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Effects of food supplementation and predator simulation on nuthatches and parids within mixed-species flocks.—Although many ornithologists have studied mixed-species flocks, few have examined spatial positioning of birds within flocks. Flocks, here defined as three or more birds that move together as a group, vary from loose associations of individuals separated by tens of meters to tight clusters of birds only centimeters apart. Variations in spacing are interesting because they may either enhance or reduce the benefits that birds acquire by flocking. For example, birds that are farther apart may have more difficulty acquiring information about food or predators from each other but may have reduced costs due to fewer aggressive interactions. Thus, spacing within flocks may reflect a balance between attractive and repulsive forces between flock members (Emlen 1952). Distances between flock members are likely to change over time scales of minutes or hours as attractive and repulsive forces vary with changes in flock size and composition (Caraco and Bayham 1982, Pearson 1989), energy reserves of flock members, or environmental factors such as habitat structure, food availability, and predation pressure (Grzybowski 1983, Prescott 1987, Pearson 1991). In this paper I examine spacing among Brown-headed Nuthatches (*Sitta pusilla*), Carolina Chickadees (*Parus carolinensis*), and Tufted Titmice (*P. bicolor*) within heterospecific flocks. The basic goal was to determine whether distances between birds varied either as food availability varied or as apparent threat of predation

varied. Three hypotheses were tested by experimentally varying food availability and apparent predator abundance. These are: (1) Nuthatches and chickadees flock less closely when these species have less overlap in their food resources; (2) Nuthatches and parids flock less closely when food is easily obtained by both species; and (3) Nuthatches and parids flock more closely when there is a relatively high likelihood of encountering a predator.

Methods.—Brown-headed Nuthatches in the present study frequently foraged on cones and on the bark of loblolly pines (*Pinus taeda*) and shortleaf pines (*P. echinada*). They typically were encountered in pairs or tight conspecific flocks of up to seven nuthatches, which were usually part of heterospecific flocks that often included chickadees, titmice, and several species of woodpeckers, kinglets, and warblers (Yaukey, unpubl. data). Parids are thought to form the nuclei of these flocks (Morse 1967, 1970). Both parids foraged in deciduous and coniferous trees at various heights; chickadees used pine cones, but not as often as nuthatches (Yaukey, pers. obser.).

Two study sites 2.7 km apart were selected in the State Botanical Garden of Georgia, and in Whitehall Forest of the Univ. of Georgia, (33°56′N, 83°24′W), near Athens, Georgia. Although these sites were not randomly selected, they were typical of habitat conditions common in the piedmont region of northern Georgia. Sites were chosen because they contained nuthatches and parids, were dominated by pines >9 m tall, and contained no human habitations or bird feeders. Both sites were extensively wooded and dominated by pines but contained roads or powerlines; the Botanical Garden had two clearings, one of which held several greenhouses. The number of different nuthatches using each site was not precisely calculated but varied daily (or hourly) from approximately two to five at the Botanical Garden and from six to twelve at Whitehall. I collected data from November to February during two winters (1989–1990, 1990–1991) at all hours of the day.

To measure distances between nuthatches and parids, I followed a flock of nuthatches (or a lone individual) and at 10-min intervals I paced the distance from the most easily visible nuthatch in the flock to the first chickadee detected. In most cases, this appeared to be the chickadee closest to the nuthatch, and highly active or vocal chickadees were probably represented more than inconspicuous ones. The birds were typically >5 m above the ground and appeared not to be alarmed by the observer. If no parids were present within 50 m, the nuthatch was recorded as not being flocked with chickadees. The same procedure was also followed to measure the distance to the first titmouse detected. In the first winter, a nuthatch was recorded only to be "not-flocked" with parids after 10 min elapsed without a parid being detected. To examine whether observations taken 10 min apart were autocorrelated, Durbin-Watson statistics (SAS Institute 1989) were calculated for these distance data from regressions (Yaukey 1991); with a few exceptions (indicated below), d values were all ≥ 1.78, indicating that there was little or no temporal autocorrelation in distance observations. I also regressed interspecific distance measurements of these species onto air temperature, wind speed, solar radiation, time of day, and date, and found few significant relationships (Yaukey 1991). Consequently, weather and time variables are omitted from the present analyses.

During the winter of 1989–1990, an experimental treatment was conducted at each site in November, followed by a non-treatment period in December, and another treatment in January. In 1990–1991, the non-treatment period at each site extended into January, and the second treatment into early February. At least 15 days elapsed between treatments and subsequent non-treatment periods. The distances between nuthatches and each parid species were compared between each treatment period and the non-treatment period at the same site in the same winter using one-tailed *t*-tests. Because data may have violated assumptions of *t*-tests in some cases, the proportion of nuthatches that flocked with either chickadees or titmice (within 50 m) was also compared using nonparametric chi-square tests with Yate's

correction (Zar 1984). The experimental design enabled treatments and non-treatments to be compared at the same site, but did not allow them to be conducted simultaneously. Although it is also possible that birds became habituated to treatments or to the observer, or that effects of treatments lingered into nontreatment periods, such effects were not evident.

The hypothesis that nuthatches and chickadees flock less closely when these species used increasingly different food resources was tested by attracting chickadees to feeders that nuthatches could not use. Sunflower seed was provided in plastic 3.7-L milk jugs bent so that they could be entered only on the wing from directly below. Jugs were hung separately in trees, at heights that ranged from about 1–9 m, at six feeding stations spread evenly across the core area of the site. During this experiment chickadees used these feeders heavily, while nuthatches did not use them, thus decreasing the overlap of their diets. If either species had been following the other closely to learn of food resources that the other species located, it should have followed less closely during the experimental treatment. Therefore, distances between chickadees and nuthatches were predicted to increase when food was provided. This treatment was conducted only at the Botanical Garden in November 1989.

The hypothesis that nuthatches flock less closely with either chickadees or titmice when food was easily obtained by both nuthatches and parids was tested by providing food for all species following a protocol similar to that used by Berner and Grubb (1985) and Grubb (1987). Sunflower seed was provided in modified plastic 3.7-L milk jugs that all species could enter through holes in their sides. Feeders were hung in groups of three, approximately 5–9 m high in trees, in three places evenly distributed in the core area of the site. Distance measurements were not collected if both the nuthatch and parid were within 10 m of a feeder that both species were using. If nuthatches had been following either parid (or vice versa) closely to acquire information about food resources by watching the other species, they should have moved apart when they were provided with food, because they did not need to rely on the other species as much. The distance between them was predicted to increase when they received supplementary food. This treatment was conducted only at Whitehall in January 1990.

The hypothesis that nuthatches would flock more closely with parids when they sensed a high likelihood of encountering a predator was tested by playing taped Sharp-shinned Hawk (*Accipiter striatus*) calls (Cornell Laboratory of Ornithology 1971). This technique was meant to simulate the presence of a hawk in the immediate vicinity rather than an actual attack. During periods of data collection, a tape of continuous hawk calls 48 sec in length was played at arbitrarily selected times spaced at irregular intervals but averaging approximately once per hour and beginning before the first observation. At Whitehall, I also played the tape whenever I switched to observing a new flock of nuthatches. The tape was played on a portable cassette recorder at 10–40 m distance from the closest nuthatch. During November 1989, the cassette recorder was hand held; subsequently, it was hung from a tree limb within 2.5 m of the ground, and I usually stood at least 10 m from it. If nuthatches and parids flocked more closely when they were more likely to encounter a predator, distances between them should have decreased when the presence of a predator was simulated. This treatment was conducted six times: at Whitehall in November 1989, at the Botanical Garden in January 1990, and at both sites in November 1990 and Jan.–Feb. 1991.

Results.—Addition of feeding stations that could be used only by chickadees had no influence on the distances between nuthatches and chickadees within flocks or on the proportion of nuthatches that flocked with chickadees (Table 1). Neither did providing food for all species affect the distances between nuthatches and chickadees within flocks or the proportion of nuthatches that flocked with chickadees (Table 1).

Addition of food that could be used only by chickadees did not affect distances between

TABLE 1

DISTANCES BETWEEN NUTHATCHES AND PARIDS WITHIN FLOCKS, AND PERCENTAGE OF NUTHATCHES THAT FLOCKED WITH PARIDS, WHEN FOOD WAS PROVIDED (FOOD), COMPARED TO NON-TREATMENT (N-T) PERIODS

		N		Mean distance (m)				Percent in flock			
Site[a]	Year	Food	N-T	Food	N-T	t	P[b]	Food	N-T	χ^2	P
					Nuthatch-chickadee interactions						
BG	Nov 89	91[c]	90	14.0	14.3	0.13	NS	96.7	93.3	0.49	NS
WF	Jan 90	80[d]	102	20.2	19.2	−0.49	NS	81.3	79.4	0.01	NS
					Nuthatch-titmouse interactions						
BG	Nov 89	85[c]	83	20.3	19.2	−0.39	NS	63.5	39.8	8.58	**
WF	Jan 90	79[d]	97	24.6	18.8	−2.25	*	54.4	52.6	0.01	NS

[a] BG: Botanical Garden, WF: Whitehall Forest.
[b] *: $P < 0.02$; **: $P < 0.01$.
[c] Treatment: food provided for chickadees.
[d] Treatment: food provided for all species.

flocked nuthatches and titmice. However, a higher proportion of the nuthatches were found flocked with titmice when food was provided for chickadees (Table 1). Flocked nuthatches and titmice were significantly farther apart when food was provided for all species as predicted (Table 1). The proportion of nuthatches that were flocked with titmice did not change when all species were provided with food.

Nuthatches were significantly closer to chickadees within flocks when predators were simulated at the Botanical Garden in January 1990 and at Whitehall in November 1990 than in their respective non-treatment periods (Table 2). However, the significance of the Botanical Garden experiment may have been overestimated, as the data showed evidence of serial autocorrelation. Three of the remaining four replicates showed some (nonsignificant) increase in the number of nuthatches observed within 5 m of a chickadee when hawk calls were played. Despite these patterns, *fewer* nuthatches were found flocked with chickadees at Whitehall in November 1990 and January 1991 and at the Botanical Garden in November 1990 than during their December non-treatment periods (two-tailed χ^2 tests, Table 2). This pattern was evident (but nonsignificant) in two of the other three predator simulation replicates. Thus, predator simulations appeared to stimulate two different responses from the birds: in some cases, nuthatches and chickadees became more tightly grouped and in others they ceased to flock together. Often, both responses were evident during the same treatment; however, neither response was particularly strong or consistent.

The proximity of nuthatches to titmice was not influenced as strongly by playing hawk calls as was the proximity of nuthatches to chickadees (Table 2). No simulations produced significant decreases in distances between birds within flocks. However, four replicates showed significant decreases in the proportion of nuthatches that were flocked with titmice. The significant results in two-tailed tests occurred at both the Botanical Garden and Whitehall during both November 1990 and January 1991 (Table 2). This pattern was also present but nonsignificant in the two other predator simulations. Thus, nuthatches and titmice appeared to move apart on several occasions, when hawk calls were played.

Discussion.—The inability of providing food, either for chickadees or for all species, to affect the distances between nuthatches and chickadees in this study suggests that inter-bird

TABLE 2

DISTANCES BETWEEN NUTHATCHES AND PARIDS WITHIN FLOCKS, AND PERCENTAGE OF NUTHATCHES THAT FLOCKED WITH PARIDS, WHEN HAWK CALLS WERE PLAYED (HAWK), COMPARED TO NON-TREATMENT PERIODS (N-T)

		N		Mean distance (m)				Percent in flock			
Site[a]	Year	Hawk	N-T	Hawk	N-T	t	P[b]	Hawk	N-T	χ^2	P
Nuthatch-chickadee interactions											
WF	Nov 89	89	102	16.4	19.2	1.39	NS	83.1	79.4	0.22	NS
BG	Jan 90	82	90	10.8	14.3	2.04[c]	*	84.1	93.3	2.81	NS
WF	Nov 90	73	91	10.4	16.2	2.71	***	64.4	86.8	10.22	***
WF	Jan 91	61	91	21.6	16.2	−1.60	NS	26.2	86.8	54.64	****
BG	Nov 90	75	77	11.3	12.7	0.69	NS	68.0	85.7	5.76	**
BG	Jan 91	59	77	12.1	12.7	0.30	NS	81.4	85.7	0.20	NS
Nuthatch-titmouse interactions											
WF	Nov 89	81	97	19.8	18.8	−0.37	NS	46.9	52.6	0.36	NS
BG	Jan 90	74	83	16.9	19.2	0.71	NS	36.5	39.8	0.07	NS
WF	Nov 90	66	75	20.6	16.3	−1.59	NS	39.4	76.0	17.95	****
WF	Jan 91	56	75	27.5	16.3	−2.47[c]	NS	23.2	76.0	33.81	****
BG	Nov 90	80	67	16.0	12.0	−0.56	NS	3.8	40.3	27.78	****
BG	Jan 91	56	67	10.2	12.0	0.41	NS	16.1	40.3	7.52	***

[a] BG: Botanical Garden, WF: Whitehall Forest.
[b] *: $P < 0.05$; **: $P < 0.02$, ***: $P < 0.01$, ****: $P < 0.001$, NS: nonsignificant.
[c] t calculated assuming unequal variances; all other t's assume equal variances.

distances were not determined by birds attempting to watch each other foraging. Although other food-supplementation studies have indicated that mixed flock participants gain some foraging benefit by flocking (Berner and Grubb 1985, Grubb 1987, Szekely et. al. 1989), these studies did not determine that the species involved watched each other to locate food. Although nuthatches and titmice did move apart when food was provided, this result should be treated with caution until it is replicated and the mechanisms are identified.

When nuthatches and chickadees were exposed to hawk calls in this study, they appeared to draw close together in some cases but to cease flocking together in others. The latter trend was also observed between nuthatches and titmice. The appearance of both flock tightening and departure from the flock in different cases raises the possibility that each action may be preferable under particular circumstances but that remaining loosely flocked might be less desirable. Although flock tightening could occur because birds converge on a single area of cover when confronted with a predator, such converging movements were not detected in the field. Most of the mechanisms that have been hypothesized to reduce the risk of predation in flocks probably are maximally effective in tight group situations. For instance, animals should group tightly to reduce risk of being singled out as prey (Hamilton 1971). Although vocal alarm responses are audible at a distance, birds that give alarms may not detect a predator until it is already upon other flock members, if those members are tens of meters away. On the other hand, flocks themselves may attract predators because they are more noisy and visible than individual birds. It is possible that the maximum risk of predation actually occurs for birds that are loosely attached to a flock and may encounter a predator attracted to the flock but derive minimal benefit from other flock

members in avoiding capture. Thus, birds that perceive a risk of predation might either leave the flock or draw close to other members but avoid being *loosely* associated with the flock.

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