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Birds often form groups that include individuals of several different species. Such heterogeneous groups may be called "mixed species flocks."

There are many different kinds of mixed species flocks. Some are composed of only two species, while others may include many more, probably over a dozen in extreme cases. Some mixed flocks are essentially transitory, while others are semipermanent, very long-sustained or dissolved and re-formed at more or less regular intervals. Some seem to be very loosely organized, while others are tightly integrated and have a complicated social structure.

Mixed species flocks are found almost everywhere, in almost all environments; but they seem to be most common and varied and probably attain the greatest structural complexity in certain regions of the humid Tropics. In such regions, most of the more complex flocks are largely or completely composed of passerines.

Mixed species flocks have been noted by almost all ornithologists and naturalists who have traveled in the Tropics since Bates (1863), Wallace (1869), and Belt (1874). Among the more recent or longer accounts of such flocks are descriptions in Chapin (1932), Davis (1946), Johnson (1954), Mitchell (1957), Moynihan (1960), Rand (1954), Slud (1960), Stanford (1947), Stresemann (1917), Swynnerton (1915), and Winterbottom (1943 and 1949). Many other, earlier, descriptions of mixed flocks are listed in Rand, 1954. Some aspects of mixed flocks have been discussed at considerable length in some or all of these publications; but the social reactions between individuals of different species within mixed flocks have not been analyzed in detail.

This paper is an attempt to provide more precise information about some of the behavior mechanisms responsible for the formation and

maintenance of certain types of mixed species flocks. It also includes some suggestions about the probable course of evolution of such flocks.

Most of the observations were made in Panamá between September 1957 and November 1960. Special attention was paid to mixed flocks of finches, tanagers, honeycreepers, and warblers. Several different types of mixed flocks of these birds are common in different habitats in Panamá. The two that were studied most intensively may be called the "blue and green tanager and honeycreeper flocks" and the "montane bush flocks." These are terms of convenience. Flocks of the first type frequently include other species in addition to blue and green tanagers and honeycreepers. Flocks of the second type are not confined to bushy habitats.

Mixed blue and green tanager and honeycreeper flocks were observed, off and on, throughout the whole period of this study. Other types of mixed flocks were observed much more briefly (see below).

THE BLUE AND GREEN TANAGER AND HONEYCREEPER FLOCKS

DESCRIPTION OF THE MOST COMMON SPECIES

Before proceeding to discuss these flocks, it may be helpful to describe the appearance of some of the species involved and to say something of their behavior apart from mixed flocks in central Panamá. This will be partly a recapitulation of data included in other publications (e.g., Skutch, 1954; Sturgis, 1928; and Moynihan, op. cit.).

Plain-colored Tanager (*Tangara inornata*).[1]—A comparatively small tanager. Sexes nearly identical in plumage: largely dull gray, with black wings and tail and bright blue patches on the upper wing coverts.

Resident in Panamá. Most common along the edges of fairly mature forest but occurring also in young second-growth forest. Primarily a bird of the treetops.

Very gregarious apart from mixed species flocks. Very restless and active. Very noisy, frequently uttering loud and sharp *tsit* call notes, which may be accelerated to produce mechanical-sounding rattles.

Palm Tanager (*Thraupis palmarum*).—A moderately large tanager. Sexes nearly identical in plumage: dull olive-green, with black wings and tail.

[1] The scientific names of all the Panamanian species cited in this paper follow Eisenmann, 1952 and 1955.

Resident in Panamá. Common both in young second-growth forest and along the edges of fairly mature forest. Primarily a bird of the treetops.

Moderately gregarious apart from mixed species flocks, several pairs or family groups sometimes occurring together. Somewhat less active and restless than the plain-colored tanager. Very noisy, frequently uttering rather plaintive-sounding *wheet* call notes. Adult males (at least) also utter twittering songs very frequently in some of the situations in which other species usually utter call notes (see Eisenmann, 1952, for a transcription of the typical song of this species in Panamá).

Blue Tanager (*Thraupis episcopus*).—Slightly smaller than the palm tanager. Sexes nearly identical in plumage; dull light blue, with brighter blue wings and tail (in the Panamanian subspecies *diaconus*).

Resident in Panamá. Most common in young, scattered, second-growth forest, but occurring also along the edges of fairly mature forest. Primarily a bird of the treetops but less markedly so than the plain-colored or palm tanagers.

Moderately gregarious apart from mixed species flocks, like the palm tanager, and similar to the palm tanager in notes and movements.

Golden-masked Tanager (*Tangara larvata*).—Similar to the plain-colored tanager in size. Sexes nearly identical in plumage; conspicuously marked with an intricate pattern of bright blue, yellow, black, and white.

Resident in Panamá. Most common in young, scattered, second-growth forest and in gardens, but occurring also along the edges of fairly mature forest. Common in bushes, near the ground, as well as in the treetops.

Only very slightly gregarious apart from mixed species flocks, seldom or never congregating in groups larger than a single family. Otherwise similar to the plain-colored tanager in behavior.

Green Honeycreeper (*Chlorophanes spiza*).—Very tanagerlike in appearance. Like the species of the genus *Tangara* in size and shape, aside from the bill. Sexes very different in adult plumage. The adult male is bright blue-green with a black head. The adult female is bright grass-green all over. Juveniles of both sexes are grass-green like the adult female.

Resident in Panamá. Distribution similar to that of the plain-colored tanager; most common along the edges of fairly mature forest. Primarily a bird of the treetops.

Also very similar to the plain-colored tanager in voice and movements, but not usually very gregarious apart from mixed species flocks.

Shining Honeycreeper (*Cyanerpes lucidus*).—Much smaller than the green honeycreeper, and much less tanagerlike in general appearance. Sexes very different in adult plumage. The adult male is blue, with black throat, wings, and tail. The adult female is green above, with a bluish head, and dirty white below, streaked with bluish. Juveniles of both sexes are similar to the adult female.

Resident in Panamá. Most common along, perhaps confined to, the edges of fairly mature forest. Primarily a bird of the treetops.

Very similar to the green honeycreeper in voice and movements. Only slightly gregarious apart from mixed species flocks.

Red-legged Blue Honeycreeper (*Cyanerpes cyaneus*).—Similar to the shining honeycreeper in size and shape. Sexes different in appearance in adult plumages. The adult male has two distinct plumages. In full nuptial plumage the adult male is a brilliant sapphire blue, with turquoise blue crown, black upper back and tail, and black wings with bright yellow edgings on the primaries and secondaries. In nonbreeding plumage the adult male is dull gray-green, with the same wings and tail as in the breeding plumage. The adult female is always dull gray-green all over. Juveniles of both sexes are similar to the adult female.

Resident in Panamá. Very common both in young, scattered, second-growth forest and along the edges of fairly mature forest. Primarily a bird of the treetops.

Very gregarious apart from mixed species flocks. Very restless and noisy, frequently uttering several different types of call notes and/or hostile notes, most of which are quite distinctive in sound.

Blue Dacnis (*Dacnis cayana*).—Rather similar to the green honeycreeper and the *Tangara* tanagers in shape, but slightly smaller. Sexes very different in appearance when adult. The adult male is bright blue (greenish in some lights) with black markings. The adult female and juveniles of both sexes are grass-green with bluish heads.

Resident in Panamá. Most common in young second-growth forest but occurring also along the edges of fairly mature forest. Primarily a bird of the treetops.

Only very slightly gregarious apart from mixed species flocks. Rather active and restless, but less noisy than the green honeycreeper or the red-legged blue honeycreeper.

Crimson-backed Tanager (*Ramphocelus dimidiatus*).—A rather large tanager (approximately the same size as the palm and blue tanagers). Very conspicuously and distinctively colored. The adult male is bright crimson and black. The adult female and juveniles of both sexes are similar but duller.

Resident in Panamá. Common both in young, scattered, second-growth forest and along the edges of fairly mature forest, both in moderately low bushes and in the treetops.

Moderately gregarious apart from mixed species flocks. Active and noisy, frequently uttering nasal *anh* notes which are quite unlike the notes of any other Panamanian tanagers or honeycreepers except the other species of *Ramphocelus*.

Summer Tanager (*Piranga rubra*).—Migratory. Absent from Panamá during the northern breeding season. Most individuals observed in Panamá seemed to be young; in more or less complete juvenal plumage, dull yellowish in color (males usually begin to assume the rosy-red adult plumage before leaving in the spring).

Fairly common in many different types of vegetation in many areas of Panamá.

Almost completely nongregarious apart from mixed species flocks in Panamá. Not very active. Moderately noisy, frequently uttering a rattling *pi-ti-ti-tuck* call.

White-lined Tanager (*Tachyphonus rufus*).—A rather large tanager. Sexes very different in appearance when adult. The adult male is black, with white underwing coverts. The adult female and juveniles of both sexes are rufous brown.

Resident in Panamá. Most common in young, scattered, second-growth forest, but common also in moderately low bushes as well as in the treetops.

Only very slightly gregarious apart from mixed species flocks. Moderately active. Not very noisy.

Fulvous-vented, Thick-billed, and Yellow-crowned Euphonias (*Tanagra fulvicrissa, T. laniirostris,* and *T. luteicapilla*).—Small to very small tanagers. The adult males of all three species are largely black glossed with steel-blue above, with yellow foreheads and yellow underparts. The adult females and juveniles of all three species are largely olive.

All three species are resident in Panamá. The fulvous-vented euphonia is most common along the edges of fairly mature forest. The thick-billed and yellow-crowned euphonias are more characteristic of young second growth.

All three species seem to be only moderately gregarious apart from mixed species flocks. They are all very active and noisy, uttering a variety of call notes almost constantly when moving.

Bananaquit (*Coereba flaveola*).—Another honeycreeper type, but very different from the blue and green honeycreepers in many respects.

Very small. Sexes nearly identical: gray above, with a black cap, and white superciliary stripes, and largely yellow below.

Resident in Panamá. Common both in young second-growth forest and scrub, and along the edges of fairly mature forest, in low bushes as well as in the treetops.

Only very slightly gregarious apart from mixed species flocks. Active. Very noisy during the breeding season, when the males may utter shrill monotonous songs for hours on end.

Yellow Warbler (*Dendroica petechia*).—All the yellow warblers observed with mixed species flocks during this study appeared to be migrants belonging to the subspecies *aestiva* which breeds in North America. They were largely yellow with rufous on the crown (but not over the whole head, as in the resident race *erithachorides*). They were observed only during the Northern Hemisphere winter.

In Panamá these warblers are widely distributed and moderately common. They are active, but silent, and almost completely nongregarious apart from mixed species flocks.

Streaked and Buff-throated Saltators (*Saltator albicollis* and *S. maximus*).—Relatively large finches. In both species the sexes are nearly identical. The streaked saltator is grayish olive above, with white superciliary stripes, and whitish below, streaked with grayish olive. The buff-throated saltator is largely olive above and gray below, with white superciliary stripes and a buff throat bordered by black.

Both species are resident in Panamá and most common in young second-growth forest. They are primarily birds of the treetops and the upper levels of moderately high shrubbery.

They are not very active or noisy, and only slightly gregarious apart from mixed species flocks.

OTHER SPECIES

The species described above are the ones that occur most frequently in the blue and green tanager and honeycreeper flocks in central Panamá, in the Canal Zone and adjacent areas.

Many other species may also occur in such flocks, but much less frequently, either because they themselves are rare, or because they are not attracted to such flocks very strongly. Among these species are the scarlet-thighed dacnis (*Dacnis venusta*), the white-winged tanager (*Tachyphonus luctuosus*), the yellow-rumped tanager (*Ramphocelus icteronotus*), the resident yellow-tailed and yellow-backed orioles (*Icterus mesomelas* and *I. chrysater*), the migrant Baltimore oriole (*I. galbula*), the clay-colored thrush (*Turdus grayi*), a variety

of flycatchers (especially the yellow-bellied elaenia, *Elaenia flavogaster*, the social flycatcher, *Myiozetetes similis*, and the rusty-margined flycatcher, *M. cayanensis*), and several different types of vireos and cotingas.

There are also some species, including the green-backed sparrow (*Arremonops conirostris*), the dusky-tailed ant-tanager (*Habia fuscicauda*), the blue-black grassquit (*Volatinia jacarina*), the variable seedeater (*Sporophila aurita*), and the yellow-bellied seedeater (*S. nigricollis*), that are associated with blue and green tanager and honeycreeper flocks in some circumstances, but are usually more or less distinctly separated by habitat preference (see below).

Finally, there are some species, such as hummingbirds, woodpeckers, and the Tovi parakeet (*Brotogeris jugularis*), that are not infrequently found in close physical proximity to blue and green tanager and honeycreeper flocks, but still appear to be essentially independent of such flocks, as their movements are seldom or never coordinated with those of the flocks.

DESCRIPTION OF THE FLOCKS

Mixed blue and green tanager and honeycreeper flocks are very widely distributed in central Panamá, but they are most characteristic of lowland areas. Some of the species of what may be called the "blue and green tanager and honeycreeper alliance" [2] seem to be absolutely confined to the lowlands. Other species of the alliance occur in both lowland and highland areas. I have seen some of them near the peaks of the highest mountains in central Panamá, around 3,200-3,400 feet above sea level, and even higher in western Panamá (see below); but all or most of them are more common in the lowlands than in the mountains. I have never seen large typical mixed blue and green tanager and honeycreeper flocks above 2,000 feet elevation in central Panamá.

Most of the species that occur in mixed blue and green tanager and honeycreeper flocks are essentially arboreal, and all the species that are regular members of such flocks are primarily "edge" birds. Most of them also prefer to remain as high above the ground as possible. Typical mixed blue and green tanager and honeycreeper flocks usually stay in or near the treetops, and never occur very far

[2] The term "alliance" will be used throughout this paper to include all the species that are regular members (see below) of a particular type of mixed flock, plus any other species that occur in that particular type of mixed flock relatively frequently.

inside the forest below the canopy. They come nearest to the ground in certain areas where tall trees are scarce. In such areas they sometimes come down to the top of low scrub, no more than a few feet above the ground. They may then be joined by such species as the green-backed sparrow and the dusky-tailed ant-tanager, which usually occur inside low scrub. These low-scrub species usually drop out of mixed blue and green tanager and honeycreeper flocks as soon as the other members of the flocks return to the trees.

All or most of the members of any given mixed blue and green tanager and honeycreeper flock are usually in approximately the same level of vegetation at any given time. This is one of the more distinctive features of such flocks (see below).

Mixed blue and green tanager and honeycreeper flocks are formed most frequently and are most often large during the nonbreeding season. Birds of many species of the blue and green tanager and honeycreeper alliance tend to associate with individuals of other species of the alliance relatively infrequently during the breeding season, as they adopt territories or (if they already own territories) they spend more and more time in the immediate vicinity of their nests; but they seldom or never stop associating completely. Every once in a while during the breeding season a mixed blue and green tanager and honeycreeper flock will be formed which is quite as large and complex as any formed during the nonbreeding season.

Mixed blue and green tanager and honeycreeper flocks are not very stable in any circumstances. Associations between individuals of different species of the blue and green tanager and honeycreeper alliance tend to be brief and are very seldom or never sustained continuously over a whole day. The composition of mixed blue and green tanager and honeycreeper flocks is also extremely variable, almost from minute to minute. Birds of different species are constantly coming together, staying together for a brief period, and then becoming separated again as some move on (perhaps going a considerable distance away) and others do not.

In spite of this short-term variability, it is quite obvious that the same birds of the same species tend to come together again and again. In favorable habitats (see below) the same birds of the same species may rejoin one another a dozen times a day and will certainly rejoin one another day after day for periods of at least several months.

None of the species of the blue and green tanager and honeycreeper alliance seems to have any special behavior patterns whose main function is to attract individuals of other species. In many or most cases,

individuals of different species just tend to stick together whenever they happen to run across one another in the course of their ordinary activities.

Mixed blue and green tanager and honeycreeper flocks can be formed at any time of the day between sunrise and sunset; but they are probably more common and larger, on the average, during early morning, when all the species of the alliance are most active, than during later periods of the day.

The social spacing of individual birds in mixed blue and green tanager and honeycreeper flocks is quite as variable as the composition of such flocks. Sometimes some or all of the members of a flock are very close together, within a few inches of one another. Oftener they are more scattered, most of them being separated from their nearest neighbors by distances of several feet or yards. Sometimes they are so widely scattered that their membership in the same flock is revealed only by their tendency to move in the same direction at approximately the same time.

The more highly integrated mixed blue and green tanager and honeycreeper flocks (which are not necessarily the flocks in which the members are nearest to one another in space) seem to be confined within certain definite ranges. In some cases, at least, the borders of these ranges seem to be directly determined by features of the vegetation or topography, rather than social contacts between adjacent flocks.

Individual birds, pairs, and larger family groups of some species may defend territories while they are part of mixed flocks (see below); but there is no joint defense of the flock range as a whole.

Most of the species of the blue and green tanager and honeycreeper alliance seem to have rather generalized feeding habits. Most of the tanagers, and probably the saltators, eat a great deal of fruit; the honeycreepers eat fruit and nectar; and all the species of the alliance eat many insects. The feeding habits of all these species seem to overlap widely. It is very common to see at least three or four species feeding on the same food at the same time in the same place. This occurs most frequently when some favored fruit or flower is particularly abundant, and when swarms of insects emerge after hatching.

It might be supposed, therefore, that the association of many of these species in mixed flocks is purely coincidental. It is conceivable that such flocks might be formed and maintained simply because many species are attracted to, and remain near, the same food sources.

There are various indications, however, that at least some (and perhaps the majority) of the associations between species of the blue

and green tanager and honeycreeper alliance are produced by some social factors, in addition to (or instead of) the direct and immediate stimulus of food.

The effects of such special social factors are obvious in the case of some associations. Birds of some species definitely do tend to join and follow birds of certain other species in places (e.g., the top branches of tall, dead, bare trees) where there is little or no food available and/or when they are obviously not in the mood to feed (as shown by the fact that they do not begin to feed immediately after joining or following).

The factors controlling the behavior of other species are more obscure. It is evident, nevertheless, that the birds of the blue and green tanager and honeycreeper alliance inhabiting any given area are relatively seldom scattered randomly among the particular parts of that area where food is most abundant at any given time. They tend to occur in "clumps," first in one part and then in another.

The minor movements of many mixed flocks are also extremely suggestive. The behavior of birds feeding in *Cecropia* trees on Barro Colorado Island may be cited as an example. These trees are common along the edges of clearings, and many or most of the trees in any particular area seem to bear fruit at almost exactly the same time. Large mixed flocks of the frugivorous members of the blue and green tanager and honeycreeper alliance frequently feed on the ripe *Cecropia* fruits. Such flocks are usually very restless. All the birds of a mixed flock may be feeding on the fruits of one particular tree, when one bird or part of the flock may suddenly fly over to an adjacent tree and begin to feed there. In such cases, the remaining members of the flock, left in the first tree, frequently (perhaps usually) fly over to the second tree sooner or later. A mixed flock may visit a dozen different *Cecropia* trees in fairly rapid succession in this way. It is also quite common for a flock to fly back and forth, visiting and feeding in these same trees again and again. In view of the frequency of such back-and-forth alternation, and the fact that the fruits of almost all the trees usually seem to be in essentially identical condition, it is difficult to believe that all the members of such a mixed flock are really looking for a different food when they move. It seems more likely that most of the members of the flock are simply reacting to the movements of the first birds to fly; and the first birds may have flown, or started to fly, for any one of several different reasons, including pure "restlessness," slight alarm, or a brief outburst of aggressiveness within the flock. Such reactions would at least suggest that some positive social

relationships are widespread among most of the species of the blue and green tanager and honeycreeper alliance.

It is difficult to believe, in any case, that birds of different species could occur together as frequently as many members of the blue and green tanager and honeycreeper alliance without forming social bonds among themselves.

Many or most of the birds in mixed blue and green tanager and honeycreeper flocks may be attracted to one another as a result of some conditioning process, having "learned" that the presence of other species is usually an indication of food in the neighborhood. Birds of the blue and green tanager and honeycreeper alliance may also tend to secure more food more easily, in the long run (although not always), when in mixed flocks than when not in mixed flocks. It is even possible that facilitation of feeding is the principal adaptive advantage of the habit of forming mixed flocks, i.e., the principal reason why such habits were selected during the evolution of many species of the blue and green tanager and honeycreeper alliance (but see comments below). Even if all these possibilities should be established as proven facts, however, they would not be evidence that the attraction of food is the sole cause of the formation and maintenance of many or most of the associations between individuals of different species in most of the mixed blue and green tanager and honeycreeper flocks observed at the present time.

There are even some indications that some slight social attraction between individuals of different species is very widespread among passerine birds in general, even species that are seldom or never found in mixed flocks. Observation of many different species of passerine birds in Panamá would suggest that an individual of almost any species may approach, or at least perform intention movements of approaching, individuals of almost any other species, especially upon first hearing or seeing the other individuals. This may be nothing more than "curiosity"; but it does tend to bring birds together, and it may be one of the sources from which more strongly gregarious tendencies have been developed in the course of evolution (see below).

All other factors being equal, the chances of one bird's approaching another bird of another species seem to be dependent upon the degree of resemblance between the two birds. Birds of different species are more likely to approach one another if they resemble one another in certain conspicuous features, such as color or voice, than if they are very different from one another in all features.

Although food may not be the only, or the principal, attraction

bringing birds of the blue and green tanager and honeycreeper alliance together, the mixed flocks of this alliance may still be considered primarily feeding groups in one sense. Almost all the birds in such flocks spend most of their time feeding, or (apparently) looking for food, as long as they remain in the flocks. (They also spend most of their time feeding and looking for food when they are not in mixed flocks.) This does not mean that birds never perform other activities in mixed flocks. Any individual or group of any species in a mixed flock may preen or perform other comfort activities, or engage in hostile disputes, or start courtship, or even just pause to rest while in the flock; but the performance of such nonfeeding patterns usually tends to reduce the cohesion of the flock. The birds performing such nonfeeding patterns tend to drop out of the flock if they continue such activities for any appreciable length of time. The flock just moves off and leaves them behind.

The only nonfeeding activities that may greatly increase the cohesion of mixed flocks are escape and mobbing reactions. Escaping and mobbing birds tend to bunch together particularly closely. Mobbing also attracts other birds in the neighborhood, and the sight of one bird escaping may induce other birds to fly in the same direction.

In the course of the present study, mixed flocks of the blue and green tanager and honeycreeper association were observed most thoroughly in three different areas:

(1) On Barro Colorado Island, in and around the large clearing of the biological station. This clearing is roughly rectangular, approximately a quarter of a mile long and 300-500 yards wide in most places, and stretches up a steep hill (approximately 275 feet high) from the shores of Gatún Lake. It is surrounded by fairly mature second-growth forest on three sides. There are also some trees and patches of shrubbery (mostly fruit trees and introduced ornamental bushes) scattered irregularly within the clearing. Mixed blue and green tanager and honeycreeper flocks are common in the trees around the edge of the clearing, and sometimes visit the trees and shrubs within the clearing, especially when the birds are crossing from one side of the clearing to the other.

(2) On the mainland, about 2 miles away, near the little town of Frijoles. In this area observations were made along approximately a half mile of railroad track and along several narrow paths leading off the track. The vegetation in this area is second growth, obviously younger than most of the forest on Barro Colorado Island. It is also extremely diverse, ranging from low scrub and gardens around houses

to moderately thick forest. There are a few cultivated fields (most of which were bare or planted with low crops at the times of observation) scattered in the midst of the forest and scrub, and a few yards of grass along both sides of the railroad track. The ground beside the railroad track is level, but the rest of the area is quite hilly. Mixed blue and green tanager and honeycreeper flocks occur in almost all the scrubby and forested parts of this area. (A peculiar feature of this area is a series of steel pylons, carrying electric cables, at regular intervals along the railroad track. Most of these pylons are separated from the nearest trees by an appreciable distance. The distribution of some birds is sometimes greatly affected by the presence of these pylons.)

(3) About 10 miles from the other two, near the town of Gamboa. The vegetation in this area is much the same as in the Frijoles area. Most of the observations in this area were made along approximately a mile of concrete road. Mixed species flocks are common along the edges of the forest and high scrub on both sides of the road.

The nature of the mixed flocks in these areas may be illustrated in more detail by the accompanying tables.

(It should be emphasized that the data in these tables are merely examples. The analyses of flocks and the behavior of individual species in the following pages are based upon many other types of counts and other observations, in addition to the data summarized in these particular tables.)

The data summarized in the first group of tables (1 to 19) were obtained by observation of birds in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959. This time of the year is the nonbreeding season for the members of the blue and green tanager and honeycreeper alliance.

Table 1 is an attempt to indicate the frequencies with which various species may occur in mixed flocks in this area at this time of the year. It is a count of the number of times individuals of the 12 most frequently observed species of tanagers, honeycreepers, and warblers were seen in mixed flocks and not in mixed flocks during the whole period of observations. This count was made as follows:

An observer walked around the clearing and counted every finch, tanager, honeycreeper, and warbler seen. Any of these birds seen in a tree or bush in which there were also one or more other birds of some other species (any other species, including nonpasserines) at the same time were counted as being in a mixed flock. The only exceptions were some birds in very large trees. In such trees a bird was

counted as being in a mixed flock only if there were one or more birds of some other species within approximately 50 feet. Any finch, tanager, honeycreeper, or warbler flying in a group with one or more birds of some other species was also counted as being in a mixed flock. Each

TABLE 1.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks.

Species	No. of times individuals seen in obviously integrated mixed flocks	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	106 (10)	478 (46)	569	1047
Palm tanagers	27 (9)	145 (48)	156	301
Blue tanagers	18 (7)	121 (45)	148	269
Golden-masked tanagers ...	9 (18)	25 (41)	36	61
Green honeycreepers	9 (8)	50 (44)	63	113
Red-legged blue honeycreepers	4 (3)	84 (73)	31	115
Blue dacnises	0	33 (50)	33	66
Crimson-backed tanagers ...	1	40 (25)	121	161
Summer tanagers	0	23 (43)	30	53
Fulvous-vented euphonias ..	1 (4)	14	11	25
Bananaquits	3 (2)	52 (39)	82	134
Yellow warblers	0	17 (18)	75	92

bird was counted individually. Thus, for instance, when two tanagers of the same species were seen together they were counted as two in the table.

Birds other than finches, tanagers, honeycreepers, and warblers were counted only when they occurred in association with the latter but were counted in the same way.

The observer made no attempt to follow any single birds or flocks.

As soon as any single bird or flock was counted, he resumed walking around the clearing. As most periods of observation lasted for several hours, the observer repeatedly retraced his steps and made counts in the same places. Many individual birds and some flocks were undoubtedly counted several times during any single period of observation. Individual birds and flocks that did not move about very much were counted repeatedly in the same places. (It should be noted, however, that the composition of mixed flocks usually changed, to a greater or lesser extent, between successive counts.) Individual birds and flocks that did move about appreciably (as most did) were often counted several times in different places, although a definite attempt was made not to count the same individuals or flocks twice within 15 minutes. Most individual birds around the clearing were also counted repeatedly on successive days.

Thus the figures shown in table 1 under the headings "Number of times individuals seen in mixed flocks" and "Number of times individuals seen not in mixed flocks" are certainly very much larger than the real numbers of individual birds seen in mixed flocks and apart from mixed flocks.

It is difficult to estimate the actual numbers of individual birds of different species in and around the clearing during the periods in which these counts were made, as few of the birds were distinctively marked or banded, and there were certainly some changes in the populations of some or all species between October and December. As a very rough estimate, I would guess that there were at least 10 plain-colored tanagers (quite possibly 16), 4 palm tanagers, 4 blue tanagers, 2 golden-masked tanagers, 5 green honeycreepers, 6 red-legged blue honeycreepers, 4 crimson-backed tanagers, 2 summer tanagers, 2 fulvous-vented euphonias, 4 bananaquits, and 2 yellow warblers in and around the clearing more or less regularly during all or most of the period between October and December. Additional individuals of all or most of these species turned up from time to time, but usually did not stay long.

(It will be noted that no finches are included in table 1. Most of the finches in and around the clearing seldom or never joined the mixed flocks of the blue and green tanager and honeycreeper alliance or went very high in the trees. The only exceptions were variable seed-eaters, some of which, especially males, did go high in the trees and were frequently associated with mixed blue and green tanager and honeycreeper flocks. They are not counted in table 1 simply because they spent most of their time on the ground or in low grass in the

clearing when they were not in the trees, and it was felt that to count only the variable seedeaters in trees would provide a very inadequate sample of the population of the area and convey a misleading impression of the behavior of the species.)

The method used in compiling table 1 (which was used in order to obtain the largest possible count of associations between species) has certain inevitable defects. It is probable, for instance, that some birds that were really associated with mixed flocks were not counted as members of such flocks simply because they did not happen to be in the same trees as the other members of their flocks when they were counted. It is also probable that some of the groups of birds that were classified as mixed flocks during this count were essentially chance aggregations of individuals that were not really reacting to one another in any significant way. Many or most of the birds in most of the groups, however, did show some tendencies to keep together, at least intermittently or for brief periods of time. Many of the groups seemed to be very well organized, composed of individuals that tended to join or follow one another in a very regular manner.

Perhaps the most conspicuous examples of groups held together by relatively strong social bonds were flocks that moved about as units, all the individuals of the group flying close together at the same time and in the same direction. The number of times individuals of different species were seen flying in such groups is also indicated in table 1 under the heading "Number of times individuals seen in obviously integrated mixed flocks."

The figures in parentheses in table 1 are percentages of the total number of times individuals of any given species were seen, both in mixed flocks and not in mixed flocks. Thus, for instance, the 106 times individual plain-colored tanagers were seen in tightly integrated mixed flocks are approximately 10 percent of the total number of times (1,047) individual plain-colored tanagers were seen, both in mixed flocks and not in mixed flocks.

Table 2 may be considered a supplement to table 1. It is a record of the same observations as those recorded in table 1, summarized in a different way.

The number of times the different species (not the individual birds) were seen in mixed flocks and not in mixed flocks is indicated in the first two columns of table 2. In order to get these figures, individual birds were not counted separately unless they were seen without any other individuals of the same species nearby. Thus, for instance, when

two or more tanagers of the same species were seen together in the same small tree at the same time they were counted as one in these columns.

The total number of times each species was seen is also indicated in table 2, in the third column. The percentage of times each species

TABLE 2.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

The number of times certain species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks, and the average number of individuals of each of these species per mixed flock and per nonmixed flock.

Species	No. of times species seen in mixed flocks	No. of times species seen not in mixed flocks	Total No. times species seen	Percentage of times species seen mixed	Average No. individuals per mixed flock	Average No. individuals per nonmixed flock
Plain-colored tanagers	172	202	374	46	2.78	2.82
Palm tanagers	126	108	234	54	1.15	1.44
Blue tanagers	96	111	207	46	1.26	1.33
Golden-masked tanagers	25	36	61	41	1.00	1.00
Green honeycreepers	50	58	108	46	1.00	1.09
Red-legged blue honeycreepers	47	22	69	68	1.79	1.40
Blue dacnises	26	32	58	45	1.27	1.03
Crimson-backed tanagers	19	65	84	23	2.11	1.86
Summer tanagers	20	27	47	43	1.15	1.11
Fulvous-vented euphonias	13	11	24	54	1.08	1.00
Bananaquits	44	68	112	39	1.18	1.21
Yellow warblers	17	75	92	18	1.00	1.00

was seen in mixed flocks is shown in the fourth column. These percentage figures were calculated by using the figures in the first and third columns.

Finally, the average number of individuals of the different species per mixed flock and per nonmixed flock is indicated in the last two columns of table 2. For this purpose every solitary individual that was seen by itself alone, without any other birds of the same or any other species nearby, was considered to form a separate nonmixed flock of its own.

Tables 3 to 6 are counts of special reactions within the mixed flocks in and around the clearing on Barro Colorado Island.

Table 3 is a partial list of interspecific following reactions observed between October 26 and December 20. For the purposes of this table, only flying reactions were counted, when a bird of one species flew after a bird of another species. In some cases, the two birds flew from one tree to another; in other cases, from one branch to another within the same tree. Only rapid reactions were counted, when one bird flew after another within 30 seconds after the first bird flew. Only

TABLE 3.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Unambiguous interspecific following reactions by tanagers, honeycreepers, and warblers. (Interspecific following reactions by finches are omitted from this table because all such reactions observed during this period were ambiguous in one way or another.)

No. of cases seen	Species following	Species being followed
15	Palm tanager	Plain-colored tanager
2	do.	Blue tanager
4	Blue tanager	Plain-colored tanager
1	do.	Palm tanager
2	Golden-masked tanager	Plain-colored tanager
1	do.	Blue tanager
3	Green honeycreeper	Plain-colored tanager
1	Summer tanager	Plain-colored tanager
1	do.	Palm tanager
2	Fulvous-vented euphonia	Plain-colored tanager
1	Bananaquit	Green honeycreeper
1	Chestnut-sided warbler	Golden-masked tanager
34		

those reactions are shown in which the following bird was a tanager, honeycreeper, or warbler (of any species—not only the ones included in tables 1 and 2).

Table 3 is also a partial list because it includes only the following reactions which were seen quite clearly and could not be misinterpreted, i.e., when it was possible to identify both the followed bird and the follower with absolute certainty. Many following reactions are omitted from this table because they were ambiguous in one way or another. Thus, for instance, none of the cases in which a bird of one species followed a group of two or more species is included in the table, as it was impossible to determine exactly which particular species was being followed in such cases. Similarly, cases in which two or

more birds of one species followed a bird of another species were counted as single cases of interspecific following, as all but one of the following birds may have been following the first follower. Thus, the actual number of interspecific following reactions in the mixed blue and green tanager and honeycreeper flocks on Barro Colorado

TABLE 4.—*Data from observations in and around the clearing on Barro Colorado Island between November 10 and December 20, 1959*

Unambiguous interspecific following and joining reactions by tanagers, honeycreepers, and warblers. (Interspecific joining as well as interspecific following reactions by finches are omitted from this table because all such reactions observed were ambiguous.)

No. of cases seen	Species following and/or joining	Species being followed and/or joined
3	Plain-colored tanager	Palm tanager
1	do.	Red-legged blue honeycreeper
1	do.	Crimson-backed tanager
19	Palm tanager	Plain-colored tanager
3	do.	Blue tanager
1	do.	Green honeycreeper
1	do.	Red-legged blue honeycreeper
1	do.	Crimson-backed tanager
5	Blue tanager	Plain-colored tanager
2	do.	Palm tanager
1	do.	Chestnut-sided warbler
4	Golden-masked tanager	Plain-colored tanager
1	do.	Blue tanager
3	Green honeycreeper	Plain-colored tanager
1	do.	Bananaquit
1	Red-legged blue honeycreeper	Green honeycreeper
1	Summer tanager	Plain-colored tanager
1	do.	Palm tanager
2	Fulvous-vented euphonia	Plain-colored tanager
1	Bananaquit	Green honeycreeper
1	Chestnut-sided warbler	Golden-masked tanager
54		

Island was certainly larger, and probably very much larger, than the number of such reactions shown in the table.

This table is set up with the following species shown on the left and the species they followed shown (separately for each following species) on the right.

Table 4 is a partial list of both interspecific following and interspecific joining reactions observed on Barro Colorado Island. For the purposes of this table, a bird was considered to have joined another

when it flew (or hopped, in a few cases) within 10 feet of the other (the other bird being perched at the time) without obviously forcing the other bird to leave. Only those interspecific joining reactions are shown in which the joining bird was a tanager or honeycreeper of any species. As in the case of the following reactions, only those joining reactions are shown which were completely clear and unambiguous. Thus, interspecific joining reactions were also actually much more common than indicated in the table.

This table was compiled by adding together all the suitable cases of

TABLE 5.—*Data from observations in and around the clearing on Barro Colorado Island between November 10 and December 20, 1959*

Unambiguous interspecific following and joining reactions by tanagers, honeycreepers, and warblers. This is a different summary of the data shown in table 4. (Interspecific following and joining reactions by birds other than tanagers, honeycreepers, and warblers are not included among the cases of being followed and/or joined.)

Species	No. of times seen following and/or joining	No. of times seen being followed and/or joined
Plain-colored tanager	5	33
Palm tanager	25	6
Blue tanager	8	4
Golden-masked tanager	5	1
Green honeycreeper	4	3
Red-legged blue honeycreeper	1	3
Crimson-backed tanager	0	2
Summer tanager	2	0
Fulvous-vented euphonia	2	0
Bananaquit	1	1
Chestnut-sided warbler	1	1

interspecific following and interspecific joining seen during the period between November 10 and December 20,[8] and it is set up in the same way as table 3.

Table 5 is a different type of partial summary of the same interspecific following and joining reactions shown in table 4. In table 5, the number of times each species was seen to follow or join and the number of times it was seen to be followed or joined are summarized separately, without indicating the other species involved in each case.

None of the interspecific following or joining reactions included in the preceding tables were accompanied by overt indications of

[8] Recording of interspecific joining reactions was not begun until November 10. This is the reason why earlier cases of interspecific following have been omitted from the summaries in tables 4 and 5.

hostility;[4] but overt interspecific hostility was not really rare in the mixed blue and green tanager and honeycreeper flocks on Barro Colorado. No interspecific contact fights, actual bill-to-bill or body-to-body struggles, were seen during the periods the flocks were studied intensively; but so-called supplanting attacks (see Hinde, 1952) were quite frequent. A supplanting attack may be said to occur when one bird flies to the spot where another bird is perched, and the other bird moves away immediately. Supplanting attacks may intergrade

TABLE 6.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Interspecific supplanting attacks by tanagers and honeycreepers. (No finches or warblers were seen to perform interspecific supplanting attacks in this area during this period of observation.)

No. of cases seen	Species supplanting	Species being supplanted
1	Plain-colored tanager	Golden-masked tanager
1	do.	Green honeycreeper
1	do.	Red-legged blue honeycreeper
1	do.	Crimson-backed tanager
1	do.	Bananaquit
25	Palm tanager	Plain-colored tanager
2	do.	Blue tanager
11	Blue tanager	Plain-colored tanager
1	do.	Palm tanager
1	do.	Fulvous-vented euphonia
1	Green honeycreeper	Plain-colored tanager
1	do.	Shining honeycreeper
2	Crimson-backed tanager	Blue tanager
49		

with joining attempts, but the difference between the two types of reactions is usually clear. Some of the supplanting attacks in the mixed flocks on Barro Colorado Island were accompanied by forward pecking or jabbing movements, obviously aggressive, by the attacking birds.

Table 6 is a partial list of the interspecific supplanting attacks observed on Barro Colorado Island between October 26 and December 20. This table is organized according to the same principles as the tables immediately preceding. Only those reactions are shown in

[4] The term "hostility" will be used throughout this paper to include all overt attack and escape behavior, as well as all reactions that seem to be produced by the interaction of attack and escape tendencies.

which a tanager or a honeycreeper was the active agent—in this case the attacker—and the specific identities of both the supplanting and supplanted birds were clear.

Table 7 is a very partial indication of the frequency with which some species failed to induce interspecific reactions when such reactions might have been expected. It is a list of the number of times species of finches, tanagers, and honeycreepers were seen to fly away from mixed flocks in a very conspicuous manner (giving loud flight calls or call notes and performing exaggerated intention movements of flight before leaving) without being followed by any other species of the flocks. These incidents were also observed between October 26 and December 20.

TABLE 7.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

The number of times species of the blue and green tanager and honeycreeper alliance were seen to leave mixed flocks in a very conspicuous manner without being followed by individuals of other species.

Species	No. of times seen
Plain-colored tanager	40
Palm tanager	9
Blue tanager	13
Red-legged blue honeycreeper	3
Bananaquit	1

Tables 8 to 19 are designed to show the frequencies with which the 12 most commonly observed species of tanagers, honeycreepers, and warblers (the same species shown in tables 1 and 2) were associated with one another in mixed flocks on Barro Colorado Island during the whole period between October 26 and December 20. Each species is treated in a separate table, showing the number of times it was seen with every other species in flocks composed of two species and in flocks composed of three or more species. Every association between two species, even in flocks of three or more species, is counted separately. Thus, for instance, if plain-colored tanagers, palm tanagers, and blue tanagers were seen together in the same flock, their group was recorded as one association between plain-colored tanagers and palm tanagers, one association between plain-colored tanagers and blue tanagers, and one association between palm tanagers and blue tanagers. The figures in these tables are counts of associations between species, not individuals. When several individuals of each of two species were seen together in the same flock, their group was counted as a single association between the two species.

TABLE 8.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between plain-colored tanagers and certain other species in mixed flocks.

Species	No. of times seen with plain-colored tanagers in 2-species flocks	No. of times seen with plain-colored tanagers in flocks of 3 or more species
Palm tanager	39	37
Blue tanager	19	31
Golden-masked tanager	5	7
Green honeycreeper	11	11
Red-legged blue honeycreeper	3	8
Blue dacnis	2	2
Crimson-backed tanager	1	7
Summer tanager	2	3
Fulvous-vented euphonia	1	4
Bananaquit	3	2
Yellow warbler	1	5

TABLE 9.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between palm tanagers and certain other species in mixed flocks.

Species	No. of times seen with palm tanagers in 2-species flocks	No. of times seen with palm tanagers in flocks of 3 or more species
Plain-colored tanager	39	37
Blue tanager	9	25
Golden-masked tanager	0	5
Green honeycreeper	0	12
Red-legged blue honeycreeper	1	12
Blue dacnis	0	2
Crimson-backed tanager	1	5
Summer tanager	2	4
Fulvous-vented euphonia	1	3
Bananaquit	3	5
Yellow warbler	0	3

TABLE 10.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between blue tanagers and certain other species in mixed flocks.

Species	No. of times seen with blue tanagers in 2-species flocks	No. of times seen with blue tanagers in flocks of 3 or more species
Plain-colored tanager	19	31
Palm tanager	9	25
Golden-masked tanager	1	5
Green honeycreeper	2	7
Red-legged blue honeycreeper	1	9
Blue dacnis	1	2
Crimson-backed tanager	2	4
Summer tanager	1	3
Fulvous-vented euphonia	2	3
Bananaquit	0	3
Yellow warbler	0	3

TABLE 11.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between golden-masked tanagers and certain other species in mixed flocks.

Species	No. of times seen with golden-masked tanagers in 2-species flocks	No. of times seen with golden-masked tanagers in flocks of 3 or more species
Plain-colored tanager	5	7
Palm tanager	0	5
Blue tanager	1	5
Green honeycreeper	0	1
Red-legged blue honeycreeper	0	2
Blue dacnis	0	0
Crimson-backed tanager	0	0
Summer tanager	0	4
Fulvous-vented euphonia	0	1
Bananaquit	0	2
Yellow warbler	0	3

TABLE 12.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between green honeycreepers and certain other species in mixed flocks.

Species	No. of times seen with green honeycreepers in 2-species flocks	No. of times seen with green honeycreepers in flocks of 3 or more species
Plain-colored tanager	11	11
Palm tanager	0	12
Blue tanager	2	7
Golden-masked tanager	0	1
Red-legged blue honeycreeper	2	7
Blue dacnis	1	1
Crimson-backed tanager	0	2
Summer tanager	0	4
Fulvous-vented euphonia	0	0
Bananaquit	9	4
Yellow warbler	0	2

TABLE 13.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between red-legged blue honeycreepers and certain other species in mixed flocks.

Species	No. of times seen with red-legged blue honeycreepers in 2-species flocks	No. of times seen with red-legged blue honeycreepers in flocks of 3 or more species
Plain-colored tanager	3	8
Palm tanager	1	12
Blue tanager	1	9
Golden-masked tanager	0	2
Green honeycreeper	2	7
Blue dacnis	2	3
Crimson-backed tanager	0	0
Summer tanager	1	2
Fulvous-vented euphonia	0	1
Bananaquit	3	6
Yellow warbler	0	5

TABLE 14.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between blue dacnises and certain other species in mixed flocks.

Species	No. of times seen with blue dacnises in 2-species flocks	No. of times seen with blue dacnises in flocks of 3 or more species
Plain-colored tanager	2	2
Palm tanager	0	2
Blue tanager	1	2
Golden-masked tanager	0	0
Green honeycreeper	1	1
Red-legged blue honeycreeper	2	3
Crimson-backed tanager	0	0
Summer tanager	1	1
Fulvous-vented euphonia	0	0
Bananaquit	0	2
Yellow warbler	2	0

TABLE 15.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between crimson-backed tanagers and certain other species in mixed flocks.

Species	No. of times seen with crimson-backed tanagers in 2-species flocks	No. of times seen with crimson-backed tanagers in flocks of 3 or more species
Plain-colored tanager	1	7
Palm tanager	1	5
Blue tanager	2	4
Golden-masked tanager	0	0
Green honeycreeper	0	2
Red-legged blue honeycreeper	0	0
Blue dacnis	0	0
Summer tanager	0	1
Fulvous-vented euphonia	0	0
Bananaquit	0	1
Yellow warbler	1	1

TABLE 16.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between summer tanagers and certain other species in mixed flocks.

Species	No. of times seen with summer tanagers in 2-species flocks	No. of times seen with summer tanagers in flocks of 3 or more species
Plain-colored tanager	2	3
Palm tanager	2	4
Blue tanager	1	3
Golden-masked tanager	0	4
Green honeycreeper	0	4
Red-legged blue honeycreeper	1	2
Blue dacnis	1	1
Crimson-backed tanager	0	1
Fulvous-vented euphonia	0	0
Bananaquit	2	3
Yellow warbler	0	2

TABLE 17.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between fulvous-vented euphonias and certain other species in mixed flocks.

Species	No. of times seen with fulvous-vented euphonias in 2-species flocks	No. of times seen with fulvous-vented euphonias in flocks of 3 or more species
Plain-colored tanager	1	4
Palm tanager	1	3
Blue tanager	2	3
Golden-masked tanager	0	1
Green honeycreeper	0	0
Red-legged blue honeycreeper	0	1
Blue dacnis	0	0
Crimson-backed tanager	0	0
Summer tanager	0	0
Bananaquit	0	0
Yellow warbler	0	0

TABLE 18.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between bananaquits and certain other species in mixed flocks.

Species	No. of times seen with bananaquits in 2-species flocks	No. of times seen with bananaquits in flocks of 3 or more species
Plain-colored tanager	3	2
Palm tanager	3	5
Blue tanager	0	3
Golden-masked tanager	0	2
Green honeycreeper	9	4
Red-legged blue honeycreeper	3	6
Blue dacnis	0	2
Crimson-backed tanager	0	1
Summer tanager	2	3
Fulvous-vented euphonia	0	0
Yellow warbler	0	3

TABLE 19.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between yellow warblers and certain other species in mixed flocks.

Species	No. of times seen with yellow warblers in 2-species flocks	No. of times seen with yellow warblers in flocks of 3 or more species
Plain-colored tanager	1	5
Palm tanager	0	3
Blue tanager	0	3
Golden-masked tanager	0	3
Green honeycreeper	0	2
Red-legged blue honeycreeper	0	5
Blue dacnis	2	0
Crimson-backed tanager	1	1
Summer tanager	0	2
Fulvous-vented euphonia	0	0
Bananaquit	0	3

Tables 20 to 27 are based upon observations in the area near Gamboa between July 12 and August 15, 1960. Many of the birds of the blue and green tanager and honeycreeper alliance appeared to have just finished breeding at this time. All the data in these tables

TABLE 20.—*Data from observations near Gamboa between July 12 and August 15, 1960*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks.

Species	No. of times individuals seen in obviously integrated mixed flocks	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	0	96 (54)	82	178
Palm tanagers	3 (1)	167 (68)	78	245
Blue tanagers	2	293 (55)	241	534
Red-legged blue honeycreepers	0	31 (48)	33	64
Blue dacnises	0	11 (69)	5	16
Crimson-backed tanagers ...	2 (1)	93 (53)	81	174
White-lined tanagers	0	1 (20)	4	5
Yellow-crowned euphonias ..	0	26 (47)	29	55
Thick-billed euphonias	0	14 (78)	4	18
Streaked saltators	0	48 (44)	62	110
Buff-throated saltators	0	36 (51)	35	71

were obtained by the same methods as the data from Barro Colorado Island.

Tables 20 and 21 show how frequently the 11 most commonly observed species of finches, tanagers, and honeycreepers (of the blue and green tanager and honeycreeper alliance) were seen in mixed flocks and not in mixed flocks, and the average number of individuals of these species per mixed flock and per nonmixed flock. Very few warblers were seen with blue and green tanager and honeycreeper

TABLE 21.—*Data from observations near Gamboa between July 12 and August 15, 1960*

The number of times certain species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks, and the average number of individuals of each of these species per mixed flock and per nonmixed flock.

Species	No. of times species seen in mixed flocks	No. of times species seen not in mixed flocks	Total No. times species seen	Percentage of times species seen mixed	Average No. individuals per mixed flock	Average No. individuals per nonmixed flock
Plain-colored tanagers	46	35	81	57	2.09	2.34
Palm tanagers	85	47	132	64	1.96	1.66
Blue tanagers	147	138	285	52	1.99	1.75
Red-legged blue honeycreepers	20	19	39	51	1.55	1.74
Blue dacnises	7	3	10	70	1.57	1.67
Crimson-backed tanagers	62	51	113	55	1.50	1.59
White-lined tanagers	1	4	5	20	1.00	1.00
Yellow-crowned euphonias	18	17	35	51	1.44	1.71
Thick-billed euphonias	9	2	11	82	1.55	2.00
Streaked saltators	40	58	98	41	1.20	1.07
Buff-throated saltators	29	29	58	50	1.24	1.21

TABLE 22.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Unambiguous interspecific following reactions by tanagers and finches. (No honeycreepers or warblers were seen to perform unambiguous interspecific following reactions in this area during this period of observation.)

No. of cases seen	Species following	Species being followed
1	Palm tanager	Blue tanager
1	Blue tanager	Plain-colored tanager
1	do.	Palm tanager
1	do.	Crimson-backed tanager
1	Variable seedeater	Plain-colored tanager

TABLE 23.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Unambiguous interspecific joining reactions by tanagers, honeycreepers, and finches. (No warblers were seen to perform unambiguous interspecific joining reactions in this area during this period of observation.)

No. of cases seen	Species joining	Species being joined
2	Palm tanager	Plain-colored tanager
2	do.	Blue tanager
3	Blue tanager	Plain-colored tanager
3	do.	Palm tanager
1	Blue dacnis	Palm tanager
1	Crimson-backed tanager	Blue tanager
1	Buff-throated saltator	Plain-colored tanager
1	do.	Blue tanager

TABLE 24.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Interspecific supplanting attacks by tanagers and finches. (No honeycreepers or warblers were seen to perform interspecific supplanting attacks in this area during this period of observation.)

No. of cases seen	Species supplanting	Species being supplanted
1	Plain-colored tanager	Yellow-crowned euphonia
1	do.	Seedeater *
2	Palm tanager	Blue tanager
1	do.	Plain-colored tanager
1	do.	Yellow-bellied elaenia
1	Blue tanager	Plain-colored tanager
1	do.	Palm tanager
1	Crimson-backed tanager	Blue tanager
1	Buff-throated saltator	Blue tanager

* This bird was almost certainly a female or juvenile male variable seedeater.

TABLE 25.—*Data from observations near Gamboa between July 12 and August 15, 1960*

The number of times species of the blue and green tanager and honeycreeper alliance were seen to leave mixed flocks in a very conspicuous manner without being followed by individuals of other species.

Species	No. of times seen
Plain-colored tanager	7
Palm tanager	5
Blue tanager	10
Red-legged blue honeycreeper	1
Crimson-backed tanager	6
Thick-billed euphonia	1
Buff-throated saltator	1
Green-backed sparrow	1
Yellow-bellied seedeater	1

TABLE 26.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Associations between some species in mixed flocks composed of only two species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Yellow-crowned euphonia	Thick-billed euphonia	Streaked saltator	Buff-throated saltator
Plain-colored tanager		2	5	0	0	1	0	1	0	0	3
Palm tanager			19	1	0	4	0	0	0	1	1
Blue tanager				1	0	12	0	1	1	3	4
Red-legged blue honeycreeper					1	2	0	0	0	1	0
Blue dacnis						0	0	0	0	0	0
Crimson-backed tanager							0	1	0	1	1
White-lined tanager								0	0	0	0
Yellow-crowned euphonia									0	0	0
Thick-billed euphonia										0	0
Streaked saltator											0
Buff-throated saltator											

TABLE 27.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Associations between some species in mixed flocks composed of three or more species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Yellow-crowned euphonia	Thick-billed euphonia	Streaked saltator	Buff-throated saltator
Plain-colored tanager		14	17	5	3	8	0	4	1	7	1
Palm tanager			31	1	3	9	0	7	4	12	1
Blue tanager				10	2	19	1	10	6	17	8
Red-legged blue honeycreeper					1	3	0	1	2	2	3
Blue dacnis						3	0	1	1	1	0
Crimson-backed tanager							1	3	1	11	7
White-lined tanager								0	0	0	1
Yellow-crowned euphonia									1	2	1
Thick-billed euphonia										0	0
Streaked saltator											3
Buff-throated saltator											

flocks at Gamboa during the period of observations. The data in these tables are arranged in exactly the same way as the corresponding data in tables 1 and 2.

Tables 22, 23, and 24 are counts of interspecific following, joining, and supplanting reactions. The following and joining reactions are not added together. Otherwise the data in these tables are arranged in exactly the same way as the corresponding information about Barro Colorado birds.

Table 25 is a count of nonfollowing reactions, as in table 7.

Tables 26 and 27 show the frequency of associations between the most commonly observed species of the blue and green tanager and honeycreeper alliance at Gamboa. The data in these tables are the same type as in tables 8 to 19, but they are arranged in a different way. All the associations between species in flocks of two species are summarized in one table, while all the associations between species in flocks of three or more species are summarized in the other table.

Tables 28 to 34 are based upon observations in the area near Frijoles between November 30, 1959, and January 19, 1960. Most of the birds of the blue and green tanager and honeycreeper alliance were not breeding throughout this period; but some of them may have begun to show a little breeding behavior toward the end of the period. These tables include the same kind of data obtained and arranged in the same way as the data on the birds at Gamboa.

Tables 35 to 39 include similar data obtained during observations near Frijoles between July 7 and August 16, 1960, just after the breeding season. Interspecific following, joining, and supplanting reactions were so rare during this period that they are all summarized in the same table. Good examples of leaving mixed groups in a conspicuous manner without being followed were so very rare that they are not shown at all.

Tables 40 to 43 are summaries of observations made in several areas. Tables 40 and 41 are summaries of all the unambiguous interspecific following and joining attempts by finches, tanagers, and honeycreepers at both Gamboa and Frijoles during all periods of observation. Table 42 is a summary of all the interspecific contact fights (in which actual blows were delivered) between finches, tanagers, and honeycreepers observed at Gamboa and at Frijoles between July 7 and August 16. No interspecific contact fights were seen at Frijoles between November and January. Table 43 is a summary of all the intraspecific contact fights (among members of the blue and

TABLE 28.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks.

Species	No. of times individuals seen in obviously integrated mixed flocks	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	2 (3)	14 (22)	50	64
Palm tanagers	0	15 (28)	38	53
Blue tanagers	3 (3)	34 (38)	56	90
Red-legged blue honeycreepers	6 (9)	23 (34)	45	68
Blue dacnises	3 (12)	9 (36)	16	25
Crimson-backed tanagers ...	3 (3)	23 (21)	88	111
White-lined tanagers	0	12 (39)	19	31
Streaked saltators	0	7 (24)	22	29
Buff-throated saltators	1 (8)	6 (50)	6	12

TABLE 29.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

The number of times certain species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks, and the average number of individuals of each of these species per mixed flock and per unmixed flock.

Species	No. of times species seen in mixed flocks	No. of times species seen not in mixed flocks	Total No. times species seen	Percentage of times species seen mixed	Average No. individuals per mixed flock	Average No. individuals per nonmixed flock
Plain-colored tanagers	12	21	33	36	1.17	2.38
Palm tanagers	10	32	42	24	1.50	1.19
Blue tanagers	24	37	61	39	1.41	1.51
Red-legged blue honeycreepers ..	11	26	37	30	1.64	1.54
Blue dacnises	5	9	14	36	1.80	1.67
Crimson-backed tanagers	20	54	74	27	1.15	1.63
White-lined tanagers	11	13	24	46	1.09	1.46
Streaked saltators	5	16	21	24	1.40	1.37
Buff-throated saltators	6	6	12	50	1.00	1.00

TABLE 30.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

Unambiguous interspecific following reactions by tanagers, and joining reactions by tanagers and honeycreepers. (No honeycreepers, warblers, or finches were seen to perform unambiguous interspecific following reactions, and no warblers or finches were seen to perform unambiguous interspecific joining reactions in this area during this period of observations.)

No. of cases seen	Species following	Species being followed
1	Palm tanager	Plain-colored tanager
1	Blue tanager	Plain-colored tanager
1	Crimson-backed tanager	Dusky-tailed ant-tanager

	Species joining	Species being joined
1	Palm tanager	Blue tanager
2	Blue tanager	Red-legged blue honeycreeper
1	do.	Plain-colored tanager
1	Red-legged blue honeycreeper	Plain-colored tanager
1	Crimson-backed tanager	Blue tanager
1	do.	Blue dacnis
1	White-lined tanager	Blue tanager
1	do.	Blue dacnis

TABLE 31.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

Interspecific supplanting attacks by tanagers and finches. (No honeycreepers or warblers were seen to perform interspecific supplanting attacks in this area during this period of observations.)

No. of cases seen	Species supplanting	Species being supplanted
3	Plain-colored tanager	Blue dacnis
2	Palm tanager	Plain-colored tanager
1	Blue tanager	Plain-colored tanager
3	do.	Red-legged blue honeycreeper
1	do.	Crimson-backed tanager
1	do.	Summer tanager
1	Streaked saltator	White-lined tanager

TABLE 32.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

The number of times species of the blue and green tanager and honeycreeper alliance were seen to leave mixed flocks in a very conspicuous manner without being followed by individuals of other species.

Species	No. of times seen
Plain-colored tanager	3
Palm tanager	1
Blue tanager	7
Red-legged blue honeycreeper	1
Crimson-backed tanager	2
White-lined tanager	4
Black-capped saltator	1
Blue-black grassquit	1

TABLE 33.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

Associations between some species in mixed flocks composed of only two species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Streaked saltator	Buff-throated saltator
Plain-colored tanager		2	0	1	0	0	0	0	0
Palm tanager			1	0	0	0	0	0	0
Blue tanager				2	0	2	2	1	0
Red-legged blue honeycreeper					1	0	0	0	0
Blue dacnis						2	1	0	0
Crimson-backed tanager							2	0	1
White-lined tanager								1	0
Streaked saltator									0
Buff-throated saltator									

TABLE 34.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

Associations between some species in mixed flocks composed of three or more species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Streaked saltator	Buff-throated saltator
Plain-colored tanager		1	5	2	1	2	1	2	2
Palm tanager			0	0	0	2	2	2	0
Blue tanager				3	1	4	3	1	3
Red-legged blue honeycreeper					1	3	0	0	2
Blue dacnis						1	0	0	1
Crimson-backed tanager							1	1	2
White-lined tanager								1	1
Streaked saltator									0
Buff-throated saltator									

green tanager and honeycreeper alliance) seen at Barro Colorado, Gamboa, and Frijoles during all periods of observations.

(It was even more difficult to estimate the numbers of individuals of different species in the Gamboa and Frijoles areas than on Barro Colorado.)

TABLE 35.—*Data from observations near Frijoles between July 7 and August 16, 1960*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks.

Species	No. of times individuals seen in obviously integrated mixed flocks	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	0	28 (68)	13	41
Palm tanagers	0	30 (28)	79	109
Blue tanagers	0	117 (49)	120	237
Red-legged blue honeycreepers	0	26 (68)	12	38
Blue dacnises	0	20 (71)	8	28
Crimson-backed tanagers ..	0	84 (48)	89	173
White-lined tanagers	0	16 (70)	7	23
Thick-billed euphonias	0	15 (100)	0	15
Streaked saltators	0	32 (38)	53	85
Buff-throated saltators	0	24 (59)	17	41

There may have been something like 16 plain-colored tanagers, 28 palm tanagers, 50 blue tanagers, 17 red-legged blue honeycreepers, 5 blue dacnises, 24 crimson-backed tanagers, 2 white-lined tanagers, 16 yellow-crowned euphonias, 8 thick-billed euphonias, 18 streaked saltators, and 13 buff-throated saltators in the Gamboa area during the periods of observation, and approximately 12 plain-colored tanagers, 14 palm tanagers, 30 blue tanagers, 12 red-legged blue honeycreepers, 7 blue dacnises, 23 crimson-backed tanagers, 8 white-lined

TABLE 36.—*Data from observations near Frijoles between July 7 and August 16, 1960*

The number of times certain species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks, and the average number of individuals of each of these species per mixed flock and per nonmixed flocks.

Species	No. of times species seen in mixed flocks	No. of times species seen not in mixed flocks	Total No. times species seen	Percentage of times species seen mixed	Average No. individuals per mixed flock	Average No. individuals per nonmixed flock
Plain-colored tanagers	18	7	25	72	1.56	1.86
Palm tanagers	25	47	72	35	1.20	1.68
Blue tanagers	67	76	143	47	1.75	1.58
Red-legged blue honeycreepers	21	7	28	75	1.24	1.71
Blue dacnises	11	4	15	73	1.82	2.00
Crimson-backed tanagers	56	55	111	50	1.50	1.62
White-lined tanagers	15	6	21	71	1.07	1.17
Thick-billed euphonias	9	0	9	100	1.67	—
Streaked saltators	28	46	74	38	1.14	1.15
Buff-throated saltators	21	13	34	62	1.14	1.31

TABLE 37.—*Data from observations near Frijoles between July 7 and August 16, 1960*

A complete list of all the unambiguous interspecific following, joining, and supplanting reactions by tanagers and finches observed. (No honeycreepers or warblers were seen to perform unambiguous interspecific reactions in this area during this period of observations.)

1 case of a blue tanager following a plain-colored tanager
1 case of a crimson-backed tanager following a blue tanager
1 case of a plain-colored tanager joining a white-lined tanager
1 case of a blue tanager joining a palm tanager
1 case of a blue tanager joining a crimson-backed tanager
1 case of a streaked saltator joining a palm tanager
1 case of a streaked saltator joining a seedeater *
1 case of a plain-colored tanager supplanting a blue dacnis
1 case of a plain-colored tanager supplanting a lesser elaenia
1 case of a streaked saltator supplanting a blue tanager

* This bird was almost certainly a female or juvenile male variable seedeater.

TABLE 38.—*Data from observations near Frijoles between July 7 and August 16, 1960*

Associations between some species in mixed flocks composed of only two species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Thick-billed euphonia	Streaked saltator	Buff-throated saltator
Plain-colored tanager		0	4	0	0	0	1	0	0	1
Palm tanager			3	0	0	2	0	1	1	0
Blue tanager				1	0	7	1	0	1	1
Red-legged blue honeycreeper					1	0	0	0	1	0
Blue dacnis						0	0	0	0	0
Crimson-backed tanager							1	1	1	2
White-lined tanager								0	0	0
Thick-billed euphonia									0	0
Streaked saltator										0
Buff-throated saltator										

TABLE 39.—*Data from observations near Frijoles between July 7 and August 16, 1960*

Associations between some species in mixed flocks composed of three or more species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Thick-billed euphonia	Streaked saltator	Buff-throated saltator
Plain-colored tanager		1	3	1	2	3	0	1	0	0
Palm tanager			6	1	2	4	2	1	4	3
Blue tanager				3	1	14	3	4	3	5
Red-legged blue honeycreeper					2	4	1	1	2	1
Blue dacnis						4	0	1	2	0
Crimson-backed tanager							1	1	5	5
White-lined tanager								0	2	1
Thick-billed euphonia									1	0
Streaked saltator										3
Buff-throated saltator										

TABLE 40.—*Summary of all the unambiguous interspecific following and joining reactions by tanagers, honeycreepers, and finches observed near Gamboa and Frijoles*

This is a summary of the data shown in tables 22, 23, 30, and 37.

No. of cases seen	Species following and/or joining	Species being followed and/or joined
1	Plain-colored tanager	White-lined tanager
4	Palm tanager	Blue tanager
3	do.	Plain-colored tanager
7	Blue tanager	Plain-colored tanager
5	do.	Palm tanager
2	do.	Red-legged blue honeycreeper
2	do.	Crimson-backed tanager
1	Red-legged blue honeycreeper	Plain-colored tanager
1	Blue dacnis	Palm tanager
3	Crimson-backed tanager	Blue tanager
1	do.	Blue dacnis
1	do.	Dusky-tailed ant-tanager
1	White-lined tanager	Palm tanager
1	do.	Blue dacnis
1	Streaked saltator	Palm tanager
1	do.	Seedeater
1	Buff-throated saltator	Plain-colored tanager
1	do.	Blue tanager
1	Variable seedeater	Plain-colored tanager
38		

TABLE 41.—*Summary of all the unambiguous interspecific following and joining reactions by tanagers, honeycreepers, and finches observed near Gamboa and Frijoles*

The same data as given in table 40, arranged in a different way. (Interspecific following and joining reactions by birds other than tanagers, honeycreepers, and finches are not included among the cases of being followed and/or joined.)

Species	No. of times seen following and/or joining	No. of times seen being followed and/or joined
Plain-colored tanager	1	13
Palm tanager	7	8
Blue tanager	16	8
Red-legged blue honeycreeper	1	2
Blue dacnis	1	2
Crimson-backed tanager	5	2
White-lined tanager	2	1
Streaked saltator	2	0
Buff-throated saltator	2	0

tanagers, 8 thick-billed euphonias, 16 streaked saltators, and 11 buff-throated saltators in the Frijoles area during observations between July 7 and August 16.

Most of these species were probably almost equally abundant during both series of observations at Frijoles. The only obvious exceptions were blue tanagers and thick-billed euphonias. They were appreci-

TABLE 42.—*Interspecific contact fights among tanagers, honeycreepers, and finches observed near Gamboa and Frijoles*

(No warblers were seen to be involved in interspecific contact fights in either area.)

No. of cases seen	More aggressive species	Less aggressive species
1	Plain-colored tanager	Variable seedeater
1	Palm tanager	Social flycatcher
3	Blue tanager	Palm tanager
1	do.	White-lined tanager
1	White-lined tanager	Crimson-backed tanager
1	Blue-black grassquit	Crimson-backed tanager
1	Clay-colored thrush	Crimson-backed tanager
1	Rusty-margined flycatcher	Yellow-crowned euphonia

TABLE 43.—*Intraspecific contact fights observed on Barro Colorado Island and near Gamboa and Frijoles*

Only fights within species of the blue and green tanager and honeycreeper alliance are shown.

Species	No.
Plain-colored tanager	9
Palm tanager	6
Blue tanager	10
Green honeycreeper	1
Red-legged blue honeycreeper	1
Blue dacnis	1
Crimson-backed tanager	1
Bananaquit	15
Buff-throated saltator	2

ably less abundant during the earlier periods of observation, between November 30 and January 19, than during the later periods.

These estimates may be too high; but there were certainly many more birds in the areas at Gamboa and Frijoles where observations were made than in the clearing on Barro Colorado Island. This was partly a reflection of the fact that the Gamboa and Frijoles areas were much larger than the clearing on Barro Colorado.

THE ROLES OF DIFFERENT SPECIES WITHIN MIXED FLOCKS

PLAIN-COLORED TANAGER

Plain-colored tanagers occur in mixed blue and green tanager and honeycreeper flocks very frequently and usually play a very significant role in such flocks. The presence of these birds in any given area tends to stimulate the formation of mixed flocks in the area; and their presence in any mixed flock tends to increase the cohesion of the flock. These effects are usually produced by the reactions of individuals of other species to plain-colored tanagers, not the reactions of plain-colored tanagers to individuals of other species. Some of the reactions of individuals of other species of plain-colored tanagers seem to be indirect results of the extreme intraspecific gregariousness of plain-colored tanagers.

Intraspecific gregariousness may be contrasted to interspecific gregariousness. Throughout this paper, the former term will be used to include all the tendencies of individuals of any given species to associate with one another. The latter term will be used to include all the tendencies of individuals of one species to associate with individuals of other species.

Flocks of 10 to 16 plain-colored tanagers are common in suitable environments, especially along the edges of fairly mature forest, during the nonbreeding season. Such flocks tend to break up during the breeding season, when individual males and pairs adopt territories; but it is still not uncommon to see groups of 4 to 6 moving about together and/or feeding together for more or less brief periods of time even during the height of the breeding season.[5] The frequency with which

[5] The territories of many tropical lowland tanagers (and many other tropical species of other groups) are more difficult to recognize and study than the territories of most related Temperate Zone species.

The conventional definition of territory is "any defended area"; but territorial defense is comparatively rare among tropical tanagers. Individual birds and/or pairs of the same species in the same general area may keep apart from one another for long periods of time, each individual or pair remaining in its own particular part of the area, without showing any overt hostility to one another. It is probable, however, that such behavior is often or usually the result of previous territorial disputes which do occur occasionally between members of the same species. A few disputes may be sufficient to fix territorial boundaries for many months, or even years. Neighboring birds may learn the boundaries of their territories after a few disputes, and may retain this learning for long periods of time without further reinforcement. The territories of many tropical birds may become "traditional" more easily than those of many migratory Temperate Zone birds simply because the tropical birds are almost completely

plain-colored tanagers associate with one another does not seem to be affected by the presence or absence of individuals of other species. None of the other species of tanagers that frequently occur in mixed flocks with plain-colored tanagers are as gregarious apart from mixed flocks as plain-colored tanagers.

Some of the social behavior patterns of plain-colored tanagers seem to be very specialized. Among these specializations are increased frequency and exaggeration of wing-flicking and tail-flicking movements (stereotyped "intention movements" of flight), extreme restlessness (plain-colored tanagers are more nearly constantly active than most other tanagers), increased frequency of call notes, loss of song (which seems to have been replaced by a variation of the call-note patterns), and various modifications and/or reductions of hostile behavior.

As a result of their frequent call notes and vigorous movements, plain-colored tanagers are usually very conspicuous—probably more so, on the average, than individuals of many other species of the blue and green tanager and honeycreeper alliance.

All or most of the specialized social behavior patterns of plain-colored tanagers seem to be adaptations to promote gregariousness (see the discussion in Moynihan, 1960) and were probably evolved originally to promote intraspecific gregariousness. Many other species of birds that are gregarious among themselves, but not usually associated with mixed species flocks, have evolved similar characters, which may promote associations between individuals of the same species in several different ways. If nothing else, a bird that is very conspicuous is more often noticed and more easily recognized by other individuals of the same species than it would be if it were less conspicuous.

Some of these specialized social behavior patterns of plain-colored tanagers also seem to affect the behavior of individuals of many other

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sedentary. There is evidence that the same pairs of some species of tropical tanagers retain, or revert to, the same territories year after year.

In the case of the more highly gregarious species, the situation is further complicated by the fact that territorial birds frequently abandon their territories at more or less regular intervals in order to join and/or follow flocks of the same or other species. Thus, the territories of many tropical tanagers may be both very stable over long periods of time, and very unstable, i.e., held only intermittently, over short periods of time.

The groups of plain-colored tanagers that are formed during the breeding season may be composed of birds that have abandoned their territories completely for the time being, and/or birds that have met in a neutral area between their territories, which they are still prepared to defend. In some cases, at least, these groups are not composed of an adult pair plus their still juvenile young of the previous breeding season.

species, to which the tanagers are undoubtedly very attractive. They are joined and followed [6] by individuals of other species very frequently, relatively much more frequently than are any other birds of the blue and green tanager and honeycreeper alliance. During the course of the present investigation the attractiveness of plain-colored tanagers was most obvious in the study area on Barro Colorado Island; but it was also quite evident at Frijoles and Gamboa, where these birds were relatively much less abundant (see table 41).

The attractiveness of the plain-colored tanager is often clearly independent of its food-finding or food-providing ability. Of all the species of the blue and green tanager and honeycreeper alliance, it is the species most often joined by birds of other species in places where there is little or no food available, and most often joined and followed by other birds that are obviously not in the mood to feed at the time. (I saw nothing to suggest that plain-colored tanagers are more efficient than individuals of many other species in finding the fruits and insects on which many members of the blue and green tanager and honeycreeper flocks feed.)

These facts would indicate that birds of other species are usually or always attracted to plain-colored tanagers by some aspect of the latter, probably behavior, as the plumage of plain-colored tanagers is particularly dull and probably does not provide many strong stimuli. The plumage may facilitate associations with other species; but it is probably not directly attractive in itself (see discussion below). The behavior patterns of plain-colored tanagers that attract individuals of other species are almost certainly the patterns that also promote intraspecific gregariousness, as plain-colored tanagers do not perform any other patterns much more frequently or conspicuously than individuals of many other species.

It has already been mentioned that many or most passerine birds show some tendency to approach birds of almost any other species. This tendency may be called "generalized" gregariousness (one type of interspecific gregariousness, as defined above), and observation of many species would suggest that it is usually more strongly stimulated by the sight and sound of conspicuously active and noisy birds than

[6] Unless specifically stated otherwise, the terms "joined" and "followed" (or "join" and "follow") are used in a rather restricted sense in this and subsequent discussions. They are applied only to reactions in which the active bird, the joiner or follower, does not appear to be hostile (or, at least, no more strongly hostile than during all social reactions).

by the sight and sound of quiet and placid birds. Thus, any species that has become conspicuously active and noisy in order to promote intraspecific gregariousness will almost inevitably tend to attract birds of other species particularly strongly. This seems to be what has happened in the case of the plain-colored tanager.

There are also some indications that generalized gregariousness is usually more strongly stimulated by the sight and sound of a group of birds than by the sight and sound of a single bird of the same species. Thus, birds of a species that has developed a high degree of intraspecific gregariousness may tend to attract individuals of other species comparatively frequently even when they are not particularly conspicuous.

A few species of the blue and green tanager and honeycreeper alliance seem to be attracted to plain-colored tanagers more strongly than would be expected on the basis of generalized gregariousness alone. Such species seem to have developed "special interspecific preferences" for plain-colored tanagers (see below). This may help to explain why plain-colored tanagers are joined and followed so very much more frequently than are individuals of any other species of the blue and green tanager and honeycreeper alliance, and by individuals of some species so much more frequently than by individuals of other species; but it is obvious that plain-colored tanagers are also very attractive to many other passerine birds that have not developed any friendly interspecific social reactions stronger than generalized gregariousness.

The relationships between plain-colored tanagers and other species in mixed blue and green tanager and honeycreeper flocks are usually essentially one way. Plain-colored tanagers join and follow individuals of other species very much less frequently than they are joined and followed by individuals of other species.

There is some evidence, in fact, that plain-colored tanagers may actually dislike being joined or followed by individuals of other species. They sometimes attack or perform intention movements of attacking some other birds with which they are associated in mixed flocks, especially such relatively small birds as variable seedeaters and blue dacnises. They do not, however, show much overt aggressiveness toward the species that join and follow them most frequently and persistently. This lack of aggressiveness is probably due to several causes. It has already been mentioned that the hostile behavior of plain-colored tanagers seems to have become modified and/or reduced in several ways, presumably as an adaptation to promote intraspecific

gregariousness.[7] More important, perhaps, is the fact that the three species that join and follow plain-colored tanagers most frequently and persistently, i.e., the palm tanager, blue tanager, and green honeycreeper, are much larger and/or much more aggressive and able fighters than plain-colored tanagers. They may intimidate plain-colored tanagers sufficiently strongly to suppress any overt expressions of aggressiveness by the latter, even when the latter are irritated by their presence.

It might be supposed, therefore, that the other species in mixed blue and green tanager and honeycreeper flocks were essentially parasitic on the plain-colored tanagers. Whatever the advantages of forming mixed flocks may be (see below), all or most of these advantages might be obtained by the other species and not the plain-colored tanagers.

This may be true in some cases, but not in all. Two types of evidence would suggest that plain-colored tanagers must also derive some advantage, at least sometimes, from their associations with individuals of other species.

The most convincing evidence in this connection is the plumage of the plain-colored tanager. It is very much duller than that of any other species of the genus *Tangara*. This dullness may be considered a type of neutral coloration, and seems to be an adaptation to facilitate associations between plain-colored tanagers and individuals of other species. The neutral coloration of the plain-colored tanager has already been discussed in an earlier paper (Moynihan, op. cit.). Part of this discussion may be quoted here:

> The dull coloration of the Plain-colored Tanager would seem to be a specific adaptation to help the species play its role in . . . mixed flocks. It seems to be effective just because of its dullness, its neutral quality. If the Plain-colored Tanager were more conspicuously colored, it might be less attractive to, or exert less influence upon, its associates of other species . . . The drab appearance of the Plain-colored Tanager probably makes it look less different to its brightly colored associates than it would if it had a distinctive bright pattern of its own. Of course, the Plain-colored Tanager might be even more effective in attracting other species if it could develop the same conspicuous colors and patterns as theirs; but most of the species with which it associates are so different from one another that it would be very difficult or impossible to mimic them all. The Plain-colored Tanager seems to have evolved a "compromise" type of coloration

[7] Observation of captive plain-colored tanagers and golden-masked tanagers under identical conditions would suggest that both the attack and escape drives of the very gregarious plain-colored tanagers are weaker, or less easily aroused, than the corresponding drives of the closely related but less gregarious golden-masked tanagers.

instead, one that is moderately different from those of almost all its associates, without being too conspicuously different from any. The fact that the compromise, neutral, coloration is drab may also have another advantage. It may make the other signal patterns of the species, the restlessness, calling, flash patterns of wings and tail, and flicking movements, relatively more effective than they would be otherwise. The drabness may allow the other characters to attract and hold a greater share of the attention of observers.

In other words, the attractiveness of plain-colored tanagers is partly a direct result of their behavior; but their behavior can only produce its full effect because their plumage is neutral, and their neutral plumage has probably been evolved as a special adaptation to permit their behavior to produce its full effect.

It may also be significant that plain-colored tanagers do sometimes join and follow individuals of other species. Such reactions are relatively very rare, but actually not too uncommon. Solitary individuals and pairs of plain-colored tanagers may also approach individuals of other species without performing clear-cut joining or following reactions of the type recorded in the accompanying tables. This may be the reason why the average number of plain-colored tanagers per mixed flock is less than the average number per nonmixed flock (see tables 2, 21, 29, and 36). It is perhaps unlikely that plain-colored tanagers would approach, join, or follow individuals of other species as frequently as they do if associations with other species were always disadvantageous, especially as any approach to individuals of other species will tend to induce these other individuals to join or follow the plain-colored tanagers in return.

PALM TANAGER

The usual social role of palm tanagers in mixed blue and green tanager and honeycreeper flocks is at least as important as that of plain-colored tanagers. In most circumstances, individual palm tanagers seem to become associated with mixed flocks approximately as frequently as do individual plain-colored tanagers, when allowances are made for the fact that the two species are seldom equally abundant in any given area. Like the plain-colored tanagers, palm tanagers also tend to stimulate the formation and increase the cohesion of mixed flocks; but the two species produce their effects in very different ways. Palm tanagers are very active joiners and followers. In most circumstances they join and follow other species relatively much more frequently than do any other tanagers of the blue and green tanager and honeycreeper alliance.

Palm tanagers also tend to perform more supplanting attacks upon individuals of other species than do any other tanagers of the blue and green tanager and honeycreeper alliance. These supplanting attacks do not, however, disturb the mixed flocks very greatly, as the supplanted individuals seldom fly very far away.

The relationships between palm tanagers and the other species of the blue and green tanager and honeycreeper alliance can be divided into two main types.

The reactions of palm tanagers to individuals of most other species seem to be nothing more than expressions of generalized gregariousness (or equally nonspecific hostility, in some cases). They do not seem to react to most other species unusually frequently or strongly.

The reactions of palm tanagers to plain-colored tanagers and blue tanagers seem to be much more specialized. Palm tanagers join, follow, and supplant plain-colored tanagers and blue tanagers [8] much more frequently than they join, follow, and supplant individuals of any other species in apparently similar social circumstances, i.e., when they are equally close to plain-colored tanagers, blue tanagers, and individuals of other species, and when these species seem to be approximately equally noisy and conspicuous. Palm tanagers also join, follow, and supplant plain-colored tanagers and blue tanagers much more frequently than do individuals of other species in similar social circumstances. These reactions would seem to be too frequent to be expressions of generalized gregariousness alone: they seem to be expressions of stronger social bonds, which might be called "special interspecific preferences."

As a rough generalization, it can be said that palm tanagers usually show a strong special interspecific preference for plain-colored tanagers, and a weaker special interspecific preference for blue tanagers; but both these preferences are rather variable, and tend to be much more obvious during some types of social reactions than during others.

In most circumstances, palm tanagers seem to join and follow plain-colored tanagers almost as frequently as they join and follow all or most other members of their own species (perhaps more frequently in many cases). They may also supplant plain-colored tanagers more frequently than they do other palm tanagers.

The relatively great frequency of supplanting attacks by palm tanagers upon plain-colored tanagers is not an indication that the former

[8] It should be stressed, again, that this discussion is an analysis of the behavior of species in central Panamá. The reactions of palm tanagers to blue tanagers may be different in parts of South America (see below).

are usually more aggressive toward the latter than toward most other members of their own species—quite the opposite in fact. It is simply because they tend to encounter plain-colored tanagers more frequently, in many environments, than any other members of their own species, except their own mates and other members of their own family groups. The comparative rarity of encounters between palm tanagers is probably an indication that they are usually more aggressive toward one another than toward individuals of any other species.

(The aggressiveness of palm tanagers toward one another is obviously variable, and often quite different, on the average, in different situations; but they do appear to be more aggressive toward one another in most circumstances than are plain-colored tanagers in the same or similar circumstances.

I have seen fairly large groups of 8 to 10 palm tanagers, with and without associated individuals of other species, in both the breeding and the nonbreeding seasons; but such groups are relatively rare. Most pairs and family groups of palm tanagers usually maintain territories during both the breeding and nonbreeding seasons—or, at least, keep well apart from one another. Such territorial birds frequently join and follow individuals of other species; but they usually stop following individuals of other species when the latter move into the territories of other palm tanagers.)

The characteristic variety of reactions by palm tanagers to plain-colored tanagers may be explained as differential responses to different stimuli presented by plain-colored tanagers.

All, or almost all, reactions between any two birds are probably at least slightly ambivalent. Thus, for instance, whenever a bird of one species sees or hears a bird of another species it is quite likely to perform some hostile patterns, at least uttering a hostile note or performing an intention movement of some hostile pattern, in addition to, or instead of, approaching or showing indications of a desire to approach the other bird in a nonhostile ("friendly") manner. Any bird presumably presents a complex of partly contradictory stimuli to any other bird that sees or hears it. Some of these stimuli are attractive, others are irritating (i.e., tend to release attack by the perceiving bird), and still others are intimidating (i.e., tend to release escape by the perceiving bird).

Palm tanagers seem to react to plain-colored tanagers as if they found them slightly less attractive, much less irritating, and very much less intimidating than other palm tanagers. This is perhaps what would be expected in view of the fact that plain-colored tanagers are

much smaller than palm tanagers but rather similar in plumage and even more active and noisy. Size is always an important factor in determining the nature of the hostile reactions between any two birds of any species; but its direct effect upon positively "friendly" reactions is usually considerably weaker.

As indicated or implied by the figures in the accompanying tables, palm tanagers tend to join, follow, and supplant blue tanagers less frequently than plain-colored tanagers when the two latter species are even approximately equally abundant. In such environments as the clearing on Barro Colorado Island, palm tanagers also tend to follow blue tanagers less closely than plain-colored tanagers and are relatively less frequently associated with blue tanagers in mixed flocks of only two species. All these facts would suggest that the social relationships between palm tanagers and blue tanagers are usually weaker than those between palm tanagers and plain-colored tanagers.

This is particularly interesting because palm tanagers and blue tanagers are strikingly similar to one another in voice, movements, and shape, as well as being very closely related. The fact that palm tanagers usually react less strongly to blue tanagers than to plain-colored tanagers is an indication that the palm tanager tends to react more strongly to the plumage patterns of the other species it encounters than to their behavior, size, or shape, and/or that the behavior patterns of the plain-colored tanager which are adapted to promote gregariousness are really remarkably effective.

Although less strong and frequent, the reactions of palm tanagers to blue tanagers are similar to their reactions to plain-colored tanagers in one important respect. Palm tanagers seem to find blue tanagers more like other palm tanagers in attractiveness than in irritating or intimidating qualities, and they usually supplant, threaten, and escape from blue tanagers relatively much less frequently than they join and follow them.

Thus, both the special interspecific preferences of palm tanagers may be said to be expressed primarily by "friendly" reactions and only secondarily by hostility. This is not true of all the special interspecific preferences of some other species (see below).

Palm tanagers join both plain-colored tanagers and blue tanagers rather frequently without starting to feed immediately afterward.

Being rather noisy and moderately restless, palm tanagers sometimes attract individuals of many other species; but this effect is seldom conspicuous. They induce overt, complete joining and following responses by individuals of other species comparatively rarely.

There may be several reasons for this. Palm tanagers are among the largest birds of the blue and green tanager and honeycreeper alliance and are probably more intimidating than such smaller species as the plain-colored tanager and the red-legged blue honeycreeper (see below). In many cases, moreover, individuals of other species are not able to join or follow palm tanagers before the palm tanagers have joined or followed them.

The dull plumage of palm tanagers may be neutral in more or less the same way as the similar plumage of plain-colored tanagers. It may be an adaptation to increase the frequency with which palm tanagers are approached by individuals of many other species probably permitting them to be approached more frequently than they would be if they were more brightly colored (unless the bright coloration were of a very special type—see below). The plumage of palm tanagers is probably not an adaptation to facilitate their associations with plain-colored tanagers alone. Palm tanagers are much more widely distributed than plain-colored tanagers (see below).

The social tendencies of palm tanagers are probably essentially the same in all environments; but they may fail to be expressed by overt behavior under certain conditions.

As their name would imply, palm tanagers show a definite preference for palm trees, nesting in the tree crowns or, less frequently, in other tall trees of similar shape, with dense crowns and bare trunks. They may also show a preference for manmade structures that have some of the same characteristics as palm trees. Near Frijoles, for instance, they were greatly attracted to the pylons along the railroad track, and some may have nested in the tops of these. Even when they nested in adjacent trees, many of the palm tanagers at Frijoles spent much of their time resting in the pylons.

Palm tanagers that have selected palm trees or similar trees or similar manmade structures as nesting sites are often reluctant to leave the vicinity of such sites during the whole period immediately before, during, and immediately after the breeding season. Other members of the blue and green tanager and honeycreeper alliance are equally reluctant to visit such trees or structures if they are far from other trees.

Thus, palm tanagers that select isolated trees or structures as nesting sites also tend to be isolated socially. They do not encounter other members of the blue and green tanager and honeycreeper alliance very frequently and usually do not follow other birds very far even when they do meet them. Such palm tanagers cannot play their usual role

in mixed flocks. They are reduced to the role of occasional and very temporary associates of the mixed flocks as long as they remain very closely attached to their nest sites.

It has already been mentioned that individuals of many species tend to associate with mixed flocks less frequently during the breeding season than during the nonbreeding season; but the palm tanagers observed in central Panamá tended to sever their connections with mixed flocks more nearly completely than all or most individuals of all or most other species. This may have been partly due to the fact that their nesting sites were more often isolated. The favorite nesting sites of palm tanagers in central Panamá are in coconut palms; and many or most of the coconut palms in this region are quite isolated from other tall trees.

In any case, the differences between the interspecific social reactions of palm tanagers during the breeding and nonbreeding seasons seem to be greater, on the average, than the differences between the corresponding reactions of any other species of the blue and green tanager and honeycreeper alliance.

The behavior of the palm tanagers at Frijoles in July and August 1960, when they were associated with mixed flocks much less frequently than individuals of many other species, was a good example of social isolation persisting immediately after the breeding season. All or almost all the palm tanagers in the Frijoles area seemed to have finished breeding before observations were begun in July 1960; but many of them were still in family groups and still more or less strongly attached to nest sites in isolated coconut palms or pylons.

BLUE TANAGER

The role of blue tanagers in mixed blue and green tanager and honeycreeper flocks is very similar to that of palm tanagers, but less unbalanced and probably less important, in most circumstances, and more nearly uniform throughout the year.

Blue tanagers tend to join, follow, and supplant individuals of many other species; but they do so relatively less frequently and less rapidly than palm tanagers in most environments. As they are also attractive to individuals of other species in much the same way as palm tanagers, they are more often joined and followed by individuals of other species than are palm tanagers in most environments. They still, however, tend to join and follow individuals of other species more often than they are joined and followed by individuals of other species.

The only species that tends to join and follow blue tanagers very

frequently is the palm tanager. In many areas blue tanagers continue to associate with mixed flocks more frequently than do palm tanagers during the breeding season, as the nesting sites of blue tanagers are usually less isolated than those of many palm tanagers. In such areas, during the breeding season, blue tanagers tend to join and follow individuals of other species *much* more frequently than they are joined and followed by individuals of other species. The role of blue tanagers in mixed flocks is much more consistently "active" in such circumstances than when palm tanagers are also frequently associated with mixed flocks.

In an earlier paper (Moynihan, 1960) it was stated that there are usually more palm tanagers than blue tanagers in mixed flocks. Subsequent observations would indicate that this is not generally true (see accompanying tables).

Blue tanagers appear to have a definite interspecific preference for plain-colored tanagers. This is probably similar to the corresponding preference of palm tanagers in quality, but averaging somewhat weaker. Blue tanagers also seem to have a special interspecific preference for palm tanagers themselves. This may be almost or quite as strong as the reciprocal preference of palm tanagers for blue tanagers, and equally similar in quality; but it is usually weaker than the preference of blue tanagers for plain-colored tanagers.

GOLDEN-MASKED TANAGER

Golden-masked tanagers were not observed very often during the present study. When they were seen with mixed flocks they showed a definite tendency to join and follow plain-colored tanagers. They may also have shown a very slight special interspecific preference for blue tanagers. (It may be significant that both golden-masked and blue tanagers have considerable amounts of bright blue in their plumages. The golden-masked tanager, the Panamanian form of the blue tanager, and the plain-colored tanager all have bright blue flash patches on the wings, which are revealed very conspicuously in flight.)

GREEN HONEYCREEPER

The behavior of green honeycreepers in mixed flocks is reminiscent of palm tanagers and blue tanagers; but by no means absolutely identical. Some aspects of the social role of green honeycreepers in mixed flocks are very distinctive. Like the palm and blue tanagers, green honeycreepers occur in mixed flocks quite frequently and tend

to approach (or try to approach) individuals of other species more often than they are approached by individuals of other species. In one way the social role of green honeycreepers is even more unbalanced than that of palm tanagers; they do not seem to be as attractive to any other species as palm and blue tanagers are to one another. In another way the social role of green honeycreepers in mixed flocks is more obviously ambivalent than that of any other common species of the blue and green tanager and honeycreeper alliance. Green honeycreepers frequently try to approach individuals of other species in an apparently nonhostile or "friendly" manner; but they also tend to be very aggressive toward individuals of other species. They are probably more often openly aggressive toward individuals of other species than are any other regular members of the mixed blue and green tanager and honeycreeper flocks.

This ambivalent behavior of green honeycreepers in mixed flocks seems to be a reflection of their behavior to one another (see Moynihan, 1960). There are indications that they are strongly attracted to one another by some sort of gregarious or general social impulse; but they seldom or never occur in stable unmixed flocks of their own species alone. This is largely owing to the fact that whenever two unrelated green honeycreepers (i.e., birds that are not members of the same pair or family group) come together, they almost always start to dispute vigorously with one another. Sooner or later (usually sooner) one bird will attack the other and drive it away.

It is quite possible that the reactions of green honeycreepers to individuals of many other species are produced by the same tendencies or internal drives as their reactions to one another; but the two types of reactions seldom take exactly the same form, i.e., they seldom include exactly the same movements, postures, or calls, in exactly the same sequence. Such differences may be due to several factors. It is obvious, for instance, that green honeycreepers seldom respond as strongly to individuals of other species as to other members of their own species, even when the quality of the response is the same in both cases. It is also evident that the social reactions of green honeycreepers are greatly affected by several aspects of the social environments in which they occur. Green honeycreepers may perform different acts, or (at least) the same acts with different frequencies, in different social environments, even when their internal motivation is the same in the different environments. This is also characteristic of the behavior of birds of all species; but it is often particularly conspicuous in the case of green honeycreepers in mixed flocks.

It is possible to recognize certain relatively minor subdivisions or subgroups, special associations of a few species, within the larger group of the blue and green tanager and honeycreeper alliance as a whole. These subgroups are not very distinct and never exclusive; but some species, including the green honeycreeper, behave slightly differently in different subgroups.

Different types of subgroups may be recognized by the use of different criteria. Perhaps the most easily distinguished are two subgroups that may be called predominantly tanager flocks and predominantly honeycreeper flocks. The former are largely composed of tanagers, especially plain-colored, palm, and blue tanagers, and include relatively few honeycreepers; while the latter are largely composed of honeycreepers, sometimes accompanied by many warblers (see below), and include relatively few tanagers.

Green honeycreepers differ from the other common honeycreepers of central Panamá in being associated with predominantly tanager flocks almost as frequently as with predominantly honeycreeper flocks.

In predominantly tanager flocks, their most conspicuous social reactions are attempts to join and follow individuals of other species. They seem to be much more strongly attracted to plain-colored tanagers than to any other species of tanager. They join and follow plain-colored tanagers relatively more frequently than they do individuals of any other common species of the blue and green tanager and honeycreeper alliance; and they occur with plain-colored tanagers in mixed flocks of only two species relatively much more frequently than with individuals of any other species of tanager. Their responsiveness to plain-colored tanagers seems to be a special interspecific preference, essentially similar to the corresponding preferences of such species as the palm tanager and the blue tanager.

The vocal patterns of the green honeycreepers may be significant in this connection. They frequently utter sharp call notes and rattling calls that are distinctly different in sound from any of the common vocal patterns of the red-legged blue honeycreeper and the blue dacnis, but very similar to the most common vocal patterns of the plain-colored tanager and the golden-masked tanager. Observation of captive birds would suggest that green honeycreepers are strongly attracted by the sound of the calls and notes of plain-colored tanagers and golden-masked tanagers that are most like their own calls and notes. There is also some evidence that the vocal repertory of the green honeycreeper is rather specialized, more so than the corresponding repertories of the red-legged blue honeycreeper and the blue dacnis.

It is conceivable, therefore, that the vocal repertory of the green honeycreeper has become increasingly similar to those of some *Tangara* tanagers, by convergent evolution, because this similarity facilitates associations with these tanagers, and such associations are usually advantageous to green honeycreepers. If so, this similarity may be considered a form of "social mimicry" (Moynihan, 1960).

(It is possible that green honeycreepers have a slight special interspecific preference for golden-masked tanagers. If so, this preference would be similar to their preference for plain-colored tanagers in quality, but probably much weaker. Under natural conditions green honeycreepers seem to join and follow golden-masked tanagers relatively much less frequently than they join and follow plain-colored tanagers.)

Green honeycreepers perform relatively few aggressive movements, but sometimes utter many aggressive calls in predominantly tanager flocks. This would suggest that they are sometimes motivated by strong aggressive tendencies in such flocks, but that these tendencies are often partly inhibited. It is probable that they find many of their companions in predominantly tanager flocks quite irritating (although presumably less irritating than other members of their own species) and also very intimidating. Most tanagers are as large as, or even larger than, green honeycreepers, and would be expected to be intimidating to the latter.

The reactions of green honeycreepers to other honeycreepers are rather more varied than their reactions to tanagers. They tend to perform many supplanting attacks upon red-legged blue honeycreepers. They may also attempt to join and follow the latter in a "friendly" manner; but such attempts are relatively very rare, and are probably nothing more than expressions of generalized gregariousness.

Green honeycreepers do not usually attack red-legged blue honeycreepers as frequently as they attack other members of their own species; but I have seen them do so in certain special circumstances, when several green honeycreepers and red-legged blue honeycreepers were feeding in the same small tree. The green honeycreepers became particularly aggressive in such circumstances. Their aggressiveness may have been released originally by their proximity to one another; but they seemed to vent this aggressiveness upon one another and upon the red-legged blue honeycreepers quite indiscriminately.

The hostility of green honeycreepers toward red-legged blue honeycreepers might be considered a peculiar form of special interspecific preference, much more limited in scope than the special interspecific

preferences of some species for plain-colored tanagers, but equally strong in its way.

As red-legged blue honeycreepers are the most common birds in predominantly honeycreeper flocks (see below), green honeycreepers tend to perform many more supplanting attacks in such flocks than in predominantly tanager flocks.

We were not able to study the social relations between green honeycreepers and blue dacnises in detail, as the latter were rather rare on Barro Colorado Island, the only area where green honeycreepers were observed with appreciable frequency during the course of the present investigation; but our observations suggest that green honeycreepers react to blue dacnises in a way that is more like their reaction to plain-colored tanagers than their reaction to red-legged blue honeycreepers. We saw green honeycreepers join and follow, or attempt to approach, blue dacnises relatively frequently, but we did not see them supplant them. This latter fact may be particularly significant because blue dacnises are appreciably smaller than green honeycreepers.

The social relations between green honeycreepers and bananaquits are essentially intermittent. Sometimes the former seem to ignore the latter almost completely, but at other times they may attempt to join, follow, and/or supplant them very frequently and persistently. (The probable explanation of this peculiar relationship is discussed below in connection with the social role of bananaquits.)

Green honeycreepers join such birds as plain-colored tanagers and bananaquits quite frequently without beginning to feed immediately afterward, even when they are not obviously very aggressive.

Female green honeycreepers are usually more aggressive than males; and there are some indications that they are associated with mixed flocks slightly less frequently than are males.

It will be noticed that relatively few cases of joining, following, and supplanting by green honeycreepers are included in the accompanying tables. This might convey a somewhat misleading impression, as green honeycreepers do attempt to join, follow, and supplant individuals more frequently than the figures in these tables would suggest. The apparent discrepancy may be explained in several ways. Most of the flocks observed when these counts were made were predominantly tanager flocks, in which green honeycreepers perform fewer overt reactions to individuals of other species than in other types of mixed flocks. Individuals of other species also tend to react to green honeycreepers by attempts at evasion. They often fly away, or at least hop to another branch, when they see a green honeycreeper approaching,

even before the green honeycreeper gets very close. They may have learned that green honeycreepers are often aggressive. In many cases, when an individual of another species retreated before a green honeycreeper in this way, the incident could not be classed as a clear-cut case of either joining or supplanting, according to the criteria used in compiling the accompanying tables.

As a general conclusion, green honeycreepers may be said to have two contradictory effects upon mixed flocks. They may tend to increase the cohesiveness and attractiveness of a mixed flock and/or tend to disrupt the flock. They may produce these effects successively or simultaneously. The disruptive effect of green honeycreepers is not, however, always as strong as might be expected. The increased calling and rapid movements provoked by, or accompanying, supplanted attacks and other aggressive patterns by green honeycreepers may tend to attract other birds in much the same way as do mobbing reactions.

SHINING HONEYCREEPER

Shining honeycreepers were not observed very frequently during the present study. They are common on Barro Colorado Island, but seldom conspicuous around the laboratory clearing. When they were seen, their behavior was more or less reminiscent of green honeycreepers.

Their social behavior apart from mixed species flocks in central Panamá seems to be quite remarkably similar to that of green honeycreepers. Shining honeycreepers have much the same range and types of display patterns [9] as green honeycreepers, and also tend to be very aggressive, and therefore only very slightly gregarious among themselves.[10]

In mixed flocks, however, the social role of shining honeycreepers seems to be less important than that of green honeycreepers. Shining honeycreepers do tend to join and follow individuals of other species, at least occasionally, but they do so relatively much less frequently than do green honeycreepers. All or most of their interspecific joining and following reactions seem to be expressions of generalized gregariousness. As far as I could tell, they do not have the special inter-

[9] The term "display" will be used throughout this paper to include all vocal patterns and all movements and postures that appear to have become specialized to subserve a signal function.

[10] Slud (1960) says that shining honeycreepers are rather strongly gregarious among themselves in part of Costa Rica; but this is definitely not true of the shining honeycreepers of central Panamá.

specific preference for plain-colored tanagers which is such a conspicuous feature of the behavior of such species as the palm tanager and the green honeycreeper. Shining honeycreepers join predominantly honeycreeper flocks much more frequently than predominantly tanager flocks.

The only birds of other species that tend to provoke unusually strong reactions from shining honeycreepers are red-legged blue honeycreepers, which they tend to supplant quite frequently, much more frequently than they supplant individuals of any other species and almost as frequently as they supplant one another. I have also seen captive female shining honeycreepers (which were in cages with males of their own species) react to wild male red-legged blue honeycreepers outside their cages in almost exactly the same way that they would react to strange males of their own species at comparable distances, i.e., they performed several displays that were largely hostile but also contained nonhostile (presumably sexual) components. It is possible, therefore, that shining honeycreepers tend to regard red-legged blue honeycreepers as nothing more than slightly subnormal or suboptimal members of their own species.

Individuals of other species seldom react very strongly to shining honeycreepers, but when they do it is almost or exactly the same way that they react to red-legged blue honeycreepers (see below). Unfortunately, I saw very few encounters between shining honeycreepers and green honeycreepers. Green honeycreepers may tend to be as aggressive toward shining honeycreepers as they are toward red-legged blue honeycreepers, but this needs to be confirmed by further observations.

RED-LEGGED BLUE HONEYCREEPER

Red-legged blue honeycreepers are highly gregarious among themselves, in much the same way as plain-colored tanagers. They also resemble plain-colored tanagers in being very restless and noisy. It might be expected, therefore, that their role in mixed flocks would be equally similar to that of plain-colored tanagers. This is not quite the case, however. Red-legged blue honeycreepers behave very much like plain-colored tanagers in mixed flocks, but their behavior does not usually produce results that are very similar to the results of the behavior of plain-colored tanagers.

Red-legged blue honeycreepers occur in mixed flocks very frequently. They occur in all types of mixed blue and green tanager and honeycreeper flocks. They are usually much more numerous than

individuals of any other species in predominantly honeycreeper flocks.

This may be illustrated by the figures in table 44, which is based upon observations of birds in two large flowering trees in the clearing on Barro Colorado Island between December 19 and December 23, 1959. During this period these trees were visited by individuals of many species of the blue and green tanager and honeycreeper alliance, separately and/or in mixed flocks. Almost all the mixed flocks seen during this particular series of observations were predominantly

TABLE 44.—*Data from observations on Barro Colorado Island between December 19 and 23, 1959*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks (predominantly honeycreeper flocks) and apart from mixed flocks.

Species	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	44 (92)	4	48
Palm tanagers	19 (70)	8	27
Blue tanagers	17 (65)	9	26
Green honeycreepers	20 (59)	14	34
Red-legged blue honeycreepers	175 (68)	82	257
Blue dacnises	42 (74)	15	57
Summer tanagers	59 (71)	24	83
Bananaquits	18 (32)	39	57

honeycreeper flocks. The figures in the table indicate the number of times individuals of the species most commonly seen during these observations were seen in mixed flocks and not in mixed flocks. These figures were compiled and are arranged in the same way as the corresponding figures in tables 1, 20, 28, and 35.

(The results of this series of observations are not included with the results of the other observations on Barro Colorado Island summarized in tables 1-19.)

Red-legged blue honeycreepers usually tend to ignore all or most of their associates in mixed flocks. They join, follow, and supplant individuals of other species comparatively rarely. They are joined, fol-

lowed, and supplanted by individuals of other species more frequently than they themselves join, follow, and supplant; but they are joined and followed relatively much less frequently than are plain-colored tanagers, and are also relatively much less common than plain-colored tanagers in obviously tightly integrated mixed flocks and in flocks composed of only two species. They do not seem to be particularly attractive to any species of tanager. With the possible exception of blue dacnises (see below), no other honeycreepers seem to behave as if they had a strong "friendly" interspecific preference for red-legged blue honeycreepers under natural conditions. I have never seen a female shining honeycreeper react to a male red-legged blue honeycreeper as a potential mate under natural conditions.

It is obvious, nevertheless, that the noisiness and rapid movements of red-legged blue honeycreepers greatly increase the conspicuousness of the mixed flocks in which they occur and probably, therefore, increase the attractiveness of such flocks to many birds of many species. It is my impression that mixed flocks that include red-legged blue honeycreepers tend to attract more birds of other species than otherwise identical flocks that do not include red-legged blue honeycreepers. In particular, migrant warblers of many species seem to be more likely to join mixed flocks that include red-legged blue honeycreepers than all or most other mixed flocks in the same environments. I am not sure of the precise social relationships between most of these warblers and red-legged blue honeycreepers. It seems unlikely that any of these warblers have any special interspecific preference for red-legged blue honeycreepers.

Red-legged blue honeycreepers may attract individuals of many other species as frequently as is possible by stimulating generalized gregariousness alone. Their social role in many mixed flocks is probably very similar to what the social role of plain-colored tanagers would be if plain-colored tanagers did not stimulate the "friendly" special interspecific preferences of some other species so strongly.

The fact that red-legged blue honeycreepers do not evoke as many nonhostile interspecific preferences as plain-colored tanagers may be due largely to the distinctive nature of some of their most common vocal patterns, which are quite different from the corresponding patterns of any other species of the blue and green tanager and honeycreeper alliance in central Panamá, and the bright and intricately patterned nuptial plumage of the males. Such characters are presumably advantageous because they help to maintain the reproductive isolation of the species. They may also tend to promote other types of social isolation as well.

It is possible that red-legged blue honeycreepers have begun to evolve certain characters to increase their attractiveness to other species. This might be one of the functions of the dull "eclipse" plumage of the males during the nonbreeding season. The males of other species of honeycreepers do not have eclipse plumages, and that of male red-legged blue honeycreepers is really quite remarkably similar to the year-round plumages of both male and female plain-colored tanagers and palm tanagers (and the eclipse plumage of male scarlet tanagers, *Piranga olivacea*).[11]

Male red-legged blue honeycreepers show more intraspecific gregariousness than do females; and they also seem to occur in mixed flocks relatively more frequently than do females.

BLUE DACNIS

Blue dacnises were not very common in any of the areas where mixed blue and green tanager and honeycreeper flocks were studied; but they appeared to contribute appreciably to the cohesion of mixed flocks, at least predominantly honeycreeper flocks, whenever they occurred in such flocks. They seemed to join and follow individuals of other species (especially red-legged blue honeycreepers) relatively frequently; and they were also joined and followed by individuals of other species (especially green honeycreepers) relatively frequently.

CRIMSON-BACKED TANAGER

All the species discussed above (with the possible or probable exception of the shining honeycreeper) may be considered regular members of mixed blue and green tanager and honeycreeper flocks. They are regular in the sense that they tend to associate with one another whenever a suitable opportunity to do so occurs, at least during the nonbreeding season. Each of these species usually approaches, or is approached by, at least one of the other species whenever they encounter one another during the nonbreeding season. Individuals of these species usually prefer to associate with individuals of other species of the group even when they have a wide choice of alternatives, i.e., when it would be just as easy for them to associate with individuals of species of other groups that have more or less similar insectivorous and/or frugivorous habits.

[11] The scarlet tanager is also the only species of its genus that has a complete eclipse plumage. It would be interesting to know if scarlet tanagers associate with mixed flocks in their winter quarters in the Tropics, and, if so, in what capacity.

The crimson-backed tanager is not quite a regular member of the mixed blue and green tanager and honeycreeper flocks in this sense.

Crimson-backed tanagers do occur in mixed flocks with blue and green tanagers and honeycreepers—so frequently, in fact, that they may be considered members of the blue and green tanager and honeycreeper alliance (see definition above). They also join, follow, and/or supplant regular members of the blue and green tanager and honeycreeper flocks occasionally, and are occasionally joined, followed, and/or supplanted by regular members of these flocks. Such clear-cut reactions are relatively rare, however. Crimson-backed tanagers are usually joined and followed by other members of the blue and green tanager and honeycreeper alliance even less frequently than are red-legged blue honeycreepers in similar social situations. Crimson-backed tanagers often appear to be purely casual associates of mixed blue and green tanager and honeycreeper flocks, keeping some distance away from all or most of the other members of such flocks, and frequently moving in different directions from the other members of the flocks. Even more significantly, crimson-backed tanagers also prefer to associate with some other species that are not members of the blue and green tanager and honeycreeper alliance (see below).

The fact that both the plumage and the most common notes of crimson-backed tanagers (see above) are very conspicuously different from the corresponding characters of any regular member of the blue and green tanager and honeycreeper flocks is probably a definite hindrance to more frequent and closer associations between crimson-backed tanagers and most other members of the blue and green tanager and honeycreeper alliance. Crimson-backed tanagers must stimulate the generalized gregariousness of many or all the other members of this alliance; but they probably do so less strongly than they would if their appearance and notes were less distinctive.

It is also possible, since crimson-backed tanagers are comparatively large birds, that they tend to alarm the smaller blue and green tanagers and honeycreepers rather strongly.

There is no evidence, however, that any of the other members of the blue and green tanager and honeycreeper alliance have developed a definite aversion to crimson-backed tanagers, as they seem to have to some related species (see below).

Blue tanagers tend to associate with crimson-backed tanagers somewhat more frequently and/or more closely than do all or most of the other members of the blue and green tanager and honeycreeper alliance. This may be due to the fact that blue tanagers and crimson-

backed tanagers have rather similar habitat preferences. Both species occur in young second-growth forest and scrub relatively more frequently than do such species as the plain-colored tanager, the palm tanager, the green honeycreeper, and the *Cyanerpes* honeycreepers.

Crimson-backed tanagers are usually very noisy and often travel in family groups or small flocks of several family groups. Mixed flocks that include crimson-backed tanagers are particularly conspicuous and tend to attract a wide variety of birds of other species not usually associated with such flocks. The other species attracted by crimson-backed tanagers are not usually the same as those attracted by red-legged blue honeycreepers. Crimson-backed tanagers seem to be especially attractive to several orioles and flycatchers.

SUMMER TANAGER

The social role of summer tanagers in mixed blue and green tanager and honeycreeper flocks is very different from the corresponding roles of any other tanagers or honeycreepers. In Panamá summer tanagers seldom associate with one another. It is relatively rare to see more than a single summer tanager in any given area at any given time.

These single summer tanagers become associated with mixed species flocks relatively frequently. They are probably associated with all types of blue and green tanager and honeycreeper flocks and with several other types of mixed flocks almost equally frequently (see below). They seem to discriminate between different types of mixed species flocks only insofar as they prefer flocks that inhabit the edges of forest or scrub and include some insectivorous or partly insectivorous species. They are largely insectivorous themselves in lowland Panamá, and are most common along the edges of forest and scrub.

Summer tanagers are seldom very conspicuous in mixed flocks. They are usually silent as long as they are associated with individuals of other species, and tend to remain on the outskirts of mixed flocks. While they are associated with mixed blue and green tanager and honeycreeper flocks, they are sometimes joined and followed by individuals of other species, especially such species as the green honeycreeper and the palm tanager which have particularly strong joining and following tendencies; but it is my impression that they usually become associated with such flocks in the first place because they themselves join the flocks.

The usual role of summer tanagers in mixed blue and green tanager and honeycreeper flocks is reminiscent of the roles of many furnariids (or dendrocolaptids) in other types of mixed flocks (see below).

Summer tanagers seem to be more nearly parasitic on their companions in mixed blue and green tanager and honeycreeper flocks than are any other birds commonly associated with such flocks.

BANANAQUIT

Bananaquits may play a rather important role in mixed flocks—but only occasionally. They are often rather silent and inconspicuous. At such times, they may occur in mixed blue and green tanager and honeycreeper flocks without having much effect upon their companions in the flocks. They may join and follow individuals of other species, or be joined, followed, and supplanted by individuals of other species; but such reactions are not usually very common.

During the breeding season, however, male bananaquits sing very frequently, and territorial bananaquits (apparently of both sexes) often engage in prolonged and noisy disputes. When bananaquits are noisy, they are joined, followed, and supplanted by individuals of other species much more frequently than when they are silent. They are particularly likely to be joined, followed, and supplanted by green honeycreepers.

It is not very clear why green honeycreepers should react so vigorously to bananaquits at times, as bananaquits do not resemble green honeycreepers in appearance or voice. The explanation may be simply that green honeycreepers react strongly to individuals of any other species that are conspicuous, and feel free to approach bananaquits because the latter are so much smaller than they are. Interestingly enough, bananaquits do not seem to have evolved any special characters for the primary purpose of either encouraging or discouraging green honeycreepers. It is possible that most bananaquits do not encounter green honeycreepers very frequently. Individuals of the two species encounter one another fairly frequently in such environments as the clearing on Barro Colorado Island; but bananaquits are also very common in certain types of second-growth vegetation in which green honeycreepers are rare or absent. Or perhaps the two species have come into contact with one another only relatively recently.

Associations between bananaquits and green honeycreepers are very seldom long sustained. This may be largely due to the fact that noisy bananaquits tend to stop vocalizing when approached by green honeycreepers.

There were some indications that some or all of the bananaquits on Barro Colorado Island tended to join and follow green honey-

creepers more frequently than they joined and followed individuals of any other species of the blue and green tanager and honeycreeper alliance. This may have been the result of conditioning. These particular bananaquits may have become used to green honeycreepers simply because they were approached by the latter so frequently.

OTHER SPECIES

There is comparatively little to be said about the other species sometimes associated with mixed blue and green tanager and honeycreeper flocks. Some of them were rather rare in the areas where these flocks were studied. None of them appears to play a very significant role in any appreciable number of blue and green tanager and honeycreeper flocks, although some of them are very important in other types of mixed flocks (see below).

The streaked saltator and the yellow warbler may be cited as examples of rather common species that have very weak generalized gregarious tendencies and/or whose generalized gregarious tendencies are usually very weakly stimulated by members of the blue and green tanager and honeycreeper alliance. The differences between the frequencies of interspecific social reactions by streaked saltators and yellow warblers and by the other species cited in the accompanying tables may be taken as a rough measure of the extent to which the latter species have become important social factors in the blue and green tanager and honeycreeper alliance.

PARTIAL SUMMARY

Many mixed blue and green tanager and honeycreeper flocks are rather complex societies. Each of the more common species of the alliance tends to play a characteristic social role, more or less distinctly different from that of every other species in the mixed flocks of the alliance. These roles are the results of complex interactions between each species and at least one (usually several) other species. Several of the species tend to react differently to each of several other species. Most of the more common species have also evolved special adaptations, of plumage and/or behavior, to facilitate the performance of their characteristic roles in mixed flocks.

The most remarkable and apparently specialized social bonds between different species in mixed blue and green tanager and honeycreeper flocks are the special interspecific preferences.

Diagrams 1 and 2 are tentative summaries of the interspecific pref-

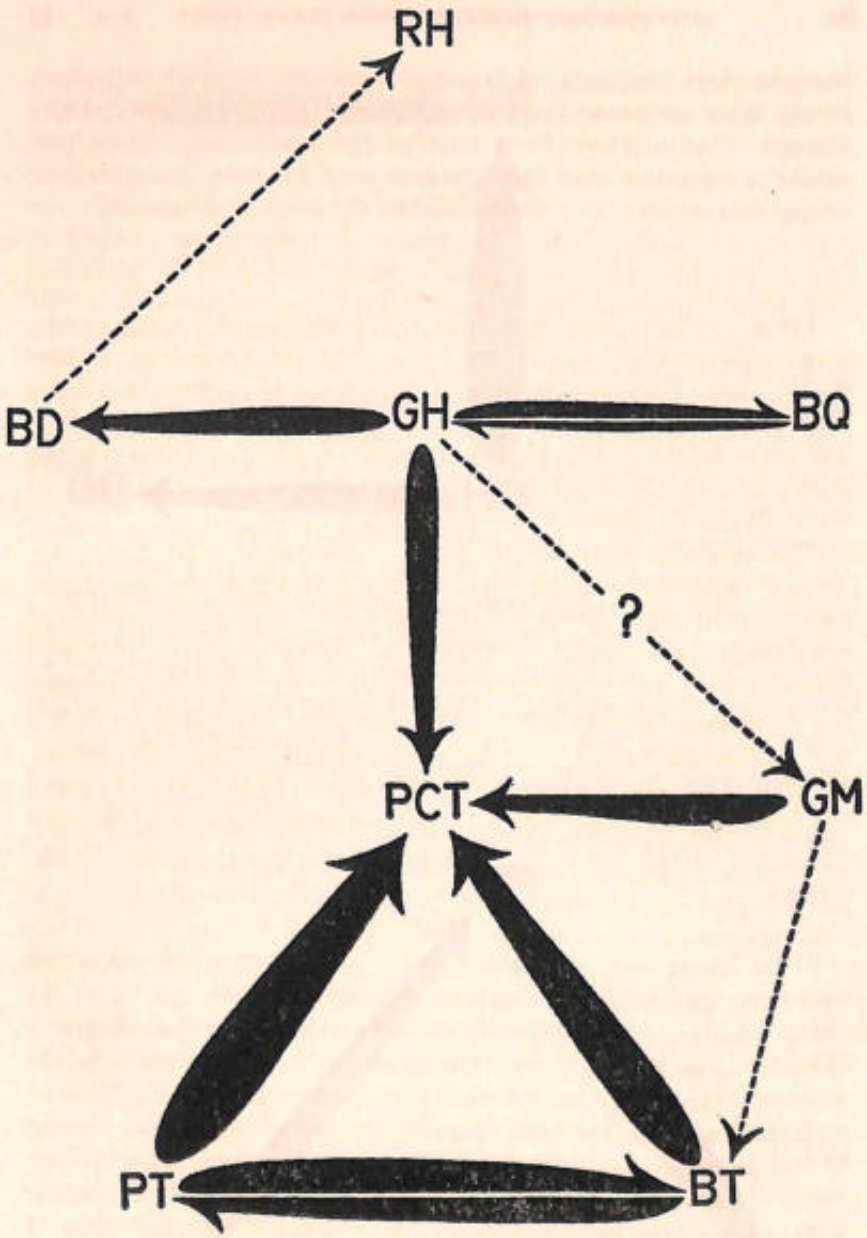

DIAGRAM 1.—The special interspecific preferences of the most commonly observed species of the blue and green tanager and honeycreeper alliance revealed by predominantly "friendly" joining and following reactions.

The species are identified by initials. RH = red-legged blue honeycreeper. BD = blue dacnis. GH = green honeycreeper. BQ = bananaquit. PCT = plain-colored tanager. GM = golden-masked tanager. PT = palm tanager. BT = blue tanager.

The arrows point from the species exhibiting a special interspecific preference to the species that is the object of this preference. The width of the arrows is roughly proportional to the apparent strength of the preferences.

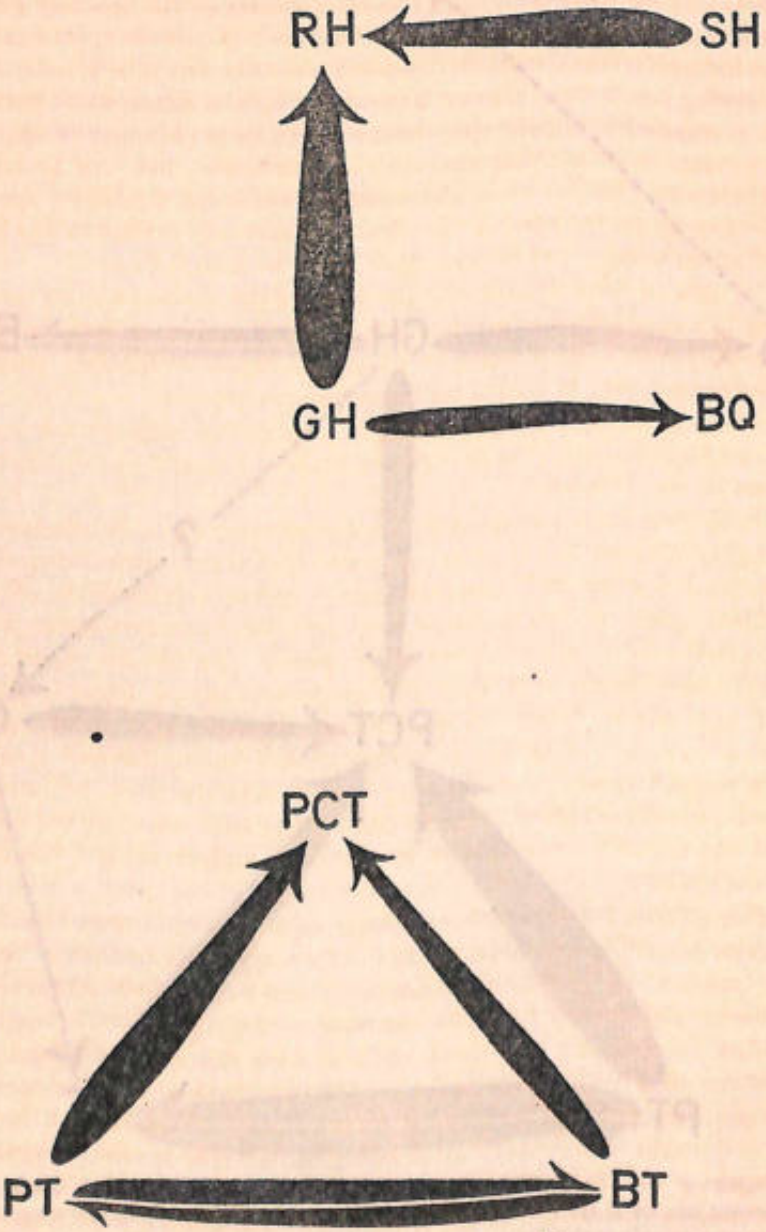

DIAGRAM 2.—The special interspecific preferences of the most commonly observed species of the blue and green tanager and honeycreeper alliance revealed by supplanting attacks and other predominantly aggressive reactions. Organized in the same way as diagram 1.

The species are identified by the same initials as in diagram 1, with one addition: SH = shining honeycreeper.

erences of the most commonly observed species of the blue and green tanager and honeycreeper alliance. Diagram 1 shows the special interspecific preferences revealed by predominantly friendly joining and following reactions. Diagram 2 shows the special interspecific preferences revealed by supplanting attacks and other predominantly aggressive reactions. Both diagrams may be incomplete; but they probably include all or almost all of the strongest and most significant special interspecific preferences of the regular members of typical mixed blue and green tanager and honeycreeper flocks in central Panamá.

In spite of their distinctness, the roles of the various species occurring in mixed blue and green tanager and honeycreeper flocks may be classified into a small number of rather broad categories. Such a classification may be useful for comparative purposes.

There have been several previous attempts to classify the social roles of species occurring in different types of mixed flocks in different areas of the Tropics.

In his first paper on mixed flocks of Rhodesian birds, Winterbottom (1943), divided the species of such flocks into two categories: "nucleus" species and "circumference" species. Individuals of the nucleus species always occurred in groups, by themselves alone, or in association with individuals of other species. Individuals of the circumference species were not highly gregarious among themselves, but did join mixed flocks. Winterbottom suggested that most mixed flocks were formed by circumference species joining nucleus species. The terms themselves would suggest that individuals of the nucleus species usually occurred at the front and/or the center of mixed flocks and the circumference species at the sides and/or toward the rear of the flocks.

Davis (1946) classified the species of mixed flocks in some Brazilian forests according to several criteria. His main categories were "regular" species and "accidental" species. These were defined as follows: "The regular species stay with the flock for long periods of time, are seldom seen away from the flock, and have the calls and behavior patterns of a flocking species. . . . The accidentals associate merely temporarily with the group as it moves along. These species do not have the calls and behavior of flocking birds." Davis also recognized categories of "migrants," species that "are present for either the breeding or the nonbreeding period," and "nomads," species that "are irregular in occurrence and vary greatly in numbers."

In a later paper, Winterbottom (1949) attempted to combine Davis's classification with his own earlier classification, and suggested

the following four main categories: (1) "nucleus" species, (2) other "regular" species, (3) "regular accidental" species, and (4) "accidental" species. He also suggested that a fifth category might be recognized: "accidental nucleus" species.

This last scheme can be used as the basis for a classification of the roles of different species in mixed blue and green tanager and honeycreeper flocks; but it needs to be revised in several ways for this purpose. The criteria for distinguishing the various categories may also be defined in more strictly behavioral terms in order to eliminate the factors that are essentially extrinsic to the mixed flocks.

An initial distinction may be made between "nuclear" and "attendant" species. Nuclear species can be defined as species whose behavior contributes appreciably to stimulate the formation and/or maintain the cohesion of mixed flocks. Individuals of such species approach individuals of other species relatively frequently and/or behave in such a way that they are particularly attractive to individuals of other species. In any case, they contribute something more than their mere presence. Nuclear species, in this sense, may or may not be regular members of the mixed flocks in which they are sometimes nuclear. They may also occur at any place in mixed flocks. Some nuclear species usually occur at the front and/or center of mixed flocks but others do not. Attendant species do much less to stimulate the formation and/or maintain the cohesion of mixed flocks. They contribute little or nothing except their presence.

Nuclear species can be divided into two main types, which may be called "active" and "passive." These may be defined as follows. Individuals of active nuclear species usually join and/or follow individuals of other species much more often than they are joined and/or followed by individuals of other species. (Many or most of the species called "other regular species" by Winterbottom would probably be classified as active nuclear species according to this definition.) Individuals of passive nuclear species are usually joined and/or followed by individuals of other species much more often than they join and/or follow individuals of other species. (All or most of Winterbottom's "nucleus" species would probably be classified as passive nuclear species according to this definition.)

It may also be convenient to divide the species occurring in any particular type of mixed flock into "regular" and "occasional" members of such flocks. The characteristics of regular members have already been mentioned. Regular members of a particular type of mixed flock usually or always approach and/or are approached by one or more of

the other species commonly occurring in that type of mixed flock whenever a suitable opportunity occurs (at least during the nonbreeding season). Occasional members of a particular type of mixed flock frequently, perhaps usually, do not approach and/or are not approached by the other species commonly occurring in that type of mixed flock when opportunities to do so occur (even during the nonbreeding season). Thus, a rare species that is a regular member of a certain type of mixed flock may actually occur in flocks of that type less frequently than a common species that is an occasional member, if the common species has many more opportunities to become associated with mixed flocks of that particular type. The term "occasional," in this sense, is probably largely synonymous with the term "accidental," as used by Davis and Winterbottom. The latter term is not used in this paper because it might convey a misleading impression. The associations between occasional members of mixed flocks and their companions in such flocks are not really fortuitous, or accidental, in the ordinary sense of the word.

The characters used to define the categories listed above are essentially relative. It is perfectly conceivable that some species might play intermediate roles in certain types of mixed flocks. This may be true of some of the species of montane bush flocks (see below). The roles of most species in mixed blue and green tanager and honeycreeper flocks, however, are so clear-cut and one-sided that they can be assigned to particular categories without any difficulty. It is possible, therefore, to summarize the roles of the various species in mixed blue and green tanager and honeycreeper flocks as follows:

The plain-colored tanager is always a regular and passive nuclear species. The red-legged blue honeycreeper is always regular and nuclear and probably always passive.

The blue tanager and the green honeycreeper are always regular and active nuclear species. The golden-masked tanager is probably similar. The shining honeycreeper may be a regular or an occasional active nuclear species.

The palm tanager is always an active nuclear species and always regular except in some environments in the breeding season.

The bananaquit is always regular. Sometimes it is a passive nuclear species. At other times it is an attendant species.

The summer tanager is always an attendant, and usually or always occasional.

The role of the crimson-backed tanager is more obviously complicated than those of all or most of the other species. It is a very

common occasional member of mixed blue and green tanager and honeycreeper flocks, and attendant in relation to the regular members of such flocks. While it is associated with mixed blue and green tanager and honeycreeper flocks, however, it sometimes functions as a passive nuclear species for other occasional members of the flocks.

The blue dacnis is apparently always nuclear and regular. It has not been observed frequently enough to determine if it is a passive nuclear and/or an active nuclear species.

Most of the remaining species are probably occasional attendant species in mixed blue and green tanager and honeycreeper flocks. Some of them are nuclear, or regular attendants, in other types of mixed flocks; but their roles in such flocks do not seem to affect their roles in the blue and green tanager and honeycreeper flocks.

DIFFERENT TYPES OF MIXED FLOCKS

The frequencies with which blue and green tanager and honeycreeper flocks are formed, and the degree of integration within such flocks, are obviously different in different environments and in the same environment at different times. This may be due partly to the fact that different species are dominant in different environments and/or in the same environment at different times. It was not possible to study this aspect of flock behavior in detail; but some of the figures in the accompanying tables may help to illustrate some of the variations that can occur.

Individuals of most species were seen in mixed flocks most frequently near Gamboa and near Frijoles in July and August of 1960, when blue tanagers were the most common of the tanagers and honeycreepers. Individuals of most species were seen in mixed flocks least frequently near Frijoles between November 1959 and January 1960, when crimson-backed tanagers were the most common of the tanagers and honeycreepers. Relatively more birds were seen in tightly integrated flocks around the clearing on Barro Colorado Island, where plain-colored tanagers were dominant, than in any of the other areas.

It seems likely that most of the birds of the blue and green tanager and honeycreeper alliance around the clearing on Barro Colorado Island were very much habituated to one another. They were confined to a relatively small area, separated from the nearest similar areas by large expanses of heavy forest and/or the waters of Gatún Lake, and tended to encounter one another again and again.

Environments like the clearing on Barro Colorado Island are rare in central Panamá now, as most of the heavy forests of this region

have been cut down; but they must have been relatively much more common before the region acquired a dense human population. It is possible that isolated clearings in heavy forest were the most important habitat of mixed blue and green tanager and honeycreeper flocks before human interference became appreciable. Many of the social behavior patterns of many species of the blue and green tanager and honeycreeper alliance may have been evolved originally as adaptations to life in mixed flocks that were more like the flocks observed on Barro Colorado Island than any of the other flocks observed in the course of the present study.

THE MONTANE BUSH FLOCKS

Montane bush flocks are much less widely distributed in Panamá than mixed blue and green tanager and honeycreeper flocks. The montane bush flocks that were studied most intensively during the present investigation are characteristic of the hills and mountains of western Panamá and seldom or never occur below 3,000 feet above sea level.

These flocks were studied on the western slopes of the Volcán de Chiriquí (El Baru), between approximately 4,500 feet and 7,500 feet above sea level (from the town of El Volcán to elevations well above the town of Cerro Punta), during four short periods of observation: between September 17 and September 21, 1958; between March 2 and March 9, 1959; between March 19 and March 30, 1960; and between October 3 and October 10, 1960. Special attention was paid to the flocks at higher altitudes, above 6,000 feet.

All or most of the upper slopes of the Volcán de Chiriquí must have been covered by heavy montane forest at one time. Much of the forest of the western slopes has been cut down within fairly recent years, but large patches remain, especially above 6,000 feet. Second-growth forest and scrub are also found in many areas. Most of the observations of mixed flocks were made along the edges of forest and scrub.

Many of the birds commonly occurring in mixed bush flocks in this region were performing reproductive behavior patterns in March; but all or most of them appeared to be in the middle of the nonbreeding season in September and October.

THE MOST COMMON SPECIES

It may be useful to describe the appearance of the most common species of the montane bush alliances in western Panamá and summarize the most distinctive features of their social behavior apart from

mixed flocks, in much the same way as was done for the most common species of the blue and green tanager and honeycreeper alliance.

Brown-capped Bush-tanager (*Chlorospingus ophthalmicus*).—A comparatively small tanager. Sexes nearly identical in plumage: largely olive above and yellow below, with brown head, conspicuous triangular white patches behind eyes, white under wings (very conspicuous in flight), and grayish-buffy throat.

Resident in Panamá. Common along the edges of forest and scrub over a wide range of altitudes, both in the treetops and in very low vegetation.

Very gregarious apart from mixed species flocks. Very restless and active. Very noisy; frequently uttering loud and sharp *tsit* call notes and mechanical-sounding rattles.

Sooty-capped Bush-tanager (*Chlorospingus pileatus*).—Very similar to the brown-capped bush-tanager in general appearance, but head largely blackish, with white postocular stripes and whitish throat.

Resident in Panamá. Usually at slightly higher altitudes than the brown-capped bush-tanager. Common along the edges of forest and scrub.

Not very gregarious apart from mixed species flocks. Similar to the brown-capped bush-tanager in voice, and almost equally active and restless.

Black-cheeked Warbler (*Basileuterus melanogenys*).—A very tanagerlike warbler. Reminiscent of *Chlorospingus* in shape. Sexes nearly identical in appearance: generally olive above and whitish below, with black cheeks, white superciliary stripes, black stripes above white superciliaries, and chestnut crown.

Resident in Panamá. Common along the edges of forest and scrub, at fairly high altitudes. Usually rather low in vegetation.

Not very gregarious apart from mixed species flocks. Very active and restless. Sometimes, but not always, very noisy.

Yellow-thighed Finch (*Pselliophorus tibialis*).—A rather large finch. Sexes nearly identical in plumage: largely blackish, with bright yellow thighs.

Resident in Panamá. Common along the edges of forest and scrub over a rather wide range of altitudes. Usually occurring relatively low in vegetation.

Not very gregarious apart from mixed species flocks. Very restless and active. Very noisy; frequently uttering twittering phrases.

Yellow-throated Bush-finch (*Atlapetes gutturalis*).—A rather large finch. Sexes nearly identical in plumage: largely black above and white below, with yellow throat and white crown stripe.

Resident in Panamá. Common along the edges of forest and scrub over a very wide range of altitudes. Usually occurring relatively low in vegetation.

Not very gregarious apart from mixed species flocks. Moderately active. Usually very quiet.

Miscellaneous Furnariidae.—Various species of furnariids, e.g., the ruddy tree-runner (*Margarornis rubiginosus*), the buff-fronted foliage-gleaner (*Philydor rufus*), and the red-faced spinetail (*Cranioleuca erythrops*) are more or less frequently associated with montane bush flocks.

All these species are somewhat similar in appearance, insofar as they all have rufous wings and tails. They are all resident in Panamá, and only very slightly gregarious apart from mixed species flocks.

Silver-throated Tanager (*Tangara icterocephala*).—A comparatively small tanager. Sexes nearly identical in plumage: largely golden yellow, with a whitish throat and black and green stripes on the back.

Resident in Panamá. Common along the edges of forest and scrub over a wide range of altitudes. Frequently occurring in treetops.

Not very gregarious apart from mixed species flocks. Very restless and active. Very noisy; frequently uttering very distinctive buzzy call notes.

Wilson's Warbler (*Wilsonia pusilla*).—A small, chunky warbler. Sexes slightly different in appearance. Male generally yellowish, with conspicuous black crown. Female without black crown.

Migrant. In Panamá from September to March (approximately). Widely distributed over a wide range of altitudes in Panamá. Common both in the treetops and in low scrub.

Almost completely nongregarious apart from mixed species flocks in Panamá. Active and noisy, frequently uttering loud "Tsit" call notes.

Slate-throated Redstart (*Myioborus miniatus*).—A flycatcherlike warbler. Sexes nearly identical in appearance: largely black above and yellow below, cheeks and throat blackish, chestnut on crown, and white tips on tail feathers.

Resident in Panamá. Common along the edges of forest and scrub over a wide range of altitudes. Occurs in almost all levels of vegetation.

Not very gregarious apart from mixed species flocks. Very active and restless. Not very noisy.

Collared Redstart (*Myioborus torquatus*).—Similar to the slate-

throated redstart in appearance, but with yellow cheeks and chin and a black breast band.

Resident in Panamá. Common along the edges of forest and scrub. Most common at slightly higher altitude than those at which the slate-throated redstart is most common. Occurs in all levels of vegetation.

Moderately gregarious apart from mixed species flocks. Very active and restless. Not very noisy.

Several other species are certainly associated with montane bush flocks at least moderately frequently. Among these are the summer tanager, the speckled tanager (*Tangara chrysophrys*), the golden-crowned warbler (*Basileuterus culicivorus*), the flame-throated warbler (*Vermivora gutturalis*), the brown-capped vireo (*Vireo leucophrys*), the blue-throated toucanet (*Aulacorhynchus caeruleogularis*), the pale-vented thrush (*Turdus obsoletus*), and various tyrannid flycatchers. Some of these species may play important roles in some montane bush flocks (see below); but they were either relatively rare in the areas where mixed montane bush flocks were studied most intensively and/or are associated with mixed montane bush flocks much less regularly or less closely than such species as the *Chlorospingus* tanagers and the yellow-thighed finch.

DESCRIPTION OF THE FLOCKS

The general social organization of most mixed montane bush flocks is similar to that of most blue and green tanager and honeycreeper flocks in the lowlands, but by no means absolutely identical.

Mixed montane bush flocks are more varied than blue and green tanager and honeycreeper flocks. They include different species at different altitudes. Some species of the montane bush alliances seem to be confined to a rather narrow range of altitudes. Other species occur over a wider range of altitudes but are not equally common throughout their ranges.

At relatively low altitudes, i.e., around 4,500-5,200 feet on the western slopes of the Volcán de Chiriquí, the montane bush flocks tend to include more species than the corresponding flocks at higher altitudes, and are rather distinctive in some other ways. These comparatively low-altitude flocks will be discussed below, after the discussion of the higher-altitude flocks.

The brown-capped bush-tanager, the yellow-thighed finch, the slate-throated redstart, various furnariids, and (sometimes) Wilson's warbler are usually the most conspicuous species in mixed bush flocks from approximately 5,200 to 6,800 feet on the western slopes of the

Volcán de Chiriquí. Above approximately 6,800 feet the brown-capped bush-tanager is more or less abruptly replaced by the sooty-capped bush-tanager, and the collared redstart becomes more common than the slate-throated redstart. In spite of their different compositions, most of the higher-altitude flocks, both above and below 6,800 feet, are essentially very similar in structure.

They are usually comparatively stable, more so than most mixed blue and green tanager and honeycreeper flocks. Individuals of all the species occurring in these montane bush flocks do tend to join and leave one another frequently, or are joined and left by one another frequently; but there are indications that individuals of some of these species tend to remain together with individuals of other species continuously for longer periods of time, on the average, than do individuals of any of the species of the blue and green tanager and honeycreeper alliance. Some of the higher-altitude mixed montane bush flocks are also long sustained as groups in spite of the fact that the individual birds in such flocks may change from time to time. This may be clarified by an example. A pair of birds of a strongly territorial species may remain associated with a mixed montane bush flock as long as the flock remains within the pair's territory and then drop out of the flock when the flock moves on; but this pair's place in the flock may be taken, immediately, by another pair of the same species, so that the specific composition of the flock is not changed by the change of individual birds.

The comparative stability of the higher-altitude mixed montane bush flocks seems to be correlated with certain other distinctive features of social behavior within such flocks. Interspecific joining and following reactions are comparatively common, more so than in all or most mixed blue and green tanager and honeycreeper flocks, while interspecific supplanting attacks are comparatively rare, much less common than in all or most mixed blue and green tanager and honeycreeper flocks.

The frequencies of some interspecific reactions in some higher-altitude montane bush flocks may be illustrated by the figures in table 45. These figures are counts of the number of times individuals of certain species were seen to be involved in interspecific joining, following, and supplanting reactions in higher-altitude montane bush flocks during approximately 25 hours of intermittent observations between October 4 and October 10, 1960, on the Volcán de Chiriquí. The method of observation used was the same as in the counts of reactions in mixed blue and green tanager and honeycreeper flocks, except that each in-

dividual montane bush flock was usually watched continuously for a considerable length of time (usually 15 minutes to 1 hour). In compiling table 45, a bird was considered to have joined another (or several others) when it approached within 10 feet of another, or others, without continuing to move after the others, and without forcing the others to move away. The joined birds were usually more or less stationary before being joined. A bird was considered to be following another (or others) when it hopped or flew steadily after the others, while the others were moving themselves.[12] Supplanting attacks were recognized by the same criteria as in the counts of similar reactions in mixed blue and green tanager and honeycreeper flocks.

TABLE 45.—*Interspecific following, joining, and supplanting reactions involving some species of the montane bush alliances in some higher-altitude mixed flocks observed between October 4 and 10, 1960*

	No. of times individuals seen in mixed flocks	No. of flocks in which seen	No. of times seen following other species	No. of times seen joining other species	No. of times seen being followed by other species	No. of times seen being joined by other species	No. of times seen supplanting other species	No. of times seen being supplanted by other species
Brown-capped bush-tanager	37	11	3	2	18	19	0	1
Yellow-thighed finch	33	16	22	7	10	6	0	0
Red-faced spinetail	4	2	10	12	1	0	0	0
Silver-throated tanager	15	7	0	2	0	0	1	3
Wilson's warbler	31	31	15	7	3	0	0	1
Collared redstart	16	10	3	9	6	0	0	0

Table 45 is a list of all the interspecific joining, following, and supplanting reactions observed, including ambiguous cases when one bird joined or followed a group composed of individuals of several other species. The figures in this table are not strictly comparable with the counts of interspecific reactions in mixed blue and green tanager and honeycreeper flocks shown in the preceding tables. The reactions of each species are listed separately in the table, without attempting to identify the other species involved in any given reaction.

Many of the higher-altitude mixed montane bush flocks seem to be formed in much the same way as all or most mixed blue and green tanager and honeycreeper flocks (but see also comments below). Like

[12] All the joining and following reactions cited in the subsequent discussion of the usual social roles of different species in mixed montane bush flocks were distinguished by the same criteria as in this count.

the mixed blue and green tanager and honeycreeper flocks, they seem to be formed more frequently and include more birds of more species, on the average, during the nonbreeding season than during the breeding season. They are also more common and tend to be larger in the early morning than at other times of the day.

Many of the higher-altitude mixed montane bush flocks seem to have definite ranges, and tend to move through their ranges along definite and rather stereotyped pathways. They tend to visit the same sites in more or less the same sequence again and again on the same day and on successive days.

Some of the members of the higher-altitude montane bush alliances seem to be purely insectivorous, but others eat fruits and seeds as well as insects. All spend most of their time feeding while they remain in the flocks. As in the case of the members of the blue and green tanager and honeycreeper alliance, however, it is obvious that individuals of different species of the higher-altitude montane bush alliances are sometimes attracted to one another by some social factor or factors in addition to, or instead of, the direct stimulus of food (see below). It was my impression, in fact, that members of the higher-altitude montane bush alliances are attracted to one another by purely social factors, apart from food, more frequently than are members of the blue and green tanager and honeycreeper alliance.

Unlike the members of most blue and green tanager and honeycreeper flocks, the members of most higher-altitude mixed montane bush flocks are frequently scattered through many different levels of vegetation. It is very common to see higher-altitude mixed montane bush flocks that include some birds feeding and moving on or near the ground, other birds feeding and moving in moderately low shrubbery, and still others feeding and moving in the treetops, all at the same time.

(Some of the mixed montane bush flocks above 6,000 feet on the Volcán de Chiriquí appeared to be accompanied by one, two, or three squirrels (probably *Sciurus granatensis*).[13] The associations between these squirrels and the mixed bird flocks were not very close, as the squirrels were always, or almost always, several feet away from the nearest birds; but the squirrels occurred in the general vicinity of mixed flocks more frequently than would seem likely by chance alone.

It may be significant, in this connection, that these squirrels are noisy animals, frequently uttering sharp chattering calls that are

[13] I am indebted to Dr. Charles O. Handley, Jr. (in litt.), for the probable identification of these squirrels.

reminiscent of the calls of some thicket-inhabiting finches (but not the finches usually occurring in mixed montane bush flocks on the Volcán de Chiriquí). The squirrels may tend to enchance the conspicuousness and the attractiveness of the mixed bird flocks with which they are associated.)

Brief observations of the lower-altitude mixed montane bush flocks on the Volcán de Chiriquí would suggest that they are usually more loosely organized than the higher-altitude mixed montane bush flocks. It has already been mentioned that the lower-altitude mixed montane bush flocks frequently include more species than the higher-altitude flocks; but they usually include relatively few individuals of the species that play the most important nuclear roles in the higher-altitude flocks. The structure of the lower-altitude mixed flocks is similar to that of the higher-altitude mixed flocks insofar as the members of the lower-altitude flocks may also occur at many different levels of vegetation; but the associations between most of the common species of the lower-altitude flocks seem to be briefer, on the average, than the associations between most of the common species of the higher-altitude flocks. Interspecific joining and following reactions seem to be comparatively rare in the lower-altitude mixed montane bush flocks; but interspecific supplanting attacks are comparatively common, much more so than in the higher-altitude mixed montane bush flocks, and perhaps as common as in mixed blue and green tanager and honeycreeper flocks.

THE ROLES OF DIFFERENT SPECIES WITHIN MIXED FLOCKS

BROWN-CAPPED BUSH-TANAGER

The usual social role of brown-capped bush-tanagers in mixed species flocks, especially at moderately high altitudes, is very similar to that of plain-colored tanagers in blue and green tanager and honeycreeper flocks.

Brown-capped bush-tanagers are frequently joined and followed by individuals of many other species, much more frequently than they themselves join and follow individuals of other species.

As in the case of the plain-colored tanagers, the usual social role of brown-capped bush-tanagers in mixed flocks seems to be largely or completely a consequence of their social behavior apart from mixed flocks. Some of the intraspecific social behavior patterns of the two

species are even more strikingly similar than their interspecific relations.

Brown-capped bush-tanagers are highly gregarious among themselves in almost exactly the same way as plain-colored tanagers. During the nonbreeding season most brown-capped bush-tanagers tend to associate with one another in rather stable groups of 4 to 8 or 10 individuals. Many or most of these groups appear to be composed of more than one family (i.e., parents and one brood of young). Individual birds, pairs, and family groups are seldom territorial during the nonbreeding season, or, at least, seldom defend territories for any appreciable continuous length of time. Some individuals, apparently adult males, may show indications of territorial defense for a few minutes, especially very early in the morning and late in the afternoon during the nonbreeding season, but such behavior is apparently always very brief at this season. During the breeding season, the larger groups of brown-capped bush-tanagers tend to break up. Pairs and apparently unmated single birds separate comparatively frequently and remain on individual territories for comparatively long periods of time. They usually spend most of the mornings, at least, on their own territories, but large groups are still re-formed occasionally, especially in the afternoons. I have seen flocks of brown-capped bush-tanagers during the later part of the courtship phase of the breeding season that were quite as large as any flocks of the same species observed during the nonbreeding season.

This high degree of intraspecific gregariousness is correlated with the usual types of movements and calls. Brown-capped bush-tanagers are very restless, almost constantly active, moving from bush to bush and tree to tree with very great rapidity. They are also very noisy (see comments below, in the discussion of the sooty-capped bush-tanager). They frequently perform exaggerated wing-flicking and tail-flicking movements, very much like the corresponding movements of plain-colored tanagers. They also utter many loud and hard call notes and rattling calls which are almost equally reminiscent of the most common calls of plain-colored tanagers. Some of these similarities between the two species are probably due to convergence, as there are indications that the genera *Chlorospingus* and *Tangara* are not very closely related to one another. *Chlorospingus* is probably more closely related to some of the bush-finches and/or the *Ramphocelus* tanagers, while *Tangara* is probably more closely related to some of the tanagers usually included in the genus *Thraupis;* and neither

Chlorospingus nor *Tangara* seems to be particularly primitive among tanagers.[14]

It seems likely, therefore, that much of the attractiveness of brown-capped bush-tanagers to individuals of other species is due to their possession of special characters that were originally evolved to promote intraspecific gregariousness. Individuals of other species are probably usually or frequently attracted to them by the same characters that attract brown-capped bush-tanagers to one another; but there are certain obvious exceptions to this general rule.

Brown-capped bush-tanagers frequently dispute among themselves, even during the nonbreeding season when they associate with one another in relatively large groups. During such disputes they usually utter many hostile vocalizations. All or most of these vocalizations seem to function as a threat during intraspecific encounters. When uttered by one brown-capped bush-tanager they usually induce other brown-capped bush-tanagers to retreat, at least temporarily.

There is some evidence that brown-capped bush-tanagers tend to utter relatively more vocal threat patterns and perform relatively fewer overt attack movements during intraspecific disputes than do many related species in similar circumstances. This may be an adaptation to promote intraspecific gregariousness, as vocal threats are probably less disruptive within a flock than overt attack movements.

Interestingly enough, the vocal threat patterns of brown-capped bush-tanagers may have an effect upon individuals of other species, which is just the reverse of their usual effect upon other brown-capped bush-tanagers. The sound of all or most of their threat calls seems to be definitely attractive to individuals of some other species. This may be illustrated by the behavior of some birds observed at approximately 5,700 feet elevation on the Volcán de Chiriquí between October 3 and October 10, 1960. There were two or three pairs of family groups of brown-capped bush-tanagers in this particular area at this time. They roosted separately at night and began to move around and feed separately at dawn. They were usually rather quiet when they first began to move around and feed, and were not usually accompanied by individuals of other species. Sooner or later, in the course of their wanderings, two of the pairs or family groups would come face to face, apparently by accident. Such encounters would induce an outburst of threat calls by some or all of the brown-capped bush-

[14] The phylogenetic relationships between different genera of tanagers and finches will be discussed in a series of separate papers (in preparation) after more detailed descriptions of their most significant behavior patterns.

tanagers involved. As soon as this outburst occurred, the brown-capped bush-tanagers were usually joined by individuals of other species, such as yellow-thighed finches or red-faced spinetails, who had been ignoring them until they became very noisy. The disputes between the brown-capped bush-tanagers usually subsided after a few minutes. The disputing birds either separated or joined up with one another to form a more or less amicable flock. In either case, some or all of the brown-capped bush-tanagers were usually followed for long periods of time after the end of the dispute by some or all of the individuals of other species that had been attracted by the sound of the dispute.

(Occasionally, but relatively very rarely, a brown-capped bush-tanager is also attracted by the sound of other brown-capped bush-tanagers uttering threat calls during a dispute. It may then fly to join the disputing birds and utter threat calls itself and/or actually begin to fight with the other birds. This would suggest that the sound of threat calls by one brown-capped bush-tanager usually or always stimulates both the attack and escape drives of other brown-capped bush-tanagers that hear the calls. The escape drives of the birds that hear such calls are probably usually or always stimulated more strongly than their attack drives; but their attack drives are apparently stimulated strongly enough to be expressed by overt activity in some cases.

There are indications that the reactions of individuals of other species that are attracted by the sounds of the threat calls of brown-capped bush-tanagers are seldom or never produced by the same motivation as the similar reactions of other brown-capped bush-tanagers. Individuals of other species that are attracted by the sounds of the threat calls of brown-capped bush-tanagers seldom or never perform hostile patterns themselves after joining the brown-capped bush-tanagers. Their reactions seem to be usually or always essentially "friendly." They apparently recognize the threat calls of brown-capped bush-tanagers as calls of a species with which they are accustomed to associate; but they seldom or never react as if they understood the hostile significance of such calls.)

The reactions of individuals of other species to the threat calls of brown-capped bush-tanagers might suggest that the usual social role of the latter in mixed flocks is largely determined by their vocal patterns rather than their movements or their physical appearance; but the effect of their vocal patterns is probably reinforced by some or all of their other characteristics. It is possible, for instance, that the

role of brown-capped bush-tanagers in mixed flocks is facilitated by their tendency to range through many different levels of vegetation. They are most often found moderately high (approximately 10 to 40 feet above the ground) in medium-sized trees and tall shrubbery; but they also occur in the tops of very tall trees and in very low shrubbery only a few inches above the ground. They probably occur at both extreme levels of vegetation more often than individuals of most other species of the montane bush alliances; and they frequently move from one extreme to the other or alternate between the two extremes very rapidly. Thus they tend to encounter a wide diversity of individuals of many different species, including species that are rather strictly confined to comparatively narrow levels of vegetation.

It is my impression that brown-capped bush-tanagers tend to play a less important role in lower-altitude mixed montane bush flocks, below approximately 5,200 feet, than in higher-altitude mixed montane bush flocks. They seem to be joined and followed by individuals of other species relatively less frequently in the lower-altitude flocks than in the higher-altitude flocks. Part or all of this difference seems to be due to the fact that brown-capped bush-tanagers are usually relatively less conspicuous in the lower-altitude flocks. They tend to be relatively rare at lower altitudes. The lower-altitude flocks also tend to include individuals of more species than the higher-altitude flocks; and some of the species that occur in lower-altitude flocks but not in higher-altitude flocks are very noisy and/or very restless. Thus the attention of the other members of the lower-altitude mixed flocks is more often distracted, i.e., diverted from the brown-capped bush-tanagers, than is that of the other members of the higher-altitude mixed flocks.

The brown-capped bush-tanager must be classified as a passive nuclear species. Its social role in mixed flocks is not, however, quite as one sided as that of the plain-colored tanager. It seems to join and follow individuals of other species slightly more frequently than do plain-colored tanagers.

The range of the brown-capped bush-tanager on the Volcán de Chiriquí overlaps that of the sooty-capped bush-tanager to some extent. Brown-capped bush-tanagers may react to sooty-capped bush-tanagers more strongly than they do to individuals of many other species. At least I have heard them begin to utter hostile calls when they heard sooty-capped bush-tanagers utter hostile calls in the distance. But such reactions are relatively very rare and very brief. I have never heard brown-capped bush-tanagers utter more than a few

hostile calls in response to sooty-capped bush-tanagers. They react to sooty-capped bush-tanagers much less frequently and less strongly than might be expected in view of the fact that the two species may occupy the same habitats, are rather similar in physical appearance, and have very similar repertories of calls, display movements, and postures. The few definite social reactions of brown-capped bush-tanagers to sooty-capped bush-tanagers probably occur when the former mistake the latter for suboptimal members of their own species.

Brown-capped bush-tanagers are more responsive to yellow-thighed finches, which are very different from brown-capped bush-tanagers in appearance and have some rather different habits, but are common throughout the range of brown-capped bush-tanagers on the western slopes of the Volcán de Chiriquí.

Brown-capped bush-tanagers react to the hostile calls of yellow-thighed finches more frequently and more vigorously than they do to those of sooty-capped bush-tanagers. I have seen single brown-capped bush-tanagers fly considerable distances to join groups of yellow-thighed finches that were disputing among themselves and uttering many hostile calls. These brown-capped bush-tanagers usually uttered many hostile calls of their own after joining the yellow-thighed finches, sometimes continuing to utter these calls as long as the yellow-thighed finches continued disputing among themselves. These incidents occurred near the upper border of the range of brown-capped bush-tanagers on the western slopes of the Volcán de Chiriquí, in which area these birds are relatively rare. It is possible, therefore, that the single brown-capped bush-tanagers that reacted so vigorously to the hostile calls of yellow-thighed finches did so because they were unable to associate with and perform their usual hostile behavior with other individuals of their own species. Their hostile motivation may have "accumulated" because it could not be vented in its usual way, and then "overflowed" upon suboptimal objects that would not have released hostility in other circumstances. The reactions of these single brown-capped bush-tanagers were particularly interesting, nevertheless, because the hostile calls of yellow-thighed finches are very different from any calls of brown-capped bush-tanagers and because the same brown-capped bush-tanagers that reacted to the hostile calls of yellow-thighed finches usually ignored all the calls of sooty-capped bush-tanagers in the same neighborhood.

I once heard a single territorial brown-capped bush-tanager near the upper border of the range of the species utter many hostile calls

which were obviously provoked by and directed toward a silent yellow-thighed finch some yards away. This reaction was presumably an even more extreme case of "overflow."

Brown-capped bush-tanagers also seem to join and follow yellow-thighed finches slightly more frequently than they do individuals of any other species; but this may be due to the fact that they are more often in closer proximity to yellow-thighed finches than to individuals of other species, as a result of the behavior of yellow-thighed finches (see below).

THE SOOTY-CAPPED BUSH-TANAGER

The sooty-capped bush-tanager is very similar to the brown-capped bush-tanager in general activity and methods of feeding as well as display patterns. It was seen in low shrubbery relatively more frequently than brown-capped bush-tanagers on the Volcán de Chiriquí; but this may have been largely or completely due to the fact that there were fewer tall trees in most of the areas where sooty-capped bush-tanagers were studied than in most of the areas where brown-capped bush-tanagers were studied.

It is perhaps remarkable, therefore, that sooty-capped bush-tanagers are much less gregarious among themselves than are brown-capped bush-tanagers. They seldom or never form flocks larger than a single family group of a pair of adults plus their most recent brood of young. Each pair or family group seems to defend its own particular territory throughout the year, including the breeding season.

Sooty-capped bush-tanagers also seem to play a less important role in mixed flocks than brown-capped bush-tanagers. They are joined and followed by individuals of other species more often then they themselves join and follow individuals of other species, and the actual frequency with which they are joined and followed is usually quite high; but they are certainly joined and followed by individuals of other species relatively less frequently than are brown-capped bush-tanagers. There are also some indications that sooty-capped bush-tanagers may join and follow individuals of other species relatively (but probably not actually) more frequently than do brown-capped bush-tanagers.

As in the case of the brown-capped bush-tanagers, the vocalizations of sooty-capped bush-tanagers seem to be more attractive than their movements to individuals of other species. They probably do not utter calls as frequently, on the average, as do brown-capped bush-tanagers, and they are sometimes almost completely silent for several minutes

at a time. (This is presumably correlated with the lesser degree of intraspecific gregariousness shown by sooty-capped bush-tanagers.) It is very obvious that they are joined and followed by individuals of other species much less frequently when they are silent, even when they are very active, than when they are vocal, even when they are not very active. The hostile calls of sooty-capped bush-tanagers, a sound very much like the corresponding calls of brown-capped bush-tanagers, also seem to be considerably more attractive to individuals of other species than many or all of their nonhostile calls (see below).

Sooty-capped bush-tanagers are sometimes attracted by the hostile calls of yellow-thighed finches in very much the same way as are brown-capped bush-tanagers. (I have not seen sooty-capped bush-tanagers react to the hostile calls of brown-capped bush-tanagers, perhaps because brown-capped bush-tanagers were relatively rare in the areas where I saw the two species together.)

The sooty-capped bush-tanager may thus be considered a passive nuclear species; but it is less effective as such than the brown-capped bush-tanager.

THE BASILEUTERUS WARBLERS

Black-cheeked warblers were not as common as bush-tanagers in the areas where mixed montane bush flocks were studied most intensively; but they were observed frequently enough to discover their usual social role in at least some types of mixed flocks.

Black-cheeked warblers seem to be approximately as gregarious among themselves as are sooty-capped bush-tanagers, which they resemble in several ways, but are more strictly confined to moderately low shrubbery. They are very much like sooty-capped bush-tanagers in physical appearance. The two species are similar in shape, and their plumage looks very much the same at a distance in the field. Both species appear to be big headed and plump bodied, generally olive in color, with blackish heads marked by light chins and whitish lines above and behind the eyes. Black-cheeked warblers are less frequently vocal than sooty-capped bush-tanagers; but their most common vocal patterns, including sharp call notes and rattles, are reminiscent of both the bush-tanagers. These similarities are not likely to be coincidental. They may be some form of mimicry.

In one area on the Volcán de Chiriquí, just below 7,000 feet, where sooty-capped bush-tanagers were quite common, black-cheeked warblers joined and followed individuals of other species, and were also joined and followed by individuals of other species moderately fre-

quently. They joined and followed individuals of other species relatively more frequently than did the sooty-capped bush-tanagers in the same area (in the same patches of shrubbery), and were joined and followed by individuals of other species relatively less frequently than were the sooty-capped bush-tanagers. The role of the black-cheeked warblers in the mixed flocks of this area appeared to be only slightly nuclear, and almost exactly intermediate between passive and active.

In another area, slightly above 7,000 feet, sooty-capped bush-tanagers were comparatively rare, and black-cheeked warblers appeared to be joined and followed by individuals of other species relatively more frequently than in the area below 7,000 feet. All the species which joined and/or followed the black-cheeked warblers above 7,000 feet also occurred in the same area as the black-cheeked warblers below 7,000 feet. This would suggest that black-cheeked warblers may take the place of sooty-capped bush-tanagers in mixed flocks in areas where the latter are rare or absent (and brown-capped bush-tanagers are absent).

There was no evidence that black-cheeked warblers have a special interspecific preference for sooty-capped bush-tanagers, or that the latter have a special interspecific preference for the former in either of the areas where the two species were seen together. It is conceivable, therefore, that one of these species has become more like the other, or that they are convergent, in voice and appearance, in order to facilitate associations with other species. It may be advantageous for the black-cheeked warbler and/or the sooty-capped bush-tanager to be joined and/or followed by individuals of other species. If associations with other species are advantageous to the black-cheeked warbler, then it may be advantageous for it to resemble the sooty-capped bush-tanager because individuals of other species tend to join and follow sooty-capped bush-tanagers. If associations with other species are advantageous to the sooty-capped bush-tanager, it may be advantageous for it to resemble the black-cheeked warbler because individuals of other species tend to join and follow black-cheeked warblers. If associations with other species are advantageous to both the black-cheeked warbler and the sooty-capped bush-tanager, the similarities between them may tend to increase the frequency and/or speed with which individuals of other species join and follow both of them, as individuals of other species may become conditioned more rapidly and easily to the essentially single set of stimuli actually presented by both the black-cheeked warbler and the sooty-capped

bush-tanager than they would to the two sets of stimuli which would be presented by the two species if they were not so similar to one another.

Black-cheeked warblers join and follow yellow-thighed finches more frequently than they do individuals of any other species and relatively more frequently than do brown-capped bush-tanagers. They may have a definite special interspecific preference for yellow-thighed finches.

Golden-crowned warblers were seen in the lower-altitude mixed montane bush flocks slightly above 5,000 feet on the western slopes of the Volcán de Chiriquí. They appeared to be rather strongly gregarious among themselves (see also Eisenmann, 1957) and to play an important nuclear role in some of the lower-altitude mixed flocks. Their usual social role in such flocks may be similar to that of brown-capped bush-tanagers in many higher-altitude mixed montane bush flocks.

YELLOW-THIGHED FINCH

Social relationships between yellow-thighed finches and individuals of many other species are extremely significant factors in the organization of most higher-altitude mixed montane bush flocks on the Volcán de Chiriquí. Yellow-thighed finches can play two different roles in such flocks, and may play either one or both of these roles simultaneously and/or successively. They probably occur in the higher-altitude mixed montane bush flocks of the Volcán de Chiriquí more frequently than individuals of any other species, and they range farther up the mountain than do brown-capped bush-tanagers.

They tend to react actively to individuals of almost all the other species they encounter. They usually join and follow individuals of most other species much more frequently than they are joined and followed by individuals of most other species. They do not, however, perform joining and following reactions equally frequently. They tend to follow individuals of most other species much more frequently than they join individuals of the same other species. The actual number of joining reactions performed by yellow-thighed finches in most higher-altitude mixed montane bush flocks is usually quite large, but always, or almost always, much smaller than the number of following reactions performed at more or less the same time. They certainly follow individuals of other species without actually joining them much more frequently than do any other members of any of the montane bush alliances.

Some other species of the montane bush alliances tend to perform many more interspecific joining reactions than interspecific following reactions (see below). The marked contrast between certain species that are primarily followers and others that are primarily joiners is one of the most characteristic features of mixed montane bush flocks, which are quite different from mixed blue and green tanager and honeycreeper flocks in this respect. All or most of the active nuclear and attendant species in mixed blue and green tanager and honeycreeper flocks cannot be classified as either followers or joiners in the same way as some species of the mixed montane bush flocks.

All other factors being equal, individuals of all or most species would probably usually prefer to follow rather than join individuals of other species. By following, a bird can associate with another bird without coming too close, which might provoke a dispute. In some circumstances, however, following tends to be more difficult than joining. The ease or difficulty of following or joining is often largely dependent upon the nature of the vegetation in which such reactions occur.

Yellow-thighed finches may be able to follow so much more frequently than to join because they are essentially birds of thickets and low shrubbery. They sometimes go fairly high into trees, 20 or 30 feet above the ground, but only in certain exceptional situations. They seldom or never do so except when there is a thick curtain of shrubberylike vegetation extending continuously or nearly continuously from the ground up to a higher level, e.g., when there are thick tangles of vines extending from just above the ground to the higher branches of trees.

Individuals of other species that also occur in thickets and low shrubbery on the Volcán de Chiriquí also tend to perform more interspecific following reactions than interspecific joining reactions as long as they remain in thickets and low shrubbery. This is true of the bush-tanagers and black-cheeked warblers, as well as individuals of several less passive species (see below). On the other hand, individuals of at least some active species of the montane bush alliances tend to perform more interspecific joining reactions than interspecific following reactions when they are in high shrubbery and trees (see below). They may also perform relatively more interspecific joining reactions when they are in high shrubbery and trees than when they are in low shrubbery and thickets.

The explanation of all or most of these differences is fairly obvious. Low shrubbery and thickets tend to be denser than high shrubbery and

trees, and twigs and branches that birds can use as perches tend to be much closer together in thickets and low shrubbery than in high shrubbery and trees. Birds moving through thickets and low shrubbery can usually regulate their distances from one another more or less at will, because they can move by very short stages, hopping or flying between perches that are only a few inches apart. Such birds can usually follow one another without joining whenever they want to. Birds moving through trees do not always have the same freedom of choice. They may have to move from tree to tree by comparatively long flights because the trees are not very close together, and may not be able to regulate their distances from one another as precisely as can birds in thickets and low shrubbery. They may have to bunch up in certain particular trees, i.e., perform joining reactions, if they are to keep in touch with one another at all.[15]

In the case of yellow-thighed finches there is also another factor involved. These birds in thickets and low shrubbery are often attracted to individuals of other species that are moving through higher vegetation more or less distinctly separated by a layer of open space from the underlying low vegetation. In such circumstances the yellow-thighed finches are usually prevented from trying to join the individuals of other species by their reluctance to move through the open space.

Although yellow-thighed finches will follow and join individuals of almost any other species, they seem to prefer to follow brown-capped bush-tanagers when the latter are common, sooty-capped bush-tanagers when brown-capped bush-tanagers are rare or absent, and black-cheeked warblers at high altitudes where brown-capped bush-tanagers are absent and sooty-capped bush-tanagers are rare or absent.

The marked special interspecific preference of yellow-thighed finches for brown-capped bush-tanagers is also shown in several other ways. Yellow-thighed finches are often attracted by the hostile as well as the nonhostile vocal patterns of brown-capped bush-tanagers. They do not seem to react as positively to the hostile calls of any other species as they sometimes do to those of brown-capped bush-tanagers.

Yellow-thighed finches also tend to follow brown-capped bush-

[15] The frequencies of interspecific reactions by members of the blue and green tanager and honeycreeper alliance are also affected by density of vegetation. Individuals of most species of this alliance tend to perform relatively more interspecific following reactions in environments such as the clearing on Barro Colorado Island, where the treetops form a continuous band of vegetation around the edge of the clearing, than in environments such as the areas near Gamboa and Frijoles, where trees are more scattered.

tanagers for longer periods of time than they do individuals of other species, and sometimes follow them at greater distances than they do individuals of other species. I have seen a pair of yellow-thighed finches in low shrubbery follow a flock of brown-capped bush-tanagers moving through trees above the shrubbery for several hours at a time, and repeatedly follow the same flock on several successive days, in spite of the fact that the brown-capped bush-tanagers were usually 30 to 50 feet above and approximately 20 feet ahead of them.

It is often particularly clear that yellow-thighed finches and brown-capped bush-tanagers are not obtaining extra food by associating with one another. In the case of the association cited immediately above, for instance, the brown-capped bush-tanagers were usually feeding on insects while the yellow-thighed finches following far below and behind them were usually feeding on fruit and other vegetable matter.

Yellow-thighed finches usually do not react to brown-capped bush-tanagers that are more than 50 feet above them, or to individuals of most other species that are as much as 30 feet above them. Thus they have almost no contact with individuals of those species of the montane bush alliances that usually remain in or near the tops of tall trees.

As a general rule yellow-thighed finches tend to follow and join individuals of all other species more frequently when the latter are being vocal than when they are silent.

Yellow-thighed finches are gregarious among themselves in much the same way and to approximately the same extent as sooty-capped bush-tanagers and black-cheeked warblers. Individual pairs and family groups seem to defend individual territories throughout the year (see below). Rather surprisingly, however, yellow-thighed finches have many characters that are strongly reminiscent of characters of other species that are more highly gregarious among themselves.

Yellow-thighed finches are remarkably conspicuous. Their generally black plumage is usually easy to see against a background of shrubbery. Their yellow thighs seem to be flash patterns, which function in the same way as the bright wing and/or tail patches of many other gregarious species. They hop very frequently, and their yellow thighs are revealed very conspicuously when they hop. They are not very shy, and are much less skulking than the other bush finches, e.g., the species of the genus *Atlapetes,* which may be their nearest relatives. They usually move in a peculiar floppy, clumsy-looking way, which tends to attract the eye of any observer. They are also noisy. They usually utter one or more types of call notes almost constantly as they move through the shrubbery. Whenever one bird of a pair

or family group comes very close to another, as happens very frequently, one (or more) of the birds usually utters a moderately loud, twittering, greeting call. During obviously hostile territorial disputes between neighboring yellow-thighed finches, the disputing birds usually utter harsher, louder versions of the same twittering call. These hostile calls sometimes appear to be attractive to individuals of several other species, in addition to the bush-tanagers cited above.

None of the other members of the montane bush alliances is as generally and consistently conspicuous as yellow-thighed finches. The conspicuous characters of yellow-thighed finches contribute greatly to the general conspicuousness of the mixed flocks with which they are associated, and sometimes seem to attract individuals of other species to themselves. It is possible that the production of either one or both of these effects is the primary function of these characters, i.e., the principal adaptive advantage they were originally evolved to secure. If so, this would be a rather unusual specialization. None of the other Panamanian finches, tanagers, or honeycreepers seems to have developed as extreme a group of conspicuous characters as an adaptation to stimulate the formation and maintain the cohesion of mixed flocks but not unmixed flocks.

It should be noted that the geographical distribution of yellow-thighed finches is not very wide (see below). It seems unlikely that they are more gregarious among themselves in other areas than they are on the Volcán de Chiriquí, where they are very abundant.

Yellow-thighed finiches are sometimes joined and/or followed by individuals of other species with some appreciable frequency; but it is probably only in certain flocks composed of yellow-thighed finches and yellow-throated bush-finches alone that they are ever consistently joined and followed by individuals of another species more frequently than they join and follow individuals of other species.

THE EFFECTS OF THE TERRITORIAL BEHAVIOR OF CERTAIN SPECIES UPON CERTAIN MIXED FLOCKS

It has already been mentioned several times that individuals of several different species are attracted by the hostile calls of yellow-thighed finches and/or sooty-capped bush-tanagers, and that mated pairs and family groups of many territorial species associate with mixed flocks. These factors interact in a rather interesting way in mixed montane bush flocks just below 7,000 feet on the western slopes of the Volcán de Chiriquí, where both sooty-capped bush-tanagers and yellow-thighed finches are common.

In this area the members of a pair or family group of sooty-capped bush-tanagers will sometimes try to follow a mixed flock, with which they have been associating while the flock was in their territory, when the flock leaves their territory. Such attempts are seldom or never successful. As soon as the members of a pair or family group of sooty-capped bush-tanagers overstep the boundary of their territory, they find themselves within the territory of another pair or family group of sooty-capped bush-tanagers. The owners of this latter territory always, or almost always, rush to defend their territory, and always, or almost always, manage to repel the intruders after a more or less prolonged dispute. Such disputes are usually accompanied by a great variety of hostile patterns by both the intruders and the defenders, including overt attack and escape movements and many hostile calls and notes. Similar incidents are common among the yellow-thighed finches in the same area. Yellow-thighed finches also try to follow mixed flocks into the territories of neighbors of their own species, and provoke similar disputes as a result.

The overt attack and escape movements performed during such disputes among sooty-capped bush-tanagers and yellow-thighed finches tend to have a disruptive effect upon any mixed flock in which, or in the immediate vicinity of which, they occur. The other members of the flock tend to scatter to get out of the way of the disputing birds, which usually fly back and forth in a very energetic manner. At the same time the hostile calls and notes of the disputing birds are so attractive to birds of other species that the other members of the flock do not usually scatter very far, and other birds that were not associated with the flock before the dispute began may come to join it. As a general rule it may be said that most of the mixed montane bush flocks of this area are never more attractive than when disputes among sooty-capped bush-tanagers and/or yellow-thighed finches are going on inside them. Thus they are most attractive just at the time when they are in greatest danger of disruption. This may tend to prolong the existence of many of these mixed flocks.

Such actions and reactions are particularly important in the flocks slightly below 7,000 feet because the territories of sooty-capped bush-tanagers and yellow-thighed finches tend to coincide in this area. The territories of both species are partly determined by the same aspects of terrain and vegetation, and boundaries are usually established where there are gaps in the shrubbery. Both species tend to react to these gaps in the same way. Every patch of shrubbery in this area that is the territory of a single pair or family group

of sooty-capped bush-tanagers is usually also the territory of a single pair or family group of yellow-thighed finches. Thus whenever a mixed flock moves over a gap in the shrubbery in this area it tends to provoke a dispute among both sooty-capped bush-tanagers and yellow-thighed finches. Similar reactions probably occur among individiuals of the same and other species associated with mixed montane bush flocks in other areas on the Volcán de Chiriquí; but they are usually or always less conspicuous.

YELLOW-THROATED BUSH-FINCH

Yellow-throated bush-finches seem to occur in mixed montane bush flocks much less frequently than either of the bush-tanagers, the black-cheeked warblers, or yellow-thighed finches, in spite of the fact that they are common over a wider range of altitudes than any of these latter species. They do, however, follow and join individuals of other species occasionally. They are most likely to follow and join yellow-thighed finches, probably at least twice as often as they follow and join individuals of any other species frequently associated with mixed montane bush flocks.

As yellow-throated bush-finches live in thickets and low shrubbery, it might be supposed that their occasional associations with yellow-thighed finches were purely coincidental; but there is some evidence that a slight but definite special interspecific preference is also involved. Yellow-throated bush-finches follow and join yellow-thighed finches relatively more frequently than do chestnut-capped bush-finches (*Atlapetes brunnei-nucha*) or large-footed finches (*Pezopetes capitalis*), which also occur in thickets in some of the same areas on the Volcán de Chiriquí.

Yellow-throated bush-finches are conspicuously colored, but shy, skulking, and quiet. They seem to be followed and joined by individuals of other species less frequently than they follow and join individuals of other species.

FURNARIIDS

A very large proportion of the species of the family Furnariidae (*sensu lato*, including the tree-creepers or dendrocolaptids) are frequently associated with mixed flocks of one type or another; but the red-faced spinetail was the only species of furnariid studied in detail during the present investigation.

Red-faced spinetails usually occur moderately high in trees, al-

though they may come down to low shrubbery from time to time. They are very inconspicuous birds, not very brightly colored, usually very quiet, and not very gregarious among themselves. Single birds, pairs, and family groups of this species are usually found widely separated from one another, and are probably territorial.

Red-faced spinetails are joined and followed by individuals of other species very rarely, but they join and follow individuals of other species very frequently. They seem to be particularly strongly attracted to brown-capped bush-tanagers, and tend to join them (at least when the latter are in trees) much more frequently than they follow them (using the terms "join" and "follow" as defined above). I have seen the same pair of red-faced spinetails join the same flock of brown-capped bush-tanagers repeatedly over a period of several hours every morning for seven successive days.

Brief observations of other furnariids on the Volcán de Chiriquí would suggest that all or most of them are similar to red-faced spinetails insofar as they tend to join and follow individuals of other species more frequently than they themselves are joined and followed. All or most of them probably also tend to join more frequently than follow.

All these species are primarily or exclusively insectivorous. Some of them, such as the tree-creepers and the ruddy tree-runners, usually or always feed on insects they find in or on the bark of trees. Such species do not seem to derive much benefit in the way of food from their associations with mixed flocks. They do not usually feed on insects stirred up by other members of the flocks.

SILVER-THROATED TANAGER

On the western slopes of the Volcán de Chiriquí, silver-throated tanagers are rather common slightly above 5,000 feet, and extend in decreasing numbers up to at least 6,000 feet. In this area they are sometimes associated with mixed montane bush flocks, but they do not seem to be regular members of such flocks, and sometimes deliberately refrain from joining them. When they do associate with mixed flocks they are seldom or never closely integrated with the other members of the flocks. They are essentially birds of the treetops, although they do come down to low shrubbery, almost to the ground, occasionally; and they seem to be more strongly attracted to the very heterogeneous lower-altitude mixed flocks, which usually include many other arboreal species, than to the less heterogeneous higher-altitude flocks, which usually include a large proportion of thicket-inhabiting birds. They seem to join and follow individuals of all or most other

species more often than they themselves are joined and followed; and they join and follow brown-capped bush-tanagers more often than they do any other common species of the montane bush alliances.

Although silver-throated tanagers are not very important members of the mixed flocks on the Volcán de Chiriquí, they seem to be associated with such flocks there more closely and more frequently, on the average, than with mixed flocks on Cerro Campana (see below).

(A few brief glimpses of a few speckled tanagers in the very heterogeneous lower-altitude mixed montane bush flocks on the Volcán de Chiriquí would suggest that their role in such flocks is probably not very different from that of silver-throated tanagers.)

WILSON'S WARBLER

This is another species that plays a very distinctive role in mixed montane bush flocks. Wilson's warblers follow and join individuals of other species much more frequently than they are followed and joined. They also tend to follow individuals of other species more frequently than they join individuals of other species. The relative frequencies of interspecific following and joining reactions performed by Wilson's warblers (at least when they are in shrubbery or low trees) are very similar to the relative frequencies of interspecific following and joining reactions performed by yellow-thighed finches; but the actual numbers of both types of reactions by Wilson's warblers are usually much less than the actual numbers of the same reactions by yellow-thighed finches in similar situations. Wilson's warblers also come close to individuals of other species much less frequently than do yellow-thighed finches.

They tend to hang about the outskirts of a remarkably wide variety of groups of other species in all the montane forest and scrub habitats above 4,500 feet on the Volcán de Chiriquí (they may also occur at lower altitudes, but I have not observed the birds of lower altitudes). During the part of the year when Wilson's warblers are in Panamá, almost every large and medium-sized mixed montane bush flock (i.e., almost every flock composed of more than two species) is accompanied by a single Wilson's warbler. Single Wilson's warblers also attach themselves moderately frequently to smaller mixed flocks and to single birds, pairs, family groups, and larger unmixed flocks of almost every other species of all the montane bush alliances, as well as some species that usually remain apart from the montane bush alliances.

It would thus appear that Wilson's warblers are almost completely undiscriminating in their choice of associates—less discriminating than any other species frequently associated with mixed montane bush flocks, with the possible exception of summer tanagers (see below). They seem to be equally satisfied to become associated with almost any other montane passerine birds. This lack of discrimination is really quite remarkable.

It is relatively very rare to see two or more Wilson's warblers close together, or associated with the same mixed flock at the same time, because they usually fight among themselves whenever they come within 10 or 15 yards of one another. They seem to be very strongly territorial in Panamá. The fights between Wilson's warblers are almost always brief and decisive. One bird attacks and the other usually flees immediately. Such fights are seldom accompanied by any unusually loud burst of calling or other displays such as are common during disputes among bush-tanagers or yellow-thighed finches. The inconspicuous nature of such fights may be advantageous, in the case of Wilson's warblers, because it may help to prevent others of this species from being attracted to, and attempting to join in, the fights when the disputing birds might be unable to repel additional intruders very promptly. (Disputes among individuals of many other species of birds are sometimes attractive to other individuals of the same species as well as other species.) Anything that helps to prevent or reduce intraspecific gregariousness is presumably advantageous in the case of Wilson's warblers in Panamá.

Wilson's warblers are quite conspicuous in other ways, however. They are brightly colored, and utter very loud call notes almost constantly (if not usually very rapidly). As neither their colors nor their notes are very different from those of many other species of the montane bush alliances, it is perhaps surprising that they are not joined and/or followed more frequently by individuals of other species. Their comparatively slight attractiveness may be due to their very slight degree of gregariousness among themselves in Panamá. As noted above, single birds are probably always less attractive than pairs or larger groups of the same species, all other factors being equal.

Wilson's warblers certainly tend to enhance the conspicuousness of the mixed flocks with which they are associated and probably, therefore, increase the attractiveness of such flocks to other birds; but they seem to contribute relatively little, directly, to increase the cohesion of the flocks.

SLATE-THROATED REDSTART

The social relations of slate-throated redstarts with individuals of other species on the Volcán de Chiriquí are somewhat reminiscent of the corresponding relations of silver-throated tanagers.

Slate-throated redstarts are very brilliantly colored and very active. They are probably more conspicuous visually than individuals of any other species of the montane bush alliances, except the closely related collared redstarts (see below). They do not, however, play a very important role in most mixed montane bush flocks.

On the western slopes of the Volcán de Chiriquí, slate-throated redstarts are common below 6,000 feet, and also occur in smaller numbers up to at least 7,000 feet. They occur in many different levels of vegetation, from just above the ground to high in tall trees. Throughout this wide range they join and follow, and are joined and followed by, individuals of many other species; but none of these reactions seems to be common enough to suggest that slate-throated redstarts have a special interspecific preference for any other species, or are the object of any special interspecific preference of any other species. Slate-throated redstarts are certainly joined and followed by individuals of other species relatively much less frequently than are bush-tanagers or black-cheeked warblers, and join and follow individuals of other species relatively much less frequently than do yellow-thighed finches, many furnariids, or Wilson's warblers. They are joined by the undiscriminating Wilson's warblers relatively more frequently than by yellow-thighed finches or furnariids.

Associations between slate-throated redstarts and individuals of other species also tend to be relatively brief and not very close, and would thus appear to be essentially "casual." In the course of their normal activities slate-throated redstarts and individuals of many other species tend to encounter one another very frequently, and they may stay more or less together for some time; but the slate-throated redstarts eventually become separated from the others without any obvious signs of reluctance on either side. They probably do associate with other species of the montane bush alliances relatively more frequently than do silver-throated tanagers; but they probably should not be classified as regular members of the mixed montane bush flocks.

Slate-throated redstarts are not very gregarious among themselves, and it is relatively very rare to see more than one or two of them associated with the same mixed flock at the same time. When they are associated with mixed flocks, they probably produce an effect that is not very different from that produced by Wilson's warblers. Slate-

throated redstarts probably also tend to enhance the conspicuousness of mixed flocks, without contributing very much, directly, to enhance the cohesion of the flocks.

COLLARED REDSTART

Collared redstarts are most common above 6,000 feet on the western slopes of the Volcán de Chiriquí; but their behavior apart from mixed flocks is very similar to that of slate-throated redstarts. It is interesting, therefore, that their usual social role in mixed flocks is much more important than that of slate-throated redstarts.

Collared redstarts tend to join individuals of other species relatively much more frequently than do slate-throated redstarts. Their usual method of joining is very distinctive. They seldom fly directly to join other birds, but make short flights to catch insects, and then tend to land beside individuals of other species when they return from their insect-catching flights. Slate-throated redstarts also make short flights to catch insects; but they do not show nearly as strong a tendency to land beside individuals of other species on their return. This peculiar type of interspecific joining behavior would be explained if collared redstarts were much more strongly attracted to individuals of other species when they themselves are flying than when they are not.

Collared redstarts may land beside individuals of almost any other species, but they seem to prefer sooty-capped bush-tanagers. Such reactions may be expressions of a definite special interspecific preference. (Collared redstarts are rare in areas where brown-capped bush-tanagers are common. It is possible that they are as strongly attracted to brown-capped bush-tanagers, when they meet them, as they are to sooty-capped bush-tanagers; but I did not see enough encounters between collared redstarts and brown-capped bush-tanagers to be able to analyze the relations between the two species.)

There are indications that the relative frequency of interspecific joining reactions (compared with interspecific following reactions) by collared redstarts is approximately the same as the corresponding frequency of similar reactions by red-faced spinetails, and much greater than the corresponding frequency of similar reactions by yellow-thighed finches or Wilson's warblers. Collared redstarts may follow individuals of other species slightly more frequently than do slate-throated redstarts; but they certainly follow individuals of other species much less frequently than they join individuals of other species. They are also followed by individuals of other species rela-

tively much more frequently than are slate-throated redstarts. It is difficult to see exactly why this should be so, as they are not very much more conspicuous or active than slate-throated redstarts. Perhaps collared redstarts are followed more frequently because they fly away from the close proximity of individuals of other species more frequently. (They are close to individuals of other species more frequently simply because they join individuals of other species more frequently.) All other factors being equal, the sight of a bird taking flight a few inches away is much more likely to induce another bird to follow than the sight of a bird taking flight a few feet or yards away.

Like slate-throated redstarts, collared redstarts are followed by Wilson's warblers much more frequently than by individuals of any other species; but they are also followed, not infrequently, by such birds as yellow-thighed finches and sooty-capped bush-tanagers, birds that seldom or never follow slate-throated redstarts. Collared redstarts may be followed by individuals of other species relatively as frequently as are sooty-capped bush-tanagers.

Collared redstarts sometimes appear to be the leaders of mixed flocks. Sometimes a whole mixed flock will move in the direction in which a collared redstart is making most of its insect-catching flights. This sort of movement is undoubtedly significant, at least in some cases; but the appearance of leadership by collared redstarts is probably often slightly deceptive. In many large flocks composed of many species, collared redstarts may lead some but not all the other members of the flocks. One or two collared redstarts, for instance, may be followed by one or two yellow-thighed finches and/or sooty-capped bush-tanagers, which are followed, in turn, by individuals of other species. In such cases, the individuals of other species do not usually continue to move after the collared redstarts if the yellow-thighed finches and/or the sooty-capped bush-tanagers go in a different direction.

(There is at least one area on the Volcán de Chiriquí, near 6,000 feet, where the birds of the local montane bush alliance are often divided into two types of flocks that are rather comparable to the "predominantly tanager" and "predominantly honeycreeper" flocks of the blue and green tanager and honeycreeper alliance. In this area there is a great deal of low scrub plus a few scattered very tall trees. The foliage of the tall trees is usually separated from the underlying scrub by a wide open space.

Most of the members of the montane bush alliance in this area tend to stay in the low shrubbery; but a few species spend consider-

able time in the tall trees. The birds high in trees may form mixed flocks that are independent of mixed flocks in the shrubbery at the same time. The higher and lower flocks may move in different directions. The high flocks are usually composed of one or two collared redstarts and one Wilson's warbler, plus a few birds of other species, such as flame-throated warblers, furnariids, and slate-throated redstarts (if present in the area). These high flocks apparently never include yellow-thighed finches or black-cheeked warblers, and seldom include sooty-capped bush-tanagers. The collared redstarts are usually the real leaders of the high flocks, as all, or almost all, the other members of the high flocks usually tend to follow the collared redstarts directly.

It should be stressed, however, that such high flocks are relatively rare and more or less atypical. All, or almost all, the birds in the high flocks in this area also go down to the shrubbery more or less frequently, where they tend to associate with more typical mixed montane bush flocks that include yellow-thighed finches and black-cheeked warblers. In other areas at the same elevation where the same species of birds occur but the vegetation is not divided into two distinctly separated strata, the birds are seldom or never divided among higher and lower flocks moving independently of one another.)

OTHER SPECIES

Flame-throated Warbler.—I did not see flame-throated warblers very frequently on the Volcán de Chiriquí and was not able to analyze their usual social role in mixed flocks. All I can say about them is that they are very conspicuous (both brightly colored and noisy), found around 6,000 feet and above, apparently usually or always territorial, more common in trees than in low shrubbery, and probably join and follow individuals of other species (at least collared redstarts) more frequently than they are joined and followed by individuals of other species.

Brown-capped Vireo.—Brown-capped Vireos were observed only at 6,000 feet and above on the Volcán de Chiriquí. In this area they are frequently associated with mixed montane bush flocks, especially flocks in trees of moderate height. They seem to join individuals of other species more frequently than they follow or are followed or joined by individuals of other species. They do not seem to exhibit any special interspecific preferences. They are very inconspicuous and not very gregarious among themselves, and so probably do not con-

tribute very much to enhance the conspicuousness of the mixed flocks with which they are associated.

Summer Tanager.—The usual social role of summer tanagers in mixed montane bush flocks on the Volcán de Chiriquí seems to be the same as in the mixed blue and green tanager and honeycreeper flocks of the lowlands of central Panamá.

Pale-vented Thrush.—This large, dull-colored, high montane species tends to have a disruptive effect on mixed montane bush flocks. Pale-vented thrushes seem to be attracted by individuals of many species of the higher-altitude montane bush alliances and/or are attracted to many of the same foods as these latter species; but they also tend to perform many supplanting attacks upon any and all other passerine birds in their immediate vicinity. Such behavior may be typical of thrushes of the genus *Turdus*. The few times that clay-colored thrushes were seen associated with mixed blue and green tanager and honeycreeper flocks they also tended to have a disruptive effect on the flocks.

PARTIAL SUMMARY

It may be useful to recapitulate briefly and summarize the usual social roles of different species in mixed montane bush flocks in the same terms as in the discussion of the species of mixed blue and green tanager and honeycreeper flocks.

Both bush-tanagers are regular members of mixed montane bush flocks and essentially passive nuclear species. They are not completely passive, however, and the sooty-capped bush-tanager is less passive than the brown-capped bush-tanager.

The collared redstart is a regular member of mixed montane bush flocks and apparently always a nuclear species. In some flocks (the "high" flocks) it is a passive nuclear species. In most flocks it is not definitely either passive or active.

The black-cheeked warbler is rather similar to the collared redstart. It is apparently always a regular nuclear species. It seems to be a passive nuclear species in some flocks and not definitely either passive or active in other flocks.

Wilson's warbler is a regular active nuclear species.

The yellow-thighed finch is a regular nuclear species. It may be an active nuclear species or a passive nuclear species, or both, depending upon the identity of the other species associated with it.

The silver-throated tanager may be an occasional active nuclear

species on the Volcán de Chiriquí. The slate-throated redstart may be an occasional nuclear species, but not definitely either passive or active.

The brown-capped vireo and some or all of the furnariids associated with mixed montane bush flocks seem to be regular attendant species. The yellow-throated bush-finch is probably a regular attendant in flocks that include yellow-thighed finches, but an occasional attendant (at best) in other mixed flocks. The summer tanager seems to be an occasional attendant species in all types of mixed montane bush flocks.

It will be noted that many of the species of the montane bush alliances are more difficult to assign to discrete categories, according to their social roles in mixed flocks, than are the species of the mixed blue and green tanager and honeycreeper alliance. The significance of this difficulty will be discussed below.

Diagram 3 is a tentative summary of the special interspecific preferences of the most common species of the higher-altitude montane bush alliances revealed by predominantly "friendly" following and/or joining reactions. It should be compared with the summary of the corresponding preferences of species of the blue and green tanager and honeycreeper alliances shown in diagram 1.

THE COLORS OF SPECIES IN MIXED MONTANE BUSH FLOCKS

There is only a restricted range of colors in the plumages of almost all the species commonly occurring in the higher-altitude mixed montane bush flocks and the majority of the species commonly occurring in the lower-altitude mixed montane bush flocks on the Volcán de Chiriquí. The plumages of these species are largely black and/or yellow (including yellow-olive), sometimes variegated with patches of brown and/or white. Bright greens, blues, and reds are lacking in the plumages of most of these species, and confined to small patches in the plumages of the others.

This general similarity of coloring may be adaptive in any one or all of several different ways. In any case, it probably tends to facilitate associations between individuals of different species. The birds of these species must become conditioned fairly early in their lives to the presence of companions that are predominantly black and/or yellow, with or without patches of brown and/or white. Some or all of these species may even be born with an innate recognition or preference for one or more of these colors. Thus an individual of any species exhibiting one or more of these colors is probably more

attractive or, at least, less irritating and/or frightening to individuals of most of the species of the montane bush alliances than an otherwise similar bird of different colors.

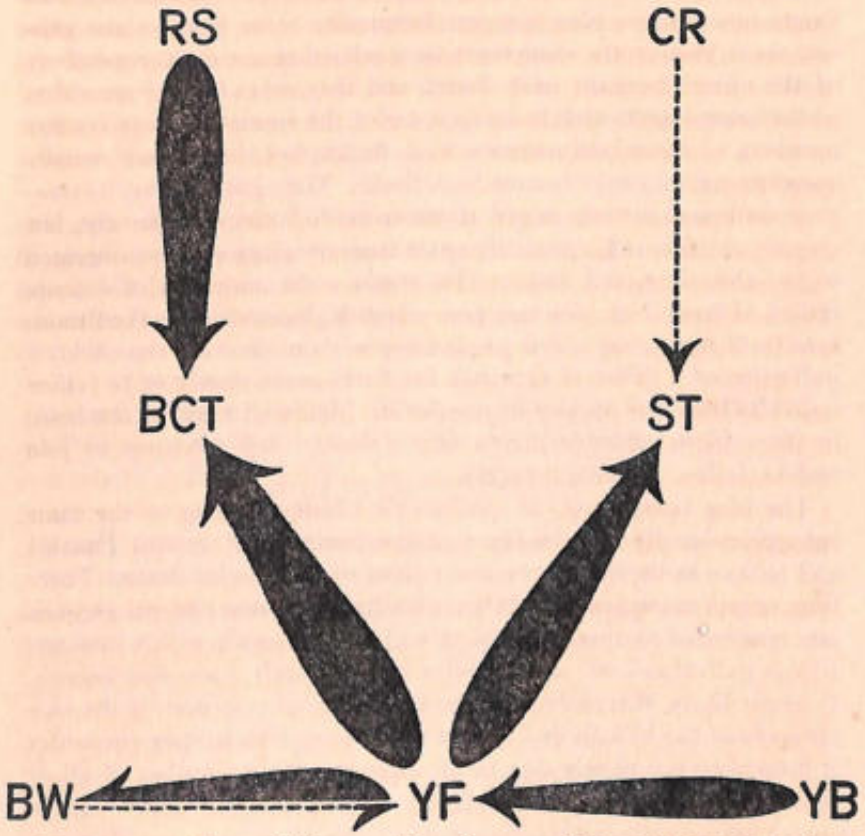

DIAGRAM 3.—The special interspecific preferences of the most common species of the higher-altitude montane bush alliances revealed by predominantly "friendly" following and/or joining reactions. Organized in the same way as diagrams 1 and 2.

The species are identified by initials. RS = red-faced spinetail. CR = collared redstart. BCT = brown-capped bush-tanager. ST = sooty-capped bush-tanager. BW = black-cheeked warbler. YF = yellow-thighed finch. YB = yellow-throated bush-finch.

Perhaps the best evidence that the similar coloring of most of the species in mixed montane bush flocks is a significant factor tending to stimulate the formation and maintain the cohesion of such flocks is provided by the behavior and social relations of certain other species that occur in the same areas but are colored very differently.

Blue tanagers occur up to 6,000 feet on the western slopes of the Volcán de Chiriquí. They may not have occurred at such high altitudes before much of the original montane forest was cut; but they seem to be well established along roads and around the town of Cerro Punta now. These blue tanagers frequently occur in the same general areas, even in the same trees, as species that are regular members of the mixed montane bush flocks, and they seem to feed on many of the same insects and fruits as some of the species that are regular members of the mixed montane bush flocks; but they do not usually associate with mixed montane bush flocks. They join the very heterogeneous lower-altitude mixed montane bush flocks occasionally, but they almost always keep strictly apart from the more closely integrated higher-altitude mixed flocks. This seems to be the result of definite choice. I have seen blue tanagers watch higher-altitude mixed montane bush flocks only a few yards away without showing the slightest indication of a desire to approach the flocks more closely or to follow individuals of any species in the flocks. Similarly, none of the birds in these higher-altitude mixed flocks showed any tendency to join and/or follow the blue tanagers.

The blue tanagers of the Volcán de Chiriquí belong to the same subspecies as the blue tanagers of the lowlands of central Panamá and behave in the same way apart from mixed species flocks. There is no reason to suppose that they do not have the same internal gregarious tendencies as the blue tanagers of the lowlands, which join and follow individuals of other species so frequently (see also below). It seems likely, therefore, that the usual lack of response by the blue tanagers of the Volcán de Chiriquí to the mixed flocks they encounter is largely or completely due to the characteristic coloration of all or most of the individuals in the flocks, a coloration that either fails to attract or actually repels (see below) the blue tanager. Many of the species in mixed montane bush flocks are not more different from blue tanagers in shape or behavior than many of the species that blue tanagers join and follow relatively frequently in the lowlands.

A few brief observations would suggest that the blue tanagers of the Volcán de Chiriquí are more strongly attracted to bay-headed tanagers (*Tangara gyrola*), which occur in small numbers slightly above 5,000 feet, than to any of the other species discussed above. It is surely not coincidental, in this connection, that bay-headed tanagers are largely bright blue and green and also tend to join mixed montane bush flocks relatively rarely. (The reactions of the blue tanagers of the Volcán de Chiriquí to bay-headed tanagers is positive evidence

that these blue tanagers really do have the same gregarious tendencies as lowland blue tanagers in central Panamá.)

Similar factors may help to explain the social isolation of two resident species of the genus *Piranga* on the Volcán de Chiriquí, the white-winged tanager (*P. leucoptera*) and the flame-colored tanager (*P. bidentata*). Individuals of both species occur in some of the same areas as many regular members of the mixed montane bush flocks; but they seem to be associated with such flocks even less frequently than are blue tanagers. They obviously do not have the special joining reactions of summer tanagers. They also seem to be definitely unattractive (at least) to all or most of the species commonly occurring in mixed montane bush flocks. This may be partly due to the fact that adult male white-winged tanagers and flame-colored tanagers are largely bright red or orange (and immature males of both species frequently show traces of the same colors).

SIGNIFICANCE OF SOME OF THE PRINCIPAL DIFFERENCES BETWEEN MIXED BLUE AND GREEN TANAGER AND HONEYCREEPER FLOCKS AND THE HIGHER-ALTITUDE MIXED MONTANE BUSH FLOCKS

Among the more obvious differences between the higher-altitude mixed montane bush flocks (which seem to be the most highly, or most thoroughly, organized type of mixed montane bush flock) and the mixed blue and green tanager and honeycreeper flocks are the following:

1. All or most of the members of a mixed blue and green tanager and honeycreeper flock are usually confined to a rather narrow level of vegetation (usually the treetops) at any given time, while the members of higher-altitude mixed montane bush flocks are frequently scattered among many different levels of vegetation at the same time.

2. Supplanting attacks by individuals of one species upon individuals of other species are relatively common in mixed blue and green tanager and honeycreeper flocks, but relatively very rare in higher-altitude mixed montane bush flocks.

3. The nuclear members of mixed blue and green tanager and honeycreeper flocks are usually completely passive or completely active, while most of the nuclear species of higher-altitude mixed montane bush flocks can be either passive or active or may play an intermediate role.

4. Mixed blue and green tanager and honeycreeper flocks usually include species that have developed an apparently highly specialized

type of dull plumage to facilitate interspecific gregariousness; but none of the species of the higher-altitude mixed montane bush alliances seems to have evolved a specialized plumage to subserve similar functions.

These differences between the two types of flocks are presumably adaptive. They may also be causally related to one another.

It has already been mentioned that mixed blue and green tanager and honeycreeper flocks are usually restricted to one rather narrow level of vegetation because most of the species occurring in such flocks are usually restricted to one and the same rather narrow level of vegetation. Higher-altitude mixed montane bush flocks often extend through several different levels of vegetation because they frequently include species that prefer different levels of vegetation and/or frequently move back and forth between several different levels. (The usual restriction of most of the species of the blue and green tanager and honeycreeper alliance to one rather narrow level of vegetation may be an indication that most of these species are more narrowly specialized, restricted to narrower ecological niches, than many or most of the species of the higher-altitude montane bush alliances; but this would be extremely difficult, if not impossible, to prove.)

The members of mixed blue and green tanager and honeycreeper flocks are not only usually restricted to one rather narrow level of vegetation, but also frequently feed on the same foods. Thus they tend to compete with one another in a very direct way. This may help to explain why interspecific supplanting attacks are so relatively frequent in mixed blue and green tanager and honeycreeper flocks.

The performance of supplanting attacks within a flock is probably often disadvantageous because such attacks tend to reduce the cohesion of the flocks in which they occur; but this disadvantage must be outweighed, in the case of many or all of the members of the blue and green tanager and honeycreeper alliances by compensatory advantages. One of these is probably increased success in competition for food. Individuals of many species of the blue and green tanager and honeycreeper alliance probably obtain more food by performing supplanting attacks than they would if they did not do so. A bird that performs a supplanting attack upon another bird of the same or a different species, when the other bird is approaching food or actually eating, will usually force the other bird to retreat, at least temporarily, and may then be able to appropriate the food itself. It seems likely, therefore, that there have been strong selection pressures, during the evolution of many species of the blue and green tanager and honey-

creeper alliance, in favor of retaining the habit of performing supplanting attacks. The frequent performance of both interspecific and intraspecific supplanting attacks is probably a primitive character, as such attacks are often performed by individuals of many species that are not very gregarious.

Andrewartha and Birch (1954) have suggested that competition between animals of different species is seldom very significant. Their discussion of this subject is not, perhaps, very convincing (see Lack, 1954, and comments by Brown and Wilson, 1956, and Hutchinson, 1959). In any case, it should be emphasized that the relations between many members of mixed blue and green tanager and honeycreeper flocks are particularly clear examples of competition. The competition between such birds is often as overt as possible.

Members of higher-altitude mixed montane bush flocks compete directly with one another less frequently than do members of mixed blue and green tanager and honeycreeper flocks. Individuals of different species in higher-altitude mixed montane bush flocks try to feed on the same foods at the same times less frequently than do individuals of different species in mixed blue and green tanager and honeycreeper flocks. Individuals of the higher-altitude montane bush alliances would probably obtain extra food less frequently by the performance of supplanting attacks than do individuals of the blue and green tanager and honeycreeper alliance. This may be the reason why the advantages of performing many interspecific supplanting attacks seem to be outweighed by the disadvantages of such behavior in higher-altitude mixed montane bush flocks (the disadvantages presumably being the same as in mixed blue and green tanager and honeycreeper flocks).

(It is possible that the total amount of competition, both direct and indirect, between species of the higher-altitude montane bush alliances is less than the total amount of competition between species of the blue and green tanager and honeycreeper alliance; but this would also be very difficult, if not impossible, to prove.)

The differences between the interspecific hostile reactions of the species of the higher-altitude montane bush alliances and those of the species of the blue and green tanager and honeycreeper alliance seem to be intrinsic at the present time. They seem to be due to internal differences between the birds themselves, not their different environments. Birds of the higher-altitude montane bush alliances may occur in social situations that seem to be essentially similar to those in which birds of the blue and green tanager and honeycreeper alliance perform many interspecific supplanting attacks. They may even be-

come involved in such situations rather frequently (but less frequently, on the average, than birds of the blue and green tanager and honeycreeper alliance). But they still do not usually perform interspecific supplanting attacks in such situations. This would indicate that the reduced frequency of interspecific supplanting attacks by members of the higher-altitude montane bush alliances is a result of basic changes in their internal hostile drives (and/or their "innate" responsiveness to hostile stimuli) in the course of evolution. Interestingly enough, the intraspecific hostile reactions of all or most species of the higher-altitude montane bush alliances do not seem to have become reduced to the same extent in the course of evolution. Individuals of all or most of these species become engaged in disputes with other birds of the same species approximately as frequently as do members of the blue and green tanager and honeycreeper alliance which show a comparable degree of intraspecific gregariousness.

The frequency of interspecific supplanting attacks in mixed blue and green tanager and honeycreeper flocks may help to explain why the social roles of most of the nuclear species of these flocks are so clear cut and one sided, and why some species have developed unusually dull plumage. Because interspecific supplanting attacks tend to reduce the cohesion of mixed flocks, the species of the blue and green tanager and honeycreeper alliance have probably been subjected to particularly strong selection pressures in favor of developing mechanisms to minimize some of the effects of interspecific supplanting attacks and/or restore the cohesion of flocks as rapidly as possible after interspecific supplanting attacks. Both the dull plumage and/or the very one-sided nature of the social roles of some species may help to accomplish these objectives. They may both permit or facilitate particularly rapid "friendly" reactions within the mixed blue and green tanager and honeycreeper flocks.

The species of the higher-altitude mixed montane bush flocks may not have been subjected to strong selection pressures in favor of the development of similar characters simply because the cohesion of their flocks is seldom subjected to the sudden shocks of interspecific supplanting attacks.

SIMPLER MIXED FLOCKS

Three other types of mixed flocks that have been studied much less intensively than blue and green tanager and honeycreeper flocks or the mixed montane bush flocks may be described very briefly, as

they are comparatively simple and their organization may reveal something of the probable course of evolution of mixed flocks in general.

MIXED FLOCKS OF SMALL FINCHES

Several species of small finches tend to associate with one another more or less frequently in various lowland areas in Panamá. Among these species are the variable seedeater, the yellow-bellied seedeater, the thick-billed seed-finch (*Oryzoborus funereus*), the blue-black grassquit (*Volatinia jacarina*), and the dark-backed goldfinch (*Spinus psaltria*).

The mixed flocks of small finches in Panamá never include as many species as the larger mixed blue and green tanager and honeycreeper flocks or mixed montane bush flocks; but they do seem to be specialized societies, not merely casual aggregations. Some aspects of the social relationships between some of these finches have already been discussed elsewhere (Moynihan, 1960). The most interesting feature of many mixed flocks of small finches is the physical resemblance between some of the species included in the flocks. The adult males of several of these species of finches, including species that do not seem to be very closely related to one another, have largely or completely black plumage. This may be "social mimicry." It is possible that one or more of these species have evolved such plumage simply to facilitate associations with other species having similar plumage.

A few additional features of the mixed flocks of small finches would suggest that their organization is most nearly similar to that of the mixed blue and green tanager and honeycreeper flocks. The finches that occur together most frequently in the lowlands of central Panamá near the Canal Zone are the variable seedeater and the blue-black grassquit. Relatively brief observations of mixed flocks composed of these two species alone would suggest that the usual social roles of both species in such flocks are very clear cut and one sided. Blue-black grassquits join variable seedeaters very frequently, but variable seedeaters seldom or never join blue-black grassquits in such flocks. (The usual social role of variable seedeaters in mixed flocks that include individuals of some other species, such as yellow-bellied seedeaters, may be rather different, at least in some respects; but I have not been able to measure the extent of this difference.) The contrasting reactions of variable seedeaters and blue-black grassquits in mixed flocks that do not include other species seem to be correlated

with their social reactions apart from mixed flocks in much the same way as the corresponding reactions of most of the nuclear species of blue and green tanager and honeycreeper flocks and some of the nuclear species of mixed montane bush flocks. Variable seedeaters resemble such passive nuclear birds as plain-colored tanagers and brown-capped bush-tanagers in showing a high degree of intraspecific gregariousness; while blue-black grassquits resemble such active nuclear birds as palm tanagers and green honeycreepers in being only slightly gregarious among themselves apart from mixed flocks.

The members of all the mixed flocks of small finches in central Panamá usually feed on the same or similar food and tend to remain at approximately the same level (on or near the ground) most of the time they are together. It is probably significant, therefore, that interspecific supplanting attacks are common in such flocks. In flocks composed of variable seedeaters and blue-black grassquits alone, the variable seedeaters frequently supplant blue-black grassquits, but blue-black grassquits seldom or never supplant variable seedeaters.

MIXED FLOCKS ON CERRO CAMPANA

Cerro Campana is an isolated mountain, west of the Canal Zone in central Panamá, which reaches an altitude of approximately 3,300 feet above sea level. Part of the upper slopes of this mountain are covered by heavy montane forest, most of which seems to be mature. The bird fauna of the montane forest on Cerro Campana above approximately 2,000 feet includes a number of species that appear to be relicts in central Panamá. Several montane species that occur on both Cerro Campana and the Volcán de Chiriquí are found at much lower altitudes on the former mountain than on the latter. Such species may have been marooned on Cerro Campana at the end of the last cold period of the Pleistocene, and have become adapted to a warmer climate.

Many tanagers and related species occur on the upper slopes of Cerro Campana. Some of these species associate with one another to form mixed flocks, the most conspicuous of which occur in the treetops and along the edges of the montane forests, usually quite high above the ground. These flocks are usually composed of silver-throated tanagers, bay-headed tanagers, and/or tawny-capped euphonias (*Tanagra anneae*). Birds of other species also occur in such flocks, but seemingly relatively less frequently. Among the other birds I have seen associated with the mixed flocks of the montane forests of Cerro Campana are blue tanagers, green honeycreepers,

black-and-yellow tanagers (*Chrysothlypis chrysomelas*) hepatic tanagers (*Piranga flava*), and various small flycatchers and (wintering) warblers. Such flocks seldom or never include more than a single individual, pair, or family group of any given species at any given time.

Unlike the other mixed flocks discussed above, these mixed flocks on Cerro Campana do not seem to be specialized societies. They appear to be essentially casual aggregations of birds that happen to be feeding more or less together in the same area but are not very strongly attracted to one another. Clear-cut interspecific following and joining reactions are relatively rare in such aggregations. Even the blue tanagers and the green honeycreepers do not join and/or follow individuals of other species very frequently on Cerro Campana. (They might join and/or follow one another very frequently if they had more chances to do so; but both species are rare in these montane forests.) None of the primarily montane species commonly occurring in these aggregations seems to have any definite special interspecific preference for any other species, and most of the associations between these species seem to be relatively brief. The species of the mixed flocks on Cerro Campana are also very diversely colored and do not seem to have developed any special type of plumage to facilitate their roles in the mixed flocks of this area.

In general, the mixed flocks of the montane forests on Cerro Campana are most reminiscent of the lower-altitude mixed montane bush flocks on the Volcán de Chiriquí, without the nuclear species which usually or frequently occur in the Chiriquí flocks.

RAMPHOCELUS FLOCKS

Different species of *Ramphocelus*, which usually do not form very close associations with birds of most other genera, do tend to associate with one another rather closely in some areas and habitats where their ranges overlap. I have seen associations between two different pairs of *Ramphocelus* species.

Mixed flocks of crimson-backed tanagers and yellow-rumped tanagers occur in many areas in central and eastern Panamá. I have observed them at rather long intervals between March 1958 and November 1960 in the Canal Zone, near María Chiquita on the Atlantic coast of central Panamá, and in Darién.

Mixed flocks of silver-billed tanagers (*R. carbo*) and black-throated tanagers (*R. nigrogularis*) were observed for a few days

between December 17 and December 24, 1958, near Iquitos in the Amazonian region of eastern Perú.

CRIMSON-BACKED TANAGERS AND YELLOW-RUMPED TANAGERS

Adult male yellow-rumped tanagers are largely pure velvety black, with whitish bills and bright lemon yellow on the lower back and rump. Adult females and young of both sexes are generally brownish, with yellow lower back, rump, breast, and belly.

Yellow-rumped tanagers show a much higher degree of intraspecific gregariousness than crimson-backed tanagers. They tend to form flocks of 8 to 12 individuals (i.e., definitely larger than a single family group of parents and one brood of young). Such flocks seem to be maintained rather steadily throughout the nonbreeding season, and also occur, at least occasionally, in the breeding season.

Like most other highly gregarious birds, yellow-rumped tanagers are very restless and noisy. Some of their more complex calls are quite distinctive, very different from any calls of any other tanager or related species occurring in the lowlands of central and eastern Panamá; but their most common notes are very similar to those of crimson-backed tanagers in sound. Both yellow-rumped tanagers and crimson-backed tanagers utter thin *tseeet* notes and nasal *anh* notes very frequently.

The habitat preferences of yellow-rumped tanagers and crimson-backed tanagers are similar in some ways and different in others. Both species prefer scrub, but yellow-rumped tanagers prefer scrub along the banks of rivers and streams, and crimson-backed tanagers prefer scrub in slightly higher and drier areas some distance away from the banks of rivers. Yellow-rumped tanagers sometimes stray away from their usual habitats, and move into typical crimson-backed tanager habitats; but such occurrences seem to be relatively rare. Crimson-backed tanagers seem to occur in typical yellow-rumped tanager habitats somewhat more frequently.

All my observations of yellow-rumped tanagers and crimson-backed tanagers in the same flocks were made in typical yellow-rumped tanager habitats. In such habitats, yellow-rumped tanagers are always much more abundant than crimson-backed tanagers.

It is usually apparent in such habitats that crimson-backed tanagers tend to stay closer to yellow-rumped tanagers than to any other tanagers, honeycreepers, or finches in the same area at the same time. They may also follow and join yellow-rumped tanagers in a clear-cut and conspicuous manner more frequently than they follow and join all

or most of the regular members of the blue and green tanager and honeycreeper flocks in the same (see below) and other habitats; but the actual frequency of such reactions is usually not very high. Crimson-backed tanagers certainly follow and join yellow-rumped tanagers much less frequently, on the average, than palm tanagers join and follow several other species of the blue and green tanager and honeycreeper alliance in central Panamá during the nonbreeding season. What the crimson-backed tanagers usually manage to do is stay in the vicinity of yellow-rumped tanagers without appearing to follow them in any regular manner or coming very close to any particular individual.

The responsiveness of crimson-backed tanagers to yellow-rumped tanagers is probably not strong enough to be considered a special interspecific preference. It is not a more frequent occurrence than would be expected as a result of generalized gregariousness, in view of the similar notes and preference for scrub of the two species.

Yellow-rumped tanagers also tend to follow and join crimson-backed tanagers relatively more frequently than they are followed and joined by the latter; but their reactions to crimson-backed tanagers are even more obviously not the results of a special interspecific preference. Yellow-rumped tanagers tend to follow and join almost all other tanagers and finches that occur in or near the scrub along river banks. Their responsiveness to individuals of so many other species seems to be a reflection of their extreme gregariousness among themselves. Their tendency to join and follow one another seems to be so strong that it frequently "overflows," to be vented upon suboptimal stimuli.

It has already been mentioned that special signal patterns and some related characters that seem to be adaptations to promote intraspecific gregariousness will usually or always tend to attract individuals of other species also, but that this attraction may be weakened by other factors. Most species are usually more strongly attracted to other species that are more or less similar to themselves than to other species that are very different. The relations between crimson-backed tanagers and most other species of the blue and green tanager and honeycreeper alliance were cited as an example. Most species of this alliance are probably attracted by the restlessness and general conspicuousness of crimson-backed tanagers, but not as strongly as they would be if the latter were not so distinctive in color and voice.

The relations between yellow-rumped tanagers and the species of the blue and green tanager and honeycreeper alliance may be an even

more striking example of the same phenomenon or, perhaps more probably, an example of definite interspecific "aversion."

The characters of yellow-rumped tanagers that seem to be adapted to promote intraspecific gregariousness are somewhat more extreme or exaggerated than the corresponding characters of crimson-backed tanagers (the "flash" patterns of yellow-rumped tanagers are even more conspicuous than those of crimson-backed tanagers, and yellow-rumped tanagers are probably even noisier, on the average, than crimson-backed tanagers); but yellow-rumped tanagers seem to attract individuals of most species of the blue and green tanager and honeycreeper alliance much less frequently than do crimson-backed tanagers, even in the most favorable circumstances. Individuals of several species that are regular members of the blue and green tanager and honeycreeper flocks (including plain-colored tanagers, palm tanagers, blue tanagers, and golden-masked tanagers) sometimes come down to the shrubbery along the edges of rivers, if there are no trees nearby. At such times they usually ignore the yellow-rumped tanagers almost completely. Even palm tanagers seem to join and follow yellow-rumped tanagers relatively very rarely.

It is conceivable that most members of the blue and green tanager and honeycreeper alliance tend to ignore yellow-rumped tanagers simply because the latter are so distinctive in voice and appearance. To the human eye and ear, however, yellow-rumped tanagers are not more different from most of the members of the blue and green tanager and honeycreeper alliance than are crimson-backed tanagers. It is perhaps more likely, therefore, that most of the members of the blue and green tanager and honeycreeper alliance have developed a specialized aversion to yellow-rumped tanagers, a special power of resistance to the attraction of their restlessness and conspicuousness. This aversion may have been developed in order to avoid being sucked down into low shrubbery too frequently. There are indications that associations with any species that is largely confined to low scrub and thickets may be disadvantageous for most members of the blue and green tanager and honeycreeper alliance.

Two other scrub-inhabiting species, the dusky-tailed ant-tanager and the dusky-faced tanager (*Mitrospingus cassinii*), are common in parts of central and eastern Panamá. Both are noisy, restless, rather gregarious among themselves, and less distinctively colored than either yellow-rumped tanagers or crimson-backed tanagers. It has already been mentioned that dusky-tailed ant-tanagers sometimes encounter many members of the blue and green tanager and honeycreeper alli-

ance in certain special circumstances. The same is true of dusky-faced tanagers. When such encounters occur, most of the members of the blue and green tanager and honeycreeper alliance, except crimson-backed tanagers (see below), tend to ignore the dusky-tailed ant-tanagers and dusky-faced tanagers in much the same way that they do yellow-rumped tanagers. (Slud, 1960, has already noted that dusky-faced tanagers are usually ignored by birds of other species in Costa Rica.) It seems likely that many or most members of the blue and green tanager and honeycreeper alliance have developed special aversions to dusky-tailed ant-tanagers and dusky-faced tanagers as well as yellow-rumped tanagers.

Such aversions are quite different from hostile interspecific preferences, such as those of green honeycreepers and shining honeycreepers for red-legged blue honeycreepers. The aversions are revealed by a conspicuous lack of overt responses, while the hostile interspecific preferences are expressed by supplanting attacks and/or other overt aggressive acts.

The habitat preference of yellow-rumped tanagers may also impede associations with other species in another way. Most members of the blue and green tanager and honeycreeper alliance (again with the exception of crimson-backed tanagers) are reluctant to remain in the scrub along the edges of rivers for any considerable length of time. They seldom remain in this environment for more than a few seconds or minutes before flying to trees or other scrub. This behavior effectively neutralizes the joining and following tendencies of yellow-rumped tanagers, simply because the latter are usually very reluctant to leave the river-bank scrub.

Although yellow-rumped tanagers do not play a significant social role in any highly integrated or very complex mixed flocks in central and eastern Panamá at the present time, they may be partly or completely preadapted to do so. It is easy to imagine how a relatively slight change in the habitat preference of yellow-rumped tanagers, or the appearance in the region of a new species that did not have a special aversion to them, or the loss of the special aversion by one of the species that already occurs in the region, would allow the yellow-rumped tanagers to play a more important nuclear role in mixed flocks (which might appear to be highly integrated from the very beginning).

(Crimson-backed tanagers occasionally associate quite closely with dusky-tailed ant-tanagers in certain scrub areas. Young crimson-backed tanagers just out of the nest seem to be more likely to form such associations than older birds. Such young birds may well be de-

ceived by the appearance of dusky-tailed ant-tanagers, which are similar to crimson-backed tanagers in shape and many of their actions, and the males of which are brownish with some red on the throat and crown. The young crimson-backed tanagers may be reacting to dusky-tailed ant-tanagers as they would to other members of their own species.)

SILVER-BILLED TANAGERS AND BLACK-THROATED TANAGERS

The silver-billed tanagers and black-throated tanagers that were observed associating with one another were relatively few in number, one family group (parents with two or three young) of each species. These two families roosted separately at night, but usually came together shortly after dawn and spent an appreciable part of every day together for at least seven consecutive days (as long as my observations continued). These birds are very similar in shape and, to a lesser extent, color (red and black). Individuals of both species utter *tseeet* notes very frequently.

The social roles of the two species in this mixed flock were not very well differentiated. Sometimes the silver-billed tanagers joined and followed the black-throated tanagers; and sometimes the black-throated tanagers joined and followed the silver-billed tanagers. Both types of reactions were quite common, in both directions. Presumably further observations would have shown that one species joined and followed the other species at least slightly more frequently than the reverse, on the average, over a long period of time; but my observations were too brief to permit a quantitative analysis of the reactions between the two species. Interspecific supplanting attacks and other hostile patterns were quite common in this mixed flock. Sometimes one species was the aggressor, and sometimes the other.

Competition for food between the two species was certainly increased when they associated with one another. When they were not together the silver-billed tanagers usually stayed in moderately to very low scrub, while the black-throated tanagers usually stayed at a somewhat higher level in low trees. When they were together, however, the individuals of both species usually moved and fed at the same level, apparently eating the same foods. This change was usually due to a change in the behavior of the black-throated tanagers, which when they were associated with the silver-billed tanagers, frequently came down into scrub that was lower than anything they visited when they were alone.

It may be significant, in this connection, that black-throated tanagers were relatively rare in the area near Iquitos (the birds that associated with the silver-billed tanagers were the only black-throated tanagers I saw in this area), while the silver-billed tanagers were comparatively common. It is possible that this area is not a very favorable environment for black-throated tanagers, or that the ones I saw had just moved into the area and may have been partly dependent upon the silver-billed tanagers' ability to discover food sources (see below).

DISCUSSION

THE ADVANTAGES OBTAINED BY MEMBERSHIP IN MIXED FLOCKS

All or almost all the authors who have discussed the functions of mixed flocks have suggested that birds become associated in such flocks in order to get food, to get protection from enemies, and/or to satisfy some gregarious motivation or instinct (see the summary in Rand, 1954). All three suggestions may be correct. It should be noted, however, that the three functions are not strictly commensurable.

The habit of associating in mixed flocks may be an adaptation to get food and/or protection, but it can hardly be described as an adaptation, in the same sense of the term, to satisfy a gregarious instinct. From an evolutionary point of view the development of a gregarious instinct that can be satisfied by association in mixed flocks is probably a means to an end, not an end in itself.[16] A bird may join individuals of other species, or allow itself to be joined by individuals of other species, because such associations satisfy its gregarious instincts; but such instincts probably have been evolved, in all or most cases, because interspecific gregariousness provides certain concrete advantages. Gregariousness seems to be a type or method of adaptation,

[16] In ethological terms, association with individuals of other species may be considered a "consummatory situation" for any bird that derives a definite satisfaction from such an association. Searching for individuals of other species to become associated with may be considered a form of "appetitive behavior." (See discussions of these terms in Tinbergen, 1951; Hinde, 1953; and Bastock, Morris, and Moynihan, 1953.) Unfortunately, there have been almost no analytical studies of the motivations impelling an individual of one species to become associated with individuals of other species. It is possible that individuals of some species have some sort of interspecific gregarious drive, which can be satisfied only by associations with individuals of other species, quite apart from any intraspecific gregarious drive or gregarious aspects of other instincts; but this has certainly not yet been proved to exist.

while food and protection are advantages that may be obtained by the adaptation.

It seems likely that many or most members of many or most mixed flocks obtain both extra food and added protection, more or less simultaneously, by their associations with one another; but the relative importance of the two advantages is probably very different for different species and for individuals of the same species at different times. This certainly seems to be true in the case of most members of the mixed flocks studied in Panamá.

Some observers of tropical mixed flocks (e.g., Chapin, 1932; Rand, 1954; Slud, 1960; and Swynnerton, 1915) have suggested that they are primarily feeding associations, that all or most birds become associated with such flocks primarily or exclusively because they tend to get more food when they are in mixed flocks than when they are not. This generalization seems to have been derived from observation of mixed flocks of birds that are primarily or exclusively insectivorous and live inside tropical forests (these were the first tropical mixed flocks to be studied).

Some of the primarily or exclusively insectivorous birds in mixed blue and green tanager and honeycreeper flocks and mixed montane bush flocks, e.g., summer tanagers, Wilson's warblers, red-faced spinetails, and the redstarts, probably obtain feeding advantages by associating with mixed flocks, and maintain such advantages nearly continuously as long as they remain within the flocks, in much the same way as do insectivorous birds inside tropical forests. The other members of mixed flocks must at least frequently serve as beaters for some of the insectivorous birds.

There are many indications, however, that the food factor is less important in the case of many other members of many mixed blue and green tanager and honeycreeper flocks and mixed montane bush flocks. The primarily frugivorous and/or nectarivorous birds probably do not obtain feeding advantages from their associations with mixed flocks as frequently or as consistently as do the insectivorous birds. It is often obvious that they are not helping one another to get food. It is difficult, in fact, to imagine how frugivorous and/or nectarivorous birds that are territorial or confined to definite home ranges could derive any considerable feeding advantages by associating with mixed flocks as long as they remain in or near their usual territories or ranges. Such birds are usually thoroughly familiar with the actual and potential sources of fruit and nectar in and near their

territories or ranges.[17] They probably encounter more competition when they associate with individuals of other species of more or less similar feeding habits than they would if they always fed by themselves alone. It seems likely, therefore, that protection from enemies is the most important advantage obtained by many members of the blue and green tanager and honeycreeper alliance and the montane bush alliances by most of their associations in mixed flocks in ordinary circumstances.

The importance of the protection factor has been doubted by some observers of mixed flocks, largely because mixed flocks are so conspicuous that predators probably notice the members of such flocks more frequently than they would notice the same birds apart from mixed flocks. This does not, however, mean that birds in mixed flocks are actually preyed upon more frequently than birds of the same species apart from mixed flocks. (As far as I am aware, there have been no quantitative studies comparing the amount of predation upon birds in mixed flocks with the amount of predation upon birds of the same species in the same environment but not in mixed flocks.) There is, in fact, some actual evidence that birds in mixed flocks are particularly efficient at discovering and/or discouraging potential predators; and various theoretical considerations would suggest that the habit of forming mixed flocks may help to protect birds from predators in several other ways.

Birds in mixed flocks are usually particularly efficient at mobbing predators. Because they usually stay rather close together, the members of a flock usually respond relatively rapidly when one member of the flock begins mobbing.

Birds in mixed flocks probably notice predators more frequently and sooner, on the average, than they would if they were not in flocks. As soon as one member notices a predator, it will usually warn all the others. (Winterbottom, 1943, did not think that such warnings produced much effect in the mixed flocks he observed in Northern Rho-

[17] In an earlier paper (Moynihan, 1960) it was mentioned that gregariousness may be particularly advantageous to birds that feed on fruits that occur in irregularly scattered masses, e.g., on scattered fruit trees far apart from one another. It may be necessary for such birds to make extensive searches over wide areas for their food, and they may tend to get more food, on the average, if they go searching in groups. The situation of most of the frugivorous members of the blue and green tanager and honeycreeper alliance and the montane bush alliances is usually quite different. They tend to feed on fruits and other vegetable materials that are fairly evenly distributed and common in the environments in which they live; and their searching for food is usually intensive rather than extensive.

desia. They do, however, seem to be very effective in the mixed flocks in Panamá. Alarm notes by one bird will at least put the other members of a flock in a state of alert.)

Birds that are not very shy by themselves will often retreat from a potential predator sooner when they are associated with shyer species in a mixed flock than when they are not in a mixed flock. Thus, for instance, the comparatively tame and unsuspicious plain-colored tanagers usually flee from an approaching human being sooner when they are in mixed flocks than when they are in similar flocks (of similar size) of their own species alone.

Predators attempting to attack a member of a flock may be distracted by the other members of the flock and hesitate for a moment, thus allowing all the members of the flock to escape. It is even possible that predators are more reluctant to try to attack a bird in a group than a solitary bird, because a group is slightly more intimidating.

Although protection may be the most important advantage obtained by many members of the blue and green tanager and honeycreeper alliance and the montane bush alliances in mixed flocks in ordinary circumstances, this does not necessarily mean that it is always the most important advantage. Even in the case of the frugivorous and/or nectarivorous birds, the discovery of food may be the most important advantage obtained by association with mixed flocks in certain special circumstances. Thus, for instance, a bird moving into a new and unfamiliar area may associate with individuals of other species in order to find the sources of food in this new area; but it may then continue to associate with the other individuals after it has discovered the food sources, and may then derive other advantages, such as added protection from predators, or no advantages at all.

It will be noted from the above account that the advantages that may be obtained by membership in mixed flocks, including both the discovery of food and protection from predators, could also be obtained by membership in flocks of a single species. This raises an interesting question. Granted that gregariousness is often advantageous in one way or another (as it obviously is), why do more species occur in mixed flocks than in unmixed flocks of their own species alone (apart from family groups)? Unmixed flocks might be easier to form and maintain, and might provide certain other social advantages that are lacking in mixed flocks. The answer to this question is probably that the members of an unmixed flock often compete with one another too strongly. Birds of the same species tend to compete with one another more strongly than birds of different species. Associa-

tion with individuals of other species in mixed flocks may provide most of the advantages that could be obtained by association with other individuals of the same species in an unmixed flock, without the disadvantages of membership in an unmixed flock.

THE ORIGIN OF HIGHLY INTEGRATED MIXED FLOCKS

On logical grounds, one might expect that highly integrated mixed flocks could develop by extension and "regularizing" of occasional associations between species that are closely related to one another phylogenetically,[18] such as the crimson-backed and yellow-rumped tanagers, and/or by strengthening and specialization of the social bonds between less closely related species that may occur together in larger but essentially casual aggregations, such as the montane forest groups on Cerro Campana. There is some evidence that the latter process may have been more important than the former in the evolution of most highly integrated mixed flocks of passerine birds.

Occasional and loose associations between species that are closely related to one another phylogenetically are common in many areas. The reasons for this are obvious. Closely related species often have similar habits and often occur in the same general habitats when they occur in the same areas. Closely related species are also often similar in appearance, at least in shape or some details of their plumage patterns. Unless inhibited or counteracted by other factors, such similarities will inevitably tend to promote or facilitate associations between closely related species whenever they come into social contact with one another. Regular and close associations between closely related species seem to be much less common among passerine birds. Closely related (i.e., congeneric) species of passerine birds seem to be linked by specialized social bonds less frequently than are less closely related species. This may also be a result of competition.

As a general rule, different species of birds that occupy the same areas and habitats can only compete with one another to a certain limited extent if they are to continue to live side by side. One species will usually or always replace another (or others) in any given area and habitat unless there is some sort of (at least partial) ecological isolation between the species. The principle of "competitive exclusion," i.e., the principle that "complete competitors cannot coexist"

[18] It will be necessary in some parts of the following discussion to use the terms "related" and "relationships" in two different senses, to refer to both phylogenetic and social relationships. The type of relationship discussed in any given passage will be specified, or should be clear from the context.

(Hardin, 1960), has been questioned or denied (see, for instance, Cole, 1960); but it does seem to be a valid generalization in the case of many species of birds (see, for instance, Lack, 1944 and 1947, and Moreau, 1948). All other factors being equal, species that are closely related to one another phylogenetically probably tend to compete with one another more strongly, in most cases, than species that are distantly related to one another, simply because the habits of closely related species (including their feeding habits) are usually more similar than the habits of distantly related species.

Although closely related species that occur in the same areas and habitats must almost certainly differ from one another in some aspects of their ecology, the ecological isolation between them can only be partial. For this reason, and because such species are usually or always similar to one another in many other characters, the ecological differences between such species probably tend to disappear in certain circumstances. Unless strongly reinforced by other factors, the partial ecological isolation between such species is almost certain to break down or become increasingly ineffective if the species should begin to associate with one another increasingly frequently and closely—as they are bound to do if they become incorporated in the same highly integrated type of mixed flock. There will thus be strong selection pressure, in many or most cases, to prevent closely related species from associating with one another very frequently and closely and/or to increase and strengthen the ecological differences between closely related species when they do associate with one another. Thus, highly integrated flocks that regularly include two or more closely related species are relatively rare (among passerines); and when they do occur, the closely related species tend to have very distinctly different feeding habits (e.g., the *Parus* species in mixed flocks in European woodlands—see Hartley, 1953; Gibb, 1954; and Snow, 1954).

Among the tanagers, honeycreepers, and finches of mixed flocks in Panamá, the most conspicuous examples of two closely related species frequently occurring in the same mixed flocks is provided by the palm tanager and the blue tanager. These two species coexist over a large part of tropical America; but they have slightly different habitat preferences, and the blue tanager seems to be slightly more insectivorous than the palm tanager (at least around the clearing on Barro Colorado Island). It is probably also significant that the palm tanager and the blue tanager are more often separated by their different habitat preferences during the breeding season, when competition be-

tween them might otherwise be most intense, than during the non-breeding season.

(One aspect of the social relationships between these two species in Panamá may possibly be typical of the social relationships between many other overlapping species of equally similar habits. Palm tanagers and blue tanagers associate with one another very frequently in Panamá; but this is probably more often due to the fact that they both tend to join and follow plain-colored tanagers than to their tendencies to join and follow one another. Their associations, in other words, are more often indirect than direct.)

It seems likely, therefore, that the first highly specialized bonds to develop during the evolution of most highly integrated mixed flocks of passerine birds were bonds between species that were not very closely related, phylogenetically (i.e., species of different genera, or even, in many cases, different families).

All or almost all highly integrated flocks of passerine birds usually or always include individuals of certain particular species that show a high degree of intraspecific gregariousness and play a nuclear role in the mixed flocks. Numerous examples may be cited. Among the flocks of tanagers, honeycreepers, and finches in Panamá, there are the plain-colored tanagers in mixed blue and green tanager and honeycreeper flocks, the brown-capped bush-tanagers in mixed montane bush flocks, the variable seedeaters in mixed flocks of small finches, and the yellow-rumped tanagers in *Ramphocelus* flocks. Among other types of flocks there are white-flanked ant-wrens (*Myrmotherula axillaris*) in mixed flocks of insectivorous birds in the lowland forests of central Panamá (Johnson, 1954, and R. H. Barth Jr., in litt.); green-headed tanagers (*Tangara seledon*) in mixed flocks of tanagers and honeycreepers in southern Brazil (Mitchell, 1957); various species of *Acanthiza*, gray fantails (*Rhipidura flabellifera*), orange-winged sittellas (*Neositta chrysoptera*), and probably some other species, in mixed flocks of insectivorous birds in Australia (Gannon, 1934, and Hindwood, 1937); white-headed vangas (*Artamella viridis*) in some mixed flocks of forest birds in Madagascar (Rand, 1936); and black-capped chickadees (*Parus atricapillus*) in mixed flocks in North American woods in winter (Odum, 1942).

More often than not there is only one species that shows a high degree of intraspecific gregariousness included in any given type of mixed flock in any given area. This would suggest that the usual course of evolution of many highly integrated mixed flocks of pas-

serine birds may be as follows. The first stage is probably usually the formation of specialized social bonds between a species that shows a high degree of intraspecific gregariousness and one or a few other species that do not show a high degree of intraspecific gregariousness. The former species is almost certain to become a passive nuclear species in the evolving flock. The subsequent history of the flock is probably largely dependent upon the nature of the other species that first become attached to the passive nuclear species. If these species become attendant species, the flock may not develop much further. If one or more of them should become an active nuclear species, however, this may provide a strong impetus to further elaboration of the flock. Active nuclear species will greatly increase the conspicuousness of the flock and contribute a variety of new stimuli, new sounds, colors, visual patterns, and/or movements, to broaden and strengthen the general effect which the flock produced upon other species in its vicinity. These additions may increase the attractiveness of the mixed flock to other species and induce the other species to become regular members of the flock in turn. If one or more of these new regular members should also become active nuclear species, this may provide another strong impetus to further elaboration of the flock. Thus, the flock may grow by a snow-balling process until all the suitable species in the area and environment have become incorporated in it in one way or another.

One of the later stages in the development of many large and complex types of mixed flocks may be the fusion of smaller types of mixed flocks, each of which grew up around a different passive nuclear species. It is possible, for instance, that the typical large blue and green tanager and honeycreeper flocks in Panamá were developed by an incomplete fusion of predominantly tanager flocks and predominantly honeycreeper flocks.

The evolution of very specialized morphological and behavioral characters, such as neutral coloration, social mimicry, and the reduction or loss of interspecific aggressiveness, by some or all of the regular members of the flock, may also be typical of the later stages in the development of many mixed flocks. Neutral coloration and the reduction of interspecific aggressiveness probably facilitate the incorporation of more new members in the flock; but social mimicry may have just the opposite effect. As social mimicry will tend to make the members of a flock more and more homogeneous in appearance and/or voice, it will probably make it more and more difficult for other species of dissimilar appearance or voice to join the flock. Social

mimicry, in other words, will tend to make a flock a closed society. It is probably significant that the largest mixed flocks of small finches in Panamá, in which social mimicry seems to be most highly developed, include fewer species than many mixed blue and green tanager and honeycreeper flocks and mixed montane bush flocks.

THE DISTRIBUTION OF MIXED FLOCKS AND THE SPECIES INCORPORATED IN SUCH FLOCKS

There seems to be a general correlation between the social roles and the geographical distribution of many tanagers and finches and some other birds that are regular members of mixed flocks in tropical America. This correlation is clear in the case of the species of the mixed blue and green tanager and honeycreeper flocks. The plain-colored tanager, which is much the most important passive nuclear species in fully-developed blue and green tanager and honeycreeper flocks, has by far the most restricted distribution of any of the regular members of such flocks. It is confined to the lowlands of Colombia, Panamá, and Costa Rica.[19] This is appreciably smaller than the range of the golden-masked tanager, which is probably closely related to the plain-colored tanager (the two species share a number of characters that are not found in other Panamanian species of *Tangara*), and occurs in many of the same habitats in Panamá, but is apparently an active nuclear species in mixed blue and green tanager and honeycreeper flocks. Various subspecies of the golden-masked tanager extend from western Ecuador to southeastern México. (Hellmayr, 1936, includes the form *nigro-cincta* in the same species; but this has been questioned by Eisenmann, 1957. If *larvata* and *nigro-cincta* are really conspecific, then the range of the species also extends over most of tropical eastern South America.) All the other, more important, active nuclear species among the more common regular members of the mixed blue and green tanager and honeycreeper flocks, i.e., the palm tanager, the blue tanager, and the green honeycreeper, are at least as widely distributed as the golden-masked tanager, extending over all or most of the lowlands of tropical Central and South America.

Similar mixed flocks of tanagers and honeycreepers occur in the

[19] Unless stated otherwise, these and the following summaries of the ranges of different species are based upon Hellmayr, 1925 (furnariids), 1935 (vireos, warblers, and honeycreepers), 1936 (tanagers), and 1938 (finches).

Hellmayr states that the plain-colored tanager is confined to Colombia and Panamá; but it has been found in northeastern Costa Rica by Slud (1960).

lowlands of southern Brazil, and have been described by Mitchell (1957). The most common birds in some of these flocks are green-headed tanagers. Mitchell suggests that they play a nuclear role in these flocks. Her description would imply that they show a high degree of intraspecific gregariousness and are usually or always passive nuclear in mixed flocks.[20] The distribution of green-headed tanagers is comparatively restricted. They are confined to the wooded regions

[20] As the social behavior and social relationships of the green-headed tanager seem to be at least roughly similar to those of the plain-colored tanager, it may be of interest to compare some of the other characters of the two species.

Like the plain-colored tanager, the green-headed tanager seems to have lost the warbling song patterns that are conspicuous in the signal repertories of many less gregarious species of *Tangara* (Butler, 1894).

Mitchell noted that most of the plumage of many of the green-headed tanagers in the flocks she watched was "mottled and nondescript." The birds with such plumage may have been young. Mitchell also cites Descourtilz (1856) who thought that green-headed tanagers take three years to attain fully adult plumage. None of the Central American species of *Tangara* seems to take as long to attain fully adult plumage (Skutch, 1954). It is conceivable, therefore, that green-headed tanagers retain their dull juvenile plumage for a relatively long period of time as an adaptation to facilitate their role in mixed flocks. Their relatively dull juvenile plumage may subserve the same function, in the same way, as the dull neutral plumage of both adult and young plain-colored tanagers.

The fully adult plumage of green-headed tanagers is even more interesting in this connection. In an earlier discussion of the plain-colored tanager, quoted above, it was suggested that the dull neutral coloration of this species is partly a compromise. Such coloration may have been evolved because plain-colored tanagers could not evolve plumage colors and patterns more like those of their most common associates in mixed flocks, simply because the colors and patterns of these associates are themselves very diverse. It is possible, however, that green-headed tanagers have been able to achieve this difficult feat. The species that associate with green-headed tanagers are also very diverse in color and pattern; but the coloration of adult green-headed tanagers is far from dull. It includes areas of orange, yellow, two or three shades of green, bright blue, violet, and black, arranged in such a way as to provide the maximum amount of "flash." Many of the other species that encounter green-headed tanagers may find some or all of the colors of their own plumages matched or nearly matched in the colors of the plumage of adult green-headed tanagers. This would be expected to render adult green-headed tanagers particularly attractive to a wide variety of other species.

The plumage of adult red-necked tanagers (*Tangara cyanocephala*), which occur in some of the same flocks as green-headed tanagers, is equally brilliant and varied, including areas of bright red, bright green, blue, and black.

It might be convenient to call plumages such as those of adult green-headed tanagers and red-necked tanagers "bright neutral" plumages, in contrast to the "dull neutral" plumages of plain-colored tanagers and young green-headed tanagers.

of southeastern Brazil, Misiones, and eastern Paraguay. Mitchell also cites a number of other species as more or less frequent associates of the green-headed tanager in mixed flocks, including the red-necked tanager, Spix's scarlet-crested tanager (*Tachyphonus cristatus*), the rufous-headed tanager (*Hemithraupis ruficapilla*), the yellow-headed tanager (*H. flavicollis*),[21] the bananaquit, and the blue dacnis. Mitchell's description would imply that all or most of these species are usually or always active nuclear or attendant species in these flocks. They are all much more widely distributed than the green-headed tanager.

Slud (1960) has described certain aspects of some mixed flocks that occur in lowland forest and scrub in northeastern Costa Rica, in an area that is more humid, or more consistently humid, than most of central Panamá. Some of these Costa Rican flocks are largely or completely composed of tanagers, honeycreepers, and/or finches. Slud cites three species of tanagers and one species of finch that are rare or absent in central Panamá but are common and tend to play nuclear roles in mixed flocks in Costa Rica. These species are the black-faced grosbeak (*Caryothraustes poliogaster*), the olive tanager (*Chlorothraupis carmioli*), the tawny-crested tanager (*Tachyphonus delatrii*), and the great shrike-tanager (*Lanio aurantius*).[22] The first three species show a high degree of intraspecific gregariousness and seem to play passive nuclear roles in all or most of the mixed flocks with which they are associated. Their social behavior would thus appear to be essentially identical with that of plain-colored tanagers in central Panamá. Great shrike-tanagers are not highly gregarious among themselves, but also seem to play a passive nuclear role in mixed flocks. All four of these passive nuclear species have comparatively restricted ranges. The black-faced grosbeak extends from southeastern México to central Panamá. The olive tanager extends from eastern Nicaragua to eastern Panamá, and has an isolated population in part of tropical Perú. The tawny-crested tanager extends from eastern Nicaragua to western Ecuador. The great shrike-tanager extends from southeastern México to western Panamá. It will be noticed that none of these species is widely distributed in the Amazonian region of South America. The ranges of these species cannot, unfortunately, be compared with those

[21] The Latin names of these purely South American species follow Pinto (1944). The English vernacular names are those used by Mitchell.

[22] Both the scientific and vernacular names of these species follow Eisenmann, 1955.

of their most important associates, as Slud does not mention which species played active nuclear roles in the flocks he observed. He does, however, state that the green honeycreeper, which is an active nuclear species in central Panamá, also occurs in mixed flocks in Costa Rica. Three of the four passive nuclear species cited by Slud are the only species of their genera in Costa Rica (and most of Central America); but there are two other species of *Tachyphonus* in Costa Rica, the white-shouldered tanager and the white-lined tanager, that do not seem to play nuclear roles in the Costa Rican mixed flocks, any more than they do in mixed blue and green tanager and honeycreeper flocks in central Panamá (see above). It may be significant, therefore, that both the white-shouldered tanager and the whilte-lined tanager are very widely distributed, much more so than the closely related but passive nuclear tawny-crested tanager. The white-shouldered tanager and the white-lined tanager extend over all or most of Amazonian South America.

(Both sexes or the adult males of the four passive nuclear species cited by Slud are largely black and/or yellow or yellow-olive. Several other tanagers and some migrant warblers that Slud observed associating with mixed flocks are also prominently marked with black and/or yellow. Such similarities are presumably not coincidental and may facilitate the formation of mixed flocks in much the same way as the similar colors of many members of the montane bush alliances.)

Finally, variable seedeaters, which are very gregarious among themselves, are much less widely distributed than blue-black grassquits, which are much less gregarious among themselves but tend to join and follow variable seedeaters in mixed flocks of small finches.

These facts would suggest that there may be a very general rule, among many different types of lowland tanagers and finches in tropical America, that species that play passive nuclear roles in mixed flocks have comparatively narrow ranges, while species that play active nuclear roles have very broad ranges.

Within the lowlands of the American Tropics, the occupation of new areas may be easier for individuals of active nuclear species adapted to lowland tropical habitats than for individuals of passive nuclear species that are otherwise equally well adapted to such habitats. Individuals of the two types of species may reach new areas equally frequently, on the average, and may be almost equally likely to secure mates in new areas (see below); but individuals of active nuclear species moving into a new area are probably much more likely to form strong social bonds with other species already established in the area

than are individuals of passive nuclear species. Individuals of active nuclear species moving into a new area probably tend to join and follow individuals of many already-established species, including passive nuclear species, other active nuclear species, and less specialized species. Individuals of passive nuclear species moving into a new area are probably not joined and followed by individuals of as many already established species. They may attract active nuclear species and less specialized species, but probably not other passive nuclear species. Individuals of active nuclear species may also tend to react to individuals of already-established species more frequently and more rapidly than individuals of already-established species react to individuals of passive nuclear species. By associating more closely with the already-established species, individuals of active nuclear species probably discover the food sources and/or potential danger spots of an area with which they are unfamiliar more rapidly than do individuals of passive nuclear species in similar circumstances.

There may also be a general, but indirect and much less consistent, correlation between the ranges and social roles of the species of the montane bush alliances of Panamá. Interestingly enough, this correlation seems to be almost the reverse of the correlation noted in the case of the tanagers and finches of the lowland flocks.

The brown-capped bush-tanager, the most important passive nuclear species of the higher-altitude montane bush flocks, and a species that shows a high degree of intraspecific gregariousness, is very widely distributed in montane and hill regions from southern México to northern Argentina. The golden-crowned warbler, which also shows a high degree of intraspecific gregariousness and may play an equally important passive nuclear role in the lower-altitude montane bush flocks, is also very widely distributed from northeastern México to eastern and southern Brazil.

None of the species of the montane bush alliances that usually or always tend to join and/or follow other species very frequently are as widely distributed as the brown-capped bush-tanager or the golden-crowned warbler. Some of them, including species that are usually active nuclear species and those that are usually attendants in mixed montane bush flocks, have comparatively very restricted ranges. The yellow-thighed finch, the ruddy tree-runner, the black-cheeked warbler, and the collared redstart, are restricted to the mountains of Panamá and Costa Rica; and several others do not extend very much farther into the mountains of northern Central America and/or north-

western South America. It will be noted that none of these species shows a very high degree of intraspecific gregariousness.

The sooty-capped bush-tanager, which is an important passive nuclear species but which does not show a high degree of intraspecific gregariousness like the brown-capped bush-tanager and the golden-crowned warbler, is also confined to the mountains of Panamá and Costa Rica.

It is possible, therefore, that the brown-capped bush-tanager and the golden-crowned warbler are more widely distributed than most of their associates, not so much because they are passive nuclear species in mixed flocks as because they are both highly gregarious among themselves. All other factors being equal, a high degree of intraspecific gregariousness probably is (or was until recently) relatively much more advantageous to most montane species than to most lowland species in most regions of tropical America.

The forest and scrub areas inhabited by most lowland tanagers and finches were probably nearly continuous, or interrupted by only relatively small areas of other habitats, over the larger part of tropical America before human settlement became very dense (see also comments below). Most of the lowland tanagers and finches of the American Tropics probably occupied all or a large part of their ranges more or less gradually. Individuals of many of these species must have been able, in many cases, to move into new areas previously uninhabited by their species without going very far from the areas in which they themselves were raised. Thus, even a single individual of a species that did not show a high degree of intraspecific gregariousness was probably often able to obtain a mate, when it moved into a new area, by attracting one from an adjacent area previously occupied by the species, or because other individuals of the same species would tend to stray into the new area on their own initiative. In such circumstances, many lowland species that did not show a high degree of intraspecific gregariousness were probably able to spread as easily as, or more easily than, many lowland species that did show a high degree of intraspecific gregariousness.

The original situation of the montane species in tropical America must have been very different. Areas of montane forest and scrub have probably always been rather scattered in much of Central and South America, and many of these cannot have been occupied by a process of gradual diffusion. In order to reach such areas, individuals of montane species must have had to make long jumps over wide expanses of unsuitable habitats. Individuals of montane species that

show a high degree of intraspecific gregariousness can probably cross such wide gaps and occupy new areas successfully more frequently than individuals of montane species that do not show a high degree of intraspecific gregariousness because they will often arrive in a new area on the other side of a wide gap in a group, from which mates can be obtained, while individuals of other species will usually arrive singly and be unable to obtain mates, as they will seldom or never be able to attract other individuals of their own species from adjacent areas, and other individuals of their own species will not be likely to stray into the new area of their own accord.[23]

The migrant species, which occur in mixed flocks in the Tropics only part of the year, have not been mentioned in the preceding discussion because they are a very special case. It might be noted, however, that most of them are quite widely distributed when in the Tropics, and tend to occur in a relatively wide variety of habitats. They all seem to be primarily joiners and/or followers when they associate with mixed flocks in the Tropics, either attendant species or not very important active nuclear species. They also tend to choose a relatively wide variety of companions of other species.

Published accounts of mixed flocks of tanagers, honeycreepers, and/or finches (with or without warblers) would suggest that such flocks are not evenly distributed throughout tropical America. More different types of mixed flocks of these birds have been noted in the lowlands of Central America and southern Brazil than in the lowlands of the Amazon basin, in spite of the fact that there are probably more genera and species of lowland tanagers and honeycreepers in the Amazon basin than anywhere else in the American Tropics. Similarly, more different types of mixed flocks of these birds have been noted in the mountains of Central America than in the central Andean region, in spite of the fact that there are more genera and species of montane tanagers, honeycreepers, and finches in the central Andes than anywhere else in the mountains of the American Tropics.

The greater number of records of mixed flocks in Central America and southern Brazil may be partly an artifact, as there have been more observers interested in avian behavior and ecology in these re-

[23] The distribution of montane species in much of tropical America is essentially insular. It has often been remarked that species of land birds that show a high degree of intraspecific gregariousness are more likely to cross water gaps and establish themselves successfully on islands than are species of otherwise similar birds that do not show a high degree of intraspecific gregariousness (see, for instance, Mayr, 1931, and Amadon, 1950).

gions than in the Amazon basin and the central Andes; but it may also reflect a real difference in the abundance of mixed flocks in these regions. Some observations of my own may be of interest in this connection.

Both palm tanagers and blue tanagers were observed very frequently near Iquitos, in Amazonian Perú, in December of 1958. According to Hellmayr (1936), both of these species in this region are subspecifically distinct from the representatives of the same species in Panamá; but most of their habits seemed to be identical with those of the Panamanian forms. The only very distinctive feature of the behavior of the Iquitos palm tanagers and blue tanagers was their very slight degree of interspecific gregariousness. Individuals of both species frequently occurred in small flocks of their own species alone near Iquitos; but they very seldom occurred in mixed flocks and never in highly integrated mixed flocks during my observations in this area. It was particularly surprising that the palm tanagers and blue tanagers near Iquitos did not associate with one another very frequently because they often fed on the same or similar foods in the same trees.

(The rarity of associations between palm tanagers and blue tanagers near Iquitos may have been partly due to the fact that there were no species of *Tangara* comparable to the plain-colored tanager in this area. Thus the palm tanagers and blue tanagers near Iquitos did not tend, or did not have the chance, to associate with one another indirectly in the same way as the same species in central Panamá. But they also joined and followed one another directly much less frequently than palm tanagers and blue tanagers in Panamá.)

As noted above, silver-billed tanagers were also very common near Iquitos. Aside from the one family that occurred in association with the family of black-throated tanagers, the silver-billed tanagers of this area seldom or never occurred in mixed flocks. They were very similar to crimson-backed tanagers in appearance and actions; but they did not seem to be nearly as attractive to individuals of other species as crimson-backed tanagers in central Panamá.

Two small finches, *Sporophila castaneiventris* and *Oryzoborus angolensis*, were observed in open scrub and grasslands near Iquitos. Neither species occurred in mixed flocks as frequently as some of the Central American species of the same genera.

Montane birds of the central Andes were studied during two brief visits to Ecuador between August 4 and August 9, 1959, and between May 19 and June 2, 1960, on the slopes of Pichincha and Atacazo above Quito, near Quito itself, and near the town of San Antonio

below Quito. There is a good deal of bush and scrub in this area, especially on Pichincha and Atacazo; and much of it is reminiscent of the montane bush on the Volcán de Chiriquí. It is inhabited by a great variety of tanagers, honeycreepers, and finches, many of which have many of the same habits as the members of the montane bush alliances on the Volcán de Chiriquí. Some of these birds are supposed to be closely related to species that associate in mixed flocks in Panamá. Among them are two species of *Thraupis, bonariensis* and *cyanocephala,* and two conspicuous and brightly colored species of *Atlapetes, leucoptera* and *rufinucha,* which feed and move through shrubbery in very much the same way as bush-tanagers on the Volcán de Chiriquí. In spite of these resemblances, the tanagers, honeycreepers, and finches of the montane bush near Quito do not seem to form mixed flocks like the mixed flocks of the montane bush alliances on the Volcán de Chiriquí. Individuals of several species frequently occur together when they feed in the same trees or shrubbery in the montane bush near Quito; but all or most of these associations seem to be purely casual aggregations. Such associations seem to be usually or always brief, and do not appear to be organized in any very regular or definite way.

These observations would suggest that mixed flocks of tanagers, honeycreepers, and/or finches may really be more common (and may even tend to be more highly organized, on the average) in Central America and southern Brazil than in the Amazonian region or the central Andes.

The tanagers and honeycreepers are certainly primarily tropical South American groups, at least at the present time. Most of the finches that occur in mixed flocks in Central America also belong to primarily tropical South American groups. Both Central America and southern Brazil seem to be marginal, partly isolated, and relatively unfavorable areas for such groups. The southern Brazilian region verges on the Temperate Zone. The forests of southern Brazil, where the mixed flocks of tanagers, honeycreepers, and finches have been noted, are partly separated from the main body of Amazonian forests at the present time by wide intervening areas of savanna and comparatively dry scrub (see, for instance, Cruz Lima, 1945, and Darlington, 1957). Central America also verges on the Temperate Zone. The tropical forests of Central America are probably less complex, providing fewer habitats, than the forests of the Amazon basin (Holdridge, quoted in Slud, 1960). Many birds of primarily North American groups have penetrated into Central America, to a greater or lesser ex-

tent, where they provide competition for birds of South American origin. The forest and scrub areas of lowland Central America are partly separated from the forests of the Amazonian region at the present time by the Andes of northwestern South America and some other physiographic barriers, while the montane forest and scrub of Central America are separated from the Andes by intervening lowland areas such as the Atrato River valley and central Panamá. Some or all of the barriers partly separating Central American faunas from South American faunas may have been less important, or may not have existed at all, during some of the climatic fluctuations of the Pleistocene; but they have certainly been intermittently effective, at least slowing the spread of many species of birds, for a considerable length of time (see Chapman, 1917 and 1926).

It is possible, therefore, that species of tanagers, honeycreepers, and neotropical finches that have developed the habit of associating in mixed flocks in any capacity or social role may tend to survive better in relatively unfavorable or partly isolated habitats and/or invade relatively unfavorable or partly isolated habitats more successfully than related and otherwise similar species that have not developed such habits.

SUMMARY

Several different types of mixed species flocks, composed of finches, tanagers, honeycreepers, and/or warblers (and sometimes species of other groups as well) are common in Panamá. Two types of these flocks were studied in some detail: mixed blue and green tanager and honeycreeper flocks in the lowlands of central Panamá, and mixed montane bush flocks on the Volcán de Chiriquí in western Panamá.

Mixed blue and green tanager and honeycreeper flocks are complex societies. Each of the species commonly occurring in such flocks tends to play a characteristic and rather consistent social role, which is more or less distinctly different from that of every other species commonly occurring in the flocks. Such roles are the results of complex interactions between each species and at least one (usually several) other species. Several of the species tend to react differently to each of several other species. Some species seem to have developed "special interspecific preferences" for certain other species. Special interspecific preferences may be expressed by apparently "friendly" joining and following reactions and/or by largely or completely hostile supplanting attacks. Some of the species commonly oc-

curring in mixed blue and green tanager and honeycreeper flocks have also developed other special characters, such as dull "neutral" plumage, to facilitate the performance of their characteristic social roles within mixed flocks.

The species that occur in mixed blue and green tanager and honeycreeper flocks can be divided into "regular" and "occasional" members of the flocks. They can also be divided into "nuclear" and "attendant" species. A species may be considered nuclear in any given type of mixed flock if its behavior contributes appreciably to stimulate the formation and/or maintain the cohesion of that particular type of mixed flock. Some species are nuclear in one type of mixed flock but not in others. The nuclear species of mixed blue and green tanager and honeycreeper flocks can be divided into "passive" nuclear species and "active" nuclear species. Passive nuclear species are usually joined and followed by other species much more frequently than they join and follow other species. Active nuclear species usually join and follow other species much more frequently than they are joined and followed by other species.

The mixed montane bush flocks that occur at higher altitudes on the Volcán de Chiriquí seem to be approximately as complex and as highly organized as mixed blue and green tanager and honeycreeper flocks; but their social structure is not identical with that of the latter in all details. Interspecific supplanting attacks are much less common in the higher-altitude mixed montane bush flocks than in mixed blue and green tanager and honeycreeper flocks. Some of the nuclear species of higher-altitude mixed montane bush flocks are not consistently passive or consistently active. Most of the differences between the social organization of the higher-altitude mixed montane bush flocks and the social organization of mixed blue and green tanager and honeycreeper flocks may be due to the fact that the members of higher-altitude mixed montane bush flocks compete directly with one another for food less frequently than do members of mixed blue and green tanager and honeycreeper flocks.

Several other types of mixed flocks, including flocks of small finches, forest birds on an isolated mountain in central Panamá, and species of the genus *Ramphocelus* were studied in less detail. These flocks appeared to be simpler and/or less highly organized than mixed blue and green tanager and honeycreeper flocks or the higher-altitude mixed montane bush flocks on the Volcán de Chiriquí.

It seems likely that most species of neotropical finches, tanagers, honeycreepers, and/or warblers obtain several advantages, including

extra food and protection from predators, by associating in mixed flocks. The additional protection from predators may be the most important advantage obtained by most of these species when they associate in mixed flocks in most circumstances.

The initial step in the evolution of most highly organized mixed flocks of passerine birds was probably the formation of special social bonds between a species that showed a high degree of intraspecific gregariousness and one or more species that did not show a high degree of intraspecific gregariousness. The former probably became a passive nuclear species in most cases. The subsequent history of such flocks was probably largely dependent upon the appearance and behavior of the other species that became attached to the passive nuclear species. Some of the characters of some species that seem to be adaptations to promote the formation and/or maintain the cohesion of a particular type of mixed flock may facilitate the incorporation of additional species as new regular members in mixed flocks of that particular type; but other characters that seem to be adaptations to subserve the same functions may tend to prevent the incorporation of additional species.

The finches and tanagers that are known to play passive nuclear roles in mixed flocks in the lowlands of central Panamá or other lowland areas of the American Tropics are less widely distributed than species that are known to play active nuclear roles in the same mixed flocks (and some closely related species that do not play any sort of nuclear role in mixed flocks). Active nuclear species of finches and tanagers that are adapted to the lowland Tropics may be able to invade new areas within the American lowland Tropics more successfully, in most cases, than otherwise similar but passive nuclear species.

Two largely passive nuclear species of the mixed montane bush flocks on the Volcán de Chiriquí are much more widely distributed than most of the other species commonly occurring in such flocks. The comparatively wide distribution of these passive nuclear species may be due to the fact that they both show a high degree of intraspecific gregariousness. On logical grounds, it might be expected that montane species that show a high degree of intraspecific gregariousness would be able to invade new montane areas in the American Tropics more successfully, on the average, than otherwise similar species that do not show a high degree of intraspecific gregariousness.

Various observations during this study, and published records, would suggest that mixed flocks of tanagers, honeycreepers, and/or finches are not evenly distributed throughout tropical America. It is

possible that species of tanagers, honeycreepers, and neotropical finches that have developed the habit of associating in mixed flocks, in any capacity or social role, may tend to survive better in relatively unfavorable or partly isolated habitats within the Tropics and/or invade such habitats more successfully than related and otherwise similar species that have not developed such habits.

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