

Distribution of birds along an elevational gradient in the Atlantic forest of Brazil: implications for the conservation of endemic and endangered species

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Summary

In this study I compare bird communities along an elevational gradient in an Atlantic forest remnant (Pico do Corcovado in Ubatuba) in coastal São Paulo state, Brazil. Forests at low elevations are structurally more complex and more diverse in plant species than those along the slopes and at higher elevations in this remnant. Consequently it is hypothesized that low elevation forests contain a greater diversity of bird species. Results from the study in the Corcovado area show clear differences in the distribution of forest birds along the elevational gradient from both qualitative and quantitative aspects. The structurally more complex forest at low elevations contains the most diverse avifauna, including several of the rarest and most threatened species. The importance of this remnant as a whole is apparent due to the high diversity observed (254 species), the high proportion of endemic species, and the extent to which the avifauna is endangered. Protection of forests at all elevations along the Serra do Mar is required to maintain diversity of bird species, particularly the many endemic and endangered species restricted to specific elevations.

Resumo

Comunidades de aves foram comparadas ao longo de um gradiente altitudinal em um remanescente florestal de Mata Atlântica (Pico do Corcovado em Ubatuba) na costa do estado de São Paulo. As florestas de baixada são mais diversas e mais complexas estruturalmente do que as florestas de encosta ou de altitude e conseqüentemente espera-se que as florestas de baixada possuam uma maior diversidade de aves. Os resultados deste trabalho na região do Corcovado mostram que existem diferenças tanto qualitativas quanto quantitativas ao longo do gradiente altitudinal. As florestas de baixada realmente possuem uma avifauna mais diversa, incluindo várias espécies endêmicas, raras e ameaçadas de extinção. A preservação deste remanescente como um todo é necessária devido à alta diversidade observada (254 espécies) e à alta proporção de espécies endêmicas e ameaçadas. A proteção de florestas em altitudes diferentes na Serra do Mar é portanto necessária para manter a diversidade de espécies de aves, principalmente espécies endêmicas e ameaçadas restritas a determinadas elevações.

Introduction

The mountains along the coast of Brazil, known as Serra do Mar, lie completely within the domain of the Atlantic forest. These mountains constitute an important biogeographical region (Cracraft 1985, Haffer 1974, 1985) and they are probably the most well-defined centre of endemism for birds and other taxa in South America (Müller 1973, Fonseca 1985, Mittermeier 1986). They comprise evergreen forests from the Rio São Francisco (Pernambuco, Alagoas) in the north, to Santa Catarina in the south, where humid forests are replaced by more arid vegetation. Parker *et al.* (1996) recognize as many as 200 endemic taxa from a total of 687 bird species in the Atlantic forest region (see also Cracraft 1985, Scott and Brooke 1985, Collar *et al.* 1987). About 140 endemics inhabit the forests (Haffer 1985), and 88 species belong to monotypic genera with no close relatives (Willis 1992).

Many birds are restricted to certain types of habitats, and their distributional patterns are thought to be strongly related to various structural and floristic aspects of the vegetation (Karr 1971, Noon 1981, Cody 1985, Levey 1988, but see Terborgh 1971). Consequently, a structurally complex forest rich in plant species is likely to house a greater diversity of bird species than a nearby, structurally more simple vegetation type. In the Atlantic forests of São Paulo state, tall forests near the ocean give way to less structurally complex forests along the slopes and mountain peaks (Câmara 1991, Joly *et al.* 1991). If bird diversity is indeed related to structural complexity, then one would expect that the most diverse avifauna would occur in narrow bands of tall forests at the base of the mountains. Here I quantitatively compared bird communities along an elevational gradient in an Atlantic forest remnant in coastal São Paulo state. My goals were to test general ideas about species distribution and diversity patterns, to look for associations between the distributions of rare and endangered bird species and of different forest types, and to draw attention to the unprotected forest at the base of the Pico do Corcovado mountain, in the Municipality of Ubatuba.

The original vegetation in the Atlantic forest region covered approximately one million km², or 12% of Brazil. Estimates of what remains range from 2% to 5% of the original forest cover, and consequently, the Atlantic forest region is one of the most threatened ecosystems in the world (Mittermeier 1988, Myers 1988, Lino 1992, SOS Mata Atlântica and INPE 1992). The deforestation process, initiated with the colonization of Brazil in the sixteenth century, was tremendously intensified during the second half of the twentieth century. Frontiers were rapidly opened due to industrialization and urban growth. Farming and cattle raising, combined with fiscal incentives for reforestation with exotic species, have further accelerated the destruction of these forests (Sick 1993, Dean 1995). As late as the beginning of the twentieth century, more than 60% of São Paulo state was still covered by forest, yet forests along the coast, as well as those on the planalto (plateau), have now virtually disappeared from the area, and only 3% of the total area of São Paulo state is still forested (SOS Mata Atlântica and INPE 1992). Not surprisingly, remaining forest patches lie in steep escarpments where access is difficult, and land is mostly unsuitable for any large-scale economic activity (SEMA 1993). Very few forest remnants exist in more accessible areas, and those continue to be destroyed at an alarming rate. Unplanned colonization as well as real estate speculation pose threats almost impossible to control. Although many

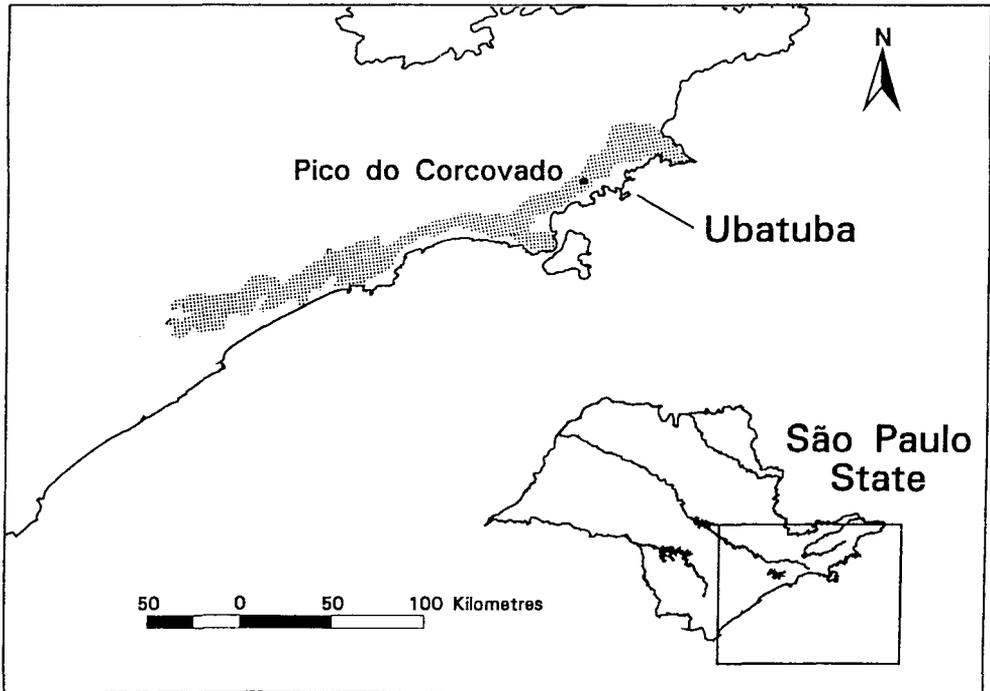


Figure 1. Pico do Corcovado area in the Municipality of Ubatuba, São Paulo State. Serra do Mar State Park along the coast is shown (stippled area).

of the remnants are part of conservation units (Unidades de Conservação; Câmara 1991), their further protection is not ensured.

Methods

Study area

The research was conducted in the Municipality of Ubatuba (São Paulo state), along a trail (c. 5 km long, <1 m wide) in the Serra do Mar that leads to the highest peak of the region, Pico do Corcovado (23°28'S 45°12'W, elevation 1,150 m) (Figure 1). This area is part of the Serra do Mar State Park (c. 314,800 ha) and is one of the few primary forest remnants that extends from sea-level to the top of the mountain range. Birds were surveyed within three elevational ranges along this trail: sea level–100 m (hereafter low), 100–950 m (hereafter mid), and 950–1150 m (hereafter high).

The climate is considered wet tropical, with rains distributed throughout the year; there are no distinct seasons, according to Koeppen's classification. Rainfall averages 1000–1500 mm/year at sea-level, but increases upslope with totals that may exceed 4,000 mm/year at the highest elevations (Câmara 1991). The climate in the mountains is mild and mean monthly temperatures average from 14 to 21 °C (Câmara 1991).

The Atlantic forest, which consists primarily of humid evergreen forests, dif-

fers markedly both structurally and floristically at different elevations (Joly *et al.* 1991, Leitão-Filho 1993). Forests at the base of the mountains (i.e. low forest) occur mostly on sedimentary soils. Vegetation is exuberant and diverse in both species and life forms, probably due to a combination of a variety of soils and stable conditions of humidity throughout the year (Câmara 1991, Joly *et al.* 1991, Leitão-Filho 1993). This forest type is restricted to very narrow bands adjacent to and at the base of the mountains. Canopy height ranges from about 10 to 30 m, with Lauraceae and Euphorbiaceae (several genera, including *Hyeronima*) being the most common tree families (J. M. Goerck unpubl. data; see also Silva and Leitão-Filho 1982). Canopy tree emergents (e.g. *Hymenaea courbaril*) reach up to 40 m in height.

Forests along the eastern slopes (i.e. mid site) occur on acid-poor soils originating from weathering of crystalline rocks, but share similar characteristics of humidity and precipitation with low elevation forests (Câmara 1991). Vegetation is very rich and diverse. Trees range from about 7 to 20 m tall, with canopy height generally decreasing with increasing elevation (J. M. Goerck unpubl. data). Common canopy families include Bombacaceae (particularly *Eriotheca*) and Sapotaceae (primarily *Micropholis*).

Highland forests (i.e. high site) as defined here, occur at elevations above 950 m at this site. Constant cloud cover and strong winds probably limit growing conditions and affect plant life forms in these forests. Consequently, they house many endemic plant species, including many in the genus *Tibouchina* (Melastomataceae) (Eiten 1992). Trees are mostly stunted with a heavy moss load. Frequent fires also influence the physiognomy of the area, and in combination with strong winds, result in many sparsely distributed gnarled trees. Compositae is the most common tree family in recently burned areas. Other common tree families in the area include Nyctaginaceae (genus *Guapira*) and Myrtaceae; canopy height generally does not exceed 10 m (J. M. Goerck unpubl. data).

Bird communities

Censuses Distribution and relative abundance of birds were documented with point counts (Verner and Ritter 1985) and tape-recordings (Parker 1991) along three 1000-m transects at different elevations (low, mid, high) corresponding to natural breaks in the vegetation. Transects were at least 200 m apart. Along each transect, 10 point count stations were established at 100-m intervals. Most birds were detected vocally and tape-recorded when possible. Location of each bird was estimated and plotted onto a trail map to avoid including the same individual twice. Only birds estimated to be within 50 m of the station were included in the analysis (i.e. limited distance point counts). Point count stations were distributed from approximately 25 to 85 m elevation in the low vegetation site, from 145 to 610 m in the mid vegetation site, and from 995 to 1050 m in the high vegetation site. All bird counts were conducted during the breeding season (September and October), when the majority of species were vocal. Counts at each station were replicated on eight different days, alternating among elevations and stations on subsequent days. Thus, stations at each elevation were surveyed at different times on different days (e.g. station 1 surveyed at 06h00 on the first

day, at 08h00 on the fourth day). Censuses lasted 10 minutes at each point (10 points/day), from before dawn until approximately 09h00. I camped at the high elevation site on five occasions; other elevations were visited mostly during the day (although, to ensure presence at a particular station before dawn, I often started fieldwork long before dawn).

General observations Data obtained from the systematic point counts were complemented by opportunistic observations on foraging and flocking behaviour. These opportunistic observations included some preliminary trips to the site in 1991 with T. A. Parker. Twenty species were seen only in 1991; these species were included in general descriptions of the bird communities, but not for quantitative comparisons (e.g. accumulation curves). Additional species were recorded during short visits in 1996 and 1997, but were not included in the general analyses. Endemic and endangered species were placed in distinct categories. Because the emphasis of this project was on the highly threatened lowland forest, more time was spent in this area: 174 hours of observations. A total of 89 and 106 hours of observations occurred at the mid and high elevation sites, respectively. Examination of species accumulation curves indicated that increased effort at mid and high elevation sites would not have drastically changed species totals. Thus, the total number of species observed during this study, although not complete, probably reflects true differences in diversity among the three elevations.

Statistical analysis

Samples at each point count station acted as the unit for statistical analyses of bird data. Variables used in statistical analyses were tested for normality (Wilk-Shapiro test) and transformed when necessary using natural logarithms. Variables also were tested for equality of variances using Bartlett's test. Non-parametric tests were used when data did not meet assumptions of normality or homogeneity of variances.

Comparisons of avifaunal composition and abundance among elevations (main factor) were done using one-way analysis of variance (ANOVA), followed by Tukey's comparisons among means tests. I determined the average number of individuals seen or heard at each point count station over eight replicate days of censuses. These average values per point count station were then used in statistical analyses that included calculation of mean values for each of the three elevational transects. The following dependent variables were considered: average number of all individuals, average number of all species, average number of endemic individuals, average number of endemic species, average number of individuals of endangered species, average number of endangered species. Two stations were omitted (one each at low and mid elevations) from this analysis because detection of some species of birds at both these stations was hampered by the presence of a nearby stream. For endangered species with 15 or more total records, distributions of observations were compared among elevations using chi-square goodness-of-fit tests. The null hypothesis was that observations are evenly distributed among sites (low, mid, and high elevation) and show no particular elevation association. No station was omitted for this analysis because all six species examined could be detected despite the presence of the stream nearby.

Results

Bird communities

General observations A total of 252 species was recorded for the Corcovado area during September 1991 and July–November 1994 (see Appendix). Two previously unrecorded species were seen in 1996 and 1997 (not included in the analyses), amounting thus to a total of 254 species. Nearly 40% (98 species) of the species observed at the site are endemic to the Atlantic forest region (cf. Parker *et al.* 1996). Of the 252 species, 158 occurred primarily in mature forests (see Appendix). The low elevation site was the most species-rich zone with a total of 224 species. Both mid and high elevation sites were similar in species numbers, with 105 and 96 bird species, respectively.

I used only bird species that occurred in mature forests for comparisons of species diversity and composition among elevations because these birds are of particular conservation concern. Other habitats surveyed are not under immediate threat, and on the contrary, may be favoured by disturbance (e.g. shrubby growth). Further, raptors and night birds, as well as latitudinal migrants that arrived late in the season (i.e. November), also were excluded from comparisons among elevations due to the low probability of recording these species.

Seventy-eight of the 98 endemic species (80%) primarily occurred in mature forest. Endangered species (i.e., those considered threatened or near-threatened by Collar *et al.* 1992) represented 13% of the whole avifauna (33 species). In addition, the majority of the listed endangered species (25 of 33) also were primarily mature forest birds. Moreover, more of these endemic (20%, 16 of a total of 78 species) and endangered (28%, 7 of 25) species were restricted to low elevation forests. Common endemic species (i.e. recorded on more than 70% of the visits) in mature forests at low elevations were Saw-billed Hermit *Ramphodon naevius* (also an endangered species), two *Drymophila* antbird species (Ferruginous Antbird *D. ferruginea* and Scaled Antbird *D. squamata*), White-eyed Foliage-gleaner *Automolus leucophthalmus*, Grey-hooded Attila *Attila rufus*, the ubiquitous Swallow-tailed Manakin *Chiroxiphia caudata*, and Chestnut-bellied Euphonia *Euphonia pectoralis*. At mid elevations, common endemics included Swallow-tailed Manakin, Greenish Manakin *Schiffornis virescens* and Hooded Berryeater *Carpornis cucullatus* (also endangered). Swallow-tailed Manakin and Hooded Berryeater were also common at high elevations, together with other endemics, Mouse-coloured Tapaculo *Scytalopus speluncae*, Rufous-backed Antvireo *Dysithamnus xanthopterus*, and White-shouldered Fire-eye *Pyriglena leucoptera*.

Point counts A total of 142 species (56% of the entire avifauna) were recorded during point counts; 94, 93, and 69 species were recorded at stations within low, mid, and high elevations, respectively. I recorded significantly more total individuals and species during point counts at low elevations than at high elevation sites. Point counts at mid elevations were intermediate (Table 1). Moreover, in general, more endemic and endangered individuals and species were recorded during point counts at low elevations than at higher sites (Table 1).

Remarkably, over one-half of all individuals (1,381 individuals, of a total of 2,410; 71 species) recorded during censuses were endemic to the Atlantic forest region. The most abundant endemic species recorded during censuses were

Table 1. Mean (\pm SE) number of individuals and bird species recorded during 10-minute point counts at three elevations. Results of one-way analysis of variance (F -value) examining differences among elevations are shown. All F -values (F) are significant at $P < 0.001$ level. Superscripts following means indicate differences between elevations using Tukey multiple comparison among means tests

Variable (number per 10-minute point count)	Elevation			F
	Low	Mid	High	
Number of individuals of all species	16.4 \pm 0.78 ^a	10.2 \pm 1.05 ^b	4.9 \pm 0.36 ^c	58.6
All species	11.2 \pm 0.43 ^a	7.0 \pm 0.63 ^b	3.7 \pm 0.27 ^c	71.0 ¹
Individuals of endemic species	9.5 \pm 0.73 ^a	5.8 \pm 0.70 ^b	2.7 \pm 0.26 ^c	33.9 ¹
Endemic species	2.7 \pm 0.13 ^a	2.0 \pm 0.15 ^b	1.2 \pm 0.08 ^c	38.5
Individuals of endangered species	1.9 \pm 0.19 ^a	1.1 \pm 0.20 ^b	0.4 \pm 0.12 ^c	19.5
Endangered species	0.5 \pm 0.03 ^a	0.6 \pm 0.05 ^a	0.2 \pm 0.06 ^b	12.8

¹ = Variances are significantly different ($P < 0.05$), but non-parametric tests yield same results.

Swallow-tailed Manakin, followed by Saw-billed Hermit, and Scaled Antbird. A total of 16 endangered species was recorded during point counts. Of these, six species occurred regularly enough (i.e. >15 observations) to compare their distributions among forest elevations. In all cases, occurrence differed significantly from that expected by chance, suggesting that these species are highly associated with certain elevational ranges (Table 2). Four of the six species examined individually were more abundant at the low site, and never recorded at the high elevation: Saw-billed Hermit, Slaty Bristlefront *Merulaxis ater*, Spot-breasted Antvireo *Dysithamnus stictothorax*, and Eye-ringed Tody-tyrant *Hemitriccus orbitatus*. Except for the Slaty Bristlefront, which is a ground-dwelling species, the others occur at the mid and understory layers in the forests. The remaining

Table 2. Total number of observations of endangered species recorded during point counts at three elevations in the Corcovado area, Ubatuba. Results of chi-square goodness-of-fit tests examining differences in distribution of species among elevations are given. N is the total number of observations for each species during point counts

Species	N	Elevation			χ^2	P
		Low	Mid	High		
Solitary Tinamou <i>Tinamus solitarius</i>	21	7	12	2	7.14	<0.05
Saw-billed Hermit <i>Ramphodon naevius</i>	81	74	7	0	123.63	<0.001
Slaty Bristlefront <i>Merulaxis ater</i>	31	21	10	0	21.36	<0.001
Spot-breasted Antvireo <i>Dysithamnus stictothorax</i>	37	24	13	0	23.41	<0.001
Eye-ringed Tody-tyrant <i>Hemitriccus orbitatus</i>	32	17	15	0	16.18	<0.001
Hooded Berryeater <i>Carpornis cucullatus</i>	27	0	16	11	14.89	<0.001

two species Solitary Tinamou *Tinamus solitarius* and Hooded Berryeater, were more abundant at mid elevations.

Discussion

During the period of this study, 254 bird species were recorded in the Corcovado area. No other study of the avifauna of the Serra do Mar along the coast of the state of São Paulo has (to my knowledge) shown such high diversity in an equally small patch of forest (<50 ha) (Camargo 1946, Müller 1966, Willis and Oniki 1981, Olmos 1989, 1996, Höfling and Lencioni 1992, Alcixo and Galetti 1997, Develey, *in press*; but see Remsen 1994 for inadequacy of comparisons of bird lists).

High species richness in the avifauna of the Corcovado area is probably due to a number of factors, including floristic and structural changes in the vegetation along the elevational gradient. Both general observations and point count data confirm that, as predicted, the more structurally diverse forest at low elevation contains the greatest number of bird species. Moreover, clear differences in the distribution of forest birds occur along this elevational gradient, thus contributing to high overall richness. In tropical forests elsewhere, changes in species composition along elevational gradients have been explained by several factors, including competition, resource availability, habitat specialization, and historical events (e.g. Terborgh 1971; 1977, Beehler 1981, Bell 1984, Loiselle and Blake 1991, Janes 1994, Repasky and Schluter 1994). In the study area, a combination of such factors is likely to be important in explaining the presence or absence of different species along the elevational gradient. Disparities in elevational distributions might be further accentuated by different intensities of human pressures. For example, Solitary Tinamou occurs at all elevations in the Corcovado area, but probably because of hunting, its population is greatly reduced at the low elevation site.

In the Atlantic forest region, patterns of endemism and the specialized habits of the avifauna, especially when considered in light of present human activities in the region, suggest that it is a highly endangered community. As mentioned earlier, many birds recorded during general observations or point counts were endemic species. Moreover, endemism is highest among forest interior species (80% of all endemics); these birds are recognized as being most susceptible to fragmentation (Lovejoy *et al.* 1986, Blake and Karr 1987, Bierregaard and Lovejoy 1989, Newmark 1991). Furthermore, several endangered endemic species known to feed primarily on insects associated with bamboo stands, (e.g. Spotted Bamboo-wren *Psiloramphus guttatus*, White-bearded Antshrike *Biatas nigropectus*, and Fork-tailed Pygmy-tyrant *Hemitriccus furcatus*) (Parker 1982, Collar *et al.* 1992), as well as species that feed primarily on seeding bamboo (Buffy-throated Seed-eater *Sporophila frontalis* and Uniform Finch *Haplospiza unicolor*) (Collar *et al.* 1992) are restricted to low elevations. Although stands of bamboo occurred at mid and high elevations, the above species were never recorded at either site. Some of these species, however, do occur at different elevations in other portions of the Atlantic forest region (pers. obs., cf. Scott and Brooke 1985, Parker and Goerck 1997).

In summary, the importance of this remnant as a whole is evident due to the

high diversity observed (254 species), the high proportion of endemic species (40%), and the extent to which the avifauna is endangered (13%). Larger populations of species both in the endemic and endangered categories appear to occur in the lower forested portions of the trail (i.e. below 100 m), thus highlighting the extreme importance of the unprotected forests at sea-level. Destruction of these forests would probably locally eradicate several species of birds due to range reductions and habitat restrictions (e.g. Russet-winged Spadebill *Platyrinchus leucorhynchus*, São Paulo Tyrannulet *Phylloscartes paulistus*). Indeed, along the Atlantic coast of Brazil, bird species dependent on primary forests at low elevations are under immense threat, as they have had their range much reduced (e.g. Black-eared Parrotlet *Touit melanonota*, *Sporophila falcirostris*) (Sick 1969). Consequences of these range reductions are that populations have become highly fragmented, and abundance may already be reduced to levels lower than those needed for long-term persistence of several species (cf. Shaffer 1987).

Specific recommendations for the Corcovado area

The small patch of primary and old secondary forest below 100 m elevation at the beginning of the Pico do Corcovado trail would benefit if incorporated into the Serra do Mar conservation unit. Existing secondary forests, such as the one in this area, when near a relict of good primary forest, likely facilitate regeneration of forest stands. This area now contains one of the only continuous tracts of primary – or near primary – forest from low to high elevations in the state of São Paulo. Protection of low elevation forests is thus required to maintain diversity of bird species, particularly the many endemic and endangered species restricted to forests below 100 m elevation region (see also Wege and Long 1995, pp. 103–104).

Enforcement of existing legislation is essential in the region, such as banning of hunting or capture of wildlife, and harvesting of any type of wild plants (orchids, palm hearts; see also Galetti and Aleixo 1998). Finally, studies like this are essential in providing the basic information needed for both government and non-government agencies to act locally.

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Appendix. Birds of the Corcovado area in the Municipality of Ubatuba, São Paulo state

The list does not include areas around Corcovado village. Abundances are provided for each elevation separately, in habitat most commonly seen. Elevations were divided in low (sea-level–100 m), mid (100–950 m), and high (950–1150 m). Habitat, sociality, and foraging position are in order of increased preference observed at this site. Threat is listed according to Collar *et al.* (1992). Taxonomic order follows Sick (1993).

Abundance: C, common (recorded on more than 70% of the visits); FC, fairly common (40–70%); U, uncommon (10–40%); S, scarce (less than 10%); P, probable, but confirmation needed.

Habitat (Hab): FM, mature forest and tall secondary forest; SG, shrubby growth and clearings; W, marshes and ponds; G, grassland; O, overhead.

Microhabitat (Mic): B, bamboo; St, streams.

Sociality (Soc): So, solitary, found alone or in pairs; Gr, gregarious, monospecific groups of more than five individuals; MF, mixed flocks.

Foraging position (FP): Te, terrestrial or on water; U, undergrowth, mainly within 5 m of the ground; M, middlestorey, mainly from 5 to 10 m above ground; Ca canopy; A, aerial.

Endemism (End): AF, Atlantic forest region.

Threat (Thr): NT, near-threatened; T, threatened.

Species	Abundance			Hab	Mic	Soc	FP	End	Thr
	Low	Mid	High						
Tinamidae (2)									
<i>Tinamus solitarius</i>	U	FC	FC	FM		So	Te	AF	NT
<i>Crypturellus obsoletus</i>	FC	FC	FC	FM		So	Te		
Fregatidae (1)									
<i>Fregata magnificens</i>	S			O		So	Te		
Ardeidae (2)									
<i>Casmerodius albus</i>	S			W		So	Te		
<i>Butorides striatus</i>	S			W		So	Te		
Cathartidae (2)									
<i>Coragyps atratus</i>	FC		U	O		Gr	Te		
<i>Cathartes aura</i>	S			O		So	Te		
Accipitridae (8)									
<i>Leptodon cayannensis</i>	S			FM		So	Ca		
<i>Harpagus diodon*</i>	S			FM		So	Ca		
<i>Accipiter striatus</i>	S			SG		So	Ca		
<i>Buteo brachyurus</i>	S	S		FM		So	Ca		
<i>Buteo magnirostris</i>	FC			SG		So	Ca		
<i>Leucopternis polionota</i>	P			FM		So	Ca	AF	NT
<i>Leucopternis lacermulata</i>	S		S	FM, SG		So	Ca	AF	T
<i>Spizaetus tyrannus</i>	U		S	FM		So	Ca		
Falconidae (2)									
<i>Herpetotheres cachimans</i>	U			FM, SG		So	Ca		
<i>Micrastur ruficollis</i>	U		U	FM		So	M		
Cracidae (1)									
<i>Penelope obscura</i>	S		S	FM		So	M		
Phasianidae (1)									
<i>Odontophorus capucira</i>	U	U	U	FM		Gr	Te	AF	
Rallidae (2)									
<i>Aramides saracura</i>	FC			W		So	Te	AF	
<i>Laterallus melanophaius*</i>	S			W		So	Te		
Columbidae (8)									
<i>Columba cayannensis</i>	U		S	SG, FM		So	Ca		
<i>Columba plumbea</i>	U	FC	C	FM		So	Ca		
<i>Columbina talpacoti</i>	S			G, SG		Gr	Te		
<i>Claravis pretiosa</i>	P			SG		So	U		
<i>Claravis godefrida*</i>	U			SG	B	So	U	AF	T
<i>Leptotila verreauxi</i>	P			SG		So	Te		
<i>Leptotila rufaxilla</i>	FC			FM, SG		So	Te		
<i>Geotrygon montana</i>	U			FM		So	Te		
Psittacidae ¹ (6)									
<i>Pyrrhura frontalis</i>	FC+	FC+	FC+	FM, SG		Gr	Ca	AF	
<i>Forpus xanthopterygius*</i>	FC			FM, SG		Gr, So	Ca		
<i>Brotogeris tirica</i>	FC+	FC+	FC+	SG, FM		Gr	Ca	AF	
<i>Touit melanonota*</i>	S			FM		So	Ca	AF	T
<i>Pionopsitta pileata</i>	U+	FC+	FC+	FM, SG		Gr	Ca	AF	NT
<i>Pionus maximiliani</i>	FC	U	U	FM, SG		So, Gr	Ca		
Cuculidae (3)									
<i>Piaya cayana</i>	U			FM, SG		So	M, Ca		
<i>Crotophaga ani</i>	U			G, SG		Gr	Te		
<i>Tapera naevia</i>	U			SG, G		So	U		
Tytonidae (1)									
<i>Tyto alba</i>	U			SG		So	Ca		
Strigidae (4)									
<i>Otus atricapillus</i>			U	FM		So	Ca, M	AF	

Species	Abundance			Hab	Mic	Soc	FP	End	Thr
	Low	Mid	High						
Strigidae (4) cont.									
<i>Pulsatrix koenigwaldiana</i>	S			FM		So	Ca	AF	
<i>Glaucidium minutissimum</i>	S			FM		So	M, Ca		
<i>Ciccaba virgata</i>	U		S	FM		So	Ca		
Nyctibiidae (2)									
<i>Nyctibius aethereus*</i>	P			FM		So	Ca		
<i>Nyctibius griseus</i>	FC			SG		So	Ca		
Caprimulgidae (2)									
<i>Lurocalis semitorquatus</i>	U	FC	U	FM, SG		So	Ca		
<i>Nyctidromus albicollis</i>	U			SG		So	Te		
Apodidae (3)									
<i>Streptoprocne zonaris</i>	U+	U+	C+	O		Gr	A		
<i>Chaetura cinereiventris</i>	FC+			O		Gr	A		
<i>Panyptila cayennensis*</i>	S			O		So	A		
Trochilidae (12)									
<i>Ramphodon naevius</i>	C+	U		FM		So	U	AF	NT
<i>Phaethornis eurynome</i>		S	S	FM		So	U	AF	
<i>Phaethornis squalidus</i>	U		U	FM		So	U		
<i>Phaethornis ruber</i>	U			SG, FM		So	U		
<i>Melanotrochilus fuscus</i>	U	S		SG		So	Ca, M	AF	
<i>Anthracothorax nigricollis</i>	U			SG		So	Ca		
<i>Lophornis sp.</i>	S			FM		So	Ca		
<i>Chlorostilbon aureoventris</i>	S			SG		So	U		
<i>Thalurania glaucopis</i>	FC	FC	U	SG, FM		So	U, M	AF	
<i>Hylocharis cyanus</i>	U			SG		So	Ca		
<i>Amazilia versicolor</i>	P			SG		So	U, M		
<i>Clytolaema rubricauda</i>			S	FM		So	M	AF	
Trogonidae (3)									
<i>Trogon viridis</i>	U	U		FM		So	Ca, M		
<i>Trogon rufus</i>	FC	U	S	FM		So	M		
<i>Trogon surrucura</i> ²	U	FC	U	FM		So	M	AF	
Alcedinidae (2)									
<i>Chloroceryle americana</i>	U			FM, W	St	So	Te		
<i>Chloroceryle inda</i>	S			FM	St	So	Te		
Momotidae (1)									
<i>Baryphthengus ruficapillus</i>	FC	U		FM		So	M	AF	
Bucconidae (2)									
<i>Notharchus macrorhynchus*</i>	U			FM		So	Ca		
<i>Malacoptila striata</i>	U			FM, SG		So	U	AF	
Ramphastidae (4)									
<i>Selenidera maculirostris</i>	U	S		FM		So	Ca	AF	
<i>Bailloniuss bailloni</i>	S	U	U	FM, SG		So, Gr	Ca	AF	NT
<i>Ramphastos vitellinus*</i>	U			FM		Gr	Ca		
<i>Ramphastos dicolorus</i>	S			FM		Gr	Ca	AF	
Picidae (8)									
<i>Picumnus cirratus</i>	FC			FM, SG		MF, So	M		
<i>Colaptes melanochlorus*</i>	S			SG		So	M		
<i>Piculus flavigula</i>	U	U		FM		So, MF	M		
<i>Piculus aurulentus</i>		U	U	FM		So, MF	M	AF	NT
<i>Celeus flavescens</i>	FC	U		FM, SG		So	M		
<i>Dryocopus lineatus</i>	U			SG		So	Ca		
<i>Melanerpes flavifrons</i>	U	U	P	FM, SG		So	M, Ca	AF	
<i>Veniliornis spilogaster</i>	U	U	S	FM, SG		MF, So	M	AF	

Species	Abundance			Hab	Mic	Soc	FP	End	Thr
	Low	Mid	High						
Rhinocryptidae (3)									
<i>Psilorhamphus guttatus</i>	U			SG	B	So	U	AF	NT
<i>Merulaxis ater</i>	FC	U		FM, SG		So	Te	AF	NT
<i>Scytalopus speluncae</i>			C	FM, SG		So	Te	AF	
Formicariidae (28)									
<i>Hypodaleus guttatus</i>	FC	U	S	FM		So	M	AF	
<i>Batara cinerea</i>		U	C	FM, SG	B	So	M, U		
<i>Mackenziaena leachii</i>			U	SG		So	U	AF	
<i>Mackenziaena severa</i>	S	S	U	FM, SG	B	So	M, U	AF	
<i>Biatas nigropectus*</i>	P			SG	B	So	M	AF	T
<i>Thamnophilus caerulescens</i>			FC	FM, SG		So	U, M		
<i>Thamnophilus ruficapillus</i>	S			SG		So	U		
<i>Dysithamnus stictothorax</i>	FC	U	S	FM, SG		So, MF	U, M	AF	NT
<i>Dysithamnus mentalis</i>	C	FC	U	FM, SG		So, MF	U, M		
<i>Dysithamnus xanthopterus</i>		U	C	FM, SG		So	M	AF	
<i>Myrmotherula gularis</i>	U	U		FM	St	So	U	AF	
<i>Myrmotherula minor</i>	S	U		FM		So, MF	M	AF	NT
<i>Myrmotherula unicolor</i>	FC	S		FM, SG		So, MF	M, U	AF	NT
<i>Herpsilochmus rufimarginatus</i>	FC			FM		So, MF	M, Ca		
<i>Drymophila ferruginea</i>	C			FM, SG	B	So, Gr	U, M	AF	
<i>Drymophila genei</i>			FC	SG	B	So	U	AF	NT
<i>Drymophila ochropyga</i>			FC	SG	B	So	U	AF	NT
<i>Drymophila squamata</i>	C	FC		FM, SG		So	M	AF	
<i>Terenura maculata</i>	FC	S		FM, SG		MF	M, Ca	AF	
<i>Pyriglena leucoptera</i>	FC	FC	C+	FM, SG		So, MF	U	AF	
<i>Myrmeciza squamosa</i>	S	FC	U	FM		So	Te, U	AF	
<i>Chamaeza campanisona</i>	S	U		FM, SG		So	Te		
<i>Chamaeza meruloides</i>	U	U	U	FM, SG		So	Te	AF	
<i>Formicarius colma</i>	FC			FM		So	Te		
<i>Grallaria varia</i>	FC	S	S	FM, SG		So	Te		
<i>Hylopezus nattereri</i>		S	FC	FM, SG		So	Te	AF	
<i>Conopophaga melanops</i>	FC	FC		FM		So	U	AF	
<i>Conopophaga lineata</i>	U	U	U	FM, SG		So	U	AF	
Furnariidae (16)									
<i>Synallaxis spixi</i>	FC			SG		So	U		
<i>Synallaxis ruficapilla</i>	FC	U		SG, FM		So	U	AF	
<i>Synallaxis cinerascens*</i>	S			SG		So	U		
<i>Phacellodomus erythrophthalmus</i>	FC			SG, FM		So	U	AF	
<i>Anabazenops fuscus</i>	U	U		FM		So, MF	M	AF	
<i>Syndactyla rufosuperciliata</i>		P	P	FM		So	U		
<i>Philydor atricapillus</i>	FC	S		FM		MF, So	M, U	AF	
<i>Philydor lichtensteini</i>	FC			FM		MF	Ca, M	AF	
<i>Philydor rufus</i>	U	U	U	FM		So, MF	Ca		
<i>Automolus leucophthalmus</i>	C	S	U	FM		So, MF	U, M	AF	
<i>Cichlocolaptes leucophrus</i>	FC	FC	U	FM, SG		So, MF	M, Ca	AF	
<i>Heliobletus contaminatus</i>			U	SG		So	M	AF	
<i>Xenops minutus</i>	U	U		FM		MF	U		
<i>Sclerurus scansor</i>	U			FM		So	Te	AF	
<i>Sclerurus mexicanus</i>	S			FM		So	Te		
<i>Lochmias nematura</i>		S		FM	St	So	Te		
Dendrocolaptidae (7)									
<i>Dendrocincla turdina</i>	FC	U		FM		MF, So	M	AF	

Species	Abundance			Hab	Mic	Soc	FP	End	Thr
	Low	Mid	High						
Dendrocolaptidae (7) (cont.)									
<i>Sittasomus griseicapillus</i>	FC	FC	U	FM		So, MF	M		
<i>Xiphocolaptes albicollis</i>	FC	U	FC	FM, SG		So, MF	M		
<i>Dendrocolaptes platyrostris</i>		U		FM		So, MF	M		
<i>Lepidocolaptes squamatus</i>	S	U	S	FM		MF	M	AF	
<i>Lepidocolaptes fuscus</i>	FC	FC	FC	FM		MF	M	AF	
<i>Campylorhamphus falcularius</i>		U	S	FM		So, MF	M, U	AF	
Tyrannidae (53)									
<i>Phyllomyias burmeisteri</i>	S	S	S	FM, SG		So	Ca		
<i>Phyllomyias griseocapilla</i>			S	FM, SG		So	M	AF	NT
<i>Camplostoma obsoletum</i>	S			SG		So	Ca		
<i>Myiopagis caniceps</i>	U			FM, SG		So	Ca		
<i>Elaenia flavogaster</i>	S		S	SG		So	Ca		
<i>Mionectes rufiventris</i>	FC+	FC	U	FM		So, Gr	U, M	AF	
<i>Leptopogon amaurocephalus</i>	FC	C	S	FM, SG		So, MF	M		
<i>Phylloscartes eximius</i>			P	FM		So	M	AF	NT
<i>Phylloscartes sylviolus</i>	U			FM, SG		So	Ca, M	AF	NT
<i>Phylloscartes ventralis</i>		P		FM, SG		So	M		
<i>Phylloscartes paulistus*</i>	FC			FM		So, MF	M	AF	T
<i>Phylloscartes oustaleti*</i>		S		FM		So	Ca	AF	NT
<i>Capsiempis flaveola</i>	FC		S	SG	B	So	M		
<i>Myiornis auricularis</i>	U	U	S	FM, SG		So	U, M	AF	
<i>Hemitriccus diops</i>	P		FC	FM	B	So	M	AF	
<i>Hemitriccus orbitatus</i>	FC	FC		FM		So	M	AF	NT
<i>Hemitriccus nidipendulus*</i>	S			FM		So	M	AF	NT
<i>Hemitriccus furcatus*</i>	U			FM, SG	B	So	M	AF	T
<i>Todirostrum poliocephalum</i>	FC			SG		So	Ca	AF	
<i>Ramphotricon megacephala*</i>	S			FM	B	So	M		
<i>Tolmomyias sulphurescens</i>	FC	FC	U	FM, SG		MF, So	M		
<i>Platyrinchus mystaceus</i>	U	U		FM, SG		So	U		
<i>Platyrinchus leucorhynchus*</i>	S			FM		So	U	AF	T
<i>Myiobius barbatus</i>	FC			FM		So, MF	M		
<i>Myiophobus fasciatus</i>	S			SG		So	M, U		
<i>Contopus cinereus</i>	U			FM, SG		So	Ca		
<i>Lathrotriccus euleri</i>	U	FC	S	FM, SG		So	M		
<i>Cnemotriccus fuscatus</i>	S			FM		So	M		
<i>Knipolegus nigerrimus</i>			U	SG		So	Ca	AF	
<i>Knipolegus cyanirostris</i>	U	U	FC	SG		So	Ca		
<i>Colonia colonus</i>	FC			SG		So	Ca		
<i>Satrapa icterophrys*</i>	S			G		So	Ca		
<i>Hirundinea ferruginea</i>	U		U	SG		So	Ca		
<i>Machetornis rixosus</i>	S			G		So	Te		
<i>Muscipipra vetula</i>			U	FM, SG		So	Ca, A	AF	NT
<i>Attila rufus</i>	C	U	S	FM		So	Ca, M	AF	
<i>Attila phoenicurus</i>	P		P	FM, SG		So	Ca		
<i>Rhytipterna simplex</i>	U	U		FM		So	M, Ca		
<i>Myiarchus swainsoni</i>	U	U	U	SG, FM		So	Ca		
<i>Pitangus sulphuratus</i>	C			SG		So	Ca		
<i>Megarynchus pitangua</i>	FC			SG, FM		So	Ca		
<i>Myiozetetes similis</i>	U			SG		So	Ca		
<i>Myiodynastes maculatus</i>	C	S		SG, FM		So	Ca		
<i>Legatus leucophaeus</i>	FC			SG		So	Ca		
<i>Tyrannus savana</i>	S			SG		So	A		

Species	Abundance			Hab	Mic	Soc	FP	End	Thr
	Low	Mid	High						
Tyrannidae (53) cont.									
<i>Tyrannus melancholicus</i>	FC			SG		So	Ca		
<i>Pachyramphus viridis</i>	FC			FM, SG		So	Ca, M		
<i>Pachyramphus castaneus</i>	S			FM		MF	Ca		
<i>Pachyramphus polychopterus</i>	U			FM, SG		MF	Ca		
<i>Pachyramphus marginatus</i>	FC	S	U	FM, SG		MF	Ca		
<i>Pachyramphus validus</i>	FC			FM, SG		So	Ca		
<i>Tityra cayana</i>	U			SG		So	Ca		
<i>Tityra inquisitor</i>	U			SG		So	Ca		
Pipridae ³ (4)									
<i>Chiroxiphia caudata</i>	C+	C+	C+	FM, SG		Gr, So	M, U	AF	
<i>Illicura militaris</i>	P	S		FM		So	M	AF	
<i>Manacus manacus</i>	C			SG, FM		So, Gr	U, M		
<i>Schiffornis virescens</i>	U	C	FC	FM, SG		So	U	AF	
Cotingidae (6)									
<i>Laniisoma elegans</i>		S		FM		So	Ca		T
<i>Carpornis cucullatus</i>		C	C	FM		So	M, Ca	AF	NT
<i>Iodopleura pipra</i>	S			SG		So	Ca	AF	T
<i>Pyroderus scutatus</i>	S			FM		So	Ca	AF	
<i>Procnias nudicollis</i>	FC	U	FC	FM		So	Ca	AF	NT
<i>Oxyruncus cristatus</i>	U	C		FM, SG		So, MF	Ca		
Hirundinidae (4)									
<i>Progne chalybea</i>	S			SG		So	A		
<i>Notiochelidon cyanoleuca</i>	FC+	U+	U+	SG		Gr	A		
<i>Neochelidon tibialis</i>	U+			SG		Gr	A		
<i>Stelgidopteryx ruficollis</i>	FC+			SG		Gr	A		
Troglodytidae (2)									
<i>Thryothorus longirostris</i>	FC			SG		So	U		
<i>Troglodytes aedon</i>	FC			SG		So	U		
Muscicapidae									
Sylviinae (1)									
<i>Ramphocaenus melanurus</i>	U	U		SG		So	U, M		
Turdinae (4)									
<i>Platycichla flavipes</i>	FC	U	FC	FM, SG		So	Ca		
<i>Turdus rufiventris</i>	FC	U	U	SG, FM		So	Te, U		
<i>Turdus amaurochalinus</i>	U			SG		So	Te, U		
<i>Turdus albicollis</i>	C+	FC+	FC+	FM		So	U		
Vireonidae (2)									
<i>Cyclarhis gujanensis</i>	C	C	FC	FM, SG		So	M		
<i>Vireo chivi</i>	C			SG, FM		So	M, Ca		
Emberizidae									
Parulinae (4)									
<i>Parula pitiayumi</i>	FC	FC		FM		So, MF	M		
<i>Geothlypis aequinoctialis</i>	U			SG		So	M		
<i>Basileuterus culicivorus</i>	C	FC	C	FM, SG		So, MF	U, M		
<i>Phaeothlypis rivularis</i>	C			FM, SG	St	So	Te		
Coerebinae (1)									
<i>Coereba flaveola</i>	FC		S	SG, FM		So	M, Ca		
Thraupinae (21)									
<i>Hemithraupis ruficapilla</i>	U	U	U	FM, SG		MF	Ca	AF	
<i>Orthogonys chloricterus</i>	U+		S	FM, SG		Gr, MF	Ca	AF	
<i>Tachyphonus cristatus</i>	FC	S		FM, SG		MF	Ca		
<i>Tachyphonus coronatus</i>	U			FM, SG		So, MF	Ca	AF	
<i>Trichothraupis melanops</i>	FC	U		FM		MF, So	M		

Species	Abundance			Hab	Mic	Soc	FP	End	Thr
	Low	Mid	High						
Thraupinae (21) cont.									
<i>Habia rubica</i>	C	FC	U	FM, SG		MF	M, U		
<i>Ramphocelus bresilius</i>	FC			SG		So	U, M	AF	
<i>Thraupis sayaca</i>	FC	FC	U	FM, SG		So, MF	Ca		
<i>Thraupis ornata</i>	U			SG	So	Ca	AF		
<i>Thraupis palmarum</i>	U			SG		So, MF	Ca		
<i>Stephanophorus diadematus</i>			S	SG		So	Ca		
<i>Pipraeidea melanonota</i>	U	S		SG, FM		So	M		
<i>Euphonia violacea</i>	FC	S		FM, SG		Gr, MF	Ca		
<i>Euphonia cyanocephala</i>			U	SG		So	U, M		
<i>Euphonia pectoralis</i>	C	FC	S	FM, SG		MF, So	M, Ca	AF	
<i>Chlorophonia cyanea</i>	P			FM		So	M, Ca		
<i>Tangara seledon</i>	FC+	U+		FM, SG		MF	Ca	AF	
<i>Tangara cyanocephala</i>	FC+	U+		FM, SG		MF	Ca	AF	
<i>Tangara desmaresti</i>		U	U	FM		MF	Ca	AF	
<i>Dacnis cayana</i>	FC			FM, SG		MF	Ca		
<i>Chlorophanes spiza</i>	U			FM, SG		So	M, Ca		
Emberezinae (6)									
<i>Zonotrichia capensis</i>	U		U	SG		So	U, T		
<i>Haplospiza unicolor</i>	S			FM, SG		So	M	AF	
<i>Sporophila frontalis</i>	U			SG	B	So, Gr	M	AF	T
<i>Sporophila falcirostris</i>	U			SG	B	So	M	AF	T
<i>Sporophila caerulea</i>	U			G, SG		Gr, So	M		
<i>Tiaris fuliginosa</i>	FC			SG		So	U		
Cardinalinae (2)									
<i>Pitylus fuliginosus</i>	U	FC	FC	FM, SG		Gr, So	M	AF	
<i>Saltator similis</i>	FC		C	SG, FM		So	M		
Icterinae (4)									
<i>Psarocolius decumanus</i>	U			FM		So, Gr	Ca		
<i>Cacicus haemorrhous</i>	S			FM		Gr	Ca		
<i>Cacicus chrysopterus*</i>	S			SG		So	Ca		
<i>Molothrus bonariensis</i>	U			SG, G		Gr	Te		
Fringillidae (1)									
<i>Carduelis magellanica</i>	S			SG		Gr	M		
Estrildidae (1)									
<i>Estrilda astrild</i>	S+			G		Gr	Ca		

* Recorded during 1991 only (information for these species refers to that year only).

+ Five or more individuals recorded on a day.

¹ Also *Triclaria malachitacea* recorded on 24 October 1996.

² Includes both subspecies *Trogon surrucura surrucura* and *T. s. aurantius*.

³ Also *Neopelma aurifrons* recorded on 30 August 1997.

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