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MULTI-SPECIES TERRITORIALITY IN NEOTROPICAL FORAGING FLOCKS

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Multi-species flocking behavior in birds assumes a wide range of forms. At one extreme are casual feeding aggregations such as those of herons and seabirds (Sealy 1973, Baltz 1977, Kushlan 1977). Showing somewhat more social and temporal cohesiveness are the restless flocks of blackbirds or sandpipers that form and dissolve on a daily basis (Recher 1966, Recher and Recher 1969, Goss-Custard 1970, Page and Whitacre 1975, Burtt and Giltz 1977). Winter foraging groups of chickadees (*Parus* sp.) and their consorts represent a further step towards continuity and organization (Morse 1970, Austin and Smith 1972, Glase 1973, Smith 1976, Hogstad 1978). These flocks form daily during the non-breeding season and may include many of the same individuals. Tropical mixed-species foraging flocks are even more constant, existing virtually year-round (Winterbottom 1943, Davis 1946, Short 1961, Moyniham 1962, McClure 1967, Wiley 1971, Buskirk et al. 1972, Fogden 1972, Croxall 1976, Partridge and Ashcroft 1976, Fairchild et al. 1977, Pearson 1977, Rubenstein et al. 1977, Greig-Smith 1978, Jones 1978).

We describe here a syndrome of flock behavior that appears to represent the endpoint of this series. It occurs in the mixed parties of small insectivorous birds that glean the understory foliage of Amazon basin forests. These flocks are an important part of the bird life of the forest. They form daily in the hour following dawn and persist until late afternoon. This pattern is followed throughout the year, regardless of the amount of current breeding activity. Many species join these flocks, though under a variety of circumstances, detailed later.

By means of color-banding and observation we have discovered that these flocks possess the following properties. First, the core membership of the main study flock at our site in southeastern Peru consisted of 12 species whose territories coincided exactly. Observations on four neighboring flocks revealed that not all of the "core" species in the main study flock are present in every flock (Tables 1 and 2). Second, membership in these flocks appeared to be limited to one family of each species (i.e., a mated pair with perhaps one or two juveniles). This means that the core species possessed nearly identical population densities over large areas. If this pattern is common, it helps to account for the unusually high equitability of netted bird samples from the Amazonian lowlands (Terborgh and Weske 1975). Third, territorial defense was communal. Boundary disputes arose infrequently when neighboring flocks happened to meet. When this occurred, a prolonged confrontation might ensue, marked by vigorous vocal activity on both sides. Otherwise, territorial songs rarely were given by most of the species. Fourth, nesting of flock members took place within the jointly-held flock territory. Young birds remained closely associated with their parents in the flock for at least several months and perhaps for as much as a year after fledging.

In addition to documenting these findings, we present data on the ecological sorting of flock members, and propose a new interpretation of the status of so-called "occasional" flock members.

METHODS

STUDY SITE

The study site was situated at 71°19′W, 11°51′S (elevation ca. 400 m) in undisturbed rainforest within 1 km of the Manu River at the Cocha Cashu Biological Station in Manu National Park. The Park includes portions of the departments of Cuzco and Madre de Dios in southeastern Peru.

The terrain in the study area (Fig. 1) is flat except for gentle depressions and rises left from ancient changes in the course of the river. In the rainy season, flooding occurs in low areas near the river and in shallow depressions in the forest.

This study was conducted in July 1974, August through November 1976, and July and August 1978. Two rainy seasons occur here: a lesser one from October into December and a greater one from February into April. July and August usually are the driest months. Approximately 2.1 m of rain fell at this site from September 1976 to late August 1977. Sections of the forest became swampy or locally flooded during the wettest periods, although none of the 8 ha used by the main study flock flooded.

The study area was primary tropical forest. The tallest trees in the canopy rose to 60 m, below which were several tree layers, as described by Richards (1952). We

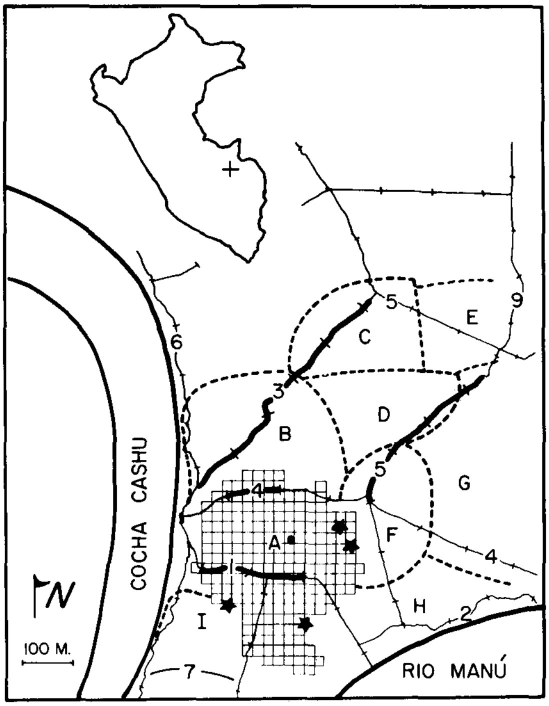

FIGURE 1. Map of study site and trail system at Cocha Cashu Biological Station, Manu National Park, Peru. Location in Peru is indicated by the cross in the inset map. The territory of the principal study flock (A), is contained within the area of the 20-m square grid. Stars mark the positions of territorial conflicts with neighboring flocks, and the dot beside 'A' pinpoints a small pool that was used frequently for bathing. Letters A through I, and the enclosing dashed lines approximately indicate the territories of nine different flocks. Thin lines and numbers designate trails. These are marked at 100-m intervals, as shown by the ticks. Netting was conducted on the heavily darkened portions of the trail system.

could walk easily through the open understory except where trees had fallen.

PROCEDURES

Birds in the understory of the study area have been aluminum-banded annually in July or August since 1973. We color-banded potential flock birds from 21 August 1976 through 3 September 1976 and from 4 July through 15 July 1978 along about 1.2 km of trails in the study area (Fig. 1). Four nestlings of three flock species also were color-banded during the 1976 study period.

Terborgh followed flocks for 100 h during July 1974, noting their composition and foraging. Munn followed several of the flocks in the netting region for a total of about 340 h from 4 September through 20 October 1976 and from 15 July through 19 August 1978. During these periods he determined which color-banded and unbanded birds comprised the different flocks.

RESULTS

FLOCK COMPOSITION

Daily study of one principal flock in both the 1976 and 1978 field seasons and of four additional flocks in the 1978 season confirmed the constancy of flock membership. The same individuals lived together day after day, and unfamiliar individuals of the core species were rarely seen within the territory. Individuals of many other species joined the flock with varying frequency, as will be discussed later.

Two species of antshrike, the Bluish-slate Antshrike (*Thamnomanes schistogynus*), and the Dusky-throated Antshrike (*T. ardesiacus*), served as nuclear species, sensu Moynihan (1962). These birds possess the full set of characteristics described by Moynihan as typical of nuclear species. Their plumage is dull and monotone, except for the female *T. schistogynus*, which is bicolored (slate gray with a brick-red abdomen). Both species are nervously active, and noisy. Frequent reversals of perch stance are accompanied by wing-flicking. Both species have relatively loud and distinctive calls that are repeated frequently throughout the day. These calls seemed to provide the rallying cry for the other species as they assembled each morning, and appeared also to signal the movements of the flock as it progressed through the forest. The territorial songs of the antshrikes differ from the calls that served to rally the flock.

As well as being the nucleus of the flock, the antshrikes appeared to direct the flock's movements. On many occasions one or another of these birds moved to and called from a spot perhaps 20–30 m from the current flock position. Other flock members almost invariably followed these leads, although not always immediately. *Thamnomanes schistogynus* seemed to be the more important of the two species at our study site by virtue of its louder, more insistent call and higher foraging position. But where it is absent (e.g., Peru's Apurimac Valley), flocks with virtually the same composition form around *T. ardesiacus*. Foraging individuals or groups of the core species are rarely found except in the presence of *Thamnomanes*. When one does encounter such groups, it usually turns out that antshrikes have been quietly resting in the vicinity all the while.

TERRITORIALITY

The principal study flock held a communal territory of about 8 ha (Fig. 1). We ascertained the boundaries of this territory by following the resident flock on 29 days for a total of approximately 213 h. After the flock was followed continuously (from dawn to dusk) for one 22-day period, its movements were mapped with reference to a 20-m grid system (Fig. 1). Territorial limits were judged from the extremities of the flock's wanderings. The locations of boundary confrontations with neighboring flocks also helped delimit the flock's territory. Individuals showed a pronounced long-term fidelity to their flocks; of 20 members of the study flock that were color-banded in 1976, 9 were observed together in the same area in 1978.

CONFRONTATIONS

Four flock confrontations occurred during the 1976 study period (Fig. 1). When the study flock encountered another flock near its territorial boundary, the lead species of antshrike immediately began giving vociferous territorial songs (very different from the location calls). The *Myrmotherula* antwrens also uttered special territorial songs. Representatives from the two flocks would assume aggressive display postures while facing one another—heads lowered, wings lowered and quivering, and tails depressed and fanned. Territorial songs would be given frequently as conspecific opponents (usually males) zipped from perch to perch, posturing dramatically. The females joined in to a lesser extent with territorial songs, noisy calls, and displays.

Male Bluish-slate Antshrikes and male White-flanked Antwrens (*Myrmotherula axillaris*) flashed otherwise-concealed white shoulder patches at their adversaries, while male and female Dot-winged Antwrens (*Microrhopias quixensis*) puffed out concealed white back patches and simultaneously fanned and cocked their white-lined tails. Each pair specifically directed its vocal and postural displays toward conspecifics in the neighboring flock. If a species was not represented in the other flock, the representatives from the study flock would continue foraging and let flockmates carry on the dispute. Very little physical combat was seen, although aerial chases were common. These confrontations often took 20 to 30 min to be resolved, as one flock slowly wandered off toward the interior of its territory.

AGGRESSION

During the 1976 observation period, fighting and agonistic display within the study flock were limited to frequent noisy encounters between two color-banded male Long-winged Antwrens (*Myrmotherula longipennis*). We do not know the relationship, if any, of these two males. The birds assumed aggressive display postures and noisily chased each other as often as seven or eight times each day, frequently flashing their concealed white shoulder patches.

DAILY SCHEDULE

The birds coalesced into a noisy flock at 06:00–06:45 (n = 15 mornings), seemingly rallying to the location calls of the antshrikes. By 07:00 the flock was foraging quietly, either in one spot or while slowly moving through the forest at an average rate of about 60 m/h (based on 188 h of following the main study flock). Foraging continued all day until the flock fragmented at 16:45–17:00, at which time many of the birds would repair to the small pool for bathing (Fig. 1). In July 1974, Terborgh noticed on several days that the flock was quieter and less active between 12:00 and 15:00, with individuals preening and resting for up to a half hour while others continued foraging.

We believe that flock members roosted separately because of the manner in which flocks formed in the morning. Only once were we able to follow flock individuals to roosting places: we watched a marked pair of Dusky-throated Antshrikes roost in low trees within 70 m of the spot where the flock rallied the following morning. In the late afternoon flocks fragmented gradually as, one by one, species left for their respective roosts. At least one group, the woodcreepers (*Dendrocolaptidae*), are known to roost solitarily in holes (Skutch 1977), and thus almost certainly did not roost with flockmates.

ECOLOGICAL SEGREGATION WITHIN THE FLOCK

The core species were all exclusively insectivorous. One might thus suppose the potential competition between them to be very intense. Nevertheless, nearly all pairs of species differed in one or more of the following foraging variables: size, foraging technique (gleaning, sallying, probing), foraging height, or foraging substrate (Table 1). Prior to observation, the seven species of *Myrmotherula* antwrens seemed the most likely to show severe interspecific competition for food; they all weigh 8–11 g, and are morphologically similar. But Plain-throated Antwrens (*M. hauxwelli*) and Pygmy Antwrens (*M. brachyura*) foraged very low and very high, respectively. White-eyed Antwrens (*M. leucophthalma*) and Ihering's Antwrens (*M. iheringi*) specialized respectively on dead leaves and on the undersides of vine stems and dead twigs.

Gray Antwrens (*M. menetriesii*) foraged higher than the two remaining congeners, *M. axillaris* and *M. longipennis*, which remain puzzling because they appeared to overlap broadly in foraging height, foraging technique, and substrate (Table 1).

The morphologically very similar *Thamnomanes* species separated in vertical foraging ranges (Table 1). In the woodcreeper assemblage, the species differ not only in weight (and presumably prey-size), but Olivaceous Woodcreepers (*Sittasomus griseicapillus*) seem to use thicker tree trunks than Striped Woodcreepers (*Xiphorhynchus obsoletus*).

BREEDING BEHAVIOR

Breeding behavior displayed by flock birds during the study period is summarized in Table 1. Breeding activity increased in October and into November. This may be associated with an increase in insect abundance that has been found to accompany the beginning of the wet season at other tropical localities (Janzen and Schoener 1968, Ward 1969, Robinson and Robinson 1970, Fogden 1972, Janzen 1973, Smythe 1974, Buskirk and Buskirk 1976).

Pairs maintained their flock membership even while breeding. The best evidence of this came from *Myrmotherula axillaris* and *M. iheringi* (Table 1). In both cases, the males and females took four or five-hour incubation shifts. The free member of the pair often would join the flock for foraging, even at distances greater than 100 m from the nest. Later, when feeding nestlings, both parents foraged within 50 m of the nest. When the flock approached the nest area, the parents would forage peacefully with their flockmates, leaving frequently to take food to the nestlings.

When two White-flanked Antwren nestlings fledged on 3 October 1976, the parents fed them in vine tangles for several days. Once the young could fly well enough, they accompanied the parents in the mixed flock, continuing to be fed regularly. By 17 November, the two fledglings had molted and from a distance resembled adult male and female antwrens; yet they still foraged with their parents in the flock. This could explain why Wiley (1971) often saw more than one male or female of a species in the antwren flocks he observed in Panama.

STATUS OF SPECIES OTHER THAN CORE MEMBERS

Core species as we define them here occur in many to all understory flocks and equally share the jointly-held flock territory. They spend virtually all of their time in the flocks. Over 30 additional species joined understory flocks with varying degrees of regularity, and under various circumstances (Table 2). Such species have been widely referred to in the literature as "occasional" or "irregular" flock members (Moynihan 1960, 1962, Short 1961, McClure 1967, Vuilleumier 1967). Our observations show, however, that many of the additional species are not just casual flock joiners. In fact, only one out of six distinguishable categories of flock-joining behavior can be fairly regarded as occasional (Table 2).

Type I: Core species present in all five surveyed flocks. Described earlier.

Type II: Core species with lower population densities than Type I species. Ten species at our study site were less numerous than the six Type I species but nevertheless seemed to forage mainly, if not exclusively, in understory flocks. Pairs of six of these species were full-time members of the 1976 study flock. At least six of the Type II species (*not* the same six) were seen consorting with different flocks on different days, and evidence suggests that some of these birds may have switched from flock to flock within a few hours. What incited birds to switch flocks was not clear. The only apparent requirement was that there were no conspecifics in the other flock.

Type III: Species with territories smaller than a flock territory. At least two species at Cocha Cashu tended to join understory flocks but maintained population densities considerably greater than those of the core species. *Myrmotherula hauxwelli* is the best example: its population density was roughly 2.5 times greater than that of congeneric core species, a fact that we have established by direct observation of banded birds, as well as from net sampling. The pairs of this antwren maintained a conventional system of close-packed territories. Much of the time the pairs foraged by themselves, but when a flock entered a territory, the owners usually would join and follow it for as long as it remained in the territory. We frequently observed disputes between neighboring pairs as a flock passed over a territorial boundary.

Type IV: Species that opportunistically join both canopy and understory flocks. Mixed-species flocks of several types occur in the Amazon forests (Willis 1977). We have mentioned only the type composed of

TABLE 1. Foraging and breeding behavior of flock species. Data from September through November 1976 and July through August 1978 on one main study flock and on four other nearby flocks.

Category and species	Mean weight (g)	Mean foraging height (N) (SD)	Foraging[1] method	Foraging substrate	Members of 1976 study flock	Breeding behavior	
						Activities	Dates[2]
TYPE I: CORE SPECIES							
Dusky-throated Antshrike (*Thamnomanes ardesiacus*)	18.0	3.10 m (184) (2.18 m)	S	surfaces of foliage, airspace	1♂, 1♀ 1 juv.	molting juvenile bird travels with parents in flock	entire period (4 Sept.–18 Nov. 1976)
Bluish-slate Antshrike (*Thamnomanes schistogynus*)	17.1	7.39 (69) (3.68)	S	surfaces of foliage, airspace	1♂, 1♀	courtship feeding, nest-building, copulation	9 Oct.–20 Oct.
White-flanked Antwren (*Myrmotherula axillaris*)	8.2	5.43 (181) (2.90)	G	foliage	1♂, 1♀	nest-building, incubation, fledge 2 young (3 Oct.), fledglings travel with flock	entire period
Long-winged Antwren (*Myrmotherula longipennis*)	9.5	4.58 (90) (2.28)	G, S	foliage, branch tips	1♂, 2♀ (1 juv. ♀?)	nest-building, courtship feeding or feeding juvenile	11 Oct.–20 Oct.
Gray Antwren (*Myrmotherula menetriesii*)	8.7	8.88 (24) (1.63)	G	foliage, vine tangles	1♂, 1♀	none seen	—
Rufous-tailed Foliage-gleaner (*Philydor ruficaudatus*)	27.0	9.31 (33) (4.16)	P, G	vine stems	1 (sex unkn.)	none seen	—
TYPE II: REGULAR FLOCK SPECIES							
Ihering's Antwren (*Myrmotherula iheringi*)	8.4	5.15 (44) (2.09)	G	undersides of dead twigs and vine stems	1♂, 1♀	nest building, incubation, fledge 1 young (8 Nov.)	3 Oct.–8 Nov.

TABLE 1. Continued.

Category and species	Mean weight (g)	Mean foraging height (N) (SD)	Foraging[1] method	Foraging substrate	Members of 1976 study flock	Breeding behavior	
						Activities	Dates[2]
White-eyed Antwren (*Myrmotherula leucophthalma*)	9.5	2.78 (89) (1.90)	G, P	dead leaves	1♂, 1♀	nest-building	15 Oct.–20 Oct.
Striped Woodcreeper (*Xiphorhynchus obsoletus*)	35.3	5.46 (24) (4.21)	P	thin tree trunks	1 (sex unkn.)	none seen	—
Olive-backed Foliage-gleaner (*Automolus infuscatus*)	42.6	1.95 (26) (1.67)	G, P	stems, dead leaves, foliage	1 (sex unkn.)	none seen	—
Plain Xenops (*Xenops minutus*)	12.5	5.97 (28) (3.33)	P Pecking	ends of broken twigs, dead vine stems	—	—	—
Tawny-crowned Greenlet (*Hylophilus ochraceiceps*)	11.9	4.82 (28) (2.49)	S, G	foliage tips	1♂, 1♀	nest-building	5 Oct.
Red-crowned Ant-Tanager (*Habia rubica*)	32.3	3.63 (42) (1.95)	G	foliage	1♂, 1♀	none seen[3]	—
TYPE III: TEMPORARY FLOCK SPECIES							
Plain-throated Antwren (*Myrmotherula hauxwelli*)	11.0	.30 (84) (.26)	G	vertical stems, ground	—	—	—
TYPE IV: SWITCHING SPECIES							
Olivaceous Woodcreeper (*Sittasomus griseicapillus*)	15.1	8.35 (27) (4.88)	P	large trunks	—	—	—
Pygmy Antwren (*Myrmotherula brachyura*)	7.0	12.51 (20) (5.05)	G	vine tangles, branch tips	—	—	—
White-winged Shrike-Tanager (*Lanio versicolor*)	18.5	15.27 (25) (7.37)	S	undersurfaces of foliage	1♂, 1♀	nest-building	18 Nov.
TYPE V: PATCH SPECIES							
Dot-winged Antwren (*Microrhopias quixensis*)	10.2	8.91 (33) (3.06)	G, S	live vine tangles, bamboo	—	—	—

[1] G = gleaning, S = sallying, P = probing.
[2] Breeding behavior observed between 4 Sept. and 18 Nov. 1976.
[3] Two other pairs of *Habia rubica* were observed in breeding activities during the 1976 study period.

TABLE 2. Categories of flock-joining behavior in understory species at Cocha Cashu.[2]

TYPE I: Core species—equal shareholders in joint territory.[3]			
Thamnomanes ardesiacus[1]	5/5	*Myrmotherula longipennis*[1]	5/5
Thamnomanes schistogynus[1]	5/5	*Myrmotherula menetriesii*[1]	5/5
Myrmotherula axillaris[1]	5/5	*Philydor ruficaudatus*[1]	5/5
TYPE II: Core species with lower population densities than Type I species. Some hold territories larger than a single flock territory and alternate regularly between two or more adjacent flocks.			
Myrmotherula iheringi[1]	2/6	Buff-throated Foliage-gleaner (*Automolus ochrolaemus*)	1/4
Myrmotherula leucophthalma[1]	3/4		
Xiphorhynchus obsoletus[1]	1/3	*Xenops minutus*	2/4
Spix's Woodcreeper (*Xiphorhychus spixii*)	1/3	Striped Woodhaunter (*Hyloctistes subulatus*)	1/4
Automolus infuscatus[1]	1/3	*Hylophilus ochraceiceps*[1]	1/3
		Habia rubica[1]	2/4
TYPE III: Temporary flock species; hold separate territories smaller than flock territory; enter and drop out as flock passes through.			
Myrmotherula hauxwelli		Black-faced Antbird (*Myrmoborus myotherinus*)	
TYPE IV: Switching species; regular members of canopy flocks that occasionally to frequently join understory flocks.			
Wedge-billed Woodcreeper (*Glyphorynchus spirurus*)		Yellow-margined Flycatcher (*Tolmomyias assimilis*)	
Sittasomus griseicapillus		Green-and-Gold Tanager (*Tangara schrankii*)	
Myrmotherula brachyura		*Lanio versicolor*	
Pink-throated Becard (*Platypsaris minor*)		Yellow-crested Tanager (*Tachyphonus rufiventer*)	
TYPE V: Patch species; occupy patchy habitats and join flocks when they pass through.			
Fasciated Antshrike (*Cymbilaimus lineatus*) (vine tangles)		*Microrhopias quixensis* (vine tangles and bamboo)	
Gray Antbird (*Cercomacra cinerascens*) (vine tangles)		Ornate Antwren (*Myrmotherula ornata*) (bamboo)	
White-shouldered Antshrike (*Thamnophilus aethiops*) (vine tangles)		Buff-fronted Foliage-gleaner (*Philydor rufus*) (riparian canebreaks)	
Black-capped Antshrike (*Thamnophilus schistaceus*) (vine tangles)		Chestnut-crowned Foliage-gleaner (*Automolus rufipileatus*) (riparian canebreaks)	
Spot-winged Antshrike (*Pygiptila stellaris*) (vine tangles)			
TYPE VI: Occasional flock species; often forage apart from flocks.			
Rufous-breasted Piculet (*Picumnis rufiventris*)		Olive-striped Flycatcher (*Mionectes olivaceus*)	
Long-tailed Woodcreeper (*Deconychura longicauda*)		Bright-rumped Attila (*Attila spadiceus*)	
Cinnamon-throated Woodcreeper (*Dendrexetastes rufigula*)		Sepia-capped Flycatcher (*Leptopogon amaurocephalus*)	
Buff-throated Woodcreeper (*Xiphorhynchus guttatus*)		Musician Wren (*Cyphorhinus arada*)	
Bar-bellied Woodcreeper (*Hylexetastes stresemanni*)		Red-billed Scythebill (*Campylorhamphus trochilirostris*)	
Black-tailed Leafscraper (*Sclerurus caudacutus*)		Orange-bellied Euphonia (*Euphonia xanthogaster*)	
Ochre-bellied Flycatcher (*Pipromorpha oleaginea*)			

[1] Core members of 1976 study flock.
[2] English names are provided only for those species *not* in Table 1.
[3] The figures to the right of the name give the number of flocks in which that species was found over the total number of adequately examined flocks, e.g. "*Myrmotherula leucophthalma* 3/4" means that 3 out of 4 flocks examined contained *M. leucophthalma.*

insectivorous birds that forage in the understory. Canopy birds also organize themselves into mixed flocks, the most prominent of which are those that form around roving omnivorous bands of tanagers (especially *Tangara* spp.) and honeycreepers. Such flocks occasionally contain large numbers of individuals (≥60) and 30 or more species at once. Tanager-honeycreeper flocks typically progress at a much faster pace than understory flocks. Several species are facultative members of both types of flocks. Some (e.g., *Platypsaris minor, Tachyphonus rufiventris*) join understory flocks infrequently while others (e.g., *Lanio versicolor, Sittasomus griseicapillus, Glyphorynchus spirurus*) alternate freely between the two flock types. One color-banded male *Lanio versicolor* associated with at least three different understory flocks from August to November 1976. An untested possible benefit of switching allegiance is that it could allow breeding individuals to choose whichever flock happened to be foraging closest to their nest site.

Type V: Species that use the forest in a patchy fashion. In a manner somewhat analogous to that of *Myrmotherula hauxwelli,* birds of certain other species in the forest usually joined flocks whenever they were passing through. These were birds that favor certain patchy situations within the forest: mid-story vine tangles, treefall openings, bamboo thickets, etc. Such species followed flocks regularly, but only as long as they remained within appropriate habitat.

Type VI: Occasional flock joiners. These are occasional flock joiners in the truest sense, species that commonly forage by themselves in the forest interior. Their presence in flocks tended to be ephemeral. Our observations do not tell whether their participation was anything more than incidental to a flock's presence in the vicinity.

DISCUSSION

The strikingly tight organization of the Amazonian understory flocks suggests a long coevolutionary history. What benefits derive from membership in the flock, and are the benefits shared equally? We will consider some of the more reasonable possibilities.

FLOCKING AS AN ANTI-PREDATOR HABIT

The forest at Cocha Cashu harbors at least six species of specialized bird-eating hawks (*Micrastur, Accipiter*), which suggests that small birds, especially gleaners whose attention is focused nearby, would benefit from cooperative anti-predator behavior (Pulliam 1973). We have some anecdotal evidence that flocking benefitted at least some species, though the benefits were not strictly mutual. For example, on 9 October 1976, the flock instantly scattered into the undergrowth when warned of the approach of a Slaty-backed Forest-falcon (*Micrastur mirandollei*) by the penetrating alarm call of a Bluish-slate Antshrike. The two *Thamnomanes* species are among the few flock members to give loud and unambiguous alarm calls (*Habia rubica* is another). Perhaps the other species profit from the vigilance of the alert, flycatching *Thamnomanes,* just as near-sighted zebras tend to associate with far-sighted ostriches on the African plains (Hesse et al. 1966). If this is so, then the benefit to the antshrikes would be of a different kind. Their followers might provide a cover of prey equally acceptable to an approaching predator (Hamilton 1971). Followers might also benefit *Thamnomanes* by providing a phalanx of beaters to flush prey.

OTHER POSSIBLE BENEFITS

Not all forest understory insectivores joined mixed flocks. Of those which did, the great majority were arboreal gleaners (as distinct from terrestrial gleaners and arboreal nongleaners, including hawkers and omnivores). This suggests that membership in the flock is limited to species whose foraging techniques are compatible. A species must move in a manner that is consistent with the course and rate of progress of the flock. This, in turn, implies that the flocks are selectively composed of ecological rivals, species that share a common diet (insects), habitat, and overall ranging pattern. It remains to be seen whether this carries any further implications for the functioning of the flock as a device for lessening interspecific competition, such as by regulating return times (Cody 1971).

The flock may also have a role in regulating intraspecific competition, though precisely how it would do this is unclear. Nevertheless, the circumstances are suggestive. How otherwise can one account for the striking equality of abundances of core members, and the extraordinarily ample territories (8 ha) of warbler-sized birds? Perhaps by cooperating in the defense of a jointly-held territory, members can enjoy the use of a larger exclusive area than they would be able to control individually. If so, this is more likely to be a derived benefit of multi-specific territoriality, rather than a primary evolutionary impetus to flock formation.

Any or all of the potential benefits we have mentioned are mutually compatible and capable of adding to the advantages of flock membership. Just as it is unlikely that any single benefit can account for all of the features of these flocks, it is possible that more than one benefit may have played a role in the evolution of the syndrome we have described, either as ultimate causes or as derived corollaries which serve to stabilize and perpetuate a most remarkable example of multi-species mutualism.

SUMMARY

We describe what appears to be an extreme case in the evolution of mixed-species foraging associations: flocks of insectivorous birds that patrol the understory of the Amazonian forest. Color-banding and long-term following of these flocks at a locality in southeastern Peru showed them to have an extraordinary degree of organization and stability.

All the flocks studied were built around a "core" membership consisting of 8–12 pairs or families of birds, each representing a different species. Other species with lower population densities were represented in some but not all of these flocks.

The 12 families of the main study flock shared a common territory of roughly 8 ha which they defended against neighboring flocks of similar composition. Territorial songs were rarely uttered except during confrontations, when each species displayed vigorously toward conspecifics in the opposing flock. The flocks appeared to be led by two species of antshrikes (*Thamnomanes*), which had the characteristics of "nuclear species." An additional 20 to 30 species were present in certain of these flocks under various circumstances.

Throughout the year, core species did virtually all of their foraging in the flocks, assembling each morning shortly after sunrise and dispersing in the late afternoon. Although these species were similar, their ecological roles, most of them as gleaners, were discernibly different. Flock members nested within the joint territory, commuting to and from the flock during incubation, but remaining close (≤50 m) to the nest when feeding young. Fledglings remained with the parental flock for at least several months. Adult birds retained membership in the same flock for at least two years. The territory of the main study flock was located in the same area in 1978 as in 1976.

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