

SENTINEL BEHAVIOR, SEASONALITY, AND THE STRUCTURE OF BIRD FLOCKS IN A BRAZILIAN SAVANNA

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Resumo. Nós investigamos a composição, o ciclo anual, a fidelidade ao local e o comportamento alimentar de aves em bandos mistos, além da importância do comportamento de sentinela do Tiê-do-cerrado, *Neothraupis fasciata*, em uma área de cerrado próxima à Brasília, Brasil. Os bandos mistos incluíram vinte e cinco espécies residentes, migratórias e transitórias, e ocorreram em todos os meses do ano, sendo mais frequentes na estação chuvosa, época em que as aves reproduziram e a maioria das espécies foram ausentes ou ocasionais nos bandos. *Neothraupis fasciata* e *Suiriri suiriri* foram as espécies nucleares dos bandos mistos, ambas com territórios permanentes. Indivíduos machos e fêmeas de *N. fasciata* desempenharam comportamento de sentinela, geralmente um de cada vez, sendo a intensidade deste comportamento significativamente menor em bandos mistos do que em associações co-específicas. Isto é consistente com a previsão de que a proteção aumentada por outras espécies resultaria em diminuição dos requerimentos para vigilância por *N. fasciata*. O comportamento de sentinela não dependeu do tamanho do grupo, tamanho do bando misto, ou época do ano. A maioria das espécies participantes dos bandos mistos foi insetívora. Não houve evidência de convergência em altura e táticas de forrageamento entre as três espécies mais frequentes dos bandos. Nós sugerimos que o fator mais importante na formação dos bandos mistos em cerrado é a proteção contra a predação.

Abstract. We investigated composition, annual cycle, site fidelity, foraging behavior of birds in mixed-species flocks, and the importance of sentinel behavior by the White-banded Tanager, *Neothraupis fasciata*, in a cerrado (savanna) near Brasília, Brazil. Mixed-species flocks, comprising up to twenty-five resident, migratory, and transitory species, occurred in all months of the year, and were most frequent during the dry season, compared to the rainy season when breeding occurred and most species were absent or occasional in the flocks. The nuclear species were White-banded Tanager and Suiriri Flycatcher (*Suiriri suiriri*), both residents with permanent territories. White-banded Tanagers showed sentinel behavior, performed by males and females usually one at a time. The intensity of the tanagers' sentinel behavior was significantly lower in mixed-species flocks compared to conspecific associations. This is consistent with the prediction that enhanced protection by other species resulted in lower requirements for vigilance by White-banded Tanagers. Sentinel behavior did not depend on group size, flock size or time of year. Most species were insectivorous. There was no evidence of convergence in foraging height or tactics among the three most frequent species. We suggest that protection from predation is a major factor in the formation of mixed species flocks in cerrado. Accepted 7 December 1995.

Key words: Sentinel behavior, mixed-species flocks, cerrado, *Neothraupis fasciata*.

INTRODUCTION

The Central Brazilian savannas (*cerrados*) cover more than 1.5 million km² Ferri (1980) and include a variety of vegetation types, of which the most typical is a tree and scrub savanna (Eiten 1972). The bird fauna is diverse, but with a fairly low level of endemism (Sick 1965, 1966; Silva 1995). Although adapted to live in open habitats, most birds species are arboreal (Sick 1966). The biology and social structure of the cerrado avifauna present many interesting questions, and mixed-species flocks are an important feature of the bird social systems in the cerrado

savannas of Central Brazil. In this study, we examined the species composition and seasonal variation in the structure of mixed-species flocks. In particular, we studied the role of the White-banded Tanager (*Neothraupis fasciata*) in the formation and function of such flocks. This tanager shows sentinel behavior, and our hypothesis was that the tanager benefitted from additional anti-predator vigilance by joining mixed-species flocks.

Mixed-species bird flocks are found in a variety of habitats, from forests to open areas such as deserts and savannas (Cody 1971, Greig-Smith

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1978, Munn & Terborgh 1979, Fry 1983, Munn 1985). The flocks have the highest structural complexity in the humid tropics, where they are largely or exclusively composed of passerine birds (Moynihan 1962). Nuclear species in such flocks are those that occur regularly and which appear to draw other species to flock with them. The functions of these flocks may be increased foraging efficiency, protection from predation, or both (Moynihan 1962, Morse 1970, 1977, Willis 1972a, b, 1973; Krebs 1973, Pulliam 1973, Gaddis 1980). In the *cerrados*, mixed flocks are widespread in the tree and scrub vegetation, and seem to be differently organized from those in Amazonia described by Munn in which the flocks have full time sentinels that only switch to non-sentinel when foraging outside the flock. Additionally, the *cerrado* flocks differ from the forest flocks in their vertical structure. In *cerrado*, flocks incorporate species from all levels, including canopy foragers, ground and shrub species, and tree trunk specialists, whereas in the Amazon canopy species form different flocks from the understory species.

Silva (1980) described the importance White-banded Tanagers in *cerrado* flocks and suggested that these flocks decreased predation and increased foraging efficiency. In this study, we analyze the relationships among flock frequency, rainfall and fruit seasonality. To test the importance of anti-predator defenses, we quantified and compared the sentinel behavior of White-banded Tanagers in conspecific groups and in mixed-species flocks.

METHODS

The field site was at the University of Brasília Ecological Station (15° 57' S, 47° 56' W), 20 km SW of Brasília, Brasil. The Station has approximately 2500 ha of natural vegetation. We worked in a tree and scrub *cerrado* (Eiten 1984, Ratter 1986) where Silva (1980) had observed the White-banded Tanager as a fundamental species in mixed-species flocks. Climate is highly seasonal, with a virtually rainless season from April through September. The annual precipitation is approximately 1600 mm (Fig. 1, data obtained from IBGE Ecological Reserve, adjoining the University property).

We established a 1900 m long transect following a 3 m wide dirt road, crossing *cerrado senso-*

stricto. This habitat is formed by a tree and scrub savanna with a widespread grass layer. The canopy cover ranges from 10 to 30% (Eiten 1972). Grassland fires are frequent, burning the grass layer completely and damaging extensively the shrubs and saplings, which resprout from unburned lateral meristems. Tree canopies do not burn, but usually the leaves dry up and fall soon after fires. From 1983 to 1987 birds were captured with 36 mm mesh mist nets, and banded with aluminum and/or plastic color bands, at various points on the transect. We performed 48 visual censuses along the entire transect, 4 times per month, between August 1986 and July 1987. At each sighting of a mixed-species flock or conspecific group White-banded Tanagers, we recorded the time, species composition, number of individuals, and location. Upon detection, we waited 10 min for habituation, recorded the total time a sentinel was present, and the flock or group composition. Conspecific groups were observed for a total of 14.71 h on 43 occasions, and mixed-species flocks for 14.09 h on 62 occasions. Each group or flock was followed for a minimum of 10 min and a maximum of 45 min. We recorded foraging heights of the three most frequent species at 5 min intervals. Sentinel behavior was recorded when one individual perched on an exposed branch of a shrub or tree, and turned its head periodically in different directions. When an observer or a predator approached, this bird usually gave alert or alarm calls (pers. observ.).

We determined the phenology of 11 species of plants (see Alves 1991 for a complete list) with fruits potentially eaten by birds by marking 3 individuals of each species and monitoring their phenology biweekly from August 1986 through October 1987.

RESULTS

Flock seasonality. We found mixed-species flocks in all months of the year. Their frequency was highest in the early dry season, between March and July, when birds were not reproducing (Fig. 1). During the breeding season, between September and early December, flocks were still present, but less frequent. In October 1986 only 4 flocks were seen in 10 h of observation, contrasting with a high of 14 flocks in 10 h recorded in April 1987. Fruit production was highest during the

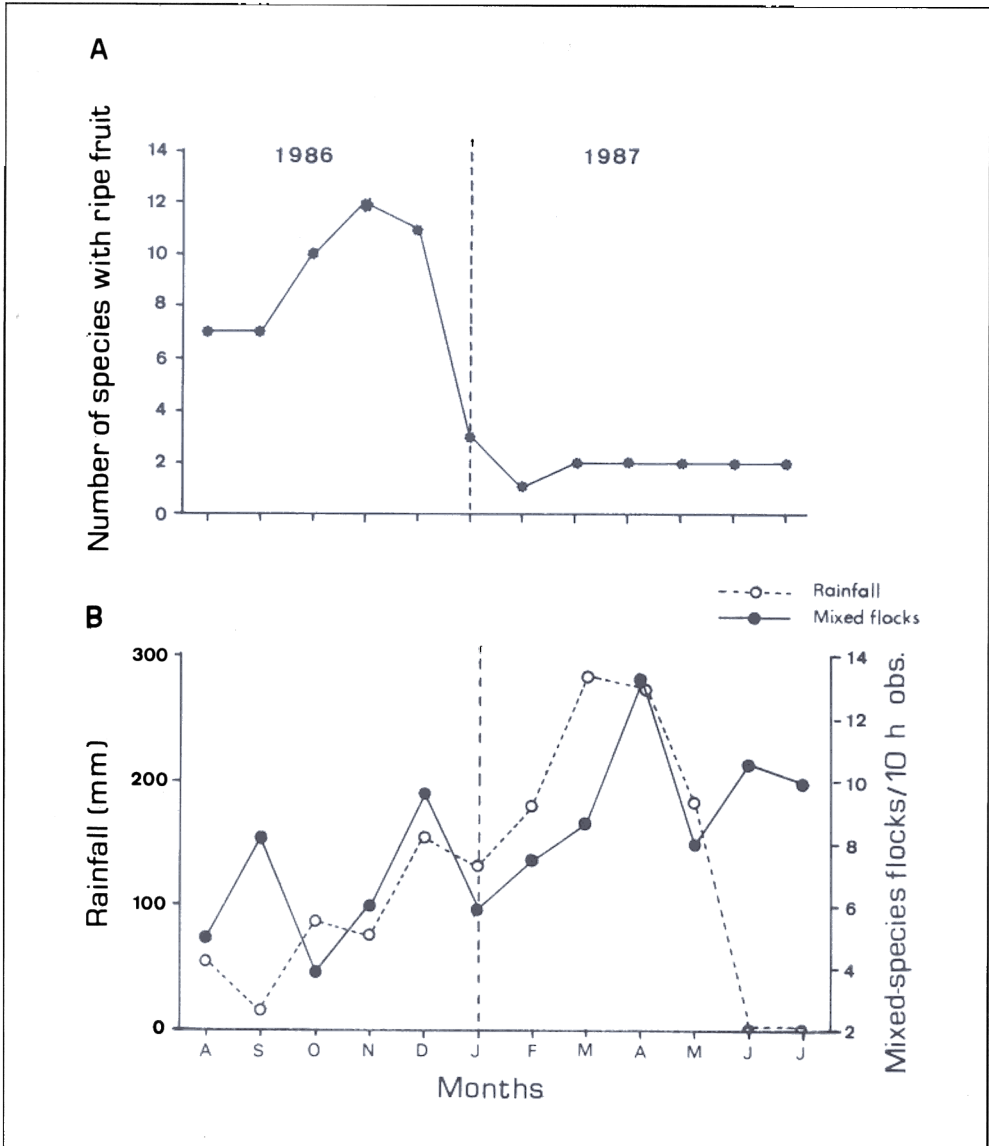


FIG. 1. Phenology, rainfall, and mixed-species flocks at the study site, August 1986 to July 1987. (A) Number of plant species with ripe fruits available to birds each month. Total sample size was 11 plant species monitored for phenology. (B) Monthly rainfall in mm and number of mixed-species flocks recorded each month per 10 h of field observation.

birds' reproductive period, when most species were absent or occasional in the flocks. The peak in flock formation probably reflects pairs and family groups returning after reproduction in December.

Flock structure. Twenty-five species were recorded in the mixed flocks with variable frequencies of occurrence and included resident, migratory, and seasonally resident species (Table 1). Nearly all were passerines, except for two hummingbirds

(*Colibri serrirostris* and *Amazilia fimbriata*) and two woodpeckers (*Colaptes campestris* and *Dendrocopus mixtus*). The largest group of passerines were tyrannids (*Xolmis velata*, *Tyrannus savana*, *Myiarchus swainsoni*, *Elaenia cristata*, *E. chiriquensis*, *E. sp.*, *Suiriri suiriri*, and *Camptostoma obsoletum*), which are conspicuous elements of the cerrado avifauna. We classified species into three categories, according to their frequency of occurrence. The species recorded in 60% or more of the sightings, were the White-banded Tanager and the Suiriri Flycatcher (*Suiriri suiriri*), considered nuclear. The four species seen in 20% to 60% of the flocks were the Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), the Grassland Sparrow (*Myospiza humeralis*), the Plain-crested Elaenia (*Elaenia cristata*) and the

House Wren (*Troglodytes aedon*), categorized as common. The remaining 19 species were considered occasionals (Table 1).

Nuclear and common species were permanent residents (Table 2). White-banded Tanagers lived in groups of three individuals on average ($\bar{x}=3.0$, S.E.=1.05) in year-round territories (one measured 4.3 hectares, Alves 1990). Suiriri Flycatchers lived usually in pairs on territories apparently larger than the tanagers'. Narrow-billed Woodcreepers had larger territories still, and one marked individual was associated regularly with up to five different Tanager/Suiriri Flycatcher mixed flocks.

The mean number of species per flock was 3.96 (S.E.=1.59). As expected, flock size and species number were highly correlated ($r=0.80$,

TABLE 1. Species presence in mixed flocks. R = resident, M = migratory, SR = seasonal resident. Total number of flocks observed was 102 (59 in the dry season and 43 in the rainy season).

Species	No. of Flocks	Total %	Dry season		Rainy season		Status
			No.	%	No.	%	
Nuclear							
<i>Neothraupis fasciata</i>	87	85.3	56	94.9	31	72.1	R
<i>Suiriri suiriri</i>	61	59.8	42	72.1	19	44.2	R
Common							
<i>Lepidocolaptes angustirostris</i>	46	45.1	27	45.8	19	44.2	R
<i>Myospiza humeralis</i>	38	37.3	21	35.6	17	39.5	R
<i>Elaenia cristata</i>	29	28.4	18	30.5	11	25.6	R
<i>Troglodytes aedon</i>	21	20.6	12	20.3	9	20.9	R
Occasional							
<i>Elaenia chiriquensis</i>	15	14.7	2	3.4	18	41.9	M
<i>Dendrocopus mixtus</i>	13	12.7	11	18.6	2	4.6	
<i>Volatinia jacarina</i>	10	9.8	0	0	10	23.3	
<i>Amazilia fimbriata</i>	10	9.8	7	11.9	3	7.0	SR
<i>Myiarchus swainsoni</i>	10	9.8	2	3.4	8		
<i>Emberizoides herbicola</i>	7	6.9	7	11.9	0	0	
<i>Elaenia sp.</i>	7	6.9	5	8.5	2	4.6	
<i>Zonotrichia capensis</i>	8	7.8	7	11.9	0	0	
<i>Colibri serrirostris</i>	8	7.8	0	0	8	18.6	SR
<i>Camptostoma obsoletum</i>	6	5.9	5	8.5	1	2.3	R
<i>Synallaxis albescens</i>	5	4.9	0	0	5	11.6	
<i>Charitospiza eucosma</i>	2	2.0	0	0	2	4.6	?
<i>Tyrannus savana</i>	3	2.9	0	0	3	7.0	M
<i>Phacellodomus rufifrons</i>	3	2.9	3	5.1	0	0	?
<i>Colaptes campestris</i>	2	2.0	2	3.4	0	0	R
<i>Tachycinetta leucorhoa</i>	1	1.0		1.7	0	0	M
<i>Xolmis velata</i>		0.1		0	1	2.3	
<i>Mimus saturninus</i>		0.1		1.7	0	0	
<i>Gnorimopsar chopi</i>		0.1			1	2.3	

TABLE 2. Number of banded individuals per species, number of recaptures, and percent recaptured in the same year and in following years.

Species	Individuals banded	Individuals recaptured	% Indiv. Recaptured	
			Same Year	Other Years
<i>Neothraupis fasciata</i>	76	32		18.4
<i>Suiriri suiriri</i>	18	7		33.3
<i>Lepidocolaptes angustirostris</i>	12	8		33.3
<i>Myospiza humeralis</i>	25	3		4.0
<i>Elaenia cristata</i>	21	11		42.9
<i>Troglodytes aedon</i>	4	1		25.0
<i>Elaenia chiriquensis</i>	82	15		2.4
<i>Dendrocopus mixtus</i>	4	3		25.0
<i>Volatinia jacarina</i>	3	0		0
<i>Myiarchus swainsoni</i>	28	10		17.9
<i>Elaenia</i> sp.	70	11		1.4
<i>Camptostoma obsoletum</i>	12	3		0
<i>Charitospiza eucosma</i>	16	2		0
<i>Phacellodomus rufifrons</i>	4			0
<i>Colaptes campestris</i>	2	0		
Total	377	107		

$P < 0.001$, Pearson correlation). The mean number of individuals per species was 2.03 (S.E. = 0.58). We seldom saw more than one adult pair of each species in a flock, and when this happened there was usually aggressive interactions between the pairs, possibly due to territorial disputes.

The composition of the flocks varied seasonally, because some species were migrants (Table 1). Several tyrannids, such as the Lesser Elaenia, the Swainson's Flycatcher, and the Fork-tailed Flycatcher (*Tyrannus savana*) were recorded only during the breeding season, starting to arrive in late August and departing by March. Two hummingbirds apparently moved in or out of the site in response to flowering cycles: the Glittering-throated Emerald (*Amazilia fimbriata*), observed in December and January and from April to July, and the White-vented Violetear, from October to December. Turnover of migrants was variable (Table 2). Lesser Elaenias had a low rate of recaptures between years. Individuals of the Swainson's Flycatcher returned to sites occupied the preceding years in subsequent rainy seasons from 1984 to 1987 (5

individuals banded in 1984 were recaptured in 1986).

Mixed-species flocks and sentinel behavior. The three most frequent species appeared to attract other species to the flocks. Suiriri Flycatchers were usually the first to be located, calling in the treetops soon after sunrise. Later they were joined by White-banded Tanagers, also calling and foraging, and this activity attracted other species to the flock. The Narrow-billed Woodcreeper's calls were frequent and audible over long distances, and probably are important in maintaining flock cohesion.

Only the White-banded Tanager, among the three most frequent species, had sentinel behavior. ♂ and ♀ performed sentinel duties, usually one at a time (Alves 1988, Alves 1990). To test the hypothesis that participation in mixed species flocks offered better anti-predator protection, we compared frequencies of sentinel behavior in conspecific groups and in mixed-species flocks for seven tanager groups. The prediction was that enhanced protection in mixed species flocks would result in lower

TABLE 3. Percentage of time spent in sentinel behavior by all individuals of White-banded tanager in conspecific groups and mixed-species flocks. t = total time observed in seconds. Sample size in brackets.

Group	Size	Sentinel behavior	
		Conspecific groups	Mixed-species flocks
4	2-4	81.35 ($t=4501$, $n=5$)	37.93 ($t=5702$, $n=12$)
	3-5	95.91 ($t=2941$, $n=2$)	86.50 ($t=2220$, $n=2$)
	2-4	73.08 ($t=4681$, $n=7$)	25.01 ($t=1140$, $n=2$)
	2-5	93.20 ($t=16741$, $n=11$)	59.08 ($t=8942$, $n=12$)
	.5	83.53 ($t=5101$, $n=2$)	48.66 ($t=11103$, $n=11$)
	4	100.00 ($t=1800$, $n=1$)	58.37 ($t=2881$, $n=2$)
		62.54 ($t=1440$, $n=3$)	89.66 ($t=1741$, $n=2$)

Wilcoxon paired-sample test, $T+=27$, $z=1$, $P(T)<0.05$

requirements for sentinel behavior by the tanagers. As predicted, the intensity of sentinel behavior was significantly lower in mixed-species flocks (Table 3).

The percentage of time in sentinel behavior showed a non significant trend to decrease with group size in conspecific groups (Kruskall-Wallis test $H=2.78$, $df=6$, $n=61$, $P=0.836$) or in mixed-species flocks (Kruskall-Wallis test $H=4.96$, $df=3$, $n=42$, $P=0.175$) (Fig. 3). There were also no significant differences between wet ($n=44$) and dry ($n=61$) seasons (Mann-Whitney $U=1045$, $z=0.9691$, $P=0.08$, two-tailed).

Foraging behavior. There was no evidence of convergence in foraging tactics or preferred substrate among the three most frequent species (Fig. 2). White-banded Tanagers foraged most frequently on the ground and in low shrubs, where they fed on insects, fruit, grains and seeds (Alves 1988, Alves 1991). Suiriri Flycatchers gleaned insects from leaves in the canopy and midstory. Narrow-billed Woodcreepers foraged on the trunks and branches of trees, poking for insects, working its way up from about 50 cm until the canopy, where it occasionally gleaned for insects among the leaves. The other species fed on a variety on sources, but most were totally or partially insectivorous.

DISCUSSION

Most suggestions as to the functions of mixed-species flocks stress the aspects of improved foraging efficiency and protection from predation (Moynihan 1962; Cody 1971; Croxall 1976; Munn 1984, 1985; Sullivan 1984a, b). Particularly in tropical regions, predation is a major selective force (Moynihan 1962). In the flocks we studied, two lines of evidence point to the importance of anti-predatory behavior in the mixed flocks. First, the most abundant nuclear species, the White banded Tanager, has well developed sentinel behavior. Second, our data also suggest that the White-banded Tanager obtains additional protection from joining other species, because it reduces the intensity of sentinel behavior in mixed-species flocks.

The increased vigilance available in mixed-species flocks has been well discussed (Metcalfe 1984). In our study site, several other species in the mixed flocks show sentinel behavior, including the Grassland Sparrow (*Myospiza humeralis*), Wedge-tailed Grass-Finch (*Emberizoides herbicola*) and Coal-Crested Finch (*Charitospiza eucosma*) (pers. observ.). If more than one species has sentinels, mixed flocks may require less vigilance on the part of each species. Alarm calls are also common in the nuclear species and may

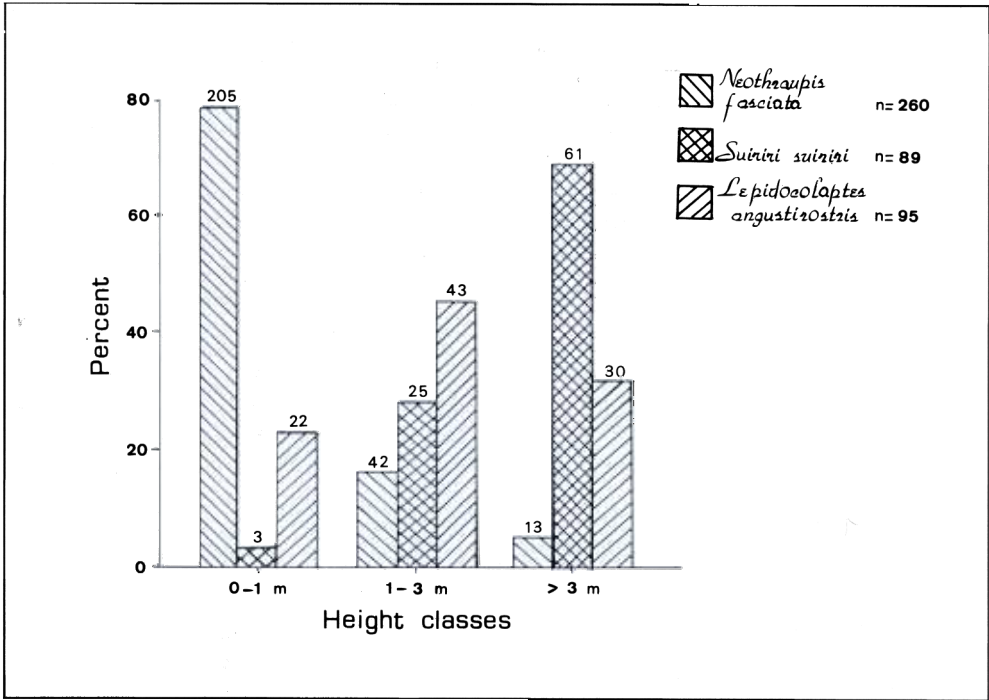


FIG. 2. Foraging frequencies of the three most common species of the flocks, in relation to height class.

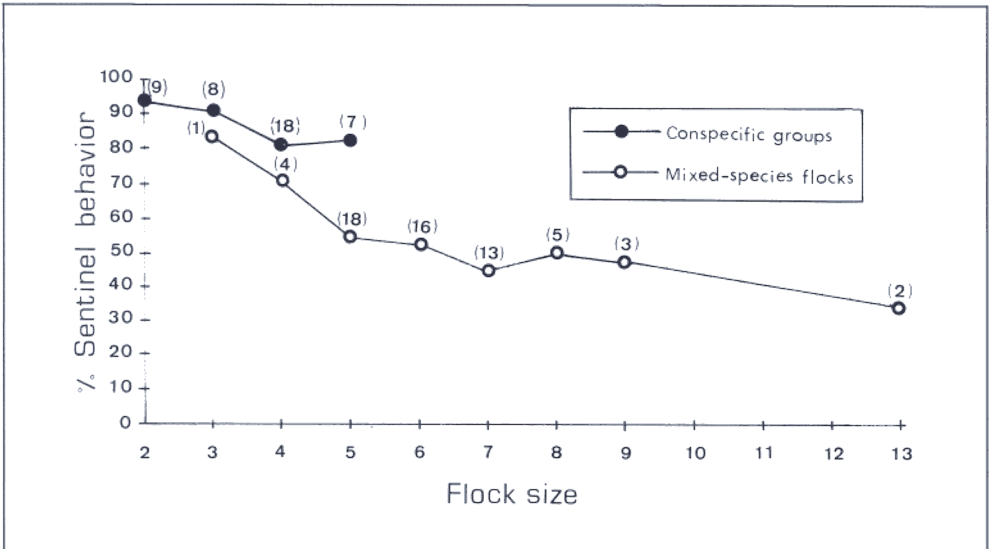


FIG. 3. Percentage of sentinel behavior of the White-banded Tanager as a function of flock size; conspecific groups and mixed-species flocks. Sample size in brackets.

add to the vigilance effect of mixed-species flocks.

The relation between mixed-species flocks and existence of sentinel behavior seems to be common in the savannas of Central Brazil. Sentinel behavior is often found in ground-foraging birds of open country, which live in small groups. These conditions may pre-adapt them to a nuclear role in mixed-species flocks of *cerrado*, by affording vigilance and group protection to joining species. The Black-throated Saltator (*Saltator atricollis*) and the Chalk-browed Mockingbird (*Mimus saturninus*) appear to have a similar role to the White-banded Tanager in other more open areas of *cerrado* that we studied. However, in forest flocks, the central species may be those with well-developed alarm calls as well as sentinel behavior (Munn 1986).

Munn (1984) studied flocks in the Amazonian forests, and suggested the existence of mutualistic associations between sentinel species and others that flush insects. In our study, we did not test for the existence of a foraging benefit in the association between species, but we feel it is made difficult by the differences in foraging strategies and spacing (and few of the flocking species are likely to flush insects). Perhaps the irregular occurrence of mixed flocks and other factors such as: a) the lack of antbirds such as species of *Myrmotherula* and *Philydor* equivalents that flush insects from dead leaves on the ground, b) the occurrence of several flycatchers (such as *Suiriri suiriri* and species of *Elaenia*) that would chase any insects they or other bird species flushed, and c) the wide spacing of flock members, some feeding on the ground, some in trunks, some in the canopy and occasionally overhead (such as *Tachycineta leucorrhoa*), would fail to create the concentration of flushed insects necessary to support a full-time specialist sentinel. Willis (1972b) presents several lines of evidence against a primary importance of the food advantage in Neotropical mixed flocks. However, birds may aggregate at temporary high quality food sources. Ferrari (1990) described a foraging association between two kite species and a marmoset in southeastern Brazil, where the kites exploited cicadas flushed by the marmosets during the highly seasonal availability of this prey.

The seasonal variation of the frequency of flocks is consistent with an earlier study at the

site (Silva 1980), which did not record groups during most of the rainy season. Declines in the frequencies of mixed flocks during the breeding season in the tropics are common (Davis 1946, Powell 1979, 1985, Bell 1980). This effect may be related to the breeding of the birds, which must spend time attending the nests, or to variations in the food supply (for example: more food availability could discourage the species to forage in groups).

The pattern of overlapping territories among different species, and the presence of a pair or family group per species in each mixed flock is consistent with data on Neotropical forest flocks (Munn & Terborgh 1979; Powell 1979; Gradwohl & Greenberg 1980; Munn 1984, 1985; Greenberg & Gradwohl 1986). Within their territories, the Spotted Antbirds (*Hylophylax naevioides*) at mixed flocks drive away trespassers of the same species (Willis 1972b).

This work supports the idea that defense against predators is a major cause of the organization of mixed-species flocks in *cerrado* areas in Brazil, and that sentinel behavior is commonly associated with the role of nuclear species in these open habitats.

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