

THE FORMATION OF ANTWREN FLOCKS ON BARRO COLORADO ISLAND, PANAMÁ

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ABSTRACT.—The nuclei of antwren flocks, studied on Barro Colorado Island, Panama Canal Zone, between October 1977 and March 1978, consisted of pairs or family groups of two species of antwrens, *Myrmotherula fulviventris* and *Microrhopias quixensis*. These species defended completely interspecifically overlapping territories and often displayed simultaneously at common boundaries. This type of association, between pairs of different species, has not been reported previously. The study site contained several abutting joint territories. Many insectivorous species of forest birds joined the antwren flocks, but most species occurred only rarely. Individual wintering *Dendroica pensylvanica* had territories that almost completely overlapped the antwren territories, but other marked attendant species had either small territories overlapping one or two antwren territories or large widely overlapping home ranges that included many antwren territories. The species with small territories, *Thamnophilus punctatus*, joined the flock only as the antwrens passed through that portion of their territory. Species with large home ranges, in particular three species of dendrocolaptids and *Xenops minutus*, moved through their home ranges by travelling with antwren flocks and passing between flocks during the territorial border displays of the neighboring antwrens. The most persistent attendant species in the flocks roosted with the antwrens.

Myrmotherula fulviventris and *Microrhopias quixensis* preferentially used areas of their territories that contained dense and continuous vine tangles, but more attendant species joined the flock, and average flock size was larger, in the portions of the antwren territory that were not preferred by the antwrens. Young antwrens probably remain with adults to learn how to forage, to detect predators, and to delay the point at which they must maintain a territory. *Myrmotherula fulviventris* and *Microrhopias quixensis* may reduce predation by flocking together. Received 21 December 1978, accepted 22 October 1979.

MIXED species flocks that form around antwrens (Formicariidae, genus *Myrmotherula*, and relatives) are common throughout neotropical forests. In lowland Panamá, pairs or small family groups of one to several antwren species often move through the forest accompanied by many species of flycatchers, woodcreepers, warblers, and other insectivorous birds. These flocks occur all year, and several attendant species are seldom found away from interspecific flocks.

Despite the importance of antwren flocks in neotropical avian communities, there has been little detailed study of their ecology. Willis (1972) gives a detailed description of flocks on Barro Colorado Island. The foraging behavior of the three antwren species of Barro Colorado Island was studied by Wiley (1971), and Jones (1977) measured foraging niche parameters and the degree of association between antwren and nonantwren species. Little is known of the integrity and mechanisms of formation of flocks, because individually marked members have not been studied for long periods of time. Buskirk et al. (1972) and Powell (1979) followed marked members of highland tropical flocks in Central America. They found that the single nucleus, or leader species, moved about a large territory and picked up attendant species, many of which held smaller territories. The structure of the flocks resulted from an interplay between movement patterns of nucleus and attendant species.

Here we report on a 5-month study of color-marked individuals in flocks of White-flanked Antwrens (*Myrmotherula axillaris*), Checker-throated Antwrens (*Myrmotherula fulviventris*), and Dot-winged Antwrens (*Microrhopias quixensis*) on Barro Colorado Island, Panamá. We will refer to these species by their specific names (*axillaris*, *fulviventris*, and *quixensis*).

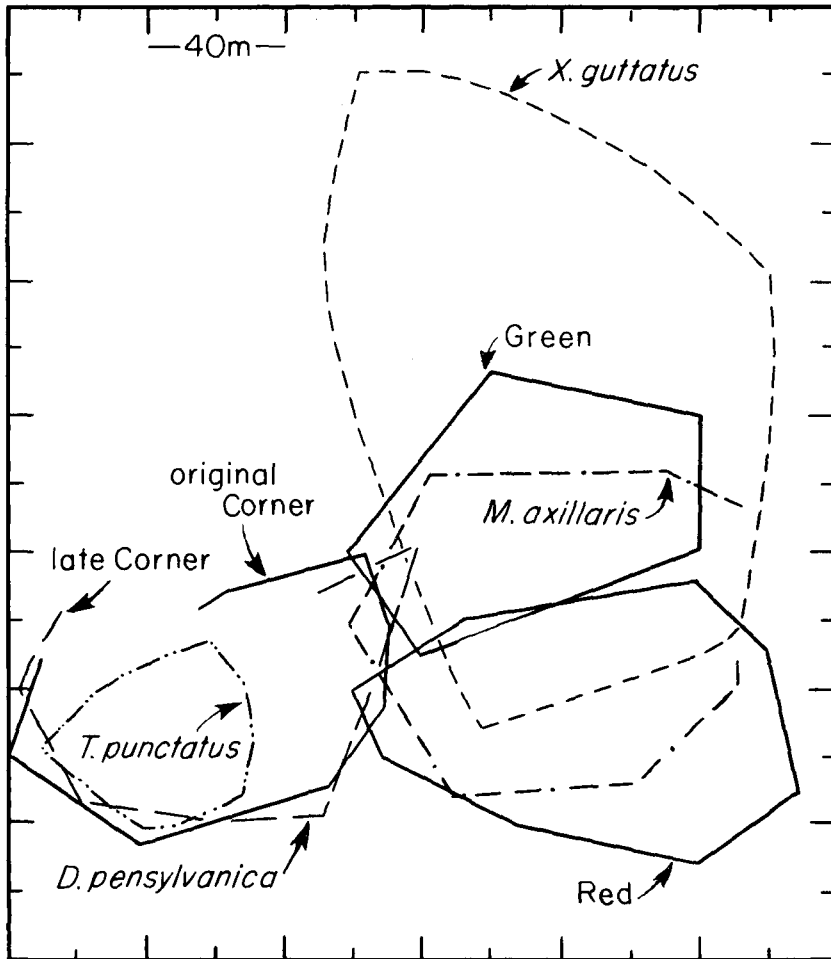


Fig. 1. Home range and territorial array of species in antwren flocks (sample sizes refer to the individual home ranges depicted): *Xiphorhynchus guttatus* ($n = 5$ resightings), *Thamnophilus punctatus* family ($n = 39$ individual resightings), *Dendroica pensylvanica* ($n = 25$ resightings), and *Myrmotherula axillaris* family ($n = 29$ resightings). The three antwren groups, Red ($n = 190$ resightings), Green ($n = 15$ resightings), and Corner ($n = 42$ resightings), are each composed of one pair or family of *Microrhopias quixensis* and one pair or family of *Myrmotherula fulviventris*. Original and Late Corner refer to the groups occupying that territory 5 months apart. All ranges are based on actual sightings; breaks in the lines indicate areas without any sightings. The home range shown for *X. guttatus* is a minimum estimate; the marked individual was the only one sighted in the study area.

METHODS

We conducted this study between 15 October 1977 and 20 March 1978 on Barro Colorado Island, Panama Canal Zone. The 1,480-ha island (Willis, pers. comm.) is covered with lowland moist tropical forest (Holdridge and Budowski 1956) under a distinctly seasonal climatic regime. The wet season lasts approximately from April through mid-December, when rainfall averages 315 mm per month; the shorter dry season averages 50 mm of rain per month (Ridgely 1976). The 5 months of observations encompassed the late wet season through the late dry season. Two types of forest are distinguishable on Barro Colorado: old growth forest at least 125 yr old, and young forest 65–90 yr old (Knight 1975). The old forest is characterized by a taller, less heterogeneous canopy (average height 30–40 m) and less undergrowth than the younger forest. Tree-fall gaps are common throughout the island and are characterized by a low

TABLE 1. Composition and percent of sightings of species in Red flock (*Myrmotherula fulviventris*) censuses, $n = 160$.

Species present	Percent sightings	
<i>Damophila julie</i>	Violet-bellied Hummingbird	1
<i>Piaya cayana</i>	Squirrel Cuckoo	2
<i>Trogon massena</i>	Slaty-tailed Trogon	3
<i>Trogon rufus</i>	Black-throated Trogon	4
<i>Electron platyrhynchum</i>	Broad-billed Motmot	3
<i>Campephilus melanoleucus</i>	Crimson-crested Woodpecker	3
<i>Glyphorhynchus spirurus</i>	Wedge-billed Woodcreeper	5
<i>Xiphorhynchus guttatus</i>	Buff-throated Woodcreeper	1
<i>Xiphorhynchus lachrymosus</i>	Black-striped Woodcreeper	11
<i>Xenops minutus</i>	Plain Xenops	15
<i>Sclerurus guatemalensis</i>	Scaly-throated Leaf-tosser	0
<i>Thamnophilus punctatus</i>	Slaty Antshrike	47
<i>Dysithamnus puncticeps</i>	Spot-crowned Antwren	2
<i>Myrmotherula axillaris</i>	White-flanked Antwren	25
<i>Myrmotherula fulviventris</i>	Checker-throated Antwren	100
<i>Microrhopias quixensis</i>	Dot-winged Antwren	63
<i>Hylophylax naevioides</i>	Spotted Antbird	3
<i>Pipra mentalis</i>	Red-capped Manakin	2
<i>Myiarchus tuberculifer</i>	Dusky-capped Flycatcher	2
<i>Empidonax virescens</i>	Acadian Flycatcher	1
<i>Terentotriccus erythrurus</i>	Ruddy-tailed Flycatcher	24
<i>Tolmomyias assimilis</i>	Yellow-margined Flycatcher	1
<i>Rhynchocyclus olivaceus</i>	Olivaceous Flatbill	2
<i>Oncostoma olivaceum</i>	Southern Bentbill	2
<i>Ornithion brunneicapillum</i>	Brown-capped Tyrannulet	2
<i>Vireo philadelphicus</i>	Philadelphia Vireo	1
<i>Hylophilus decurtatus</i>	Lesser Greenlet	37
<i>Mniotilta varia</i>	Black-and-White Warbler	12
<i>Dendroica pensylvanica</i>	Chestnut-sided Warbler	44
<i>Dendroica castanea</i>	Bay-breasted Warbler	27
<i>Geothlypis formosus</i>	Kentucky Warbler	4
<i>Setophaga ruticilla</i>	American Redstart	2
<i>Tachyphonus luctuosus</i>	White-shouldered Tanager	4
<i>Eucometis penicillata</i>	Gray-headed Tanager	2

canopy ringed by dense vine tangles. Barro Colorado Island has approximately 40 km of trails, each of which is marked at 100 m intervals. The steep sides of the island level to a broad plateau at the center. The plateau was chosen as the site of a detailed study of marked individuals, because the gentle topography was conducive to census routes away from trails. Our study site consisted of 6 ha of mainly young forest with an average canopy height of 22.5 m on the northeast edge of the plateau. We marked 2.5 ha of the study site with a 20-m grid system to facilitate accurate sightings of individual birds. All weights used in this paper are from Karr (1971).

CENSUS ROUTES

Plateau site census.—Ten mist nets were placed at points in the plateau study area where we had observed flocks foraging low in the understory. Species captured that might occur in an antwren flock were individually color marked. From 6 November to 4 March, a total of 85 individuals were banded in 740 net-hours. We censused regularly, totaling a minimum of 500 h, the area within and adjacent to the study area and attempted to resight marked individuals. We recorded the time of day and location within the grid system of all individuals within 20 m of marked birds. All estimates of home range size (Fig. 1) were based on the Plateau site census (Single flock census points not included).

Single flock census.—For a more detailed study of flock dynamics and species turnover we followed a single pair of *fulviventris* marked with red leg bands ("Red *fulviventris*") for 80 h during the dry season, between 31 December and 12 March. Observations were distributed evenly between 0615, when the birds first called from their roost, and 1830, when they settled to roost. Sufficient distance was maintained between the observer and birds that the birds never alarmed at nor mobbed the observer.

Any individuals clearly moving with the antwrens were considered members of the flock. Individuals within 20 m of the antwrens but that did not move with them were noted but not considered in the

analyses. Each 0.5 h, species composition of the flock, location within the grid system, and vertical foraging height range of certain species were recorded. Time of day, location, and species involved in any change in flock membership also were recorded. Species composition of Red flock for the 80-h period is shown in Table 1.

STRUCTURAL ANALYSIS OF VEGETATION

Measurements of vegetation were taken throughout the 2.3-ha area that was used by Red *fulviventris*. Within each 20 × 20-m quadrat, the unit used in the regression analysis (see below), vegetation structure was measured at four evenly spaced preselected points. A 2-m rod held at breast height was used as the radius for each sample circle. As we moved the rod through the circle, we recorded the diameter at breast height (dbh) of each vertical vine and tree that the rod touched. For the purposes of the analysis, trees were separated according to dbh into three size classes: small (0 < dbh ≤ 5 cm), medium (5 < dbh ≤ 20 cm), and large (dbh > 20 cm); we did not differentiate size classes for vines. The mean and standard deviation of each of the various size classes for each quadrat were used in the analysis. In this manner, we included a measure of overall density and variability of each class of vegetative structure within each quadrat. In addition we recorded the diameter and height range for all dense (estimated to be 75% or more closed to light; 100% would be black) vine tangles between 3 and 18 m. The vine tangle index for each quadrat used in the multiple regression was chosen to reflect the roughly conical shape of vine tangles on the study site:

$$\sum_{i=1}^{n=4} \sqrt{(\text{vertical height range} \times \text{diameter})}$$

Height to the top of the canopy was estimated, and the estimates were calibrated with a 200-mm telephoto lens. The center of the territory was determined by drawing the smallest possible rectangle around the peripheral sightings of *fulviventris* and using the center of the rectangle. The distance of each quadrat from the center of the territory was measured from the center of each quadrat. Twelve variables were used in the multiple regression: mean and standard deviation of trees 0 < dbh ≤ 5 cm, 5 < dbh ≤ 20 cm, and dbh > 20 cm; mean and standard deviation of all vertical vines of canopy height; the vine tangle index; and the distance of each quadrat from the center of the territory.

THE ANTWRN SPECIES

Myrmotherula fulviventris (Checker-throated Antwren) is one of the least sexually dimorphic species of antwrens. The 10.5-g birds have drab brown backs and buffy undersides. The male has a black and white checkered throat. Iris color proved to be useful for aging males; irides of females are golden-brown, of immature males, light gray, and of adult males, dark brown. We discovered this relationship between male age and iris color from three banded juvenile males. *Fulviventris* forage almost exclusively by probing their bills into dead curled leaves (Wiley 1971, present study). Foraging heights range from 0.5 m to 25 m and average 10.5 m ($n = 126$; $SD = 5$ m). These birds give a soft *chip*, which serves as a contact note for the pair or family group as it moves through dense vegetation; a louder faster version is used in territorial displays.

Microhopias quixensis (Dot-winged Antwren) weighs 8.1 g and is strongly sexually dimorphic. Males are jet-black with white spots on the wing coverts and tips of the tail feathers; females resemble males but have bright rufous undersides from throat to under-tail coverts. Individuals of this species forage mostly by gleaning and hover-gleaning at live vegetation and take insects from the undersides of leaves. Foraging heights range from 2 to 30 m, and average 13.5 m ($n = 72$; $SD = 4.5$ m). This species is more easily heard than seen because it has a loud and distinctive call note, and individuals spend most of their time in the densest part of thick vine tangles. The family group was a territory that completely overlapped with Red *fulviventris* (Fig. 1) was distinguished from other *quixensis* on the study area by the presence of a young male that begged noisily for 4 months.

RESULTS

HOME RANGE PATTERNS WITHIN ANTWRN FLOCKS

The basic unit or nucleus of the antwren flock consists of pairs or families of *fulviventris* and *quixensis* with completely overlapping territories. There were five such co-defended territories on the plateau study area; "Red Group" was chosen for

intensive study because its central location within the study site allowed us to monitor the entire territory.

The *quixensis* family group with the young begging male spent 63% of the 80-h census travelling with the Red *fulviventris* pair. These two species also roosted in the same tree on the eight occasions that roosts were observed. Many other attendant species also roosted with the antwrens: *Thamnophilus punctatus*, *Xenops minutus*, *Xiphorhynchus lachrymosus*, *Myrmotherula axillaris*, *Dendroica pensylvanica*, and *Glyphorhynchus spirurus*. *T. punctatus* usually roosted on the same branch as *fulviventris*, and the others roosted within 15 m; by 0630 all species would be moving together as a flock.

Pairs or families of *quixensis* and *fulviventris* defended common boundaries in conspicuous territorial border displays. All observed border interactions occurred on the southeast side of the territory (\bar{x} = 2.3 displays per day) where three other territories of antwren groups abutted. Frequently, the Red group displayed successively with each of the other groups, and occasionally three antwren groups displayed simultaneously. Observations by Willis (1960) suggest that this phenomenon of co-defended territories may occur in other species of tropical birds.

Quixensis have loud contact notes, and, as they approached their border, we could hear the neighboring *quixensis*. The contact notes got louder and more rapid as the two *quixensis* groups discovered each other's presence and rushed to display. Displays were always directed toward members of the same sex; this held true for all observations of antwren border interactions throughout the island. If young were present, they fluttered around the periphery singing and occasionally displaying for 1–2 min. The displays of adults lasted from 5 to 45 min (usually 15–20 min), and the birds sang as they left the boundary. They rarely touched in the displays, and no grappling was observed. This lack of overt aggression was also characteristic of the *fulviventris* displays.

Fulviventris usually moved to the border to display after *quixensis* had started. They have softer contact notes, and it may take longer for neighboring pairs to discover each other. Displays of *fulviventris* were less vigorous than *quixensis* displays. Males always participated, but females occasionally did not display or moved away from the border to continue foraging. *Fulviventris* usually stopped displaying before *quixensis*, and, as they moved away from the border, they called loudly and slowly. Both species usually displayed in the same tree and each appeared to direct displays toward conspecifics only. The displays took place in dense vine tangles at the same region along the border each time. In both species, once display positions were reached, neither group advanced further.

Border displays were the predominant territorial behavior for both species, although *fulviventris* males occasionally chipped loudly, while in the center of their territories, in response to the distant fast chipping of neighboring conspecifics.

Home range patterns of attendant species.—Home ranges of most of the marked attendant species were either smaller than one antwren territory or were larger and included three or more antwren territories (Fig. 1). *Dendroica pensylvanica*, a migrant, was the only attendant species present whose territorial boundaries coincided with those of the antwrens. Each of the three individual *D. pensylvanica* (with recognizable plumage patterns in the study area) had a territory that overlapped almost completely with the territory of a different antwren group (51 total resightings of *D. pensylvanica*, not including sightings on Red flock census). *Thamnophilus punctatus* (15 marked individuals in 7 pairs or families, 33 resightings of pairs or

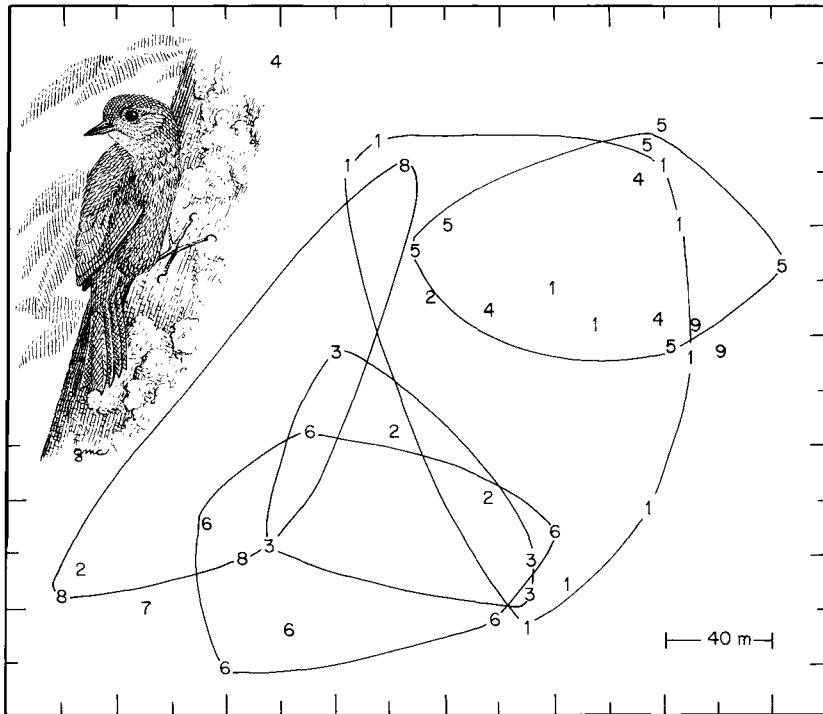


Fig. 2. Home ranges of nine *Glyphorhynchus spirurus*. Each number indicates a different individual; lines indicating minimum home-range estimates are drawn for five individuals.

families) held smaller territories. Other species, such as *Dysithamnus puncticeps*, *Geothlypis formosus*, *Sclerurus guatemalensis*, and *Empidonax virescens*, also appeared to hold smaller territories, but we did not have enough marked individuals to confirm this. It was possible for more than one pair or family group of *T. punctatus* to have a territory totally or partially included in one antwren territory.

The third species of antwren, *axillaris*, had a territory the equivalent size of 2–3 *fulviventris-quixensis* territories (51 resightings of 3 marked individuals in 2 family groups; these were the only family groups in the study area). This may reflect the differential habitat preference of this species. It usually forages in the open understory, while the other two antwrens usually forage higher and in dense vine tangles. The following species appeared to have large and widely overlapping home ranges: 2 species of dendrocolaptids, *Xiphorhynchus lacrymosus* (1 marked individual, at least 2 unmarked were on the study site) and *Glyphorhynchus spirurus* (14 marked individuals, 40 total resightings); *Xenops minutus* (4 marked individuals, 6 total resightings); and *Dendroica castanea* (6 marked individuals, 6 total resightings, and many different unmarked birds sighted). We caught many of these species in the same net and resighted them in the same area. Many individuals of the flycatcher *Terentotriccus erythrurus* were caught, (eight individuals marked, one resighting), but we did not have enough resightings of any one individual to estimate home range size.

The pattern of sightings of marked *Glyphorhynchus spirurus* (Fig. 2) show widely overlapping home ranges. No areas of exclusive use can be discerned. In addition, five other *G. spirurus* were marked and never resighted. The low number of re-

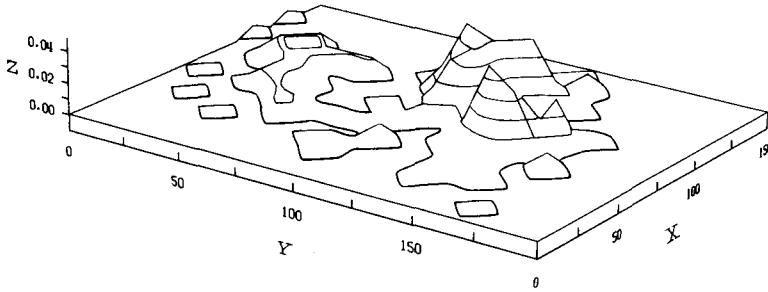


Fig. 3. Topographic map of *Myrmotherula fulviventris* territorial use. The axes X and Y are in meters, and Z is the proportion of total sightings ($n = 160$).

sightings of individuals also indicates that home ranges were probably much larger than the study area. A number of different *G. spirurus* could be seen in each antwren flock; during the Red flock census, *G. spirurus* was observed in 5% of the census periods, and this consisted of 4 different marked (and 1 or more unmarked) individuals.

Movement patterns.—As the antwrens moved through their territory, other species joined and left them within the constraints of their own spacing systems. The species with larger home ranges, in particular the dendrocolaptids, appeared to move through their larger home ranges by moving from antwren flock to antwren flock. It was possible to locate a marked individual with an antwren flock at one end of the study area and observe it over the course of a few hours in a series of antwren flocks as it moved to the other end of the study area. Species with smaller territories, such as the antshrike *Thamnophilus punctatus*, moved with the antwrens only as the flock passed through the antshrike's territory.

Antwrens participated several times daily in the conspicuous territorial border displays. Families of *fulviventris* and *quixensis* displayed simultaneously at their mutual boundaries, and occasionally other species such as *axillaris* and *T. punctatus* displayed also, if their territorial borders coincided with an antwren border. The dendrocolaptids and *Xenops minutus* engaged in lengthy and vociferous chases if they met conspecifics in the next antwren flock, but displays in these species did not appear to be boundary oriented. These species were generally solitary within flocks during our study (98%, $n = 107$).

TERRITORY USE PATTERNS OF *MYRMOTHERULA FULVIVENTRIS*

The total area covered by Red *fulviventris* during 80 h of observation was 2.3 ha. The range of area used during an 8-h period of observation, however, was 0.6–1.2 ha. Additionally, the antwrens used a small portion of their territory disproportionately more than they used the rest of the territory; 10 of the 57 quadrats used by the antwrens, or 18% of the total area, was used 67% of the time (Fig. 3).

To determine the habitat characteristics of the areas preferred by antwrens, we performed a stepwise multiple regression between antwren territory use, measurements characterizing vegetation structure, and the distance of each quadrat from the border of the territory. The two variables with the greatest r^2 values (from a total of 12 variables) were the presence of dense vine tangles ($r^2 = 0.29$, $P < 0.01$), and the distance from the edge of the territory ($R^2 = 0.09$, $r^2 = 0.140$, $P < 0.05$).

The multiple R^2 was 0.38. This is strong evidence that *fulviventr*s preferentially use areas with dense and abundant vine tangles. Moreover, antwrens appear to prefer areas of exclusive vine tangles, i.e. those closest to the center of their territory. Two other factors that were not reflected in the regression probably figure importantly in the way in which antwrens use territories. First, the antwrens commonly used the same routes for travelling between areas with vine tangles; thus, quadrats used commonly as corridors should have high antwren-use values and low vine-tangle values. Second, quadrats that were isolated and had high vine-tangle values may not have been as attractive to the antwrens as contiguous quadrats with high vine-tangle values.

Each large concentration of vine tangles around a major light gap supported one antwren group on the plateau study site; antwren groups on other parts of Barro Colorado Island were also found consistently in areas with dense vine tangles. Suitable habitat for *fulviventr*s territories appeared to be a limited resource. Evidence for this came from the death in a mist net of the adult male *fulviventr*s of Corner group. The female and young *fulviventr*s subsequently disappeared, but the *quixensis* and a marked *Thamnophilus punctatus* family remained. Within 1 week we marked a new immature male and female *fulviventr*s in the territory. The immature male was replaced sequentially by three other immature males, one of which had dispersed from Red group. Over the course of 5 months, the male *fulviventr*s in Corner group changed four times and the female changed once. Figure 1 shows the original territories of the first pair and territory of the last pair of *fulviventr*s in Corner group. The size and placement of the territory did not change appreciably. The apparent scarcity of suitable habitat and difficulty of the young *fulviventr*s in holding a territory may explain why young birds stay with their parents for extended periods of time.

USE OF THE ANTWREN TERRITORY BY ATTENDANT SPECIES

Although the Red *fulviventr*s pair spent most of its time in a limited portion of its territory, these were not necessarily the areas where attendant species joined the antwrens. To test whether attendant species occurred with antwrens in the preferred or nonpreferred portion of their territory, we tabulated the number of attendant species in Red group in each census period and compared the distributions from heavily used to less heavily used quadrats. It would be preferable to compare, on a quadrat by quadrat basis, the average number of attendant species to the number of census visits for each quadrat. Less frequently used quadrats, however, will display a greater variation in mean number of species because of sampling error. To avoid this problem, we calculated the overall distributions with less than six sightings of *fulviventr*s and those of six or more sightings. The analysis considers only species with home ranges larger than the antwren territory, because only these species could exhibit a completely independent selection of quadrats. Thus, *Dendroica pensylvanica*, *Thamnophilus punctatus*, *Dysithamnus puncticeps* and *Microrhopias quixensis* were excluded from this analysis. The average number of species was significantly higher (Mann-Whitney U -test with normal approximation, $U = 3,889$, $t = 2.88$, $P < 0.005$) in antwren nonpreferred quadrats (2.2 species per flock) than in antwren preferred quadrats (1.35 species per flock). We interpret this to indicate that attendant species occurred in antwren flocks more frequently (relative to *fulviventr*s presence) in areas away from the antwren-preferred vine tangles.

TABLE 2. Sightings of attendant species in the Red *Myrmotherula fulviventris* territory. Preferred quadrats are those in which *M. fulviventris* was sighted six or more times in 160 censuses. Nonpreferred quadrats are those in which *M. fulviventris* was sighted less than six times.

Species	Number of censuses species was present	Number of sightings in preferred quadrats	Number of sightings in non-preferred quadrats	Difference between species sightings and <i>Myrmotherula fulviventris</i> sightings (χ^2 test)
<i>Myrmotherula fulviventris</i>	160	107	53	—
<i>Microrhopias quixensis</i>	105	86	19	$0.025 > P > 0.01$
<i>Thamnophilus punctatus</i>	77	57	20	N.S.
<i>Dendroica pensylvanica</i>	72	39	33	$P < 0.005$
<i>Hylophilus decurtatus</i>	62	33	29	$P < 0.005$
<i>Dendroica castanea</i>	44	26	18	N.S.
<i>Myrmotherula axillaris</i>	38	30	8	$0.10 > P > 0.05$
<i>Terenotriccus erythrurus</i>	37	23	14	N.S.
<i>Xenops minutus</i>	26	6	20	$P < 0.005$
<i>Mniotilta varia</i>	20	11	9	$0.05 > P > 0.025$
<i>Xiphorhynchus lachrymosus</i>	19	10	9	$0.10 > P > 0.05$

Our direct observations also indicate that more species joined the flock in the areas without many vine tangles. We recorded every time a bird joined the flock (this includes between census periods), and 46% of these joinings ($n = 96$) occurred in the nonpreferred quadrats, which had 33% of the census sightings ($\chi^2 = 4.19$, $0.05 > P > 0.025$).

This pattern of attendant species joining *fulviventris* away from their preferred vine tangles is predominant but not universal for species that join antwren flocks (Table 2). Of the 10 species that foraged most commonly with Red *fulviventris* (including those species with small territories), four species (*Dendroica pensylvanica*, *Hylophilus decurtatus*, *Xenops minutus*, and *Mniotilta varia*) significantly ($P < 0.05$) preferred quadrats where the antwrens occurred infrequently. Four species (*Dendroica castanea*, *Thamnophilus punctatus*, *Xiphorhynchus lachrymosus*, and *Terenotriccus erythrurus*) showed no clear preference for the quadrats with respect to antwren use. Only two species (*Microrhopias quixensis* and *Myrmotherula axillaris*) showed preference for the quadrats used more frequently by Red *fulviventris*, and this was significant only for *quixensis*. The preference of *quixensis* for joining *fulviventris* when in vine-tangled areas reflects the strong dependence of this species on dense vegetation. The results for *axillaris* (the least common antwren) are surprising, because elsewhere on Barro Colorado Island this species generally preferred more open understory. In fact, the low foraging height of this species when with Red group ($\bar{x} = 6.9$ m, $n = 17$) indicates that this species may not have been in the dense vine tangles when they were foraging with Red group. It is also possible that *axillaris* were actually joining the flock for reasons irrespective of habitat; they may have been taking advantage of the ability of *quixensis* to detect a different set of predators.

We propose three possible reasons why attendant species may prefer not to forage in the dense vine tangles preferred by *fulviventris* and *quixensis*: (1) The attendant species may not be able to maneuver through the vine tangles as easily as the antwrens. Certain large-bodied species may not be able to fit physically through the dense foliage. Species that have a large foraging distance (*Terenotriccus erythrurus* mean attach distance to capture an insect = 3 m, $n = 28$) or species that commonly leap or sally to obtain insect prey may not be able to forage in dense vine tangles.

(2) *Fulviventris* move more slowly through areas with vine tangles than through relatively open understory. The attendant species that need to move more rapidly while foraging may not be able to support themselves by searching a small area intensively. (3) It may be more difficult for attendant species to locate and follow antwrens through dense vine tangles. The only instances in which the observer lost Red flock occurred when the flock disappeared into dense vine tangles and contact notes of the antwrens could not be heard. This was a problem primarily during the mid-dry season, when noise made by winds and ever-present cicadas made it necessary to watch the antwrens continuously while in dense vine tangles to keep from losing them. Any attendant species not foraging close to the antwrens, or an "intensively foraging" species (Willis 1972), may encounter the same difficulties.

DISCUSSION

The nuclei of the antwren flocks we studied on Barro Colorado Island were formed by the close association of family groups of *fulviventris* and *quixensis*. The existence of family groups that last for extended periods has been described for many species of tropical forest birds (Skutch 1967, Fogden 1972). During the 5 months of this study, we observed family groups in marked or otherwise identifiable *fulviventris*, *quixensis*, *axillaris*, and *Thamnophilus punctatus*. These associations, of a pair of adults and 1 or 2 young birds, lasted for at least 4–6 months. The young begged occasionally and were fed by both parents. Antwrens appeared to breed year around, for we saw newly fledged birds from November through March. The peak of breeding activity reported for insectivorous forest birds on Barro Colorado Island occurs in the late dry season and beginning of the wet season (March–June) (Eisenmann 1952, Oniki 1975). Our marked pairs of *fulviventris* and *quixensis* commenced courtship feeding and nest building after the young of the previous year had dispersed. It is possible, however, that an adult pair has young birds with it throughout most of the year. The young birds appeared to have a minimal role in territorial maintenance while with their parents.

A probable explanation for the extended period during which the young birds remain with their parents is the limited availability of suitable habitat. It is apparently necessary for antwrens to use certain habitat features, such as vine tangles, and there appears to be intense competition for these features. It was shown above that, for *fulviventris*, suitable habitat patches for territories (vine tangles) may be limited; perhaps this applies to other species as well. It is probably more difficult for a young bird than an old bird to hold a territory. It may also be advantageous for young birds to stay with parents to learn how to forage and detect predators (Fogden 1972). The young antwrens and antshrikes may remain with their parents for both of the above reasons.

The reasons behind the persistent association of *fulviventris* and *quixensis* are less obvious than the factors promoting maintenance of family groups within these species. It is unlikely that any direct advantage is gained in food location through local enhancement (e.g. Krebs 1972). The two species, *quixensis* and *fulviventris*, probably show no overlap in foraging microhabitat because *quixensis* forages exclusively on live vegetation and *fulviventris* forages exclusively on dead vegetation. It is possible that they are learning the location of areas of high insect abundance, but it is unlikely that this is a major factor promoting interspecific flocking in these species. The territories of these species are small, and the birds traverse them many

times daily. It is also possible that *quixensis* and *fulviventris* are searching for different types of insects because they exploit different microhabitats. Arguments concerning efficient harvesting of resources (Short 1961) or niche shifts (Morse 1970) could not apply in this situation.

Increased predator avoidance may be the factor uniting these two species, but the specific mechanisms may be complex. Each species displays three basic responses to potential predators that may aid the other species: detection, alarm, and mobbing. Family groups of antwrens are conspicuous even when they are moving alone through the vegetation, and the presence of two family groups may not be twice as conspicuous to predators. The negative effects of travelling in a group may, in this case, be outweighed by increased vigilance of the group to predators. Because the two species have different mean foraging heights and use different microhabitats, each species may be vigilant to different predators.

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