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Composition of mixed-species bird flocks and abundance of flocking species in a semideciduous forest of southeastern Brazil

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RESUMO. **Composição de bandos e abundância de aves participantes de bandos mistos numa floresta semidecídua do sudeste do Brasil.** Foram estudados bandos mistos de aves num fragmento de mata semidecídua de 1400 ha, localizado no município de Anhembi, São Paulo, durante abril e junho de 1996. Foram realizados censos de bandos para avaliar a frequência de ocorrência de espécies de aves em bandos mistos. Na mesma trilha utilizada para a observação de bandos, foram realizadas amostragens quantitativas de avifauna pelo método de levantamento quantitativo por pontos de escuta. Um total de 91 espécies foi registrado nos pontos (N = 35), sendo que destas apenas 48 (52,7 %) foram observadas em bandos mistos (N = 45), notadamente insetívoros de folhagem de subosque (25,4 %). Espécies com uma alta frequência de ocorrência em bandos também tendem a ser as mais abundantes na área de estudo ($r = 0.70$, $F = 48.63$, $P < 0.001$). Das 51 espécies observadas em bandos apenas 27 (52,9 %) foram registradas em mais de 10 % dos bandos. Uma análise multivariada de ordenação (RA) dos padrões de associação dessas 27 espécies revelou que três grupos podem ser distinguidos: subosque e estrato médio (com 20 espécies), dossel (4) e "marrom" (3). Os resultados obtidos permitem associar a composição e a estrutura de bandos mistos na área de estudo a dois fatores principais: abundância e padrões especiais de associações das espécies participantes.
PALAVRAS-CHAVE: Amazônia, bandos mistos, levantamento quantitativo, leste brasileiro.

ABSTRACT. Mixed-species flocks were studied in a forest fragment (1,400 ha) in interior São Paulo state. A quantitative avifauna survey was also undertaken at the same site, in order to assess the relative abundance of flock species'. A total of 91 species was recorded on point counts. Of these, 48 (52.7 %) also followed mixed flocks; most of these species were understory foliage gleaning insectivores (25.4 %). Frequency of occurrence of species within mixed-flocks, of which a significant percentage were understory foliage-gleaning insectivores (25,4%), usually increased with abundance ($r = 0.70$, $F = 48.63$, $P < 0.001$). Association patterns between species that occurred in more than 10 % of censused flocks were analyzed through a multi-variate ordination procedure (RA). Three groups emerged: understory and mid-level (with 20 species), canopy (four species), and "brown" (three species). The results showed that flock composition and structure were primarily influenced by species abundance and special patterns of association among flocking species.
KEY WORDS: Amazonia, eastern Brazil, mixed-species flocks, quantitative bird survey.

Neotropical mixed species bird flocks are found throughout many forested, wooded and even open habitats of Central and South America (Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Powell 1985, Hutto 1987, Poulsen 1996). Typically, these flocks are understood as associations centered around a nuclear species which is responsible for the cohesion of the flock. In Amazonia, understory mixed flocks are intimately tied to the presence of antshrikes (Thamnophilidae) of the genus *Thamnomanes* which acts as a sentinel, providing anti-predatory benefits to the flock (Munn and Terborgh 1979).

Stotz (1993) presented evidence that in Espírito Santo, eastern Brazil, the antshrike *Thamnomanes caesius*, althought present, does not play the same pivotal role in mixed species flocks as in Amazonia. He also pointed out that mixed species flocks in eastern Brazil are less stable in terms of species composition, weakly differentiated between understory and canopy flocks and without full-time flock members. Other studies from eastern Brazil (Machado 1991, P. Develey in prep.) also reported a lower stability when compared to Amazonian flocks.

In this study I assess the composition of mixed species flocks and associate frequency of occurrence of a given species in flocks with its abundance in the study area. I also analyze patterns of association among species within flocks in order to evaluate the processes responsible for flock composition and structure in low stability mixed-species bird flocks of southeastern Brazil.

STUDY SITE AND METHODS

Study area. Flocks and birds were censused in the largest (1,400 ha) forest fragment of the Fazenda Barreiro Rico (22°45´S, 48°09´W; 500-600 m elevation) near Anhembi, São Paulo, in southeastern Brazil. Fieldwork was carried out in 25-27 April and 1-7 June 1996. Annual rainfall is about 1,500 mm concentrated from October to March (summer).

Vegetation is composed of semideciduous Atlantic forest with a canopy of 20-25 m and emergent trees of about 35 m. Patches of secondary forest are widespread, especially near edges.

Flock composition. I followed a total of 45 flocks along a single 3 km trail and its immediate vicinity. While following flocks, I recorded all bird species observed until I lost the flock. I followed flocks continuously for up to 45 min, but most were followed for only 9-15 min. Mixed species flocks were defined as associations of two or more species in proximity, moving in the same direction for at least five minutes without external resource concentration (Stotz 1993).

Bird counts. Birds were censused with unlimited distance point counts (Blondel *et al.* 1981), modified for tropical areas (Vielliard and Silva 1990). Thirty point counts (spaced by 50 m) were placed along the same 3 km trail used for following flocks. Five points were run from 20 min before dawn to 2-3 hr after sunrise. Each point count lasted 20 min and was done at least 200 m from the next census point. Starting point and direction were randomized by lottery. At the points, all birds heard or seen were recorded. The index of point abundance (IPA) of a species at the study site was calculated by dividing the number of contacts with a particular species by the total number of points censused (n = 35). One contact means the detection of an individual, pair or group (no matter the size or makeup) of a given species in the vicinity of the point (Vielliard and Silva 1990).

Statistical analyses. Simple linear regression using a confidence interval of $P = 0.95$ was used to evaluate the variation of bird abundances according to the regularity of occurrence within flocks. Inspection of frequency histograms indicated that bird abundances and frequency of occurrence in flocks deviated from normality. Data were normalized with the arcsine transformation. The significance of the regression was tested by an analysis of variance (ANOVA) at the level of significance of 5 % (Zar 1996). A multivariate statistical procedure was employed to assess patterns of association among species within flocks. Species recorded in more than 10 % of the flocks were ordinated with the reciprocal averaging method (RA). Analyses followed Ludwig and Reynolds (1988) and were performed using the PC-ORD 2.01 computer package.

RESULTS

Flock composition. A total of 51 species were recorded in mixed flocks at Barreiro Rico (Appendix). Mean flock species richness was 10.2 (s.d. = ± 5.1) ranging from 2 to 24 species. Most flocking species are understory insectivores (25.4 %), followed by trunk insectivores (15.6 %) and canopy insectivores (13.7 %).

Most species recorded in flocks do not regularly join flocks (figure 1). Only 27 species were recorded in at least 10 % of the flocks. Again, understory insectivores were dominant,

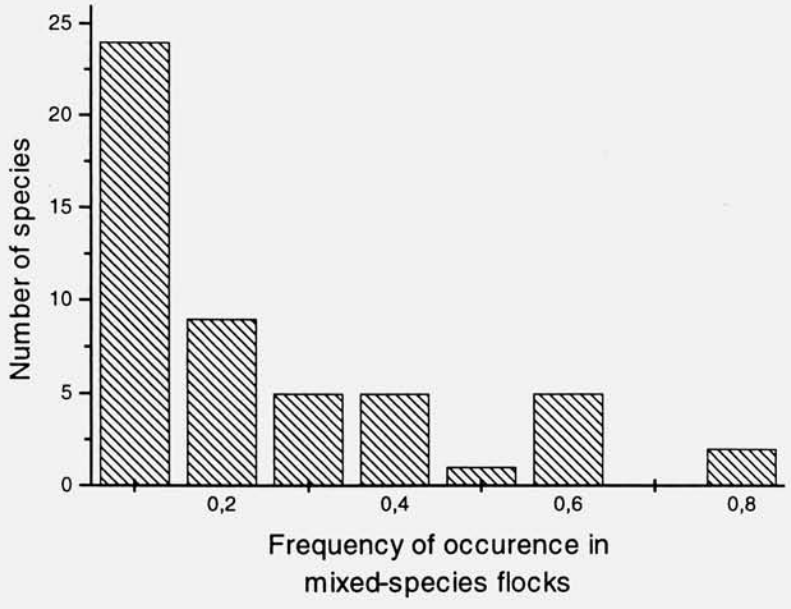

Figure 1. Number of species that occured in each of the eight categories representing different proportions that a bird was observed following mixed-species flocks.

accounting for 37 % of the species. Only two species, *Herpsilochmus rufimarginatus* and *Basileuterus hypoleucus*, were recorded in more than 70 % of the flocks showing that flock composition at Barreiro Rico is highly variable.

Dominant groups in flocks are Tyranniinae, Thamnophilinae, Thraupinae, Dendrocolaptinae, and Furnariinae.

Abundance of flocking and non-flocking species. Ninety-one species were recorded on point counts. Of these, 48 species (52.7%) were also observed following mixed species flocks (index of abundance given in the appendix). Three species recorded at mixed flocks were not recorded in point counts: *Mackenziaena severa, Hylophilus poecilotis* and *Parula pitiayumi*. These species are assumed to have a lower abundance than one contact (record) in 35 points, i.e. IPA = 0. The proportion of mixed species flocks within which any of the 51 species was observed could be predicted on the basis of its index of abundance ($r = 0.70$, $F = 48.63$, df = 49, $P < 0.001$; figure 2). In fact, the four commonest species within flocks (*Dysithamnus mentalis*, *Herpsilochmus rufimarginatus*, *Hemitriccus orbitatus* and *Basileuterus hypoleucus*) were among the six most common species at the study site, showing that abundance and regularity of occurrence in flocks were closely associated.

Most of the 43 non-flocking species recorded on point counts were frugivores (24.4 %), including common species at Barreiro Rico (*Columba cayennensis, Pionus maximiliani* and *Ramphastos toco,* for example). Omnivores (22 %) and nectarivores (17 %, mainly hummingbirds, family Trochilidae) were also among the commonest non-flocking species. Among the 13 insectivore species not observed following mixed flocks, four were trunk insectivores (Picidae), three were terrestrial insectivores (Cuculidae, Formicariidae and Conopophagidae), three were salling insectivores (Tyranniinae), three were nocturnal (Caprimulgidae and Strigidae) and one was aerial (Hirundinidae).

Patterns of association among flocking species. Ordination of species using RA based on presence-absence of 27 species recorded in more than 10 % of the flocks produced three axes with low eigenvalues and variances (table 1) indicating that the segregation among species is also low.

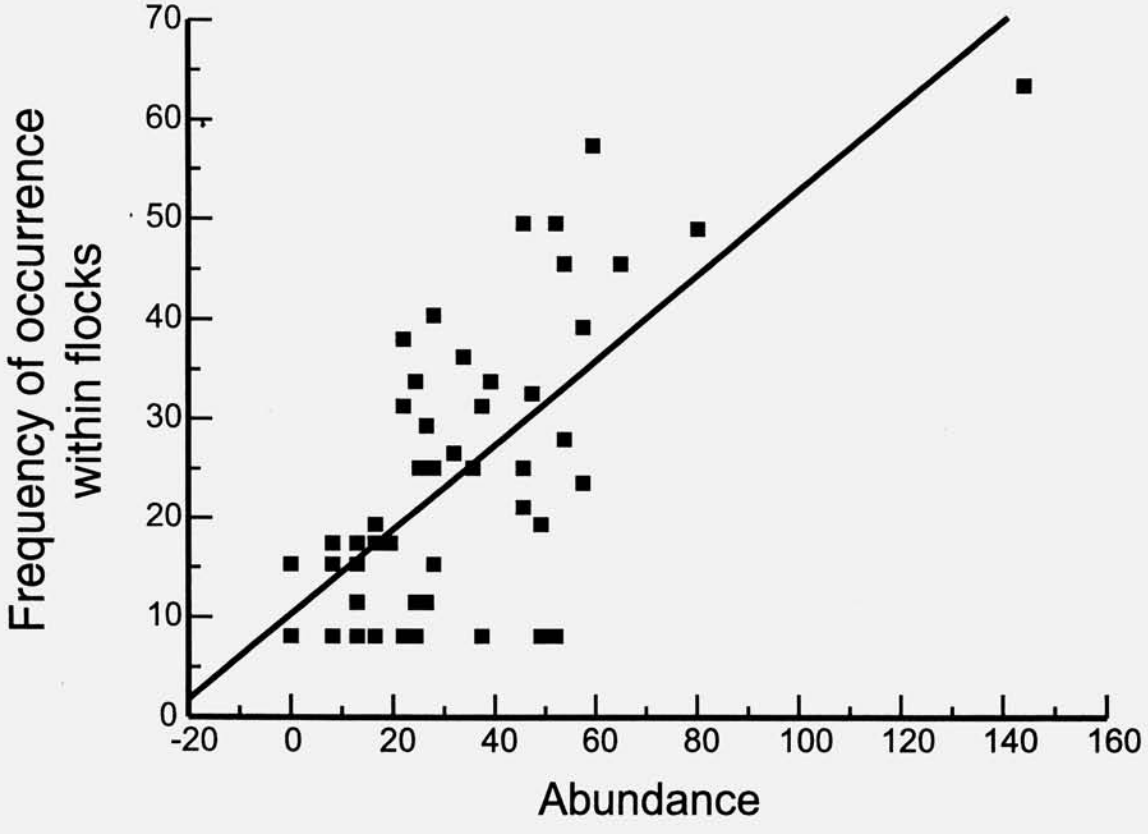

Figure 2. Proportion of 45 flocks occupied by each of the 51 flocking species as a function of its abundance in the study area. Data on both axes were normalized with the arcsine transformation. ($r = 0.70$, $F = 48.63$, df = 49, $P < 0.001$).

Table 1. Reciprocal averaging eigenvectors and variance for analysis of association among the 27 species found in 10 % or more of flocks.

Axis	1	2	3
Eigenvalue	.233	.196	.164
% of variance	20.1	6.6	16
Cumulative % of variance	____	26.7	42.7

The first axis separates two main groups (figure 3, table 2): canopy species (a) and "brown" species (c) from understory - midlevel species (b). The first axis showed that there is not a strong distinction between canopy and understory mixed species flocks. Instead, many canopy, midlevel and understory species occur within the same flocks. The second axis separates "brown" species (c; *Automolus leucophthalmus, Lepidocolaptes fuscus* and *Habia rubica*) from other species groups, showing that it corresponds to a conspicuous association among species within flocks at Barreiro Rico.

DISCUSSION

Mean flock species richness at Barreiro Rico is similar to that reported from Floresta Rio Doce, Espírito Santo, also in eastern Brazil (9.8 species; Stotz 1993). Machado (1991) reported a lower mean (5.4 species) from montane forest of São Paulo State. Mean flock species richness is higher in Amazonia when compared to southeastern Brazil (Stotz 1993). Because the total number of species in flocks is very dependent on the size of flock samples, direct comparisons between Amazonian and eastern Brazilian

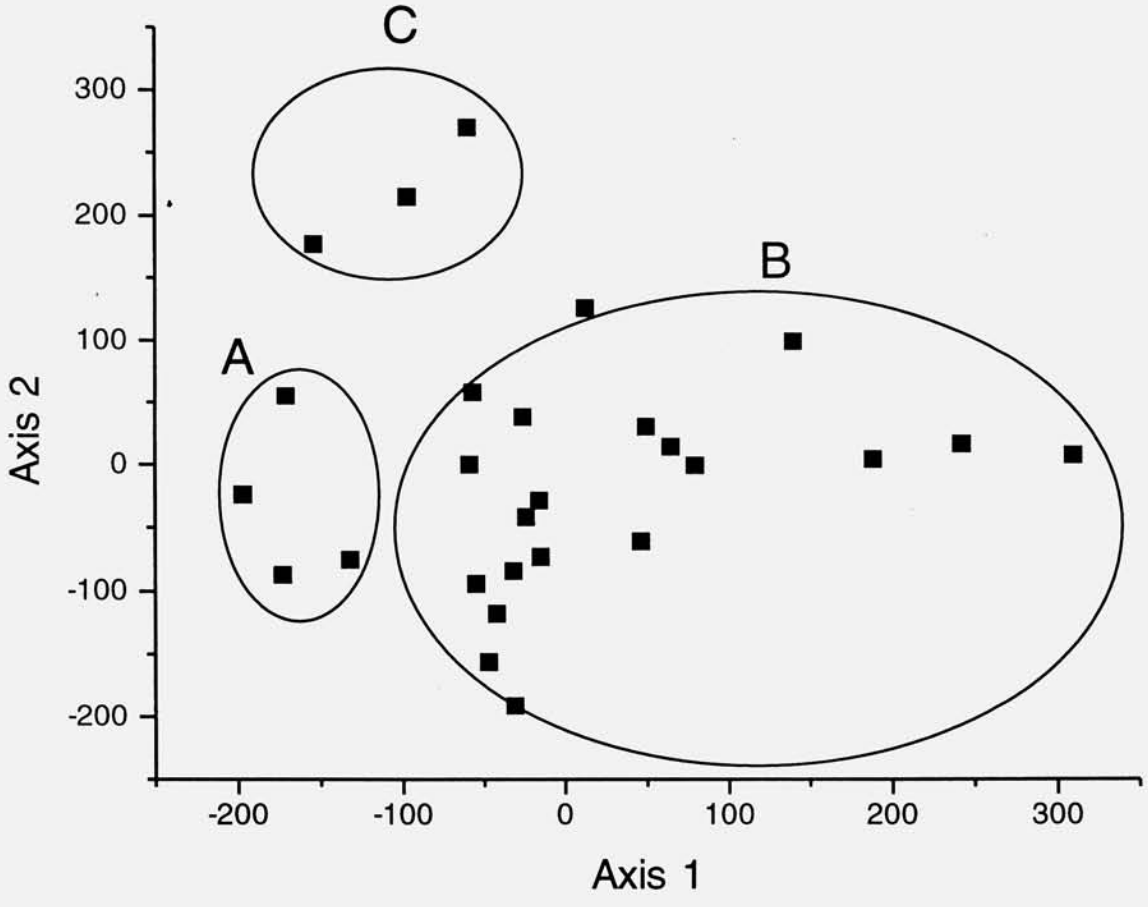

Figure 3. Ordination with reciprocal averaging of the 27 species found in 10 % or more of flocks by associations with other species within flocks. Letter designations gives species groups. (A = canopy species, B = understory and midlevel species, and C = "brown" species). See table 2 for group membership.

Table 2. Species groups produced by the reciprocal averaging ordination (RA) of the 27 species found in 10 % or more of flocks. See table 1, figure 3 and results.

Group A (canopy species)	Group B (understory-midlevel species)	Group C ("brown" species)
Myiopagis caniceps	*Piaya cayana*	*Automolus leucophthalmus*
Cyclarhis gujanensis	*Trogon surrucura*	*Lepidocolaptes fuscus*
Conirostrum speciosum	*Picumnus albosquamatus*	*Habia rubica*
Hemithraupis ruficapilla	*Synallaxis ruficapilla*	
	Philydor lichtensteini	
	Sittasomus griseicapillus	
	Thamnophilus caerulescens	
	Dysithamnus mentalis	
	Herpsilochmus rufimarginatus	
	Terenura maculata	
	Drymophila ferruginea	
	Leptopogon amaurocephalus	
	Myiornis auricularis	
	Hemitriccus orbitatus	
	Todirostrum poliocephalum	
	Platyrinchus mystaceus	
	Tolmomyias sulphurescens	
	Schiffornis virescens	
	Basileuterus hypoleucus	
	Trichothraupis melanops	

are yet difficult (Stotz *in litt.* 1996).

Flocks reported from southeastern Brazil lacks the set of full-time members (core species) which are so characteristic among Amazonian flocks (Munn and Terborgh 1979, Powell 1985, Machado 1991, Stotz 1993). Consequently, flock membership in eastern Brazil seems to be less restrictive (leading to a higher total number of species) but less stable (leading to a lower mean flock richness) when compared to Amazonia.

Flock composition and structure is so highly variable at Barreiro Rico that the abundance of a given forest insectivore species is a good predictor of its regularity of occurrence within flocks (figure 2). Though I did not individually mark birds, my preliminary observations indicated also a lack of flock territoriality at Barreiro Rico. Even the most regular flocking species, *Basileuterus hypoleucus*, apparently followed flocks only within the limits of its own territory. In many instances I observed within the same flock different pairs of the same species as the flock moved. Similarly, flock composition changed gradually as the flock moved. In many flocks I followed, no single species was observed all the time within the flock. These same patterns were observed in flocks with marked birds studied in the Ecuadorian Andes (Poulsen 1996a,b) indicating that this is a possible rule in non-Amazonian mixed-species flocks.

The most regular flocking species, *Basileuterus hypoleucus* (recorded in 80 % of the flocks) and *Herpsilochmus rufimarginatus* (recorded in 71 % of the flocks), do not fully meet the attributes of nuclear species proposed originally by Moynihan (1962): species capable of influencing the formation and cohesion of the flocks. Probably other common species forage together with the most common species at the study site (*Basileuterus hypoleucus*), but this species does not maintain the cohesion of the flocks through continuous calls and active behavior as do *Thamnomanes* spp. antshrikes in Amazonia (Powell 1985).

It is not surprising that given the circumstances of lack of truly nuclear or core species and absence of flock territoriality, mixed species flocks at Barreiro Rico are composed of collections of whichever species happen to co-occur within the home range of the most abundant species. Hutto (1994) observed the same pattern of flock composition and structure in Western Mexico, but he considered the two most regular flock members (present in 89 % and 84 % of the flocks, respectively) to be nuclear species which influenced flock formation. Other data for Central America (Powell 1979) and the Andes (Poulsen 1996a,b) also suggest that mixed-species flocks there are also less stable and highly variable.

Poulsen (1996a) attributed the instability of mixed-species focks in the Ecuadorian Andes and Atlantic forest to the low stature of the vegetation when compared to Amazonia. He pointed out that a low vegetation structure would allow understory and canopy flocks to join one another, preventing a striking differentiation as observed for Amazonian flocks. This hypothesis seems to work for the mixed species flocks in the mainly secondary vegetation of Barreiro Rico. Though

at Barreiro Rico canopy species form a somewhat tight cluster (figure 3, A), there is not a significant segregation among species within flocks (table 1), with many flocks composed of associations between midlevel, trunk and understory insectivores (figure 3, B; table 2).

However, behavioral features of the flocking species also influence patterns of association among species. At Barreiro Rico a striking association occurred between species that share the same pattern of dominant brown plumage color (figure 3, C): *Automolus leucophthalmus*, *Lepidocolaptes fuscus* and *Habia rubica* (the more common female plumage birds are entirely plain brown while males are predominantly dull red). Willis (1989) also studied cases of species with similar plumage coloration that are found together in mixed flocks of montane cloud forests of southeastern Brazil. Willis (1989) attributed these associations to anti-predatory benefits: moving groups of birds which share the same coloration pattern but differ in techniques of avoiding predation are less vulnerable to a predator expecting a single escape response. These associations might work as mimicry and consequently the birds involved share a convergent plumage color. It is interesting to note that these three species also flock together in other areas (Parque Estadual Intervales and Estação Ecológica Juréia-Itatins; pers. obs., P. Develey, pers. comm.). Other species with dominant brown plumage (*Anabacerthia amaurotis* and *Philydor rufus*) also flock together with *Habia* in other forest types such as subtropical montane forests of southern Brazil (Bencke 1996).

Historical, ecological and behavioral processes seem to be responsible for the differences between Amazonian and non-Amazonian flocks. Nuclear, sentinel, core species, inflated home range sizes and multispecies territoriality appear to be attributes restricted to Amazonian flocks (Munn and Terborgh 1979, Powell 1985, 1989, Stotz 1993). I suggest that other types of associations (such as between species that share the same main plumage color) might occur in flocks lacking stability and active sentinel species. Mixed species-flocks from non-Amazonian neotropical forests (yet little studied) can provide important clues to the understanding of the causes of the mixed species flocking behavior.

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APPENDIX

Abundance, guild and frequency of occurrence of flocking species in mixed species bird flocks at Fazenda Barreiro Rico, SP, Brazil.

Family and species	Guild[1]	Frequency[2]	Abundance[3]
Cuculidae			
Piaya cayana[4]	Mi	0.11	0.08
Trochilidae			
Melanotrochilus fuscus	N	0.02	0.37
Trogonidae			
Trogon rufus	O	0.02	0.17
*Trogon surrucura**	O	0.11	0.57
Momotidae			
Baryphthengus ruficapillus	O	0.02	0.57
Picidae			
*Picumnus albosquamatus**	Ti	0.20	0.28
Piculus flavigula	Ti	0.07	0.02
Furnariinae			
*Synallaxis ruficapilla**	Ui	0.27	0.37
Xenops rutilans	Ti	0.09	0.05
Xenops minutus	Ti	0.04	0.05
*Philydor lichtensteini**	Ti	0.31	0.17
*Automolus leucophthalmus**	Ui	0.18	0.17
Dendrocolaptinae			
*Sittasomus griseicapillus**	Ti	0.51	0.65
Dendrocolaptes platyrostris	Ui	0.02	0.14
Xiphocolaptes albicollis	Ti	0.04	0.17
*Lepidocolaptes fuscus**	Ti	0.27	0.14
Thamnophilidae			
Mackenziaena severa	Tgi	0.02	0
*Thamnophilus caerulescens**	Ui	0.40	0.71
*Dysithamnus mentalis**	Ui	0.58	0.97
*Herpsilochmus rufimarginatus**	Mi	0.71	0.74
*Terenura maculata**	Mi	0.42	0.22
*Drymophila ferruginea**	Ui	0.29	0.54
Pyriglena leucoptera	Ui	0.02	0.62
Tyranninae			
Elaenia obscura	Eo	0.02	0.02

APPENDIX

(continued)

Family and species	Guild[1]	Frequency[2]	Abundance[3]
*Myiopagis caniceps**	Ci	0.18	0.34
Myiopagis viridicata	Mi	0.09	0.11
Camptostoma obsoletum	Eo	0.04	0.05
*Leptopogon amaurocephalus**	Ui	0.38	0.14
*Myiornis auricularis**	Ui	0.58	0.51
*Hemitriccus orbitatus**	Ui	0.51	0.82
*Todirostrum poliocephalum**	Mi	0.15	0.71
*Platyrinchus mystaceus**	Ui	0.18	0.51
*Tolmomyias sulphurescens**	Mi	0.31	0.40
Lathrotriccus euleri	Ui	0.07	0.22
Sirystes sibilator	Ci	0.02	0.05
Piprinae			
*Schiffornis virescens**	Uo	0.13	0.51
Manacus manacus	Uo	0.04	0.20
Cotinginae			
Laniisoma elegans	O	0.07	0.05
Vireonidae			
*Cyclarhis gujanensis**	Ci	0.22	0.65
Hylophilus poecilotis	Ci	0.02	0
Parulinae			
Parula pitiayumi	Ci	0.07	0
Basileuterus flaveolus	Tei	0.09	0.08
*Basileuterus hypoleucus**	Ui	0.80	1.62
Thraupinae			
Dacnis cayana	Eo	0.02	0.05
*Conirostrum speciosum**	Ci	0.18	0.22
*Hemithraupis ruficapilla**	Ci	0.24	0.20
Euphonia chlorotica	Eo	0.02	0.08
Ramphocelus carbo	Eo	0.02	0.05
*Habia rubica**	Uo	0.35	0.31
Tachyphonus coronatus	Eo	0.09	0.02
*Trichothraupis melanops**	Uo	0.58	0.62

[1] Guild codes; **Ci** - Canopy insectivores. **Eo** - Edge omnivores. **Mi** - Midlevel insectivores. **N** - Nectarivore. **O** - Omnivores. **Tei** - Terrestrial insectivores. **Tgi** - Forest tangle insectivore. **Ti** - Trunk and twig insectivores. **Ui** - Understory insectivores. **Uo** - Understory omnivores. Classification based primarily on Willis (1979) and personal observations.

[2] Frequency of species occurrence within mixed species flocks, i.e. number of flocks occupied for a given species divided per the total of flocks observed.

[3] Species abundances as measured by the IPA (index of point abundance, see methods).

[4] An asterisk means that the species in question was recorded in more than 10 % of the total of flocks observed.