EFFECTS OF FOREST FRAGMENT SIZE AND SUCCESSIONAL STAGE ON MIXED-SPECIES BIRD FLOCKS IN SOUTHEASTERN BRAZIL[1]

MARCOS MALDONADO-COELHO AND MIGUEL Â. MARINI

Departamento de Biologia Geral, ICB, C.P. 486, Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil, 30161-970, e-mail: marini@mono.icb.ufmg.br

Abstract. We analyzed patterns of species richness, size, structure, and composition of mixed-species flocks in relation to forest fragment size and forest successional stage during dry and rainy seasons, at the state of Minas Gerais, southeastern Brazil. Three forest fragments (1.7, 50, and 200 ha) were used for fragment size analysis, and two fragments (200 and 300 ha) were used for successional stage analysis. Fragment size and season affected flock richness, size, stability, and composition. In the 1.7-ha fragment, flock species richness, size, and stability were significantly different only during the rainy season. Fragment successional stage also influenced flock richness and size, although season did not. Flock composition also had changes related to fragment successional stage. Fragment geometry seems to be an important factor influencing flock structure and composition.

Key words: Atlantic Forest, Brazil, foraging behavior, forest fragmentation, mixed-species flocks, seasonal effects.

INTRODUCTION

Forest fragmentation causes several biotic and abiotic changes in biological communities (Lovejoy et al. 1986, Terborgh 1992). These include disruption of dispersal and migration patterns, invasion of forested areas by non-forest organisms, several edge effects, decline in the size and gene pool of animal and plant populations, and a decrease in species richness (Bierregaard et al. 1992). A consequence of habitat fragmentation, local species extinction, is caused by direct and indirect effects. The direct effects include genetic depletion, demographic changes, and increased edge effects. Indirect effects include alteration of one or more trophic levels in an ecosystem, hence, changing the relative and absolute abundance of predators and prey (Terborgh 1992).

Possible effects on trophic chains may alter the composition and structure of mixed-species bird flocks. These flocks are multispecific associations widespread worldwide, which may increase foraging efficiency of birds, decrease their predation risk, or a combination of both (Buskirk 1976, Powell 1985, Munn 1986). Mixed-species flocks of insectivorous birds usually have a leader (or nuclear) species, some regular (or central) species, and many irregular (or

occasional) species (Munn and Terborgh 1979). Few effects of habitat fragmentation on bird behavior have been reported, particularly bird foraging behavior (Bierregaard and Lovejoy 1989), territory size of species (Rappole and Morton 1985), and dispersion patterns of ant-following birds and mixed-species flocks (Lovejoy et al. 1986, Bierregaard and Lovejoy 1988). Successional vegetation stages also may affect mixed-species bird flocks positively (Cymeris 1991), negatively (Munn 1985), or neutrally (Croxall 1976).

In this study, we evaluated characteristics of mixed-species bird flocks (flocks hereafter) at four forest fragments in southeastern Brazil, to test whether flock richness, size, stability, and structure differ between (1) fragments of different size and (2) fragments at different successional stages. Because the climate of our study region is seasonal, we also evaluated flock characteristics between rainy and dry seasons.

METHODS

STUDY AREA

We conducted this study from December 1996 to January 1999 in fragments of the Atlantic Forest (900 m) near Belo Horizonte, Minas Gerais, Brazil. The four forest fragments studied (1.7, 50, 200, and 330 ha) were located at the "Áreas de Proteção Especial para Proteção de Mananciais da Mutuca e do Barreiro" (19°50'S,

43°50'W), referred to hereafter as Barreiro and Mutuca, owned by the Minas Gerais State Water Company (COPASA). The region has a strong seasonal weather with a well defined rainy season from October to March and a dry season from April to September.

The four forest fragments are embedded in a matrix of disturbed cerrado grasslands, totaling 2,656 ha of protected areas. The first three fragments are located at Barreiro and are between 200 to 400 m from each other. The 330-ha fragment is located at Mutuca, 600–700 m away from the 50 and the 200-ha fragments and is a younger secondary successional stage (90 years, Pedrali, pers. comm.) with a continuous 10–15 m high canopy and a dense understory. The 200-ha fragment is at a more advanced successional stage (150 years), which was evident by the presence of 20–30 m high emergent trees above a 20-m high canopy, and a more open understory. The two smallest fragments have circular shapes resembling in structure the 200 ha-forest.

OBSERVATIONS OF MIXED-SPECIES FLOCKS

Flocks were searched for along roads, trails, and water courses in the fragments' interiors and borders from early morning until mid-afternoon. Flocks were located and followed until lost from sight, mostly because of steep terrain or dense understory. Flock observations were conducted with 7 × 35 mm binoculars. Bird associations were considered as flocks following Stotz's (1993) definition: an association of two or more species moving in the same direction for at least 5 min., without an external concentration of resources. For each flock we recorded number of species and individual and species behavior.

DATA ANALYSIS

The effects of fragment size and season on flock richness and size were compared between the 1.7, 50, and 200-ha fragments by two-way ANOVA. The effects of fragment age and season on flock richness and size were compared between the 200 and the 330-ha fragments also by a two-way ANOVA. A posteriori multiple comparisons were conducted with Tukey approximations. Results are reported as significant if $P \leq 0.05$.

Chi square tests with Yates' correction were employed to test differences in flock leadership between fragments of different size and successional stage during dry and rainy seasons separately, and also between these two seasons at the same fragment. Fisher exact tests were used in cases where sample sizes were small.

Frequency associations among species in flocks during the dry and the rainy season were estimated as the percentage of flocks in which the species were recorded in a specific season. Species were classified as nuclear when they were present in more than 50% of the flocks and showed behaviors characteristic of nuclear species as described by Moynihan (1962), such as frequent vocalizations and alarm calls. Regular species were those that did not show the characteristics determined by Moynihan and were present in 10–49% of the flocks. The third category of occasional species, are those regularly encountered away from flocks, following flocks rarely or only for brief periods (sensu Stotz 1993), and present in less than 10% of the flocks. One species was considered as leader when it was the first species that crossed an open space and was followed by other species, and as sentinel when they gave alarm calls and flycatched.

RESULTS

Forty-one bird species were detected in 137 flocks after 371 hr of observation (Tables 1 and 2). More species were recorded during the rainy season ($n = 38$) than during the dry season ($n = 32$), during 205 and 166 observation hours, respectively. Flock structure was similar in all fragments independent of size and succession stage, and we identified three types of flocks at the study sites: (1) understory-midstory-canopy insectivores ($n = 89$), (2) midstory-canopy insectivore ($n = 43$), and (3) understory-midstory insectivore ($n = 5$). The most represented groups in the flocks were flycatchers (Tyrannidae, $n = 14$ species), ovenbirds (Synallaxinae, $n = 5$ species), tanagers (Thraupinae, $n = 7$ species), and antbirds (Formicariidae, $n = 4$ species) (Table 1). The most frequent species attending flocks were Basileuterus hypoleucus (White-bellied Warbler), Hemithraupis ruficapilla (Rufous-headed Tanager), Trichothraupis melanops (Black-goggled Tanager), and Philydor rufus (Buff-fronted Foliage-gleaner) (Table 1).

AREA AND SEASON EFFECTS

The effects of fragment size, season, and the interaction of these two variables were all significant for species richness and flock size (Table

TABLE 1. Flock role and frequency (%) of bird species at mixed flocks in the four forest fragments during the dry and the rainy seasons at the study site. Species are organized in decreasing overall frequency order.

Species[a]	Flock role[b]	330 ha		200 ha		50 ha		1.7 ha		Total	Number of flocks
		Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy		
White-bellied Warbler (Basileuterus hypoleucus)	N,L	66.6	80.0	66.6	81.5	77.2	66.6	100.0	40.0	72.3	99
Rufous-headed Tanager (Hemithraupis ruficapilla)	N,L	53.3	50.0	80.0	59.2	77.7	60.0	87.5	86.6	68.6	94
Black-goggled Tanager (Trichothraupis melanops)	N,L,S	86.6	87.5	73.3	48.1	33.3	93.3	81.2	40.0	65.6	90
Buff-fronted Foliage gleaner (Philydor rufus)	N	66.6	31.2	73.3	55.5	83.3	60.0	0	26.6	50.3	69
White-barred Piculet (Picumnus cirrhatus)	R	33.3	18.8	33.3	51.8	55.5	60.0	50.0	33.3	43.0	59
Black-capped Antwren (Herpsilochmus atricapillus)	R	0	0	40.0	55.5	66.6	73.3	68.7	26.6	43.0	59
Yellow-olive Flycatcher (Tolmomyias sulphurescens)	R	53.3	12.5	66.6	33.3	38.8	53.3	68.7	13.3	41.6	57
Mottle-cheeked Tyrannulet (Phylloscartes ventralis)	R	33.3	62.5	40.0	7.4	5.5	13.3	50.0	40.0	29.2	40
Rofous-browed Peppershrike (Cyclarhis gujanensis)	R	40.0	37.5	26.6	3.7	22.2	20.0	37.5	6.2	22.6	31
Red-eyed Vireo (Vireo olivaceus)	R	40.0	31.2	13.3	22.2	0	40.0	0	26.6	21.2	29
Variable Antshrike (Thamnophilus caerulescens)	R	26.6	25.0	33.3	14.8	27.7	20.0	18.7	0	20.4	28
Streaked Xenops (Xenops rutilans)	R	20.0	6.2	20.0	14.8	27.7	60.0	0	0	18.2	25
Lesser Woodcreeper (Lepidocolaptes fuscus)	R	0	0	33.3	33.3	5.5	26.6	0	0	17.5	24
Gilt-edged Tanager (Tangara cyanoventris)	R	26.6	37.5	13.3	11.1	0	13.3	31.2	13.3	17.5	24
Sepia-capped Flycatcher (Leptopogon amaurocephalus)	R	6.4	18.7	26.6	18.5	11.1	20.0	37.5	0	17.5	24
Olivaceus Woodcreeper (Sittasomus griseicapillus)	R	0	31.2	66.6	11.1	11.1	20.0	0	0	16.8	23
Plain Antvireo (Dysithamnus mentalis)	R	0	0	26.6	22.2	11.1	6.6	62.5	0	16.8	23
White-eyed Foliage-Gleaner (Automolus leucophthalmus)	R	20.0	12.5	6.6	7.4	16.6	26.6	0	0	10.9	15
Southern Beardless Tyrannulet (Camptostoma obsoletum)	O	0	0	13.3	3.7	27.7	13.3	6.2	0	8.0	11
Long-tailed Tyrant (Colonia colonus)	O	0	0	13.3	3.7	27.7	13.3	6.2	0	8.0	11
Rufous-capped Spinetail (Synallaxis ruficapilla)	O	0	0	20.0	14.8	5.5	6.6	0	0	6.6	9
Little Woodpecker (Veniliornis passerinus)	O	6.6	12.5	0	0	0	20.0	0	6.6	5.1	7
Fawn-breasted Tanager (Pipraeidea melanonota)	O	26.6	6.2	13.3	3.7	0	0	0	0	5.1	7
Tropical Pewee (Contopus cinereus)	O	0	0	20.0	0	11.1	6.6	0	0	5.1	7
Blue Dacnis (Dacnis cayana)	O	0	0	13.3	3.7	0	6.6	12.5	0	4.3	6

[a] Species whose frequency was <4% included White-winged Becard (Pachyramphus polychopterus), Bananaquit (Coereba flaveola), Rufous-crowned Greenlet (Hylophilus amaurocephalus), White-shouldered Fire-eye (Pyriglena leucoptera), Gray Elaenia (Myiopagis caniceps), Greenish Elaenia (Myiopagis viridicata), White-crested Tyrannulet (Serpophaga subcristata), Sooty-fronted Spinetail (Synallaxis frontalis), Gray-headed Tody-flycatcher (Todirostrum poliocephalum), Squirrel Cuckoo (Playa cayana), Gray-hooded Flycatcher (Mionectes rufiventris), Hepatic Tanager (Piranga flava), Purple-throated Euphonia (Euphonia chlorotica), Streaked Flycatcher (Myiodynastes maculatus), Ruby-crowned Tanager (Tachyphonus coronatus), and Green-backed Becard (Pachyramphus viridis).

[b] N = Nuclear species, L = Leader species, S = Sentinel species, R = Regular species, O = Occasional species.

TABLE 2. Observation effort and characteristics of the flocks detected in each fragment studied during dry and rainy seasons.

Fragment size (ha)	Seasons	Number of observation hours	Number of flocks observed	Total number of species	Mean ± SE number of species	Mean ± SE number of individuals
	Dry	33	16	15	7.1 ± 0.5	14.3 ± 1.2
1.7	Rainy	42	15	14	3.6 ± 0.4	6.6 ± 0.8
	Total	55	31	29	5.4 ± 0.4	10.5 ± 1.0
	Dry	40	18	22	6.2 ± 0.8	12.2 ± 1.5
50	Rainy	44	15	27	7.2 ± 0.7	12.6 ± 1.1
	Total	84	33	49	6.7 ± 0.5	12.4 ± 0.9
	Dry	45	15	28	8.5 ± 0.7	15.3 ± 1.1
200	Rainy	62	27	30	7.0 ± 0.5	14.1 ± 0.9
	Total	107	42	53	7.6 ± 0.4	14.6 ± 0.7
	Dry	48	15	19	6.2 ± 0.7	12.8 ± 1.6
330	Rainy	57	16	22	5.8 ± 0.4	11.2 ± 1.0
	Total	105	31	41	6.0 ± 0.4	12.0 ± 0.9
Size comparison	Dry	118	49	28	7.2 ± 0.4	13.8 ± 0.7
	Rainy	148	57	32	6.2 ± 0.3	11.8 ± 0.7
Succession stage	Dry	93	30	32	7.4 ± 0.5	14.1 ± 1.0
comparison	Rainy	119	43	32	6.6 ± 0.4	13.0 ± 0.7
All		371	137	41	6.5 ± 0.2	12.6 ± 0.5

3). The effects were due to a pronounced decline of flocks in the 1.7-ha fragment during the rainy season when compared to the two larger fragments for species richness (Tukey test, $P = 0.01$

TABLE 3. ANOVA table for effects of fragment size and season and of fragment successional stage and season on mixed-species flock richness and size. Season refers to dry and rainy. Size refers to three fragments: 1.7, 50, and 200-ha fragments. Successional stage refers to early succession forest (330-ha) and late succession forest (200-ha).

Parameters	Effects (df)	F	P
Richness	Size (1)	6.2	0.002
	Season (2)	5.6	0.019
	Size × season (2)	5.0	0.007
Size	Size (1)	6.6	0.001
	Season (2)	8.4	0.004
	Size × season (2)	6.0	0.003
Richness	Season (1)	2.3	0.133
	Successional stage (1)	7.3	0.008
	Successional stage × season (1)	0.6	0.419
Size	Season (1)	1.3	0.246
	Successional stage (1)	5.0	0.027
	Successional stage × season (1)	0.0	0.826

and $P < 0.001$ for 1.7 vs. 50 ha and 1.7 vs. 200 ha, respectively) and flock size ($P = 0.01$ and $P < 0.01$ for 1.7 vs. 50 and 1.7 vs. 200 ha, respectively, Fig. 1a and 1b).

No significant differences were found between the 1.7 and the 50 and 200-ha fragments in flock richness and flock size (Tukey test, all pairwise comparisons $P > 0.70$) during the dry season. The 50 and 200-ha fragments also did not show significant differences during the dry and the rainy season in flock species richness and flock size (Tukey tests, all $P > 0.20$).

During the rainy season, both flock richness (Tukey test, $P = 0.01$) and flock size ($P < 0.001$) were significantly smaller than during the dry season in the 1.7-ha fragment. Flocks in the 50 and the 200-ha fragments did not show significant differences between the dry and rainy season in species richness (Tukey test, both $P > 0.50$; Fig. 1a) and size (both $P > 0.95$, Fig. 1b). Hence, these results reveal that mixed flocks in the smallest fragment were influenced by both area and season.

The total number of species detected in flocks at the smaller fragments relative to larger ones decreased if the species recorded in more than 15% of flocks in each season were considered separately. During the dry season, the 1.7-ha
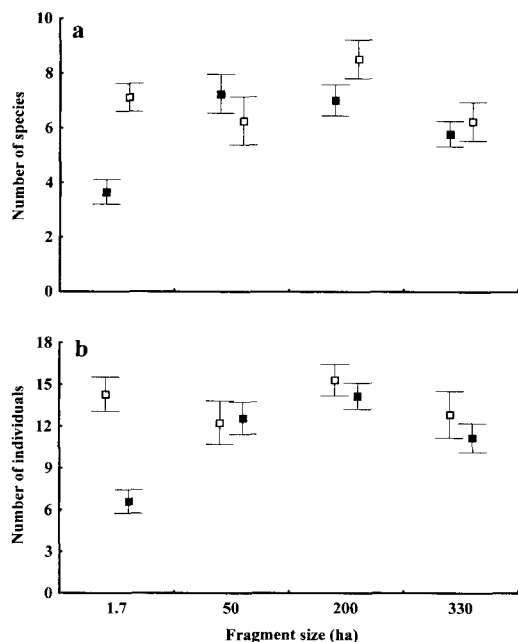
FIGURE 1. Mean (± SE) of (a) flock richness (number of species) and (b) flock size (number of individuals) at four forest fragments studied during rainy (solid squares) and dry (open squares) seasons.

fragment had 28% (n = 9) fewer species and the 50-ha fragment had 9% (n = 3) fewer species than the 200-ha fragment. During the rainy season, the 1.7-ha fragment had 29% (n = 11) fewer species than the 200-ha fragment, but the 50 and the 200-ha fragments had the same number of species (Table 1). With the exception of *P. rufus,* all the nuclear and many regular species increased their frequencies in flocks during the dry season in relation to the rainy season in the 1.7-ha fragment (Table 1). At the 50-ha fragment, *T. melanops* had a low attendance during the dry season, but was the most frequent species during the rainy season.

FOREST SUCCESSIONAL STAGE AND SEASON EFFECTS

The comparison between young (330 ha) and late (200 ha) succession fragments indicated that the effect of successional stage was significant for flock richness and flock size, but season and the interaction between successional stage and season had no significant effect on flock richness or size (Table 3). The weak effects of season and successional stage × season interaction can be explained by the similar seasonal variation patterns of flock species-richness and size in both fragments. This is reinforced by nonsignificant differences in flock richness and size between the dry and rainy seasons on these two fragments (Tukey test, all P > 0.30). The significant effect of succession stage on flock species richness and size explains the higher number of species recorded in the late-succession-fragment flocks in both dry and rainy seasons (Table 2, Fig. 1a and 1b).

For species recorded in more than 15% of flocks, the early-successional-stage forest had 30% (n = 6) fewer species during the dry season and 17.6% (n = 3) fewer species during the rainy season than the later succession forest. At the 330-ha fragment, *Sittasomus griseicapillus* (Olivaceus Woodcreeper) was absent during the dry season, but was recorded during the rainy season (Table 1). The same was observed for *Hylophilus amaurocephalus* (Rufous-crowned Greenlet), an occasional flock species. *Dysithamnus mentalis* (Plain Antvireo), *Lepidocolaptes fuscus* (Lesser Woodcreeper), and *Herpsilochmus atricapillus* (Black-capped Antwren) were not found in the early-succession-fragment flocks, and no species was exclusively found in the 330-ha forest.

FLOCK SPECIES COMPOSITION IN FRAGMENTS

Flocks in the 1.7-ha fragment showed a reduction in frequency of association and absence of many regular species during at least one of the two seasons, when compared with the 50 and 200-ha fragment (Table 1). For example, *P. rufus* was absent during the dry season and this species together with *Tolmomyias sulphurescens* (Yellow-olive Flycatcher), *Thamnophilus caerulescens* (Variable Antshrike), *Leptopogon amaurocephalus* (Sepia-capped Flycatcher), and *D. mentalis* had a lower frequency of association during the rainy season at this fragment. Some regular species were never recorded at the smaller fragment, such as *Xenops rutilans* (Streaked Xenops), *L. fuscus, S. griseicapillus,* and *Automolus leucophthalmus* (White-eyed Foliagegleaner), revealing that fragment size can affect selectively flock species.

Comparisons of flock composition between the two large forest fragments (200 and 330 ha) of different successional stages reveal that during the dry season some nuclear and regular species (such as *B. hypoleucus, T. melanops, P. ru-*

TABLE 4. The results of chi-square and Fisher exact tests for fragment size and fragment successional stage analyses in relation to the times when the Black-goggled Tanager (*Trichothraupis melanops*) was registered as flock leader. Size refers to three fragments: 1.7, 50, and 200-ha fragments. Successional stage refers to early successional forest (330-ha) and late succession forest (200-ha).

Analyses	Season (df)	Test	P
Size	Dry (2)	0.58[ab]	0.743
	Rainy (2)	13.86[a]	0.001
Successional stage	Dry (1)	-	1.000[c]
	Rainy (1)	0.01[a]	0.846

[a] Chi-square test (χ^2). For one degree of freedom Yates' correction for continuity was employed.
[b] More than one-fifth of fitted cells are sparse (frequency <5), although test was not significant.
[c] Fisher Exact test.

TABLE 5. Chi-square and Fisher exact tests for comparisons between dry and rainy seasons at 1.7, 50, 200, and 300-ha fragments in relation to the times when the Black-goggled Tanager (*Trichothraupis melanops*) was registered as flock leader. All df = 1.

Fragment (ha)	Season	Number of flocks	% leading	P
1.7	Dry	11	68.7	0.001[a]
	Rainy	2	13.3	
50	Dry	14	77.7	0.698[b]
	Rainy	10	66.6	
200	Dry	10	66.6	1.000[b]
	Rainy	19	70.3	
330	Dry	11	73.3	0.706[b]
	Rainy	10	62.5	

[a] Chi-square test, χ^2 = 7.6.
[b] Fisher Exact test.

fus, and *T. sulphurescens*, Table 1) show similar occurrences in both fragments. However, a difference in composition between the flocks of the early and late-succession fragments during the dry season can be explained by the loss of four regular (*H. atricapillus, L. fuscus, S. griseicapillus*, and *D. mentalis*), and many occasional [such as *Camptostoma obsoletum* (Southern Beardless Tyrannulet), *Colonia colonus* (Long-tailed Tyrant), *Synallaxis ruficapilla* (Rufous-capped Spinetail), *Contopus cinereus* (Tropical Pewee), and *Dacnis cayana* (Blue Dacnis)] flock species in the early succession fragment during this season (Table 1). During the rainy season, some nuclear and regular species showed a similar frequency of occurrence in both fragments (such as *H. ruficapilla, B. hypoleucus*, and *L. amaurocephalus*, Table 1). The differences in flock composition between these fragments are due to the loss of some regular species at the early-succession fragment during the rainy season (Table 1) together with an increase in the frequencies of occurrence of other species at this fragment [such as *Cyclarhis gujanensis* (Rufous-browed Peppershrike), *Tangara cyanoventris* (Gilt-edged Tanager), and *Phylloscartes ventralis* (Mottle-cheeked Tyrannulet)].

Four species [*T. melanops* (65.6% of the flocks), *H. ruficapilla* (68.6% of the flocks), *B. hypoleucus* (72.3% of the flocks), and *P. rufus* (50.3% of the flocks)] were considered nuclear in the flocks observed because they showed an important role in the maintenance of flock cohesion through their high frequency of flock attendance and intense vocalizations. Fourteen

species were considered regular and 23 occasional (Table 1). Three of the four nuclear species behaved as leaders (*T. melanops, H. ruficapilla*, and *B. hypoleucus*), and only one (*T. melanops*) behaved as a sentinel.

Trichothraupis melanops, in spite of being the third most common species in the flocks (Table 1), may be considered the most important nuclear species and leader of flocks at our study site. Characteristics such as highly conspicuous behavior within the flocks, frequent vocalizations, and quick flights from one flock extremity to the other, together with a neutral-color plumage and the fact that other species follow *T. melanops*, reinforce its role as a nuclear flock leader. At the canopy level, only *H. ruficapilla* acted as a leader, even though it did not behave as a sentinel.

Among the flocks in which it was possible to identify the leader (*n* = 93), *T. melanops* assumed this role in 93.5% (*n* = 87) of them. It did not show differences in this role during the dry season between the 1.7, 50, and 200-ha fragments. However, during the rainy season, *T. melanops* had a significantly lower participation as leader on the 1.7-ha fragment compared to the 50 and the 200-ha fragments (Table 4). No differences were found in *T. melanops*' participation as a leader between the early and the late-succession-stage fragments, during the dry and rainy seasons (Table 4). During the rainy season, *T. melanops*' participation as a leader was significantly less than during the dry season in the 1.7-ha fragment. No significant differences were detected at the 50, 200, and 330-ha fragments between the dry and rainy season (Table 5). *Trichothraupis melanops* and *B. hypoleucus* appar-

ently had fewer vocalizations and conspicuous movements during the rainy season in the 1.7-ha fragment than during the dry season at this fragment and during both seasons at the other two larger fragments. *Hemithraupis ruficapilla* had the highest ($n = 4$) participation as leader at the 1.7-ha fragment during the rainy season. *Basileuterus hypoleucus* had the same participation ($n = 2$) as *T. melanops* in the 1.7-ha fragment during the rainy season. However, *H. ruficapilla* and *B. hypoleucus* were recorded as leaders in our study only in the 1.7-ha fragment during the rainy season. Hence, *T. melanops*' behavior was different from the general pattern only inside the 1.7-ha fragment during the rainy season, given that it behaved frequently as leader in the 1.7-ha-fragment flocks during the dry season, and in the other fragments at both seasons.

DISCUSSION

EFFECT OF AREA

Several studies have shown that habitat fragmentation causes the loss of species (reviews in Offerman et al. 1995, Laurance and Bierregaard 1997); however, similar effects on mixed-species flocks are poorly known, except for some qualitative studies in Amazonia (Lovejoy et al. 1986, Stouffer and Bierregaard 1995) and Central America (Rappole and Morton 1985). In our study, fragmentation effects were most evident only in the 1.7-ha fragment, mainly during the rainy season, when we detected significant differences in flock species richness, size, and structure (Fig. 1a and 1b, Table 1). Similar results in relation to the loss of species attending flocks were detected by Rappole and Morton (1985) and Stotz (1993) in 1.8 and 10-ha forest fragments in Caribbean Mexico and Amazonian localities, respectively; in both cases, five years after fragment isolation, the flocks disappeared. Bierregaard et al. (1989) and Stouffer and Bierregaard (1995) affirmed that mixed-species flocks do not persist in fragmented forests, even in areas larger than the flock home range. Contrary to what we found at the 1.7-ha fragment, Bierregaard and Lovejoy (1989) recorded the loss of species of both mixed-species flocks and ant followers in fragments of 1 and 10 ha after 1–2 years of isolation. Two questions arise from these data: (1) Which factors are allowing flocks to persist at our 1.7-ha fragment? and (2) Which

factors influence the striking seasonal variation at the 1.7-ha fragment, given that a similar pattern was not detected at larger fragments?

Fragment geometry may be one explanation for our finding, because the 1.7-ha fragment is located between the 50 and the 200-ha fragments about 200 m distant from both and may be a stepping stone for several species when crossing between fragments (Marini, unpubl. data). Lovejoy et al. (1986) also recorded several ant-following birds crossing open areas of 100–150 and 300 m between a 10-ha fragment and a continuous forest. An area of dense vegetation (savanna-like cerrado) between the 1.7 and the 50-ha fragments may have facilitated the dispersal of some individuals, as observed for *P. rufus* and *H. ruficapilla*. Bierregaard and Lovejoy (1988), and Stouffer and Bierregaard (1995) found that vegetation density around fragments, and not the size and isolation of fragments, affected the recolonization of fragments by small mammals, Euglosinae bees, flock attending birds, and ant-following birds.

Another explanation may be abundance of food resources at the 1.7-ha fragment enough to attract flocking species. Bierregaard et al. (1992) showed that foliage density and insect abundance were higher in the understory than in the canopy of forest fragments, however, the opposite was detected at the continuous forest. This may be occurring in the 1.7-ha fragment because mixed-species flocks were observed foraging at lower heights in this forest than in the larger fragments. In the three largest forest fragments, flocks avoided the edges as reported for Amazonian forest fragments (Stouffer and Bierregaard 1995). However, flocks were seen at edges of the 1.7-ha fragment. Lovejoy et al. (1986) found changes in foraging activities from the interior to the edge of a 1-ha fragment after 6 months of isolation, probably due to changes in microclimatic conditions and insect abundance. We may have observed a similar change in foraging behavior.

Lastly, the presence of the four nuclear species, even with altered foraging behavior, may be responsible for the existence of flocks at the 1.7-ha forest fragment. In Amazonian fragments, flocks became less cohesive after the disappearance of the leader and sentinel species, Cinereous Antshrike (*Thamnomanes caesius*) (Stouffer and Bierregaard 1996). Nuclear species are important in maintaining cohesion of mixed-spe-

cies flocks due to their cohesive role as thoroughly discussed before (Powell 1979, Stotz 1993). Our results suggest that for attendant flock species, fragmentation affects seasonal movements on a landscape scale as found for two hummingbird species (Stouffer and Bierregaard 1996).

At the 50, 200, and 330-ha fragments, flock size did not differ between seasons, contrary to other studies in the Atlantic Forest (Davis 1946, Develey 1997, Machado 1999), and to the seasonal pattern found for the 1.7-ha fragment. In Central America and the Amazon, all studies showed a decrease in flock richness and size during the breeding season (Powell 1979, 1985). Explanations for the lack of difference in flock richness and size between seasons at ours and other study sites could be related to differences in reproductive behavior (such as participation of both sexes, period and duration of reproductive attempts) or foraging (e.g., prey availability, diet) of flock participants, as proposed by Powell (1979) and Develey (1997). These explanations may also explain differences in flock characteristics among Neotropical regions.

Due to the absence of seasonal variation in flock size at the 50 and 200-ha fragments, seasonal variation detected at the smaller fragment may be due to a different seasonal resource utilization at this fragment by wide-ranging species and individuals from the two larger fragments.

The seasonal variation of flock characteristics at the 1.7-ha fragment may be related to seasonal changes in territory defense, food abundance, and post-fledging dispersal. During the breeding season (rainy season), species may be reproducing preferentially in larger fragments, avoiding the smaller one, because of insufficient area to establish territories, whereas during the dry season, due to a possible weaker territory defense, species can be utilizing the small forest fragments as a home-range extension. Insect abundance in tropical regions is lower during the dry season (Tanaka and Tanaka 1982, Young 1994), thus, birds may spread their home range during periods of low food abundance, using the 1.7-ha fragment more often during the dry season. Develey (1997) showed that all territories of seven flock species in Atlantic Forest of southeastern Brazil were larger than 2.6 ha. Terborgh et al. (1990) estimated the territory size of 144 species in an Amazonian bird community, and found that no species had territories

smaller than 3 ha. These studies reinforce the potential lack of territory sustainability at the 1.7-ha fragment.

Alternatively, the higher richness and size of the 1.7-ha flocks during the dry season can be due to dispersion from larger fragments of juvenile birds without territories that could wander into the isolated fragment and thus associate with flocks. However, juvenile dispersion may be restricted in fragmented forest landscapes, and field data are necessary to support this hypotheses.

Seasonal changes of behavior of nuclear species (*T. melanops* and *B. hypoleucus*), such as less conspicuous movements and fewer or no vocalizations, may explain the change in size and stability of the flocks at the 1.7-ha fragment during the rainy season. During the dry season, *T. melanops* did not show behavioral changes, maintaining the leader role as in the other fragments, and probably was responsible for the high stability of these flocks (some flocks were followed for more than an hour). In Amazonian fragments, flocks became less cohesive and disintegrated after the disappearance of the leader and sentinel *Thamnomanes caesius* (Stotz 1993).

EFFECT OF AREA ON FLOCK COMPOSITION

The lack of some species in flocks at the 1.7-ha fragment may be related to area and isolation effects. The 1.7-ha fragment may be too small for most forest species to establish stable territories throughout the year. Two woodcreeper species (*L. fuscus, S. griseicapillus*) and two ovenbirds (*A. leucophthalmus, X. rutilans*) were absent from flocks. All of these species have territories larger than 1.7 ha, as shown by Develey (1997) in another area of Atlantic Forest of southeastern Brazil. Two other studies attributed the lack of flocks in a 1.8-ha Mexican fragment and in 1 and 10-ha Amazonian fragments (Rappole and Morton 1985, Stouffer and Bierregaard 1995) to an insufficient area to support territories. Fragmentation in our study affected the species selectively, with some species being more resistant (nuclear and regular species) and others being more susceptible (woodcreepers and some ovenbirds) to forest area reduction.

EFFECT OF FOREST AGE

Even though structure and stability did not differ between flocks of the more advanced (older) succession fragment (200 ha) in relation to the

less advanced (younger) forest succession fragment (330 ha), species richness, size, and composition did change. These differences were due to the lack of some species in the younger fragment and an unequal species participation frequency between these fragments.

With the exception of *S. griseicapillus* (absent only during the dry season), three regular species were absent in flocks of the younger forest. After 105 hours of flock observation at this fragment, *H. atricapillus*, *L. fuscus*, and *D. mentalis* were never recorded. Mist-netting surveys conducted in this forest also have not recorded the first two species (Marini, unpubl. data). This may be related to the different forest structures and habitat selection by these species. After two years of study, Greenberg (1996) did not register *D. mentalis* in a selectively logged forest fragment in Mexico. *Lepidocolaptes fuscus* may be absent from the 330-ha fragment due to the lack of larger trees and the consequent lower, average trunk width (Brooke 1983). Similarly, some species of woodcreepers are possibly the most affected by a niche reduction in forests of lower height (Terborgh 1977). *Sittasomus griseicapillus*, however, uses trees with a higher girth variance (Brooke 1983), which would presumably allow this species to utilize a variety of forest types, like immature secondary forests. The lack of these three species in the 330-ha fragment is probably due to the low resilience of these species to habitat perturbation. Thiollay (1992) found that bird communities at three forests at French Guyana did not recover after 40, 80, and 100 years of selective logging. In a study conducted in northeastern Mexico, flock composition differed between three forest habitats due to differences in local abundance of both resident and migrant species (Gram 1998). In Asian forests, Croxall (1976) concluded that there were no differences in flock composition between a primary and a secondary forest, but the primary forest had more species attending the flocks and the secondary forest had more individuals. However, we did not find this pattern in our study. Species and individual numbers were higher at the older forest in both seasons (Fig. 1a and 1b). The lack of seasonal effects on mixed-flocks size in relation to forest succession stage reveals that fragments at these successional stages show similar patterns of seasonal variation in flock size.

Even though we did not find differences in behavior of nuclear and leader species between old and young forests, this was observed between three forest habitats by Gram (1998) in northeastern Mexico for a resident and migratory nuclear species. She attributed this behavioral change to differences in flock-species composition and abundance together with a possibly unequal distribution of resources at the three forest habitats.

In conclusion, we found strong effects only in the 1.7-ha fragment during the rainy season when the mixed-species bird flocks showed major changes in stability, richness, and size. The results also show that size and richness of flocks can be affected by fragment successional stage. Particularly, medium-sized (50 ha) and young (90 years old) forest fragments may have important conservation roles because they hold structured and stable flocks. Also, small forest fragments may function as stepping stones and temporary habitats for flocking species during periods of low food abundance.

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