

## INTERSPECIFIC BIRD FLOCKS IN TROPICAL HIGHLAND PANAMA

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TROPICAL mixed-species bird flocks have been the subject of numerous investigations (e.g., Swynnerton, 1915; Winterbottom, 1943, 1949; Davis, 1946; Wagner, 1959; Short, 1961; Moynihan, 1962a; McClure, 1967; Vuilleumier, 1967; Willis, 1967). With the exception of Willis (1967) these studies have depended upon observations of unbanded birds, and hence information on flock organization and movements has been inferential. Our study of montane mixed flocks containing color-marked birds evaluates temporal flock composition and cohesiveness, home range, and daily activity cycles.

An initial development of mixed flock studies was the distinction of different roles played by the several species in flock formation and maintenance. It is generally agreed (Winterbottom, 1943, 1949; Rand, 1954; Moynihan, 1962a) that mixed flocks can be separated into two major components: a nucleus species component that includes one or several intraspecifically gregarious species (Winterbottom, 1943) and an attendant species component that includes any number of species that regularly join the nucleus species (Rand, 1954).

In the following discussion, the unmodified term "flock" is applied only to intraspecific aggregations, while the terms "mixed flock" and "interspecific flock" denote only interspecific aggregations.

### STUDY AREA AND METHODS

This study was conducted at the Florida State University Volcán de Chiriquí Field Station at Nueva Suiza, 3 km south of the town of Cerro Punta, Chiriquí Province, Panama (elevation 1,680 m). The wooded study area (Figure 1) was separated by open fields and gravel roads from most surrounding forests. The area contained approximately 3.6 ha on the horizontal plane and centered on a steep south-facing hillside rising about 45 m from base to crest. A dense second growth woodland covered the hillside. Its average canopy height was 15 m, with several emergents reaching higher. A large fallen tree at the base of the cliff produced a relatively large opening in the canopy. The wood's edge along the base of the hill consisted of thick bushes, predominantly *Miconia* sp. (Melastomaceae) and *Piper* sp. (Piperaceae), ranging from 2 to 5 m in height. The eastern end of the tract had recently been cut over and was covered primarily with thick second growth shrubs and bamboo up to 5 m tall. Several scattered trees remained uncut. An abandoned coffee finca covered most of the southeastern portion. Invading shrubs, primarily *Piper* and *Miconia*, and small trees growing among the coffee plants produced a nearly continuous stand of dense brush about 4 m high.

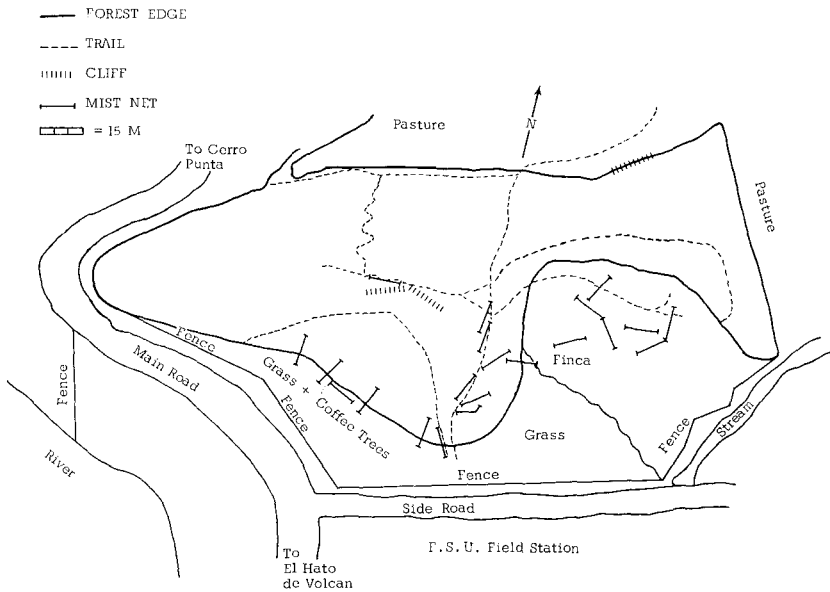


Figure 1. Cerro Punta study area. Topographic and vegetational features.

Subdivisions of the study area were designated (Figure 2), and trails were cut and cleared to permit following the birds with minimal disturbance. Initial studies, concurrent with these physical preparations on 12, 13, 15, and 16 December 1968, established the presence of several mixed-species flocks in the area. During this period we found it difficult to maintain prolonged contact with the flocks and impossible to determine the identity of individual birds. On 18 and 19 December we netted and color-banded birds within the study plot. On 21 December we resumed observations and continued daily through 31 December except for 25 and 26 December. We followed interspecific flocks as continuously as possible, and monitored their movements, changes in size, species and individual composition, and activity levels. Field work, amounting to approximately 30 man-hours daily, began shortly before dawn and terminated after dark. Two researchers frequently followed mixed flocks simultaneously and often followed two mixed flocks concurrently.

During the study we netted and color-banded birds (12 to 125 net-hours daily, average 75) in a brushy tract adjacent to the south boundary of our study area and separated from it by an open grassy strip approximately 20 m wide. This banding allowed us to evaluate the movements of individuals of different species into and out of our study area.

On 1 and 2 January we collected representative individuals of some species in the flocks to determine sex and breeding condition from gonadal state.

The period of our study coincided with the start of the dry season in western Panama. Heavy overcast and light rain characterized the first week of the study. Thereafter skies generally were clear during night and morning hours, with day-to-day variations in the amount of fair weather clouds during late morning and after-

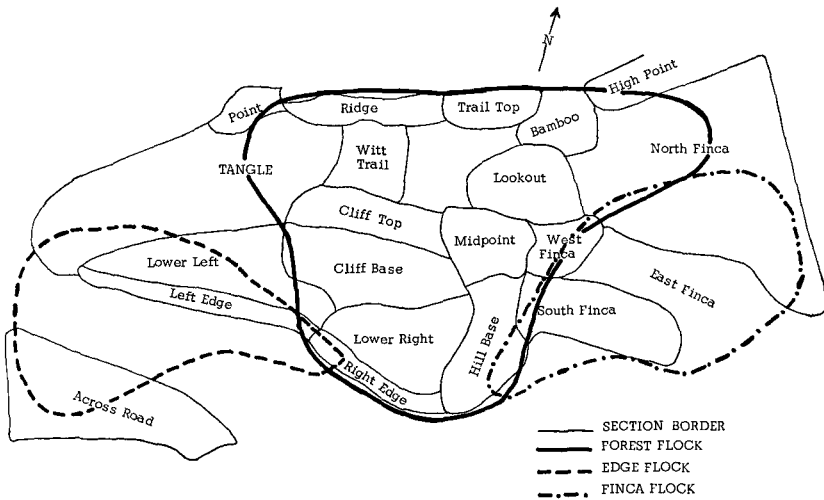


Figure 2. Cerro Punta study area. Locations and *Chlorospingus ophthalmicus* flock home ranges.

noon. Midday temperatures were about 70°F and were highest on those days with little cloud buildup. On two afternoons late in the study light showers occurred.

## RESULTS

During the 2-day color-banding operation on the study plot we marked 12 of the 14 Common Bush-Tanagers (*Chlorospingus ophthalmicus*) in three flocks. Our subsequent studies centered on these three flocks; 16 percent of the birds attendant to these bush-tanager flocks were color-banded.

### NUCLEUS SPECIES COMPONENT

The nucleus species component in each of the mixed flocks was composed of a single species, the Common Bush-Tanager. This tanager is a rather dull-colored, gregarious, and widely-distributed species (Mexico to Argentina of humid montane regions. Skutch (1967) describes its life history in Costa Rica, and Moynihan (1962a, 1962b) adds many ethological details for the race (*C. o. novicius*) found in western Panama.

The 4 days of following flocks prior to color-banding indicated that the Common Bush-Tanagers in our study area separated into small intraspecific flocks. After color-banding, we established that these groups were stable and independent flocks maintaining distinct, slightly overlapping, home ranges (Table 1). Lack of gonadal development showed that the species was not breeding at this time. This is consistent

TABLE 1  
DISTRIBUTION OF INDIVIDUAL COMMON BUSH-TANAGERS IN STUDY AREA<sup>1</sup>

Sections	Color-banded individuals												
	Finca Flock				Forest Flock				Edge Flock				
	A	B	C	D	E	F	G	H	I	J	K	L	
Across road										2	2	1	2
Left edge					—	—	1	1		12	17	18	13
Lower left					—	—	1	1		3	5	5	4
Right edge					—	1	11	2		1	1	1	3
Tangle					3	1	1	4		3	3	3	3
Point					—	1	—	1					
Lower right					3	3	4	4					
Cliff top					9	8	12	13					
Whitt trail					5	2	2	4					
Ridge					—	2	—	3					
High point					—	2	—	1					
Trail top					1	—	1	2					
Bamboo					—	4	1	1					
Lookout					3	4	4	7					
Midpoint					5	6	6	12					
Cliff base					1	2	—	2					
Hill base					9	8	12	12					
South finca	1	3	1	4	1	2	1	3					
West finca	6	6	2	6	1	2	1	3					
North finca	2	2	1	2	1	1	1	1					
East finca	4	3	4	4	2	1	1	1					
	5	3	5	5									

<sup>1</sup> A count was tabulated each time an individual was recorded in a new section or for each 30-minute period that an individual was seen to remain within a section.

with Skutch's (1967) observations of nesting in Costa Rica from March to June.

The three flocks of bush-tanagers containing color-banded birds maintained home ranges entirely within the study area. These flocks were named according to the location of their ranges (Figure 2). The "Finca Flock" consisted of 1 male and 3 females, all of which were color-banded. They occupied approximately 0.8 ha including the finca and its periphery. The "Edge Flock" included 5 birds, 2 females and 3 unsexed, of which 4 were color-banded. This flock restricted its movements to approximately 0.8 ha including the southwest edge and lower portions of the study site. The "Forest Flock" was also composed of 5 birds, 2 females and 3 unsexed, of which 4 were color-banded. This flock's principal range was in the wooded areas, but it also visited portions of the West and South Finca and Right Edge. The home range of the Forest Flock was somewhat greater than 1.6 ha.

Two additional flocks of the bush-tanagers, consisting of approximately six individuals each, included parts of the study site in their ranges.

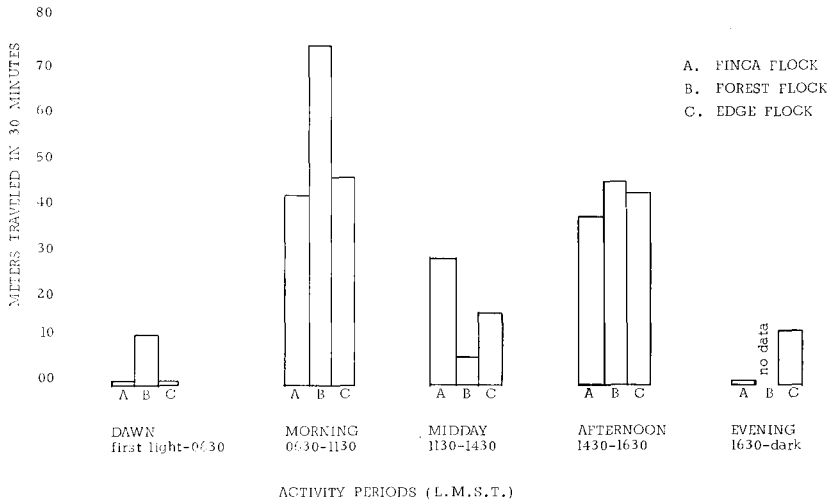


Figure 3. Average distances covered by flocks in 30-minute intervals during each activity period.

Neither flock was netted at the outset, so we ignored them except to note their presence. One of these flocks regularly occurred in the north-eastern sector, the other in the northwest corner. On one occasion this second flock entered the range of the Forest Flock and toured a major part of that range with the Forest Flock. All of the 12 bush-tanagers color-banded at the beginning were present at the end of the study. With only one exception (see below) these birds were never seen or netted outside the study area.

From a total of more than 50 hours of observations, a temporal pattern in the daily activities of bush-tanagers was apparent. This daily cycle could be divided into five periods (Figure 3) characterized by different levels of activity and organization: dawn, morning, midday, afternoon, and evening.

Individual birds began and ended their daily activity at the same site. All the individuals of both the Finca Flock and the Edge Flock roosted in loose groups within their ranges, but individuals of the Forest Flock roosted at widely separated localities as much as 75 m apart. Two of these roosted in the Right Edge area, one in the North Finca, another at Clifftop, and the fifth bird 15 m beyond the southern boundary of the study tract. Thus four of the five members of this flock roosted near the boundaries of the flock's home range, and the remaining one spent the night where the flock was never seen as a group. Once we located a roosting site, we found the occupant there

repeatedly. The roosting site of each bird was checked three or more times, with the exception of one bird checked only twice. All individuals roosted in dense bushes within 3 m of the ground.

Bush-tanager activity began at dawn, approximately at 06:00 Local Mean Solar Time. The ensuing dawn period of activity lasted up to 30 minutes. During this period the birds were active and vociferous. Individual activity was not integrated into flock activity and consisted of flitting around in the bushes and low tree branches near the roosting site. Only a small amount of feeding occurred during this period.

At about 06:30 the bush-tanager activities began to shift to integrated flock movements. For members of the Forest Flock, which were widely dispersed at the onset of each day, the beginning of this shift in activity was exhibited by movement away from their respective roosts and a greater emphasis on feeding. Union by these individuals into an integrated flock was sometimes not completed until 09:30. Members of the Edge and Finca Flocks made this shift from individually-oriented movements to integrated flock movements more quickly. These flocks were usually functioning as units by 07:00.

Usually a flock traveled through its entire home range during the morning activity period, but it only visited a portion of this terrain during the afternoon. In other respects, the afternoon activity period was similar to the morning one. Periods of low level activity characterized by drifting movements (Hinde, 1952; Marler, 1956) and decreased intensity of vocalizations alternated with higher levels of activity characterized by integrated movements and increased calling. We also noted escape movements (Marler, 1956) during which the flock flew to cover and then remained silent and motionless for a time. Disturbance by the observers or the appearance of raptors elicited escape behavior.

An extended period of greatly reduced activity separated the morning and afternoon activity periods. Each flock repeatedly spent this midday period at the same location. All three midday roost sites were in dense foliage. Each flock remained quiet during this period, and individual birds reduced feeding activity to short bouts interspersed with intervals of almost complete inactivity. During a feeding bout the birds moved to the outer edge of the foliage, fed briefly, then quickly returned to the center of the foliage.

Light intensities began to drop rapidly around 17:00. At this time the bush-tanagers began to return to roost. These birds occasionally performed long silent flights during their return. After reaching their roosts, they called briefly, and then became inactive and quiet. The Edge and Finca Flocks appeared to go through a short period of non-integrated activity similar to, but less pronounced than the dawn activity

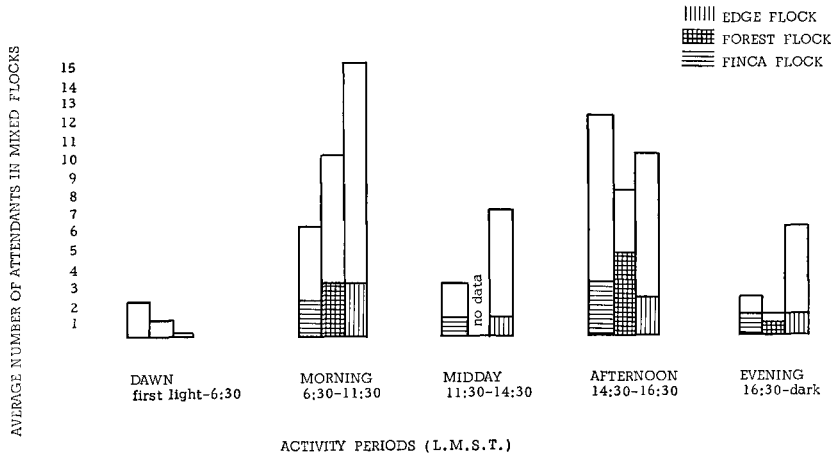


Figure 4. Average flock size at respective times of the day. The clear area denotes joiners and short-term followers and the hashing denotes long-term followers.

period before quieting down for the night. This activity ended by 17:45. Visible skylight disappeared about 18:30.

An overall pattern in a flock's movement within its home range did not recur from day to day, though each flock followed preferred pathways. The presence of alternative routes permitted variability in movement patterns. The Forest Flock, because of its larger and more diverse home range, had a greater number of alternative routes and hence more varied movement patterns than did the other two flocks. We did not find the stereotyped movement patterns suggested by Moynihan (1962a) and reported by McClure (1967).

#### ATTENDANT SPECIES COMPONENT

Mixed-species assemblages were highly variable in size. Generally mixed flocks contained 8 to 15 birds, though on one occasion a group held at least 50 birds. The size of the nucleus species component of each flock is constant, so this variability is due to fluctuations in the size of the attendant species component.

The attendant species component is largest during morning and afternoon and sharply decreases or disperses entirely at midday and in the evening (Figure 4). During the midday period some of the individuals remain inactive in the vicinity of the bush-tanagers, but whether their behavior is still integrated with that of the nucleus species remains unclear.

The relationships of attendant species to the intraspecific flocks of bush-tanagers were highly variable and can best be defined by the

TABLE 2  
CLASSIFICATION AND RELATIVE FREQUENCY OF ATTENDANT SPECIES IN MIXED-SPECIES  
FLOCKS

Species <sup>1</sup>	Attendant classification <sup>2</sup>	Relative frequency (N = 212) (percent)
Silver-throated Tanager ( <i>Tangara icterocephala</i> )	J	63
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	S	44
Slate-throated Redstart ( <i>Myioborus miniatus</i> )	S	30
Red-faced Spinetail ( <i>Cranioleuca erythrops</i> )	L	29
Yellow-thighed Finch ( <i>Pselliophorus tibialis</i> )	L	27
Philadelphia Vireo ( <i>Vireo philadelphicus</i> )	J	26
Brown-capped Vireo ( <i>Vireo leucophrys</i> )	S	25
Black-throated Green Warbler ( <i>Dendroica virens</i> )	J	22
Golden-winged Warbler ( <i>Vermivora chrysoptera</i> )	L	16
Black-and-White Warbler ( <i>Mniotilta varia</i> )	J	15
Golden-crowned Warbler ( <i>Basileuterus culicivorus</i> )	S	15
Flame-throated Warbler ( <i>Vermivora gutturalis</i> )	L	13
Red-headed Barbet ( <i>Eubucco boucierii</i> )	L	13
Barred Becard ( <i>Pachyramphus versicolor</i> )	L	12
Spot-crowned Woodcreeper ( <i>Lepidocolaptes affinis</i> )	S	11
Black-cheeked Warbler ( <i>Basileuterus melanogenys</i> )	S	11

<sup>1</sup> Only those species that occurred in more than 10 percent of the samples are listed.

<sup>2</sup> J = joiners, S = short-term followers, L = long-term followers.

propensity of species to join or follow the bush-tanager flocks (Moynihan, 1962a). We measured this propensity by a different set of criteria than Moynihan used. We considered an individual to have "joined" if it was within the vicinity of a flock. An individual "followed" if we recorded it with a particular flock in consecutive censuses of the mixed flock from two or more locations.

The Red-headed Barbet, Barred Becard, Red-faced Spinetail, Golden-winged Warbler, Flame-throated Warbler, and Yellow-thighed Finch regularly joined and followed bush-tanager flocks over extended distances. These six species were rarely represented by more than two individuals per mixed flock. Single color-banded individuals of the Red-faced Spinetail and Yellow-thighed Finch consistently followed the Forest Flock during much of the day, day after day, throughout the study. A second Red-faced Spinetail was seen repeatedly with the Finca Flock. Neither of these spinetails moved with any other flock. Likewise this



particular Yellow-thighed Finch occurred only with the Forest Flock. Banded individuals of two other species in this group of long-term followers, the barbet and becard, changed from one mixed flock to another. None of the resident Flame-throated Warblers or wintering Golden-winged Warblers were color-banded. Our classification of these two species as long-term followers is inferential and it was impossible to determine whether individuals of these species associated with more than one flock.

Another group of species, including the Spot-crowned Woodcreeper, Brown-capped Vireo, Slate-throated Redstart, Golden-crowned Warbler, and Black-cheeked Warbler regularly joined flocks but showed only moderate tendencies to follow them. These short-term followers accompanied mixed flocks only briefly and for short distances or restricted their association to joining the flock without following it.

A major group of attendant species joined but usually did not follow the bush-tanager flocks. Most notable of these joiners are the Mountain Elaenia (*Elaenia frantzii*), Olive-striped Flycatcher (*Mionectes olivaceus*), Silver-throated Tanager (*Tangara icterocephala*), and Blue-Gray Tanager (*Thraupis episcopus*). These species joined interspecific flocks, but either remained after the flock departed or left before the flock moved on. Only occasionally did members of these species follow the flock for even a short distance.

Of nine species of North American migrants observed, only the Golden-winged Warbler regularly followed flocks for extended distances. The relationships of the others varied. The Black-and-white Warbler, Black-throated Green Warbler, and Summer Tanager (*Piranga rubra*) were joiners but normally not followers. In many cases individuals of a species designated as a short-term follower joined but did not follow flocks. Only the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) among the migrant species failed to join mixed flocks.

Many local woodland passerine species neither joined nor followed the bush-tanager flocks. This group included the Ochraceous Wren (*Troglodytes ochraceus*), Gray-breasted Wood-Wren (*Henicorhina leucophrys*), Black-faced Solitaire (*Myadestes melanops*), Clay-colored Robin (*Turdus grayi*), Mountain Robin (*T. plebejus*), Ruddy-capped Nightingale-Thrush (*Catharus frantzii*), and Long-tailed Silky-flycatcher (*Ptilogonys caudatus*). None of these species exhibited any obvious reaction to the bush-tanager flocks.

The relative tendency to follow flocks does not correlate with the frequency of attendant species in the mixed flocks. Relative frequencies were obtained from 212 sample counts of birds associating with bush-tanager flocks (Table 2). As the Silver-throated Tanager was the most

numerous and conspicuous species in the avifauna, its relatively high frequency in mixed flocks may have been due more to chance or brief encounters than to deliberate association with the mixed flocks. In comparison, the tallies for the barbet, becard, spintail, and finch are derived from repeated observations of a few marked individuals.

#### DISCUSSION

The term "home range" rather than "territory" has been used here because we are not certain how the Common Bush-Tanager flocks establish their range boundaries. This is in accordance with Marler and Hamilton's (1966: 171) definition of a home range as site occupied by a species during the course of the annual cycle without regard to the way the boundaries are maintained.

We did not find any overt interflock aggression in spite of frequent contact and occasional mixing of adjacent flocks. Typically when two flocks came into contact at a common boundary, a marked increase in vocalizations, possibly of a threatening nature occurred, but supplanting or fighting did not. In most instances flock identities and home ranges held constant at these times. Contact between flocks did not last longer than 20 minutes, except on one occasion when two flocks integrated into a single flock for at least 90 minutes. The composite flock foraged and toured a large portion of the range of one of the flocks. We later found these two flocks separate and on their respective ranges.

Agonistic behavior in the form of attacks between individual bush-tanagers belonging to the same flock was frequent. These attacks led to either supplanting or to submissive behavior, characterized by motionless cringing of the bird under attack. Loud vocalizations normally accompanied this behavior, as reported by Moynihan (1962a).

As this investigation was an intensive study at one site in the broader area encompassed by Moynihan's (1962a) observations of montane mixed-species flocks, a number of useful comparisons can be made. Our findings confirm Moynihan's impressions that the nonbreeding Common Bush-Tanagers form flocks that are both stable in composition and home range. In addition the correlation between the activity level of the nucleus species and the size of the attendant species component suggested by Moynihan (1962a) is supported by quantitative data in this study (Figure 5). When the nucleus species component was moving rapidly, the attendant species component was larger, principally through the incorporation of more short term following and joining species. On the basis of this correlation, the regular pattern of fluctuation in size of the attendant species component can be accounted for the daily activity cycle of the nucleus species component (see Figures 3 and 4).

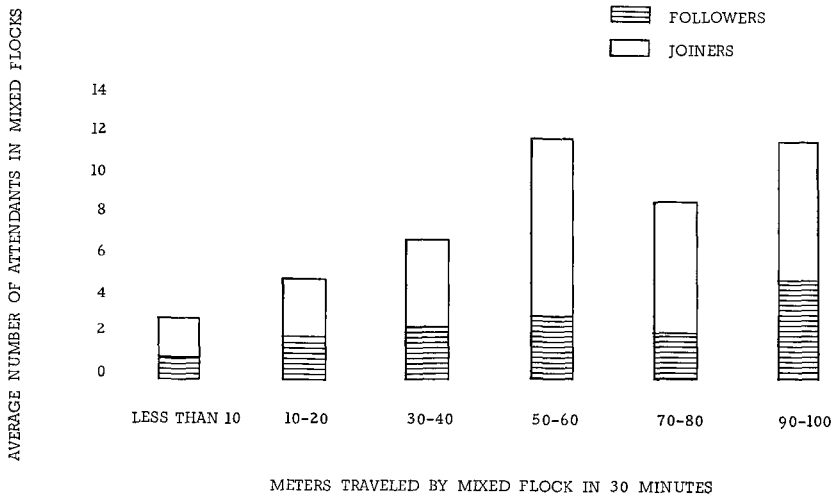


Figure 5. Correlation between average flock size and rate of movement. A summary of observations of the three color-banded flocks.

Our classification of attendant species according to their relative propensities to join or follow mixed flocks is somewhat inferential, as only a small proportion of individuals of these species were color-banded. Nevertheless this classification does illustrate the wide variety of behavioral responses made to mixed flocks by attendant species. Intraspecific variability in flocking behavior also occurs. For example, the response of individual color-banded Yellow-thighed Finches to mixed flocks varied from nearly continuous to infrequent association.

The composition of the nucleus and attendant species components of the mixed flocks we studied was similar to those Moynihan (1962a) describes. The difficulties we experienced in applying Moynihan's definitions of these social roles operationally to members of the mixed flocks led us to adopt the older definitions of nucleus and attendant species (Winterbottom, 1943; Rand, 1954).

Moynihan (1962a) held nucleus species to be those "whose behavior contributes appreciably to stimulate the formation and/or maintain the cohesion of mixed flocks." He defined attendant species to be those that "contribute little or nothing except their presence" and thus "do much less to stimulate the formation and/or maintain the cohesion of mixed flocks." These definitions are difficult to apply as their use necessitates subjective interpretation. The definition of a nucleus species as one that is intraspecifically gregarious and around which mixed flocks are formed and maintained (Winterbottom, 1943) was more useful to us in

classifying the various species within the flock. In conjunction with this definition Rand's (1954) use of attendant species to refer to those species that form interspecific associations with nucleus species follows directly.

All definitions suggested to date have failed to provide a precise means for measuring the effect of each flock member on flock size and cohesion. Similarly criteria for the degree to which each attendant increases or decreases the conspicuousness or acceptability of a mixed flock to other potential attendants (i.e. through the quality and intensity of its vocalizations and displays) are lacking in these definitions. Future understanding of the dynamics and evolution of interspecific flock systems rests on defining and quantifying objectively the social roles of species based on characteristics that effect flock genesis and cohesion.

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#### SUMMARY

Small intraspecific flocks (four to six birds per flock) of the Common Bush-Tanager (*Chlorospingus ophthalmicus*) acted as nucleus components in interspecific foraging flocks at 1,680 m elevation in the vicinity of Cerro Punta in western Panama. These intraspecific flocks were stable groups of individuals and maintained closely spaced, slightly overlapping home ranges. Each flock foraged throughout the entire extent of its range daily.

Individual *C. ophthalmicus* roosted at the same site each night. The members of two flocks roosted in loose groups while those of a third roosted singly or in pairs at widely scattered sites near or just beyond the boundaries of the flock's home range.

*C. ophthalmicus* was active during the morning and late afternoon but was inactive during midday. Each flock of this species spent the midday period each day at the same location within its range. The courses these flocks followed during foraging periods varied from day to day.

The relationships of other species to *C. ophthalmicus* flocks varied. Some species joined and followed flocks almost continuously. Other birds showed no reaction to the flocks. Several types of intermediate

response occurred. The size and organization of the interspecific flocks depended upon the activity levels of the *C. ophthalmicus* component. When the *C. ophthalmicus* were active and calling intensely, the mixed-species flock was large. During periods of inactivity by the *C. ophthalmicus*, the mixed flock decreased in size.

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