the seeds.

Brown-headed Nuthatches cracked seeds by sliding them under thick bark scales and hammering upon them. Consequently these birds had to visit regularly the part of the habitat frequented by the Pine Warblers in order to process this food. Attempts to crack seeds on the outer parts of limbs met with little success. Thus, though the overlap of foraging distribution between the two species in mixed flocks did not change significantly with the availability of pine seeds, the overlap of spatial distribution increased sharply, and the possibility of contact between the two species became greater than before. For present purposes, spatial distribution will be considered the sum of

TABLE IV. Frequency of visits to longleaf pine cones in mixed flocks

Species	Before heavy crop			During heavy crop		
	Total foraging	Trips to cones	Percentage of total foraging	Total foraging	Trips to cones	Percentage of total foraging
Brown-headed Nuthatch	131	9	6.9	181	60	33.1
Pine Warbler	162	0	0.0	347	9	2.3

foraging observations plus seed cracking observations. Each successful foraging trip to a pine cone involved a subsequent trip to either a trunk or the proximal part of a limb. Though other activities such as preening and aggressive behavior were observed, the majority of time was spent in foraging or cracking seeds.

If the figures of Table IV are added to those of trunks and proximal parts of limbs in Table III in approximately equal amounts for the Brown-headed Nuthatches, an approximation of their spatial distribution will be obtained. Since Pine Warblers only cracked seeds on the proximal parts of limbs, the pertinent observations in Table IV should be added to that single category in Table III for this species.

Pine Warblers cracked seeds like Brown-headed Nuthatches, though with considerably less efficiency. One individual was observed hammering unsuccessfully upon a single seed for more than 5 min. Many of the seeds eaten by Pine Warblers were sprouted ones that probably had been picked up off the ground.

The increased spatial overlap was accompanied by a significant heightening of hostile behavior between the two species (Table V; $P < .01$ for Brown-headed Nuthatch, $P < .05$ for Pine Warbler). The Pine Warbler was the more aggressive of the two species, and it attacked Brown-headed Nuthatches on the wing from some distance. When they met at close range, the nuthatches almost always prevailed.

TABLE V. Frequency of attacks on opposite species in mixed flocks in longleaf pines

Species	Before heavy crop		During heavy crop	
	Fights per 100 foraging observations	Total foraging	Fights per 100 foraging observations	Total foraging
Brown-headed Nuthatch	0.8	131	3.3	181
Pine Warbler	0.6	162	2.0	347

TABLE VI. Observations of Brown-headed Nuthatches in and away from mixed flocks in longleaf pines during 1964-65[a]

Date	Flocks with nuthatches	Groups of nuthatches away from flock
Nov. 6	3	4
11	3	3
29	4	2
Dec. 7	3	9
16	3	10
Jan. 4	3	7
11	3	2
17	3	3
23	2	1
30	5	6

[a]The height of the seed season occurred in December.

Attachment of Brown-headed Nuthatches to mixed flocks

At the height of the seed season the strength of attachment of Brown-headed Nuthatches to mixed flocks reached a minimal point, revealed both by the number of times that individuals were seen away from mixed flocks (Table VI), and by their increased tendency to become separated from flocks while they were under observation. This factor probably prevented an even greater increase of hostilities.

Before the season of seed abundance, Brown-headed Nuthatches readily kept up with flock movement. However, at the height of seed abundance they often lagged behind and not infrequently became separated from flocks, as a result of their strong tendency to remain feeding for extended periods of time in a small area, often even on a single cone or cone cluster. Nevertheless, almost all flocks still contained Brown-headed Nuthatches. There was a tendency for the groups of Brown-headed Nuthatches away from mixed flocks at the height of the season to be made up of one to two birds, in contrast to the usual four to eight birds found in pure and in mixed flocks. As January progressed, the seed crop began to fail, and the foraging behavior of some groups of nuthatches began to return to that exhibited before the height of the seed season.

Stomach contents

Twenty-one Brown-headed Nuthatches and 15 Pine Warblers were collected at regular intervals during the fall and winter of the 1964-65 season in a forest similar to the study area and about 3 km away. Since it was impossible to tell whether these birds had been alone or with the other species for a considerable period of time before collecting, the information obtained was of limited value in this study. However, Brown-headed Nuthatches and Pine Warblers obviously shared most items of animal food, the most common including sawfly larvae (Diprionidae), small Coleoptera (mostly Scolytidae), Coccidae, and small spiders. During the heavy seed crop, both species fed on the seeds, though these items were much more frequent in the nuthatch stomachs than in those of Pine Warblers, some being packed with seeds to the exclusion of all other food at the height of the season. In no Pine Warbler stomach examined did the seeds exceed 50% of the total food contents, and most individuals contained 0 to 30% seeds at this time. Soft, sprouted seeds, probably picked off the ground, formed a principal part of the seed contents in stomachs of this species during and following intermittent periods sufficiently warm to induce this change.

Predation

During 2 years of intensive field work in the study area I did not note any indication of predation upon either Brown-headed Nuthatches or Pine Warblers. Sparrow Hawks (*Falco sparverius*) would occasionally fly over the pines, eliciting alarm reactions, but never was one observed to attack. No other potential predators were seen in the area. Norris (1958) did not note any predation during his study on Brown-headed Nuthatches. His data suggest, however, that most mortality occurred during the nesting season.

Population density

One might expect that the great increase of readily available food during the heavy seed crop would result in net immigration of the species that fed most heavily upon them. However, no evidence of a change in density could be detected in Brown-headed Nuthatches, the species that fed most heavily upon the seeds. On a 50-acre (20.2 ha) sample census plot, a total of 7 to 10 birds was seen repeatedly before the seed crop matured and during the various phases of its maturation. The winter density of 17.2 birds per 100 acres (40.5 ha) is well within the range of densities compiled for this species by Norris (1958). He concluded that this species is quite sedentary, and these data also suggest this.

No increase of Pine Warblers could be attributed to the crop. Although the winter density of 9.3 birds per 100 acres was only slightly more than half the density of the Brown-headed Nuthatch population in the same area, the tendency of any Pine Warbler to be a member of a mixed flock was much greater than it was for Brown-headed Nuthatches (Table I). Thus, nearly equal numbers of both species were found in mixed flocks. Occasional large numbers of this species (15 to 20 per flock) in the middle and latter part of January 1965, as the seed crop was waning, probably represented a change in the population, but in response to stimuli other than the seed crop. These birds contained enlarged gonads in several instances at this time.

Relationship with other species

Since much of their time is spent in mixed flocks, Brown-headed Nuthatches and Pine Warblers necessarily are in company with several additional species of birds. Some data (Tables VII, VIII) were gathered on the foraging behavior and hostile activities of these other species, which suggest the importance of their effects upon the foraging distribution of Brown-headed Nuthatches and Pine Warblers.

Table VII indicated a high frequency of foraging in the sparse oak understory by several species, even though this growth probably comprises less than 5% of the tree vegetation by volume. The pattern was repeated in the mixed pine-deciduous forest, where a foraging preference heavily in favor of deciduous growth also occurred (Table IX). However, it will be noted that the Pine Warbler was exclusively a pine tree forager in both instances. Thus this species and the Brown-headed Nuthatch were almost entirely dependent upon pines for food in this region, and this factor alone reduced potential competition appreciably.

Only two other species, White-breasted Nuthatches (*Sitta carolinensis*) and Brown Creepers, did over 90% of their foraging on longleaf pines (Table VII). Both species utilized the trunk heavily. The White-breasted Nuthatch was not a common species in the pinelands, being found in less than one-fourth of the flocks counted, and usually with a frequency of only one per flock. However, when it was present, a higher level of hostility existed between it and Brown-headed Nuthatches than between any other pair of species. Nevertheless, the total contact between these two species was small in comparison to the opportunity

TABLE VII. Percentage frequency of foraging positions in mixed flocks in longleaf pines

Foraging position	Downy Woodpecker	Carolina Chickadee	Tufted Titmouse	White-breasted Nuthatch	Brown Creeper	Golden-crowned Kinglet	Ruby-crowned Kinglet	Myrtle Warbler
Ground	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0
Deciduous	30.0	46.4	48.8	6.1	10.0	15.4	90.5	51.7
Pine branch								
distal half	30.0	16.3	11.2	3.0	0.0	84.6	9.5	28.2
proximal half	33.3	17.9	32.9	18.3	4.0	0.0	0.0	19.6
Pine cone	0.0	12.8	2.4	3.0	0.0	0.0	0.0	0.0
Pine trunk	6.7	1.0	4.7	69.6	86.0	0.0	0.0	0.5
Total no. observations	30	196	170	33	50	26	74	209

TABLE VIII. Number of interspecific attacks (per 100 foraging observations of Brown-headed Nuthatches and Pine Warblers) in longleaf pines[a]

Species	Brown-headed Nuthatch		Pine Warbler	
	On	By	On	By
Carolina Chickadee	0.0	1.3	0.4	0.4
Tufted Titmouse	0.0	0.0	0.6	0.2
White-breasted Nuthatch	1.9	1.0	0.0	0.0
Brown-headed Nuthatch	—	—	1.4	1.5
Pine Warbler	2.6	2.2	—	—
Total no. observations	312	312	509	509

[a]No hostile behavior was observed between Brown-headed Nuthatches or Pine Warblers and any other species in flocks.

TABLE IX. Percentage of foraging in deciduous vegetation by mixed flocks in pine-deciduous forest

Species	Per cent foraging in deciduous vegetation	Total no. observations
Downy Woodpecker	71.4	56
Carolina Chickadee	75.8	150
Tufted Titmouse	85.3	133
White-breasted Nuthatch	—	0
Brown-headed Nuthatch	—	0
Brown Creeper	68.1	47
Golden-crowned Kinglet	71.4	40
Ruby-crowned Kinglet	84.8	106
Myrtle Warbler	71.6	53
Pine Warbler	0.0	52

of meeting a Pine Warbler. No difference in Brown-headed Nuthatch foraging was noted between the flocks that contained White-breasted Nuthatches and the ones that did not.

With its highly specialized beak, the Brown Creeper is in a position to exploit food supplies not easily available to the other species in this heavily ridged bark. It also probably captured food available to both nuthatches and Pine Warblers on the trunk. Brown Creepers appeared actively to avoid close contact with other species.

Carolina Chickadees and Tufted Titmice showed a preference for deciduous growth, both species doing nearly 50% of their foraging in this scattered cover. Neither species occurred regularly on trunks and, even when on large branches, these birds seldom removed scales of bark in the manner of Brown-headed Nuthatches and Pine Warblers. The longer bills of both the nuthatch and warbler may enable them to forage more effectively in the large longleaf pine needle clusters than do Carolina Chickadees and Tufted Titmice. Foraging overlap between the two groups of species occurs primarily in the use of the surface of large and small limbs.

Pine Warblers occasionally made aggressive contact with chickadees and titmice in the process of foraging, but hostilities remained at a consistently low level. Hostile actions between chickadees and Brown-headed Nuthatches were only noted when the chickadees ventured to the pine cones for seeds.

No hostile contact was noted with any other species. The Myrtle Warbler (*Dendroica coronata*) was, however, a potential competitor. It hawked frequently for insects during favorable weather and was basically a gleaner when in the trees. Myrtle Warblers were only sporadically present and when found were often in numbers of 30 or more. When in such abundance, they demonstrated a strong tendency to spread out through the entire habitat (excluding trunks), and thus showed little tendency to work selectively in any particular part of the habitat. The Downy Woodpecker (and other woodpeckers) have access to food occurring deeper in the bark than where the Brown-headed Nuthatch and Pine Warbler can reach readily, but all these species probably shared food found near the surface. Both kinglets were almost exclusively foliage gleaners, and the Ruby-crowned Kinglet was largely confined to the sparse deciduous growth. Golden-crowned Kinglets were infrequent in this forest and not present each winter.

Discussion

A number of characteristics suggest that Brown-headed Nuthatches and Pine Warblers are important factors regulating each other's distribution in the habitat while in each other's presence: (1) the dissimilar foraging distributions of these two somewhat similarly foraging species when together, and the accompanying low level of hostility (considering their potentially aggressive nature); (2) the increase of hostile behavior between the two species that accompanied a change in spatial distribution prompted by an irregular food supply; and (3) the more similar foraging distribution of the two species when not in the presence of the other.

The demonstrated displacement in foraging when together suggests that Brown-headed Nuthatches and Pine Warblers share too many ecological similarities to search efficiently for food through a large part of the habitat when in each other's company. When foraging differently part of the time, they doubtless obtain a greater part of the available food in this rather poor foraging area than they would if both species were always together in a single part of the habitat. At times that Brown-headed Nuthatches are foraging independently of Pine Warblers, they probably manage to obtain some food on the large limbs and trunks that is not readily available to the Pine Warblers. Pine Warblers might similarly discover food not obtained by Brown-headed Nuthatches by foraging more frequently on the peripheral parts of trees in the occasional periods that they are away from Brown-headed Nuthatches, though their time away from that species is limited. The data indicate that this displacement decreases interspecific hostilities. Stomach contents of both species show that the variety of food items taken was rather similar. Thus it appears likely that the demonstrated spatial segregation is the result of competition for food between the two species. No suggestion was found that predators or parasites remove enough of these individuals to reduce competition significantly, as has been found in experimental studies by Utida (1953) on weevils and Park (1955) on flour beetles. The two species thus probably depress each other's population densities.

The observations indicate that, although some competition for food may be expected from most, if not all the other members of the flocks, nowhere is it potentially as keen and as constant as between these two species. No other spatial modifications similar to those of the Brown-headed Nuthatches in the presence and absence of Pine Warblers were noted in the relations of the other species to Brown-headed Nuthatches and Pine Warblers.

Brown-headed Nuthatches forage more frequently in the foliage than do other nuthatches found in the Pine Warbler's range, whereas Pine Warblers forage much more frequently on large limbs and trunks (often in a nuthatch-like manner) than do most other species in the flocks studied. A considerable convergence in foraging behavior exists between the two species, and results in a greater foraging overlap between them than between Pine Warblers and other more logical competitors, such as chickadees, titmice, and kinglets.

The seemingly paradoxical placement of Pine Warblers proximally and of Brown-headed Nuthatches distally when together may be largely the result of their respective hostile behaviors. Pine Warblers were extremely aggressive and generally performed winged attacks, which usually were successful against Brown-headed Nuthatches. Brown-headed Nuthatches, however, usually performed simple supplanting attacks, which consisted of replacing another bird at close range. Pine Warbler attacks against Brown-headed Nuthatches were quite successful in the open proximal parts of the branches, but were less effective in the heavily foliated distal parts. Not only was it more difficult for a bird to launch an aerial attack through this foliage; it was a simpler matter for the attacked individual to avoid this maneuver than if it were in the open. Thus the distribution observed may have been the result of incomplete dominance of each species over the other.

One might expect hostile behavior to increase at times of food shortage if foraging remained similar. Unfortunately not enough observations of hostilities were made during the season in which few cones were produced to determine whether such an increase occurred as food became scarcer. At times of such a shortage, Hartley (1953) and Gibb (1960) reported an increase in fighting for food among different species of titmice. Hostile behavior between the Brown-headed Nuthatches and Pine Warblers at times that seeds were not available was of low frequency in comparison to that occurring in the heavy seed season, however. The noticeable increase in hostile behavior during the heavy seed season apparently was the result of an increase in spatial overlap, in response to the abundant food source. Overlap was minimal outside of the seed season when the two species were in each other's company.

Hostile behavior when food was abundant would not effectively serve as the mechanism by which

the birds maintain the pressure for differentiation into discrete feeding areas, though this phenomenon may easily serve in such a manner when food supplies are low. If food were at a premium the energy expenditure in such an increase of hostile behavior might be extremely detrimental to the species concerned.

Though the birds studied did not occupy an extremely rigorous climate, occasional critical periods occurred. During many winters, periods of a few days are experienced in which the temperature does not rise above freezing. These spells completely prevent the movement of invertebrate prey and increase the energy demand of the individual. Less frequent snow or ice storms increase the difficulty of foraging; these often occur at times of minimum day length, as do cold spells. Although these conditions are not as extended or severe as in the north, neither are the individuals as well equipped to live under critical conditions (see Scholander 1955). With such a low variety and abundance of insects in longleaf pine forests, it appears likely that at times during the winter an additional premium for the most effective type of foraging possible would exist. Division of the habitat with a minimum of hostile actions rather than by wasting energy and time in frequent fighting would be of particular importance at such times, if there were no abundant seed crop. Under severe conditions one would then expect foraging between the two species to be more different than during more favorable weather. Though insufficient data were gathered properly to test this supposition, such results were obtained in mixed titmouse flocks by Hartley (1953) and Gibb (1954, 1960).

When an abundant food source appears, it provides such a convenient source of energy that no difficulty is experienced in procuring a sufficient amount to support an individual engaged in almost any activity. Then the spatial pattern became more similar in the Brown-headed Nuthatches and Pine Warblers, and hostile actions between them increased. However, the increase of activity resulting from additional hostilities at this time could be compensated for by the increased available food.

Where Brown-headed Nuthatches occur in species of pines that produce seeds more regularly than do longleaf pines and where more than one species of pine occurs, these seeds provide a more stable winter diet than they do in the longleaf pine forest. Burleigh (in litt) stated that in areas of mixed pines the nuthatches congregated upon the species that was in seed. For a highly sedentary species like the Brown-headed Nuthatch, possession of such an ability would not be of apparent use in the midst of extensive unbroken longleaf pine forests.

Although geographical and ecological species displacement has been reported and advanced as evidence of interspecific competition in several groups of animals, this evidence is less direct in nature than that arising from experiments conducted in the laboratory. In the field these species are geographically isolated from one another or they occupy different parts of the habitat. It is thus difficult actually to prove that interspecific competition is largely or partly responsible for the existing relationships, because of the other possible explanations that exist, even though circumstantial evidence for competition may be strong. Hutchinson (1957) pointed out that though animal communities appear qualitatively to be constructed as if competition were regulating their structures, difficulties and unexplored possibilities nearly always exist even in the best studied cases.

Errington (1956) discussed the difficulties of conclusively eliminating environmental factors in field studies of interspecific competition. The situation described in this paper contains fewer possibilities of an alternate explanation than most such field studies, since Brown-headed Nuthatches and Pine Warblers were studied foraging in a homogeneous habitat at the same time. The small variety of food items available in longleaf pines limit the number of possible variables. Although additional species of birds usually were present with these two species when they were together, it appears improbable that they exerted more than a slightly modifying effect.

Though the Brown-headed Nuthatch-Pine Warbler problem involves a displacement in foraging between the two species when together, this separation is of short duration, and the species may be studied in the same area with and without each other. The division of the habitat between the two species is also only partial when they occur in common flocks, so that ample opportunity exists to observe their behavioral interactions. This study thus afforded an unusual opportunity to study species both with and away from their presumed competitors, a necessary step to be completely sure that the behavior observed was caused by coassociation of the species (Park 1954).

A case of mutual avoidance was noted between two butterflies of the genus *Danaus* (Brower 1962), where the selection of the species of milkweed used by an individual for oviposition was to a large part dependent upon the presence or absence of the other species of butterfly. However,

Brower felt that the monarch (*D. plexippus*) was a fugitive species (Hutchinson 1951), because of the nature of the displacements and because of the migratory tendency of most of the monarch population, while the queens (*D. gilippus*) are sedentary. No information suggested that either the Brown-headed Nuthatch or the Pine Warbler could be considered fugitive species. The apparent sedentary nature of both species, the relative permanency of their respective densities, the wide range of sympatry, and the condition of incomplete reciprocal dominance all suggest a balanced relationship between them.

Snow (1949) found that when Great Tits (*Parus major*) were present in a mixed flock, Crested (*P. cristatus*) and Willow (*P. atricapillus*) Tits foraged at a low level, but that when Great Tits were absent, the other two species foraged at all heights. Hartley (1953) also noted that when Marsh Tits (*P. palustris*) were present they prevented Blue Tits (*P. caeruleus*) from foraging at low heights. An interspecific flock hierarchy exists in such mixed flocks, which is correlated with size, the larger species usually being dominant (Colquhoun 1942; Morley 1953). In the closely related tits studied by Snow and Hartley, a clear example of dominance apparently existed, in contrast to the Brown-headed Nuthatch-Pine Warbler situation.

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