

Avian distribution in treefall gaps and understorey of *terra firme* forest in the lowland Amazon

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We compared the bird distributions in the understorey of treefall gaps and sites with intact canopy in Amazonian *terra firme* forest in Brazil. We compiled 2216 mist-net captures (116 species) in 32 gap and 32 forest sites over 22.3 months. Gap habitats differed from forest habitats in having higher capture rates, total captures, species richness and diversity. Seventeen species showed a significantly different distribution of captures between the two habitats (13 higher in gap and four higher in forest). Gap habitats had higher capture rates for nectarivores, frugivores and insectivores. Among insectivores, capture rates for solitary insectivores and army ant followers did not differ between the two habitats. In contrast, capture rates were higher in gaps for members of mixed-species insectivore flocks and mixed-species insectivore–frugivore flocks. Insectivores, especially members of mixed-species flocks, were the predominant species in gap habitats, where frugivores and nectarivores were relatively uncommon. Although few canopy species were captured in gap or forest habitats, visitors from forest mid-storey constituted 42% of the gap specialist species (0% forest) and 46% of rare gap species (38% forest). Insectivore, and total, captures increased over time, but did so more rapidly in gap than in forest habitats, possibly as a response to gap succession. However, an influx of birds displaced by nearby timber harvest also may have caused these increases. Avian gap-use in Amazonian *terra firme* forests differs from gap-use elsewhere, partly because of differences in forest characteristics such as stature and soil fertility, indicating that the avian response to gaps is context dependent.

The influence of treefall gaps on the distribution of tropical forest birds is expected to differ among forests (Schemske & Brokaw 1981, Levey 1988) depending on treefall frequency, distribution of gap sizes and regeneration time (e.g. Garwood *et al.* 1979), all of which are influenced by soil type, topography and climate (Hallé *et al.* 1978). In addition, the distinction between gap and forest understorey may be less pronounced in deciduous than in evergreen forests with denser canopies (Levey 1988). This may explain the higher proportion of avian habitat specialists (i.e. gap vs. understorey) found by Levey (1988) in a Costa Rican evergreen forest with dense canopy, in contrast to findings of

Schemske and Brokaw (1981) in a more deciduous Panamanian forest with a more sparse canopy. Also, canopy differences may have contributed to a greater abundance of fruit and frugivores in gaps than in forest understorey in the Costa Rican forest, vs. the Panamanian forest, where frugivore abundance was similar in gap and forest. In contrast, no gap species were encountered among the birds of a Puerto Rican evergreen forest with relatively low stature and few gaps (Wunderle *et al.* 1987). Thus, the role of treefall gaps in influencing avian distributions differs with forest type; however, the relative importance of the various factors responsible for differences in gap use are poorly understood due to a paucity of studies in different forest types.

The response of understorey birds to treefall gaps in Amazonian *terra firme* forests is expected to differ

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from responses found in Central American and Caribbean forests because of forest-specific environmental traits. For example, the relatively tall stature of *terra firme* canopy trees (30–50 m) may produce larger treefall gaps there than in forests of lower stature, such as those in which avian gap-use has been studied. Tall stature also enhances vertical stratification of the bird community (Terborgh 1980, Stiles 1983). In tall stature forests, canopy species forage over a narrow stratum of foliage and are less likely to move to ground level, even in gaps, than are mid-storey species that forage across a greater breadth of strata closer to the understorey (Walther 2002). In addition, the low incidence of flowering and fruiting in the understorey of Amazonian *terra firme* forests relative to the situation in other neotropical forests (Gentry & Emmons 1987) may make *terra firme* gaps especially important resource hotspots, differentially attracting nectarivores and frugivores, which are otherwise relatively rare in the understorey of these forests (Bierregaard 1990a, 1990b; Henriques *et al.* 2003). Finally, large mixed-species flocks of insectivores are characteristic of Amazonian forests (Bates 1863; Munn & Terborgh 1979), and are expected to congregate in gaps or gap edges that support dense foliage and vine tangles. These areas provide food and foraging substrates for leaf gleaning insectivores, a guild that constitutes a high proportion of the flock species (Munn & Terborgh 1979, Gradwohl & Greenberg 1980).

We compared avian distributions in treefall gaps and intact forest understorey of an Amazonian *terra firme* forest and compared the results with similar studies from other forest types. Our study was designed to answer a number of questions: (1) Are particular understorey species distributed differently in gaps and understorey of intact forest? (2) Do gaps have assemblages of birds that differ in composition, diversity, evenness or species richness from those in the forest understorey? (3) Are gap and understorey species found in other strata or habitats? (4) What is the source of rare species in the two habitats? (5) How does bird distribution in these two habitats vary with development over a short time period (approximately 2 years)? Because the core avifauna (*sensu* Remsen 1994) of *terra firme* forest in the Tapajós National Forest comprised 274 species (42% of these have been captured in understorey mist-nets; Henriques *et al.* 2003), this area presented an excellent opportunity for assessing how gaps contribute to avian diversity in a species-rich biota.

METHODS

Study area

This study was conducted in the Tapajós National Forest (henceforth Tapajós Forest), a 560 000-ha forest managed by the Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis. The Tapajós Forest is located near the mouth of the lower Tapajós River in the western part of the state of Pará. It is bounded by the Tapajós River to the west, the Santarém–Cuiabá Highway (BR-163) to the east and the Cupari River to the south (Fig. 1).

The climate, soils and vegetation of the Tapajós Forest are described in Silva *et al.* (1985), Daly and Prance (1989), Silva (1989) and Parrotta *et al.* (1995). Average annual rainfall is 1920 mm, with the heaviest rains from December to May and a short dry season (August to October) in which monthly precipitation is less than 60 mm. Average monthly temperatures vary from 24.3 to 25.8 °C.

Terra firme or dry land forest constitutes 33% of the Tapajós Forest. Here, trees grow on a low-fertility soil type known as Dystrophic Yellow Latosol (Silva 1989). Our study was conducted in the *terra firme* forest accessible at km 83 on the Santarém–Cuiabá Highway, where forest covers gently undulating upland terrain and is characterized by emergent tree species such as *Bertholletia excelsa*, *Couratari* spp., *Dinizia excelsa*, *Hymenaea courbaril*, *Manilkara huberi*, *Parkia* spp., *Pithecellobium* spp. and *Tabebuia serratiolia* (Silva *et al.* 1985). Canopy heights of the undisturbed forest range from approximately 30 to 40 m, with occasional emergent species reaching approximately 50 m. Palms are rare and the understorey is relatively open with frequent occurrence of shrubs *Rinorea flavescens*, *R. guianensis* and *Duguetia echinophora* (Silva 1989).

A system of roads and trails provides access to the forest at km 83. Here, our study occurred on a 5000-ha grid (3°21'21"S, 54°56'58"W) established for demonstration forestry. Netting was conducted in two adjacent 100-ha control blocks (C-2 and C-3). Each block was bounded by undisturbed *terra firme* forest on three sides, and a fourth side (north) adjoined a block subject to selective logging. Here, low impact selective logging (at approximately 40 m³/ha) continued through the study. Both control blocks were bisected by a small stream. All net sites in the blocks were situated at least 30 m from the stream and from the block border adjoining the selectively logged area.

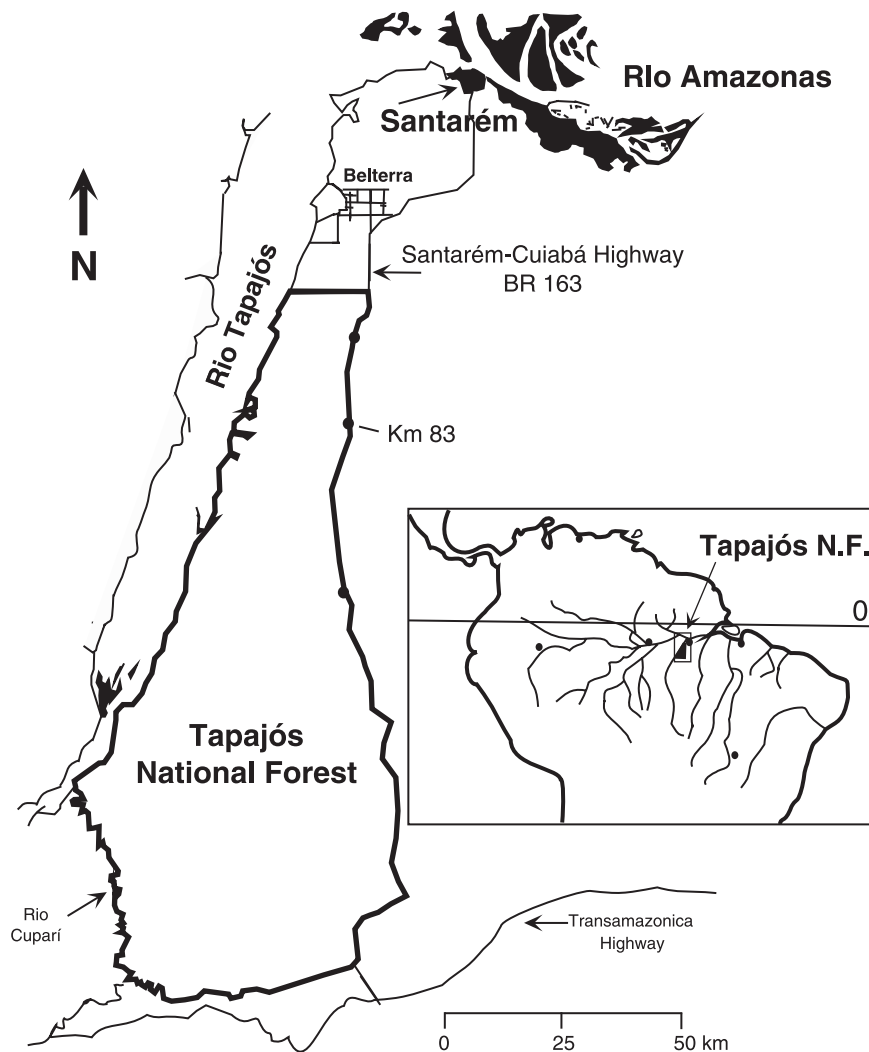


Figure 1. Location of the Tapajós Forest in Pará Brazil. The map from Henriques *et al.* (2003) shows km 83 along the Santarém–Cuiabá highway (BR-163) where the forest was entered to conduct the study.

Field methods

We sampled birds by using mist-nets to enable comparison with previous gap-use studies (Schemske & Brokaw 1981, Willson *et al.* 1982, Wunderle *et al.* 1987, Levey 1988). Use of mist-nets was justified in these studies because it allows similar and simultaneous sampling of numerous sites and avoids the difficulties of detecting and identifying birds by sight and sound. In addition, observers may differ in their field identification abilities and may easily miss species that rarely vocalize or are difficult to see. The use of mist-nets circumvents some of these problems and allows comparisons among studies in different forests by different

observers. Moreover, the method focuses on understorey birds, which is the group of birds most relevant for study. Mist-nets do not, however, obtain a random sample of bird species (see Karr 1981, Bierregaard 1990a, 1990b; Remsen & Good 1996). Because the effectiveness of mist-nets differs among species, it is wise only to compare capture rates within a species or within a group of behaviourally similar species (Karr 1981, Bierregaard 1990a, 1990b). We have previously discussed biases of netting in relation to the Tapajós *terra firme* forest (Henriques *et al.* 2003). In the present study, we interpret the results of mist-netting in relation to these biases and in light of knowledge of the avifauna obtained by field observations over a 9-year period.

Two different understorey forest habitat types were selected for net placement on the basis of physiognomies: natural treefall gap and undisturbed forest (henceforth gap and forest). A gap is 'a vertical hole in the forest extending through the canopy to within 2 m of the forest floor' (Brokaw 1982b). Forest sites were established under continuous forest canopy and initially located at least 25 m from the nearest gap. Two or more mist-nets (various combinations of 6-m or 12-m length nets) were set at each net site to provide a total length of 24 m. Nets were arranged in various configurations (e.g. at right angles, T-shaped, L-shaped or straight line) to fit within gaps; nets in forest sites were set to match these configurations. All nets were set to 2.6 m height and contained four shelves and 35-mm mesh.

Sampling occurred in two large blocks (1000 m × 1000 m). Each block was subdivided into four quadrats in which net sites were located to ensure adequate dispersion of sampling effort throughout a block. In each block, four pairs (gap and forest) of net sites were located within a quadrat. Sites were located at least 30 m apart, and distances between gap and forest within a pair were less than distances to other sites within a quadrat (total of 16 gap and 16 forest net sites per block; Fig. 2).

Birds were sampled during eight 2-day mist-netting sessions: 19–31 August 1999; 9–16 December 1999; 21–28 March 2000; 20–28 June 2000; 7–14 September 2000; 2–9 December 2000; 11–18 May 2001; and 12–18 June 2001. Although intervals between netting sessions were not equal (mean = 87 days ± 38 sd, range 25–153 days), we found no evidence for a relationship between capture rates and interval length ($r = -0.27$; $P = 0.55$), suggesting that learned net-avoidance did not interfere with capture rates, and indeed capture rates actually increased during the study.

During a session, nets at each site were opened in half of a block (eight gap and eight forest sites) for two consecutive days (06:00–14:00 h, day 1; 06:00–12:00 h, day 2) and operated simultaneously before moving to the other sites in the other half of the block. Thus a session involved 8 days to sample the two blocks, although netting days were not always consecutive. Open mist-nets were inspected at least every hour, and all captured birds, with the exception of hummingbirds, were ringed with a numbered aluminium ring or coloured plastic ring before release. We clipped a tail or wing feather of hummingbirds before release to identify recaptures during a netting session. All birds were identified to species; age and sex were determined when possible. New captures as

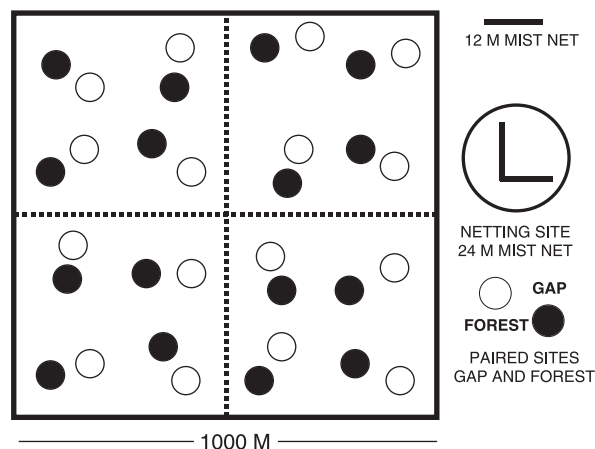


Figure 2. Schematic diagram showing arrangement of net sites in a 100-ha block of *terra firme* forest in the Tapajós Forest, Brazil. Sampling occurred in two 100-ha blocks. Each block was subdivided into four quadrats. Four pairs (gap and forest) of net sites were situated in each quadrat. Each net site contained 24 m of net set in various configurations, such as the L-shaped pattern shown in the diagram.

well as recaptures were recorded. Capture rates from gaps are interpreted as minimum values because gap nets were exposed to direct sunlight for much of the day, thereby reducing capture effectiveness relative to nets in the shaded forest understorey.

Foliage height profiles were used to quantify vegetation structure at the end of the study (June 2001), using a modification of the methods of Schemske and Brokaw (1981). Profiles at each of the 64 sites were obtained by establishing two parallel transects, one on each side of a net, situated 2 m from the net and equal in length to the sampled net. A 3-m pole (2.0 cm diameter) marked at 0.5-m intervals was placed vertically at each sample point (13 per transect). We recorded the presence or absence of foliage touching the pole within each height interval. For height intervals above 3 m, we sighted along the pole and recorded the presence or absence of foliage along the sight line of the pole and estimated height intervals. Height intervals above the ground (in metres) were: 0–0.5, 0.5–1, 1–2, 2–3, 3–4, 4–6, 6–8, 8–10, 10–12, 12–15, 15–20 and > 20. An estimate of percentage cover was based on these data for each height interval. Overall canopy cover was also obtained with a spherical densiometer held 1 m from the ground at each site in mid June 2001. Canopy cover was estimated in the four cardinal directions in the middle of each net, and an average percentage cover was calculated per site. Gaps were measured on 10–26 June 2001 and the area was calculated as

the maximum length (L) of the gap times the longest right-angle distance (W) across the opening (width).

Analysis

Capture rates are used as an index of abundance and presented as captures/1000 net hour, where net hour refers to 12 m of net open for 1 h. We excluded all recaptures of individuals during the same 2-day session, but included recaptures between sessions. Analysis of capture rates involved a doubly repeated-measures (time, eight sessions; habitat, forest vs. gap) ANOVA with a model II treatment factor (block). The ANOVAs were conducted for capture rate per site for particular species, as well as for diet guilds based on a previous ecological classification (Bierregaard 1990b, Henriques *et al.* 2003). Generally, P values without reference to a statistical test pertain to results of the repeated-measures ANOVA.

Guild classifications included both a simple and a complex categorization of species (Bierregaard 1990a, Henriques *et al.* 2003). Simple guilds included insectivores, frugivores and nectarivores. Complex guilds involved a subdivision of some of the simple guilds, and included army ant followers, solitary insectivores, solitary insectivore–frugivores, mixed-species insectivore flocks, mixed-species insectivore–frugivore flocks, solitary frugivores, solitary frugivore–insectivores, and mixed-species frugivore–insectivore flocks. The term solitary can refer to species in which pairs may forage together but do not join flocks.

For comparison with previous studies (i.e. Schemske & Brokaw 1981, Willson *et al.* 1982, Wunderle *et al.* 1987, Levey 1988), we conducted chi-squared tests on capture numbers to assess differences between gap and forest. This analysis runs the risk of bias and a false conclusion that habitat differences exist if a few nets dominate the total captures and skew the results (Hurlbert 1984). Moreover, combining recaptures from all sessions results in lack of independence in the data and disregards the nature of pairing gap and forest sites. These are not problems for the repeated-measures ANOVA, but we provide results from both tests and note discrepancies when they exist.

In general, we estimated parametric values (i.e. means and standard errors) for each of a number of biodiversity indices using a bootstrap approach (Manly 1991) written in Matlab (Mathworks 1995). Biodiversity measures included Camargo's (1993) index of evenness, Shannon's index of diversity (Pielou 1975), Berger and Parker's (1970) index of dominance, species richness (i.e. cumulative number of

unique species), and rarity (i.e. the number of species with a relative frequency of capture less than the inverse of species richness; Camargo 1993, Gaston 1994). The Berger-Parker Index was scaled by calculating its inverse to ensure that large values of all indices represented high levels of biodiversity (Stevens & Willig 2000). Simulations for estimating parameters of biodiversity for gap and forest were conducted by randomly selecting N individuals, with replacement, from a universe defined by the corresponding species abundance distribution separately for gap and forest. N was equal to the total number of individuals in net samples from a particular habitat type, and each of the four indices of biodiversity was calculated on the basis of these data. This process was iterated 1000 times, followed by calculation of the mean, median and standard error for each index in each habitat type.

A t -test was used to evaluate the significance of the difference in mean gap area between the two blocks. Row $\times$ column tests of independence (G -statistic) were used to compare the distribution of species or individuals among guilds between gap and forest. A chi-squared goodness of fit test was used to evaluate whether gap and forest sites had an a priori 50 : 50 distribution of captures for all species combined. A chi-squared contingency test assessed differences in species or guild composition between blocks and habitats. A Kolmogorov–Smirnov two-sample test was used to compare rank abundance distributions between habitats. Spearman rank correlation (r) was used to evaluate the association of capture rates (all species combined and individual species) with time. Statistical tests follow Sokal and Rohlf (1995) using SPSS (1990).

We tested whether the variation in foliage development differed among groups, defined by combinations of block and habitat type, by conducting Bartlett's test of homoscedasticity for each of five foliage height classes (percentage cover at 0–0.5 m, 0.5–1.0 m, 1.0–2.0 m, 2.0–3.0 m and 3.0–4.0 m) and at the level of the canopy (spherical densiometer reading). To assess whether mean differences in these same characteristics of vegetative structure differed with respect to habitat type and block, we conducted a repeated-measures ANOVA with block as a model II between-subjects treatment factor.

Terms

We follow Levey (1988) in the designation of habitat specialists. We use the terms 'gap specialist' or 'forest

specialist' to designate species that showed a statistically significant larger number of captures in a particular habitat. The term 'gap species' is used for a species with more total captures in gap than forest, and 'gap-only' species are taxa captured exclusively in gaps. 'Forest species' and 'forest-only' species were similarly defined. These terms do not imply that the species exclusively occurs in a single habitat. Note also that species are referred to by their scientific names throughout this paper.

Our habitat classification system for birds follows that of Cohn-Haft *et al.* (1997) and Henriques *et al.* (2003). Terrestrial birds are those that forage primarily on the ground. Understorey birds are species that forage mostly within 5 m of the ground in shrubs and small trees in closed canopy forest. Mid-storey birds generally forage above 5 m, but below the canopy.

RESULTS

Vegetation

As expected, the vertical distribution of foliage differed considerably between gap and forest (Fig. 3).

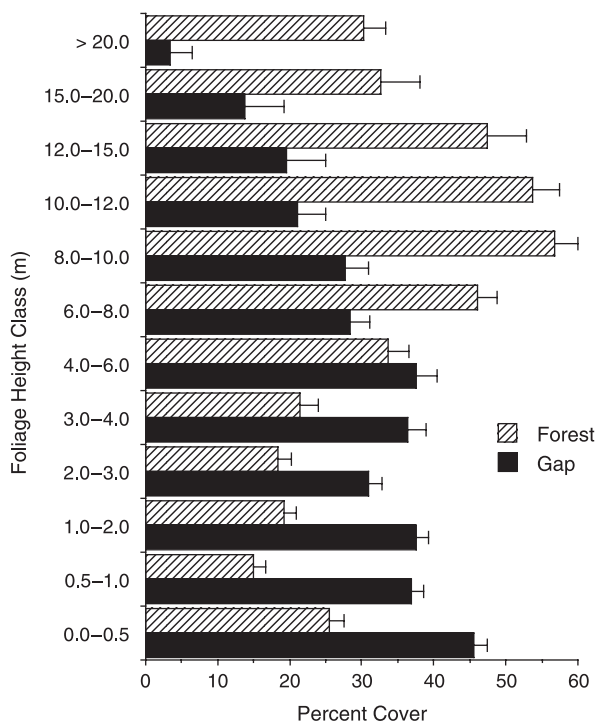


Figure 3. Foliage height profiles for 32 treefall gap and 32 forest net sites of *terra firme* forest in the Tapajós Forest, Brazil. Mean $\pm$ se are for percentage cover in each height class.

Most of the foliage in gaps occurred within 6 m of the ground. Foliage density was significantly greater in gap than forest at each of the height classes that spanned 0–4 m (0–0.5 m, $F_{1,30} = 45.96$, $P < 0.001$; 0.5–1.0 m, $F_{1,30} = 93.60$, $P < 0.001$; 1.0–2.0 m, $F_{1,30} = 35.12$, $P < 0.001$; 2.0–3.0 m, $F_{1,30} = 19.53$, $P < 0.001$; 3–4 m, $F_{1,30} = 29.58$, $P < 0.001$). In contrast, most of the foliage above forest nets occurred between 6 and 20 m. The denser canopy above forest nets was also reflected in a significant difference ($F_{1,30} = 104.76$, $P < 0.001$) in spherical densiometer readings (mean = $5.32\% \pm 0.23$ se of the canopy open above forest sites vs. mean = $12.43\% \pm 1.05$ se above gap sites). In addition, gap sites had greater relative variation among sites in canopy openness than did forest sites (gap CV = 34 vs. forest CV = 18). All but one measure of vegetation structure (i.e. foliage height density from 0.5 to 1.0 m) exhibited heteroscedasticity that at least approached significance ($P < 0.10$). In all cases, the variance among gap sites within blocks was greater than the variance among forest sites within blocks. In addition, all measures of vegetation structure differed between gap and forest sites in a consistent manner (i.e. a significant habitat effect in the absence of a habitat-by-block interaction). Although gaps differed in size from an estimated 65–700 m² (mean = $280 \text{ m}^2 \pm 37$ se) no significant ($t = 0.15$, $df = 30$, $P = 0.88$) difference in gap size existed between blocks (C-2, $286 \text{ m}^2 \pm 53$ se; C-3, $275 \text{ m}^2 \pm 52$ se).

Birds

In 14 336 net h during eight netting sessions over 22.3 months, we recorded 2216 captures representing 116 species in 25 families. We averaged 277 captures per session (range 196–368) with an average of 60 species per session (range 51–68). Of the 116 species captured, the five most common species (32% of captures) were the woodcreeper *Glyphorhynchus spirurus* (7.5%), the antwren *Myrmotherula longipennis* (7.0%), the woodcreeper *Dendrocincla merula* (6.5%), and the manakins *Pipra rubrocapilla* (5.6%) and *P. iris* (5.5%). Captures in gap and forest, as well as diet guild designation for each species, are given in the Appendix.

The total numbers of captures were significantly higher in gap than forest (1256 vs. 960, respectively, $\chi^2 = 39.3$, $df = 1$, $P < 0.001$). Total capture rates in gap and forest (Fig. 4) were dependent on time (T–H interaction, $F_{7,210} = 2.42$, $P = 0.021$), with gap capture rates during a netting session greater than (three sessions) or equal to (five sessions) those in forest

(i.e. positive synergism). Total capture rates increased over time in gaps ($r = 0.74$, $n = 8$, $P = 0.04$), but not in forest ($r = 0.31$, $n = 8$, $P = 0.46$). Temporal patterns of species richness in both habitats were almost identical to those of total capture rates (Fig. 4) and similarly displayed a significant time-by-habitat interaction ($F_{7,210} = 2.20$, $P = 0.04$, positive synergism). In addition, the species richness per session increased over time in gaps ($r = 0.81$, $n = 8$, $P = 0.015$), whereas no temporal pattern occurred in forest ($r = 0.31$, $n = 8$, $P = 0.46$). Diversity (H') per netting session was significantly ($F_{1,30} = 25.09$, $P < 0.001$) greater in gaps than forest, and diversity was affected consistently by time ($F_{7,210} = 4.72$, $P < 0.001$).

Species accumulation was most rapid in the first 100 captures in both gap and forest (Fig. 5). Accumulation of species in gaps surpassed those in forest after approximately 200 captures, and reached a plateau at approximately 80 species in the forest as compared with 107 species in gaps. The cumulative species curve for combined data from gap and forest rose most quickly prior to 100 species, but increased at a slow and constant rate through 116 species. The jackknife procedure based on sampling with replacement predicted a species richness of 93 and 75 species for gap and forest, respectively, assuming an infinite number of samples (Fig. 5).

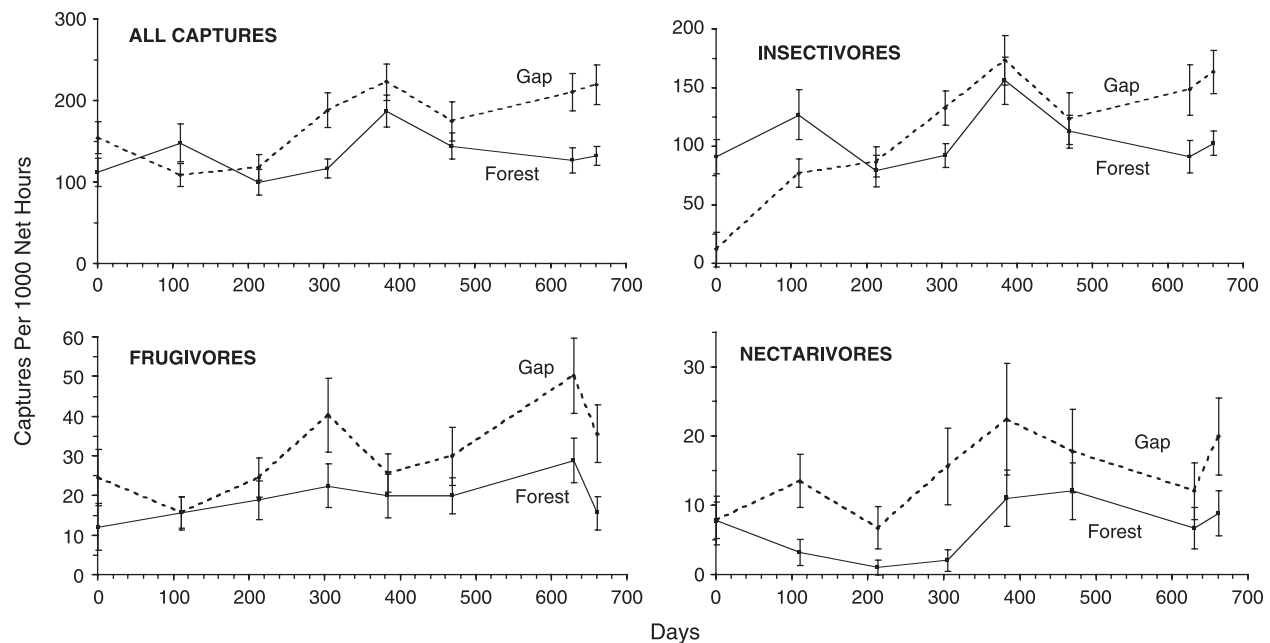


Figure 4. Mean ($\pm$ se) captures per 1000 net hours in gap and forest sites of *terra firme* forest in the Tapajós Forest, Brazil, during eight netting sessions from 19 August 1999 to 18 June 2001. Zero refers to the first netting session and median days are shown for each of the eight netting sessions. Capture rates during this period are shown for all captures, all insectivores, all frugivores and all nectarivores.

Habitat associations

Habitat associations were detected in 17 species (Table 1), and habitat had a consistent effect on the capture rates of 15 species (ANOVA, $P < 0.10$). In two other species (the antwren *Myrmotherula menetriesii*, and the tanager *Tachyphonus surinamus*) capture

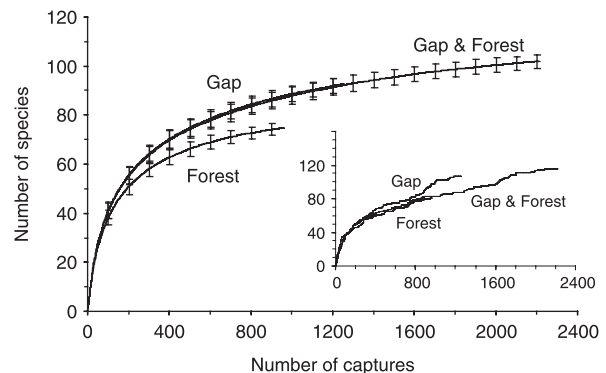


Figure 5. Species richness relative to the cumulative number of bird captures estimated from a jackknife procedure involving sampling with replacement for mist-net samples from gap and forest sites of *terra firme* forest of the Tapajós Forest, Brazil. The inserted graph shows the observed relationship of species richness and the cumulative number of captures from gap and forest nets. Error bars represent 1 se.

Table 1. Species of birds captured more frequently in gap or forest nets in *terra firme* forest in the Tapajós Forest, Brazil and their diet guild classification. Test statistics and *P*-values are provided for chi-squared test and repeated-measures ANOVA.

Species	No. of captures		Chi-squared		ANOVA		Complex diet guild ^a
	Gap	Forest	χ^2_1	<i>P</i> (chi-squared)	<i>F</i> _{1,30}	<i>P</i> (ANOVA)	
<i>Phlegopsis nigromaculata</i>	19	7	5.54	0.02	3.10	0.09	AA
<i>Pipra iris</i>	78	43	10.12	0.001	4.69	0.04	F
<i>Pipra rubrocapilla</i>	91	34	25.99	< 0.001	26.79	< 0.001	F
<i>Galbula cyanicollis</i>	6	0	6.00	0.01	7.11	0.01	I
<i>Hypocnemis cantator</i>	22	4	12.46	< 0.001	5.00	0.03	I
<i>Myrmotherula leucophthalma</i>	67	19	26.79	< 0.001	17.78	< 0.001	MFI
<i>Myrmotherula longipennis</i>	93	63	5.77	0.02	8.32	0.007	MFI
<i>Myrmotherula menetriesii</i>	22	3	14.44	< 0.001	7.98	0.008	MFI
<i>Thamnomanes caesius</i>	43	24	5.39	0.02	9.90	0.004	MFI
<i>Thamnophilus schistaceus</i>	21	2	15.70	< 0.001	9.16	0.005	MFI
<i>Tachyphonus surinamus</i>	16	0	16.00	< 0.001	5.35	0.03	MFIF
<i>Phaethornis longuemareus</i>	28	5	16.03	< 0.001	10.91	0.002	N
<i>Thalurania furcata</i>	33	15	6.75	0.009	6.50	0.02	N
<i>Dendrocincla merula</i>	57	88	6.63	0.01	5.85	0.02	AA
<i>Hylophylax poecilonota</i>	41	67	6.26	0.01	4.31	0.05	I
<i>Malacoptila rufa</i>	5	15	5.00	0.03	2.90	0.09	I
<i>Platyrinchus coronatus</i>	12	32	9.09	0.003	4.89	0.038	I

^aDiet guild based on classification in Henriques *et al.* (2003). AA = ant follower, F = solitary frugivore, I = solitary insectivore, MFI = mixed species flock insectivore, MFIF = mixed species flock insectivore frugivore, N = nectarivore.

rates in gaps were always greater than or equal to those in forest, but the magnitude of gap preference varied through time (T–H interaction, positive synergism). Generally, results of the repeated-measures ANOVA were consistent with those of the chi-squared analysis, although significance levels differed somewhat between the two tests (Table 1). Given the relative consistency of the two tests, we designated habitat specialists (i.e. gap specialists or forest specialists) as those species for which significance level was $P \leq 0.10$ and was less than 0.05 in at least one of the tests. Consequently, of 17 habitat specialists, 13 preferred gap and four preferred forest.

A minimum of six captures is required to detect a significant difference between gap and forest captures, assuming a 5% level of significance (Fisher exact test). Fifty-eight species met this criterion. Therefore we would expect 2.9 species ($58 \text{ species} \times 0.05$) to show differences in number of captures between gap and forest due to chance. From chi-squared analyses (Table 1), we found that 17 of the 58 species (29%) were captured more often ($P < 0.05$) in one habitat or the other (13 gap, four forest). This was significantly more than expected ($\chi^2 = 82.76$, $df = 1$, $P < 0.001$) from random effects (i.e. 2.9 species).

Seventy-two species were captured more frequently in gap than forest (gap species) vs. 28 species

captured more frequently in forest than gap (forest species), a significant difference from a 50 : 50 distribution of captures ($\chi^2 = 27.68$, $df = 1$, $P < 0.001$). Thirty-one species were captured only in gaps (gap-only species) vs. six species captured only in forest (forest-only), which also differed significantly from a 50 : 50 distribution of captures ($\chi^2 = 16.89$, $df = 1$, $P < 0.001$).

For a few species, the differences between gap and forest depended on block (block $\times$ habitat interaction). For instance, the hermit hummingbird *Phaethornis longuemareus* was captured only in gaps in control 2, but in both gaps and forest in control 3 (block $\times$ habitat, $F_{1,30} = 5.96$, $P = 0.02$). In contrast, captures were registered only in gaps for the antshrike *Thamnophilus aethiops* in control 3, but in both habitats in control 2 (block $\times$ habitat, $F_{1,30} = 8.24$, $P = 0.007$).

Affinities of habitat specialists and rare species

Habitat distributions of Tapajós birds were summarized in Henriques *et al.* (2003), facilitating an independent evaluation of the habitat breadth of captured species, as well as a determination of potential sources of rare species (Table 2). The 13 gap specialists occurred most frequently in forest understorey,

Table 2. Habitat associations of bird species cross-classified by affinity for gap or forest, in *terra firme* forest in the Tapajós Forest, Brazil. Percentages do not sum to 100 because a species may be typical of more than one habitat type. Habitats used by particular species are classified in Henriques *et al.* (2003). The terms 'gap specialist' or 'forest specialist' designate species that showed significantly more captures in a particular habitat (Table 1). The term 'gap species' refers to species with more total captures in gap than forest and 'forest species' refers to species with more total captures in forest than gap.

Classification	No. of species	Percentage					
		Terrestrial	Understorey	Midstorey	Canopy	Forest edge	Second growth
Gap specialists	13	8	69	46	0	23	54
Forest specialists	4	0	75	25	0	0	25
Gap species	72	7	56	46	11	15	22
Forest species	28	7	54	32	14	11	18
Gap rare species	79	11	44	46	15	13	13
Forest rare species	58	12	52	38	16	12	21

followed by mid-storey, second growth and forest edge. Forest specialists (four) were too rare or few to generalize regarding habitat associations. The distribution of gap species (i.e. gap > forest captures) and forest species (i.e. forest > gap captures) in other habitats is similar, with each group most typically found in the understorey, followed by mid-storey and second growth habitats, with least frequent occurrences of both groups in edge, canopy or terrestrial sites.

The distribution of habitat affinities of rare species (Table 2) captured in forest sites corresponded to the distribution of habitat affinities of those designated as forest species (i.e. forest > gap captures). However, less correspondence was found in the distribution of habitat affinities of rare species captured in gaps compared with gap species (i.e. gap > forest captures), at least for the percentage of species typical of the forest understorey (44.0% of rare gap species vs. 56.0% gap species) and typical of second growth (12.7% of rare gap species vs. 22.2% gap species).

Habitat associations by diet guild

Capture rates were significantly higher in gap than forest in three of the eight complex dietary guilds: solitary frugivores, nectarivores and mixed-species insectivore flocks (Fig. 6). No diet guilds had higher captures in the forest than in gaps.

Nectarivores: in general, nectarivores were captured more frequently in gaps than forest ($F_{1,30} = 17.76$, $P < 0.001$, Fig. 4). This bias was significant for the hummingbird *Thalurania furcata* and the hermit *Phaethornis longuemareus*, and approached significance ($F_{1,30} = 3.87$, $P = 0.06$) for the hermit *P. superciliosus*.

Nectarivores showed a significant ($F_{1,30} = 4.44$, $P = 0.04$) block-by-habitat interaction, in which preference for gaps was stronger in B2 than B3. Much of this interaction is attributable to captures of the hermit *Phaethornis longuemareus*, which exhibited a significant ($F_{1,30} = 5.96$, $P = 0.02$) B–H interaction.

Solitary frugivores: capture rates of solitary frugivores were significantly ($F_{1,30} = 15.63$, $P < 0.001$) higher in gaps than in forest as a result of the significantly higher gap capture rates of manakins (*Pipra iris* and *P. rubrocapilla*).

Solitary frugivore–insectivores: captures of solitary frugivore–insectivores did not differ significantly ($F_{1,30} = 1.09$, $P = 0.30$) between gap and forest.

Solitary insectivore–frugivores: captures of solitary insectivore–frugivores showed an inconsistent temporal pattern of response to the two habitats (Fig. 6) in which gap captures were greater than forest captures in three sessions, with the reverse occurring in four sessions (i.e. H–T interaction, negative synergism, $F_{7,210} = 2.06$, $P = 0.05$). This interaction is due mostly to captures of the flycatcher *Mionectes macconnelli*, in which the dominance of captures shifted between gap and forest in different netting sessions (H–T interaction, $F_{7,210} = 2.08$, $P = 0.05$).

Mixed-species insectivore–frugivore flocks: the significant habitat-by-time interaction ($F_{7,210} = 3.73$, $P = 0.001$, positive synergism) in this guild is mostly due to captures of the tanager *Tachyphonus surinamus* (Fig. 6).

Solitary insectivores: captures of solitary insectivores did not differ significantly ($F_{1,30} = 0.01$, $P = 0.91$) between gap and forest, although captures of some members of the guild differed significantly between habitats. For example, gap captures were significantly greater than forest captures for the jacamar

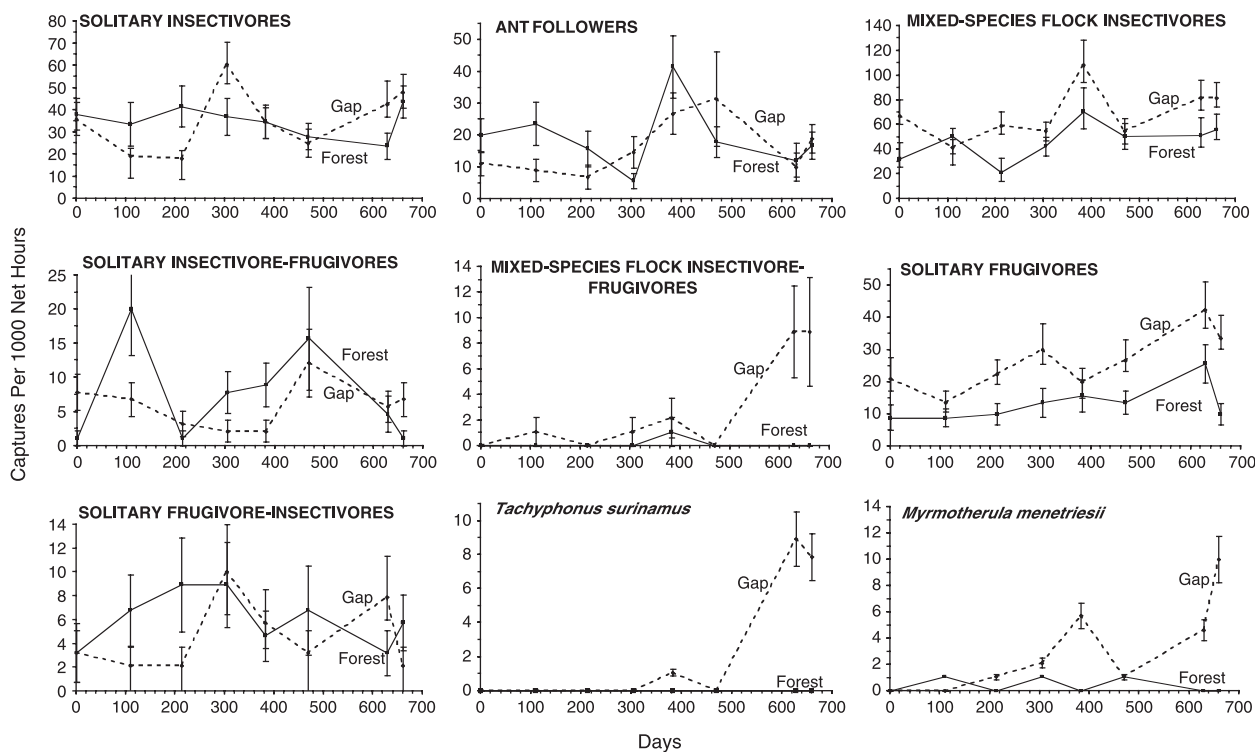


Figure 6. Mean ($\pm$ se) captures per 1000 net hours in gap and forest sites of *terra firme* forest in the Tapajós Forest, Brazil, during eight netting sessions from 19 August 1999 through 18 June 2001. Zero refers to the first netting session and median days are shown for each of the eight netting sessions. Capture rates during this period are shown for solitary insectivores, ant followers, mixed species flock insectivores, solitary insectivore–frugivores, mixed species flock insectivore–frugivores, solitary frugivores, solitary frugivore–insectivores, *Tachyphonus surinamus* and *Myrmotherula menetriesii*.

Galbula cyanicollis and the antbird *Hypocnemis cantator*, whereas forest captures of the antbird *Hylophylax poecilonota* were significantly greater than those in gaps. Interspecific heterogeneity of response to habitats resulted in no habitat association at the guild level.

Ant followers: although the number of captures of the ant-following guild did not differ ($F_{1,30} = 0.84$, $P = 0.37$) between gap and forest, the number of captures of the obligate ant-following woodcreeper *Dendrocincla merula* was significantly higher in forest than gaps. In contrast, captures of the antbird *Phlegopsis nigromaculata* were higher in gap than forest. Again interspecific heterogeneity in the habitat association diminished the strength of associations at the guild level.

Mixed-species flock insectivores: constituents of the mixed-species insectivore flock guild were captured significantly ($F_{1,30} = 21.90$, $P < 0.001$) more often in gaps than forest. A number of species (antshrikes *Thamnophilus shistaceus* and *Thamnomanes caesi*, and antwrens *Myrmotherula longipennis* and

M. leucophthalma) evinced this same pattern. In contrast, captures of the antwren *Myrmotherula menetriesii* showed a positive synergism between habitat and time. The number of gap captures increased more rapidly with time in gap compared with forest (Fig. 6). In general, block effects were rare in this guild and only the antshrike *Thamnophilus aethiops* showed a significant ($F_{1,30} = 8.24$, $P = 0.007$) habitat-by-block interaction in which all captures in block 3 were in gaps ($n = 9$), but most (4 of 5) captures in block 2 were in forest.

Relative abundance of diet guilds

Two gap specialists were frugivores, nine were insectivores and two were nectarivores (Table 1). The distribution of these gap specialists among diet guilds (15.4% frugivores, 69.2% insectivores, 15.4% nectarivores) was indistinguishable ($G = 0.15$, $df = 2$, $P = 0.93$) from the distribution of other species with six or more captures (12.0% frugivores, 79.0% insectivores, 9.0% nectarivores). Similarly, the representation of

diet guilds for the 72 species captured only in gaps (13.9% frugivores, 73.6% insectivores, 12.5% nectarivores) did not differ significantly ($G = 0.01$, $df = 2$, $P = 1.0$) from the guild representation of 28 species captured only in the forest (14.3% frugivores, 82.1% insectivores, 3.6% nectarivores). Finally, the representation of diet guilds for all species captured in gaps ($n = 108$ species, 12.0% frugivores, 78.7% insectivores, 9.3% nectarivores) did not differ significantly ($G = 0.26$, $df = 2$, $P = 0.88$) from the distribution for all species captured in forest ($n = 83$ species, 14.5% frugivores, 77.1% insectivores, 8.4% nectarivores). Thus the simple guild structure in gaps did not differ from that in forest.

The distribution of captures differed significantly between gap and forest. For example, the representation of the three simple dietary guilds differed significantly between gap and forest ($G = 15.39$, $df = 2$, $P < 0.001$). Gap ($n = 1255$) differed from forest ($n = 960$) in having higher proportions of frugivores (17.6 vs. 14.4%) and nectarivores (8.3 vs. 5.0%), but a lower proportion of insectivores (74.1 vs. 80.6%). For the eight complex dietary guilds, representation differed significantly between gap and forest ($G = 148.48$, $df = 7$, $P < 0.001$). Gap captures ($n = 1255$) differed from forest captures ($n = 960$) in having higher proportions of mixed-species insectivore flock members (40.4 vs. 33.5%), frugivores (15.5 vs. 9.9%), nectarivores (8.6 vs. 5.0%), and mixed-species insectivore–frugivore flock members (1.6 vs. 0.1%), but lower proportions of ant followers (9.4 vs. 14.3%), solitary frugivore–insectivores (2.7 vs. 4.5%), solitary insectivores (21.5 vs. 27.1%), and solitary insectivore–frugivores (0.0 vs. 5.6%).

Diversity

Bird assemblages in gap and forest differed with respect to several measures of diversity, as indicated by non-overlapping 95% confidence intervals from bootstrap simulations (Table 3). For instance, gaps had greater richness and diversity and more rare species (79 species vs. 58 species) than did forest. The prevalence of rare species in gaps relative to the forest was also evident in rank abundance distributions, which differed significantly between habitats (Kolmogorov–Smirnov test, $Z = 1.701$, $n = 114$, $P = 0.006$).

Time effects

Capture rates varied, but increased from the first netting session in August 1999 (130 captures/1000

Table 3. Bootstrap estimates of bird species richness, Camargo's index of evenness, Shannon's index of diversity, Berger–Parker index of dominance (scaled) and rarity, based on mist-net samples in gap and forest sites in *terra firme* forest in the Tapajós Forest, Brazil.

		Bootstrap estimates			
Measures	Empirical index	Mean	Median	Lower 95% CI	Upper 95% CI
Forest					
Richness	83	74.80	75	70	78
Evenness	0.37	0.39	0.39	0.37	0.41
Diversity	3.69	3.64	3.64	3.56	3.71
Dominance	10.91	10.57	10.61	8.89	12.31
Rarity	58	53	53	49	59
Gap					
Richness	108	92.56	93	87	98
Evenness	0.33	0.37	0.37	0.34	0.39
Diversity	3.84	3.79	3.79	3.73	3.85
Dominance	13.48	12.80	12.80	11.00	14.58
Rarity	79	66.46	66	60	73

net h) through June 2001 (180 captures/1000 net h). Time had a significant effect on capture rates of several diet guilds including all frugivores ($F_{7,210} = 3.54$, $P = 0.001$), solitary frugivores ($F_{7,210} = 3.99$, $P < 0.001$), nectarivores ($F_{7,210} = 2.18$, $P = 0.04$), solitary insectivores ($F_{7,210} = 2.86$, $P = 0.007$), ant followers ($F_{7,210} = 3.29$, $P = 0.002$), mixed-species flock insectivores ($F_{7,210} = 4.68$, $P < 0.001$) and mixed-species flock insectivore–frugivores ($F_{7,210} = 3.66$, $P < 0.001$). Captures increased with time in at least one habitat for several guilds including: all frugivores (gaps, $r = 0.77$, $n = 8$, $P = 0.03$), solitary frugivores (gaps, $r = 0.74$, $n = 8$, $P = 0.04$; forest, $r = 0.66$, $n = 8$, $P = 0.08$), mixed-species flock insectivores (forest, $r = 0.69$, $n = 8$, $P = 0.06$), and mixed-species flock insectivore–frugivores (gaps, $r = 0.68$, $n = 8$, $P = 0.06$). Captures of all insectivores (Fig. 4) were dependent on time (T–H interaction, $F_{7,210} = 2.33$, $P = 0.03$), with gap capture rates during a netting session greater (six sessions) or less (two sessions) than those in forest (i.e. positive synergism). Capture rates of all insectivores increased over time in gaps ($r = 0.81$, $n = 8$, $P = 0.02$). Time had a significant effect on capture rates of 13 species, most of which increased during the study (Table 4).

Block effects

Few significant block effects were found, and none was evident for total captures, species richness or diversity. Of the diet guilds, a block effect ($F_{1,30} =$

Table 4. Species that showed a significant change in capture rates over eight netting sessions in gap or forest sites of *terra firme* forest in the Tapajós Forest, Brazil. Spearman rank correlation between capture rates and time are shown for gap and forest separately. Test statistics and *P* values are shown for a repeated-measures ANOVA in which a consistent effect of time or positive time by habitat interaction (*Myrmotherula menetriesii*, *Tachyphonus surinamus*) occurred.

Species	<i>r</i>		ANOVA	
	Gap	Forest	$F_{7,210}$	<i>P</i>
<i>Dichrozona cincta</i>	0.44	-0.15	2.23	0.030
<i>Dendrocincla merula</i>	0.53	-0.10	3.87	0.001
<i>Geotrygon montana</i>	0.30	0.09	2.49	0.020
<i>Hylophylax poecilonota</i>	0.34	-0.04	2.91	0.006
<i>Myiobius barbatus</i>	0.12	0.72*	3.60	0.001
<i>Myrmotherula leucophthalma</i>	0.55	0.43	3.66	0.001
<i>Myrmotherula longipennis</i>	0.55	0.46	3.90	0.001
<i>Myrmotherula menetriesii</i>	0.84**	-0.17	2.84	0.008
<i>Phaethornis superciliosus</i>	0.73*	0.11	2.44	0.020
<i>Phlegopsis nigromaculata</i>	0.24	0.29	2.41	0.020
<i>Pipra iris</i>	0.25	0.42	1.82	0.040
<i>Pipra rubrocapilla</i>	0.88**	0.49	2.97	0.005
<i>Tachyphonus surinamus</i>	0.76*	0.00	4.27	< 0.001

* $P \leq 0.05$; ** $P < 0.01$.

4.25, $P = 0.05$) only occurred for nectarivores, and specifically for the hermit hummingbird *Phaethornis superciliosus* ($F_{1,30} = 4.12$, $P = 0.05$). Block effects also occurred in the captures of two insectivores (the flycatcher *Attila spadiceus*, $F_{1,30} = 5.00$, $P = 0.03$; the antwren *Myrmotherula longipennis*, $F_{1,30} = 6.50$, $P = 0.02$) and a frugivore (the manakin *Pipra iris*, $F_{1,30} = 8.20$, $P = 0.008$). In contrast to capture rates, blocks differed in species composition of gaps ($\chi^2 = 78.32$, $df = 33$, $P < 0.001$) and of forest ($\chi^2 = 66.06$, $df = 33$, $P < 0.001$). Differences between blocks also occurred with respect to the composition of simple ($\chi^2 = 16.74$, $df = 3$, $P < 0.001$) and complex ($\chi^2 = 28.73$, $df = 8$, $P < 0.001$) guilds in gaps, but not in forest (simple, $\chi^2 = 0.717$, $df = 3$, $P = 0.717$ and complex, $\chi^2 = 5.101$, $df = 8$, $P = 0.747$).

DISCUSSION

A non-random distribution of captures between the understoreys of treefall gaps and intact forest was expected for some bird species, given differences between gap and forest in vegetation structure and plant species composition (Brokaw 1982a, 1985), detritus (Whitmore 1978), microclimate (Hallé *et al.* 1978, Chazdon & Fetcher 1984) and productivity (Hallé *et al.* 1978). Birds may respond to these dif-

ferences, particularly if they result in variation in food resources (e.g. Blake & Hoppes 1986, Martin & Karr 1986, Levey 1988) and microclimate (Karr & Freeman 1983). Indeed, 29% of 58 species in the Tapajós Forest with adequate sample size ($n \geq 6$) corroborated this expectation. However, 29% is somewhat low compared with the range (16–71%) from previous studies (Table 5). This suggests that for many Amazonian species, the environmental contrast between *terra firme* habitats may not have been as great as in Costa Rica (45%) or Puerto Rico (71%). Alternatively, species with strong habitat associations may be rare in the Tapajós Forest.

Of the species in *terra firme* forest that showed a non-random distribution of captures between habitats, the majority (76%) were captured more frequently in gap than forest sites. This is consistent with previous findings (Table 5). In addition, as evident in both Panama and Costa Rica, species exclusive to one habitat (i.e. gap only or forest only) and species with more captures in one habitat than the other (i.e. gap species or forest species) showed a gap bias in captures. Moreover, species richness at net level was higher in gap than forest, a difference observed in most other studies.

Gaps compared with intact forest had higher total capture rates, as well as higher capture rates for each of the simple diet guilds. The attractiveness of gaps compared with understorey has been attributed to the presence of more 'edge' habitat, more foliage at net level and higher productivity of gaps (Schemske & Brokaw 1981). Higher productivity in the understorey of gaps than in the intact forest could result in productivity hotspots, similar in function to islands of fertility in some deserts (Charley & West 1975). These productivity hotspots may be especially evident on low fertility soils of *terra firme* forests such as those of the Tapajós, where the heavily shaded understorey may further limit flowering and fruiting. Here the higher productivity of gaps, relative to the surrounding forest understorey, may result in even greater clumping of food resources to which birds are attracted (e.g. Blake & Hoppes 1986, Martin & Karr 1986, Feinsinger *et al.* 1988, Levey 1988), resulting in local hotspots of activity and biodiversity.

Distribution of foraging guilds

Flowers and fruits appeared to be more common in gaps than understorey, but both were relatively scarce (J.M.W. pers. obs.), as also observed in *terra firme* forest north of Manaus (Gentry & Emmons

Table 5. Summary of avian gap studies based on mist netting in tropical forests including this study (Tapajós) and studies in Panama (Limbo Hunt Club; Schemske and Brokaw, 1981); Costa Rica (La Selva; Levey, 1988), and Puerto Rico (El Verde; Wunderle *et al.* 1987).

Trait	Tapajós	Limbo Hunt Club	La Selva	El Verde
Mean Gap Size (m ²)	280	130	>89 ¹	117
Total Species in Gap Captures	107	66	77	10
Total Species in Forest Captures	81	53	60	11
Total Captures Gap	1256	409	997	112
Total Captures Forest	960	417	63	69
Percent Species Nonrandom Distribution ²	29% (17/58)	16% (5/31)	45% (19/42)	71% (5/7)
Percent gap specialists ³	76%	60%	89%	57%
Percent gap species ⁴	72% (72/100)	67% (42/63)	71% (55/77)	43% (6/14)
Percent gap only species ⁵	84% (31/37)	73% (19/26)	72% (28/39)	50% (3/6)
Diet Guilds of Gap Specialists				
Frugivores	15.4% (2/13)	20% (1/5)	58% (10/17)	20% (1/5)
Nectarivores	15.4% (2/13)	20% (1/5)	23.5% (4/17)	40% (2/5)
Insectivores	69.2% (9/13)	60% (3/5)	17.6% (3/17)	40% (2/5)

¹Gap size not given, but greater than gap mean of 89 m² at La Selva (Levey 1988).

²Percentage of species with sufficient sample size ($n \geq 6$ captures, Fisher exact test) that showed a nonrandom distribution of captures between gap and forest.

³Percentage of birds with a nonrandom distribution that showed a gap bias in captures.

⁴Percentage of species with more captures in gaps than forest. Basis of the percentage is the total number of species that had more captures in one of the habitats (gap or forest).

⁵Percentage of species captured only in gaps. Basis of the percentage is the total number of species that were captured in only one habitat.

1987). This scarcity may be a reason for the low relative abundances of nectarivores and frugivores in samples from Manaus (Bierregaard 1990b) and Tapajós (Henriques *et al.* 2003). Although capture rates of nectarivores and frugivores were each higher in gaps than forest, differences in their respective relative abundances between the two habitats were low. Even in gaps, where they were expected to be relatively abundant, nectarivores and frugivores each comprised only 15% of the gap-specialist species. The relative abundances of nectarivores and frugivores in gaps occurred within the low range of values from similar studies (Table 5).

As in other tropical forests (e.g. Karr *et al.* 1990), insectivores constituted the predominant foraging guild based on species richness and captures in either gap or forest habitats. However, capture rates for all insectivores were higher in gap than forest sites. Much of this may be attributable to the dense foliage in gaps and the shift in foliage to lower strata, which provides a substrate on which to glean prey, as well as perches for aerial sallying. Nevertheless, not all insectivores showed equivalent habitat associations, as evident when subdivided into guilds based on sociality and presence of fruit in the diet.

Mixed-species flocks of insectivores are the most conspicuous group of birds in the Tapajós Forest (Henriques *et al.* 2003), as well as the predominant

guild in gap and forest habitats. The guild's size is influenced by inclusion of species that only occasionally join flocks (facultative members), in addition to obligate or core species. Although the most dominant guild in both gap and forest habitats, members of mixed-species insectivore flocks were captured at a higher rate and had a higher relative abundance in gap than in forest sites. The concentration of members of mixed-species insectivorous flocks in gap or gap edges has been observed previously (e.g. Munn & Terborgh 1979), especially in disturbed sites with vine tangles (Gradwohl & Greenberg 1980) or small perches (Buskirk 1969).

Foliage-gleaning insectivores of the forest understorey generally forage in larger groups than do species that forage on other substrates or use different capture manoeuvres, many of which forage singly or in pairs (Greenberg & Gradwohl 1985). Foliage gleaners, such as many antwrens (*Myrmotherula* spp.), are core members of mixed-species flocks and commonly glean insects from foliage, stems or vine tangles (Gradwohl & Greenberg 1980). Antwrens were among the most frequently captured birds in gaps, where their captures surpassed those in the understorey. In addition, two rare antwren species (*M. axillaris* and *M. ornata*) were caught only in gaps. Although not as abundant in Costa Rican gaps as in *terra firme* gaps, two other antwren species also

showed a gap bias in captures in Costa Rica (Levey 1988).

The presence of a nuclear species (the antshrike *Thamnomanes caesi*) in gaps or gap edges may contribute to the attractiveness of gaps to insectivores in mixed-species flocks. As a nuclear species (*sensu* Moynihan 1962), *T. caesi* plays an important role in attracting other insectivores and directing flock movements (Powell 1985, Stotz 1993). The more frequent capture of *T. caesi* in gap than forest suggests its prevalence at net level in gaps. This antshrike's conspicuous movements and vocalizations at net level probably attracted other insectivores, increasing the probability of capture in gaps. However, when foraging in the forest, *T. caesi* occurred mostly in the foliage of the mid-canopy, just above the nets, where it may have attracted flock members to this vertical stratum, reducing the likelihood of capture in understorey nets.

Other insectivore guilds such as solitary insectivores, ant followers and insect-frugivores did not differentiate between gap and forest, although some constituent species showed non-random distributions of captures between the two habitats. For example, although ant-following birds may occur in second-growth habitats (Borges & Stouffer 1999) and were captured in gap and forest alike, species differed in gap use, possibly in relation to differences in foraging mode and vegetation structure. The denser vegetation of gaps may hinder movement and foraging of the ant-following woodcreeper *Dendrocicla merula*. This may explain the forest bias in captures of this species, as it requires an open area of ground around vertical trunks and saplings to which it clings before darting to the ground to capture prey. In contrast, the denser gap vegetation did not deter antbirds that perch on smaller stems, such as *Rhematorhina gymnops* (captured in both habitats) and *Phlegopsis nigromaculata* (captured mostly in gaps).

Change in captures over time

Gap vegetation undergoes rapid development, at least in the early seres (e.g. an estimated 4 years after formation, Fraver *et al.* 1998). Consequently, some bird species might respond to these changes, even within the 2-year duration of our study. Consistent with this was our finding that captures of all insectivores and total captures increased over time, but did so more rapidly in gap than forest habitats. In addition, two species (antwren *Myrmotherula menetriesii*, tanager *Tachyphonus surinamus*) exhibited increases

in captures in gaps over time, while remaining unchanged in abundance in forest.

Increases in captures over time may have resulted from an influx of birds that were displaced by selective logging activities from adjacent forest. Such pulses in local avian abundance have occurred in Amazonian fragments as adjacent forest was cleared (Bierregaard & Lovejoy 1989, Bierregaard 1990a). Supporting the influx hypothesis is our finding that most species with capture rates that changed showed increases with time. In addition, two forest specialists (e.g. woodcreeper *Dendrocicla merula*, antbird *Hylophylax poecilonota*) increased during the study, as might be expected from an influx of displaced forest birds. It is difficult to distinguish between increases in captures due to local changes (e.g. succession in gaps) or events that transpired in the surrounding area of the study (e.g. nearby timber harvest).

Contribution of canopy and mid-storey birds to gaps

In some tropical forests, canopy species follow the contour of the canopy as it descends to the ground in gaps (Orians 1969, Pearson 1971, Greenberg 1981). These species forage in the foliage–air interface, a boundary where direct sunlight first strikes vegetation. As an area of high resource concentration, this interface is an important foraging zone (Stiles 1979, 1983), which if followed from canopy to gap by many taxa could account for a high proportion of gap specialist species (e.g. Wunderle *et al.* 1987). However, none of the gap specialists occurs in the Tapajós canopy.

Similar to results from our study, canopy species were relatively rare among gap species in lowland forests in Panama (Schemske & Brokaw 1981) and Costa Rica, where 24% of the gap specialists also occurred in the canopy (Levey 1988). The prevalence of canopy species at net level in gaps, however, depends on forest type (Wunderle *et al.* 1987, Levey 1988). For instance, canopy dwellers predominated in gaps in an evergreen forest in the hurricane belt where tree height was relatively low (20–24 m), gaps were rare and understorey gap specialists absent (Wunderle *et al.* 1987). Moreover, gap frugivores in montane forest in Costa Rica may spend most of their time in the canopy consuming fruit, thereby obscuring the distinction between gap and canopy species (P. Feinsinger and K.G. Murray pers. comm. cited in Levey 1988). Nevertheless, for the continental lowland tropical forests studied so far, gap specialists

are mostly birds of low vegetation levels, a few of which may follow the foliage–air contour into the canopy, rather than being canopy dwellers that follow the contour into gaps.

We found that 46% of gap specialists and 46% of gap species also occurred in the forest mid-storey. The mid-storey's proximity to the ground and the greater breadth of strata used by mid-storey birds, compared with canopy dwellers (Walther 2002), increases the likelihood of mid-storey birds straying into gaps and forest understorey. Moreover, mid-storey birds may shift downwards at midday (Pearson 1971, 1977, Walther 2002), increasing the likelihood of capture. Some descending mid-storey birds may avoid the relatively open forest understorey with its limited cover, but follow the more dense foliage of the gap edge to net level. This may be the response of gap specialists such as members of mixed-species insectivore flocks (i.e. *Myrmotherula leucophthalma*, *M. menetriesii*, *Thamnomanes caesioides*) and members of mixed-species insect–frugivore flocks, such as the tanager *Tachyphonus surinamus*. The manakin *Pipra rubrocapilla* behaved similarly, except that displays by males suggest that the mid-storey may be used primarily for leks, with gaps used as foraging areas (L.M.P.H. & J.M.W. unpubl. obs.).

Rare species

As in previous netting studies in tropical forests (e.g. Karr *et al.* 1990) most species in samples were rare. The distribution of rare species was not homogeneous with respect to gap and forest sites. Gaps harboured more rare species than did forest (79 vs. 58). This was reflected in the higher diversity, greater evenness and lower scaled dominance in gaps compared with forest. The greater number of rare species in gap than forest may reflect the greater within-habitat variability of gaps than forest sites. However, some species may be rare because mist-nets do not capture a representative sample of the bird community (e.g. Karr 1981, Bierregaard 1990a, 1990b; Remsen & Good 1996). We have previously estimated that approximately 37% of rare species in understorey of *terra firme* forest were rare due to sampling bias associated with mist-netting (Henriques *et al.* 2003).

Gap size

Size, in addition to stage of succession, is an important factor for attracting gap specialists. For example, large gaps may be more attractive than small gaps to

fruit-eating species because of higher densities of fruiting plants in large gaps (Levey 1988). The inclusion of larger treefall gaps might have resulted in the identification of additional gap specialists. For instance, likely additions to the list of gap species include the finch *Arremon taciturnus* and the grosbeak *Cyanocopsa cyanooides*, which were observed most frequently in larger gaps (J.M.W. unpubl. obs.). *C. cyanooides* is a gap specialist in Panama (Schemske & Brokaw 1981), and a congener to the finch *A. aurantirostris* that is a gap specialist in Costa Rica (Levey 1988). Finally, the number of canopy species using gaps may increase as gap size increases as observed for the flycatcher *Tyrannopsis luteiventris* (L.M.P.H. & J.M.W. unpubl. obs.).

The relative scarcity of forest understorey specialists in this and previous studies may be due to small sample sizes and low power. However, these factors alone may not fully explain the relative rarity of forest understorey specialists that avoid treefall gaps. For many understorey species in intact forests, treefall gaps or at least gap edges may not be avoided regularly over the range of gap sizes studied by us. All of the Tapajós understorey specialists had at least some captures in gaps. The flycatcher *Platyrinchus coronatus* was the only understorey specialist that occurred in Central American sites, although it was absent from gaps in Costa Rica (Levey 1988). Avoidance of gaps by understorey species probably increases with increasing gap size, at least at the early stages of gap succession, given the reluctance of many forest understorey birds such as ant followers (i.e. some antbirds and woodcreepers) to cross open areas (e.g. Willis & Oniki 1978). However, after only a few years of plant succession (e.g. 5 years), ant followers may move through previously open areas (Stouffer & Bierregaard 1995).

Gap specialist birds

Twenty-one species (8% of the 274 species of the core avifauna of the Tapajós *terra firme* forest; Henriques *et al.* 2003) are gap species. This estimate is based on the 13 species captured more frequently in gap than forest habitats (i.e. gap specialists), as well as the antshrike *Thamnophilus aethiops* in which a block $\times$ habitat interaction indicated a gap bias in one of two blocks. Several other species that were represented poorly in net samples also occurred in gap or gap edge, including the antbirds *Cercomacra nigrescens* and *Myrmeciza hemimelaena*, the antpitta *Myrmothera campanisona*, the flycatcher *Myiozetetes*

luteiventris, the gnatcatcher *Ramphocaenus melanurus*, the finch *Arremon taciturnus*, and the grosbeak *Cyanocopsa cyanoides* (L.M.P.H. & J.M.W. unpubl. obs.). No gap species in the Tapajós *terra firme* forest are exclusive to treefall gaps.

Contribution of gaps to avian diversity in forests

The distribution and diversity of birds in tropical forests is influenced by the heterogeneity of structures and resources associated with treefall gaps. However, as indicated by differences in avian gap-use among various neotropical forests, the avian response to gaps is dependent on context. For instance, the tall stature of *terra firme* forest results in greater vertical stratification of the bird community, which may result in the relative rarity of canopy species in gaps. The larger average area of gaps in tall stature *terra firme* forest compared with those in other forests presumably contributed to the capture of more gap specialist species than found in most other studies. Nonetheless, Tapajós gaps were not sufficiently large to inhibit visits by many forest understorey species. The overall scarcity of flowers and fruits in Tapajós gaps undoubtedly contributed to the low numbers of frugivores and nectarivores among gap specialists, and the low relative abundance of these guilds in gaps. Despite the relative scarcity of nectarivores and frugivores, both guilds had higher capture rates in gap than forest habitats, presumably due to a greater abundance of flowers and fruits in gaps than in the forest understorey. The predominance of insectivores, especially those that participate in mixed-species flocks and concentrate in gaps, distinguished the lower strata of *terra firme* forest from those of previous studies of gap-use. Thus gaps in tall stature *terra firme* forest on low-fertility soils with dark understoreys, such as those of the Tapajós, may be especially important productivity hotspots to which a variety of birds are attracted.

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APPENDIX

Birds captured in gap and forest sites of *terra firme* forest of the Tapajós Forest, Brazil, during eight netting sessions from 19 August 1999 to 18 June 2001. The sequence and nomenclature for species in non-Passeriformes families follows Sick (1997). For Passeriformes, the sequence and nomenclature for families and species follow Ridgely and Tudor (1989, 1994), with minor modifications adopted by Sick (1997). Guild and microhabitat classification follows Henriques *et al.* (2003).

	Gap	Forest	Guild ^a	Microhabitat ^b
TINAMIDAE				
<i>Crypturellus variegatus</i>	1	1	f	t
ACCIPITRIDAE				
<i>Accipiter bicolor</i>	0	1	svli	c
<i>Leucopternis albigollis</i>	1	0	svli	c
FALCONIDAE				
<i>Micrastur ruficollis</i>	1	2	svli	u
<i>Micrastur gilvicolis</i>	6	6	svli	c
PSOPHIDAE				
<i>Psophia viridis</i>	0	2	fi	u
COLUMBIDAE				
<i>Geotrygon montana</i>	14	13	f	t, u
TROCHILIDAE				
<i>Glaucis hirsuta</i>	0	2	n	ef
<i>Threnetes leucurus</i>	1	0	n	u
<i>Phaethornis superciliosus</i>	19	11	n	u, ef
<i>Phaethornis bourcierii</i>	13	11	n	u
<i>Phaethornis longuemareus</i>	28	5	n	u
<i>Campylopterus largipennis</i>	4	3	n	c, ef
<i>Florisuga mellivora</i>	1	0	n	c
<i>Thalurania furcata</i>	33	15	n	tf
<i>Hylocharis saphirina</i>	1	0	n	ef
<i>Heliothryx aurita</i>	1	1	n	c
TROGONIDAE				
<i>Trogon violaceus</i>	1	0	mfif	m, ef
<i>Trogon rufus</i>	2	1	mfif	m
MOMOTIDAE				
<i>Baryphthengus ruficapillus</i>	1	2	if	m
<i>Momotus momota</i>	0	1	if	m
GALBULIDAE				
<i>Galbula cyanicollis</i>	6	0	i	m
BUCCONIDAE				
<i>Bucco capensis</i>	1	0	i	m
<i>Malacoptila rufa</i>	5	15	i	m
<i>Monasa morphoeus</i>	1	1	svli	m
RAMPHASTIDAE				
<i>Selenidera gouldii</i>	1	0	f	c
<i>Ramphastos vitellinus</i>	0	1	f	c
FURNARIIDAE				
<i>Xenops minutus</i>	18	13	mfi	u, m
<i>Phylidor erythrocercus</i>	1	0	mfi	u
<i>Phylidor ruficaudatus</i>	9	3	mfi	u
<i>Phylidor pyrrhodes</i>	2	1	mfi	u
<i>Automolus infuscatus</i>	23	26	mfi	u, ef
<i>Automolus ochrolaemus</i>	7	2	i	u
<i>Sclerurus mexicanus</i>	2	3	i	u
<i>Sclerurus rufifigularis</i>	5	7	i	u
<i>Sclerurus caudacutus</i>	9	9	i	u
DENDROCOLAPTIDAE				
<i>Dendrocincla fuliginosa</i>	10	6	i	u, m
<i>Dendrocincla merula</i>	57	88	aa	u

APPENDIX *Continued*

	Gap	Forest	Guild ^a	Microhabitat ^b
<i>Deconychura longicauda</i>	7	8	mfi	u
<i>Deconychura stictolaema</i>	6	13	mfi	u
<i>Glyphorhynchus spirurus</i>	85	82	mfi	u, m
<i>Hylexetastes uniformis</i>	5	8	aa	m
<i>Dendrocolaptes certhia</i>	1	3	aa	m
<i>Dendrocolaptes picumnus</i>	1	0	aa	m
<i>Xiphorhynchus spixii</i>	19	27	mfi	u, m
<i>Xiphorhynchus guttatus</i>	3	3	mfi	c, m
<i>Campylorhamphus procurvoides</i>	1	0	mfi	c, m
THAMNOPHILIDAE				
<i>Cymbilaimus lineatus</i>	3	0	mfi	u, m, ef
<i>Taraba major</i>	1	0	i	ef
<i>Thamnophilus aethiops</i>	10	4	mfi	u
<i>Thamnophilus schistaceus</i>	21	2	mfi	u
<i>Pygiptila stellaris</i>	1	0	i	u
<i>Thamnomanes caesi</i>	43	24	mfi	u
<i>Microrhopias quixensis</i>	1	1	i	m, u
<i>Myrmotherula hauxwelli</i>	18	10	mfi	u, m
<i>Myrmotherula leucophthalma</i>	67	19	mfi	u, m
<i>Myrmotherula ornata</i>	2	0	mfi	m, u
<i>Myrmotherula axillaris</i>	1	0	mfi	ef
<i>Myrmotherula longipennis</i>	93	63	mfi	u
<i>Myrmotherula menetriesii</i>	22	3	mfi	u, m
<i>Cercomacra cinerascens</i>	1	0	i	c, m
<i>Cercomacra nigrescens</i>	1	1	i	tf, ef, m
<i>Myrmoborus myotherinus</i>	1	0	i	u
<i>Dichrozona cincta</i>	6	4	i	t
<i>Hylophylax naevia</i>	8	12	i	u
<i>Hylophylax punctulata</i>	6	4	i	u
<i>Hylophylax poecilonota</i>	41	67	i	u
<i>Hypocnemis cantator</i>	22	4	i	u, ef, tf
<i>Sclateria naevia</i>	2	1	i	u
<i>Schistocichla leucostigma</i>	2	0	i	u
<i>Myrmeciza hemimelaena</i>	2	3	i	u, tf, ef
<i>Myrmornis torquata</i>	2	4	i	t
<i>Rhegmatorhina gymnops</i>	32	31	aa	u
<i>Phlegopsis nigromaculata</i>	19	7	aa	u
FORMICARIIDAE				
<i>Formicarius analis</i>	1	1	i	t
<i>Myrmothera campanisona</i>	1	1	i	t, tf
<i>Hylopezus macularius</i>	1	1	i	t
CONOPOPHAGIDAE				
<i>Conopophaga aurita</i>	9	12	i	t
TYRANNIDAE				
<i>Mionectes macconnelli</i>	33	47	if	u
<i>Lophotriccus galeatus</i>	2	0	i	m
<i>Corythopsis torquata</i>	4	3	i	u
<i>Platyrrhynchus platyrhynchus</i>	14	13	i	u, m
<i>Platyrrhynchus saturatus</i>	11	5	i	u, m
<i>Platyrrhynchus coronatus</i>	12	32	i	u
<i>Rhynchociclus olivaceus</i>	1	0	i	m
<i>Ramphotrigon ruficauda</i>	1	3	i	m
<i>Onychorhynchus coronatus</i>	7	7	i	u
<i>Myiobius barbatus</i>	25	16	mfi	u
<i>Terenotriccus erythrurus</i>	9	4	i	m, u
<i>Attila spadiceus</i>	1	3	i	c, m
<i>Rhytipterna simplex</i>	3	1	i	m
<i>Pachyrhamphus marginatus</i>	1	0	if	m

APPENDIX *Continued*

	Gap	Forest	Guild ^a	Microhabitat ^b
PIPRIDAE				
<i>Schiffornis turdinus</i>	15	16	fi	u
<i>Tyranneutes stolzmanni</i>	1	0	f	m
<i>Manacus manacus</i>	1	1	f	u
<i>Pipra iris</i>	78	43	f	tf, ef
<i>Pipra rubrocapilla</i>	91	34	f	u, m
COTINGIDAE				
<i>Phoenicircus carnifex</i>	0	2	f	c, m
<i>Laniocera hypopyrha</i>	2	1	if	m
<i>Lipaugus vociferans</i>	2	0	fi	m
TROGLODYTIDAE				
<i>Cyphorhinus aradus</i>	25	13	i	t, u
SYLVIIDAE				
<i>Ramphocaenus melanurus</i>	5	0	mfi	m, u
TURDIDAE				
<i>Catharus minimus</i>	1	0	if	u
<i>Turdus albicollis</i>	7	19	fi	u
VIREONIDAE				
<i>Hylophilus ochraceiceps</i>	8	8	i	m, u, tf
EMBERIZIDAE				
PARULINAE				
<i>Basileuterus rivularis</i>	1	0	i	m
THRAUPINAE				
<i>Lanio versicolor</i>	7	5	mfi	c, m
<i>Tachyphonus cristatus</i>	1	0	mfif	c, m
<i>Tachyphonus surinamus</i>	16	0	mfif	m
<i>Habia rubica</i>	5	3	fi	m
<i>Cyanerpes caeruleus</i>	2	0	n	c
EMBERIZINAE				
<i>Oryzoborus angolensis</i>	1	0	f	t, u, ef
<i>Arremon taciturnus</i>	4	3	if	u, ef
CARDINALINAE				
<i>Cyanocompsa cyanooides</i>	4	3	fi	u

^aGuild: aa = ant follower, f = solitary frugivore, fi = solitary frugivore–insectivore, i = solitary insectivore, if = solitary insectivore–frugivore, mfi = mixed species flock insectivore, mfif = mixed species flock insectivore–frugivore, n = nectarivore, svli = small vertebrates and large insects.

^bMicrohabitat: t = terrestrial, u = understorey, m = mid-storey, c = canopy, ef = edge of forest, tf = treefall.