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COOPERATIVE ROLES IN MIXED FLOCKS OF ANTWRENS (FORMICARIIDAE)

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Interspecific flocks of birds, so characteristic of the tropics although also occurring in temperate zones, often show features related to exploiting particular food resources, to reducing the risks of predation, and to maintaining flock organization by means of communication. Reviews by Rand (1954), Short (1961), and Moynihan (1962) suggest that flocking has potentially counteracting effects both on the efficiency of foraging and on the risks of predation. Under certain conditions, flocking might enhance the foraging efficiencies of some or all the participating individuals. For instance, individuals might capture insects flushed by other members of the flock (Swynnerton, 1915; Brosset, 1969), or flocks might exploit patches of abundant food more efficiently than solitary individuals could. Yet flocking also increases the chances of competition for food among flock members. Presumably in order to reduce this competition, related species in flocks often clearly differ in their feeding habits, especially in flocks of insectivorous birds (Moreau, 1948; Willis, 1966a, 1966b; Vuilleumier, 1967; Morse, 1967, 1969; Brosset, 1969). Flocks composed of several species with different feeding habits might well generate less competition among the participating individuals than would single-species flocks of the same size (Moynihan, 1962).

Flocking might also increase the efficiency of detecting, mobbing, or distracting predators (Miller, 1922; Tinbergen, 1951: 168–170; Kruuk, 1964). Yet a flock probably draws the attention of predators more than solitary individuals would, especially if the flock includes noisy or visually conspicuous species (Stresemann, 1917). Nevertheless, visual and auditory signals are critical for maintaining contact among the members of a flock, for attracting recruits to a flock, or for spacing individuals (Moynihan, 1960, 1962). Conspicuous colors, flash patterns, sharp calls, and restless movements, all of which facilitate locating and recognizing the individual bird, thus have a double effect. In addition to promoting flock integration, they must also attract predators. In general, adaptations that reduce the risks of predation, as well as those that reduce competition for food among flock members, should facilitate the evolution of flocking behavior. Yet flocks must compromise between adaptations that reduce predation and those that increase effective communication among flock members.

Observations of White-flanked, Checker-throated, and Dot-winged Antwrens (*Myrmotherula axillaris*, *M. fulviventris*, *Microrhopias quixensis*; Formicariidae), in small flocks on Barro Colorado Island, Panama, suggest that the two congeneric species have cooperative roles in the flocks, in order to promote both the maintenance of flock cohesion and effective mobbing of predators, a synergic interaction not reported previously among related, flocking species. The three antwren species also manifest clear differences in foraging behavior, which presumably reduce competition among them for food resources.

Johnson (1954), Slud (1960, 1964), and Skutch (1946, 1969) have reported that these three species flock regularly in Costa Rica and Panama. The flocks I studied foraged at medium elevations (1–10 m above ground), well below the canopy, in relatively mature forest.

PROCEDURES

Between 9 and 23 February 1969, I encountered as many as nine different flocks each day. Each flock was watched quietly for several minutes to an hour, depending on the ease of observation. My studies usually involved flocks in different places scattered throughout the forested parts of the island, and thus presumably different birds. To quantify foraging behavior I timed with a stopwatch sequences of 6–10 flits by one bird (each change of perch was a flit) and noted the foliage density and any movements to capture prey. I recognized three classes of foliage density based on the obstruction of my view by the foliage within ½ m of the bird: (1) less than about 50 per cent closed, (2) about 50–90 per cent closed, and (3) almost totally closed. Movements to capture prey included (1) gleaning, or plucking a prey item from a leaf, (2) sallying either to pluck an item from a leaf or from midair, (3) pecking the bark of a branch, and (4) investigating or probing in hanging dead leaves. The antwrens usually discovered me before I found them, and at first they often showed signs of uneasiness. Therefore, before collecting data, I allowed the birds to resume active foraging. Occasionally I recorded data several times from one individual. Whenever this was done, observations were recorded at least a minute apart and only if the bird had moved 5 m in the meantime. As the birds foraged very actively, after a minute they had usually changed to another tree. I collected data on at least 40 individuals of *Myrmotherula axillaris*, 22 *M. fulviventris*, and 27 *Microrhopias quixensis* in a total of 32 flocks. The sexes were about equally represented in the samples of all three species. About 1/5 of my data comes from flocks in which I detected only one species of antwren. Since these data show the same trends as the data from known mixed flocks, I have combined them for the following account. I found no differences in the foraging behavior of males and females in any of the species.

I recorded vocalizations with a Nagra III PHO tape recorder and a Sony F96 dynamic microphone and analyzed them on a Kay 6061-B Sound Spectrograph with the wide-band filter.

DESCRIPTIONS OF THE FLOCKS

I can only approximate the composition of these flocks for two reasons: quiet birds were easily overlooked in the foliage; and I watched different flocks for different lengths of time, a few of them quite briefly. I have depended primarily on records of 29 flocks that I studied after I could reliably distinguish both sexes of all three species of antwrens.

The three species were found together in about one-third (10/29) of the flocks, while in another 10/29 I detected only one of the species. *Myrmotherula axillaris* was recorded in 21 of the 29 flocks, *Myrmotherula fulviventris* in 17/29, and *Microrhopias quixensis* in 20/29. The flocks included 2–8 individual antwrens, though usually no more than one male and one female of each antwren species. As the birds flitted in the foliage and flew from tree to tree, the male and female of each species usually remained closer to each other (1–5 m) than to other antwrens present. Individuals of different species often drifted 10–20 m apart. However 10 of 29 flocks definitely included more than one antwren of the same sex and species. Some of these records might represent small family groups, but 7 of the 10 cases involved two male-plumaged birds of the same species in one flock (*axillaris* twice, *fulviventris* twice, *quixensis* three times). In three of these seven instances I noted intraspecific aggression (see below), although I never saw aggression in other situations. These observations suggest that the flocks usually included only one mated pair or a small family group of each species of antwren, and these individuals perhaps excluded other conspecifics by aggression.

Although the wide spacing of the birds gave the flocks a diffuse appearance, as a flock moved slowly through the forest all the antwrens went along. A flock sometimes fed in one area perhaps 25 m in diameter for up to 30 minutes and then quickly moved away through the forest, all the antwrens disappearing in the same direction. Another indication of the cohesion of the flocks was the tendency for all three species of antwrens to approach me and begin calling when I disturbed them by walking near. So although the antwrens often spaced themselves rather far apart while foraging, they converged into a smaller compass while mobbing me.

I identified 22 other species of birds in association with antwren flocks (Appendix); 14 of these species (marked with asterisks) followed the flock movements, while the others seemed only temporarily or even accidentally associated with the antwrens. Slaty Antshrikes (*Thamnophilus punctatus*), another formicariid, although the most frequent associates of the antwrens, usually remained behind when the antwrens moved. The Plain Xenops (*Xenops minutus*, Furnariidae) was the most common species that clearly followed the flocks. In only 5 of 29 flocks did individuals of other species outnumber antwrens. So far as I could determine, none of these species that accompanied the antwrens had an important role in regulating the behavior of the flocks.

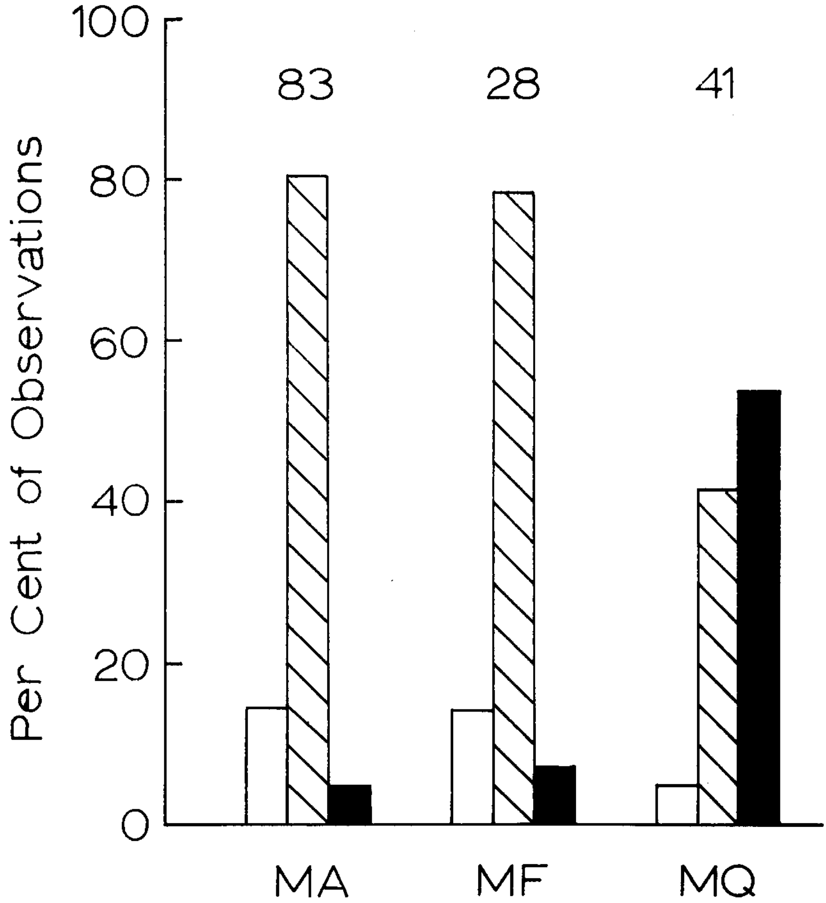

Figure 1. Foliage densities preferred by three species of antwrens. Black bars, densest foliage; hatched bars, foliage of intermediate density; clear bars, sparse foliage (see Procedures for details). The number above each column is the number of observations for each species. MA, *Myrmotherula axillaris*; MF, *M. fulviventris*; MQ, *Microrhopias quixensis*. MQ differs significantly from both MA and MF ($P < 0.01$ in both cases; $\chi^2 = 39.63$ and 12.30 respectively, 2 df). MA and MF do not differ significantly ($P > 0.9$; $\chi^2 = 0.13$, 2 df).

FORAGING BEHAVIOR

Antwrens of all three species flitted to a new perch every 1.0–4.4 seconds, with means for the three species lying between 2.24 and 2.35 seconds. In their choices of foliage density the two species of *Myrmotherula* hardly differed, but both contrasted with *Microrhopias*, which preferred the densest foliage (Figure 1). In techniques used to obtain

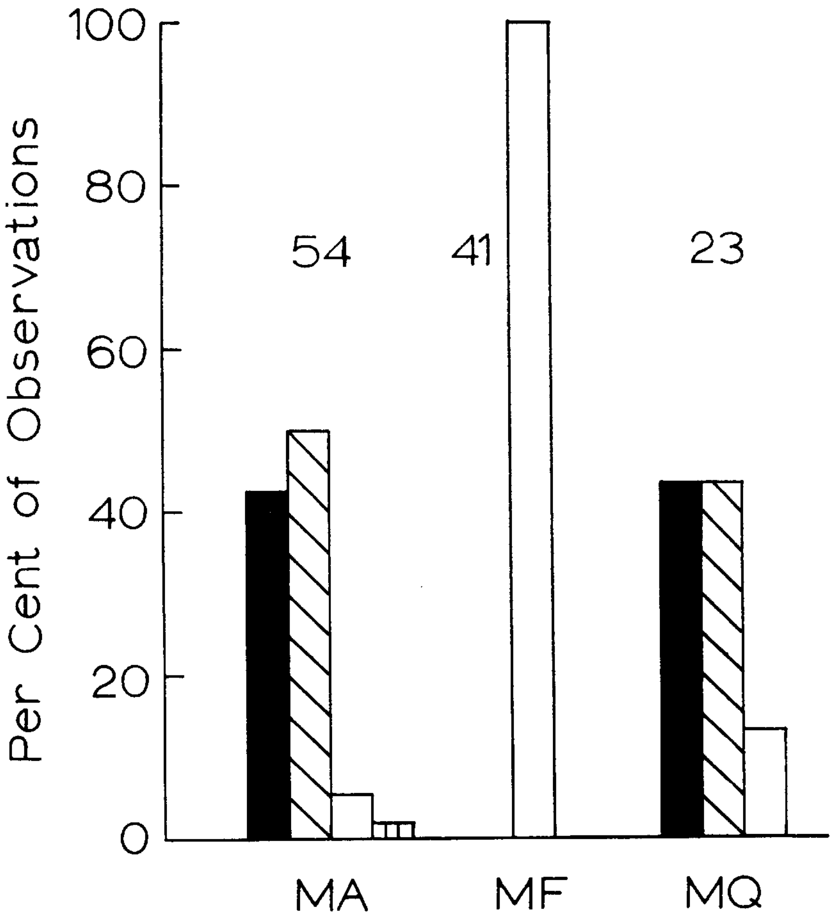

Figure 2. Prey capture techniques of three species of antwrens. Black bars, sallying; diagonally hatched bars, gleaning; clear bars, probing dead leaves; vertically hatched bar, pecking bark on a branch. Otherwise the notation is the same as in Figure 1. MF differs significantly from both MA and MQ ($P < 0.001$ in both cases; $\chi^2 = 82.61$ and 51.82 respectively, 2 df), while MQ and MA do not differ significantly ($P > 0.5$; $\chi^2 = 1.27$, 2 df).

prey, on the other hand, *M. axillaris* and *Microrhopias* hardly differed, while *M. fulviventris* relied virtually exclusively on probing dead leaves (Figure 2). Thus the two species that preferred the same foliage densities differed in their techniques of prey capture.

Foraging *Myrmotherula axillaris* typically flitted from perch to perch amongst the foliage of lower story trees, 2–10 m above ground. Between flits a bird peered at the nearby leaves, tilting and craning its head several times. A bird caught small food items by plucking them from the upper or lower surface of a leaf without leaving its perch, or by flying forth, sometimes to the distance of a meter, and snatching a prey item either in midair or from the undersurface of a leaf. After such a sally the bird usually tumbled downward fluttering for a meter or so before regaining its stability and flying to a new perch. *Microrhopias quixensis* also flitted in the lower story trees, where they preferred the densest foliage, often in tangles of vines. Instead of peering and craning like *axillaris* on each perch between flits, *Microrhopias* turned abruptly from side to side through a wide arc, maneuvers that might permit the bird to see farther in dense foliage. Perhaps owing to its longer tail, *Microrhopias* was more adept at sallying than *M. axillaris.* It could hover neatly near a leaf, then fly straight to a new perch without the fluttering tumble seen in *axillaris. Myrmotherula fulviventris* often hung obliquely or upside down to probe the curled dead leaves on trees in the understory. James Karr (pers. comm.) and Skutch (1969) had previously noticed that *fulviventris* forages preferentially in dead leaves.

PLUMAGE PATTERNS AND VOCALIZATIONS

Male *Myrmotherula axillaris* and both sexes of *Microrhopias quixensis* have black and white patterns that are conspicuous among the greens and browns of the forest. Basically these birds are black, or in female *Microrhopias* black and chestnut, with white spotting on their wing coverts. In addition, all have flash patterns. *M. axillaris* males reveal white flanks when they lift their wings, and the long tail feathers of *Microrhopias* have conspicuous white tips. In contrast, drab plumages characterize female *M. axillaris* and both sexes of *M. fulviventris,* all of which are brown with buff spotting on their wing coverts. Thus of the three species, the only male with drab plumage is *M. fulviventris.*

The vocalizations of *M. fulviventris,* however, are conspicuous. When I approached a flock, or when a flock approached me, the most frequent calls were loud, sharp "tseeks" (Figure 3a) from both sexes of *fulviventris.* This call resembles those other passerines use when mobbing predators. It shares with them the sudden changes of pitch which should make it easy to locate (Marler, 1956). Although I could not actually measure the intensities of the antwrens' vocalizations, this "tseek" call of *M. fulviventris* struck me as the loudest, as well as the most easily located, of the three species' vocalizations. Usually the calling stopped quickly if I remained still, though occasionally a bird would approach uttering loud "tseeks" and apparently mob me. In similar circumstances both sexes of *M. axillaris* gave a softer, mewing "pew pew pew" or "pew

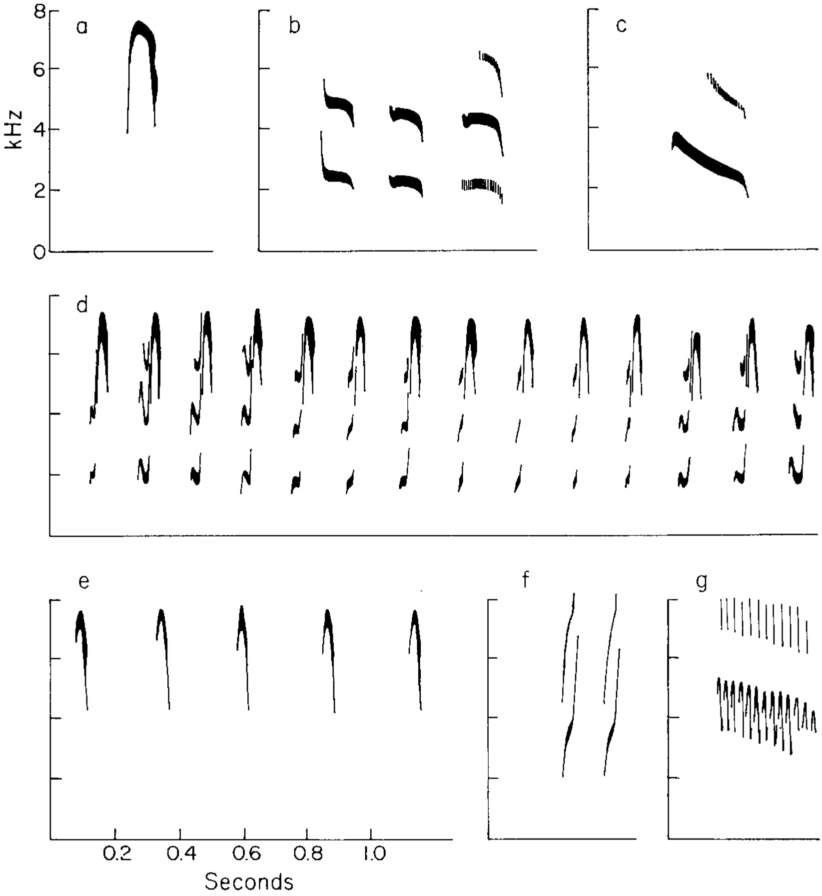

Figure 3. Vocalizations of antwrens: tracings of spectrograms made with the wide bandpass filter. The ordinate is frequency in intervals of 2 Khz; the abscissa is time in intervals of 0.2 seconds. (a) "Tseek," *Myrmotherula fulviventris*; (b) "pew pew pew," *Myrmotherula axillaris*; (c) "peeeu," *Microrhopias quixensis*; (d) fast sequence, *M. fulviventris*; (e) slow sequence, *M. fulviventris*; (f) "whit whit," *M. axillaris*; (g) rattle, *M. quixensis.*

pew" (Figure 3b), the first note slightly higher in pitch. Both sexes of *Microrhopias* produced a distinctive "peeeu" (Figure 3c), longer and clearer than the notes of *axillaris.* Each of these calls was species-specific and readily recognized.

Twice I saw prolonged encounters between two male *M. fulviventris,* one of which I tape-recorded. In both instances much supplanting and chasing occurred. Males ruffled their black and white throat feathers, flicked their wings, and nervously jerked their bodies from side to side. Three vocalizations were noted each time: (1) the loud "tseek" described above; (2) a rapid sequence, "tseetseetseetsee. . .," with almost 6 notes per second (Figure 3d); and (3) a slower sequence, "tsee tsee tsee tsee," with about four notes per second, the first note often slightly higher and more emphatic (Figure 3e). This slow sequence I also heard on occasions when I had no indication of the presence of more than a pair of *M. fulviventirs*, so this vocalization might have the advertising function typical of many birds' songs.

Twice I witnessed encounters between two or three male *Microrhopias*. Both times I saw chases and constantly heard the "peeeu" note described above. One male before starting a chase adopted a head-forward posture with his wings raised, his white interscapular feathers ruffled, and his tail partly fanned.

Time after time I noted that, except when alarmed by my approach or engaged in intraspecific aggression, the flocks were very quiet; nothing could be heard but soft chips, probably "contact" notes. All three species uttered these chips at irregular intervals. *M. axillaris*, for instance, had a soft, double "whit whit" (Figure 3f). Occasionally, with unknown stimulus, a *M. axillaris* would utter several "pew pews," or a *M. fulviventris* would produce one or two slow sequences of "tsee tsee tsee tsee," or a *Microrhopias* a few "peeeus." *Microrhopias* several times produced a weak, dry rattling (Figure 3g). Otherwise only weak chips informed me of the antwrens' presence.

DISCUSSION

As flocking has counteracting consequences both for obtaining food and for avoiding predators, different compromises might evolve. For some species, flocking might confer advantages in exploiting a food resource that override the disadvantages of increased competition for food among the flocking individuals and increased risks of predation. For other species, flocking might confer advantages in reducing the risks of predation that override the disadvantages of somewhat reduced foraging efficiency and increased competition for food. My observations could not confirm whether flocking by the three species of antwrens confers advantages in exploiting food resources, in avoiding predators, or both. However I did note adaptations that would reduce any disadvantages of competition for food and exposure to predators, yet permit effective intraflock communication.

The three species of antwrens exhibited complementary feeding habits. In the combination of its techniques of prey capture with its choice of foliage, each species differed from the other two. These flocking antwrens have thus apparently reduced the disadvantages of interspecific competition for food. Furthermore, intraspecific antagonism might regulate the number of conspecifics in each flock and thus regulate intraspecific competition. The wide spacing of individuals within a flock should also help to minimize competition among them.

The Plain Xenops also has characteristic foraging habits. They feed, as Skutch (1969) describes, by clinging to slender, hanging, dead twigs and vines while pecking at the rotting bark. The behavior of the greenlet (*Hylophilus decurtatus*, Vireonidae) and certain wintering North American warblers (*Dendroica, Vermivora*; Parulidae) resembled the flitting, gleaning, and sallying of the antwrens more closely, but I have no quantitative data for assessing how much these species might overlap the antwrens' feeding habits.

When mobbing me, the antwrens used their loudest calls and tended to keep in the open and closer together than when foraging. These mobbing reactions are probably the basis for Johnson's (1954) impression that antwren flocks are noisy. Usually my first contact with a flock came when the antwrens suddenly began calling loudly as they converged around me. A natural predator would probably elicit similar behavior. In contrast, an undisturbed flock ordinarily used only soft, chipping notes, behavior that made the flocks inconspicuous when they were out of sight in the forest.

The antwrens' plumages and vocalizations suggest how these species compromise between effective intraflock communication and the risks of predation. Visually the most conspicuous members of antwren flocks were male *M. axillaris*, but acoustically *M. fulviventris* surpassed the other two species, both with its occasional slow sequences of "tsee tsee tsee tsee" and with its piercing "tseek" when the flock was alarmed. The calls of *M. axillaris* and *Microrhopias*, although they could become insistent, were in comparison more difficult to locate and probably softer. Thus among the three antwrens, the most conspicuous vocalizations appear in the species with the least conspicuous plumage.

Again the Plain Xenops fits well into antwren flocks. A drab bird, resembling *M. fulviventris* in general hue, its calls if anything exceed those of *fulviventris* in intensity and piercing quality. In fact its calls superficially resemble two of those of *fulviventris*: an almost ringing "tsik" and a ringing rattle that rises slightly in pitch.

The salient calls of *fulviventris* featured prominently in mobbing, and this species' drab plumage might in part compensate for the risks involved in using these conspicuous, easily located calls. Male *axillaris* with their bold plumage and their preference for more open foliage probably provide visual signals that maintain flock cohesion, although their bold plumage patterns might also function in epigamic or agonistic interactions or even serve to flush insects. Perhaps in compensation for this visual conspicuousness of the male, *axillaris* has less easily located calls. If antwrens routinely used sharp calls to maintain flock cohesion, their calls might well attract predators to the flock from a distance through the forest. Although both sexes of *Microrhopias* have bold patterns, they frequent the densest foliage, so their patterns probably serve to maintain visual contact only over short distances, for instance between mates.

Thus the two *Myrmotherula* antwrens seem to have cooperative roles that enhance both maintenance of contact among individuals within a flock and mobbing responses to predators. Male *M. axillaris* appear to have a special role in maintaining flock cohesion by means of visual signals, while the loud calls of *M. fulviventris* enhance the effectiveness of mobbing.

Moynihan (1962, 1968) has discussed another type of coadaptation among certain regularly flocking species: the convergent or parallel evolution of similar plumage patterns or colors in order to facilitate interspecific communication within flocks. Male *Myrmotherula axillaris* and *Microrhopias quixensis* provide a good example of two regularly flocking species with similar plumage patterns. Here too coadaptation might result in synergy among regularly flocking species.

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Summary

Observations of mixed flocks of antwrens (*Myrmotherula axillaris, M. fulviventris,* and *Microrhopias quixensis*; Formicariidae) in Panama suggest that the two congeners have cooperative roles in the flocks. The sharp vocalizations of *fulviventris* should enhance mobbing of predators, while the flash patterns of male *axillaris* should promote maintenance of flock cohesion by visual contact. The three species differ significantly in their foraging behavior, which presumably reduces interspecific competition for food.

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APPENDIX

Other Species Associating with 44 Antwren Flocks

In the following list the name of each species is followed by three numbers, respectively the number of flocks in which the species was seen, the total number of individuals in all flocks, and the maximum number of individuals in any one flock. Asterisks mark species that clearly followed the flocks' movements, and daggers indicate species that breed in temperate North America.

Slaty Antshrike (*Thamnophilus punctatus*) 15, 25, 3; Plain Xenops (*Xenops minutus*)* 9, 12, 3; Chestnut-backed Antbird (*Myrmeciza exsul*) 5, 7, 2; Brown Woodcreeper (*Dendrocincla fuliginosa*)* 5, 5, 1; Buff-throated Woodcreeper (*Xiphorhynchus guttatus*)* 4, 6, 2; Gray-headed Greenlet (*Hylophilus decurtatus*)* 4, 6, 2; Spotted Antbird (*Hylophylax naevioides*) 4, 4, 1; Black-tailed Trogon (*Trogon rufus*) 3, 4, 2; Gray-chested Dove (*Leptotila cassinii*) 2, 2, 1; Black-and-White Warbler (*Mniotilta varia*)*† 2, 2, 1; Kentucky Warbler (*Oporornis formosus*)*† 2, 2, 1; White-shouldered Tanager (*Tachyphonus luctuosus*) 2, 3, 2; White-whiskered Puffbird (*Malacoptila panamensis*) 1, 1, 1; Rufous Motmot (*Baryphthengus ruficapillus*) 1, 1, 1; Scaly-throated Leafscraper (*Sclerurus guatemalensis*) 1, 1, 1; Spot-crowned Antvireo (*Dysithamnus puncticeps*)* 1, 1, 1; Dusky-capped Flycatcher (*Myiarchus tuberculifer*) 1, 2, 2; Golden-crowned Spadebill (*Platyrinchus coronatus*)* 1, 1, 1; Worm-eating Warbler (*Helmitheros vermivora*)*† 1, 1, 1; Tennessee Warbler (*Vermivora peregrina*)*† 1, 1, 1; Chestnut-sided Warbler (*Dendroica pennsylvanica*)*† 1, 1, 1; Bay-breasted Warbler (*Dendroica castanea*)*† 1, 1, 1; unidentified small tyrannids* 6, 6, 1; unidentified *Dendroica**† 3, 3, 1.