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Vigilance towards raptors by nuclear species in bird mixed flocks in a Brazilian savannah

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Abstract

A nuclear or leader species is the one around which foraging activity is organized. In the campo-cerrado (Brazilian savannah) up to four bird species (*Saltator atricollis*, *Cypsnagra hirundinacea*, *Mimus saturninus*, and *Neothraupis fasciata*) may function as nuclear or leader species in mixed species flocks. The aim of this study was to assess the features shown by these nuclear species. I quantified parameters of sociality, communication and alertness of nuclear bird species in mixed flocks with different composition. Parameters related to sociality (mean intraspecific group size) and communication (frequency of contact calls) were not correlated with the leadership. On the other hand, the most alert species was in the front of a given mixed flock most of the time. The leader species spent more time in vigilance and gave most alarm calls due to approaching raptors earlier. The results of this study strongly suggest that the alertness of a species is the major character of nuclear bird species in mixed flocks of the campo-cerrado.

Keywords: mixed flocks, sentinels, vigilance, nuclear species, Brazilian savannah.

Introduction

Studies have shown benefits to birds in mixed flocks mainly due to better protection and/or foraging advantages (Pullian, 1973; Powell, 1974; Sullivan, 1984a,b; Hogstad, 1988; Waite & Grubb, 1988; Carrascal & Moreno, 1992). The formation and cohesion of bird mixed-species flocks result from species responses to one another (Powell, 1985). In this respect nuclear or leader species play a significant role enhancing flock cohesion and stability (Powell, 1985; Hutto, 1994; Monkkonen et al., 1996; Dolby & Grubb, 1999).

Generally nuclear species occur together in groups larger than the ones of attendant species. They are conspicuous in plumage, contact calls and movements (Moynihan, 1962; Greig-Smith, 1978; Powell, 1985). Also, nuclear species are commonly followed by the other species (Greig-Smith, 1978; Munn & Terborgh, 1979; Powell, 1985). Besides those features, some studies found the nuclear species are the most alert species in mixed flocks (Munn & Terborgh, 1979; Gaddis, 1980; Greig-Smith, 1981; Sullivan, 1984a,b; Alves & Cavalcanti, 1996). Thus, their increased perception to detect raptors was thought of as the major cause to bird attraction to mixed flocks (Gaddis, 1980; Greig-Smith, 1981).

Although many studies stressed the existence as well as the role of nuclear species, specific behavioral parameters associated with the nuclear function are poorly known among tropical bird mixed flocks (Powell, 1985; Hutto, 1994). *Saltator atricollis* is a conspicuous species of dry semi-open habitats of Brazil, such as the 'cerrado'. Unlike other saltators, *S. atricollis* commonly perch on tops of bushes and trees while foraging (Ridgely & Tudor, 1989; Sick, 1997). Also, three other species from cerrado (*Cypsnagra hirundinacea*, *Mimus saturninus* and *Neothraupis fasciata*) regularly perch prominently, and together with *S. atricollis* may be included in mixed flocks (Ragusa-Netto, 1999) in the 'campo-cerrado' (a kind of open cerrado [Brazilian savannah], Eiten, 1994). Pilot observations on mixed flocks with *S. atricollis* in the campo-cerrado, showed in most of the cases *S. atricollis* as the obvious flock nucleus. However, in some cases *M. saturninus* or *C. hirundinacea* led mixed flocks.

Unlike in tall rain forest, birds in the open cerrado frequently forage on or close to the ground (Ridgely & Tudor, 1989; Sick, 1997; Ragusa-Netto, 1999), being highly

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exposed to raptors (Ragusa-Netto, 1999). Due to a high risk of predation, species with an increased perception of raptors may be exploited by less alert ones (Munn & Terborgh, 1979; Gaddis, 1980; Greig-Smith, 1981; Sullivan, 1984a,b). If birds on exposed perches are on guard (Wickler, 1985; Ferguson, 1987; McGowan & Woolfenden, 1989), the sentinel behavior may be the major feature for mixed flock cohesion in the campo-cerrado. Thus, the aim of this study was to assess the leader species of mixed flocks including *S. atricollis* in the campo-cerrado, and to examine how features (sociality, communication and alertness) are consistent with the role of leader species.

Material and Methods

Study area

This study was developed in a 'campo-cerrado' (Brazilian savannah) in Brotas (São Paulo State, 22°12′S, 47°55′W, altitude 750 m). The site is approximately 1500 ha (included in a 4600 ha reserve) and vegetation consists of bushes and small trees (height ± 1–6 m) interspersed with open grassy areas. Bushes and trees cover less than 20% of the area (Eiten, 1994). Mean annual temperature is 19.7°C. A higher mean temperature is recorded in January and February (±22.5°C). In June and July mean temperature is 16.3°C. During this period, the day-break temperature often drops to 2°C or less and frost may occur. A large number of trees and bushes simultaneously drop their leaves. Mean annual rainfall is around 1430 mm, with 1200 mm between October to March. There is a wet-hot season extending from October to March and a dry-cold season from April to September (source: meteorological service of RIPASA; reforestation and cellulose company next to the study area).

Observations of mixed flocks

In order to find *S. atricollis* I used 11.5 km of permanent access trails in the campo-cerrado. I positioned twelve points along the trails from where I started walking. Each point was 1000 m from the nearest one. I randomized by lot (without replacement) the starting point and direction to be followed. Observations were made from 07:00 to 12:00 h and from 13:00 to 18:00 h (totalling 50 h/month). When I found *S. atricollis* within a mixed flock, direct observations were conducted, so that only one mixed flock was studied in each period. If I lost the mixed flock from view within 1 h, I discarded the observation period. I also discarded the observation period if the leader species started confrontations towards conspecifics before 1 h had passed. In that case, I abandoned the mixed flock and tried to study another one. If confrontations started after 1 h, I interrupted the observation and took it as replicate for statistical analysis. This was done to assure the observation of only one mixed flock per period since birds were not colour ringed and to avoid any effect of confrontations on time spent by birds on exposed perches. I watched birds through 8 × 30 binoculars and dictated observations into a portable recorder for later transcription. Before observing a mixed flock, I waited 5–10 min to allow the birds to become habituated. After that, I recorded: a) bird species, b) flock size, c) time with at least one prominently perched bird of any of those four species, d) calls given by prominently perched birds, e) encounters between raptors and mixed flocks, and f) bird reaction to raptors. If *S. atricollis* was found in groups out of mixed flocks, I observed the group, following the procedures described above, mainly to record time with birds prominently perched and encounters with raptors, as well as bird reactions to raptors.

I observed prominently perched birds for regular rotating movements of the head holding the bill horizontally positioned, because the performance of those movements suggested that the bird was searching. As a prominently perched bird may indicate vigilance (Wickler, 1985; Ferguson, 1987; McGowan & Woolfenden, 1989), I assumed that this duty was accomplished by such a bird only if, besides watching about, it gave alarm calls earlier than foraging birds, which implies a higher perception of danger.

As both contact and alarm calls may be recorded from prominently perched birds (Wickler, 1985; McGowan & Woolfenden, 1989), in this study the criterion used to distinguish one from the other was bird response. Commonly alarm calls trigger instantaneous evasive responses while contact calls do not trigger evasive responses. I also attempted to determine the causes of alarm calls, which bird species gave them, as well as whether it was foraging or prominently perched.

All raptors seen (also presumably by birds) while a mixed flock was observed were recorded as an encounter between raptors and mixed flocks. *S. atricollis* was assumed to be in a mixed flock if there was an individual of at least one other species located within 10 m and the two or more birds appeared to be joining or following one another (Hutto, 1994). The semi-open vegetation made it possible to distinguish that one species started and conducted conspicuous mixed flock displacement (birds flew 20 m or more from a foraging patch to another). Consequently, in this study, a species was assumed to be a leader if it was in the front of mixed flocks in more than 50% of the conspicuous displacements, during a period of observation. Also, a species was considered as nuclear if it was joined and followed by others species (Moynihan, 1962; Munn & Terborgh, 1979; Powell, 1985), whereas attendant ones led no mixed flocks.

I conducted observations on mixed flocks including *S. atricollis* from April 1994 to March 1996. Once the leadership of those mixed flocks was determined, I studied mixed flocks without *S. atricollis* from March to September 1996, to assess the pattern of leadership and to compare the mean number of species per flock, according to leader species. These mixed flocks might include *C. hirundinacea* and/or *N. fasciata*. Field procedures to study those mixed flocks were the same described above. As mixed flocks with *N. fasciata* (*S. atricollis* and *C. hirundinacea* absent) showed less cohe-

sion, I standardized observations on those mixed flocks to 1 h only.

Results

Size and composition of mixed flocks

From April 1994 to March 1996 I found *S. atricollis* within mixed flocks 162 times. *S. atricollis* was also found in conspecific groups (25 times), mainly from November to January while breeding. Additionally, 63 mixed flocks without *S. atricollis* were studied from March to September 1996 (33 included *N. fasciata* and 30 *C. hirundinacea* and *N. fasciata*). I observed mixed flocks with *S. atricollis* directly, for a total of 425 h (mean observation periods were 2 h 30 min) and for 72 h those including *C. hirundinacea* and *N. fasciata* (also for 2 h 30 min, on average). Mixed flocks including *N. fasciata* were observed for 33 h. In the mixed flocks with *S. atricollis* up to 34 species were recorded. Almost all were passerines mainly from Emberizidae and Tyrannidae (12 and 7 species respectively, Table 1). The mean (±SD) species number was 9.2 ± 3.5 and the mean mixed flock size was 24.1 ± 10.9 birds. The species number and mixed flock size were highly correlated ($rs = 0.88$, $p < 0.001$, Spearman correlation). Table 2 shows the species recorded in the mixed flocks without *S. atricollis*. In those ones including *C. hirundinacea* and *N. fasciata* or only *N. fasciata*, average species number was 5.5 ± 1.8 and 3.8 ± 1.7 respectively. Mean mixed flock size was 14.4 ± 4.4 and 8.2 ± 3.1 respectively (correlations, $rs = 0.71$, $p < 0.05$, and $rs = 0.86$, $p < 0.01$, respectively).

Behavior of prominently perching species

The prominently perched birds of the species *M. saturninus*, *C. hirundinacea*, *N. fasciata* and *S. atricollis* constantly turn their heads, first to one side, then to the other, holding the bill horizontally positioned. Most alarm calls recorded when raptors were present were given by prominently perched birds (see results below). The alarm calls stimulated all birds to head for cover. Two or more birds from different species were recorded simultaneously on exposed perches for less than 5% of the time birds were prominently perched ($n = 152$ mixed flocks in which *S. atricollis* was with at least one of the three other species).

When a prominently perched bird left its position, it resumed foraging. However, those birds were not observed leaving the perch towards a prey. I observed prominently perched birds starting to chase conspecifics 14 times. Besides being uncommon, these events were almost always ($n = 11$) recorded in *N. fasciata*.

Encounters with raptors

In the study site, raptors were common and, at encounters with mixed flocks, eight species stimulated birds to give alarm calls (Table 3). I recorded 194 encounters between those raptors and mixed flocks with *S. atricollis*. In 49% of them, the birds gave alarm calls. Prominently perched birds gave 86% of the alarm calls (the remaining were given by foraging birds). Foraging birds gave alarm calls before the ones prominently perched only twice, so that most alarm calls given by foraging birds occurred when no bird was prominently perched. Falcons attacked mixed flocks 14 times (10 attacks by *Falco sparverius* and four by *F. femoralis*; one attack every 30 h, on average). Successful attacks were prevented due to prominently perched birds' alarm calls, which warned all flock members in time to head for cover.

Table 1. The occurrence of species in mixed flocks with *Saltator atricollis* ($n = 162$) in campo-cerrado. Mean (±SD) group size is also provided. For the species recorded less than three times in mixed flocks only the mean is given.

Species	Occurrence (%)	Group size
Saltator atricollis	100	3.7 ± 1.4
Emberizoides herbicola	84	2.2 ± 0.9
Neothraupis fasciata	83	3.8 ± 1.1
Synallaxis albescens	83	1.7 ± 0.5
Melanopareia torquata	70	1.2 ± 0.4
Ammodramus humeralis	69	1.3 ± 0.5
Cypsnagra hirundinacea	63	3.4 ± 1.2
Zonotrichia capensis	59	3.2 ± 1.6
Coryphospingus cucullatus	38	2.0 ± 0.3
Formicivora rufa	35	2.1 ± 0.5
Volatinia jacarina	34	3.2 ± 1.8
Suiriri suiriri	30	1.9 ± 0.6
Sporophila bouvreuil	27	7.5 ± 5.6
Mimus saturninus	24	5.0 ± 1.9
Camptostoma obsoletum	24	1.1 ± 0.3
Picoides mixtus	18	1.2 ± 0.4
Troglodytes aedon	10	1.3 ± 0.5
Furnarius rufus	9	2.1 ± 0.9
Sporophila plumbea	9	1.9 ± 0.5
Elaenia flavogaster	9	1.4 ± 0.5
E. cristata	9	1.3 ± 0.5
Sporophila caerulescens	8	2.8 ± 1.5
Sicalis citrina	7	2.1 ± 0.5
Veniliornis passerinus	6	1.7 ± 0.5
Colaptes campestris	5	2.1 ± 0.8
Sporophila leucoptera	4	1.9 ± 1.1
Picumnus albosquamatus	3	1.6 ± 0.5
Cyclarhis gujanensis	3	1.0 ± 0.0
Serpophaga subcristata	2	1.2 ± 0.5
Polystictus pectoralis	2	1.3 ± 0.6
Alectrurus tricolor	2	2.5 ± 1.0
Piaya cayana	1	1.0
Nystalus chacuru	1	1.0
Colaptes melanochloros	1	1.0

Leader species

I recorded *M. saturninus* in only 24% ($n = 39$) of the mixed flocks. However, it was always the leader in spite of group

Table 2. The occurrence of species in mixed flocks led by *Cypsnagra hirundinacea* ($n = 30$, left) in campo-cerrado, and in the ones led by *Neothraupis fasciata* ($n = 33$). Mean (±SD) group size is also provided. For the species recorded less than three times, only the mean is given.

Species	Occurrence (%)	Group size	Species	Occurrence (%)	Group size
Cypsnagra hirundinacea	100	4.1 ± 1.5	*Neothraupis fasciata*	100	3.8 ± 1.1
Neothraupis fasciata	100	3.6 ± 0.9	*Ammodramus humeralis*	73	1.3 ± 0.5
Emberizoides herbicola	97	2.3 ± 1.4	*Emberizoides herbicola*	73	1.9 ± 0.7
Melanopareia torquata	70	1.0 ± 0.2	*Zonotrichia capensis*	39	2.3 ± 2.0
Synallaxis albescens	60	1.4 ± 0.5	*Synallaxis albescens*	36	1.3 ± 0.5
Ammodramus humeralis	53	1.1 ± 0.3	*Melanopareia torquata*	33	1.0 ± 0.0
Zonotrichia capensis	20	2.2 ± 1.5	*Camptostoma obsoletum*	6	1.0
Suiriri suiriri	13	1.3 ± 0.5	*Volatinia jacarina*	6	3.0
Picoides mixtus	10	1.6 ± 0.6	*Coryphospingus cucullatus*	3	2.0
Camptostoma obsoletum	7	1.0 ± 0.0	*Formicivora rufa*	3	2.0
Sporophila plumbea	7	2.0	*Polystictus pectoralis*	3	1.0
Alectrurus tricolor	3	3.0	*Troglodytes aedon*	3	1.0
Veniliornis passerinus	3	1.0			
Volatinia jacarina	3	8.0			

Table 3. Raptors which stimulated birds to give alarm calls, and respective rate of encounters ($n = 194$) with mixed flocks in campo-cerrado ($n = 162$).

Species	Encounters (%)
Falco femoralis	26.5
F. sparverius	25.0
Milvago chimachima	14.2
Elanus leucurus	13.6
Rupornis magnirostris	10.1
Rhinoptynx clamator	4.6
Buteo albicaudatus	4.0
Herpetotheres cachinnans	2.0

size (pure groups within mixed flocks; ranged from 2–9 birds) and low percentage of contact calls given by their prominently perched birds. Those birds were present for nearly 50% of the observation time and gave earlier 92% of the alarm calls ($n = 12$) in the presence of raptors (Fig. 1). The same trend was verified in other 72 mixed flocks in which *S. atricollis*, *C. hirundinacea* and *N. fasciata* were included. Mean group size was similar for those three species. Prominently perched birds of *S. atricollis* and *C. hirundinacea* were present for nearly 30% and 25% of the observation time, respectively. *Saltator atricollis* was the first to give 80% of the alarm calls ($n = 34$) recorded at encounters with raptors, and regularly gave contact calls while prominently perched (Fig. 1). *Saltator atricollis* led most of those mixed flocks (64%, $\chi^2 = 5.10$, $p < 0.025$), whereas none was led by *N. fasciata*. Also, *S. atricollis* always led either mixed flocks in which *C. hirundinacea*, *M. saturninus* and *N. fasciata* were absent ($n = 10$) or the ones in which it was with *N. fasciata* (*C. hirundinacea* and *M. saturninus* absent, $n = 33$).

Mixed flocks including *C. hirundinacea* and *N. fasciata* (*M. saturninus* and *S. atricollis* absent, $n = 30$) were always led by *C. hirundinacea*. Prominently perched birds of *C. hirundinacea* were present 41 ± 17% of the observation time while the ones of *N. fasciata* only 1.2%. Alarm calls were recorded in 54% of the encounters between raptors and those mixed flocks ($n = 24$). All of them were given by prominently perched birds of *C. hirundinacea*. *Neothraupis fasciata* only led mixed flocks without *C. hirundinacea*, *M. saturninus* and *S. atricollis* ($n = 33$). In this case, prominently perched birds of *N. fasciata* were present 32 ± 12% of the observation time and gave all alarm calls recorded in the presence of raptors ($n = 5$). No other species was observed leading mixed flocks (>1300 h of observations). Therefore, the other 30 species recorded in mixed flocks might be identified as attendant species.

I compared the mean number of species present in mixed flocks composed by equivalent species, whose birds used exposed perches to watch about, in order to evaluate whether different leader species were associated with the same number of attendant species. Those comparisons were made between mixed flocks led by *S. atricollis* including *N. fasciata* ($n = 27$, sampled from March to September) and mixed flocks led by *C. hirundinacea*, also including *N. fasciata* ($n = 30$). On average, the number of species was higher in mixed flocks with *S. atricollis* (9.3 ± 2.8 versus 5.5 ± 1.8 species, Mann-Whitney *U*-test, $z = 4.70$, $p < 0.001$). I also compared mixed flocks led by *S. atricollis* in which there was no other species whose birds used exposed perches to watch about ($n = 7$, sampled in the same period cited above) and mixed flocks led by *N. fasciata* ($n = 33$). The mixed flocks led by *S. atricollis* included a larger average number of species (8.3 ± 1.5 *versus* 3.8 ± 1.7 species, Mann-Whitney *U*-test, $z = 3.83$, $p < 0.001$).

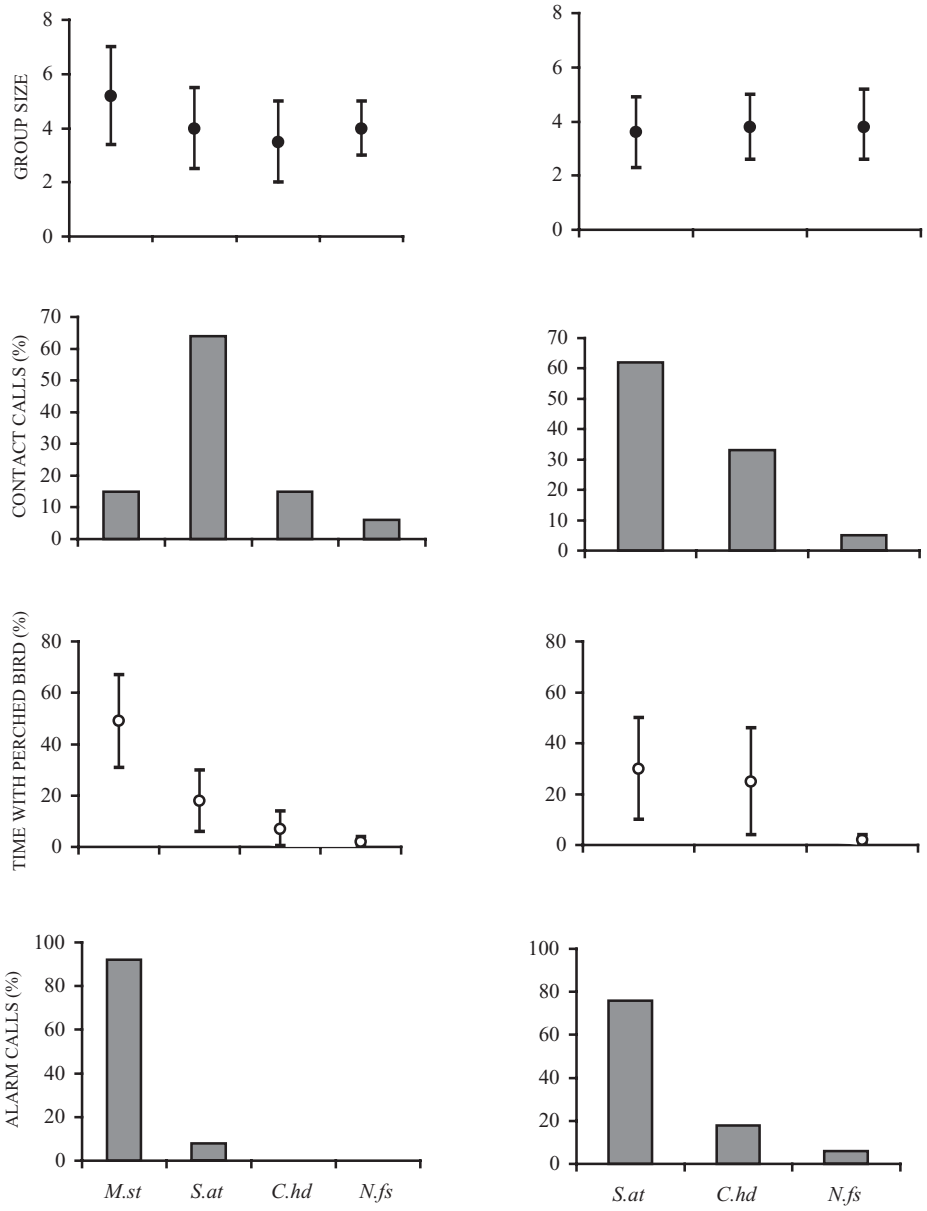

Fig. 1. Comparison of four behavioral parameters of nuclear species occurring together in mixed flocks with (left, $n = 23$) and without (right, $n = 72$) *Mimus saturninus*. From top to bottom: mean group size (±SD), rel. frequency of contact calls given by prominently perched birds ($n = 130$), performance as nuclear species within the flock (percent of observation period) and relative frequency of alarm calls ($n = 12$) given in the presence of raptors. *Mimus saturninus* (*M.st*), *Saltator atricollis* (*S.at*), *Cypsnagra hirundinacea* (*C.hd*) and *Neothraupis fasciata* (*N.fs*) when in the same mixed flock. Right, the same parameters in mixed flocks including *Saltator atricollis*, *Cypsnagra hirundinacea* and *Neothraupis fasciata* (contact calls, $n = 374$; alarm calls, $n = 34$).

Discussion

Vigilance

Vigilance among prominently perched birds has been found in some species. Predation avoidance is thought to be the main function of those birds because their advantageous position increases perception of predators (Wickler, 1985; Ferguson, 1987; McGowan & Woolfenden, 1989). McGowan and Woolfenden (1989) showed in Florida scrub jay (*Aphelocoma coerulescens*) the existence of a sentinel system as well as the sentinels' efficiency to alert to danger (through alarm calls) the other foraging birds.

In this study, the main function of birds recorded prominently perched may also be vigilance. The continuous movements of the head in all directions is consistent with this interpretation. Furthermore, in most cases, they gave alarm calls earlier than the foraging birds, which suggests an enhanced perception of raptors. Also, birds of different

species overlapped to only a small percentage in the time they spent on exposed perches, and the large differences in mean time they were on exposed perches according to the presence of other species which also used exposed perches, suggest mutual exploitation of guarded periods (Metecalf, 1984; Beveridge & Deag, 1987; Popp, 1988).

It is nevertheless worth considering alternative explanations that may cause birds to use prominent observation points. Birds might use exposed perches to enhance the detection of a prey below or a prey flushed by other flock members. However, those birds were not looking down, and I never observed them capture a prey immediately after leaving an exposed perch. Also, while in mixed flocks, they never chased flushed prey. In the campo-cerrado, the species recorded using prominent perches chased flying ants and termites only during the wet season, after heavy rain fall when those insects were abundant and most species were breeding. During that period mixed flocks were rare (Ragusa-Netto, 1999). In addition, if birds were prominently perched mainly for foraging, I would expect to observe birds regularly resuming an exposed perch after an attempt or a successful capture of a prey (as in the case of many Tyrannidae; Fitzpatrick, 1980). As a result, birds simultaneously prominently perched would presumably be more common.

The prominently perched birds might be monitoring foraging performance of mixed flock members in order to copy successful foragers. If this were so, prominently perched birds commonly would leave their position to follow a successful forager closely, or to chase them from an appropriate substrate, as in the case of temperate mixed flocks (Morse, 1970; Krebs, 1973). However, as mentioned above, prominently perched birds were looking around and not towards a specific point. Moreover, neither agonistic interactions between birds from different species, nor foraging in close proximity to one another suggesting copy behaviour were observed (Hutto, 1994).

Birds of mixed flocks in campo-cerrado may be territorial (for *N. fasciata* see Alves, 1990) as are birds of neotropical mixed flocks elsewhere (Wiley, 1971; Willis, 1972; Munn & Terborgh, 1979; Powell, 1979, 1985, 1989; Greenberg & Gradwohl, 1986; Poulsen, 1996). In a such semi-open habitat, birds might use exposed perches to spot territorial intruders. However, *M. saturninus* was recorded prominently perched for longer periods, and no agonistic interactions were observed. In contrast, most agonistic interactions were recorded in *N. fasciata*, whose individuals were observed for less time prominently perched. For *S. atricollis*, *C. hirundinacea* and *N. fasciata*, the mean time employed on exposed perches was different according to mixed flock composition (Fig. 1, and mixed flocks without *S. atricollis*). Thus, it seems unlikely that those species employed more time to the detection of conspecifics, by using exposed perches, in the absence of other species which also used exposed perches to look around. Nevertheless, a change with the ability to perceive raptors is likely (Metecalf, 1984; Beveridge & Deag, 1987; Hogstad, 1988; Popp, 1988).

Nuclear species

The cohesion and stability of bird mixed flocks is enhanced by the nuclear species, because mixed flocks lacking nuclear species are more likely to be small and weakly united (Moynihan, 1962; Powell, 1979, 1985; Hutto, 1994). In the campo-cerrado, the four potential leader species of mixed flocks showed, in common, both larger group size and birds which more frequently used exposed perches to look around (hereafter sentinels). Although group size of species such as *Zonotrichia capensis*, *Volatinia jacarina* and *Sporophila bouvreuil* was similar or even larger than the ones of the leaders, those species led no mixed flock. Thus, group size alone may be poorly related to bird attraction to mixed flock and its leadership. If group size was meaningful to bird attraction, I would expect that the species whose group size was the largest at a given mixed flock was the leader. In many cases two or three *S. atricollis* were present at a mixed flocks while groups of *N. fasciata* included 5–7 birds. Despite this fact, *N. fasciata* always followed *S. atricollis*.

The amount of contact calls given by sentinels (assumed in this study as an estimator of communication) was apparently weakly related to bird attraction. The contact calls were both more conspicuous and regularly given by *S. atricollis*. Although those calls may function to make fellow group members aware that they are being covered (Wickler, 1985; Rasa, 1986; Manser, 1999) and might be exploited by other species (Sullivan, 1984b; Monkkonen et al., 1996), *M. saturninus* always led mixed flocks in spite of giving at least four times less contact calls than *S. atricollis*, when in the same mixed flock.

The time employed by each species in vigilance and the responses through alarm calls were the most consistent parameters to mixed flock leadership in campo-cerrado. All comparisons showed a higher propensity for flock leadership by the most alert species in a given mixed flock. *Mimus saturninus* and *N. fasciata* were the two extremes of this pattern. *Neothraupis fasciata* always followed the other species with sentinels. On average, time guarded by this species was shortest, making it more similar to the attendant ones, except in those mixed flocks where it was the leader. Even in mixed flocks in which the other species with sentinels was *C. hirundinacea*, another tanager similar both in body and group size, the time employed in vigilance by *N. fasciata* was very short.

Saltator atricollis, the main subject of this study, was out of mixed flocks only while breeding. Even at that time, some birds tried to follow it. However, the frequent trips to the nest apparently jeopardized mixed flock organization. Due to the low occurrence of *M. saturninus* in mixed flocks, *S. atricollis* led most of those mixed flocks in which it was included. In fact, most alarm calls recorded in this study were given by *S. atricollis* (66%, $n = 95$), including those when raptors unsuccessfully attacked mixed flocks. This species meets such features as large groups, regular display of

contact calls and, most important, high alertness, which probably made it the best reference to the other flocking species which presumably benefited by exploiting the shelter close to them.

Munn and Terborgh (1979) described the role of *Thamnomanes* spp. in Amazonian mixed flock. These birds led mixed flocks and were the most alert species. The flycatching *Thamnomanes* scanned about (with an erect posture) to search for prey while most other species (mainly gleaners) closely focused on vegetation. Due to this foraging behaviour, *Thamnomanes* more readily detected approaching predators and gave unambiguous alarm calls which were used by all species to avoid predation. In temperate mixed flocks the parids (*Parus* spp.) are the most alert species (Morse, 1970), and their alarm calls are recognized by all participating species (Gaddis, 1980; Sullivan, 1984b). Greig-Smith (1981) showed that up to 10 species exploited alarm responses (flights and calls) given by *Saxicola torquata*, which support the concept of alertness as the main feature to the attraction of species to mixed flocks. While in mixed flocks, attendant species also increased food intake, since personal efforts in vigilance were reduced due to the exploitation of the vigilance of nuclear species (Sullivan, 1984a; Dolby & Grubb, 1999).

In the campo-cerrado, encounters between raptors and mixed flocks were common, imposing a high degree of threat to birds (Morse, 1973). The species with sentinels more readily gave alarm calls due to potential danger, while attendant species, many of them foraging on or close to the ground among grasses (Ridgely & Tudor, 1989, 1994; Sick, 1997; Ragusa-Netto, 1999), were not recorded giving alarm calls. So, the perception of attendant species may be restrained if compared to those of the leader species. The instantaneous evasive reactions by all flock members to alarm calls from different species suggests heterospecific exploitation of information towards predation avoidance (Powell, 1974; Gaddis, 1980; Greig-Smith, 1981; Sullivan, 1984b). The exploitation both of signals and vigilance is most likely among species which share the same habitat and are similar in size, life cycle and vulnerability (Metecalf, 1984; Sullivan, 1984b; Hogstad, 1988; Popp, 1988). In order to decrease the risk of predation, while scanning less and presumably increasing time to foraging (Pullian, 1973) in the highly seasonal campo-cerrado, birds were presumably attracted to mixed flocks mainly due to increase protection from predators.

Although in the strictest sense nuclear species are not needed for mixed flock organization, both their role for cohesion maintenance and influence on the size of mixed flocks are widely accepted (Vuilleumier, 1970; Powell, 1979, 1985; Hutto, 1994; Monkkonen et al., 1996; Dolby & Grubb, 1999). In the campo-cerrado the leader species probably is more than a sharp focus of movement and direction (Austin & Smith, 1972). In fact, the leader species presented an increased perception of raptors and consequently improved the safety in mixed flocks.

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