

Multispecies antbird societies in lowland forests of Surinam and Ecuador: stable membership and foraging differences

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(With 5 figures in the text)

Flocks of insectivorous birds in the understory of lowland wet forest in Surinam and eastern Ecuador regularly included two species of antshrikes in the genus *Thamnomanes* (*ardesiacus* and *caesi**us*) and four species of antwrens in the genus *Myrmotherula* (in Surinam, *axillaris*, *menetriesii*, *longipennis*, and *gutturalis*; in Ecuador, the first two plus *hauxwelli* and *ornata*) (Formicariidae), as well as a number of other species particularly in the families Furnariidae and Dendrocolaptidae. Each flock included only a pair or occasionally a small group of each species. Although the individuals in a flock often spread over an area 30 m in diameter, the *Myrmotherula*, *Thamnomanes* and several other species moved cohesively through the forest. Each flock persisted throughout a day and, over periods of at least a week, recurred within the same largely exclusive range in the forest. The two *Thamnomanes* species had distinctive vocalizations that provided the primary signals for flock cohesion and alarm calls. Although most of the species of *Myrmotherula* had loud vocalizations, these were uttered too infrequently to contribute to flock cohesion and played no role in reactions to predators. In Central America, on the other hand, where *Thamnomanes* does not occur, *M. fulviventris* produces loud vocalizations, that resemble those of *Thamnomanes*, during disturbances to a flock. The species of *Myrmotherula* in each locality segregated ecologically in two dimensions, height of foraging above ground and preference for foraging in live or dead foliage. A shift in the foraging height of *axillaris* depending on the presence or absence of *longipennis* in the same flock suggested that competition for food has favoured ecological segregation of foraging height by these species. *Thamnomanes*–*Myrmotherula* flocks attain an unusual degree of cohesiveness and integration of foraging specialities in comparison with other mixed aggregations of animals.

Contents

	Page
Introduction	128
Study areas and procedures	128
General behaviour of flocks	129
Composition of flocks	129
Flock movements and ranges	132
Communication within a flock	133
Foraging behaviour	136
Discussion	139
Ecological differentiation of flocking species	139
Advantages of flocking	140
Communication within flocks	141
Stable membership of flocks	143
References	144

Introduction

As a substantial literature now documents, animals of different species often associate in coherent groups. Although striking examples of multispecies groups occur among ungulates, primates, and coral reef fish, it is among birds that this phenomenon has received the most detailed attention. Studies have focussed on adaptations for obtaining food and avoiding interspecific competition in mixed flocks of birds and on adaptations for promoting the cohesiveness of these flocks by means of interspecific communication (Moynihan, 1962, 1968; Morse, 1970, 1978).

Small flocks with antwrens in the genus *Myrmotherula* (Formicariidae) in lowland forests of Central America include a pair or a small group, probably a family, of each of three species of antwrens (*Myrmotherula axillaris*, *M. fulviventris*, and *Microrhopias quixensis*) (Johnson, 1954; Slud, 1960; Wiley, 1971; Karr, 1971; Willis, 1972; Jones, 1977). These three species have clear differences in their foraging behaviour, which presumably reduce competition among them for food. In comparison to *axillaris*, *quixensis* forages higher above the ground and in denser foliage, while *fulviventris* preferentially explores dead leaves hanging in the understory (Wiley, 1971; Willis, 1972; Jones, 1977). In addition, the two congeneric species seem to have cooperative roles in maintaining flock cohesion and mobbing predators (Wiley, 1971). *M. fulviventris*, a species with drab plumage in both sexes, produces conspicuous vocalizations during disturbances to a flock, while *M. axillaris* has less conspicuous calls but bold male plumage patterns that could promote flock cohesion. Several instances of intraspecific aggression suggested that the one pair of each species in a flock tended to exclude other conspecific antwrens from the flock. These antwrens, particularly the two species of *Myrmotherula*, have thus evolved coadaptations for particularly well organized mixed flocks.

Flocks with antwrens in lowland forests in South America are considerably more complex than those in Panama. The genus *Myrmotherula* includes some 30 species in northern South America, of which as many as 10 species occur in one location (Pearson, Tallman & Tallman, 1977). Pearson (1977) has shown that syntopic species forage at characteristic heights above ground and differ in the density of foliage used for foraging, although species can overlap widely in both respects. In addition to antwrens, flocks of insectivorous birds in the understory of lowland forests usually include antshrikes in the genus *Thamnomanes* (Willis, 1972, 1977).

Both in Surinam and in eastern Ecuador, flocks in the understory of lowland wet forest regularly included four species of *Myrmotherula* and two species of *Thamnomanes*. Usually only one pair or a small group of each species accompanied a flock. The composition of these flocks was remarkably consistent both for flocks in the same general locations on different days and for flocks at different locations in the study areas. The regularity of the membership in these flocks and the association of four congeners raised questions about the long-term stability of the flocks, the differentiation of foraging habits of the congeners, and the adaptations for communication that assured the coherence of the flocks.

Study areas and procedures

Flocks were studied in nearly undisturbed lowland forests: in Surinam, at the base of the Voltzberg (4°41' N, 56°11' W), a basalt outcropping in the Raleighvallen Natuurreservaat (elevation about 80 m, annual rainfall about 2000 mm), for three days in 1973 (28–30 July) and nine days in 1974 (19–27 July); in Ecuador, about 1 km north of the settlement at Limoncocha

(0°24' S, 76°38' W), Napo Province (elevation 400 m, annual rainfall about 3000 mm), for eight days in 1978 (between 10 and 25 March). In both locations, the forest canopy was generally continuous 20–30 m above ground, and scattered emergents reached at least to 40 m. Palms 4–12 m tall were numerous in the understory. Within 1 m of the ground grew numerous woody seedlings and herbaceous monocots. In 1974, approximately 50 hours were spent in the field following and searching for antwren flocks. In 1978, approximately 30 hours were spent.

For these studies an endeavour was made to follow a flock for one to two hours at a time. The flocks only occasionally moved rapidly, so by walking quietly through the forest an observer had no trouble staying near or actually within a flock. In 1974, flocks were followed for at least 30 min on 10 instances, for a total of 12.5 hours. In addition seven more flocks were encountered at times when they could not be followed and a total of two hours were spent with three flocks in order to taperecord vocalizations. Altogether about 16.5 hours were spent in contact with flocks; the remaining time in the field was spent searching for flocks primarily by walking slowly along 1.5 km of trails.

In 1978 10 flocks were followed for at least 30 min for a total of 10.1 hours. In addition flocks were contacted on 10 other occasions at times when they could not be followed. Altogether 12 hours were spent in contact with flocks.

In both localities, the calls of all species of *Myrmotherula* and both species of *Thamnomanes* were learned, with one exception explained below, and thus the presence of these species could be detected much more reliably than by sight alone. In order to determine field marks for both sexes of all these species, collections in museums were examined prior to field work in 1974 and 1978. Trails and stream courses were mapped, so that a flock's location could usually be ascertained within 10–20 m.

General behavior of flocks

The individuals in *Thamnomanes-Myrmotherula* flocks did not necessarily stay close together. Although on occasion an entire flock could feed in an area no more than 15 m in diameter, a flock regularly spread over an area 30 m or more across. An individual's nearest neighbour was sometimes 10 m away. Usually individuals of the same species remained closer together than did individuals of different species. The wide spacing of individuals gave these flocks a diffuse character. Nevertheless, these flocks were extremely cohesive: the *Myrmotherula*, *Thamnomanes* and several other species moved together through the forest.

Hours spent searching for flocks revealed that they were usually widely separated. Flocks were easily detected within about 30 m of the outlying individuals and occasionally from greater distances. If an observer remained quiet and moved as little as possible, a flock often loitered in one location for 10–30 min before drifting onward. On occasion, a flock would undertake a rapid progression some 50–100 m through the forest. Both in Surinam and in Ecuador, flocks tended to move slowly or remain stationary particularly in the dense vegetation around an opening created by a fallen tree or a stream. The denser vegetation at intermediate levels in these sites seemed to attract the flock.

Composition of flocks

Both in Surinam and Ecuador, almost every flock included two species of *Thamnomanes* (*ardesiacus* and *caesi*us) and four species of *Myrmotherula* (*axillaris*, *menetriesii*, *gutturalis* and *longipennis* in Surinam; the first two of these species plus *hau*xwelli and *ornata* in

Ecuador). These species were never encountered away from a flock, with one exception. In Ecuador a pair of *T. ardesiacus* was found alone at 07.15 hrs. No flock was ever encountered before 07.45 hrs.

In Ecuador, Peru, and Bolivia, Pearson (1977) found *M. axillaris* and *M. menetriesii* in flocks in 79% and 89% of observations respectively. In Ecuador, *M. ornata* and *M. hauxwelli* were in flocks on only 59% and 10% of his observations. In the present study none of these species was ever encountered away from flocks, although the calls of each except *ornata* were known. Pearson's procedure, however, differed substantially from the one used in the present study: he followed a prescribed path through the forest and did not systematically follow these species when encountered. Owing to the wide spacing of individuals in *Thamnomanes*-*Myrmotherula* flocks, an observer on a prescribed path might discover only one or two of the species at the edge of a flock and miss others that could be 20-30 m away. *M. hauxwelli* seemed particularly likely to be at the periphery of a flock, although they went with the flock as it moved.

In the present study, in contrast, the observer remained with any *Myrmotherula* or *Thamnomanes* by staying quiet and moving as little as possible. This procedure always revealed that these species were accompanying flocks. In following a flock, the observer would often not see a particular species for 10-20 min at a time, owing to the wide spacing of individuals. Although most species had calls that could be heard 20-30 m away, a species often did not use its loud calls for periods of 10-20 min. Over a period of 30 min, however, it could be verified repeatedly that the species was present in the flock. In addition, the observer could confirm that individuals followed the flock during its movements, in contrast to a number of other species that were observed in only one location and did not follow movements of the flock. Thus repeated sightings and observations of individuals following the flock's movements served to distinguish species that remained with a flock from those that did not.

For each of the species of *Thamnomanes* and *Myrmotherula*, no more than four individuals occurred in the same flock and usually no more than one male and one female. All observed flocks included at least a pair of each species of *Thamnomanes*. On one occasion in Ecuador, a flock definitely included three male *ardesiacus*. There were no signs of intraspecific antagonism.

In Surinam all four species of *Myrmotherula* accompanied the flocks observed for at least 30 min, with one interesting exception. A flock observed in the same area (B, Fig. 1) on four separate days never included *longipennis*, a readily detected species in other flocks.

On one occasion two male *menetriesii* and on another occasion two male *axillaris* were observed near each other; in neither case did intraspecific antagonism occur. A flock observed in the same area (A, Fig. 1) virtually every day of the study in 1974 included three female-plumaged *longipennis*. Evidently two of these were juveniles, as one female-plumaged bird and the male fed the others on several occasions. Aside from this family group of *longipennis*, a pair of each species of *Myrmotherula* was the rule in these flocks.

In Ecuador, a pair of each of three species (*axillaris*, *menetriesii*, *hauxwelli*) accompanied every flock observed for at least 30 min. For *axillaris* and *menetriesii*, mates were seldom observed less than 2 m apart and often found more than 5 m apart. On several occasions a male and female *hauxwelli* were seen less than 2 m apart, but usually one bird was seen at a time. On six occasions, 10-15 m apart, birds answered each other's calls. *M. ornata* was found during only three of ten observation periods at least 30 min long. This species

was seen on two other occasions with flocks and never alone. Because the loud call of this species was never learned, this species must have been overlooked much more than the congeners. On three occasions a male and female were less than 1 m apart. *M. erythrura* also joins these flocks at Limoncocha (E. O. Willis, pers. comm.), although it is not common there (Pearson, Tallman & Tallman, 1977; Tallman, 1979). Thus in eastern Ecuador *Thamnomanes*–*Myrmotherula* flocks regularly contain three species of *Myrmotherula* (*axillaris*, *menestriesii* and *hauxwelli*) and often two others (*ornata* and *erythrura*).

Both in Surinam and in Ecuador, a number of other species regularly stayed with *Thamnomanes*–*Myrmotherula* flocks. Most frequently encountered were several woodcreepers (in Surinam, *Glyphorhynchus spirurus*, *Xiphorhynchus guttatus*, *X. pardalotus*, *X. obsoletus*, and *Lepidocolaptes albolineatus*; in Ecuador, the first two of the preceding species plus a fourth *Xiphorhynchus*), foliage-gleaners (in Surinam, *Automolus ochrolaemus* and *Philydor erythrocerus*; in Ecuador, *P. erythrocerus* and *P. pyrrhodes*), a xenops

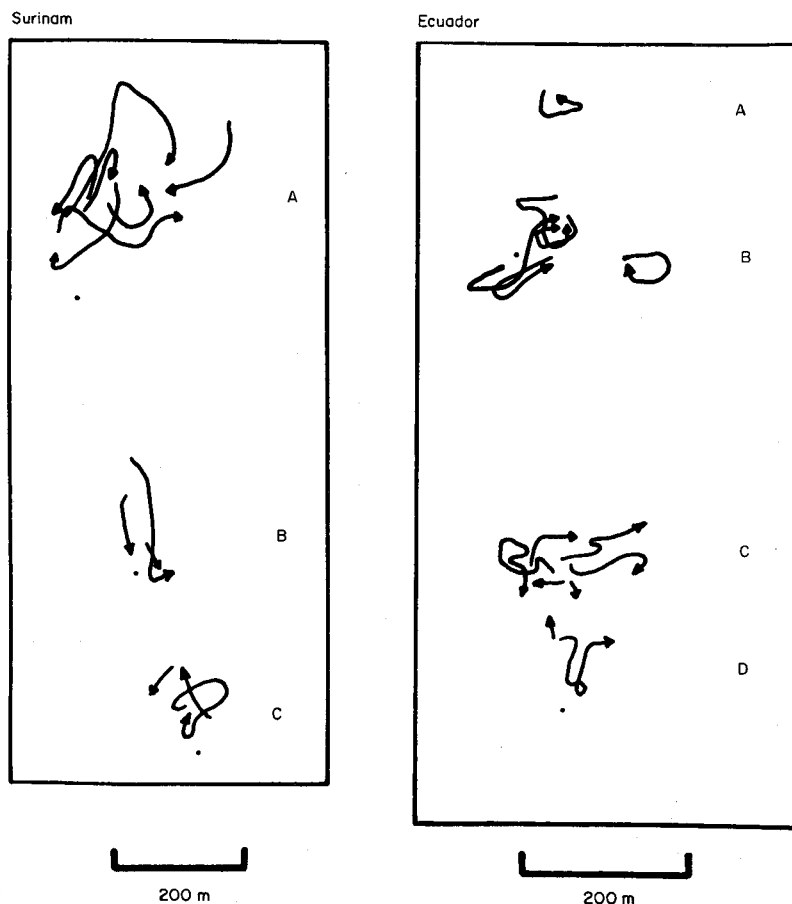


FIG. 1. Maps of the locations and movements of flocks in study areas in Surinam (left) and Ecuador (right). Each line with an arrow indicates the movements of a flock followed continuously; a dot indicates the location of a flock encountered at a time when it could not be followed. The tracks of flocks and the spaces between them are drawn to scale.

(*X. minutus*), in Surinam a small flycatcher (*Myiobius barbatus*), and in Ecuador an ant-tanager (*Habia rubica*) and a manakin (*Tyrannneutes stolzmanni*). None of these species was detected as frequently in the flocks as the *Thamnomanes* and *Myrmotherula* species. The only one that occurred in almost all flocks, both in Surinam and in Ecuador, was the woodcreeper *G. spirurus*, often in pairs that stayed within 10 m or so of each other. Occasionally two foliage-gleaners of the same species associated closely (*A. ochrolaemus*, *P. pyrrhodes*, *P. erythrocerus*). Otherwise these species were encountered one at a time (see Davis, 1946).

In Surinam shrike-tanagers (*Lanio fulvus*) often stayed in the lower parts of the canopy above a *Thamnomanes*–*Myrmotherula* flock. Sometimes a few other tanagers (*Tangara gyrola* most often), other antwrens (*Herpsilochmus* species, *Myrmotherula brachyura*), and greenlets (*Hylophilus muscicapinus*) would join them. Most of the time, however, *Thamnomanes*–*Myrmotherula* flocks had no association with birds in the canopy. In Panama antwren flocks also associate on occasion with small flocks that form around greenlets in the canopy (Willis, 1972). In Surinam, these combined flocks sometimes remained in the same area, often in the dense vegetation along a stream course, for 30 min or more at a time. Eventually, however, the antshrike–antwren assemblage would move away through the forest without its canopy associates. In Ecuador there were no similar associations of *Thamnomanes*–*Myrmotherula* groups with canopy species.

Many species of the forest undergrowth were temporarily included in *Thamnomanes*–*Myrmotherula* flocks but remained behind when the flocks moved. Most important in this category were a number of species of antbirds: in Surinam, *Thamnophilus murinus*, *Cymbilaimus lineatus*, *Hypocnemis cantator*, *Pernostola rufifrons*; in Ecuador, *T. schistaceus*, *Hylophylax naevia*).

Flock movements and ranges

Both in Surinam and in Ecuador flocks frequented the same limited areas day after day. Observations of flocks for one to two hours at a time provided evidence that flocks occupied exclusive areas some 200–400 m in diameter. Flocks often turned back more or less in the direction in which they had come after traveling several hundred metres in one general direction (Fig. 1, left). In addition, the tracks of flocks initially located in the same general area tended to form a cluster with turnaround points on all sides. In Surinam three such clusters were established, each presumably the result of one flock's movements on different days. Here each of the clusters was separated by a substantial distance in which flocks were never detected, although the areas between these flocks were traversed on many occasions. In Ecuador three clusters of paths were found, each presumably the result of movements of one flock (B–D, Fig. 1, right). One additional path (A, Fig. 1, right) perhaps belonged to another flock. Here two flocks seemed to occupy adjacent but exclusive ranges (C,D, Fig. 1, right). On two occasions, it was confirmed that flocks were about 200 m apart in these two areas. Both times, following an observation period with one flock, the other flock was quickly encountered. On the other hand, the area between B and C (Fig. 1, right) was crossed on many occasions without encountering a flock.

In Surinam some additional information suggested that individual birds tended to stay in the same range each day. Thus one flock (A, Fig. 1, left) on every occasion included

a family group of *M. longipennis*, while flock B never included this species, and flock C always included only a pair.

These observations suggest that a flock persists throughout a day and, over periods of at least a week, recurs within the same largely exclusive range in the forest. Furthermore, the consistent membership of these flocks makes it likely that the same individuals of the *Thamnomanes* and *Myrmotherula* species constitute the flock each day.

Communication within a flock

Coherent social groups require easily locatable signals that permit individuals to stay in spatial proximity. In addition, individuals in social groups often produce special alarm signals when a predator is detected. In order to analyse these two forms of communication in *Thamnomanes*–*Myrmotherula* flocks, this section presents brief descriptions of the vocalizations used by the regular members of these flocks and then discusses the use of these vocalizations in four situations: during the observer's first contact with a flock and on other occasions when the observer moved conspicuously while near members of a flock; during periods without any apparent disturbance to the flock; during rapid movements by the flock; and during reactions to flying raptors.

Each species of *Thamnomanes* had two distinctive vocalizations used by both sexes. For *ardesiacus*, the explosive "kseea" (Fig. 2(B)) varied considerably in intensity, sometimes quite soft but on occasion piercingly loud. Birds often uttered this call, particularly loud versions, at the moment of taking flight to a new perch. The "keeer" call of *ardesiacus* (Fig. 2(A)) was used less frequently than "kseeas". Birds often mixed these two kinds of calls when apparently undisturbed, but "keeer" calls were particularly frequent in response to terrestrial predators. A bird that approached or remained near the observer often repeated this call; on one occasion a domestic dog that trotted beneath a flock in Ecuador evoked repeated "keeer" calls.

For *caesius*, "whut" calls (Fig. 2(F)), often repeated at intervals of about one second, were usually rather soft, audible about 30 m in the forest. The abrupt "staccato rattle" (Fig. 2(E)), which began with one or two notes like "whut" calls, had considerable variation in intensity. Like the "kseea" of *ardesiacus*, loud instances of the "staccato rattle" usually occurred immediately on taking flight to another perch. On three occasions *caesius* delivered a modified version of "whut" calls, which were transliterated "huep" (Fig. 2(G)). This version, in which the individual notes often had more prolonged onset, consisted of almost regularly repeated notes that persisted for minutes at a time. On these occasions, all during light rain, the vocalizing birds remained motionless on their perches.

All of the *Myrmotherula* species in Surinam and Ecuador produced brief, abrupt notes, so soft that they carried only 10–15 m in the forest. These notes were transcribed as "cht" or "tsk" (see Fig. 2(I),(K) for examples). There seemed to be species-specific characteristics to these short calls, but they proved to be so difficult to record that this possibility could not be confirmed. One species in Surinam (*gutturalis*) rarely produced any calls other than these soft brief notes; on a few occasions individuals of this species delivered short, sharp trills and "tsee tsee" calls, which were never successfully recorded. In Ecuador one species (*ornata*) never produced calls during the observations other than soft short notes. Both in Surinam and in Ecuador, the other three regular *Myrmotherula* species in the flocks produced distinctive calls, easily audible 15–20 m away, although not so piercing as the calls of *Thamnomanes*.

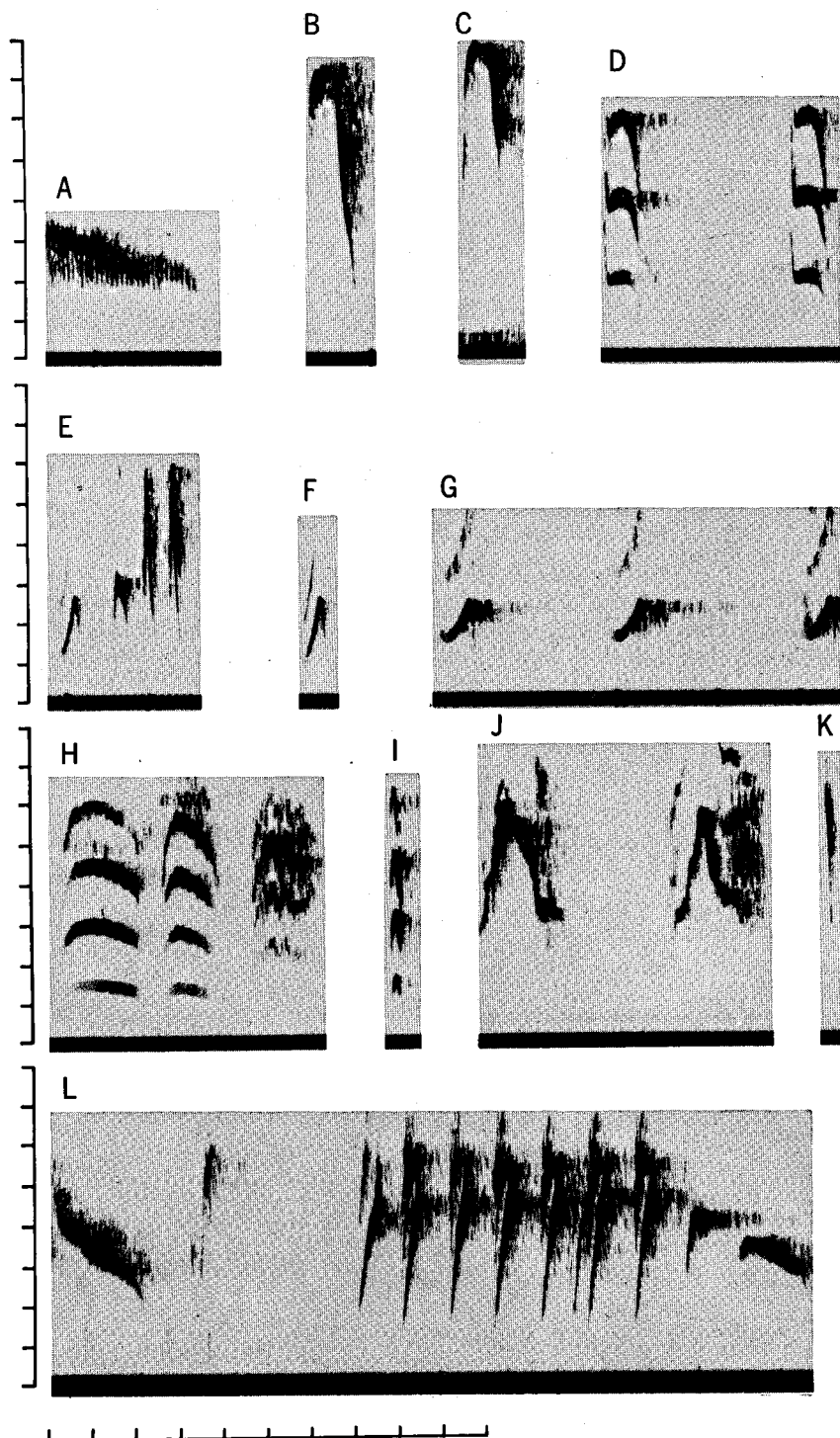


FIG. 2. Sound spectrograms of the vocalizations of *Myrmotherula* and *Thamnomanes* species. (A) "keer", *T. ardesiacus*. (B) "kseea", *T. ardesiacus*. (C) "tseek", *M. fulviventrus* (Panama, Wiley, 1971). (D) "peeu peeu", *M. axillaris*. (E) "staccato rattle", *T. caesioides*. (F) "whut", *T. caesioides*. (G) "huep" calls, *T. caesioides*. (H) "peeu peeu", *M. longipennis*. (I) "cht", *M. longipennis*. (J) "weel" calls, *M. longipennis*. (K) "tsk", *M. menetriesii*. (L) "peeu pipipipi peeu", *M. menetriesii*. All sonagrams prepared from recordings in Surinam, (except C). Vertical scale, 0–8 kHz in 1 kHz intervals; horizontal scale, 1 sec in 0.1 sec intervals.

M. axillaris produced a short train of nasal calls, "pee-u pee-u pee-u", very similar to those heard in Panama (Fig. 2(D); Wiley, 1971). Often a male and female *axillaris* used these nasal notes to call back and forth. *M. longipennis* in Surinam also produced a series of nasal calls, but each note was usually longer than those of *axillaris* (Fig. 2(H)). In addition the juvenile birds in one flock, and possibly also the adult female, persistently produced soft, variable calls, "weel" (Fig. 2(J)). In Ecuador *hauxwelli* had a brief, sharp rattle; on several occasions two birds used this call to answer each other from a separation of 10–15 m. *M. menetriesii* had the most distinctive call of all of these species: a variable combination of short glissandos and brief trills, "pee-u pipipipi pee-u" (Fig. 2(L) is an example). Both sexes used this call, although often only one bird would call repeatedly. Once two called from 8 m apart, and on another occasion two called back and forth from 10 m.

On the observer's first encounter with a group, *Thamnomanes* usually uttered a burst of loud vocalizations. If the observer remained motionless or moved slowly, these loud calls subsided quickly, usually within 15 sec. A record was kept of the vocalizations heard during the first 10 sec after contact with a flock on 17 instances in Ecuador. In all cases either the loud "staccato rattle" of *caesius* or loud "kseea" calls of *ardesiacus* were heard. Altogether, "kseea" calls occurred in the first 10 sec 11 times, "staccato rattles" nine times, and "keer" calls five times. In this circumstance, the antshrikes always used the loud versions of these calls. When the observer moved rapidly or conspicuously while near a flock, the same pattern recurred: a brief outburst of loud calls from *Thamnomanes*.

After the observer remained still for 30 sec, the most frequent calls heard were soft versions of "kseea" calls of *ardesiacus*, often uttered repeatedly at irregular intervals of 1–10 sec. Soft versions of "keer" calls of *ardesiacus* and "staccato rattles" or "whut" calls of *caesius* occurred much less regularly, although all of these calls were sometimes uttered repeatedly. On occasion both species of *Thamnomanes* remained silent for as long as 30 min, but only when the flock was not moving.

In order to document the prevalence of different vocalizations during periods of no disturbance to a flock, vocalizations were tabulated during one-minute intervals while following flocks in Ecuador. The observer remained motionless for 30 sec preceding each sample; the samples were spaced 5 min apart. Altogether 78 such samples were obtained, 5–13 during each of eight observation periods on flocks in all locations (A–D, Fig. 1, right). The calls of *T. ardesiacus* occurred most frequently (Fig. 3), especially soft versions of "kseea" calls. This call was also most often the only vocalization heard during a one minute interval. Calls of *T. caesius*, *M. menetriesii* and *axillaris* occurred less frequently. Of the *Myrmotherula* species, only *menetriesii* was heard on at least one quarter of the one-minute samples.

During rapid movements by the flock through the forest, "kseea" calls occurred more frequently than at any other time, including some loud versions. Rapidly repeated "kseea" calls were characteristic of this situation. The other vocalizations of *Thamnomanes* also occurred more frequently at these times.

In contrast, loud "staccato rattles" of *caesius* were the most characteristic alarm call for aerial predators. Twice in Ecuador an abrupt burst of "staccato rattle" coincided with many birds diving from the middle layers of the forest toward the ground. Immediately afterwards, absolute silence prevailed for about one minute. On one of these occasions a small raptor, probably a small species of *Micrastur* or *Accipiter*, sliced through the

middle layers of the forest. In three such alarms in Surinam the most prominent vocalization was a sharp rattle from shrike-tanagers in the lower canopy.

In summary, *T. ardesiacus* had a special role in producing vocal signals that could serve to maintain the cohesion of a flock. During periods without disturbance soft versions of the "kseea" call were uttered regularly. During fast movements initiated by the flock, the "kseea" call of *ardesiacus* occurred particularly frequently. *T. caesius*, *M. menetriesii* and *M. axillaris* played subsidiary roles in producing calls that could orient the flock members. In reactions to predators only the *Thamnomanes* species figured prominently, both species in reactions to the observer's sudden presence and *caesius* especially in reactions to flying raptors. In Surinam, *M. gutturalis* vocalized much too infrequently to contribute to flock cohesion and played no role in reactions to predators. In Ecuador, *M. hauxwelli* and *ornata* likewise made no real contribution to flock cohesion or alarm reactions.

Foraging behaviour

The four species of *Myrmotherula* that occurred together regularly in *Thamnomanes*—

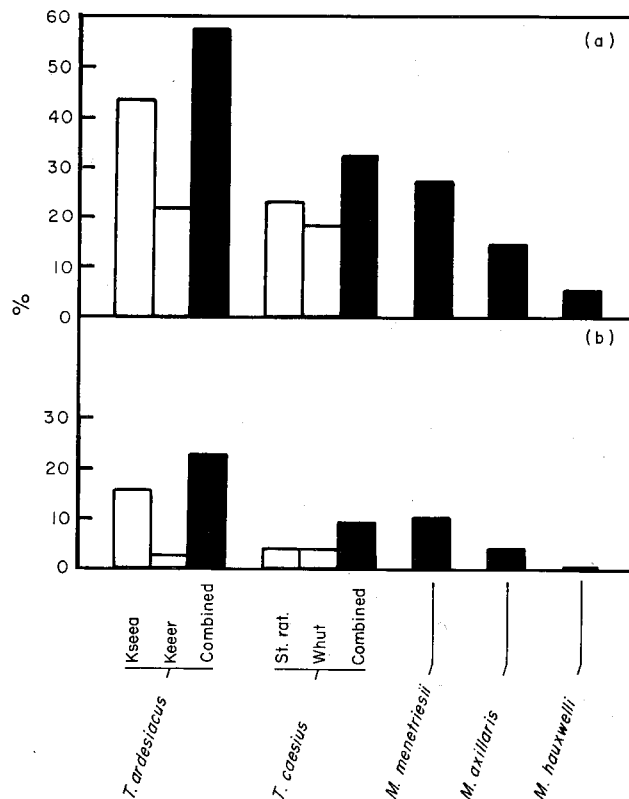


FIG. 3. Prevalence of vocalizations by *Thamnomanes* and *Myrmotherula* species in undisturbed flocks in eastern Ecuador; (a) percent of one-min intervals in which vocalizations by each species occurred; (b) percent of one-min intervals in which vocalizations by each species occurred and no others occurred. For the three *Myrmotherula*, only the loud vocalizations of each species are considered.

Myrmotherula flocks had clear differences in foraging behaviour. In Surinam, each *Myrmotherula* differed from its congeners either in foraging height above ground or in special techniques used for searching or for capturing prey.

The data for each antwren observed in an undisturbed flock included its height above ground, the density of foliage in its vicinity, any attempts to capture prey, and any specialized foraging techniques were recorded. Each antwren was watched as long as possible, 10–90 sec, but information on height and foliage density was recorded only once unless the bird moved to a new tree, flew at least 5 m, or 60 sec elapsed. About half of the information came from individuals in flock A (Fig. 1) and the rest from individuals in flocks B and C about equally. There is no indication in the data that birds in different flocks behaved differently, except in one case discussed below. Techniques used to capture prey included (1) gleaning, simply plucking a small arthropod from the surface of a leaf or twig, by far the most frequent technique of capture by all species of *Myrmotherula*, (2) sallying, flying 0.5–2 m to snatch an item from the undersurface of a leaf (or rarely from mid-air) and then proceeding to a new perch without stopping, (3) hovering, stationary flight below a leaf while plucking small items, (4) fluttering, flying forth to snatch an item beneath a leaf but tumbling downward after stopping in flight, and (5) searching in curled dead leaves hanging in the understory. Foliage density in the vicinity of a foraging

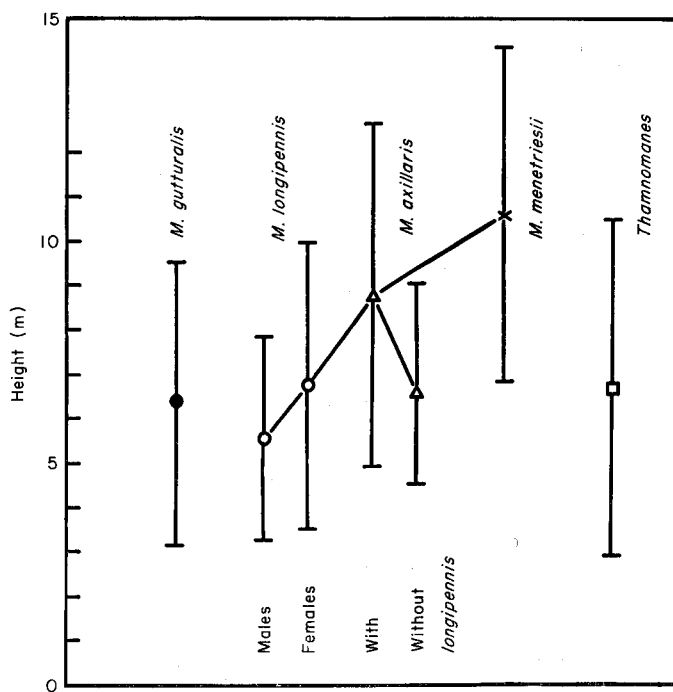


FIG. 4. Foraging heights of four *Myrmotherula* species and two *Thamnomanes* (combined) in Surinam. Vertical lines indicate one standard deviation on either side of the mean. Diagonal lines connect significant differences between means (t -test, $P < 0.05$). Observations for the two *Thamnomanes* species are combined. Observations of male and female *M. longipennis* are separated, as are observations of *M. axillaris* in two flocks with *longipennis* present and one flock without *longipennis*.

bird was judged by the obstruction of the observer's view by the foliage within 0.5 m of the bird: (1) less than about 50% closed, (2) about 50–90% closed, and (3) almost totally closed (see Wiley, 1971). Altogether this study obtained 160 observations of foraging height for *longipennis*, 52 for *axillaris*, 51 for *menetriesii*, and 32 for *gutturalis*.

The information on the heights of foraging antwrens showed that *gutturalis* and *longipennis* foraged at approximately the same height (about 6 m above ground) (Fig. 4). Male and female *longipennis* differed slightly but significantly ($t = 2.49$, $P < 0.02$) (Fig. 4). The information revealed no differences between sexes in the other species. *M. menetriesii* consistently foraged higher than the other species (10.6 m on average).

M. axillaris foraged significantly higher than *longipennis* in flocks A and C in which *longipennis* also participated (Fig. 4). In these two flocks *axillaris* averaged 8.8 m above ground, significantly higher than female *longipennis* ($t = 2.73$, $P < 0.02$). In contrast, in flock B, in which *longipennis* never occurred during the observations, *axillaris* used significantly lower perches (6.8 m, $t = 2.05$, $P < 0.05$) than in the other two flocks. Thus in the flock without *longipennis*, *axillaris* moved down to occupy virtually the same foraging level occupied by *longipennis* in other flocks.

Myrmotherula species also differed clearly in foraging techniques. In order to adjust for differences in the number of times foraging information was recorded for each species, the number of instances in which a species used a particular technique was divided by the total number of records of foraging height for that species. This normalized rate approximated the frequency of each technique in about 30 sec (roughly the average duration of observations).

M. gutturalis differed from all the other *Myrmotherula* by concentrating on dead leaves, sites almost never visited by the other species (Fig. 5). All the remaining three species obtained prey most frequently by gleaning from green foliage. All three also occasionally sallied from their perches to snatch items, which often involved stopping in flight and then fluttering downward awkwardly. *M. longipennis* was the only species that regularly hovered

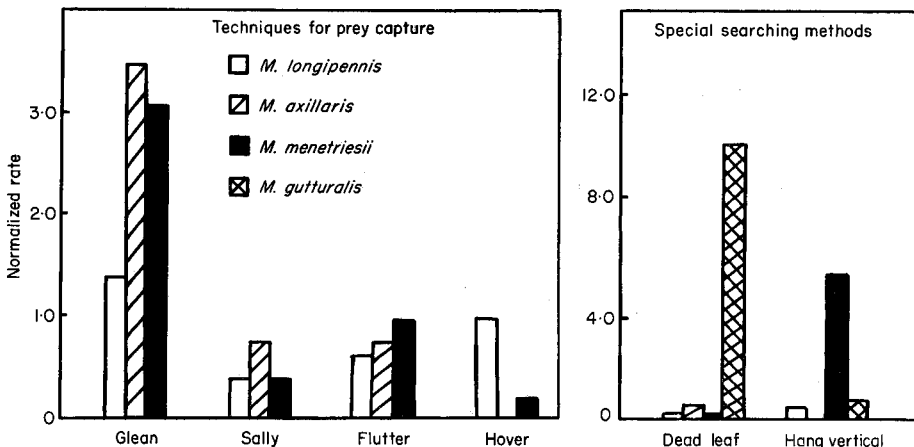


FIG. 5. Specializations for foraging by four species of *Myrmotherula* in Surinam. The vertical axis indicates a normalized rate, the number of observed instances of each technique or searching method divided by the number of foraging observations of each species. Note the comparatively high rates of hovering by *M. longipennis*, searching in dead leaves by *M. gutturalis*, and hanging vertically by *M. menetriesii*.

neatly beneath a leaf to pluck food items (Fig. 5). *M. menetriesii* had a different specialty, hanging vertically downward from its twig, an action almost never performed by the other species. *M. axillaris* had no technique for searching or capturing prey that it used substantially more than any other species.

In Surinam, all four species of *Myrmotherula* in flocks spent most of their foraging time in foliage of intermediate density. *M. longipennis* and *axillaris* used the densest category of foliage on only 2% of the records for each. *M. menetriesii* tended to occur in the densest foliage more often (16% of the records), as Pearson (1977) noted in Ecuador.

The two *Thamnomanes* foraged similarly. Both perched on relatively open branches in the understory, where they remained still while looking intently in one direction then another. Both sexes had similar distributions of foraging heights, from near the ground to 8 m and occasionally higher (Fig. 4). After peering around intently from one perch, a bird flew straight to another perch. The modal distance for these flights was 2 m; few were greater than 5 m or less than 1 m. The two most frequent techniques for capturing prey were sallying from a perch to snatch an item in mid-air and hovering beneath a leaf to take prey. Although these two *Thamnomanes* species alternated perching and sallying to snatch insects from foliage or mid-air, they differed from many other Neotropical birds that perch and sally. *Thamnomanes* changed perches at frequent intervals and rarely returned to the same perch.

Discussion

Ecological differentiation of flocking species

Mixed flocks of insectivorous birds often include more than one species in the same genus, a situation first emphasized by Moreau (1948). Indeed the *Thamnomanes*–*Myrmotherula* flocks in South American forests are not unique in regularly containing four congeners (see Gibb, 1954; MacDonald & Henderson, 1977). In flocks of insectivorous birds, congeners that regularly occur in the same flock in most cases differ clearly in their foraging behaviour. Differences include the height of foraging above ground (Moreau, 1948; MacDonald & Henderson, 1977), the substrate used for foraging (the parts of a tree or the nature of the foliage) (Morse, 1978; MacDonald & Henderson, 1977; Gibb, 1954; Morse, 1967, 1970), and special foraging techniques (Morse, 1978).

In Ecuador three of the *Myrmotherula* species in flocks segregate by height of foraging above ground. As Pearson (1977) showed, *menetriesii* averages about 12 m above ground, *axillaris* about 6 m, and *hauxwelli* about 1 m. There are some indications that *menetriesii* and *axillaris* might differ in more than one dimension of their foraging behaviour. In particular, Pearson (1977) indicated that *menetriesii* prefers denser foliage than *axillaris*. In Surinam, the present study suggested that this difference was a slight one. In addition, *menetriesii* was much more acrobatic on a perch, often hanging down vertically while seeking food underneath leaves.

To demonstrate that these differences result from competition among the *Myrmotherula* species, one would like to show that their behaviour differs more in mixed flocks than when each forages alone. The few such comparisons available in the literature for other species (Morse, 1967, 1970, 1978; Austin & Smith, 1972; Willis, 1966) indicate that species of insectivorous birds in mixed flocks do adjust their foraging behaviour to reduce overlap with socially dominant species in the same flock. Such information is difficult

to obtain for the flocking *Myrmotherula*, however, because those species that occur regularly in mixed flocks almost never forage alone. However, comparison of flocks with different memberships in Surinam provides some direct evidence that *Myrmotherula* adjusted their heights of foraging to reduce overlap with congeners in the same flock.

In Surinam, ecological segregation of the *Myrmotherula* species in mixed flocks was less clear than in Ecuador, primarily owing to the presence of two species (*longipennis* and *axillaris*) at intermediate heights. In flocks with both *longipennis* and *axillaris*, *longipennis* foraged at virtually the same height used by *axillaris* in Peru, Ecuador, and Panama (Terborgh in MacArthur, 1972; Pearson, 1977; Jones, 1977) and *axillaris* foraged higher than *longipennis* but lower than *menetriesii*. Furthermore, *axillaris* had no special foraging technique, although both *menetriesii* and *longipennis* had specialities. *M. axillaris* and *longipennis* have similar relationships in flocks in eastern Peru (Munn & Terborgh, in press). Thus *axillaris*, without any noticeable specialization, squeezed its vertical distribution between those of two other species, a particularly unfavourable situation for ecological coexistence (MacArthur, 1972).

In Surinam *axillaris* foraged lower in the one flock in which *longipennis* did not occur, evidence that competition with *longipennis* influenced the vertical foraging distribution of *axillaris*. A change in the distribution of foliage in the forest in the area occupied by this flock is not likely to explain this change in the behaviour of *axillaris*: no relevant difference was noticed in the forest occupied by the three flocks in Surinam; in addition, two other *Myrmotherula*, *menetriesii* and *gutturalis*, had similar vertical foraging distributions in all three flocks.

One species of *Myrmotherula* in Surinam (*gutturalis*) foraged at intermediate heights, widely overlapping *longipennis* and *axillaris*, but searched almost exclusively in dead leaves hanging in the understory, locations almost completely ignored by *longipennis* and *axillaris*. In Ecuador, *ornata* has a vertical foraging distribution very similar to that of *axillaris* (Pearson, 1977), but it too concentrates on dead leaves. *M. erythrura* also specializes on dead leaves (E. O. Willis, pers. comm.). In addition, in Panama and in eastern Peru one species of *Myrmotherula* differs from its congeners in strict specialization on dead leaves (Wiley, 1971; Munn & Terborgh, in press). Thus throughout the Neotropics the species of *Myrmotherula* that regularly join flocks segregate in two dimensions, foraging height and substrate.

The clear differences in foraging behaviour among the *Myrmotherula* species in the same flock, together with the evidence that *longipennis* displaces *axillaris* from its preferred foraging zone in Surinam, indicate that the *Myrmotherula* occurring together in a flock have usually evolved adaptations to minimize competition among them for food.

Advantages of flocking

Several of the possible advantages of flocking seem not to apply to *Myrmotherula-Thamnomanes* flocks. The species that occur in these flocks, including the associated woodcreepers and ovenbirds, are not likely to act as beaters for each other (see Swynnerton, 1915; Winterbottom, 1943; Brosset, 1969), because individuals are rarely close enough to benefit from insects flushed by another individual. Of the species present, the two *Thamnomanes* are most likely to benefit from insects flushed by others. These flocks are also unlikely to have advantages in locating patches of food. Since the members of a flock

rarely, if ever, separate during daylight, a flock is not likely to discover any new large-scale patches of food (larger than a flock) much sooner than each member could alone. Small-scale patches also appear not to influence relations between species of antwrens, since foraging individuals of different species seldom approach each other closely. The possibility that these flocks could reduce wasted time by coordinating rates of return to exploited areas (see Cody, 1971) also seems implausible. The species of *Myrmotherula* differ so clearly in their foraging behaviour that each species could regulate its own rates of return independently of other species.

On the other hand, increased efficiency in surveillance for predators seems to offer clear advantages for these flocks. All individuals reacted promptly to alarm calls within the flock. *Thamnomanes caesius* seemed to have the most prominent role in giving the alarm for flying raptors, although in Surinam shrike-tanagers also gave similar alarms.

These flocks thus fit Willis's (1972) and Buskirk's (1976) prediction well: small, actively foraging insectivores tend to assemble in flocks in order to counteract their exposure to predators while feeding. Each individual might benefit either by reduced vulnerability to predation (Hamilton, 1971; Vine, 1971; Williams, 1964; Pulliam, 1973; Page & Whitacre, 1975) or by more time for feeding rather than surveillance (Murton, Isaacson & Westwood, 1971; Powell, 1974; Feare, Dunnet & Patterson, 1974). As Morse (1973, 1977, 1978) points out, the effects of flocking on foraging and predator avoidance are not completely separable.

Communication within flocks

All *Myrmotherula* and *Thamnomanes* species in these flocks relied primarily on vocal signals to maintain contact between mates and with the flock. Often mates were closer together than either was to other species in the flock. Consequently, acoustic signals for communication between mates were often inconspicuous. The soft, short calls of all *Myrmotherula* species are examples. *M. axillaris*, *menetriesii*, *longipennis*, and *hauxwelli* also used louder, more complex calls for contact between mates on occasions when the two individuals had separated 10 m or more. Often an individual answered its mate, or mates called back and forth repeatedly. *M. gutturalis* in Surinam and *ornata* in Ecuador never called in this fashion during the observation periods. In these two species, mates stayed closer together than in the other *Myrmotherula*, so that contact between mates perhaps rarely required a loud call. Visual signals played a role in communication between mates over distances of more than a few metres only in *M. axillaris*. In this species, bold white flank plumes flashed when the male flicked his wings, a conspicuous signal to distances of about 15 m.

In order for the members of a flock to remain together, some have to produce signals that allow accurate localization over distances of at least 10–20 m, since individuals of different species are often this far apart. These signals have to recur frequently, particularly when a flock is moving. The calls of the two *Thamnomanes* species were the most important signals with these characteristics. Certain of the *Myrmotherula* species provided some supplementary signals that could promote flock cohesion: the white flanks of *axillaris* and the complex calls of *menetriesii*. No other *Myrmotherula* species repeated its loud calls frequently enough to provide reliable signals for flock cohesion.

Note that *Thamnomanes* used the same calls for alarm and for contact between flock

Stable membership of flocks

In comparison to other mixed flocks of insectivorous birds, the *Thamnomanes-Myrmotherula* flocks of lowland forests in South America are unusual in the regularity and stability of membership, the coherence of the flocks over periods of at least a week, and their use of exclusive ranges. In Surinam and in Ecuador the present study suggests that each flock consisted of the same individuals day after day and restricted itself to a well defined range. Others have documented these features of antwren flocks in Panama and in Peru (Munn & Terborgh, in press; Gradwohl & Greenberg, in preparation).

Many observers of other multispecies flocks of insectivorous birds have felt that flocks recurred in the same area day after day and used the same routes or limited area (Bates, 1864; Swynnerton, 1915; Stanford, 1943; McClure, 1967; Willis, 1972; MacDonald & Henderson, 1977). It is not clear, however, whether or not these flocks have resulted from persistent associations of the same individuals. Flocks of tits in winter in England regularly include six or more species, but flock composition varies considerably (Morse, 1978). The flocks that form around three-striped warblers *Basileuterus tristriatus* in the understory of subtropical forests in Central America change membership continually. Each member joins and then leaves as a flock passes through its territory (Powell, 1979). The birds that accompany raiding army ants in lowland neotropical forests assemble opportunistically, according to the availability of swarms in the vicinity of each bird's territory (Willis, 1967, 1972; Willis & Oniki, 1978). Multispecies associations of other vertebrates also usually have considerable variation in membership, with little indication that the same individuals of different species associate persistently. Mixed schools of coral reef fish are an example (Ehrlich & Ehrlich, 1973; Barlow, 1974; Itzkowitz, 1977).

Persistent associations of individuals of different species do occur among *Cercopithecus* monkeys in mature lowland forests in Africa (Gautier & Gautier-Hion, 1969; Struhsaker, 1969; Gartlan & Struhsaker, 1972; Marler, 1973; Gautier-Hion & Gautier, 1974; Gautier-Hion, 1978). In Gabon, a mixed troop of *C. nictitans* and *C. pogonias* associated 97% of the time over a three-month period. Some groups include three species of *Cercopithecus*, which differ in foraging height and diet (Gautier-Hion, 1978). These primarily frugivorous monkeys thus share with *Thamnomanes-Myrmotherula* flocks a persistent association of the same individuals in multispecies groups that occupy a limited range, but the *Thamnomanes-Myrmotherula* groups are much more complex in their membership.

These forest *Cercopithecus* species, like the antwrens and antshrikes, have species-specific, loud calls. These probably serve both to regulate intergroup spacing and as "rallying calls" that coordinate the movements of group members (Struhsaker, 1969; Gautier, 1969; Marler, 1973). In addition, these species have softer, less complex calls ("phased grunts", Marler, 1973) used for relatively short-range coordination of group movements, analogous to the soft, short calls ("cht", "tsik") of the *Myrmotherula* species and the soft versions of calls of the *Thamnomanes* species. Additional loud calls by the forest *Cercopithecus* monkeys serve for alarm. More information is needed on the rates with which different *Cercopithecus* use their calls in multispecies associations and on the contributions of the different associated species in coordinating group movements and giving alarm.

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understory of lowland forests in South America, these flocks represent an important form of social and ecological organization in the insectivorous birds of Neotropical forests.

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REFERENCES

- Austin, G. T. & Smith, E. L. (1972). Winter foraging ecology of mixed insectivorous bird flocks in oak woodland in southern Arizona. *Condor* **74**: 17–24.
- Barlow, G. W. (1974). Extraspecific imposition of social grouping among surgeon fishes (Acanthuridae, Pisces). *J. Zool., Lond.* **174**: 333–340.
- Bates, H. W. (1864). *The naturalist on the river Amazon*. London: Murray. 2nd ed. (Reprinted 1962, Berkeley: University of California Press).
- Brosset, A. (1969). La vie sociale des oiseaux dans une forêt équatoriale du Gabon. *Biologia gabon.* **5**: 29–69.
- Buskirk, W. H. (1976). Social systems in a tropical forest avifauna. *Am. Nat.* **110**: 293–310.
- Cody, M. L. (1971). Finch flocks in the Mojave Desert. *Theor. Pop. Biol.* **2**: 142–158.
- Davis, D. E. (1946). A seasonal analysis of mixed flocks of birds in Brazil. *Ecology* **27**: 168–181.
- Ehrlich, P. R. & Ehrlich, A. H. (1973). Coevolution: heterotypic schooling in Caribbean reef fishes. *Am. Nat.* **107**: 157–160.
- Feare, C. J., Dunnett, G. M. & Patterson, I. J. (1974). Ecological studies of the rook (*Corvus frugilegus* L.) in north-east Scotland—food intake and feeding behaviour. *J. appl. Ecol.* **11**: 867–896.
- Gartland, J. S. & Struhsaker, T. T. (1972). Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa. *J. Zool., Lond.* **168**: 221–266.
- Gautier, J. P. (1969). Émissions sonores d'espacement et de ralliement par deux cercopithèques arboricoles. *Biologia gabon.* **5**: 117–145.
- Gautier, J. P. & Gautier-Hion, A. (1969). Les associations polyspécifiques chez Cercopithecidae du Gabon. *Terre et Vie* **2**: 164–201.
- Gautier-Hion, A. (1978). Food niches and coexistence in sympatric primates in Gabon. In *Recent advances in primatology 1 Behavior*: 269–286. Chivers, D. J. & Herbert, J. (Eds). London: Academic Press.
- Gautier-Hion, A. & Gautier, J. P. (1974). Les associations polyspécifiques de Cercopithèques du plateau de M'passa, Gabon. *Folia primatol.* **22**: 134–177.
- Gibb, J. A. (1954). Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis* **96**: 513–543.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *J. theoret. Biol.* **31**: 295–311.
- Itzkowitz, M. (1977). Social dynamics of mixed-species groups of Jamaican reef fishes. *Behav. Ecol. Sociobiol.* **2**: 361–384.
- Johnson, R. A. (1954). The behavior of birds attending army ant raids on Barro Colorado Island, Panama Canal Zone. *Proc. Linn. Soc. N.Y.* **63–65**: 41–70.
- Jones, S. E. (1977). Coexistence in mixed species antwren flocks. *Oikos* **29**: 366–375.
- Karr, J. R. (1971). Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.* **41**: 207–233.
- MacArthur, R. H. (1972). *Geographical ecology*. New York: Harper and Row.
- Macdonald, D. W. & Henderson, D. G. (1977). Aspects of the behaviour and ecology of mixed-species bird flocks in Kashmir. *Ibis* **119**: 481–491.
- Marler, P. (1973). A comparison of vocalizations of red-tailed monkeys and blue monkeys, *Cercopithecus ascanius* and *C. mitis*, in Uganda. *Z. Tierpsychol.* **33**: 223–247.
- McClure, H. E. (1967). The composition of mixed-species flocks in lowland and sub-montane forests of Malaya. *Wilson Bull.* **79**: 131–154.

- Moreau, R. E. (1948). Ecological isolation in a rich tropical avifauna. *J. Anim. Ecol.* **17**: 113–126.
- Morse, D. H. (1967). Foraging relationships of brown-headed nuthatches and pine warblers. *Ecology* **48**: 94–103.
- Morse, D. H. (1970). Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.* **40**: 119–168.
- Morse, D. H. (1973). Interactions between tit flocks and sparrowhawks *Accipiter nisus*. *Ibis* **111**: 591–593.
- Morse, D. H. (1977). Feeding behavior and predator avoidance in heterospecific groups. *Bioscience* **27**: 332–339.
- Morse, D. H. (1978). Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. *Ibis* **120**: 298–312.
- Moynihan, M. (1962). The organization and probable evolution of some mixed species flocks of neotropical birds. *Smithson. misc. Collns* **143**: 1–140.
- Moynihan, M. (1968). Social mimicry: character convergence versus character displacement. *Evolution* **22**: 315–331.
- Munn, C. A. & Terborgh, J. W. (In press). Multi-species territoriality in neotropical foraging flocks. *Condor*.
- Murton, R. K., Isaacson, A. J. & Westwood, N. J. (1971). The significance of gregarious feeding behaviour and adrenal stress in a population of wood-pigeons *Columba palumbus*. *J. Zool., Lond.* **165**: 53–84.
- Page, G. & Whitacre, D. F. (1975). Raptor predation on wintering shorebirds. *Condor* **77**: 73–83.
- Pearson, D. L. (1977). Ecological relationships of small antbirds in Amazonian bird communities. *Auk* **94**: 283–292.
- Pearson, D. L., Tallman, D. & Tallman, E. (1977). *The birds of Limoncocha, Napo Province, Ecuador* (revised edition). Quito: Instituto Linguístico de Verano.
- Powell, G. V. N. (1974). Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* **22**: 501–505.
- Powell, G. V. N. (1979). Structure and dynamics of interspecific flocks in a neotropical mid-elevation forest. *Auk* **96**: 375–390.
- Pulliam, R. H. (1973). On the advantage of flocking. *J. theoret. Biol.* **38**: 65–70.
- Slud, P. (1960). The birds of Finca 'La Selva,' Costa Rica: a tropical wet forest locality. *Bull. Am. Mus. nat. Hist.* **121**: 49–148.
- Stanford, J. M. (1943). Bird parties in the forest of Burma. *Ibis* **89**: 507–509.
- Struhsaker, T. T. (1969). Correlates of ecology and social organization among African cercopithecines. *Folia primatol.* **11**: 80–118.
- Swynnerton, C. F. M. (1915). Mixed bird-parties. *Ibis* **1915**: 346–354.
- Tallman, D. A. (1979). *Ecological partitioning by antbirds of a moist tropical forest in Amazonian Ecuador*. Ph.D. Dissertation, Louisiana State University.
- Vine, I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behavior. *J. theor. Biol.* **30**: 504–522.
- Wiley, R. H. (1971). Cooperative roles in mixed flocks of antwrens (Formicariidae). *Auk* **88**: 881–892.
- Williams, G. C. (1964). Measurement of consociation among fishes and comments on the evolution of schooling. *Publs Mich. St. Univ. Mus. (Biol. Ser.)* **2**: 351–383.
- Willis, E. O. (1966). Interspecific competition and the foraging behavior of plain-brown woodcreepers. *Ecology* **47**: 667–672.
- Willis, E. O. (1967). The behavior of bicolored antbirds. *Univ. Calif. Publs Zool.* **79**: 1–132.
- Willis, E. O. (1972). The behavior of spotted antbirds. *Ornith. Monogr.* **10**: 1–162.
- Willis, E. O. (1977). Lista preliminar das aves da parte noroeste e áreas vizinhas da Reserve Ducke, Amazonas, Brasil. *Revta bras. Biol.* **37**: 586–601.
- Willis, E. O. & Oniki, Y. (1978). Birds and army ants. *Ann. Rev. Ecol. Syst.* **9**: 243–263.
- Winterbottom, J. M. (1943). On woodland bird parties in northern Rhodesia. *Ibis* **85**: 437–442.