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Functional Roles in Mixed-Species Foraging Flocks: A Field Manipulation

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Mixed-species foraging flocks occur in a variety of habitats (Winterbottom 1949, Moynihan 1962, McClure 1967, Morse 1970, Greig-Smith 1978, Powell 1985, Eguchi et al. 1993), and participants in such flocks are thought to acquire foraging and predator-avoidance advantages (McClure 1967, Morse 1977, Barnard and Thompson 1985). Descriptions of mixed-species flocks often include attempts to categorize participating species according to their presumed functional roles in the flocks. Some species, referred to as nuclear or core species, appear to facilitate flock formation and to initiate flock movements. Other species, known as satellite or attendant species, seem to behave as flock followers (Winterbottom 1943, Moynihan 1962, McClure 1967, Morse 1970, Austin and Smith 1972, Buskirk 1976, Powell 1985, Hutto 1994).

Such functional roles have been applied to members of mixed-species flocks that form during the winter within the assemblage of bark-foraging birds in eastern North America (Morse 1970). Developing during early autumn, these flocks typically consist of two parids, Tufted Titmouse (*Baeolophus bicolor*) and either Carolina (*Poecile carolinensis*) or Black-capped (*P. atricapillus*) chickadee, and several additional species, including Downy Woodpecker (*Picoides pubescens*) and White-breasted Nuthatch (*Sitta carolinensis*). Within these flocks, the parids have been classified as nuclear species, whereas the woodpeckers and nuthatches have been categorized as satellite species (Morse 1970, Sullivan 1984a).

Although observational evidence suggests that nuclear species facilitate flock cohesion (Moynihan 1962, Morse 1970, Powell 1985), this hypothesis has received little experimental support (but see Monk-konen et al. 1996). We predicted that if parids maintain flock cohesion, then woodpeckers and nuthatches (i.e. satellite species) would occur together less often within isolated woodlots from which titmice and chickadees had been removed than in control woodlots in which these nuclear species were present. By removing parids from woodlots, we manipulated flock size and flock composition. Therefore, our results could be interpreted as being attributable to either variable. Although we would have preferred to hold group size constant in treatment and control

woodlots, intraspecific aggression of White-breasted Nuthatches and Downy Woodpeckers prohibited us from adding extra satellite individuals to woodlots from which we had removed parids.

Methods.—We conducted the experiment during the winters of 1995–1996 and 1996–1997 in woodlots within the agricultural landscape of Union and Delaware counties, Ohio. These topographically flat deciduous forest fragments consisted primarily of oaks (*Quercus* spp.), ashes (*Fraxinus* spp.), shagbark hickory (*Carya ovata*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*). Each woodlot was completely surrounded by cultivated fields, lacked any connection to other woodlands, and was so small that it contained only one mixed-species flock. During the study period, such flocks were never observed to cross open ground into neighboring woodlots. In addition to the species mentioned above, the study woodlots usually contained one or two Red-bellied Woodpeckers (*Melanerpes carolinus*) and occasionally a Hairy Woodpecker (*Picoides villosus*) or Brown Creeper (*Certhia americana*).

Sixteen woodlots were used in the experiment. Before each field season, four of the eight woodlots to be used in that year were randomly assigned to the control group and four to the parid-removal group. Control woodlots averaged $5.3 \pm \text{SD of } 2.2$ ha in size, and removal woodlots averaged 5.5 ± 2.1 ha. Each woodlot was used only once.

From mid-December to mid-January each year, we trapped and mist netted birds attracted to feeders and wire-mesh suet cages. All Downy Woodpeckers and White-breasted Nuthatches were fitted with USFWS bands and uniquely colored plastic leg streamers for individual identification. Chickadees and titmice in control woodlots were similarly marked, but those in treatment woodlots were removed and released approximately 50 km away in suburban Columbus, Ohio.

Observations of flocking behavior took place during two-hour visits to woodlots conducted between 0800 and 1600. To balance sampling across time of day and season, we alternated visits to treatment and control sites. Each woodlot was visited 10 times, or until new parids began arriving in the treatment woodlots in late February during the juvenile dispersal period (T. C. Grubb pers. obs.). During each visit, we assigned the location of individually marked birds to one of the 25×25 -m blocks that formed a grid that covered the entire area of the woodlot.

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TABLE 1. Number of individual nuclear (i.e. titmice and chickadees) and satellite species present per woodlot initially (i.e. before removal) and on average per visit over the course of the observation period in eight control (i.e. parids not removed) and eight treatment (i.e. parids removed) woodlots. Values are $\bar{x} \pm \text{SE}$.

Species	Observation period	Control	Treatment
Nuclear species			
Parids	Initial	6.9 \pm 1.1	6.5 \pm 0.5
	Average per visit	6.1 \pm 1.1	0.4 \pm 0.1
Satellite species			
Downy Woodpecker	Initial	3.4 \pm 0.4	2.6 \pm 0.3
	Average per visit	3.4 \pm 0.4	2.6 \pm 0.3
White-breasted Nuthatch	Initial	1.9 \pm 0.1	1.6 \pm 0.5
	Average per visit	1.9 \pm 0.1	1.5 \pm 0.5

Upon entering a woodlot, we usually located birds by sound. To minimize chances that our presence in woodlots would cause the birds to move before their positions could be recorded, we identified the location of each bird as quickly as possible instead of using predetermined transects. The same entry point was used for each visit, and all color-marked birds consistently were located within two hours.

Pravosudov and Grubb (1999) found that the benefits of flocking begin accruing with a group size of two. Therefore, we defined a satellite bird association as an instance in which at least one Downy Woodpecker and at least one White-breasted Nuthatch were recorded within the same or adjacent 25 \times 25-m block. Because we conducted multiple surveys in each woodlot, we based our analyses on the proportion of visits to each treatment or each control woodlot during which we observed a satellite association. Species comprising mixed-species flocks are nonrandomly distributed in space (Monkkonen et al. 1996). Furthermore, bark-foraging birds may be nonrandomly distributed in woodlots owing to such factors as differential exposure to wind and solar radiation (Grubb 1975). Consequently, we confined our analyses to differences in satellite bird associations between control and treatment groups.

We used analysis of covariance (ANCOVA) to test for a difference between the mean proportion of visits (arcsine-transformed) to treatment and control woodlots during which at least one satellite association was observed. To control for different numbers of satellite individuals among woodlots (Table 1), we included the number of satellite individuals per ha in each woodlot as a covariate in our ANCOVA model. The woodlot served as our unit of statistical independence.

Results.—Except for two titmice during the first winter and two titmice and one chickadee during the second winter, all parids were removed from the eight experimental woodlots during the initial capture period (Table 1). The average number of parids removed per treatment woodlot was 5.6. During the observation period, 73 and 74 visits were made to treatment ($\bar{x} = 9.1 \pm 0.9$ visits) and control ($\bar{x} = 9.3 \pm 0.9$ visits) woodlots, respectively.

The proportion of woodlot visits during which at least one White-breasted Nuthatch and one Downy Woodpecker were observed in association was significantly higher in control than in treatment woodlots (control, $\bar{x} = 0.81 \pm 0.18$; treatment, $\bar{x} = 0.44 \pm 0.16$; $F = 6.27$, $df = 1$ and 13 , $P = 0.026$). During a mean of 82.4 \pm SE of 6.5% of the visits, at least one woodpecker and one nuthatch were in the same block as the majority of the parid group, or in blocks adjacent to the parid group.

Discussion.—Downy Woodpeckers and White-breasted Nuthatches associated with each other more often in control than in the treatment woodlots from which parids were removed. In addition, both species were found in close proximity to parids during most of our visits to control woodlots. These results suggest that the presence of parids enhances association between the satellite species, and they support the hypothesis that parids facilitate flock cohesion.

An alternative explanation for our data, however, is that reduced flock size alone produced the reduction in association between nuthatches and woodpeckers. It is possible that a critical group size needs to be reached before flocking behavior is stimulated between these species. Because the benefits of flocking begin to accumulate with just two individuals (Pravosudov and Grubb 1999), satellite species seeking benefits specific to group size without regard to group composition should have been just as likely to form groups with each other in treatment woodlots as in control woodlots. The enhanced stimulus provided by increased group size alone, however, may promote flock participation by woodpeckers and nuthatches.

The chickadees and titmice of North American mixed-species flocks have several attributes in common with other nuclear species (Moynihan 1962, Hutto 1994). These parids (1) lead heterospecifics more often than they follow (Morse 1970), (2) consistently associate with conspecifics (Hogstad 1989) as well as with heterospecifics (Morse 1970), and (3) give more frequent and conspicuous alarm calls than do woodpeckers or nuthatches (Sullivan 1985). Parids with comparable properties are thought to behave as nuclear species in

other mixed-species flocks (Greig-Smith 1978, Szekely et al. 1989, Monkkonen et al. 1996).

Monkkonen et al. (1996) found that heterospecifics were attracted differentially to playbacks of Willow Tit (*Parus montanus*) calls relative to control calls. Similarly, Downy Woodpeckers and White-breasted Nuthatches may be attracted to Tufted Titmouse and Carolina Chickadee vocalizations. This possibility may explain how parids facilitate flock cohesion.

We do not claim, however, that parids actively recruit woodpeckers and nuthatches to flocks. It is possible that being followed by other species is a selectively neutral by-product of the communication system of parids that is exploited by woodpeckers and nuthatches. In a playback experiment, Sullivan (1984b) found that woodpeckers responded to playbacks of parid alarm calls by freezing and then increasing their rate of head cocking. After an alarm reaction, they resumed their foraging activity more quickly when the alarm-call playback was followed by playback of parid contact calls (Sullivan 1984b). Sullivan's (1984b) experiment showed that Downy Woodpeckers reduced their vigilance rates in response to the information contained in parid vocalizations. This behavior also may be exhibited by White-breasted Nuthatches, and exploitation of vocal communication may be a primary benefit gained by both satellite species when they flock with titmice and chickadees.

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