ORNITOLOGIA NEOTROPICAL 18: 75–97, 2007

MIXED-SPECIES FLOCKS OF BIRDS IN THE CERRADO, SOUTH AMERICA: A REVIEW

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Resumo. – Bandos mistos de aves no Cerrado, América do Sul: uma revisão. – Revisões sobre bandos mistos de aves geralmente examinam informações obtidas em várias regiões do mundo, não focando avifaunas de ecossistemas particulares. Este trabalho teve como objetivo revisar informações sobre bandos mistos encontrados no Cerrado. Publicações (n = 28) mencionaram 172 espécies participando de bandos mistos, em várias fitofisionomias e regiões. Estudos mais detalhados foram conduzidos somente em cerrado sensu stricto e campo cerrado. Membros de bandos foram vistos consumindo frutos, néctar, insetos e sementes. Bandos com até 16 espécies e 40 indivíduos foram registrados. Doze espécies de seis famílias já foram apontadas como espécies nucleares. Em geral, são aves de coloração contrastante, que também ocorrem em grupos mono-específicos quando ausentes de bandos mistos. Há evidência de que o risco de predação é um fator levando à formação de bandos mistos em campo cerrado e cerrado *sensu stricto*. Também, ataques predatórios por espécies de *Falco* foram flagrados. Bandos mistos são menos freqüentes e têm menor número de indivíduos e de espécies durante a época reprodutiva do que no período não-reprodutivo das espécies. Avaliações da avifauna conduzidas em várias escalas espaciais revelaram que a participação em bandos mistos é uma estratégia adotada por uma porção considerável da avifauna encontrada no Cerrado. Entre as sugestões para pesquisas futuras está o aproveitamento do ambiente do Cerrado (seus mosaicos de vegetação, sua grande extensão e a forte sazonalidade de seu clima) para pesquisar aspectos da biologia de bandos mistos pouco estudados ao redor do mundo.

Abstract. – Reviews on mixed-species flocks usually examine information obtained in several regions around the world, not focusing the avifauna of particular ecosystems. This study aimed to review information on mixed-species flocks found in Cerrado. Publications (n = 28) mentioned 172 species participating in mixed-species flocks in several vegetation physiognomies and regions. More detailed studies were conducted only in cerrado *sensu stricto* and "campo cerrado" vegetation. Flock members were found consuming fruits, nectar, seeds and insects. Flocks with up to 16 species and 40 individuals were recorded. Twelve species of six families were considered as nuclear species. In general, these are birds with contrasting coloration that also occur in mono-specific groups in absence of mixed-species flocks. There is evidence that predation risk is a factor leading to the formation of mixed-species flocks in savanna vegetation. Also, predatory attacks by *Falco* species were noted. Mixed-species flocks are less frequent and have lower number of species and individuals during the breeding season than in the non-breeding season. Assessments conducted at several spatial scales revealed that the participation in mixed-species flocks is a strategy adopted by a large part of the bird species richness found in Cerrado. Among suggestions for future research is the consideration of the Cerrado environment (its mosaics of vegetation, its great extension and its strongly seasonal climate) for studying aspects of the biology of mixed-species flocks poorly investigated world-wide. *Accepted 1 October 2006*.

Key words: Birds, Cerrado, mixed-species flock, Neotropical region, savanna.

INTRODUCTION

Mixed-species flocks of birds are related to two major advantages gained by flock members – reduced predation risks and increased foraging efficiency (Morse 1970, 1977; Diamond 1981, Powell 1985, Terborgh 1990, Thiollay 1999). According to these reviews, birds enhance these two benefits in several ways through the acquisition of information and protection from other birds participating in these inter-specific associations.

Mixed-species flocks have been found on all continents (Greig-Smith 1978, Bell 1980, Hutto 1987, Latta & Wunderle 1996, Thiollay 1999, Hino 2000, Tellería *et al.* 2001). In the Neotropical region, they have been recorded in a diverse range of ecosystems or regions, such as Amazonia (Powell 1979, Gradwohl & Greenberg 1980, Munn 1985, Stotz 1993, Jullien & Thiollay 1998, 2001), the Atlantic Forest (Machado 1999, Develey & Peres 2000), Patagonia (Vuilleumier 1967) and Andes (Poulsen 1996, Bohórquez 2003).

In the Cerrado province, detailed investigations on mixed-species flocks have been conducted since the 1980s (Silva 1980, Silva & Oniki 1988, Alves & Cavalcanti 1996, Ragusa-Netto 1997, 1999, 2000, 2002; Tubelis 2004, Tubelis *et al.* 2006). Additionally, several publications concerning the avifauna of the Cerrado provide brief information on these flocks (Alves 1990, Willis & Oniki 1990, 1991; Cavalcanti 1992, Marini 1992, Ridgely 1994, Parker & Willis 1997, Sick 1997, Vasconcelos *et al.* 1999, Olmos & Boulhosa 2000, Pearce-Higgins 2000, Ragusa-Netto 2001, Silveira *et al.* 2001, Willis 2003, Lopes 2004).

Some aspects of its avifauna and landscapes make Cerrado an interesting region for the study of mixed-species flocks. First, a diverse range of habitat requirements shown by the numerous species found in Cerrado (Willis & Oniki 1990, Silva 1995, Macedo 2002) favor the study of mixed-species flocks in diverse situations. For example, these associations can be examined within vegetation patches (Alves & Cavalcanti 1996, Ragusa-Netto 2000), as well as across boundaries formed by the juxtaposition of distinct habitats (Tubelis *et al.* 2006). Second, Cerrado is marked by a strongly seasonal climate (Eiten 1993), with consequent seasonal changes in resource availability (Oliveira 1998, Pinheiro *et al.* 2002). Thus, Cerrado might be an interesting region to examine seasonal formation of flocking – a question often investigated worldwide (Morse 1970, Powell 1985). Third, Cerrado harbors a high species richness of avian predators (Silva 1995), birds that might lead to the formation of mixed-species flocks around the world (Terborgh 1990, Thiollay 1999).

Reviews on mixed-species flocks tend to consider information obtained world-wide, not focusing particular ecosystems (Morse 1970, 1977; Diamond 1981, Powell 1985, Terborgh 1990). On the other hand, two reviews on the biology of mixed-species flocks in the Neotropical region (Develey 2001, Jullien & Thiollay 2001) have emphasised the Amazon and the Atlantic Forest. Recently, social aspects of the Cerrado's avifauna have been reviewed (Macedo 2002), but mono-specific groups were the major focus. Thus, studies of mixed-species flocks in Cerrado remain unreviewed in details.

This study reviews the information on mixed-species flocks in the Cerrado province. First, I review data related to the Cerrado environment and its resources: 1) the geographic distribution of records within this province, 2) the use by mixed-species flocks of different vegetation physiognomies, 3) the food items consumed by flock members. Additionally, I use the compiled records to investigate patterns of habitat use, sociality and habit (forest or non-forest species) among the nuclear species. Also, the compiled information was used to examine the propor-

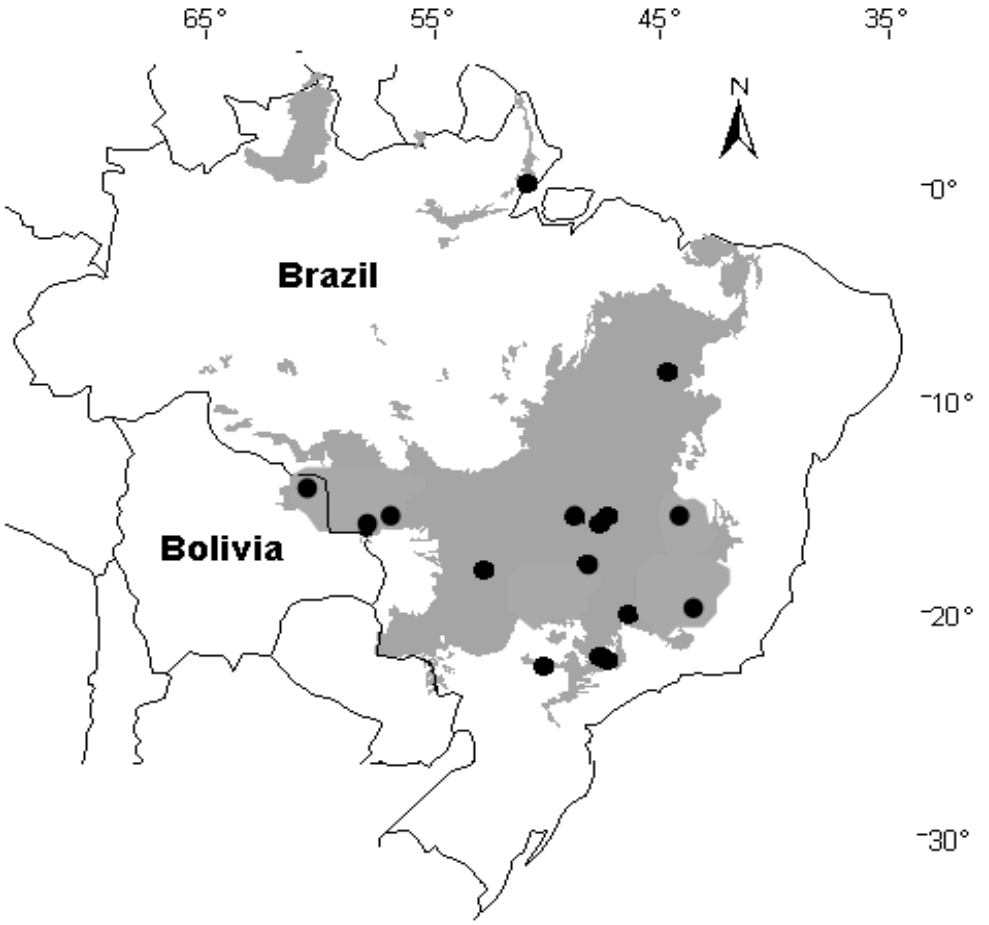

FIG. 1. Geographical distribution of localities (black spots) in which mixed-species flocks of birds have been found in the Cerrado, South America.

tion of species participating in mixed-species flocks at three spatial scales in Cerrado. The next topics reviewed in this paper include three major aspects of mixed-species flocks often investigated around the world: the number of birds and species found in mixed-species flocks, evidence of advantages gained by participation in mixed-species flocks, and the seasonal occurrence of these flocks. Also, I present a general overview and provide suggestions for future research of mixed-species flocks in Cerrado.

METHODS

Cerrado. This South American vegetation province occupies about 2,000,000 km^2 in Brazil, Bolivia and Paraguay (Fig. 1). Its vegetation covers most of the highlands of central Brazil and extends through peninsulas and disjunct patches to Caatinga, Amazonia, Chaco and the Atlantic Forest (Eiten 1972, 1993; Cavalcanti 1999a, Oliveira & Marquis 2002).

Landscapes in the Cerrado are usually

dominated by cerrado *sensu lato*, which encompasses a range of vegetation physiognomies varying from open grasslands to woodlands and forests (Eiten 1972, 1993; Ribeiro & Walter 1998, Oliveira-Filho & Ratter 2002). Grasslands without shrubs or trees are called "campos limpos", while "campos sujos" are those with scattered shrubs and few trees. Savanna vegetation with intermediate and higher densities of shrubs and trees are called "campo cerrado" and cerrado *sensu stricto*, respectively. "Cerradão" is forest, with higher and denser trees and a much reduced ground layer (Eiten 1972, 1993; Ribeiro & Walter 1998, Oliveira-Filho & Ratter 2002).

Besides cerrado *sensu lato*, other major vegetation physiognomies are found in uplands, such as semi-deciduous forests, deciduous forests and rocky grasslands. Gallery forests, marshes, floodplain grasslands and "veredas" (wet grasslands with scattered shrubs and palm trees) occur in valleys (Eiten 1972, 1993; Ribeiro & Walter 1998, Oliveira-Filho & Ratter 2002). Additional information on vegetation and landscapes can be found in Sano & Almeida (1998), Cavalcanti (1999a) and Oliveira & Marquis (2002).

Mixed-species flocks. They are inter-specific bird associations that forage within a giving area, keeping the group cohesion even when changing directions; they are guided by species that often display alarm calls and sentinel behavior – the nuclear species (Morse 1977, Powell 1985, Terborgh 1990, Stotz 1993, Jullien & Thiollay 1998). Although these flocks are often called mixed-species flocks (e.g., Alves & Cavalcanti 1996, Parker & Willis 1997, Silva *et al.* 1997, Tubelis *et al.* 2006), they also receive other denominations, such as mixed species bird flocks (e.g., Develey & Peres 2000), mixed flocks (e.g., Cavalcanti 1992), mixed bands (e.g., Dubs 1992), bird mixed flocks (e.g., Ragusa-Netto 2000, 2002) and "bandos mistos" (e.g., Silva & Oniki 1988, Willis & Oniki 1990). All publications mentioning the occurrence of such flocks in Cerrado (Fig. 1) were included in this review. Mixed-species flocks are very different from ant-following bird groups (Willis & Oniki 1978) and bird aggregations in a given area as a result of localized food resources (e.g., water, fruiting trees, swarming insects), whose records were not included in this review. Also, records in Cerrado of several species foraging together but with no comment on interactions in mixed-species flocks (e.g., Bagno & Rodrigues 1998, D'Angelo 2000) were not included. The nomenclature of bird species follows Sigrist (2006).

Literature review. The literature review was based on the bibliography of Oniki & Willis (2002), the "Bibliografia Recente da Ornitologia Brasileira" published regularly in "Araraajuba" (the former journal of the Brazilian Society of Ornithology) until 2002, and the Zoological Records.

RESULTS AND DISCUSSION

Regional distribution of records of mixed-species flocks in the Cerrado. A total of 28 publications has reported the occurrence of mixed-species flocks in Cerrado. These associations have been found through most of the Cerrado region (Fig. 1; Appendix 1). In central Brazil, published records come from the Distrito Federal (Silva 1980, Alves 1990, Cavalcanti 1992, Marini 1992, Ridgely 1994, Alves & Cavalcanti 1996, Lopes 2004, Tubelis 2004, Tubelis *et al.* 2006) and Goiás (Ridgely 1994, Sick 1997, Tubelis 2004). Investigations in west Cerrado areas have been conducted in Bolivia (Pearce-Higgins 1996, 2000) and in Brazilian Mato Grosso (Silva & Oniki 1988, Willis & Oniki 1990, Dubs 1992, Parker & Willis 1997). Records in northern Cerrado are restricted to the states Amapá (Silva *et al.* 1997) and Piauí (Silveira *et al.* 2001). Those in

south-eastern Cerrado are from São Paulo (Willis & Oniki 1993, Ragusa-Netto 1997, 1999; Olmos & Boulhosa 2000, Ragusa-Netto 2000, 2001, 2002; Willis 2003) and Minas Gerais (Willis & Oniki 1991, Silveira 1998, Vasconcelos *et al.* 1999). Further research is probably going to increase the number of localities with records of these associations, as participation in mixed-species flocks appears to be a strategy widespread in Cerrado.

Despite numerous records throughout most of its extension, studies comparing mixed-species flocks in different regions or localities are rare in Cerrado. Silva *et al.* (1997) reported that the species composition of flocks found in cerrado *sensu stricto* vegetation in northern Cerrado (Amapá) is similar to those flocks recorded in central Brazil (Distrito Federal). Tubelis (2004) compared mixed-species flocks of forest species found in savannas adjacent to forests in Caldas Novas (Goiás) and the Distrito Federal. Flocks were guided by the same nuclear species in both localities. It was suggested that differences in the number of species found in mixed-species flocks of both localities could result from the size of gallery forests and the vegetation structure of adjacent savannas (Tubelis 2004).

Use of vegetation physiognomies. Mixed-species flocks were recorded in a diverse range of native physiognomies (Appendix 1). Forest vegetation included gallery forest (Silva & Oniki 1988, Willis & Oniki 1991, Cavalcanti 1992, Dubs 1992, Marini 1992, Tubelis 2004), dry forest (Willis & Oniki 1990, 1991) and "cerradão" (Olmos & Boulhosa 2000). Non-forest vegetation comprised cerrado *sensu stricto* (Silva 1980, Silva & Oniki 1988, Alves 1990, Willis & Oniki 1991, Ridgely 1994, Alves & Cavalcanti 1996, Silva *et al.* 1997, Silveira *et al.* 2001, Lopes 2004, Tubelis 2004, Tubelis *et al.* 2006), rocky "cerrado" (Tubelis 2004), "campo cerrado" (Parker & Willis 1997, Vasconcelos *et al.* 1999, Ragusa-Netto 1999, 2000, 2001, 2002), grasslands (Silva & Oniki 1988, Willis & Oniki 1990, 1993; Ridgely 1994, Silveira 1998, Vasconcelos *et al.* 1999), marshes (Sick 1997) and wet grasslands (Pierce-Higgins 1996, 2000). Thus, more studies have been done in open vegetation than in forests. Mixed-species flocks have not yet been studied in rocky grasslands and "veredas" (Appendix 1).

Records in managed or exotic vegetation were in orchards and plantations (Silva & Oniki 1988), pastures with scattered trees (Ragusa-Netto 1997) and in eucalypt plantations with recovering native understory (Willis 2003) (Appendix 1). It was not determined if flocks could establish whole territories within patches of such vegetation or if they were using them as additional foraging areas.

Despite the recording of mixed-species flocks in a wide range of native and exotic vegetation (Appendix 1), no studies made comparisons between different habitats in Cerrado. Thus, the biology of mixed-species flocks in different native physiognomies and the response of mixed-species flocks to man-induced changes in native vegetation remain unknown in Cerrado.

Food items consumed by flock members. Studies recorded a diverse range of resources eaten by birds joining mixed-species flocks. Fruits included those of Melastomataceae (Silva & Oniki 1988), *Ficus* sp. (Willis & Oniki 1990), *Miconia albicans*, *M. fallax*, *M. ferruginata*, *M. rubiginosa*, *Miconia* sp., *Byrsonima lancifolia* and *Qualea parviflora* (Tubelis 2004), and unidentified species (Cavalcanti 1992, Alves & Cavalcanti 1996). Inflorescences of *Mabea* sp. (Willis & Oniki 1990), *Mabea fistulifera* (Olmos & Boulhosa 2000), *Caryocar brasiliense, Phoradendron crassifolium*, *Qualea grandiflora* and *Roupala montana* (Tubelis 2004) also were major resources used by flock members. The consumption of seeds by mixed-flock mem-

TABLE 1. Taxa considered as nuclear species of mixed-species flocks in Cerrado, with information on their habits, sociality when not in mixed-species flocks, use of vegetation physiognomies, and the source of information. An asterisk (*) indicates species endemic to Cerrado (according to Cavalcanti (1999a) and Silva (1995)), while the sign (**) indicates that the species was considered as a probable nuclear species by the respective authors.

Families/species	Habits	Sociality	Vegetation	Sources
Dendrocolaptidae				
Lepidocolaptes angustirostris	Open vegetation	Pairs	Cerrado *sensu stricto*	2
Tyrannidae				
Suiriri suiriri	Open vegetation	Groups	Cerrado *sensu stricto*	2, 11, 26
Mimidae				
Mimus saturninus	Open vegetation	Groups	Campo cerrado	14, 24
Thraupidae				
Cypsnagra hirundinacea *	Open vegetation	Groups	Campo cerrado	21, 24
Lanio versicolor (**)	Forest		Gallery forest	2
Ramphocelus carbo (**)	Forest		Gallery forest	2
Neothraupis fasciata *	Open vegetation	Groups	Cerrado *sensu stricto*, Campo cerrado	1, 2, 3, 11, 21, 24
Tangara cayana	Forest	Groups	Cerrado *sensu stricto,* Gallery forest	27,28
Dacnis cayana	Forest	Groups	Cerrado *sensu stricto,* Gallery forest	27,28
Hemithraupis guira	Forest	Groups	Cerrado *sensu stricto* Gallery forest	27,28
Emberizidae				
Sporophila nigricollis	Open vegetation	Groups	Campo grassland	2
Cardinalidae				
Saltator atricollis *	Open vegetation	Groups	Campo cerrado	21,22,24

[1] Reference codes: 1, Silva (1980); 2, Silva & Oniki (1988); 3, Alves (1990); 11, Alves & Cavalcanti (1996); 14, Ragusa-Netto (1997); 21, Ragusa-Netto (2000); 22, Ragusa-Netto (2001); 24, Ragusa-Netto (2002); 26, Lopes (2004); 27, Tubelis (2004); 28, Tubelis *et al.* (2006).

bers was reported but the plant species were not identified (Silva & Oniki 1988, Willis & Oniki 1990, Alves & Cavalcanti 1996, Silveira 1998). Similarly, some studies mentioned flock members preying on unidentified insects (Alves & Cavalcanti 1996, Silveira *et al.* 2001, Tubelis 2004). In general, studies did not mention the bird species feeding on the resources, nor the species (especially seeds and arthropods) consumed. Further, there was no quantification of the food resources consumed by mixed-flock members.

No studies examined the consumption of food items by particular bird species when in and out mixed-species flocks, as examined in Costa Rican forests (Valburg 1992). Similarly, relationships between flock formation and food availability (e.g., Poulsen 1996) also were not examined in Cerrado. Investigations like these could contribute to the understanding of the advantages of participation in mixed-species flocks in Cerrado.

Despite the apparent dominance of studies reporting mixed-species flocks feeding on arthopods in the Neotropical region (e.g., Powell 1979, Gradwohl & Greenberg 1980,

Munn 1985, Hutto 1987, Machado 1999, Tellería *et al.* 2001, Bohórquez 2003), a considerable proportion (5/8) of the studies conducted in Cerrado mentioned the consumption of plant resources by flock members (see above). Thus, investigations aiming to examine the influence of food availability on flock formation and structure in Cerrado should take into account plant and animal components of the biota. This suggestion is reinforced by the recording of the consumption of insects, flowers and fruits by members of particular mixed-species flocks (Willis & Oniki 1990, Tubelis 2004).

The nuclear species. According to major reviews, the nuclear species are those that guide and keep the cohesion of mixed-species flocks (Morse 1970, Diamond 1981, Powell 1985, Terborgh 1990). Eleven out of 28 publications mentioning the occurrence of mixed-species flocks in Cerrado identified their nuclear species (Table 1). Twelve species belonging to six families of the order Passeriformes have been considered as nuclear species of mixed-species flocks in Cerrado. Most of them are members of the sub-order Passeri. Among them, there was a predominance of tanagers (Thraupidae) as nuclear species (Table 1).

The nuclear species in Cerrado are social bird species (Table 1) as they occur in groups of three or more individuals when not participating in mixed-species flocks (Alves 1990, Ridgely 1994, Sick 1997, Ragusa-Netto 1997, 2001; Lopes 2004). The only exception is *Lepidocolaptes angustirostris* which occurs alone or in pairs during most of the year (pers. observ.). However, the role of this woodcreeper as a nuclear species is secondary as *Neothraupis fasciata* and *Suiriri suiriri* are the major nuclear species in cerrado *sensu stricto* patches (Silva 1980, Silva & Oniki 1988, Alves & Cavalcanti 1996). Similarly to these findings of my review, Greig-Smith (1978) had noted in savanna woodlands in Ghana that the most frequent species in mixed-species flocks occur in mono-specific groups when out of these inter-specific associations.

Land birds found in Cerrado can be classified as forest species and non-forest species (Lins 1994, Cavalcanti 1999b). Only five (42%) of the nuclear species are forest birds (Table 1). Two of them (*Lanio versicolor* and *Ramphocelus carbo*) were detected by an investigation conducted in forests (Silva & Oniki 1988). However, the other three species (*Hemithraupis guira*, *Tangara cayana* and *Dacnis cayana*) were pointed out by a study conducted in savannas (Tubelis 2004) which examined forest-savanna movements by forest birds. Thus, this relatively low number of forest nuclear species found until now in Cerrado results, in part, from the low number of detailed studies in forests.

Ten of the 12 nuclear species have been found leading flocks in open vegetation (Table 1). This prevalence of nuclear species in savanna vegetation is result of a series of detailed observations in savannas (Silva 1980, Alves & Cavalcanti 1996, Ragusa-Netto 1999, 2000, 2001, 2002; Tubelis 2004, Tubelis *et al.* 2006). On the other hand, only five nuclear species were found in forests (Table 1). Although Tubelis (2004) and Tubelis *et al.* (2006) sampled savannas, mixed-species flocks also were seen in adjacent gallery forests. These numbers of nuclear species in both savanna and forest vegetation strongly reflect the numbers of detailed investigations conducted in these physiognomies, as identification of nuclear species requires intensive observations or sampling.

Future detailed research of mixed-species flocks in Cerrado will likely reveal further nuclear species, especially if conducted in forest, grassland and other vegetation still poorly sampled. Several species are expected to be revealed as nuclear species. This because nuclear species in Amazonia and the Atlantic

Forest, such as *Philydor rufus*, *Thamnomanes caesius*, *Habia rubica*, *Hemithraupis ruficapilla*, *Trichothraupis melanops*, *Basileuterus culicivorous* and *Basileuterus hypoleucus* (see review in Develey 2001), also might lead mixed-species flocks in Cerrado. Further, some studies reported the occurrence of flocks formed uniquely by *Sporophila* species in Cerrado (Willis & Oniki 1993, Ridgely 1994, Pearce-Higgins 1996, Sick 1997, Silveira 1998, Pearce-Higgins 2000). Also, research in regions not yet studied in detail might reveal other nuclear species.

Co-occurrence of forest and savanna birds in mixed-species flocks. Bird movement between adjacent vegetation physiognomies is a major phenomenon in Cerrado landscapes (e.g., Cavalcanti 1992, Lins 1994, Tubelis *et al.* 2004). As a consequence, a particular vegetation patch might be used by species typical of other patches. For example, forest bird species might use adjacent savanna vegetation, and savanna birds might use adjacent gallery forests. Thus, forest and non-forest (savanna) bird species (Lins 1994, Cavalcanti 1999b) might occur in a given mixed-species flock. Records of mixed-species flocks with birds typical of distinct landscape units (forest and savanna bird species) are shown below.

A forest woodpecker (*Picumnus* sp.) was seen flocking with savanna birds in cerrado *sensu stricto* (Silva 1980). Willis & Oniki (1990) recorded the forest species *Turdus amaurochalinus* foraging in canopies with species of forest edges (*Thraupis palmarum* and *T. sayaca*). Also, *T. sayaca*, *T. palmarum* and *Coryphospingus cucullatus* joined forest species in dry forests (Willis & Oniki 1990). The forest species *Myiarchus swainsoni* was found with savanna birds in cerrado *sensu stricto* (Alves & Cavalcanti 1996). Olmos & Boulhosa (2000) mentioned *Thraupis sayaca* with the forest species *Dacnis cayana* and *Tangara cayana* as common flock members in "cerradão". The forest species *Veniliornis passerinus* was recorded with bird species of open physiognomies in "campo cerrado" (Ragusa-Netto 2000, 2002). Silveira *et al.* (2001) mentioned flocks formed by savanna birds and forest species (*Piranga flava* and *Hemithraupis guira*) in cerrado *sensu stricto.* In this same habitat, six forest bird species (*Veniliornis passerinus*, *Picumnus albosquamatus*, *Cyclarhis gujanensis*, *Serpophaga subcristata*, *Piaya cayana* and *Colaptes melanochloros*) were among the less frequent participants of savanna bird flocks (Ragusa-Netto 2002). Further, *Elaenia flavogaster*, *Elaenia chiriquensis*, *Camptostoma obsoletum*, *Thraupis palmarum, Lepidocolaptes angustirostris* and *Coryphospingus cucullatus* joined forest bird flocks in adjacent cerrado *sensu stricto* patches at Distrito Federal (Tubelis 2004). *Thraupis sayaca* also was found flocking with forest species in similar patch-matrix movements at Caldas Novas (Tubelis 2004).

With the exception of Tubelis (2004), these studies did not mention co-occurrence of species typical of distinct landscape units (e.g., forest and savanna species) in the same flock. Although these events have been recorded occasionally, they illustrate the influence of habitat proximity on the species composition of mixed-species flocks in Cerrado. Such flocks with species of distinct landscape units will likely be found more often if observations are conducted close to boundaries between forest, savanna and/or vegetation associated with aquatic environment.

Despite the recording of forest and non-forest (savanna) bird species in a given flock, similar records did not occur for nuclear species. In cerrado *sensu stricto*, detailed studies identified three forest nuclear species (*Hemithraupis guira, Tangara cayana* and *Dacnis cayana*) and three savanna nuclear species (*Lepidocolaptes angustirostris*, *Neothraupis fasciata* and *Suiriri suiriri*) (Table 1). However, taxa of these two groups of nuclear species were always found in distinct flocks. Thus, the guidance of particular mixed-species flocks by both forest

and savanna nuclear species has not been reported. The reasons for this fact could be seen as venues of future research.

Participation of the bird species in mixed-species flocks. A total of 172 bird species has been observed in mixed-species flocks in Cerrado (Appendix 2). Species of the order Passeriformes were dominant, as only 18 (10.5%) of the species are non-passerines. Families with higher numbers of species in these bird associations were Tyrannidae, Thraupidae, Emberizidae, Thamnophilidae and Furnariidae, with 32, 27, 24, 13 and 11 species, respectively (Appendix 2). The participation of the bird species richness in mixed-species flocks could be evaluated at three spatial scales.

An assessment at a macro scale could be done, after discarding records outside the Cerrado core area (Willis & Oniki 1990, 1991; Dubs 1992, Willis & Oniki 1993, Pearce-Higgins 1996, Ragusa-Netto 1997, Silva *et al.* 1997, Vasconcelos *et al.* 1999, Olmos & Boulhosa 2000, Pearce-Higgins 2000, Ragusa-Netto 2000, 2001, 2002; Willis 2003). A participation of 18% was observed, as 153 of the 837 species recorded in the Cerrado core area (Silva 1995) have been found in mixed-species flocks (Appendix 2). When families (e.g., Ardeidae, Columbidae, Caprimulgidae and Apodidae) whose species have not been recorded in mixed-species flocks in Cerrado (Appendix 2) are not considered, the participation of the avifauna in mixed-species flocks raises to 28% (153/550).

Two regions characterised by both extensive inventories and considerable knowledge on mixed-species flocks permitted the assessment of participation of the avifauna at a regional level. In the Estação Ecológica Serra das Araras, 100 (43%) of the 233 species recorded were found in mixed-species flocks (Silva & Oniki 1988). Also, of 355 bird species recorded in four protected reserves in the Distrito Federal (Braz & Cavalcanti 2001), 71 (20%) have been found in mixed-species flocks (Silva 1980, Alves 1990, Cavalcanti 1992, Marini 1992, Ridgely 1994, Alves & Cavalcanti 1996, Lopes 2004, Tubelis 2004, Tubelis *et al.* 2006). These proportions raises to 60% (100/167) and 33% (71/216), respectively, after discarding families whose species have not yet been found in mixed-species flocks in Cerrado (Appendix 2).

Two studies examined the participation of the avifauna in mixed-species flocks at a local level. Of 38 species recorded in a cerrado *sensu stricto* patch in the Distrito Federal, 14 (37%) were recorded in mixed-species flocks (Silva 1980). Tubelis *et al.* (2006) showed that 50% of 66 forest bird species using savannas adjacent to gallery forests at Distrito Federal joined mixed-species flocks. These percentages raise to 64% and 82%, respectively, when considering only those taxa whose families had species found in mixed-species flocks in Cerrado (Appendix 2).

Although these proportions probably will change with further inventories and studies of mixed-species flocks, it can be noted that participation in mixed-species flocks is a major strategy adopted by a considerable part of the avifauna in the Cerrado. The high tendency of the Cerrado avifauna to flock in such interspecific associations became more evident when assessments considered only families whose species were noted in mixed-species flocks.

Also, participation of the avifauna in mixed-species flocks tended to be lower at greater than at smaller spatial scales. This might result mainly of three factors. First, assessments conducted at greater scales included avifaunas of a diverse range of habitats, while those conducted at local scales included only birds found in cerrado *sensu stricto* – a vegetation where birds often form mixed-species flocks (Appendix 1 and 2). Second, estimates at the Cerrado core area and

regional scales involved detailed and non-detailed observations on mixed-species flocks, while estimates at local scales involved only detailed observations on these flocks. Third, characteristics of the avifauna might be involved, as tendencies to participate in mixed-species flocks vary among bird species. For example, participation of savanna bird species in mixed-species flocks was lower (64%) than that of forest bird species (82%) in cerrado *sensu stricto* patches at Distrito Federal (Silva 1980, Tubelis *et al.* 2006). This difference observed in savanna vegetation might result from the fact that savanna birds are in their major habitat, while forest birds are in a habitat that provide less protection than their major (forest) habitat.

Flock size, flock species richness and flock formation. Information on the number of species found per flock (flock species richness) was present in more studies than on the number of birds per flock (flock size) (Appendix 1), probably due to difficulties in censusing individuals. Mixed-species flocks with higher number of species were recorded in "campo cerrado" (Ragusa-Netto 2002), cerrado *sensu stricto* (Tubelis 2004) and gallery forests (Marini 1992). On the other hand, flocks with low species richness (e.g., those with only two or three species) were found in a wide range of vegetation physiognomies, such as grasslands, "campo cerrado", cerrado *sensu stricto*, gallery forests, marshes and managed vegetation (Appendix 1). Larger flocks also were recorded in several habitats, such as grasslands, "campo cerrado", cerrado *sensu stricto* and gallery forests (Appendix 1).

Besides vegetation and the richness of bird communities, the level of detail of each study might influence flock size and species richness. For example, numerous studies observed flocks just briefly, thus likely contributing to reports of flocks with few (two or three) species. On the other hand, flocks with only two or three species can be frequently formed in Cerrado, as reported in detailed studies (Silva 1980, Ragusa-Netto 1997, Tubelis 2004).

Four studies in patches of cerrado *sensu stricto* (Silva 1980, Alves & Cavalcanti 1996) and "campo cerrado" (Ragusa-Netto 2000, 2002) dealt with the relationships between species richness and bird abundance in mixed-species flocks. All of them found a positive correlation between flock size and flock species richness. It was suggested that flock size increases due to the entry of new species, as usually only a group of each species is present in each flock. Interestingly, the number of species and the number of birds in a mixed flock can vary according to the nuclear species of these associations (Ragusa-Netto 2002).

Another factor causing variation in mixed-species flocks is seasonality. Detailed investigations that examined the seasonal occurrence of mixed-species flocks were conducted in the Distrito Federal. In a cerrado *sensu stricto* patch, Silva (1980) made observations during a 12-month period and recorded flocks of savanna bird species only between January and August. Contrastingly, similar mixed-species flocks were recorded in all months of a year period in this same vegetation (Alves 1990, Alves & Cavalcanti 1996). An investigation carried out in gallery forests recorded mixed-species flocks of forest bird species in basically all months of a year (Marini 1992). Further, forest flocks left gallery forests to forage in adjacent savannas throughout the year (Tubelis 2004, Tubelis *et al.* 2006). These studies sampling flocks year round suggest that mixed-species flocks are formed during both the breeding and non-breeding seasons of forest and savanna bird species in central Cerrado. Probably, their absence during a 4-month period (Silva 1980) might have resulted from a relatively lower sampling effort done in that period.

Some of these studies also examined seasonal variation in the frequency of occurrence of mixed-species flocks. Considering comparable sampling efforts, Silva (1980) contrasted the recording of 14 flocks in March (nonbreeding period) with that of only three in August (early breeding period). In the same area, the frequency of occurrence of flocks was higher in the early dry season, when birds were not reproducing (Alves 1990, Alves & Cavalcanti 1996). Similarly, forest flocks were recorded more frequently in adjacent savannas during the non-breeding than the breeding period of species (Tubelis 2004, Tubelis *et al.* 2006). Further investigations were considered necessary to verify the roles of the higher abundance of food resources and of the breeding activities in the lower frequency of occurrence of mixed-species flocks during the breeding period (Alves & Cavalcanti 1996, Tubelis 2004).

Studies that have not conducted samples year round could be divided in two major categories. First, were investigations that conducted detailed observations for several months, during the nonbreeding period of species. These studies examined flocks between June and September (Ragusa-Netto 1997) and from March to September (Ragusa-Netto 1999, 2000, 2002), probably to achieve information when flocks are more frequent. The second category included numerous studies whose major objectives focused diverse aspects of the avifauna, other than the seasonal formation of mixed-species flocks. Thus, they provided occasional findings of these mixed-species flocks, usually reporting the month in which they were found (Appendix 1). Considering all the information on seasonal occurrence revealed by these investigations, it can be noted that mixed-species flocks have been found in all months of the year in Cerrado (Appendix 1). This is true for flocks of forest species as well as for those of open-habitat birds. Thus, the compilation of these scattered records confirms the fact that mixed-species flocks can be found year round in Cerrado, as has been reported for Neotropical forests (e.g., Powell 1979, Jullien & Thiollay 1998, Develey & Peres 2000).

Evidence of advantages of participation in mixed-species flocks. The hypothesis of increased foraging efficiency as an advantage gained by members of mixed-species flocks (Morse 1977, Diamond 1981, Powell 1985, Terborgh 1990) has been tested by only one study in Cerrado. In pastures with scattered trees, the pecking rate of a species (*Furnarius rufus*) was significantly higher in mixed-species flocks than when foraging alone or in mono-specific groups (Ragusa-Netto 1997). It was suggested that the vigilance provided by sentinels of the nuclear species (*Mimus saturninus*) allowed *F. rufus* to spend more time with feeding activities.

The anti-predatory hypothesis in the formation of mixed-species flocks (Morse 1977, Diamond 1981, Powell 1985, Terborgh 1990) has been tested by more studies. In a cerrado *sensu stricto* patch of the central Cerrado, the intensity of sentinel behavior by a nuclear species (*Neothraupis fasciata*) was significantly lower in mixed-species flocks than in monospecific groups (Alves & Cavalcanti 1996). This pattern was consistent with their prediction that enhanced protection gained with the presence of other species leads to lower vigilance by this nuclear species. In a "campo cerrado" patch in eastern Cerrado, the time spent in sentinel activities by a nuclear species (*Cypsnagra hirundinacea*) was positively related to the rate of encounters between mixed-species flocks and avian predators (Ragusa-Netto 2000). In central Cerrado, the proportion of forest bird species participating in mixed-species flocks when foraging in adjacent savannas (cerrado *sensu stricto*) was higher at greater distances from gallery forests (Tubelis *et al.* 2006). This tendency of being in mixed-spe-

cies flocks at more distant savanna vegetation was interpreted as a reluctance to forage alone or in mono-specific groups at greater distances from cover (forest). Thus, participation in mixed-species flocks was considered a strategy adopted by forest species to reduce predation risk in less protective savanna vegetation (Tubelis *et al.* 2006).

Further evidence of predation risk to flock members has been obtained by observations of attacks by four species of avian predators in open habitats. Fourteen unsuccessful predatory attacks (ten by *Falco sparverius* and four by *F. femoralis*) on mixed-species flocks were recorded in a "campo cerrado" patch in eastern Cerrado (Ragusa-Netto 1999, 2000, 2001, 2002). Near this same study area, I. Sazima (pers. com.) observed a successful attack by *F. femoralis* (Ragusa-Netto 1997). Two studies provided some data on the frequency of occurrence of such predatory attacks in Cerrado. Silva (1980) informed that no predator attacks on mixed-species flocks were recorded during 444 h of observation in cerrado *sensu stricto.* One predatory attack was recorded every 30 h, on average, in "campo cerrado" patches (Ragusa-Netto 2002).

Additionally, there are reports of flock members escaping to cover in response to the presence of avian predators in three open vegetation physiognomies. These events involved *Falco rufigularis* and *F. femoralis* in grasslands (Willis & Oniki 1990), *F. femoralis* and *F. sparverius* in "campo cerrado" (Ragusa-Netto 1999, 2000, 2001, 2002) and *Cyanocorax cristatellus* in cerrado *sensu stricto* (Silva 1980). These movements into cover in response to predator approaches were induced by alarm calls displayed by sentinels of nuclear species, which included *Mimus saturninus*, *Neothraupis fasciata*, *Cypsnagra hirundinacea* and *Saltator atricollis* in "campo cerrado" (Ragusa-Netto 1999, 2000, 2001, 2002). In this habitat, the time spent with sentinel activities by nuclear species was proportional to the rate of encounters with avian predators (Ragusa-Netto 2002). This study recorded eight species of avian predators threatening mixed-species flocks: *Buteo albicaudatus*, *Rupornis magnirostris*, *Elanus leucurus*, *Herpetotheres cachinnans*, *Milvago chimachima*, *Falco femoralis*, *F. sparverius* and *Rhinoptynx clamator* (Ragusa-Netto 2002). Despite evidence of threat by birds, no studies mentioned non-avian predators threatening mixed-species flocks in Cerrado.

The compilation of information brought by studies involving advantages of participation in mixed-species flocks leads to three major conclusions. First, predation risk is an important factor influencing bird communities in Cerrado's woodland savannas. Indirect evidence for this fact was brought by detailed studies involving distinct approaches (e.g., Alves & Cavalcanti 1996, Ragusa-Netto 2002, Tubelis *et al.* 2006). Additionally, ten bird species of four families (Accipitridae, Falconidae, Strigidae and Corvidae) have been noted threatening or attacking members of mixed-species flocks in "campo cerrado" and cerrado *sensu stricto.* Second, sentinel behavior and alarm calls appear to be frequent anti-predatory mechanisms shown by the nuclear species of mixed-species flocks inhabiting savanna woodlands in Cerrado (e.g., Alves & Cavalcanti 1996, Ragusa-Netto 2000, 2002). Third, advantages gained with the formation of mixed-species flocks around the world – increased foraging efficiency and reduced predation risks – were noted in Cerrado. Also, a study at forest-savanna boundaries argued that an additional advantage might benefit members of mixed-species flocks. Tubelis *et al.* (2006) have shown that the formation of mixed-species flocks played an important role in promoting the use of adjacent savannas by forest birds. Based on this fact, they pointed out a novel advantage gained with participation in these inter-specific associations – greater use of adjacent vegetation patches.

Overview. Of 28 publications reporting the occurrence of mixed-species flocks in Cerrado, only nine (32%) stated in the objectives their aim of studying these bird associations (Appendix 1). Of these, Silva & Oniki (1988) elaborated a list of species participating or not in mixed-species flocks in Serra das Araras. The other eight studies involved detailed sampling schemes and were carried out at Distrito Federal (Silva 1980, Alves 1990, Alves & Cavalcanti 1996, Tubelis 2004, Tubelis *et al.* 2006) and in Brotas-SP (Ragusa-Netto 1997, 2000, 2002). Therefore, detailed investigations on mixed-species flocks were conducted exclusively in the central and southeastern regions of Cerrado, despite the recording of these flocks through most of its extension.

Of these eight detailed investigations, five examined mixed-species flocks inhabiting cerrado *sensu stricto* vegetation in the Distrito Federal, while three investigated flocks in "campo cerrado" vegetation in Brotas (Appendix 1). This fact leads to two major conclusions. First, potential effects of regional variation and habitat on flock structure and biology would be confounded in eventual comparisons of results obtained by these two groups of detailed studies. Second, aspects of the biology of mixed-species flocks have been examined in details only in savanna woodlands, thus remaining relatively poorly investigated in forests, grasslands ("campo limpo" and "campo sujo") and other native vegetation.

Aspects of the biology of mixed-species flocks more often investigated in details were advantages of flock formation (Silva 1980, Alves 1990, Alves & Cavalcanti 1996, Ragusa-Netto 1997, 2000, 2002; Tubelis *et al.* 2006) and seasonal variation in flock structure and formation (Silva 1980, Alves & Cavalcanti 1996, Tubelis 2004, Tubelis *et al.* 2006). They are aspects usually examined in major reviews of mixed-species flocks (Morse 1970, 1977; Diamond 1981, Powell 1985, Terborgh 1990). On the other hand, the diet and feeding habits of flock members, regional variation in mixed-species flocks, and the use of distinct vegetation patches by flocks are among aspects of their biology not yet examined in details in Cerrado. Information on these poorly studied aspects results of eventual records reported in studies focusing aspects of the avifauna other than the biology of mixed-species flocks.

All publications reviewed in this study provided information on the locality/region, and habitat where mixed-species flocks were found (Appendix 1). Information on the period of the year in which mixed-species flocks were recorded was provided less often, only in 24 (86%) of the 28 publications assessed. Only four studies (Dubs 1992, Ridgely 1994, Ragusa-Netto 2001, Willis 2003) have not indicated the period of the year in which flocks were found (Appendix 1). Information on the number of species found per flock was provided in only 15 (54%) of the 28 publications included in this review. Only six publications (21%) provided information on the number of birds found per flock. Information on the period of flock occurrence, and on the species richness and bird numbers found per flock was published since the earliest to the most recent publications involving records of mixed-species flocks in Cerrado (Appendix 1). Thus, no tendencies for the study of particular aspect of the biology of mixed-species flocks appear to have occurred along the history of investigations on these bird associations in Cerrado. The same is true for studies with detailed sampling schemes and those involving only brief information (Appendix 1).

Several records of mixed-species flocks in Cerrado have been presented only briefly in 19 (68%) non-detailed studies on these associations. These studies focused, for example, inventories of species (e.g., Willis & Oniki 1990, Pearce-Higgins 2000), bird-plant interactions (e.g., Olmos & Boulhosa 2000) or

aspects of the biology of particular taxa (e.g., Marini 1992, Parker & Willis 1997, Vasconcelos *et al.* 1999, Lopes 2004). Despite not answering complex questions on mixed-species flocks, these studies contributed to the understanding of aspects such as the occurrence of mixed-species flocks within Cerrado, the use of vegetation physiognomies, the period of their occurrence, and the species richness and bird abundance found per flock (Appendix 1). Further, 41 (24%) of the bird species found in mixed-species flocks in Cerrado have been recorded exclusively by these 19 studies that have not shown detailed data on these flocks (Appendix 2). Thus, brief comments on the occurrence and biology of mixed-species flocks would be welcome in future studies on the Cerrado avifauna.

Of the 28 publications, only eight (Silva 1980, Alves 1990, Alves & Cavalcanti 1996, Ragusa-Netto 1997, 2000, 2002; Tubelis 2004, Tubelis *et al.* 2006) provided information on the criteria used to identify nuclear species. Also, these eight publications were the only studies to define when a bird was participating or not in a mixed-species flock. Therefore, near three quarters of the 28 studies did not make clear statements on the criteria used to identify mixed-species flocks and their nuclear species. Despite this fact, I considered their data because I assumed that authors of these 20 publications were aware of definitions of nuclear species and mixed-species flocks. However, I suggest that future publications cite references (e.g., Powell 1985, Stotz 1993) or mention criteria regarding definitions of mixed-species flocks and nuclear species.

Considering the evidence of predation threat to bird species brought by detailed investigations in savannas, the importance of nuclear species for their survival became more evident. Thus, bird species functioning as nuclear species of flocks in native habitats should receive more research and conservation attention because of their role in assisting numerous bird species.

Some interesting aspects of the biology of mixed-species flocks were not included in this review due to the low number of studies. Among them were the use of vegetation strata by species (Silva 1980, Alves & Cavalcanti 1996), flock movement (Silva 1980), territory of flocks (Alves & Cavalcanti 1996), inter-specific aggressions (Silva 1980) and the role of different species in the vigilance towards avian raptors (Ragusa-Netto 2002). Their achievements also should receive the attention of investigators of mixed-species flocks.

Suggestions for future research. Numerous interesting suggestions for future investigations of the biology of mixed-species flocks have been proposed recently by Greenberg (2000). To avoid being repetitive, my suggestions focus on the Cerrado environment and knowledge of its avifauna. My suggestions for future research on mixed-species flocks in Cerrado are: (1) Identification of nuclear species leading mixed-species flocks in different habitats and regions; (2) improvement of knowledge of major food items consumed by flock members, especially for the nuclear species; (3) patch-matrix and inter-patch movements by mixed-species flocks examined in a diverse range of boundaries and situations in the diverse range of land mosaics found in Cerrado (this kind of research will likely bring new insights on the biology of mixed-species flocks, as most research conducted world-wide has involved flocks foraging within a single vegetation patch); (4) examination of flock responses to habitat and landscape changes essential for their appropriate conservation in protected reserves and in human-modified landscapes; (5) co-occurrence of birds typical of distinct landscape units in a given mixed-species flock as indicator of aspects of flock cohesion still poorly investigated world-wide; (6) basic questions regard-

ing the biology of mixed-species flocks, such as their seasonal occurrence, their size, their species composition, their home range, and the advantages gained with flock formation addressed in Cerrado, especially in forests, grasslands, marshes and other less sampled vegetation; (7) given the huge dimensions of Cerrado, studies comparing regional variation in flock structure and guidance providing relevant information on factors involved in their organisation; (8) during surveys, observers could try to distinguish two situations: birds in mixed-species flocks and birds outside these associations. Acquisition of these two types of information in a given sample or study site would permit the examination of the propensity of species to join mixed-species flocks. This aspect is still poorly investigated world-wide, probably due to difficulties in obtaining data, but might be possible in structurally less complex vegetation (e.g., grassland and savanna).

Overall, researchers could consider aspects of the Cerrado environment (e.g., its great extension, its patchy environment, and its strongly seasonal climate) to study aspects of the biology of mixed-species flocks poorly investigated world-wide.

ACKNOWLEDGMENTS

I thank many people that provided comments and suggestions since the early phases of this review: R. B. Cavalcanti, A. Cowling, P. F. Develey, C. Donnelly, R. Gabon-Lima, S. Gilmore, P. MacDonald, R. H. F. Macedo, P. Olsen and M. N. Sato. I also thank Claudinha Melo, M. Â. Marini, Y. Oniki, J. W. Pearce-Higgins and A. Tubelis for helping with references. T. C. Anacleto, R. McNeil, Y. Oniki, J. Ragusa-Netto, P. Warden-Hutton, E. O. Willis and two anonymous reviewers greatly improved this manuscript. I was granted fellowships from CNPQ (process no. 200102-00/1) and FAPESP (process no. 05/00773-3) during the elaboration of this manuscript.

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APPENDIX 1. Studies that recorded mixed-species flocks in Cerrado, with information on their study area, on the vegetation physiognomies used by flocks, on their seasonal occurrence, and on the species richness and bird abundance found per flock. Studies were grouped according to the country where they were conducted and then listed in chronological order. Questions examined by studies involving detailed sampling schemes also were provided.

Country /Sources	Study area	Vegetation	Seasonal occurrence	Numbers of species	Number of birds	Question
Brazil						
1	Faz. Água Limpa, DF	Cerrado *ss*	Jan to Aug	2 to 6, mean = 3.8	4 to 27, mean = 11.5	Seasonal variation Advantage
2	E. E. Serra das Araras, MT	Gallery forest	Jan, Feb and/or Mar	–	Up to 30	
		Forest	Jan, Feb and/or Mar	4 to 8		
		Cerrado *ss*	Jan, Feb and/or Mar	–	10 to 15	
		Campo sujo and limpo	Jan, Feb and/or Mar	–	Up to 40	
3	Faz.Água Limpa, DF	Cerrado *ss*	All months of year	–	–	Advantage
4	Porto Limão, MT	Dry forest	Jul	–	–	
	Serras das Araras, MT	Forest (?)	Jun, Jul, Sep or Oct	–	–	
	Pontes e Lacerda, MT	Grassland and forest	Aug	–	–	
5	Januária, MG	Cerrado *ss*	Sep	–	–	
		Forest	Sep	–	–	
6	Faz. Água Limpa, DF	Gallery forest	Dry season	–	–	
7	Cerrado bordering the Pantanal, MT	Forest	–	–	–	
8	Faz. Água Limpa, DF	Gallery forest	Near year round	3 to 11, mean: 5.0	–	
9	Itirapina, SP	Grasslands	Nov	3	–	
10	Brasília NP, Brasília, DF	Cerrado *ss*	–	–	–	
	Emas NP, GO	Grassland	Oct	–	–	
11	Faz. Água Limpa, DF	Cerrado *ss*	Year round	Mean ± s.d. = 3.9 ± 1.6	–	Advantage Seasonal variation
12	Serra das Araras, MT	Campo cerrado	Jan	3	–	
13	Brotas, SP	Pasture with trees	Jun to Sep	2	–	Advantage
14	Emas NP, GO	Marshes	Oct	3	–	

APPENDIX 1. Continued.

Country /Sources	Study area	Vegetation	Seasonal occurrence	Numbers of species	Number of birds	Question
15	Around Macapá, AP	Cerrado *ss*	Oct and/or Nov	–	–	
16	Serra da Canastra NP, MG	Grassland	Oct	3	–	
17	Espinhaço Range, MG	Campo cerrado	Jul	4	–	
		Grassland	Jan	4	13	
18	Assis, SP	Cerradão	May and/or Jun	–	10 to 20	
19	Brotas, SP	Campo cerrado	Mar to Sep	Mean ± s.d. = 5.5 ± 1.8	Mean ± s.d. = 14.4 ± 4.7	Advantage
20	Brotas, SP	Campo cerrado	–	–	–	
21	E. E. Uruçcuí-Una, PI	Cerrado *ss*	Jan and Jul	–	–	
22	Brotas, SP	Campo cerrado	Mar to Sep	Mean ± s.d. = 9.2 ± 3.5	Mean ± s.d. = 24.1 ± 10.9	Advantage
		Campo cerrado	Mar to Sep	Mean ± s.d. = 5.5 ± 1.8	Mean ± s.d. = 14.4 ± 4.4	
		Campo cerrado	Mar to Sep	Mean ± s.d. = 3.8 ± 1.7	Mean ± s.d. = 8.2 ± 3.1	
23	Horto, Rio Claro, SP	Eucalypt plantation	–	4	–	
24	E. E. de Águas Emendadas, DF	Cerrado ss	Dec to May	2 to 4	–	
25	Four reserves, DF	Cerrado ss	Breeding and non-breeding	2 to 16, 4.5 ± 3.2	–	Seasonal variation
	Caldas Novas, GO	Cerrado ss	June, Aug and Nov	2 to 7, 3.3 ± 1.9	–	
26	Four reserves, DF	Cerrado ss	–	–	–	Advantage Seasonal variation
Bolivia						
27	Noel Kempff Mercado NP, Santa Cruz	Wet campos	Aug and/or Sep	–	–	
28	Noel Kempff Mercado NP, Santa Cruz	Wet campos	Aug and/or Sep	–	–	

[1]**Reference codes:** 1, Silva (1980); 2, Silva & Oniki (1988); 3, Alves (1990); 4, Willis & Oniki (1990); 5, Willis & Oniki (1991); 6, Cavalcanti (1992); 7, Dubs (1992), 8, Marini (1992); 9, Willis & Oniki (1993); 10, Ridgely (1994); 11, Alves & Calvalcanti (1996); 12, Parker & Willis (1997); 13, Ragusa-Netto (1997); 14, Sick (1997); 15, Silva *et al.* (1997); 16, Silveira (1998); 17, Vasconcelos *et al.* (1999); 18, Olmos & Boulhosa (2000); 19, Ragusa-Netto (2000); 20, Ragusa-Netto (2001); 21, Silveira *et al.* (2001); 22, Ragusa-Netto (2002); 23, Willis (2003); 24, Lopez (2004); 25, Tubelis (2004); 26, Tubelis *et al.* (2006); 27, Pierce-Higgins (1996); 28, Pierce-Higgins (2000).

APPENDIX 2. Bird species recorded in mixed-species flocks in Cerrado, with the source of information. The nomenclature and sequence of species follows Sigrist (2006).

Species	Reference[1]	Species	References
Cuculidae		*Glyphorynchus spirurus*	2
Piaya cayana	2,24	*Hylexetastes perrotii*	2
Crotophaga ani	2	*Xiphorhynchus picus*	2
Trochilidae		*Xiphorhynchus guttatus*	2
Colibri serrirostris	11	*Lepidocolaptes angustirostris*	1,2,11,16,23,26,27
Amazilia fimbriata	11	*Lepidocolaptes squamatus*	5
Trogonidae		Furnariidae	
Trogon viridis	2	*Furnarius rufus*	14,18,24
Trogon curucui	2	*Synallaxis* sp.	1
Momotidae		*Synallaxis frontalis*	27
Electron platyrhynchum	2	*Synallaxis albescens*	2,11,16,21,24
Momotus momota	2	*Synallaxis rutilans*	2
Bucconidae		*Synallaxis gujanensis*	2
Notharchus macrorhynchos	2	*Phacellodomus rufifrons*	1,11
Nystalus chacuru	1,2,24	*Philydor rufum*	27
Monasa nigrifrons	2	*Philydor dimidiatum*	2,8
Monasa morphoeus	2	*Automolus leucophthalmus*	25
Picidae		*Hylocryptus rectirostris*	27
Picumnus sp.	1	*Xenops rutilans*	2
Picumnus albosquamatus	24,27	Tyrannidae	
Picoides mixtus	11,21,23,24,26	*Mionectes oleagineus*	2
Veniliornis passerinus	21,24,27	*Hemitriccus striaticollis*	2
Colaptes melanochloros	24	*Poecilotriccus latirostris*	2
Colaptes campestris	1,2,11,24	*Phyllomyias fasciatus*	27
Melanopareiidae		*Myiopagis caniceps*	25
Melanopareia torquata	21,24	*Elaenia* sp.	1,11
Thamnophilidae		*Elaenia flavogaster*	24,27
Thamnophilus punctatus	2	*Elaenia parvirostris*	2
Thamnophilus caerulescens	2,8,27	*Elaenia cristata*	2,6,11,16,23,24
Thamnophilus torquatus	2	*Elaenia chiriquensis*	6,11,16,27
Dysithamnus mentalis	2	*Camptostoma obsoletum*	11,21,24,27
Myrmotherula hauxwelli	2	*Suiriri suiriri*	1,2,11,16,21,24,26
Formicivora grisea	2	*Suiriri islerorum*	26
Formicivora rufa	13,23,24	*Serpophaga subcristata*	24
Cercomacra nigrescens	2	*Polystictus pectoralis*	13,24
Pyriglena leuconota	2	*Euscarthmus rufomarginatus*	13
Myrmoborus myiotherinus	2	*Phylloscartes roquettei*	5
Myrmeciza atrothorax	2	*Culicivora caudacuta*	13
Rhegmatorhina hoffmannsi	2	*Tolmomyias sulphurescens*	2,27
Hylophylax poecilonotus	2	*Myiophobus fasciatus*	2
Conopophagidae		*Lathrotriccus euleri*	2
Conopophaga lineata	2	*Xolmis velatus*	11
Dendrocolaptidae		*Alectrurus tricolor*	13,21,24
Dendrocincla fuliginosa	2	*Myiodynastes maculatus*	2
Sittasomus griseicapillus	2,25,27	*Tyrannus savana*	11

APPENDIX 2. Continued.

Species	Reference[1]	Species	References
Casiornis rufus	27	*Piranga flava*	23,27
Casiornis fuscus	5	*Habia rubica*	25
Myiarchus swainsoni	11,16	*Eucometis penicillata*	27
Myiarchus ferox	27	*Tachyphonus rufus*	2,7,8,27
Myiarchus tyrannulus	16	*Lanio versicolor*	2,7
Ramphotrigon ruficauda	2	*Ramphocelus carbo*	2,27
Attila bolivianus	2	*Thraupis sayaca*	2,4,19,27
Cotingidae		*Thraupis palmarum*	2,4,7,27
Xipholena punicea	2	*Neothraupis fasciata*	1,2,3,10,11,13,15,16,
Pipridae			18,21,23,24,26
Neopelma pallescens	2	*Tangara mexicana*	2
Tyranneutes stolzmanni	2	*Tangara chilensis*	2
Piprites chloris	2	*Tangara cayana*	2,19,27,28
Antilophia galeata	2,8,27	*Tangara cyanicollis*	2
Tityridae		*Dacnis lineata*	2
Schiffornis sp.	2	*Dacnis cayana*	2,19,27,28
Tityra cayana	2,27	*Cyanerpes caeruleus*	2
Tityra semifasciata	2	*Cyanerpes cyaneus*	2
Pachyramphus polychopterus	2,27	*Chlorophanes spiza*	2
Vireonidae		*Hemithraupis guira*	2,4,23,27,28
Cyclarhis gujanensis	2,24,27	*Hemithraupis ruficapilla*	25
Vireo olivaceus	2,27	*Hemithraupis flavicollis*	2
Hylophilus muscicapinus	2	*Conirostrum speciosum*	4,25,27
Hirundinidae		Emberizidae	
Tachycineta leucorrhoa	11	*Zonotrichia capensis*	11,21,24
Troglodytidae		*Ammodramus humeralis*	1,2,11,16,18,21,24
Thryothorus genibarbis	2	*Sicalis citrina*	24
Thryothorus leucotis	2,8	*Sicalis flaveola*	2
Troglodytes musculus	1,2,11,13,24	*Sicalis luteola*	4
Polioptilidae		*Emberizoides herbicola*	1,2,11,12,16,18,21,
Polioptila dumicola	27		24
Turdidae		*Embernagra longicauda*	18
Turdus leucomelas	8,27	*Volatinia jacarina*	2,11,12,21,24
Turdus amaurochalinus	2,4,27	*Sporophila plumbea*	21,24
Turdus albicollis	2	*Sporophila nigricollis*	2
Mimidae		*Sporophila caerulescens*	24
Mimus saturninus	11,13,14,18,24	*Sporophila leucoptera*	2,24
Coerebidae		*Sporophila nigrorufa*	12
Coereba flaveola	2,4,27	*Sporophila bouvreuil*	17,24
Thraupidae		*Sporophila hypoxantha*	9,12,15
Schistochlamys melanopis	10	*Sporophila ruficollis*	9,12
Cissopis leverianus	2	*Sporophila palustris*	10,15
Nemosia pileata	25,27	*Sporophila hypochroma*	12,15,17
Cypsnagra hirundinacea	2,13,16,18,21,23,24	*Sporophila cinnamomea*	10
Trichothraupis melanops	8,27	*Sporophila melanogaster*	9,17

APPENDIX 2. Continued.

Species	Reference[1]	Species	References
Sporophila sp.	4,20	*Basileuterus flaveolus*	2,8
Oryzoborus angolensis	2	Icteridae	
Arremon taciturnus	2	*Cacicus cela*	2
Charitospiza eucosma	1,11	*Icterus cayanensis*	2,4
Coryphospingus cucullatus	4,24,27	*Icterus jamacaii*	2
Cardinalidae		*Gnorimopsar chopi*	2,11
Saltator similis	4,8,27	Fringillidae	
Saltator atricollis	2,22,23,24	*Euphonia chlorotica*	27
Parulidae		*Euphonia violacea*	2
Parula pitiayumi	2,4,27	*Euphonia rufiventris*	2
Basileuterus hypoleucus	2,8,25,27		

[1] **Reference codes:** 1, Silva (1980); 2, Silva & Oniki (1988); 3, Alves (1990); 4, Willis & Oniki (1990); 5, Willis & Oniki (1991); 6, Cavalcanti (1992); 7, Dubs (1992); 8, Marini (1992); 9, Willis & Oniki (1993); 10, Ridgely (1994); 11, Alves & Cavalcanti (1996); 12, Pearce-Higgins (1996); 13, Parker & Willis (1997); 14, Ragusa-Netto (1997); 15, Sick (1997); 16, Silva *et al.* (1997); 17, Silveira (1998); 18, Vasconcelos *et al.* (1999); 19, Olmos & Boulhosa (2000); 20, Pearce-Higgins (2000); 21, Ragusa-Netto (2000); 22, Ragusa-Netto (2001); 23, Silveira *et al.* (2001); 24, Ragusa-Netto (2002); 25, Willis (2003); 26, Lopes (2004); 27, Tubelis (2004); 28, Tubelis *et al.* (2006).