



Birds of Many Feathers: The  
Formation and Structure of Mixed-  
Species Flocks of Forest Birds

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Considering the differences in the social and ecological requirements of the different participants, the cohesive movement of animal groups is an amazing phenomenon. Associations composed of many species, each with its own intraspecific social organization and species-specific requirements, seem even more improbable. Yet mixed-species fish schools (Ehrlich and Ehrlich 1973; Alevizon 1976), ungulate herds (Fitzgibbon 1990), primate troops (Gartland and Struhsaker 1972; Terborgh 1983; Peres 1992a; Cords, chap. 4, this volume), and bird flocks are commonplace.

Nowhere else in the animal kingdom is the phenomenon of mixed-species associations more widespread than it is in birds. Mixed-species associations of birds are particularly well developed in forests, occurring from the most diverse tropical forest to the species-poor taiga. During the nonbreeding season in particular, a majority of bird species participate in mixed-species flocks. Mixed-species forest flocks contrast with flocks found in open habitats (blackbirds, shorebirds, finches, etc.) in their smaller and more consistent sizes, more regular membership, the presence of a consistent flock home range, and participation by a small number of individu-

als of each species (Terborgh 1990). Because of these attributes, forest flocks make a logical focus for a chapter on the regulation of group formation and movement.

I approach this topic as a researcher who published a small amount on mixed-species flocking a number of years ago; the phenomenon—which I encounter at all my study sites—still never fails to fascinate me. However, as exciting as it is to see a species-rich bird flock, it is surprising to note that, a spattering of good studies aside, the field of mixed-species flock studies has stagnated. The composition of many flock systems has been inventoried, the behavior and ecology of different species has been described for a few flock systems, and the costs and benefits accrued to individuals have been examined for a few focal species. However, the integration of these different levels of flock organization has rarely been achieved. Therefore, the goal of this chapter is in some small way to renew interest in flocking research by first reviewing our knowledge and assumptions about how mixed-species flocks work and then suggesting ways to build new integrated approaches to mixed flock behavior.

I begin by critiquing traditional approaches to defining species-specific roles in flock formation. I then discuss the rich literature on the potential costs and benefits of flock participation and how these relate to the proximate mechanisms of flock formation and movement. Finally, I sketch out a vision of future work on the mixed-species flock phenomenon that integrates considerations of proximate mechanisms of formation with those of ultimate causation.

### **An Encounter with a Mixed-Species Flock**

Mixed-species flocks are incredibly varied in their composition and structure. However, given that there is no “typical” mixed flock system, I will give the reader a more tangible feel for what it is like to encounter and follow mixed flocks by describing an encounter with an understory flock on Barro Colorado Island, Panama—the site where I have conducted most of my mixed-species flock work.

The first impression most people have when walking through a lowland tropical forest is how few birds there seem to be. However, as you continue through the forest, the drone of cicadas is occasionally interrupted by the soft contact notes and the rustling of foliage made by a flock of birds in the dense canopy. At first it seems that

only a few birds are darting between trees, but as you watch patiently, more and more slip silently ahead of you.

Although we usually notice bird flocks at their most conspicuous—moving rapidly through trees—antwren flocks spend much of the day slowly milling about areas of dense vine vegetation around old treefall gaps. At the core of the flock are three species of small insect-eating birds known as antwrens—so named because someone thought they looked like wrens and they are related to birds that follow army ants. In fact, they are ecological equivalents of temperate zone warblers. Checker-throated antwrens (*Myrmotherula fulviventris*) usually occur in pairs and quietly chip as they spend their lives probing into dead, curled leaves that hang in the understory vegetation. In family groups, white-flanked antwrens (*Myrmotherula axillaris*) move rapidly through the low- to mid-forest strata, giving an oddly musical “whit” note while acrobatically gleaning arthropods from live foliage. Dot-winged antwren (*Microrhopias quixensis*) pairs or families forage through the densest vegetation, keeping up a constant patter of loud contact notes. For hours, the pairs and family groups of the three antwren species and a few other birds—perhaps a hulking slaty antshrike (*Thamnophilus punctatus*) or a diminutive olive flycatcher, the southern bentbill (*Onocostoma olivaceum*)—perch quietly at the edge of a black hole of tropical vegetation.

Then, seemingly inexplicably, the antwrens increase their chipping and pewing and begin to move rapidly toward the sound of a neighboring flock. During the rapid advance to the territorial interaction, more species join the flock—a tiny, ochraceous ruddy-tailed flycatcher (*Terenotriccus erythrurus*), a green and yellow black-throated trogon (*Trogon rufus*) in the canopy, perhaps a few spotted antbirds (*Hylophylax naivoides*) near the forest floor. Occasionally you catch a glimpse of a robin-sized woodcreeper as it flies from trunk to trunk, disappearing around the back of a large tree. Struggling to keep up, you find the antwrens in an intense interaction with another antwren flock. Two checker-throated antwren males are perched side by side chipping, bodies waving back and forth, with throat feathers expanded so that the checkering looks more like a large black patch. Occasionally the two chase each other while producing loud “keek” notes. Dot-winged antwrens puff up and fan their wings and tails while singing (sweet notes ending in a musical trill), and chase through the dense foliage—males facing

off with males, and females with females, while the young birds watch. Out of corner of your eye you can see the brown flash of woodcreepers and furnariids chasing as well.

The flock drifts away from the border interaction as the last dot-winged antwren continues its raspy agonistic vocalizations. Moving back to the dense vine tangle at the core of their territory, the antwrens enter the thickest vegetation, where they and a few other species fluff up to spend the night. If you return to the roost shortly before dawn, you will hear the antwrens and some of the other species singing—for many species, it is the only time of the day (apart from border interactions) they utter a song. As light begins to filter into the somber understory, the antwrens and their attendant species start to mill slowly about the vine tangle, searching for their arthropod prey.

### Feeding Aggregations versus Cohesive Flocks

Mixed-species flocks consist of many species moving through the forest together in search of dispersed food. However, although multispecies associations are common among forest birds, many are actually feeding aggregations, brought together by a specific resource, rather than the presence of other birds (flocks). Two examples of feeding aggregations that have been studied in detail are birds visiting fruiting and flowering trees (Leck 1971) and those following swarms of army ants in tropical forests (Willis 1972; Willis and Oniki 1978). In the latter case, birds jockey for position in front of the swarm, where arthropods are flushed by waves of ants scouring the leaf litter and lower stems of understory saplings. That the ant-following aggregation is not a cohesive social grouping of birds does not signify an absence of social interactions. The long-term research of Willis (1972) has exposed a complex interspecific dominance hierarchy, in which the more specialized “professional” ant-following birds (usually members of the true antbird family, Formicariidae) dominate the foraging zone directly in front of the swarm and the many subordinate species are found farther above or to the sides of the swarm. In addition, some species—particularly antbirds—are quite noisy, providing a cue for a variety of bird species to locate swarms (Willis 1972; Willis and Oniki 1978).

The hallmarks of a true mixed-species flock are that the birds travel together and that the benefits accruing to an individual joining the association are derived primarily from the behavior of other

birds rather than from the presence of a food source. Furthermore, individuals of different species in mixed flocks usually use different food resources (Diamond and Terborgh 1967). However, the distinction between aggregation and flock is often not a clean one: birds may readily switch between moving in flocks and feeding in aggregations as the distribution of food changes from scarce and dispersed to abundant and patchy. The frugivorous birds that occur in aggregations at fruiting trees (Leck 1971) may also occur in highly organized canopy foraging flocks that move between fruiting trees (Moynihan 1962; Munn 1985). Experiments with food supplementation show that in temperate zone forests, mixed flocks of chickadees and other species break up and form local aggregations with more aggressive interactions (Bock 1969; Berner and Grubb 1985). Although aggregations brought together by a particular resource do not have complex mechanisms for maintaining group cohesion, aggregations still comprise complex dominance interactions, and animals potentially communicate information regarding the approach or presence of predators.

### Flock Composition

The species richness and composition of mixed flocks can be characterized in two ways: by the total number of species regularly participating in mixed-species flocks in a given locality, or by the mean number of species participating in a particular flock at one time (table 18.1). Tropical localities, particularly in humid and lowland areas, may boast as many as 50–100 participating species versus 10–15 for temperate flocks (table 18.1; Odum 1942; Davis 1946; Gibb 1954; McClure 1967; Morse 1970; Buskirk et al. 1972; Munn and Terborgh 1979; Gradwohl and Greenberg 1980). However, individual flocks in the Tropics may be on average only marginally more diverse than those found at temperate zone sites; tropical flocks vary and change often as less common species join and drop out. In addition, most tropical forests have two or more basic flock types; for example, Willis (1972), Greenberg (1984), and Munn (1985) describe the existence of canopy and understory associations in lowland Neotropical forests. A third association—one of honeycreepers and small tanagers—moves between flowering and fruiting trees of the outer canopy. Often the first two flock types come together, and occasionally these are joined by the third, forming “mega-flocks” of remarkable diversity (Greenberg 1984; Munn 1985). A similar array



Table 18.1 Characteristics of some mixed-species flocks

Flock type and location	Flock size	Total species	Flock core*	Some core species	Reference
European tit	15	9	N	Tits, goldcrest	Morse 1978
North American tit	13-23	15	2N	Titmouse, chickadee	Morse 1970
Panamanian antwren flock	7	34	MST	2-3 antwrens	Gradwohl and Greenberg 1980
Amazonian understory	30-35	48	MST	Antshrikes, antwrens, furnuriids	Munn and Terborgh 1979
Amazonian canopy	?	53	MST	<i>Lanio</i> , <i>Tachyphonus</i> tanagers, greenlet	Munn 1985
Highland Costa Rica understory	8	43	N	<i>Basileuterus</i> warbler	Bell 1983
New Guinea understory					Bell 1983
Peninsular Malaysia	35	109	?		McClure 1967
Borneo	12	62	N	Babblers, drongos, flycatchers	Laman 1992
Australia	10	59	N	Thornbill, fairy wren	Bell 1980
African savanna	10-20	56	N	Tit, <i>Eremomela</i> warbler	Greig-Smith, 1978
Kashmir	?	15	N	<i>Phylloscopus</i> warblers, tits	McDonald and Henderson 1972

\*N = nuclear species; 2N = two or more nuclear species; MST = several species with same territory.

of different flock types has been described for the forests of New Guinea (Bell 1983; Diamond 1987). On the other hand, McClure (1967) found that mixed flocks in Malaysia consist of understory, mid-level, and canopy species that move together consistently.

The average number of individuals participating in mixed flocks is fairly consistent throughout the world, usually ranging from ten to thirty (Davis 1946; Morse 1970; Buskirk et al. 1972; Munn and Terborgh 1979; Powell 1979). Although larger flocks have been reported (McClure 1967; Bell 1983), most forest flocks are moderate in size, suggesting an upper limit determined by the ability to maintain group cohesion and consistent movement (Buskirk 1976). In addition, some observers (Morse 1970) have found that flock speed greatly increases with flock size, further suggesting that resource disturbance or depletion may be operating.

A high proportion of forest species join mixed-species flocks at least occasionally. This proportion varies: Hutto (1994) found that canopy birds participated in mixed-species flocks in proportion to their overall abundances in a tropical dry forest habitat. Greig-Smith (1978) found that a majority of species did not join the savanna flocks he studied. In moist tropical forests, species that are not found in flocks are often stationary sentinel foragers, have exceedingly small home ranges, or consume large fruits or other resources not used by mixed flock species (Buskirk 1976).

#### Behavioral Roles in Flock Formation

Although considerable effort has gone into classifying species according to the "role" they play in mixed flock formation, most of this work has been conducted without marked individuals or attempts to follow the activities of flocks for long periods of time (but see Buskirk et al. 1972; Munn and Terborgh 1979; Gradwohl and Greenberg 1980; Munn 1985; Powell 1985). Five distinct concepts have been incorporated into different classification schemes: (1) intraspecific gregariousness of the species; (2) "attractiveness" to other species (Moynihan 1962; McClure 1967); (3) whether the species follows or leads other species (Moynihan 1962; Morse 1970; Buskirk et al. 1972; Powell 1979; Diamond 1987); (4) the frequency of the species in flocks (regular versus accidental: Davis 1946; Buskirk et al. 1972; Bell 1983); and (5) the percentage of time a species occurs in mixed-species flocks (Morse 1970; Willis 1972; Powell 1979). The terminology commonly used to describe mixed flock behavior can be found in table 18.2.

Table 18.2 Common terminology used in mixed-species flock research

Term	Definition
Aggregation	A group of birds at a resource patch that does not travel together between patches
Alarm call	A conspicuous call given in the presence of a predator (usually a flying predator)
Attendant species	A species that joins and follows flocks
Beat	A predictable daily movement pattern
Contact calls	Soft call notes frequently given without agonistic or defense context
Core species	The set of species found in most individual flocks in a particular habitat or habitat stratum
Flock	A group of birds that move together while foraging for dispersed food
Flock territory	Territory of the nuclear or core species
Leader species	A species that coalesces the flock or is followed by other species
Multispecific territory	The territory of a flock made up of more than one species sharing the same boundaries; generally does not involve cooperative defense
Nonflocking species	Species that seldom join flocks
Nuclear species	Intraspecifically gregarious species joined by solitary or pair-forming species
Sentinel species	Species that produce conspicuous and early alarm vocalizations upon detecting a predator
Social mimicry	Hypothesized interspecific convergence of social signals to promote gregariousness

### *Nuclear Species*

Because of the often superficial nature of mixed-species flock research (i.e., no marked birds or long-term following of flocks), the most commonly used term to describe the species around which flocks form—nuclear species—has permeated the literature without a rigorous definition. The nuclear label is usually applied to species that are in most of the flocks at a particular location and forest stratum, show evidence of leading the flock, and are intraspecifically gregarious and noisy. Most researchers believe there to be considerable intercorrelation between these attributes. For example, intraspecifically gregarious species, particularly those whose own flocks comprise family groups, often are more vocal than species that occur solitarily, with well-developed mobbing behavior and predator alarm notes (Mönkkönen, Forsman, and Hella 1996). This vocal behavior may make them attractive to other species.

Examples of nuclear species include chickadees and tits, various species of babblers and thornbills, bulbuls, *Chlorospingus*, *Tachyphonus*, and *Tangara* tanagers, *Campylorhynchus* wrens, antwrens,

*Basileuterus* warblers, and *Hylophilus* greenlets. All of these form single-species flocks that attract a following of other, more solitary species. The demographic composition of these single-species flocks is quite diverse. Some (antwrens, wrens, greenlets, African tits, and American titmice) occur in nuclear or extended family groups. Temperate zone tits (Ekman 1979; S. M. Smith 1991) and *Chlorospingus* tanagers (R. Greenberg, pers. obs.) often form non-breeding groups of unrelated individuals or pairs that separate during the breeding season. In some areas, flocks of presumably unrelated migratory wood warblers appear to form a nucleus that attracts other species (Greenberg 1984; Hutto 1994). The diversity of social organization within the flock nucleus reminds us that perhaps, under many circumstances, mixed flocks form opportunistically around any gathering of birds that reaches critical mass and momentum. Discussions of possible adaptations that promote interspecific gregariousness should always entertain this, more mundane, hypothesis.

Moynihan (1962) defined nuclear species as those whose members lead and seldom follow other birds. Morse (1970) developed matrices based on the relative proportion of individuals and species led or followed. The relative frequency of leading and following has not been quantified for birds in most flock systems, but is accepted on an intuitive level as the fundamental attribute for defining flock roles. One senses the frustration of determining flock leadership—particularly in large, diverse tropical associations—in a comment by McClure (1967, 135): “at times babblers would lead or they might be overrun by the flycatchers, cuckoo-shrikes and minivets above them, and at other times pseudopodes of species stream ahead at different levels.” Observations of flocks crossing habitat gaps may facilitate quantification of the leadership role of flock members (T. Grubb, pers. comm.). Such observations would lead to more representative conclusions in areas where dominant flock members freely cross gaps than in tropical flocks, where only a select subset of species do so (Poulson 1994).

Most workers have restricted the classification of behavioral roles to nuclear and attendant species—that is, leaders and followers. However, Moynihan’s original system was a bit more complex, including a second tier of (active) nuclear species that followed the primary (passive) nuclear species but were sufficiently gregarious and noisy to attract other, more solitary species. Regardless of whether this more complicated classification system is warranted,



it is common to find mixed flock systems with two or more species that are found in most of the flocks and are themselves intraspecifically gregarious. Examples include *Basileuterus*-led flocks in Central America (Buskirk et al. 1972; Powell 1985), multispecies tit flocks in temperate Eurasia and North America (Morse 1970; Ekman 1979; Pravosudov 1987), antwren flocks of the Central American lowland tropical forest understory (Willis 1972; Gradwohl and Greenberg 1980), and *Hylophilus decurtatus*/*Tachyphonus luctuosus* flocks of the lowland forest canopy (Willis 1972). Finally, some tropical flocks have a nucleus that consists of individuals of a number of species that are not themselves intraspecifically gregarious (Munn and Terborgh 1979; Powell 1989).

#### *Home Ranges of Nuclear and Attendant Species*

A few studies of Neotropical flocks (Buskirk et al. 1972; Munn and Terborgh 1979; Powell 1979; Gradwohl and Greenberg 1980) have examined flock participation based on long-term following of color-marked individuals. These studies have, by and large, concluded that intraspecific social interactions are paramount in determining the participation of individuals in mixed flocks. The movement pattern and range of a particular flock system is defined by those of the nuclear species, whose space use is ultimately determined by intraspecific interactions. The joining by attendant species is highly constrained by their intraspecific spacing behavior as well. Working in the understory of the Central American highland forests, Buskirk et al. (1972) and Powell (1979) found that most attendants had smaller territories than the nuclear species and were found in flocks when the nucleus spent a significant amount of time within the smaller attendant territories. Gradwohl and Greenberg (1980) reported that in the lowlands of Panama, attendant species joining a core of two to three antwren species had both smaller territories (e.g., slaty antshrike) and larger home ranges (wedge-billed woodcreeper, *Glyphorhynchus spirurus*) or territories (buff-throated woodcreeper, *Xiphorhynchus guttatus*) than the antwrens. Birds with small territories joined flocks when the nuclear species passed through their territory. Those with larger ranges were seen in mixed-species flocks more regularly, since they moved through the forest by hopping from one flock to the next when the nuclear species interacted at territorial boundaries. Territoriality often regulates the numbers of a particular species in a mixed-species flock: either one, a pair, or a family group depending upon whether indi-

viduals or pairs maintain territories in the species. In addition to the above observations of territoriality in tropical attendant species, Sullivan (1984) reported that downy woodpeckers (*Picoides pubescens*), a common associate of North American tit flocks, defended individual territories against conspecifics. Even in nonterritorial species, such as the wedge-billed woodcreeper, intraspecific intolerance restricts the number of individuals in a flock to one (Gradwohl and Greenberg 1980).

The difference between the highland Central American *Basileuterus* and lowland antwren flocks may relate to the specific relationship between the home range size of the nuclear species and that of other common forest species. Apparently most highland forest species have small territories, whereas lowland species often have large ranges, and the antwren territories are relatively small themselves. We will not be able to generalize any patterns until detailed mapping of territories is completed for many more flock systems.

#### *Seasonality of Flock Formation*

Because mixed flocks form out of a complex interaction of the home ranges of attendant and nuclear species, the size and range of flocks varies considerably with seasonality of movement of the nuclear species. Temperate zone flocks are primarily a winter phenomenon. Flocks break up entirely during the breeding season and late summer, and fall flocks are unstable in composition, subjected to postbreeding influxes of migratory birds (Morse 1970). In contrast to winter flocks, where overt aggression is rare and dominance interactions take the form of subtle supplantations, interspecific chasing is common in postbreeding flocks. Tropical flocks persist throughout the year (Davis 1946; Moynihan 1962; Willis 1972; Gradwohl and Greenberg 1980). Powell (1979) found that highland flocks almost completely disappeared during the breeding season of the nuclear species (*Basileuterus*). However, Munn and Terborgh (1979) and Gradwohl and Greenberg (1980) found that even when breeding, members of the nuclear species often remained with the flock. Furthermore, the long and asynchronous breeding season of many tropical birds means that, particularly in flock systems with more than one nuclear species, there will usually be species between nesting efforts that can form the core of a flock. However, the flocks are generally smaller during the breeding season. For example, the home ranges of attendant species are often smaller, so opportunities to join flocks are reduced (R. Greenberg, pers. obs.). More criti-

cally, the velocity and range of movement of the nuclear species can change profoundly between seasons. J. Gradwohl and R. Greenberg (unpub.) followed antwren flocks during the nonbreeding and breeding seasons in 1985 and found that the nuclear species (antwrens) moved considerably more slowly and covered a much smaller area during the breeding season—even when the pair was between nesting efforts. In the nonbreeding (dry) season, antwrens covered more area at a much greater velocity, increasing their range by trespassing on neighboring territories. The reduced movement and home range size during the breeding season probably can be ascribed to the increase in food abundance, which allows nutritional requirements to be met in a smaller area. The behavioral adjustments birds make when they join flocks are summarized in table 18.3.

#### *Vocalizations Promoting Flock Formation and Cohesion*

Although McClure (1967) and Gradwohl and Greenberg (1980) found that the core species of flocks roost together, some flocks apparently spend the night apart and come together during the morning. T. Grubb (pers. comm.) and Munn (1985) both reported that a particular species (titmice and antshrikes, respectively) produces loud calls in the morning that attract other species.

Once the flock has coalesced, the activity of the nuclear species appears to promote further flock cohesiveness and momentum. Although this has yet to be rigorously tested, vocalizations appear to play a central role. Many of the gregarious nuclear species are “noisy” as they move through the forest; a familiar example is the complex vocal repertoire of flocking tits (*Parus*) (S. M. Smith 1991). In a tropical example, the dot-winged antwren—one of the nuclear species of Central American antwren flocks—gives short “pew” notes almost continuously, which are punctuated by longer “pachuka” notes when it moves between trees. It is these notes that allow ornithologists, and presumably birds, to locate flocks as they move slowly through dense vegetation. Loud notes of the *Thamnomanes* antshrikes promote flock coalescence and movement in understory flocks in Amazonian forests (Munn and Terborgh 1979; Wiley 1980), as do those of tufted titmice (*Parus bicolor*) in temperate tit flocks (T. Grubb, pers. comm.). Bell (1983) and Diamond (1987) made reference to a leader call in babblers of New Guinea, and McDonald and Henderson (1972) reported that the continuous notes of the western crown-warbler (*Phylloscopus occipitalis*) of

Table 18.3 Possible behavioral adjustments associated with mixed-species flock formation

Behavior	Example	Intraspecific function	Interspecific function
Frequent contact calls	Antwrens, tits	Facilitates group movement or spacing	Used by attendants to track flock
Loud and early alarm call	Tits, <i>Thamnomanes</i> antshrike	Reduces risk of predator attack	Used by attendants; perhaps allows reduced vigilance and greater time for foraging
Territorial adjustment	Antwrens, core of Amazon flocks, some tit flocks	Territory determined by flocking behavior and may adjust territory size from optimal with respect to foraging or density-dependent nest predation	Ensures consistent association with other flock species
Heterospecific following	Many attendant species		Facilitates the maintenance of association with mixed flocks
Adjustment of foraging velocity	Unknown	Speed of movement adjusted, perhaps away from optimal as determined by prey depletion or required search time	“

*continues*



Table 18.3 (continued)

Behavior	Example	Intraspecific function	Interspecific function
Low interspecific aggression Reliance on territorial boundary interactions	Tropical understory flocks Tropical forest flocks	Allows individuals to assess status of conspecifics in neighboring territory (flock switching is the dominant form of dispersal)	Temporally restricts the use of song; reduces conspicuousness
Irregular flock movement	Tit flocks, antwren flocks, highland tropical flocks	Reduces the predictability of flock location in time and space	
Regular flock beats Foraging site divergence	Possibly Malaysian flocks Temperate zone flocks	Minimizes temporal overexploitation of patches ?	Reduces probability of being attacked by dominant; may increase predation risk for subordinates; reduces probability of foraging at already visited site; allows dominant to monopolize best site
Foraging site convergence	Some temperate flocks Highland Costa Rica	?	May result from copying or to facilitate following

Kashmir attracted attendant species. In my experience, the contact notes given by individuals of gregarious nuclear species are similar whether they are in a mixed or a single-species flock (see also Greig-Smith 1978). However, I am unaware of a detailed and quantified study of the call repertoire of a species in and out of a mixed-species association. In contrast to calls that promote gregariousness, Powell (1979) suggested that certain vocalizations (song and sibilant flight call) of the three-striped warbler (*Basileuterus tristriatus*) discourage attendants from joining because they indicate likely movement out of the attendant's small territory.

If all this discussion of the role of vocalizations in the formation of mixed-species flocks seems anecdotal, it is because it is largely anecdotal. The function of particular vocalizations, or of the vocalizations of particular species, could be tested with playback experiments or vocal muting (McDonald 1989) experiments. The one experimental study of the effect of a particular vocalization was on the formation of loose mixed feeding groups during the breeding season in Finland, using the territorial song of the willow tit (*Parus montanus*: Mönkkönen, Forsman, and Hella 1996). The researchers studied foraging aggregations among different species of boreal forest birds during the breeding season. Species were differentially attracted to the song of the willow tit—a species that they demonstrated was joined disproportionately by other boreal forest insectivores. The degree of distinction made by the joining birds is unclear, since the experimental comparisons were made with the song of a North American tyrant flycatcher and a piece of classical music. However, the results of the experiment do not support the idea that special vocalizations are required to promote the formation of tit flocks.

#### *Do Plumage Patterns Promote Interspecific Gregariousness?*

A number of authors have pointed to plumage characteristics that might promote interspecific gregariousness. Moynihan (1962) argued that dull coloration may reduce the visual conspicuousness of vocally conspicuous species while promoting interspecific gregariousness. His idea, which has received no rigorous experimental testing, is that dull coloration promotes the approach of other species by reducing hostile reactions that might be released in the presence of bright colors. Moynihan illustrated the potential importance of dull coloration with the example of the red-legged honeycreeper (*Cyanerpes cyaneus*), the only species in the honeycreeper complex



in which males molt into a dull nonbreeding plumage. (This is, in fact, quite unusual for nonmigratory tropical birds.) This bird is quite gregarious intraspecifically and is an important member of canopy tanager-honeycreeper flocks. Although his findings were not quantified, Moynihan argued that this species is considerably more vocal than other honeycreepers. The argument that dull coloration promotes gregariousness was developed in an analysis of plumage changes in Neotropical migratory songbirds by Hamilton and Barth (1962) as well. These hypotheses are intriguing, but are very difficult to test. Looking over the sample list of nuclear species provided above (see table 18.1), which range in color from black and white to olive and gray or brown to yellow, it is hard to see a strong common thread. It would be interesting to see whether the proportion of brighter colors (for example, bright reds) among these species is statistically different from the relative abundance of other dominant colors in forest avifaunas.

Gregarious species also often have flash patterns in their plumage that are conspicuous when the bird flies. This can be easily seen in the white outer tail feathers of a number of flocking pipits and wagtails (Motacillids) and emberizid finches, mainly open-country species; such flashes are uncommon among leaders of forest bird flocks. Often these plumage features are inconspicuous until piloerection or flight exposes the feature. Examples of such plumage characteristics are the white flanks of the white-flanked antwren, the white shoulder patches of the otherwise black white-shouldered tanager (*Tachyphonus luctuosus*), the blue shoulder patches (greater wing coverts) of the plain-colored tanager (*Tangara inornata*), and the wingbars of the white-winged tit (*Parus leucomelas*) found in African savanna flocks (Greig-Smith 1978). Although some authors (Moynihan 1962; Wiley 1971) have argued that flash patterns facilitate mixed flock cohesion, the association between such patterns and mixed flocking is weak. These patterns are particularly important in maintaining flock formation in synchronized flights, but such displays are not characteristic of forest flocks. Many of the nuclear species of forest flocks lack any such pattern, and for those that have them, these patterns may function in a number of contexts, such as foraging and intraspecific agonistic interactions (common in antbirds, for example).

#### *Signal Convergence in Mixed-Species Flocks*

Members of mixed-species flocks might show convergence of signals to promote group cohesion (Moynihan 1962, 1968). Based on

what he posited is the economy of signals, Moynihan argued that species should converge on similar plumage patterns to promote positive associations. Although it is reasonable that a bird would have an easier time following a limited number of color patterns, the mechanism for individual selection of a convergent color pattern is more problematic. One could posit that a bird that sports a coloration more similar to that of a species it regularly follows is allowed to approach more closely than one that has a strikingly divergent pattern. Although no evidence from forest bird flocks is available to evaluate this idea, Caldwell (1981) presented some intriguing experiments on mixed flocks of foraging herons. When she presented life-like models, she found that snowy egrets (*Egretta thula*) attracted the most individuals and species of foraging herons. Herons foraging near snowy egrets improve their foraging success, perhaps because the snowys stir up the substrate and flush fish. Immature little blue herons (*Hydranassa caerulea*) are white and are allowed to approach snowy egrets, resulting in increased foraging success. However, adult little blues are dark-colored, are attacked by snowy egrets, and as a result, are more successful when solitary than when foraging in association with egrets. All this occurs without a measurable decrease in the success of the snowy egrets.

Moynihan (1968) cited several examples of flocks that consist of apparently conspicuously and similarly colored birds. In the canopy of lowland forests in Panama, flock members are generally blue, green, or blue-gray; in the second-growth forests of the highlands, flocks consist of black and yellow species. The social mimicry hypothesis rests on the assumption that shared plumage patterns are disproportionately more similar than one would expect of random assemblages of species from the same habitat—an analysis that has not been conducted for any flock system. With the exception of plumage patches that are covered by erectable feathers, avian coloration is not readily changeable and must function in many ways simultaneously. The social mimicry hypothesis would be most convincing if color patterns could not be demonstrated to have some other function, such as crypticity, with more obvious adaptive value. For example, the blue and green colors of canopy honeycreepers might appear to constitute convergence on a bright color. But these colors may actually be difficult to detect in a tropical forest canopy (Endler 1985). For this reason, it has proved difficult to rigorously distinguish between the social mimicry hypothesis and other reasonable explanations.

In another example of an alternative explanation for convergent

plumages, Greig-Smith (1978) argued that the core species in African savanna flocks often share predominantly black and white patterns, possibly because these species are unpalatable. Hypotheses can also be advanced for the convergence on black and brown patterns described for understory flocks in New Guinea (Diamond 1987). The nuclear species (babblers) in these flocks are predominantly black or brown, or both, and the followers (for example, drongos) are black. This, Diamond argued, was a striking example of apparent social mimicry, and he reiterated the arguments of Moynihan (1968). Of course, brown and black could be cryptic coloration for tropical understory vegetation. Furthermore, at least two leader species of the genus *Piohui* were more recently found to be poisonous (Dumbacher et al. 1992) and involved in an apparent Müllerian mimicry complex. This finding leaves open the possibility that the shared brown and black patterns that Diamond described are actually part of a Batesian mimicry complex.

The likelihood of convergence in vocal signals is also unclear. The economy of signals idea would best apply to situations in which a mistake that causes a slow or inappropriate response results in a large cost to the responding individuals. Therefore, calls associated with predator detection and avoidance are an obvious place to look. Alarm notes to flying predators and mobbing notes to stationary predators often share acoustic properties among mixed flock members. However, as Marler (1957) argued long ago, there are functional explanations for similarity in vocal responses to predators—an argument that, with some modifications, stands today. Alarm notes to aerial predators are often short in duration and given at a high and narrow frequency band. These sharp notes usually cause other flock members to freeze. Presumably the bird giving the alarm gains some advantage by reducing the conspicuousness of the entire flock, and for some species, by warning relatives. Mobbing notes are generally longer in duration, with a broader and lower frequency band. Alarm and mobbing calls are selected to provide the minimum and maximum amount of locational information, respectively, to a potential predator, which accounts for much of the interspecific similarity in their respective structures.

It is less clear why birds cannot easily respond to a variety of "contact" notes—calls given by foraging birds not necessarily in the presence of a predator or in an overtly aggressive context. One could argue that giving a convergent call note might facilitate closer

following by heterospecifics. However, it is likely that such contact notes function primarily as intraspecific signals within a flock—to promote either following or avoidance. Senders of so-called contact notes may also be advertising to conspecifics that a flock is already occupied. If intraspecific interactions dominate, then one would expect the contact notes of different species to diverge to minimize confusion or misidentification on the part of the intended conspecific receivers. As far as I know, the divergence or convergence of contact notes within the context of mixed-species flocks has not been systematically studied. However, the likely reason for the lack of such studies is that the contact notes of flock members are readily distinguished by human observers. Begging notes of juveniles also show great species-typical variation, at least among members of antwren flocks (R. Greenberg, pers. obs.). It could be a costly waste of time (and in the presence of kleptoparasites, time may be of the essence) for adults carrying prey to young in a mixed flock not to be able to readily and rapidly determine the location of their own young.

With regard to intraspecific convergence, there is evidence (Nowicki 1983, 1989) that the "chickadee-dee" calls used for mobbing and territorial interactions by members of chickadee flocks tend to converge rapidly among flock members and diverge from those of other flocks. Similar copying has been found in intraspecifically gregarious finches (Mundinger 1970) and budgies (Farrabaugh, Linzenbold, and Dooling 1994). These convergent calls in budgies and finches are thought to synchronize group movement—and an individual may benefit by not looking or sounding different from other flock members as the group flies in unison. However, in the case of chickadees, convergence in an aggressive vocalization may reduce mistaken intragroup attacks in intergroup agonistic interactions.

#### *Do Species Evolve in Response to Flock Role?*

Does the mixed-species social environment shape specific adaptations, such as visual or vocal signals? Or do mixed-species flocks develop idiosyncratically around any group of birds that provides critical mass and momentum, so that no long-term alteration of communication systems is necessary or advantageous? Moynihan (1968), Cody (1971), and Diamond (1987) have all proposed that some species have evolved signals and behavior patterns specifically adapted to promote interspecific gregariousness. Moynihan's argument is somewhat contradictory on this point. On the one hand, he

posits that certain features of nuclear species are general adaptations, shared by many nuclear species, to facilitate other species joining them and hence to promote the formation of mixed-species flocks. On the other hand, he suggests that all species commonly occurring together in a particular flock type converge upon special patterns that distinguish that flock type. The most parsimonious mechanism of flock formation is that the various attendant species evolve plumage, vocalization, or behavior patterns that allow them to approach and follow the nuclear species. Both of these suggestions place paramount importance on interspecific interactions in shaping signals. Alternatively, the adaptations of nuclear species that promote gregariousness may have primarily been shaped by intraspecific interactions.

The assumptions of these two views are different and rest strongly upon the degree of symmetry in the advantages gained by nuclear and attendant species through mixed-species flock formation. The evolution of features in individuals of nuclear species that somehow encourage other species to follow them presupposes that the individuals of nuclear species enjoy some net benefits from the presence of the attendant species. It is easier to assume that the species that actively join or follow the nuclear species derive benefits from this association. The social mimicry hypothesis is reasonable if the signals of the attendant species converge to facilitate their following response, even if—or particularly if—the nuclear species does not benefit from the association.

#### *Dominance and Flock Role*

Although it is probably safe to assume that the attendant species gain a net advantage from associating with the nuclear species, the converse assumption is more problematic. The relative dominance of flock participants and the importance of dominance-mediated access to resources are critical to understanding the costs and benefits accruing to the nuclear species. There has been at least one experimental confirmation that members of a small and subordinate nuclear species (Carolina chickadee, *Parus carolinensis*) do in fact experience a cost in association with a larger, dominant species (tufted titmouse: Crimprich and Grubb 1994). The cost was measured by removing titmice from isolated woodlots and measuring the regrowth of chickadees' plucked outer tail feathers. Although the experiment was conducted on only one associated species, the results at least suggest the possibility that sometimes nuclear species must merely tolerate the presence of other species, rather than

actively attracting them. Although the experiment raises this possibility, the results were more narrow. The experiment tested the effect on chickadees of the presence of titmice in the same habitat patch, not the cost of actually flocking together. In addition, the results of an analysis of possible benefits (vigilance) were ambiguous.

Mixed flocks are often characterized by few overt agonistic interactions (Morse 1970; Munn and Terborgh 1979; Powell 1979) except intraspecific territorial skirmishes. The few studies that have examined the dominance of nuclear versus attendant species paint a diverse picture for different flocks. For example, the *Thamnomanes* antshrikes and *Lanio* shrike-tanagers are thought to be critical in the coalescence of the complex Amazonian flocks and are strongly dominant to other species. In North American winter flocks, the two tit species are subordinate to some common attendants (woodpeckers and nuthatches: Waite and Grubb 1988; but see Sullivan 1984 for a report of black-capped chickadees [*Parus atricapillus*] kleptoparasitizing woodpeckers) and dominant to kinglets. Suhonen (1993) and Alatalo (1981) found tits to dominate goldcrests and treecreepers, causing the latter to forage farther out on limbs, thereby increasing their predation risk. Since nuclear species vary greatly in size, and size is known to be an important determinant of dominance, I see no reason to believe that they are consistently dominant or subordinate to their common attendants.

#### **Possible Foraging Benefits of Participation in Mixed-Species Flocks**

When considering hypotheses about the benefits and costs of mixed flocking, it is critical to remember that the presence of species-typical foraging specialization is one of the main ways in which these flocks differ from single-species flocks. Mixed-species flocks, particularly in the Tropics, often contain resource specialists that hunt insects in particular strata or microsites, such as dead leaf curls, bark, dead or live twigs, or tree boles, or attack prey in specialized ways (long-distance strikes, hanging, reaching, etc.).

Foraging niche generally correlates with flock role. Nuclear species are often foraging microhabitat generalists. Tits provide a good example of this; they use a diversity of foraging maneuvers to extract prey from a wide variety of sites. Attendant species use specialized foraging techniques (such as long-distance aerial strikes) or specific foraging sites. In tropical flocks, the intraspecifically gregarious nuclear species are most often simple gleaners of live foliage—an abundant microhabitat, but one that supports relatively low prey abundances. Species that either capture arthropods with



long-distance attacks or search relatively rare microhabitats, such as dead twigs, epiphytes, dead curled leaves, or bark, are generally solitary or occur in pairs and fit the attendant species behavioral syndrome (Buskirk et al. 1972; Willis 1972; Greenberg and Gradwohl 1985). These authors argued that their smaller intraspecific group size is a response to greater sensitivity to intraspecific competition (rarer foraging sites, or longer foraging attack radii).

#### *Location of Specific Foraging Sites*

One commonly suggested potential benefit of flocking is learning where food is located from other flock members. There is little field evidence that birds in mixed flocks learn about the distribution of food from other flock members; however, experiments with captive tits showed that members of two generalist species (black-capped and chestnut-backed chickadees [*Parus rufescens*]) might gain information on productive foraging sites from each other (Krebs 1973). The possibility that tit species learn from each other in the wild is particularly interesting in light of the specialization that has been reported among conspecifics in a flock (Vanbuskirk and Smith 1989). Convergence of foraging niches of birds in flocks has been put forward as evidence that birds join flocks to learn about the specific locations of food (local enhancement) or, perhaps more commonly, to learn what types of foraging sites are productive at a particular time "site enhancement" (Morse 1978). Waite and Grubb (1988) present evidence from aviary experiments that both types of copying can occur in mixed-species flocks consisting of tits, woodpeckers, and nuthatches. Their experiment showed that attendant species (woodpeckers and nuthatches) pay attention to the foraging success of the more generalized tit species, at least in a confined aviary situation. However, more data from the field are required to determine the importance of copying behavior.

#### *Limits to Social Facilitation: Stereotypy and Neophobia*

Perhaps rather than focusing on the small body of evidence for copying—which at this point is largely restricted to tit species—a more interesting question to consider is how individual birds retain their species-specific specializations in the context of a mixed flock. What prevents birds, particularly young birds, from attending to the foraging success of species with highly divergent foraging strategies? Responses of birds to the foraging behavior of other birds should be a fruitful area for research. One could hypothesize that

the specialized attendant species of tropical flocks are highly resistant to social facilitation. Although learning mechanisms between birds with different degrees of foraging specialization have not been well studied, I have conducted a few experiments that are relevant.

The Carolina chickadee is a nuclear species that shows a high degree of foraging plasticity. The worm-eating Warbler (*Helmitheros vermivorus*) is a highly specialized attendant species during the nonbreeding season, occurring solitarily in mixed flocks and feeding almost exclusively from dead curled leaves. I presented a large number of objects (including dead leaves, live leaves, boxes, tubes, chenille stems, etc.) to naive fledgling warblers and tits housed in flight cages and recorded their preferences for exploring these objects (Greenberg 1987a) (these were dependent young and no food reward was involved). The worm-eating warblers all showed highly similar preference rankings, whether they had been reared with conspecifics or with chickadees. The chickadees showed highly divergent preferences between rearing groups, but converged upon a preference ranking within groups. The mechanism for the convergence was unclear—only a small portion of visits to objects were made simultaneously by more than one chickadee. The experiment suggests that chickadees have relatively unstereotypic preferences that are easily shaped by their social environment, as opposed to the highly stereotypic preferences of the warbler.

It has been hypothesized (Greenberg 1984) that neophobia (fear of novelty) plays a central proximate role in controlling foraging specializations: individuals of more specialized species have an aversion to approaching unfamiliar foraging sites or feeding on unfamiliar foods. I tested the hypothesis that the more specialized chestnut-sided warbler (*Dendroica pensylvanica*) would approach a productive but novel feeding site more readily in the presence of the intraspecifically gregarious and generalized bay-breasted warbler (*Dendroica castanea*), a species that it commonly associates with on the wintering grounds (Greenberg 1987b). The chestnut-sided warblers did not decrease their aversion to novel stimuli in the presence of the non-neophobic species.

#### *Avoiding Exploited Sites*

Foraging competition is discussed below as a probable cost of mixed flock participation. However, since interspecific competition may occur anyway, participation in flocks may be a way to monitor the resource use of potential competitors (Morse 1970; Austin and

Smith 1972). By avoiding substrates or sites already being used by another species, birds in mixed flocks may actually enhance their foraging efficiency. Divergence in foraging sites has been reported for temperate zone flocks, but this is a difficult hypothesis to distinguish from a behavioral competition hypothesis (see below under foraging costs) or one regarding dominance and predation (Suhonen, Halone, and Mappes 1992; Suhonen 1993).

#### *Flushing of Prey and Kleptoparasitism*

Kleptoparasitism—stealing food from subordinates—can be an important source of food, and hence a benefit, for a few behaviorally dominant flock species, at a substantial cost to subordinate flock members. J. Gradwohl and R. Greenberg (unpub.) observed that the slaty antshrike frequently stole large food items from the smaller antwrens. The association between antshrikes and antwrens is particularly strong during the breeding season, when adults handle many large prey items. Antshrikes tended to station themselves between male and female antwrens during periods of nuptial feeding, and the antwrens moved into dense vine tangles and performed evasive maneuvers to avoid attacks by antshrikes. Munn and Terborgh (1979) and Munn (1985) found that the leader species of Amazonian flocks, *Thamnomanes* antshrikes in the understory and white-winged shrike-tanagers (*Lanio versicolor*) in the canopy, depend heavily upon prey flushed by or stolen from other flock members. Munn (1986) further suggested that the antshrikes use a deceptive alarm call to induce subordinate birds to drop prey, which are then kleptoparasitized. Similar “deceptive” use of alarm calls has been reported for tits (Moutsouka 1980; Møller 1988). Møller found that during periods of inclement weather, great tits (*Parus major*) gave alarm calls when no predators were seen by the human observer. These calls were given at feeders in the presence of finches and allowed the tits access to food or facilitated food theft. The published studies on deceptive alarm calls are suggestive, but leave a number of unanswered questions. As both Munn (1985) and Møller (1988) point out, the advantages of using deceptive alarm calls are highly frequency dependent. If foraging is common and predation is rare, the caller risks habituating the target species, which would reduce the efficacy of the “false alarm” as well as the efficacy of the real alarm call.

Kleptoparasitism of live prey has not been documented in temperate flocks, where winter prey is usually small. However, Waite and Grubb (1988) suggested that kleptoparasitism by large atten-

dant species against subordinate nuclear species (chickadees and titmice) could be common. In addition, it seems possible that birds pilfer food from caching species. One captive study looking for interspecific pilfering failed to find interspecific interactions, however (Suhonen and Iniki 1992).

#### *Optimal Movement Patterns*

In one of the few attempts to apply optimization models to bird flocks, Cody (1971) proposed that mixed finch flocks move through a range in such a way as to optimize the harvesting of resources with respect to their renewal. When resources were abundant, he found that flocks moved more rapidly, turned more frequently, and that the angles of flock turns were larger, which brought the flocks back to previously visited areas more frequently. The desert flocking system was studied further by Eichinger and Moriarty (1985), who correlated movement patterns with topography, specifically the presence of desert washes. Even in a seemingly simple system, the construction of movement models that disentangle resource use strategies from patchiness of the environment is difficult.

The movement of mixed-species flocks has so rarely been charted over a number of days that we cannot assess the possibility that there exist long-term movement “strategies.” A few observers, such as McClure (1967) in Malaysia, have found that flocks follow regular “beats.” In general, mixed flock movements are irregular and seemingly haphazard, with no tendency to avoid previously visited areas at regular intervals. Based on his own experience and earlier accounts, Gaddis (1980) concluded that chickadee/titmice-led flocks are irregular in their movement, with no clear pattern of speed or direction. He proposed that this irregularity was in itself a strategy to make the location of the flock unpredictable to predators. In a particularly careful study of flock movement, Powell (1979) found that flock movement approximates a random walk with a bias toward forward motion, and that a dominant feature of flock movement is movement to territorial boundary interactions. The nuclear species of mixed-species flocks maintain territories, to a large degree, by face-to-face interactions with neighboring groups that reestablish traditional territory boundaries. Gradwohl and Greenberg found that in the dry season, antwren flocks move slowly through a few core areas (dense vine tangles) and intermittently make forays to territorial boundaries (or into neighboring territories if neighboring flocks are temporarily absent from the boundary area). In many core flock species, such as the antwrens, song is

restricted to a brief predawn period and to boundary interactions. It is tempting to speculate that song is restricted to these times to reduce the possibility that the location and movement of the flock will be monitored from a distance by predators.

The overall patterns of territory use by Powell's highland flocks and by Gradwohl and Greenberg's lowland flocks are quite different. The former flocks use the territory evenly, suggesting some mechanism for regulating space use, whereas the latter flocks' space use is very patchy, with individuals concentrating their activity on a few core areas. Without more detailed following in conjunction with habitat sampling, it is impossible to generalize about strategies of space use by mixed flocks.

#### *Spatial Memory of Flocking Species*

Perhaps certain species are joined by others to take advantage of their special spatial cognitive abilities. The development of spatial memory has been an important area of recent research in avian behavioral ecology. However, this work has not been conducted in the context of group movement per se, but rather in the area of food storage and caching. Food caching is not known for participants in tropical flocks, but is widespread in common flock species in temperate forests (Sherry 1989; Krebs et al. 1996). Spatial memory over a few days has been demonstrated, and longer-term memory is possible as well. Species that store food have a well-developed hippocampus compared with related nonstoring species. It seems possible that if mixed flocks have an emergent strategy for optimizing the time between visits to particular parts of the flock territory, this strategy might be based on the spatial memory of individuals of the nuclear species.

#### *Learning from the Locals*

Species may join a mixed flock because the locally territorial species are familiar with favorable or safe areas in which to forage. This hypothesis works best for attendant species that have large home ranges compared with the nuclear or other attendant species. Where the nuclear species has a territory larger than its attendants', it seems unlikely that the attendants would join to "learn" about features of their territory.

#### **Possible Antipredation Advantages of Participating in Flocks**

Although it has been proposed that flocking can reduce the risk of predation to participants in a number of ways, for forest flocks, the

primary mechanism is increased vigilance and the ability to take advantage of the alarm calls of certain species (see Powell 1985 for review). The nuclear species, with their well-developed and conspicuous vocalizations, may be particularly attractive sources of information on the presence of predators. Both Morse (1970) and Gaddis (1980) showed that individuals of two tit species consistently alarmed first and most vociferously, with a loud whistle, when accipiters attacked mixed flocks. The whistled alarm causes all flock members to freeze, thereby reducing the conspicuousness of both the individual and the overall flock. Attendants in flocks are often species that forage intensively by examining surfaces or probing into specific microhabitats (Willis 1972; Buskirk 1976), whereas species with less intensive foraging behavior join flocks less commonly, and presumably are more vigilant.

A number of studies have examined the role of group vigilance within single-species flocks (Powell 1974; Siegfried and Underhill 1975), and interspecific changes in vigilance have been documented for simple mixed flock systems (Barnard and Thompson 1985). Sullivan (1984) first carefully tested the vigilance hypothesis in forest flocks by examining video footage of foraging downy woodpeckers in and out of mixed flocks, and found that vigilance time was much reduced in this bark-searching insectivore when it associated with other species. The decreased need for vigilance by attendants can also be seen as a feeding advantage, as the downy woodpeckers in flocks spent more time foraging. Areval and Gosler's (1994) finding that the solitary attendant treecreeper (*Certhia familiaris*) restricted its foraging zone, but increased its feeding rates, as mixed flock size increased suggested that the treecreeper depends upon the greater surveillance for predators found in larger flocks (see also Henderson 1989). However, it has never been demonstrated that intraspecifically gregarious nuclear species change their vigilance behavior when joined by attendant species. In fact, Carolina chickadees showed no significant change when tufted titmice were removed from flocks (Crimprich and Grubb 1994). However, Hogsted (1988) reported reduced vigilance in willow tits (*Parus montanus*) when they participated in mixed flocks.

As the number of birds increases in a flock, not only does the probability of detection of a predator increase, but so does the possibility of "false" alarms—calls given mistakenly when no predator is actually present. There is a cost in lost foraging time to responding to inappropriate alarms. Recent work by Lima (1995) suggested that assessing whether an alarm is valid is a complex pro-



cess in sparrows in mixed flocks, and that alarms gain salience if several birds alarm and flush. The ambiguity of alarm information is therefore an issue—one that has not been addressed in forest flocks.

### Costs of Flock Participation

#### *Foraging Disturbance and Competition*

Several studies of temperate zone flocks (Morse 1970; Alatalo 1981; Crimprich and Grubb 1994) have shown that birds adjust their foraging sites when they join flocks. These adjustments appear to be a result of aggression or the threat of aggression, or of exploitative competition—the superior ability of some species to harvest arthropods from particular foraging sites. Crimprich and Grubb (1994) demonstrated through a removal experiment that Carolina chickadees expand their foraging sites in the absence of titmice. However, the choice of foraging sites may be based on relative safety from predation as well as on food resource availability (Suhoenen 1993). Buskirk (1976) indicated that birds actively converge upon a single foraging height stratum to join flocks. But there have been no reports of changes in the use of particular foraging sites.

Competition from other species should be viewed as a cost of mixed flock participation. However, because different species tend to forage in different sites, mixed-species flocking allows birds to gain the benefits of flocking with less competition than they would experience in single-species flocks. The actual resource depletion by insectivorous flocking species has only rarely been measured, but may be great (Gradwohl and Greenberg 1982).

The effect of temporary disturbance may be profound as well. Based on observations of captive checker-throated antwrens (J. Gradwohl and R. Greenberg, unpub.) we found that, upon disturbance, arthropods may retreat into a dead curled leaf after an initial visit and become more difficult to find. Although long-term prey abundance may not be seriously depressed, birds may have to let areas “rest” before arthropods are easily located again. The effect of this type of competition should be most pronounced between members of the same species, hunting in the same microhabitats. Valburg (1992) found that the common bush tanager (*Chlorospingus ophthalmicus*) formed large, single-species flocks when feeding on fruit (where such disturbance-based competition is minimal), but participated in smaller single-species groups within mixed-species flocks when searching for arthropod prey. A number of au-

thors (e.g., Ekman 1979) have argued that in temperate zone tit flocks, within-species group size declines as more congeners occur together, suggesting that species gain flocking advantage with reduced intraspecific competition. Aggression is generally much greater within tit species than between, and between tit species than between tits and attendants (Morse 1970). Waite and Grubb (1988) suggested that tits gain an advantage by flocking with dominant attendants because interactions with them are fewer than with conspecifics or congeners.

#### *Nonoptimal Movement Patterns*

I have discussed the possibility that movement across flock territories is optimized when birds join flocks. However, movement with flocks may impose a cost on birds that are required to move through areas at speeds or with return times that are inappropriate for their particular foraging strategy. Munn and Terborgh (1979) argued that flocks consist of species that have generally compatible movement patterns when foraging. Incompatible movement patterns may explain why some gregarious species (such as dusky-faced tanagers, *Mitrospingus cassinii*, in Panama) attract few followers. However, as pointed out by Hutto (1988), even for species that move through the habitat at similar speeds, the adjustment of movement patterns away from the optimal may be a cost of flocking. Buskirk (1976) reported that slate-throated redstarts (*Myioborus miniatus*) use simple gleaning rather than aerial maneuvers when they join flocks; he proposed that the aerial maneuvers cannot be accomplished in a rapidly moving flock.

The issue becomes more complicated because the speed of flocks is not constant. In fact, Morse (1970) showed that tit flocks with more individuals move faster. Although Powell (1980) found no such relationship in his highland tropical flocks, Greenberg and Gradwohl (1980) found that antwren flocks with more forward momentum contained more species. The reason for this flock size/velocity relationship is unclear. One explanation might be that more birds cause more disturbance and force birds to change foraging sites more quickly. In this case, the upper limit of flock size may be reached when birds can no longer sustain their foraging at high flock speeds. Another explanation is that more species require higher flock speeds to sustain their foraging, and as the nuclear species moves more rapidly, more attendants are able to join. Obviously both the generality and the mechanism of a flock size/velocity relationship require further study.

### *Flock Conspicuousness*

Despite the well-developed alarm behavior of some flocking species, flocks themselves provide a tempting target for predators. A predator locating a flock has a number of targets, and it is difficult for a flock to melt away into the forest the way a solitary bird can. It is interesting that observers have generally not found raptors that track mixed-species flocks (I am assuming that nonavian predators would be unable to track flocks over great distances). Predators are able to station themselves at food resources or track feeding aggregations (such as at fruiting or flowering plants, bird feeders, ant swarms). For example, ant-following aggregations are often joined for long periods by barred forest falcons (*Micraster ruficollis*: Willis and Oniki 1978; R. Greenberg, pers. obs.). Foraging flocks may be a less tempting target for a following raptor because participants have more options for different patterns of movement than birds whose movements are determined by the vagaries of an ant swarm. Furthermore, ant-following birds produce noisy agonistic vocalizations as they jostle for position.

Movement and behavioral strategies for discouraging the following of flocks by avian predators may include spending time in dense and perhaps safer patches (e.g., the vine tangles of antwren flocks), moving rapidly and irregularly away from these areas, and reducing the use of long-distance vocalizations in favor of short-distance contact notes and border interactions. The strategies flocks employ to discourage following by avian predators would be a fascinating line of research.

### **Costs and Benefits and the Nuclear/Attendant Paradigm**

There are many varied potential costs and benefits to joining mixed flocks, centering on detection of predators and enhancement of foraging efficiency on the one hand and increased competition on the other. It is not surprising that different costs and benefits accrue to birds in different flock systems and to birds of different species within a flock. One can probably safely assume that the attendant species that actively join flocks receive a net benefit from the association. It is more challenging, however, to understand the costs and benefits experienced by the individuals that are joined. It is conceivable that nuclear species benefit from attracting individuals of other species through an increase in the diversity of vigilant individuals and the ability to monitor a wider range of foraging sites. It is equally conceivable that nuclear species gain minimally from the

presence of attendant birds and actually experience a net cost due to the increase in competition or the attraction of predators. Carefully exploring the costs and benefits for species with different flock roles will be a formidable task for future research.

### *Decision Making Within Nuclear Species Groups*

The strong species-specific role in apparent flock leadership begs the question of which individual birds determine the pattern of flock movement and how this is conveyed to other flock members. Little research has focused on the decision-making process within the social group of the nuclear species. However, Mostrom (1993) and S. M. Smith (1991) examined the relationship between dominance status and tendency to initiate movements in groups of Carolina and black-capped chickadees, respectively, and found no relationship. Their work, as well as other studies (notably, Odum 1942), failed to detect a strong tendency for particular individuals to initiate group movements. Without such a tendency, the possibility of correlating demographic attributes with group leadership is meaningless. In addition, although chickadees are followed by most attendant species and are generally considered to be nuclear, it appears that they, in turn, usually follow titmice (Morse 1970). T. Grubb (pers. comm.) suggested that the dominant male titmouse may play the greatest role in flock movement and coalescence.

### *Beyond the Nuclear/Attendant Paradigm: Flock Leaders versus Sentinel Species*

Wiley (1971) suggested that the nuclear/attendant dichotomy may be inadequate to describe the potential complementary roles species play in the functioning of mixed-species flocks. His work focused on flocks with a nucleus of two species of *Myrmotherula* antwrens. He argued that one congener, the white-flanked antwren, by virtue of its sociability and conspicuous plumage pattern (black with white flank flashes, as described above), promotes the cohesion of flocks. A second species, the checker-throated antwren, is cryptically colored and follows the white-flanked, but acts as a sentinel species, giving a sharp "peeet" call in the presence of predators (a call that is often used in high-intensity territorial interactions as well). It is not clear how selection would act on individuals of the two species to shape these complementary roles. Perhaps the association of the two species did not involve any evolutionary adjustments, and it is just fortuitous that two species with these character-

istics are found commonly in the same forest. However, the details of the particular relationship outlined by Wiley are not well established. Further work has shown that the strongest association is between the checker-throated and dot-winged antwrens. Attendant species probably follow the continuous contact notes of the dot-winged antwren. Checker-throated antwrens are highly specialized dead leaf foragers and are probably less effective at detecting predators than are the other antwrens (J. Gradwohl and R. Greenberg unpub.).

The concept of sentinel species, however, has been supported by research on mixed-species flocks in Amazonian forests. Munn and Terborgh (1979), Wiley (1980), and Powell (1989) found that antshrikes in the genus *Thamnomanes* were sentinel foragers with the best-developed alarm call in the flocks. They provided some anecdotal evidence that *Thamnomanes* give alarm calls to which other flock members respond. However, as I stated previously, they also suggested that these antshrike species function as flock leaders: their calls coalesce dispersed flocks, and other flock members follow when these species give calls away from the flock. Therefore, since the call notes of one species serve both as a warning system and a mechanism of group coalescence, the concept of complementary roles as suggested by Wiley for antwren flocks does not apply to the Amazonian flocks.

Bell (1983) and Diamond (1987) provide another possible example of complementary roles in New Guinea bird flocks. The leader species (often babblers) gain from the sentinel behavior and loud alarm calls of drongos. Croxall (1976) found that the loud calls of drongos are important in flock formation, but did not discuss alarm calls in particular.

It should be remembered, however, as we discuss stable and perhaps coevolved relationships between species in the core of a mixed flock system, that it is likely that many attendant species join mixed-flock systems opportunistically—that they are attracted to any group of birds moving through their forest.

#### *Beyond the Nuclear/Attendant Paradigm: Multispecific Territories*

The most surprising discovery concerning the formation of complex mixed-species flocks is that the core often consists of a number of species that defend the same territorial boundaries. This phenomenon was found in understory flocks in Panama (Gradwohl and Greenberg 1980) and Peru (Munn and Terborgh 1979), where three

and sixteen species respectively occupied multispecific territories. Munn (1985) further demonstrated that canopy flocks in the same Peruvian forest consisted of a core of species that codefended territories, although the territories were larger and less aggressively defended than those of understory flocks. Multispecific territories are not restricted to tropical forests: temperate tit flocks sometimes have two or three species in such a system (Ludescher 1973; Ekman 1979; Bardin 1984; Pravosudov 1987). Studies of marked members of the core of these multispecific associations have been carried out for from a few to up to 14 years (Greenberg and Gradwohl 1997). All studies suggest that the boundaries of these associations are extremely stable, maintaining their salience far longer than the tenure of particular birds.

#### *Multispecific Territories and Population Ecology*

We can assume that species that join multispecific territorial systems do so at some energetic cost. If optimal territory size is dependent upon the abundance and distribution of resources, and resource abundance and distribution vary considerably with the body size, foraging strategy, nesting behavior, and so forth of individual species, then it is unlikely that the optimal territory size will be identical for all participating species. Added to this assumption is the observation that the sizes and locations of multispecific territories are extremely stable, despite annual fluctuations in rainfall and food supply. Greenberg and Gradwohl (1986) reported that annual adult survival showed considerable yearly variation in two species (checker-throated antwren and slaty antshrike), and that this variation was correlated with the amount of rainfall during the late rainy season (the more rain, the higher the disappearance rate). If territory did not precisely regulate the breeding population, one would not expect stable populations and territories unless the number of young produced each year exactly matched the mortality rate. However, at least in the checker-throated antwren, the number of recently fledged young recruited into flocks showed very little year-to-year variation and thus could not balance the fluctuating turnover in adults. These observations suggest that territory size in these species is not finely adjusted to resources, either between species or through time. Greenberg and Gradwohl (1986) argued that this system is a prime example of populations that are socially regulated well below the carrying capacity for the participating species. Powell (1989) extended this argument to suggest that the high diversity



of flock-participating species may be a result of large territory sizes with respect to resource abundance, which would reduce intraspecific competition and allow a number of specialist species to coexist on the same territories.

The core species of multispecific territorial associations (Munn and Terborgh 1979; Gradwohl and Greenberg 1980) appear to be highly consistent and ecologically regulated in composition. Simulation studies by Graves and Gotelli (1993) based on flock censuses by Munn (unpub.) uncovered some strongly nonrandom patterns, in which ecologically similar congeners (*Xiphorhynchus*, *Myrmotherula*, *Hylophilus*, and *Automolus*) co-occur significantly less often than expected in the same flocks. This analysis suggests that interspecific competition may regulate flock membership. However, no habitat data were presented in this study, and the species could instead be responding to subtle variations in forest structure.

#### *Decision Making in Multispecific Territorial Associations*

The existence of multispecific territories greatly complicates the question of how group movement is coordinated between a number of species. Up to this point I have argued that the movement pattern results from behavioral asymmetries between nuclear and attendant species. However, when a number of species occupy precisely the same home range, then movement coordination becomes the equivalent of a single-species coordination problem. The question is, which bird decides where in this complex territory to go next? The question is more complex than that for a single-species system because the participants have a much greater diversity of resource needs. In our (Greenberg and Gradwohl) studies of antwrens in Panama, we were unable to answer this question quantitatively. However, after many thousands of hours spent observing these groups, I am left with the impression that each antwren species is capable of initiating movement. Movement is often pseudopodic, with one or another of the antwren species moving out from the core. When the different species of antwrens are separated, each species calls antiphonally with the other to facilitate flock coalescence.

In contrast, as I stated earlier, the Amazonian understory flocks are formed and led by the activity and vocalizations of one or two antshrike species. The details of flock roles in these multispecific territorial associations may provide some insight into the evolution of these systems. The coalescing of a number of core species around one or two sentinel species turns out to be quite similar to the nu-

clear/attendant model. It differs only in that some of the attendant species have become sufficiently dependent upon the information provided by the sentinels to adjust their territories so as to assure constant association. The roles in antwren flocks, which appear to have a core of several species with more egalitarian or even complementary role relationships, suggest that these flocks develop from the mutual adjustment of the territorial boundaries of the core species. Detailed study of the bi- or multispecific territorial tits (Ludescher 1973; Ekman 1979; Bardin 1984; Pravosudov 1987) would be instructive. V. V. Pravosudov (pers. comm.) believed that the Siberian tit (*Parus cinctus*) was more numerous, dominant, and tended to lead in its association with willow tits.

Mixed flock territorial systems may represent a near obligatory mutualism (Munn and Terborgh 1979), which would set the stage for the evolution of complementary roles. On the other hand, it is equally plausible that the associations are the result of learned facultative adjustments of individuals. For example, the migratory chestnut-sided warbler spends up to 7 months of the year in the antwren flocks of Barro Colorado Island, where it defends the same territorial boundaries as the core species. Yet in nearby second-growth woods, warbler territories are one-tenth the size and unrelated to the territories of any other species. It has been argued that by adjusting their territory location and boundaries to those of ecologically similar resident birds, migrants can use the resident birds as cues for locating stable resources (Morton 1980; Greenberg 1984).

#### *Proximate Factors in Multispecific Territory Establishment and Maintenance*

What determines the locations of the stable and shared boundaries of multispecific territories? In the short run, replacement of individuals is slow, and the territories are maintained by the behavior of the remaining flock members and their neighbors. In the long term, what maintains these territories has yet to be determined. Are their boundaries traditional ones carried over from when the participating species first colonized an area of mature forest, or are they somehow determined by structures within the forest? Over a much shorter time frame, settlement pattern has been shown to have a profound effect on the size and configuration of territories. Krebs (1971) conducted a removal experiment on great tits (*Parus major*) and found that if a series of territorial occupants were removed simultaneously, new birds established a new array composed of

smaller territories. However, one-by-one removal of birds resulted in an array similar to the original. In stable multispecific territorial systems, we could be observing territorial arrays constrained by settlement patterns over very long periods of time. The alternative is the possible presence of stable habitat features. This possibility seems unlikely considering the continued occurrence of treefall gap succession. However, the habitat features that form the core of the antwren territories are areas of vine tangles, which may have a much longer existence than other parts of a tropical forest. In our studies of antwrens, there was one period when three sets of territorial individuals of both core species of antwrens disappeared. The territorial array then consisted of fused territories within the already existing external boundaries. When the population recovered and the fused territories split, the same internal boundary was reformed. That pairs of both of the core species disappeared and then were replaced to re-form the exact original territories suggests that boundaries are at least in part formed around some intrinsic structure in the forest. Perhaps, then, the different species in these flock systems defend the same territories because of individual responses to similar cues. This idea needs to be tested, but seems unlikely, given the different ecological requirements and body sizes of all the species involved. Furthermore, convergent territory boundaries do not seem to occur in bird communities where no mixed-species flocking is involved.

### Future Research Directions

In my mind, the fundamental issue facing mixed-species flock research is: to what degree does participation in mixed-species flocks select for behaviors or attributes that do not evolve in response to intraspecific interactions? A research program that addresses this fundamental question would integrate the analysis of flock behavior at the level of the individual, species, and whole flock: a daunting task—particularly for a Ph.D. candidate looking for a “doable” topic. Therefore, in table 18.4, I lay out some key questions that, if answered, should improve our understanding of mixed flock formation.

### Conclusions

For forest birds, involvement in multispecific associations is the rule during the nonbreeding season in the temperate zone and throughout the year in the tropics. For many intraspecifically solitary spe-

Table 18.4 Some hypotheses or questions for future research on mixed-species bird flocks

- A. Do flocks use their territories in an even, random, or patchy manner? If the latter, do the peaks of usage correspond to particular habitat features, territory centers, or territory boundaries?
- B. Do flocks move about the territory in predictable beats or variable and irregular paths? If the beat is regular, does this result in regularly spaced return times to specific areas? If the path is erratic, is the movement relatable to interactions with neighboring groups, or is it a tactic to evade tracking by predators?
- C. Is short-distance flock progression generally led by particular individuals and species, or is leadership shared evenly among a number of species? Do the leadership roles of species change with context (i.e., moving toward boundary, in core area, etc.)?
- D. Does flock formation depend upon the presence of particular species, as determined by removal experiments or their equivalent, and if so, when numerous flock systems are compared, do these species share behavioral traits? Alternatively, are there a number of species whose presence is sufficient to generate flock formation?
- E. Are certain vocalizations particularly efficacious for flock formation and movement?
- F. Does net benefit correlate with importance in flock formation as determined in C–E?
- G. Are roles in food finding, predator detection, and flock coalescence complementary between core flock members?
- H. In flocks in which core members have complementary roles, are net benefits more similar than in flocks in which one species performs most of the key functions?
- I. Are there vocalizations or behaviors of core flock members that function exclusively or primarily in an interspecific context, or are most behaviors shaped primarily by intraspecific interactions?
- J. Do mechanisms underlying social learning of resource distribution vary with flock role?

cies, such associations form the dominant social unit. These associations vary in their cohesion and stability. At their simplest, associations form around an attractive food resource, and interspecific interactions center primarily on conflict resolution and dominance relationships. Mixed-species flocks range from those that form when a number of species join a gregarious leader species, to those that have a leadership core of several species, to those that have a core of species that share and defend the same territorial boundaries. The last appears to reflect the greatest behavioral commitment to a mixed-species association because, unlike other mixed flock systems, it requires a complete adjustment of movement patterns and home range use to participate.

Mixed-species associations demand many of the same behavioral adjustments that are at the core of single-species group formation. However, the nature of these adjustments is often qualitatively

different between single- and mixed-species groups. Participants in single-species groups of vertebrates are morphologically similar and share the same basic ecological requirements. Differences in resource and home range use are based largely on quantitative differences or on variation in social status. Participating species in mixed-species groups show large qualitative differences in morphology and ecological requirements. These differences, essentially, make coordination of movement potentially more expensive, but reduce the effect of exploitative resource competition. They also open the possibility for individuals to play markedly different roles in detecting and mobbing predators and locating food sources. Furthermore, they underlie potentially large asymmetries in the costs and benefits of group formation.

Asymmetries of advantages and disadvantages between species have been postulated in numerous studies of mixed-species flocks, but rarely analyzed experimentally. This is an area of mixed flock formation research that is ripe for the picking. Asymmetry in roles in the maintenance of group cohesion is another area in which exciting work could be accomplished. Most researchers have viewed flocks as consisting of leader species, which play a central role in group movement and decision making, surrounded by a constellation of species that follow these species. However, within the stable core of mixed-species flocks we find the possibility of co-leadership—a phenomenon that has been rarely studied.

The most exciting possibility is that the multispecific social unit has exerted an important selective force on the communication systems and color patterns of the participating species. So far, evidence for the possibility that flock members have undergone significant coevolutionary changes is scant. It is my impression that mixed-species flocks form where the selective pressure to flock is great and under conditions consistent with the demands of intraspecific interactions. However, the natural historical observations suggest over and over again that these flock systems have overriding importance in the survival of forest birds, so coevolution of traits in flocking species remains a compelling possibility.

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#### CHAPTER NINETEEN



#### Keeping in Touch at Sea: Group Movement in Dolphins and Whales

RACHEL SMOLKER

#### A Dolphin's Day

We first come across Snubnose and Bibi, two male bottlenose dolphins as they are traveling rapidly out to the north, diving, surfacing, and breathing in perfect synchrony. Just out of synchrony, slightly farther apart, but keeping pace with them, is Sicklefin, another male and the third member of the alliance. Eighty meters to the west, and moving in parallel, are two more males, Wave and Shave. They are Snubnose, Bibi, and Sicklefin's "second-order alliance" partners. These two alliances will shadow each other's movements from a distance for much of the day, occasionally joining forces. We know that Snubnose, Bibi, and Sicklefin are "up to