

# STRUCTURE AND DYNAMICS OF INTERSPECIFIC FLOCKS IN A NEOTROPICAL MID-ELEVATION FOREST

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**ABSTRACT.**—Mixed-species flocks of marked individuals were studied for 3 yr in a middle-elevation neotropical forest. Most flock participants maintain pair bonds and defend territories throughout the year. Residents only follow flocks that are in their territories, so intraspecific group size of flocks is limited primarily to pairs and pairs with young. When a flock leaves the territory of one of its members, the member generally drops from the flock, and the neighboring conspecific, whose territory has just been entered, may join. The propensity for birds to join varies with season, time of day, climate, species composition of the flock, and proximity of the passing flock.

A three- to four-fold annual cycle in interspecific flock participation is primarily a consequence of more frequent and consistent flocking by year-round residents. Larger mixed-species flocks are not the result of shifts in population structure or densities. Nonresidents from local sources and North American migrants play minor roles in increased flock size.

Mixed flocks are structured groupings whose membership is limited to a few resident individuals of relatively few species. A given flock at any time of the year will consist of some subset of those individuals, with identity of the subsets depending on the flock's location. *Received 29 June 1978, accepted 20 December 1978.*

GROUPING by neotropical birds into interspecific flocks is a widely occurring phenomenon that has attracted the attention of biologists for at least a century (Bates 1863). In spite of the abundance of publications dealing with flocking, however, little is known about the mechanics of multispecific flock formation. In this paper, I examine factors that influence the structure and dynamics of mixed-species flocking.

Multispecific groups of birds are generally categorized as either flocks or aggregations. Aggregations are groupings that incidentally form when individuals are drawn together by environmental factors such as resource patches, sources of water for bathing and drinking, or threatening organisms that elicit mobbing behavior. In contrast, flocks are groupings whose cohesion is dependent on members' responses to one another, that is, a flock generates its own *raison d'etre*. Hypothesized selective advantages for forming mixed flocks are numerous and controversial. Briefly, flocking is thought to enhance foraging or decrease the likelihood of being captured by a predator. Foraging may be enhanced by facilitating the location of food-rich areas (Moynihan 1962) or areas with few competitors (Morse 1970). Proximal flock members may flush prey (Belt 1874) or demonstrate the suitability of additional prey species (Leck 1971). Flocking may permit more systematic resource harvesting (Cody 1971), reduce interspecific aggression (Austin and Smith 1972), or facilitate reduction of niche overlap (Morse 1967). Mixed flocking may allow more effective defense against intraspecific trespassing by virtue of mistaken identity and incorrect assessment of defenders' group size (Darwin 1845, Charles Munn pers. comm.). The potential for flocks to reduce predation susceptibility is as diverse. Flocks may produce confusion or threat of physical damage for the predator (Olson 1964) or reduce

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the predator's capacities to launch surprise attacks on intended prey (Bates 1863). Following flocks may allow birds to learn the locations likely to harbor predators (Moynihan 1962).

To date, objective measures of the relative importance of proposed flocking advantages have proven elusive. Balancing foraging efficiency against predation evasion is frustrated by the absence of simultaneous measures of food and predation stresses. While it is difficult to measure the ultimate determinants of flocking, it is possible to quantify proximate factors that may alter the balance between joining and ignoring flocks. Environmental parameters, such as time of day and year, or flock-related factors, such as composition, location, and movement rate, are proximate factors, the measurement of which will provide an understanding of the dynamics and structure of interspecific flocking and ultimately may help to identify the adaptive significance of these groupings.

Species that associate with mixed flocks have been categorized relative to the roles they play in group formation or maintenance. A nuclear species (Moynihan 1962), or central focus of the group, contributes to the cohesion of the flock. Attendant species are those whose presence does not correlate with the propensity of other species to participate in a flock. I designated a species to be nuclear if its presence correlated with a greater propensity of at least two other species to be present. This definition deliberately avoids the necessity of sorting out leadership roles, a process that proved difficult with the flocks I studied. Furthermore, I have avoided Moynihan's (1962) differentiation between joining and following and have simply defined a bird to be part of a flock if it remained with the group for at least two consecutive censuses recorded in different locations. This set of criteria assures that the bird has moved with the flock regardless of whether it led or followed.

#### STUDY AREA AND METHODS

The study area was situated at 1,580 m in a Lower Montane Wet Forest (Holdridge 1967 and pers. comm.), Puntarenas Province, Costa Rica. The site was bordered on the east by a vast tract of continuous pristine forest, the Monteverde Cloud Forest Biological Preserve; on the north by a wooded pasture; and on the south and west by limited forest interspaced with wooded pastures. Local climate was nonseasonal relative to temperature but highly seasonal with respect to the distribution of wind and precipitation. From November until middle February, most days were marked by prevailing easterly winds 16–80 kmph. These winds were frequently accompanied by heavy cloud cover and windblown moisture that amounted to little accumulation, usually less than 7 mm in 24 h, but that kept leaf surfaces dripping and the forest floor damp. Wind intensities decreased from February until April. Most days in April were relatively calm with clear skies. Heavy rains began either in mid- to late-April or May and continued intermittently until winds again increased in late October. A mean annual rainfall,  $2,437 \pm 593$  mm, was recorded for 12 yr at a weather station located in slightly drier habitat, 1.5 km from the study area.

The study-area forest was characterized by four strata of vegetation. Average height of the canopy was approximately 20 m. Common trees were representatives of Lauraceae, Sapotaceae, Moraceae, and Symplocaceae. Understory trees, up to 8 m in height, were primarily Melastomaceae, Rubiaceae, Apocynaceae, Solanaceae, and Urticaceae. Dense 3–5-m stands of shrubs, primarily Melastomaceae, Solanaceae, and Acanthaceae, filled in light gaps, while vegetation beneath the closed canopy was characterized by a scattering of 1–2-m plants of the families Rubiaceae, Palmae, Solanaceae, Acanthaceae, Piperaceae, and Liliaceae. Trees and shrubs were lightly covered with epiphytes, principally of the taxa Bryophyta, Pteropsida, Orchidaceae, and Gesneriaceae. Some climbing vines, particularly Araceae, Cyclanthaceae, and Leguminosae, were present on most large trees.

Field work was conducted from April 1970 until December 1971 and from September 1972 until October 1973. A grid of narrow paths was cut through the ground cover over most of the 11.7-ha study area. These trails enabled me to observe and follow interspecific flocks unobtrusively, so the birds quickly became habituated to my presence. The squares formed by intersecting trails ( $23 \times 23$  m) were the basis

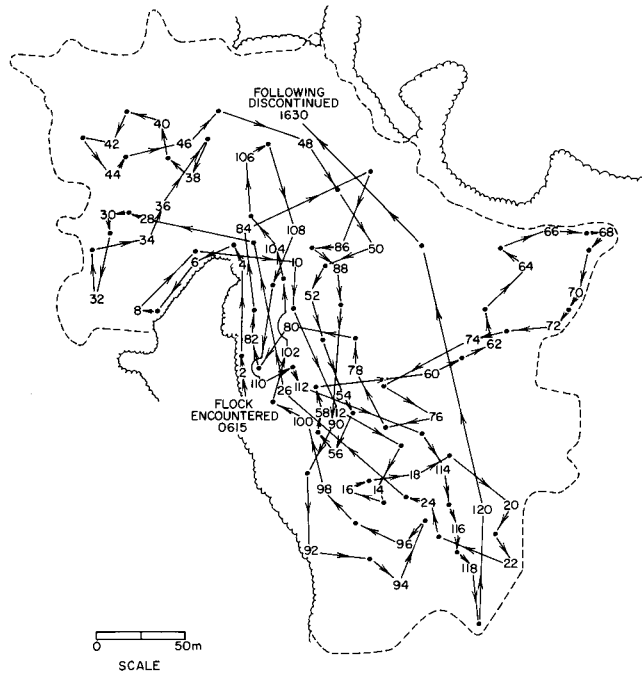


Fig. 1. Course traveled by mixed flock from 0615 until birds roosted at 1630 on 24 November. Numbers represent flock locations at time of censuses made at 5-min intervals throughout the day. Arrows indicate the direction of travel.

for a Cartesian coordinate system used to plot locations. Location within squares was estimated to the nearest 7 m in the X and Y directions. To capture and color-band understory residents, 5–20 mist nets were employed periodically for 1–3 days in succession. I individually marked 734 birds of 42 species that participated in mixed flocks. Banding success varied by species and season. In general, at least one and often both members of most pairs were color-banded. Immatures and new arrivals sometimes remained unbanded for several months before a reduction in wind intensity permitted banding.

Data were collected during 700 h of observations while following flocks on the study area. Grid location and individual composition of the flock were recorded at 5-min intervals. Also, at each census I recorded three characteristics of weather: cloud cover (heavy, partial, light, clear, or fog), wind intensity (rated from 0 for no wind to 6 for wind strong enough to sway large trees), and precipitation (heavy, light, drizzle, drip, or none). Between 5-min censuses, I collected the following behavioral information: intra- and interspecific agonistic interactions; foraging height; food items taken; vocalization types; bathing, preening, and sunning behavior; interactions with potential predators; and intra- and interspecific communication with warning calls. An additional 1,000 h were spent on the study area searching for nests, making behavioral observations, and observing marked birds that were not in flocks. Flock movement rates were determined by dividing linear distance between consecutive censuses by the elapsed time. Mathematical analysis of the data was based primarily on 373 h of observations of a single flock. For the sake of simplicity I refer to a flock by its principal nucleus species contingency. Because data from consecutive censuses of the same flock may be correlated, I analyzed all data for autocorrelation (Anderson 1942). Statistical analyses used censuses that, temporally, were far enough apart to eliminate autocorrelation. Observations of four other mixed flocks were used to corroborate findings.

## RESULTS

Mixed flocks composed of small insectivores and omnivores were prominent in the understory during most of the year. Because birds participating in these flocks foraged primarily in the understory, (0–10 m), they could be followed for long periods

TABLE 1. Foraging behavior and characteristics of flock participation of species that formed mixed-species flocks in the understory of the study area. Symbols for foraging behavior (Aerial = insects captured from the air; Foliage = arthropods gleaned from foliage and branchlets; Ground = arthropods and plant materials obtained from on the ground; Rummage = search through detritus and epiphytes for arthropods; Stalk = glean arthropods from surfaces of trunks and major branches (T) or smaller stems and branches (S); Veg = feed on reproductive parts of plants).

Species	Foraging behavior <sup>a</sup>	Frequency of association	Mean number per 100 associates	Interspecific group size (±SD)	Duration of association (min ± SD)
<b>Permanent residents that are regular associates</b>					
Three-striped Warbler ( <i>Basileuterus tristriatus</i> )	Foliage	100	28.8	2.3 ± 0.5	
Spotted Barbtail ( <i>Premnoplex brunnescens</i> )	Stalk (S+T)	75	16.9	1.8 ± 0.8	109.4 ± 95.5
Gray-breasted Wood-Wren ( <i>Henicorhina leucophrys</i> )	Rummage, Stalk (S)	44	11.8	2.1 ± 0.9	33.6 ± 33.5
Golden-crowned Warbler ( <i>Basileuterus culicivorus</i> )	Foliage	34	9.2	2.2 ± 0.8	64.6 ± 76.8
Chestnut-capped Brush-Finck ( <i>Atlapetes brunneinucha</i> )	Ground, Stalk (S)	26.4	5.9	1.8 ± 0.7	22.1 ± 23.8
Common Bush-Tanager ( <i>Chlorospingus ophthalmicus</i> )	Rummage, Veg	20.2	5.0	2.0 ± 0.9	13.5 ± 11.7
Slate-throated Redstart ( <i>Myioborus miniatus</i> )	Aerial, Foliage	19.2	3.5	1.4 ± 0.5	14.2 ± 16.6
Lineated Foliage-gleaner ( <i>Syndactyla subalaris</i> )	Rummage, Stalk (T+S)	17.5	2.5	1.1 ± 0.3	55.2 ± 55.8
Red-faced Spinetail ( <i>Cranioleuca erythropis</i> )	Stalk (S), Rummage	13.6	3.0	1.8 ± 0.7	29.2 ± 41.7
Spotted Woodcreeper ( <i>Xiphorhynchus erythropygius</i> )	Stalk (T)	13.2	2.0	1.2 ± 0.4	46.0 ± 55.4
Olivaceous Woodcreeper ( <i>Sittasomus griseicapillus</i> )	Stalk (T)	11.7	1.7	1.2 ± 0.4	41.5 ± 52.1
<b>Common permanent residents that are occasional associates</b>					
Ochraceous Wren ( <i>Troglodytes ochraceus</i> )	Rummage, Stalk (S)	6.6	1.0	1.2 ± 0.5	8.5 ± 7.7
Prong-billed Barbet ( <i>Semnorhis frantzii</i> )	Veg, Foliage	0.2	0.1	1.4 ± 0.8	5.0
Rufous-winged Woodpecker ( <i>Piculus simplex</i> )	Stalk (T+S)	0.4	0.1	1	8.3 ± 3.7
Bright-rumped Attila ( <i>Attila spadiceus</i> )	?	0.1	0.1	1	5
Yellowish Flycatcher ( <i>Empidonax flavescens</i> )	Aerial	0.2	0.1	1	5.8 ± 2.8
White-throated Spadebill ( <i>Platyrinchus mystaceus</i> )	Aerial	1.8	0.2	1	11.7 ± 14.9
Eye-ringed Flatbill ( <i>Rhynchocyclus brevirostris</i> )	Aerial	5.7	1.0	1.3 ± 0.8	20.5 ± 30.7
Olive-striped Flycatcher ( <i>Mionectes olivaceus</i> )	Veg	2.0	0.2	1	11.5 ± 18.7
Azure-hooded Jay ( <i>Cyanolyca cucullata</i> )	?	1.1	0.1	2.6 ± 0.5	8.6 ± 5.8
Black-faced Solitaire ( <i>Myadestes melanops</i> )	Veg	0.8	0.1	1	5.9 ± 2.6
Black-headed Nightingale-Thrush ( <i>Catharus mexicanus</i> )	Ground, Stalk (S)	0.1	0.1	1	5
Slaty-backed Nightingale-Thrush ( <i>Catharus fuscater</i> )	Ground, Stalk (S)	0.4	0.1	1	5
Bananaquit ( <i>Coereba flaveola</i> )	Veg, Foliage	0.1	0.1	1.1 ± 0.4	10.0 ± 4.0
Golden-browed Chlorophonia ( <i>Chlorophonia callophrys</i> )	Veg	0.1	0.1	2.0	5
Silver-throated Tanager ( <i>Tangara icterocephala</i> )	Veg, Stalk (S)	0.1	0.1	1.2 ± 0.3	5.7 ± 2.3

TABLE 1. Continued.

Species	Foraging behavior <sup>a</sup>	Frequency of association	Mean number per 100 associates	Interspecific group size (±SD)	Duration of association (min ± SD)
<b>Nonresident associates</b>					
Plain Antvireo ( <i>Dysithamnus mentalis</i> )	Foliage	8.5	1.6	1.5 ± 0.5	49.9 ± 57.0
Streak-breasted Treehunter ( <i>Thripadectes rufobrunneus</i> )	Rummage, Stalk (S)	7.2	0.9	1.1 ± 0.3	60.0 ± 49.2
Wedge-billed Woodcreeper ( <i>Glyphorhynchus spirurus</i> )	Stalk (T)	0.1	0.1	1.0 ± 0.0	17.0 ± 13.6
Brown-billed Scythebill ( <i>Campylorhamphus pusillus</i> )	Stalk (T)	5.6	0.7	1.0 ± 0.1	127.2 ± 99.5
Spectacled Foliage-gleaner ( <i>Anabacerthia variegaticeps</i> )	Stalk (S)	1.5	0.1	1.0 ± 0.0	90.8 ± 85.7
Slaty Antwren ( <i>Myrmotherula schisticolor</i> )	Rummage	4.6	0.6	1.0 ± 0.0	240.1 ± 96.6
Barred Becard ( <i>Pachyramphus versicolor</i> )	?	0.3	0.1	1.0 ± 0.0	15.0 ± 4.5
Ruddy-capped Nightingale-Thrush ( <i>Catharus frantzii</i> )	Ground Stalk (S)	0.4	0.1	1.0 ± 0.0	5.9 ± 3.5
Lesser Greenlet ( <i>Hylophilus decurtatus</i> )	Foliage	1.7	0.1	1.8 ± 0.3	42.5 ± 24.0
Spangle-cheeked Tanager ( <i>Tangara dowii</i> )	Veg	0.2	0.1	3.1 ± 0.5	5.7 ± 2.6
Sooty-faced Finch ( <i>Lysurus crassirostris</i> )	Ground	0.6	0.1	1.0 ± 0.0	40.0 ± 2.5
<b>Seasonal Migrant Associates</b>					
Black-and-white Warbler ( <i>Mniotilta varia</i> )	Stalk (S+T)	1.4	0.2	1.0 ± 0.1	10.6 ± 10.9
Golden-winged Warbler ( <i>Vermivora chrysoptera</i> )	Foliage	6.4	0.9	1.2 ± 0.4	17.5 ± 16.7
Black-throated Green Warbler ( <i>Dendroica virens</i> )	Foliage	0.4	0.1	1.0 ± 0.0	10.0 ± 7.6
Kentucky Warbler ( <i>Oporornis formosus</i> )	Ground	4.6	0.6	1.0 ± 0.0	82.5 ± 8.5
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	Foliage	2.5	0.3	1.0 ± 0.0	8.2 ± 13.3
Summer Tanager ( <i>Piranga rubra</i> )	Veg, Aerial	0.8	0.1	1.0 ± 0.0	6.4 ± 2.9

<sup>a</sup> Species that were associated with the mixed flocks too infrequently to accurately determine their foraging behavior while flocking are denoted by a question mark (?).

despite dense vegetation. Mixed flocks were continually changing associations that moved through the forest on courses frequently crossing, but rarely retracing previous paths (Figs. 1, 2). Species that participated in mixed flocks fed primarily on arthropods, which they captured by a variety of methods including foliage-gleaning, stalk-gleaning and probing, rummaging (i.e. searching through detritus and epiphytes), terrestrial foraging, and limited amounts of flycatching. Several species augmented their diet with fruiting material from shrubs and epiphytes and fleshy flowers from herbs and palms (Table 1; described in detail by Buskirk 1972).

The principal nuclear species on the study area was the Three-striped Warbler (see Table 1 for scientific names of all avian species treated in the text, tables, and figures), a large dull-colored parulid, which remained in single pairs or pairs with young throughout the year. A congener, the Golden-crowned Warbler, also functioned as a nucleus for mixed flocks. Its use of the study area, however, was re-

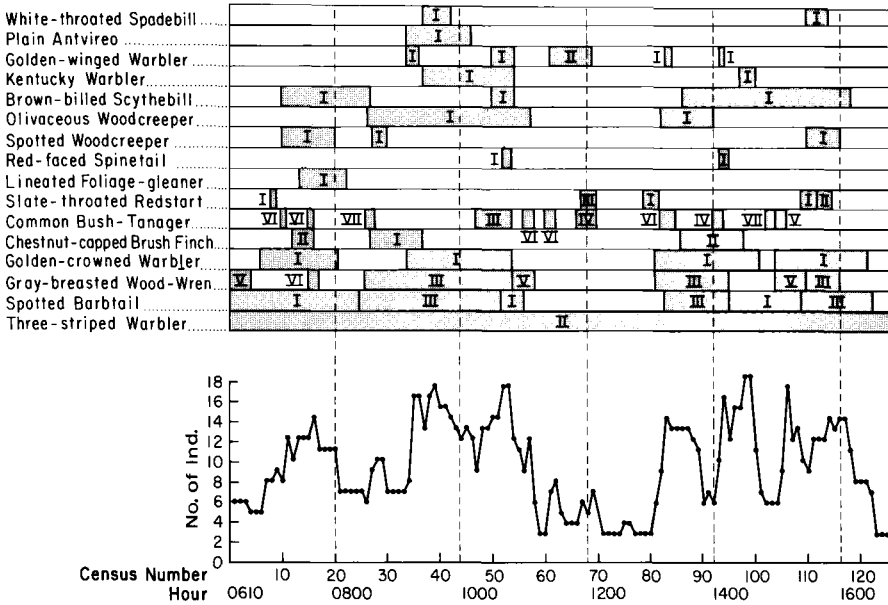


Fig. 2. Dynamics of mixed flock as determined in censuses taken 5 min apart on 24 November. Census numbers correspond to the locations in Fig. 1. Rectangles represent presence of participating individual, pair, or pair and young, whose identity is indicated by the roman numerals.

stricted primarily to the edges. Mixed flocks that contained neither Three-striped nor Golden-crowned Warblers were unstable and tended to disintegrate rapidly. Observations on the study area away from these warblers confirmed that understory mixed flocks rarely occurred in their absence. Therefore, it was possible to monitor most interspecific flocking in the understory by following the Three-striped Warblers.

Mixed flock formation varied seasonally (Fig. 3). Flocking was at its lowest ebb from March through July, when most insectivorous species bred (Powell 1977, Skutch 1967). The few birds that joined followed for short periods (Table 2). Mean flock size was largest between November and February (Scheffe's multiple contrasts,  $P < 0.01$ ; Fig. 3). Resident individuals that were present throughout the year accounted for 73% of the increase in monthly mean flock size (Fig. 4). The remaining increase resulted from association by seasonal residents. These were either species that bred locally, but not on the study area (transients), or seasonal migrants (Table 1). Flocks also exhibited a daily cycle in individual and species participation (Spearman's rank correlation coefficient,  $r = 0.3345$ ,  $P < 0.001$  for both size and species composition,  $n = 428$ ). During the morning (0530–0800) and late afternoon (1400–1645), flock size was significantly smaller than during the rest of the day (Scheffe's multiple contrasts,  $P < 0.01$ ). Between July and October, flocks exhibited less daily variation in size than between November and February (Scheffe's multiple contrasts,  $P < 0.01$ ).

Flock size was directly proportional to the number of species present ( $r = 0.95$ ,  $P < 0.01$ , slope = 0.56; Fig. 5). Flocks were composed primarily of pairs, single individuals, and in a few cases pairs with young. Although 42 species participated in mixed flocks on the study area, 90.3% of the birds recorded in flocks were of 11



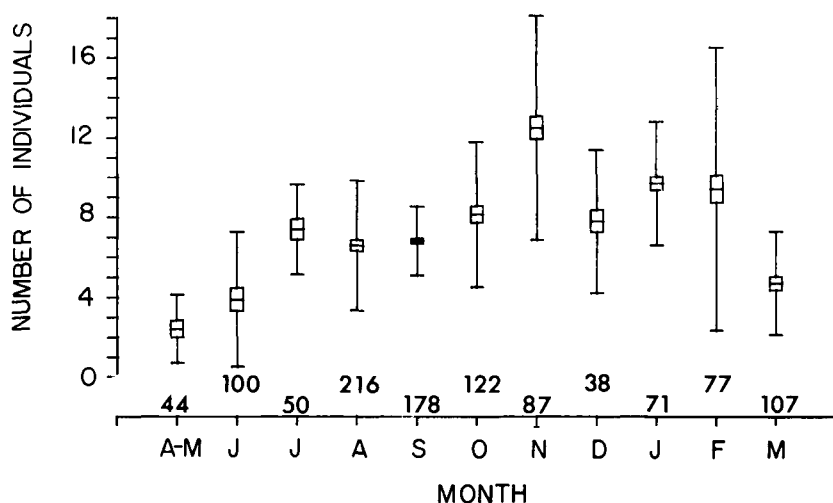


Fig. 3. Mean monthly mixed flock size (number of individuals) between the hours of 0800 and 1400. Means, 95% confidence interval of the mean,  $\pm$ SD, and  $n$  are given.

species ( $n = 27,004$ , Table 1). These species, the common flock participants, were all permanent residents; most defended territories throughout the year (Powell 1977). Therefore, the 27,004 sightings of flocking birds on the study area were repeated observations of approximately 27 pairs or pairs with their young. Some species were represented by a single pair, others by as many as nine pairs. Residents only associated with flocks that were in their territories. When a flock left a resident's territory, the resident generally dropped from the flock; 65% of 1,186 departures by color-marked residents were at or within 10 m of territory boundaries. The impact of territorial restriction on resident flocking species was inversely proportional to territory size (linear regression,  $r = 0.90$ ; Table 3). Species with smaller territories left flocks primarily at boundaries, while attendants with larger ranges frequently left flocks that were still in their territory. Transient species that participated in mixed flocks did not defend territories, so they could follow a flock through its entire range. Transients demonstrated a wide diversity of mixed-flocking propensities.

TABLE 3. Size of home range and its impact on participation in mixed-species flocks by the 10 most frequent attendant species.

Species	Area of home range, ha ( $n$ )	Departures from flocks at home range boundaries, % ( $n^a$ )
Spotted Barbtail	2.9 (1)	48 (179)
Gray-breasted Wood-Wren	0.7 (6)	78 (340)
Golden-crowned Warbler	4.1 (1)	40 (174)
Chestnut-capped Brush-Finch	0.8 (2)	82 (76)
Common Bush-Tanager	0.5 (6)	75 (228)
Slate-throated Redstart	0.8 (3)	76 (76)
Lineated Foliage-gleaner	2.6 (1)	45 (29)
Red-faced Spinetail	2.4 (1)	40 (52)
Spotted Woodcreeper	3.0 (1)	49 (35)
Olivaceous Woodcreeper	3.5 (1)	54 (26)

<sup>a</sup> Total departures by marked individuals.



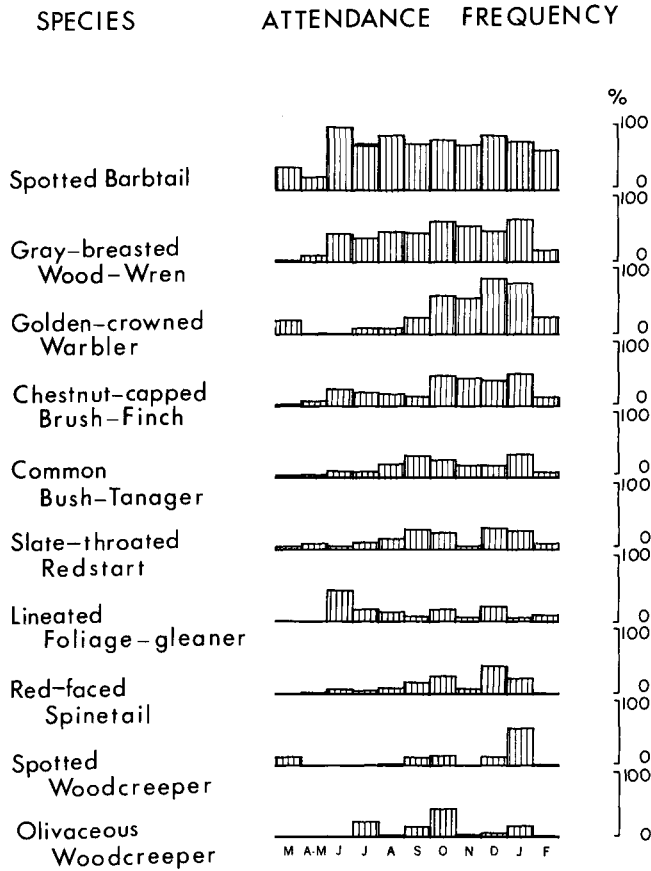


Fig. 4. The frequency with which the 10 most common mixed-flock attendant species associated with mixed flocks during each month of the year.

Some species followed for long periods, while others typically joined for a few minutes (Table 1). Seasonal migrants, largely from North America, arrived at the study site in September and early October and left in March. They had differing tendencies to participate in understory flocks. The most common winter visitants, Black-throated Green Warbler, Wilson's Warbler, and Black-and-White Warbler, joined resident mixed flocks infrequently and, as participants, remained for short intervals (Table 1). Only the Kentucky Warbler and Golden-winged Warbler consistently participated in Three-striped Warbler flocks.

I have analyzed in greater detail flock-following by three of the most common resident flock attendants: Gray-breasted Wood-Wren, Common Bush-Tanager, and Chestnut-capped Brush-Finch. The duration of mixed-flock visits to territories of these species varied from 5 to 100 min, but 72% lasted less than 15 min ( $n = 898$ ). The likelihood that any of these three species would join a flock correlated with two factors: the length of time the flock was in their territory (linear regression,  $r = 0.9$ ,  $P < 0.01$ , slope = 1.5; Fig. 6) and whether or not a conspecific was associated with the flock when the flock entered the territory. Birds joined a flock sooner and closer to the edges of their territory when conspecifics were with the flock as it entered ( $\chi^2 = 26.94$ ,  $P < 0.01$ ).

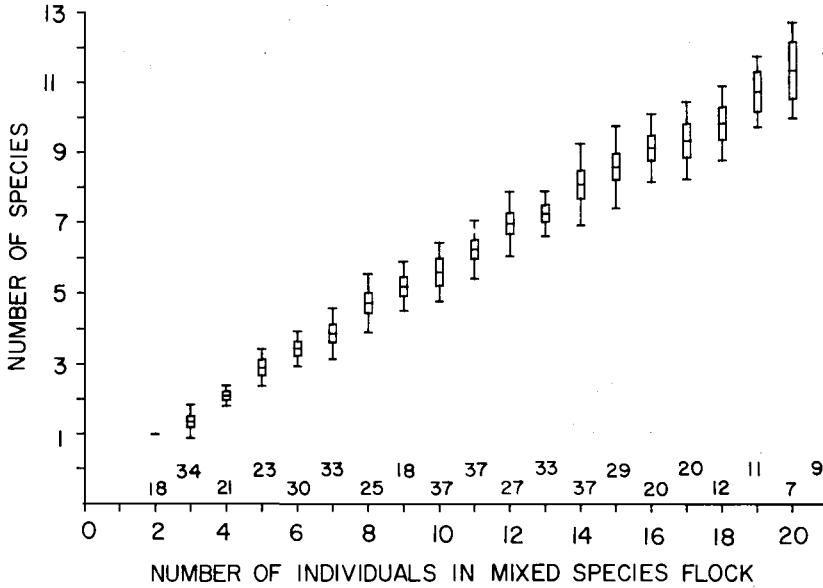


Fig. 5. Composition (number of species to number of individuals) of mixed-species flocks composed primarily of permanent residents. Mean, 95% confidence interval of the mean,  $\pm$ SD, and *n* are given.

The rate at which interspecific flocks moved through the study area was variable ( $5.4 \pm 2.4$  m/min). Flock movement rates, measured as 5-min averages (i.e. distance of group's movements between 2 consecutive censuses), ranged from less than 1 m/min to over 80 m/min. The flock moved less than 7 m/min 81% of the time, however. More rapid movement was associated with interrupted foraging and integrated flight, i.e. all birds flying in the same direction (Hinde 1952). These flights preceded interfamily agonistic conflicts by Three-striped Warblers, trips by Three-striped Warblers to water or roost, or a flight over a piece of the forest to resume foraging at a new location. Rate of movement was independent of previous movement rates ( $P > 0.05$ ).

TABLE 4. Frequency of participation by attendant species relative to rate of movement of mixed-species flock. The first column for each month gives the correlation between attendance and all rates of movements by flocks; the second column gives correlation between attendance and movements up to 7 m/min (the maximum rate when flock members are foraging).

Species	Regression coefficient					
	September		November		February	
	All rates	$\leq 7$ m/min	All rates	$\leq 7$ m/min	All rates	$\leq 7$ m/min
All attendant species	.15	.03	.20 <sup>a</sup>	.01	.11 <sup>a</sup>	.03
Spotted Barbtail	.09 <sup>a</sup>	.00	.11	.00	.06	.07
Gray-breasted Wood-Wren	.09 <sup>a</sup>	.01	.16 <sup>a</sup>	.01	.09 <sup>a</sup>	.02
Golden-crowned Warbler	.04	.06	.12 <sup>a</sup>	.04	.07	.01
Chestnut-capped Brush-Finch	.04	.06	.16 <sup>a</sup>	.12 <sup>a</sup>	.15 <sup>a</sup>	.00
Common Bush-Tanager	.06	.06	.03	.05	.04	.05
Slate-throated Redstart	.02	.06	.11 <sup>a</sup>	.01	.00	.05
Red-faced Spinetail	.04	.02	.03	.07	.01	.01
Spotted Woodcreeper	.04	.04	.03	.05	.03	.05
Olivaceous Woodcreeper	.04	.04	.17 <sup>a</sup>	.00	.08	.00

<sup>a</sup> Lower frequency of attendance in faster moving flocks, linear regression,  $P < 0.01$ .

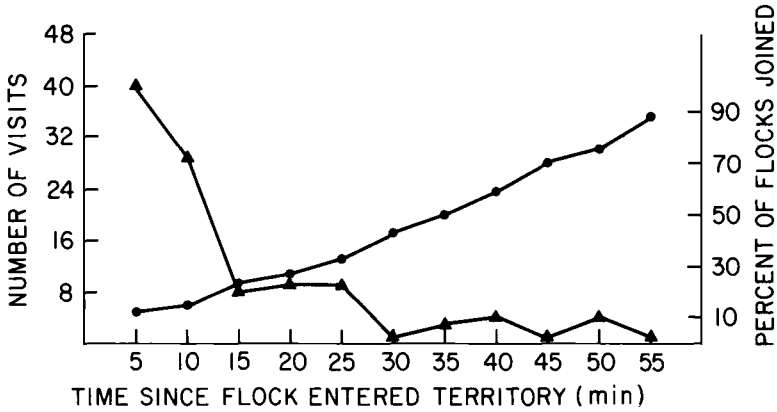


Fig. 6. Duration of visits by mixed-species flocks to attendants' territories (▲), and the relationship between a flock's time in a territory and the likelihood the territory owner will join (●),  $y = 1.5x - 1.0$ ,  $r = 0.9$ .

There was a weak negative correlation between rate of movement and group size (Pearson correlation =  $-0.01$ ,  $P < 0.01$ ). The correlation was significant, however, only for analyses that included all observations. There was no significant correlation between flock size and group movement rates of less than 7 m/min (Table 4). Attendance by some of the common flock participants correlated negatively with movement rate. With one exception, however, all were significant only when movement rates of greater than 7 m/min were included in the analyses (linear regression,  $P > 0.01$ ; Table 4).

Seven types of behavior by Three-striped Warblers were investigated relative to their potential impact on mixed flocks (Table 5). Of these, use of flight calls and primary song correlated with subsequent decreases in flock size; a third, the use of warning notes, was correlated with increases in group size.

Species other than the Three-striped Warbler may influence mixed-species flock composition. Five species were present more often when Golden-crowned Warblers were also present (Table 6, species 1, 2, 6, 7, and 9;  $\chi^2$ ,  $P < 0.01$ ). Two species were present more often in flocks that contained Common Bush-Tanagers ( $\chi^2$ ,  $P < 0.01$ ; Table 6, species 8 and 9). Species that foraged in the interior of the forest

TABLE 5. Relationship between behavior of Three-striped Warblers and changes in mixed-species flock size. Change was measured by comparing flock size at the time of the behavior with flock size at the subsequent census 5 min later.

Action by Three-striped Warbler	Change in flock size	Significance $t(n)$
<b>VOCALIZATION</b>		
Low intensity contact notes	$-.31 \pm 1.9$	1.73 (108)
Flight call	$-.62 \pm 2.2$	2.82 <sup>a</sup> (100)
Primary song	$-.42 \pm 2.7$	2.85 <sup>a</sup> (154)
Warning notes	$+.23 \pm 1.8$	2.66 <sup>a</sup> (434)
<b>BEHAVIOR</b>		
Sunning	$-.15 \pm 2.2$	0.40 (18)
Preening	$+.21 \pm 1.9$	0.48 (19)
Feeding fledglings	$+.11 \pm 1.9$	0.77 (168)

<sup>a</sup> Significant at 0.05 level.

TABLE 6. Interspecific association in mixed flocks by common attendant species during nonbreeding season. Numbers in parentheses are  $\chi^2$  values for observations during the entire day (0615–1630). Numbers without parentheses are  $\chi^2$  values for observations between 0800 and 1400.

Species	Species number <sup>a</sup>	Spotted Wood-creeper <sup>c</sup>	Red-faced Spinetail	Lineated Foliage-gleaner	Slate-throated Redstart	Common Bush-Tanager	Chestnut-capped Brush-Finch	Golden-crowned Warbler	Gray-breasted Wood-Wren
Spotted Barbtail	1	(7)		5 (4)	4 (16 <sup>b</sup> )	4 (45 <sup>b</sup> )	4 (18 <sup>b</sup> )	79 <sup>b</sup> (149 <sup>b</sup> )	45 <sup>b</sup> (55 <sup>b</sup> )
Gray-breasted Wood-Wren	2	3 (0)	-32 <sup>b</sup> (10)	1 (1)	6 (10)	0 (61 <sup>b</sup> )	6 (33 <sup>b</sup> )	18 <sup>b</sup> (29 <sup>b</sup> )	
Golden-crowned Warbler	3	27 <sup>b</sup> (22 <sup>b</sup> )	4 (16 <sup>b</sup> )	23 <sup>b</sup> (6)	25 <sup>b</sup> (43 <sup>b</sup> )	3 (76 <sup>b</sup> )	1 (13 <sup>b</sup> )		
Chestnut-capped Brush-Finch	4	-5 (0)	0 (4)	3 (1)	0 (2)	-5 (47 <sup>b</sup> )			
Common Bush-Tanager	5	33 <sup>b</sup> (139 <sup>b</sup> )	15 <sup>b</sup> (220 <sup>b</sup> )	0 (0)	0 (108 <sup>b</sup> )				
Slate-throated Redstart	6	1 (0)	-5 (1)	1 (12)					
Lineated Foliage-gleaner	7	127 <sup>b</sup> (147 <sup>b</sup> )	0 (1)						
Red-faced Spinetail	8	1 (24 <sup>b</sup> )							

<sup>a</sup> Referred to by number in text.

<sup>b</sup> Significantly different from value expected by chance at 0.01 level.

<sup>c</sup> Species number 9.

(Table 6, species 1 and 2) were observed more often together and less often with Red-faced Spinetails, a species that foraged on the forest edges and around openings.

Data collected with each observation made it possible to examine the relationship between weather conditions and flock composition. Of three parameters recorded, increasing precipitation and wind intensity were inversely correlated with group size (Spearman's rank correlation for both,  $P < 0.01$ ). Cloudiness showed no significant correlation with flock size. Attendance by seven of the 11 most frequent flocking species was reduced during periods of heavy wind and precipitation ( $\chi^2$ ,  $P < 0.01$ ; Table 7). The Spotted Barbtail was similarly affected by windy weather but not by precipitation.

## DISCUSSION

Characteristics of this understory avian community enhanced the analysis of interspecific flocking behavior. Permanent territoriality and limited migration mini-

TABLE 7. Association between intensity of wind and precipitation and the frequency of participation in mixed-species flocks by the 10 most common attendant species.

Species	Precipitation ( $\chi^2$ )	Wind ( $\chi^2$ )
Spotted Barbtail	4.5	11.8 <sup>a</sup>
Gray-breasted Wood-Wren	45.7 <sup>a</sup>	14.7 <sup>a</sup>
Golden-crowned Warbler	17.5 <sup>a</sup>	21.0 <sup>a</sup>
Chestnut-capped Brush-Finch	2.2	5.7
Common Bush-Tanager	0.5	1.2
Slate-throated Redstart	27.1 <sup>a</sup>	17.3 <sup>a</sup>
Lineated Foliage-gleaner	53.6 <sup>a</sup>	25.2 <sup>a</sup>
Red-faced Spinetail	51.2 <sup>a</sup>	79.2 <sup>a</sup>
Spotted Woodcreeper	8.1 <sup>a</sup>	8.2 <sup>a</sup>
Olivaceous Woodcreeper	46.2 <sup>a</sup>	86.1 <sup>a</sup>

<sup>a</sup> Species less likely to be present with increasing intensity of precipitation or wind,  $\chi^2$ ,  $P < 0.01$ .

mized changes in the density and composition of the flocking population. As the principal nuclear species was territorial, there was only one flock nucleus available to most potential flock joiners. Monitoring this nucleus provided an accurate measure of the propensity of species to associate with mixed flocks.

The three- to four-fold annual cycle in tropical mixed-flock formation cannot be attributed to influx or redistribution of the population, as is the case in temperate zone flocks (Odum 1942, Hinde 1952, Fretwell 1969, Cody 1971). Seasonal migrants and offspring provide limited sources of recruits. Winter residents from North America associate infrequently with understory mixed flocks. Most local offspring leave their parents within a few months after fledging and thereafter are limited to participating in mixed flocks when territorial defenders, inclusive of their own parents, are absent. Post-breeding adults, when accompanied by recently fledged young (Spotted Barbtail, Slate-throated Redstart, Spotted Woodcreeper, Olivaceous Woodcreeper, and Lineated Foliage-gleaner), frequently forage separately, each adult accompanied by a fledgling. When separated in this way, only a single adult and fledgling participate in a flock concurrently. Mean monthly intraspecific group size varied from 2.1 individuals per species in July, the end of the breeding season, to 1.7 individuals per species in February, when breeding begins again.

The confinements of territoriality generally limit pairs to associating with a single mixed flock that comes through their territory. Individuals absent from a flock in their territory cannot be flocking elsewhere. Thus, the observed cycles in mixed flocking are actual changes in flocking propensities of attendant birds. This contrasts with other flocking studies, which have been unable to determine the whereabouts of nonparticipating individuals. Earlier studies could not exclude the possibility that absentees were participating in other mixed flocks or smaller monospecific flocks (Pulliam et al. 1974). I found that seasonal increases in flock size are principally a consequence of more frequent (Fig. 4) and consistent (Table 2) flocking by permanent residents. Except while incubating, nesting Three-striped Warblers continue to be conspicuous, yet they are generally alone during the breeding season (Fig. 3). Their movements are restricted to a limited area while they have nestlings and recently fledged young, however. This attachment to a specific site, nest, or recently fledged young probably deters other birds from following the warblers. Nests of the other flocking species, all of which nest concurrently with Three-striped Warblers, are scattered throughout the study area. As predation pressure probably selects for this dispersed pattern of nest sites (Tinbergen 1952), other flocking species will have to fly extra distances to join Three-striped Warbler families.

The daily cycle in mixed-flock size results from a reduction in flock attendance by most species during early and late hours of the day. This trend in flocking propensities suggests that factors influencing daily tendencies to associate in flocks are general rather than species-specific. Influencing factors might be environmental rhythms, such as the increased windiness that typifies early and late daylight hours on the study area; they might be indicative of temporal patterns in nuclear species behavior that make the flock nucleus less compatible for co-association; or the cycle could be a manifestation of behavioral attributes of the attendants themselves, such as more stereotyped feeding behavior and reduced compatibility with nuclear species foraging patterns.

Moynihan (1962) suggested that intraspecific territoriality could have an impact on attendant participation in tropical mixed-species flocks. Buskirk et al. (1972) observed that flock composition was restricted to the same individuals. In the present

study, territoriality is a major factor influencing the composition of understory mixed flocks. Most participants are represented in mixed flocks singly, in pairs, or as pairs with offspring. Territoriality imposes a constant turnover of participants as the group moves through the understory. The loss of participants from a flock is, to a large degree, a fixed phenomenon that occurs whenever the flock crosses the territorial boundary of an attendant species. Because flocks cross some boundary every few minutes, flocks have a consistently changing individual composition, even though species composition is relatively stable. Spatial restrictions imposed by year-round territoriality do more than restrict intraspecific group size; they reduce the tendency of residents to join flocks that are in their territories. Several pieces of evidence suggest that birds selectively join mixed flocks that are in their territories. First, individuals demonstrate a greater propensity to join flocks that include conspecific birds. This cannot be explained by increased flock conspicuousness, as the more rapid joining occurs only with the presence of conspecific birds. Second, intraspecific confrontations between nuclear species, loud, conspicuous interactions that can be heard for more than 75 m, do not increase flock size (Table 5). If ignorance of the mixed-flock's position limited participation by attendants, the conspicuous agonistic behavior should correlate with an increase in flock size. Third, daily and annual cycles in flock size, which result from changes in flocking propensities of attendant species, are a reflection of selective joining. And fourth, attendant species within audible distance of flocks frequently fail to join. I followed attendant species that failed to join flocks that were in their territories and that were clearly audible to me.

The hypothesis that attendants selectively participate in interspecific flocks explains why, even during periods of maximum flock development, the number of birds participating is lower than expected relative to the populations of attendant species. The typically short period that Three-striped Warbler families remain in attendant species' territories probably makes it unprofitable for potential attendants to pursue mixed flocks in order to join them. Most visits by the nuclear species to territories of common attendant species lasted less than 15 min (Fig. 6). Interruption of feeding and systematic foraging patterns, the energetic costs of moving to the flock's location, and increased exposure to predation while moving to the flock's location are all possible costs that could deter an individual from pursuing mixed flocks, if participation is likely to be of short duration.

Two vocalizations in the repertoire of Three-striped Warblers are associated with decreases in the number of participants in mixed-species flocks. The decrease associated with flight calls probably reflects the context in which these vocalizations are utilized. Flight calls are given by Three-striped Warblers whenever they fly 25 m or more in a single flight. Territorial constraints will prevent some attendant species from following the warblers when they fly. Attendant species with the smallest home ranges are most affected by rapid rates of movement. The negative correlation between flock size and the use of primary song by Three-striped Warblers is probably a consequence of the rapid flights that are associated with intergroup interactions. Primary song is used almost exclusively in the context of interfamily interactions, which often involve flight to a territory boundary while repelling trespassers. Again, territorial constraints prevent some attendant species from following.

The size of mixed flocks and the rate at which they move are generally considered correlated variables. Hypotheses explaining the correlation suggest that large flocks move faster (or slower) because of inherent qualities of group size. Gibb (1960) and

later Morse (1970) suggested that positive correlation between rates and flock size is due to the need of larger groups to cover more new foraging substrate than smaller groups. Buskirk (1972) suggested that large flocks move more slowly because they become disorganized.

In the current study, movement rate and flock size were independent in flocks moving at rates indicative of foraging (less than 7 m/min). Flock size decreased when movement rates were rapid (above 7 m/min). Because resident mixed flocks are augmented by interspecific rather than intraspecific recruitment, foraging substrate depression rates are dependent on interspecific food niche overlap. The level of competition for food resources is difficult to measure, as it is always possible that data collected were not sufficiently sensitive to register overlap. Buskirk (1972) classified foraging behavior of principal flock participants on the study area by measuring seven substrate, posture, and activity parameters: foraging movements, method of capture, foraging height, substrate size, substrate cover, texture, and orientation (see Buskirk, 1972, Tables 2, 7, 12, 13, and Fig. 9). He concluded that the principal flock participants overlap very little in food niches. Therefore, the failure to find a correlation between flock size and movement rate does not contradict Gibb's hypothesis. Movement rate may still be dependent on resource depression rates, but the latter are independent of flock size in the resident flocks. Rapid movement probably leads to decreases in flock size because the rapidly moving group encounters various participants' territorial boundaries more frequently, so more birds are forced to leave somewhat more rapidly than new ones are recruited.

#### CONCLUSIONS

The proximate correlates of mixed-species flock formation are a combination of spatial, temporal, climatic, and behavioral factors. Flock composition is controlled in large degree by intraspecific social organization. Permanent territoriality and pair bonding impose strict limits on intraspecific group size, making interspecific diversity the principal determinant of flock size. Maximum potential flock size is therefore somewhat larger than twice the number of consistent flocking species resident in the area. This maximum is rarely attained, however. Mean size of the flocks I studied was less than half the potential based on the number of consistent flocking species found throughout the area. The discrepancy between predicted and observed values results, in part, from members constantly being forced to leave the flock when it crosses territorial boundaries. Every few minutes the flock leaves an attendant's territory and enters that of a conspecific neighbor. The likelihood that an owner of a newly entered territory will join a mixed flock is directly proportional to the time the flock is in its territory.

The time lag appears to be an expression of the costs and benefits of joining the flock. While the ultimate costs and benefits of participating in flocks (i.e. predation evasion vs. foraging efficiency) have thus far eluded more than subjective analysis (i.e. Morse 1977, Buskirk 1976, Powell MS), proximate factors influencing flocking propensities can be tested statistically. I have shown that individuals are more likely to join flocks that contain trespassing conspecifics and that they have a greater propensity to flock during the nonbreeding season and a reduced propensity to flock in early morning, late afternoon, and during periods of inclement weather (wind and rain). Finally, I have shown that flock composition and nuclear species behavior influences the likelihood of other species joining the flock.

Resident mixed flocks are not random assortments of birds that happen to aggregate; instead, each flock is a structured grouping whose membership is limited to a few resident individuals of a relatively few species. A given flock at any time of the year will consist of some subset of those individuals. Total membership for the 11 resident species that made up 90% of a typical flock was 27 pairs. Subsets were limited to one pair per species. Identity of the pairs depended on the flock's location within its home range.

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