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# Diversity, biomass, and trophic structure of a central amazonian rainforest bird community

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## RESUMO: Diversidade, biomassa, e estrutura trófica de uma comunidade de aves de floresta tropical na Amazônia central.

As comunidades de aves da Amazônia estão entre as mais ricas do mundo. Mesmo assim, relativamente pouco é conhecido sobre a organização da comunidade inteira na escala local ou sobre diferenças dentro do Bioma Amazônia. Esses dados são fundamentais não só para compreender os processos que geram e mantêm a biodiversidade tropical, mas também como base para avaliar alterações antropogênicas na floresta amazônica. Aqui apresentamos uma descrição da comunidade inteira de uma parcela de 100 ha de floresta de terra firme no Projeto Dinâmica Biológica de Fragmentos Florestais, perto de Manaus, Brasil, baseada de levantamentos *spot-map* e capturas de rede de neblina entre outros, aumentados com métodos adicionais de campo e de análise. Embora nossos resultados são de uma única parcela e um único ano, os nossos métodos e interpretação refletem quase 30 anos de pesquisas ornitológicas no local. Registramos 228 espécies na parcela, das quais 207 foram consideradas parte da avifauna *core* da região. A densidade mediana foi de cinco indivíduos/100 ha. Apenas 13 espécies (6% das espécies *core*) atingiram densidades de  $\geq 20$  indivíduos na parcela, e 55 espécies (27%) tiveram  $\leq 2$  indivíduos. Nenhuma espécie teve território menor do que 3 ha; tamanho de território mediano foi de 11 ha para as 103 espécies para as quais poderíamos fazer estimativas razoáveis. Medidos por números de espécies ou indivíduos, a parcela foi dominada por insetívoros (54% de espécies, 62% de indivíduos). Biomassa, no entanto, foi dominada por frugívoros e granívoros (59%). Comparado com dados disponíveis de outros locais da floresta amazônica, o nosso sítio parece ter riqueza comparável de um conjunto semelhante de espécies, mas densidade menor e variação em ocorrência local maior. Nossos resultados sugerem que a área necessária para suportar populações de muitas espécies será ainda maior na Amazônia central do que na Amazônia ocidental.

**PALAVRAS-CHAVE:** Amazônia, comunidade de aves, biomassa, riqueza de espécies, floresta tropical.

**ABSTRACT:** Amazonian forest bird communities are among the richest in the world. Even so, relatively little is known about the organization of the entire avian community at local scales or about differences across Amazonia. These are fundamental data not only for understanding the processes generating and maintaining tropical diversity, but also as a baseline for evaluating anthropogenic changes to Amazonian forests. Here we provide a description of the entire bird community for a 100 ha plot of *terra firme* forest at the Biological Dynamics of Forest Fragments Project, near Manaus, Brazil, based on spot-map and mist net surveys augmented by additional field and analytical techniques. Although our results are from a single plot surveyed in a single year, our methods and interpretation reflect nearly 30 years of ornithological research at the site. We found 228 species on the plot, of which 207 were considered part of the core regional avifauna. Median density was five individuals/100 ha. Only 13 species (6% of the core species) had densities  $\geq 20$  individuals on the plot, although 55 species (27%) had  $\leq 2$  individuals. No species had territories smaller than 3 ha; median territory size was 11 ha for the 103 species for which we could make reasonable estimates. Measured by numbers of species or individuals, the plot was dominated by insectivores (54% of species, 62% of individuals). Biomass, however, was dominated by frugivores and granivores (59%). Compared to available data from other Amazonian forests, our site appears to have comparable richness of a similar set of species, but lower density and greater patchiness. Our results suggest that the area required to support populations of many species will be even greater in central Amazonia than in western Amazonia.

**KEY-WORDS:** Amazonia, bird communities, biomass, species richness, rainforest.

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Our understanding of Amazonian birds has increased extraordinarily in recent decades. Distributions, including dramatic rediscoveries and range extensions, are constantly being refined (e.g., Cohn-Haft 1993, Aleixo *et al.* 2000, Lane *et al.* 2006, Naka *et al.* 2007). Research focus on habitat specialization has revealed distinct avifaunas

associated with savannas, flooded forest, and sandy soil forests (Borges and Carvalhaes 2000, Alonso and Whitney 2003, Aleixo and Poletto 2007, Cintra *et al.* 2007). Phylogeographic studies show the evolutionary relationships of Amazonian birds to their relatives in Atlantic Forest and across the Andes, as well as the role of rivers

in shaping evolutionary trajectories (Aleixo 2004, Bates *et al.* 2008, Cabanne *et al.* 2008, Burney and Brumfield 2009, Patane *et al.* 2009).

Despite these advances, community ecology of birds in *terra firme* forest has seen much less progress. The explosion in resources essential for survey work, particularly recordings and field guides, has made it much easier to assemble accurate and relatively complete species lists. This information is essential to describe distributions and patterns of species richness, but species lists alone do little to help answer some of the fundamental mechanistic questions about tropical communities, either in general or specifically for birds, such as how this fantastic diversity is maintained, how communities are organized, or how diversity and productivity are related (Chesson 2000, Currie *et al.* 2004, Swenson and Enquist 2009, Gomez *et al.* 2010, Kraft and Ackerly 2010).

Community patterns are understood much better for Amazonian trees than for birds, thanks to survey work across a network of forest plots where data include spatial arrangements, growth, and mortality of individual trees (*e.g.*, Muller-Landau *et al.* 2006). To make similar progress with birds, we need comparable data – particularly abundance, biomass, and spatial arrangement within plots large enough to include a representative sample of the entire community. As Terborgh *et al.* (1990) emphasized in their landmark paper on the birds of Cocha Cashu, Peru, accurate surveys of Amazonian bird communities require multiple techniques and a considerable effort of time, both as preparation and in the field. Extremely rare species require special consideration, as they likely have little to do with community organization, perhaps representing vagrants from other habitats. For this reason, Remsen (1994) advocated the importance of identifying the core avifauna of resident species to be compared across sites, a concept that was useful to help understand the differences between central and western Amazonian avifaunas (Cohn-Haft *et al.* 1997).

Detailed descriptions of bird communities are essential not only for understanding ecological patterns, but also for their more pressing role as baseline information as Amazonia is increasingly modified by human activity, including roads, agriculture, fire, climate change, hunting, and the synergism of these activities (Lewis *et al.* 2004, Fearnside 2005, Gardner *et al.* 2007, Peres and Palacios 2007, Hubbell *et al.* 2008). Data collected now from minimally disturbed sites likely will represent the best approximation of the former state of Amazonia as it transitions into a possibly turbulent 21<sup>st</sup> century.

Quantitative descriptions of entire bird communities are available for a very few Amazonian sites: plots in Peru (Terborgh *et al.* 1990), Ecuador (English 1998), and French Guiana (Thiollay 1994) are all we know of that include species richness, density, and abundance. Other papers have described relative species richness and some

proxy for abundance, such as detections via netting, spot-maps, or point counts, especially in the context of examining effects of forest perturbation (*e.g.*, Barlow *et al.* 2007, Blake 2007, Borges 2007), but these do not permit comparisons of density, biomass, or territory size across studies.

Here we describe the bird community of a 100 ha plot of continuous *terra firme* forest at the Biological Dynamics of Forest Fragments Project (BDFFP), near Manaus, Amazonas, Brazil. This effort builds on 30 years of research at the BDFFP, including bird recordings (Naka *et al.* 2008), development of techniques for aging and sexing mist-netted birds (Bierregaard 1988, Ryder and Wolfe 2009, E. I. Johnson *unpublished data*), mixed-species flock surveys (Develey and Stouffer 2001, P. C. Stouffer *unpublished data*), and radio-telemetry (Stouffer 2007, P. C. Stouffer *unpublished data*). We provide the following community metrics for our plot: 1) species richness; 2) density; 3) biomass; and 4) territory size. From these data, we calculate species richness and biomass contribution by foraging guild. We also refine the description of the core forest avifauna for the area of the BDFFP. Our goal is to provide the details necessary for future comparisons with other intensive plot surveys.

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## METHODS

### Study site

We conducted our study at the Biological Dynamics of Forest Fragments Project (BDFFP), approximately 80 km north of Manaus, Amazonas, Brazil (02°30'S, 60°00'W). The area annually received 2714 mm ( $\pm$  22 mm SE) of rain each year from 2006-08, but had a long-term average of about 2500 mm from 1966-90 (Stouffer and Bierregaard 1993). The dry season lasts from June to December with the driest months in July through September and the wettest months in February through May. The annual mean temperature is 26.7°C. We conducted the study between 3 June and 10 November 2008, which is during the breeding season for most species at the BDFFP (E. I. Johnson *unpublished data*). Although the BDFFP is well known for its studies of forest fragmentation, much of the landscape is still largely forested; we conducted this study at a continuous forest site called KM41 (or reserve 1501). The forest is primarily comprised of *terra firme* lowland rainforest. Soils are generally nutrient-poor sandy or clay-rich ferrasols typical of the region (Chauvel *et al.* 1987). The canopy is approximately 35 m tall with emergents reaching 55 m. The understory is relatively open and dominated by palms. There is some topographic variation within our study plot with plateaus on either side of a small stream that

bisects the plot. In recent years a series of strong storms created a 4 ha gap and several smaller canopy gaps. There are also a variety of small gaps in various stages of succession. The area of the BDFFP is described in more detail by Lovejoy and Bierregaard (1990) and Gascon and Bierregaard (2001).

### Modifying the Manaus core species list

We created a list of core *terra firme* species slightly modified from the Cohn-Haft *et al.* (1997) list of the avifauna of the BDFFP, based on results from our plot and the additional > 10 years of sampling at the BDFFP since that list was published. We define core *terra firme* species as those that regularly breed and forage in mature *terra firme* forest and its components such as gaps, small streams, and airspace above the canopy, but not species associated mainly with ponds or anthropogenic disturbance such as roadside edges, pastures, and large areas of second growth. We also do not include seasonal long-distance boreal or austral migrants.

### Species richness and density estimations – Overview

Our goal was to estimate species richness and individual species densities within a 100 ha patch of continuous *terra firme* lowland rainforest. With these data, we also generated biomass and territory size estimates, which are described in more detail below. In general, we follow the methodology described in detail by Terborgh *et al.* (1990), Thiollay (1994), and Robinson *et al.* (2000). We used a variety of sampling techniques to determine the number of individuals and species within our 100 ha study plot; for many species the combination of approaches provided a better density estimation than did any sampling technique on its own. For several species, we were able to improve upon previous methods to generate more accurate density estimates by utilizing mark-recapture techniques, radio-telemetry, and newly-developed aging and sexing criteria for captured birds (Ryder and Wolfe 2009, E. I. Johnson *unpublished data*). We note any significant deviations from previous methods below. Taxonomy follows Remsen *et al.* (2011).

### Species richness and density estimations – Spot-mapping

Spot-mapping was our primary source for detections, especially for species that hold typical territories. We noted locations of birds in reference to the gridded trail system, with perpendicular trails intersecting every 100 m to create 1 ha blocks. We divided each 1 ha block

into four quarters, each 50 × 50 m, and noted the location of birds at this scale. Because many territories did not fall entirely within the study plot, we counted territories in 1/4 territory increments. For species with typical territories, we multiplied the number of territories by two to estimate the number of individuals.

We conducted spot-mapping at all hours of the day, focusing our effort and coverage during the morning hours (1 hour before to 2 hours after sunrise) and the late afternoon (± 1 hour of sunset). Often 2 or 3 observers spot-mapped in different areas of the plot simultaneously, which helped elucidate distinct territories. When possible, we noted counter-singing to help determine territory boundaries. We used playback for some species that were infrequently detected or to help identify color-banded birds (*see Species richness and density estimations – Mist netting*) after the bird was initially detected by song or call. We frequently observed dependent young with paired adults, but do not include birds obviously < 12 months old in our calculations.

In addition to singing territorial species, spot-mapping allowed us to estimate the density of birds that follow understory mixed-species flocks. At our study site, flocks are led by two *Thamnomanes* spp. that sing and give rally calls in the early morning to gather flocking species. These gathering areas are found in the same location each morning (Jullien and Thiollay 1998), allowing us to determine the number of mixed-species flocks in the study plot. We also followed some mixed-species flocks later in the day, noting the location and composition of these flocks. These observations and a study of 15 flocks, also at KM41 (P. C. Stouffer and P. Develey *unpublished data*), allowed us to determine directly (for flocks well followed) or estimate (from the previous work at KM41) the composition of flocks in our plot.

As in other studies, estimating canopy flock species' densities was more difficult. These species have different home ranges than understory flocks, some can be difficult to detect by voice, and they do not fall into mist-nets. In addition, it is likely that canopy flock home ranges overlap with two or more understory flocks, adding confusion (Munn 1985). Spot-mapping locations of singing birds helped resolve the number and composition of canopy flocks. Flocks of canopy frugivore/omnivores (*e.g.*, *Tangara* and *Cyanerpes*) are even more vagabound than typical canopy flocking insectivores, despite often associating with canopy insectivores. Because these species are small, have weak, indistinct voices, and have widespread movements, it was difficult to get accurate density estimates, and we very conservatively estimated their numbers. We are confident, however, that we found all the resident species (*see Results*), and because most canopy flock frugivores are small-bodied (Appendix), overall biomass estimates should be minimally affected by difficulties in estimating their abundance.

### Species richness and density estimations – Mist netting

We conducted six rounds of mist netting during the study period using 12 m ATX-type (36 mm mesh) mist-nets. Each round of mist netting consisted of using three lines of 16 nets in the interior of the plot and four lines of four nets around the edge of the plot. Interior net lines were > 350 m apart and > 100 m from the plot border. Each round of netting took three or four consecutive days to complete (one line of 16 nets plus one or two lines of four nets was opened each day). Nets were open from 0600 to 1400.

We aged and sexed captured birds using plumage, molt, and skull criteria (E. I. Johnson *unpublished data*). Each bird also received an aluminum band and two color bands with the exception of large birds (*e.g.*, hawks) and hummingbirds. Resighting color-banded birds during spot-mapping greatly improved our ability to understand space use and delineate territory boundaries of many understory species.

Mist-netting also allowed us to estimate the number of territories of some understory species that did not hold typical territories or were difficult to detect, an improvement over previous studies. For three common species (*Glyphorhynchus spirurus*, *Pithys albifrons*, and *Pipra pipra*), we used recapture data to estimate the density of adult birds using a Jolly-Seber mark-recapture model for open populations in program MARK (White and Burnham 1999). Because we mist-netted during a single dry-season, we assumed that within-season population growth ( $\lambda$ ) and apparent survival ( $\Phi$ ) were negligible; we fixed  $\lambda$  to 1.0 and  $\Phi$  to 1.0 to reduce the number of parameters and increase precision in estimating recapture probability ( $\rho$ ) and density ( $n$ ). Experimentation with models that had  $\Phi$  fixed to 0.95 or 0.90 had less support than the model of  $\Phi = 1.0$ , as did models with  $\lambda$  fixed to 1.05 or 0.95 (E. I. Johnson *unpublished data*). Decreasing  $\lambda$  and  $\Phi$  to < 1 also increased  $n$ , thus our methodology is conservative with respect to estimating bird density.

### Species richness and density estimations – Radio-telemetry

We opportunistically placed radios on 8 species captured in mist nets (1-5 individuals per species) to determine their territory size and location. Even when only one individual of a species was followed, this provided information to determine territory boundaries based on spot-map registrations (*e.g.*, Stouffer 2007). It also allowed us to estimate territory size for three rare and difficult-to-detect species (*Malacoptila fusca*, *Frederickena viridis*, and *Onychorhynchus coronatus*).

### Species richness and density estimations – Other estimation techniques

In the following sections, we describe how we estimated the number of individuals for species that do not hold typical territories and were not regularly mist-netted.

#### Group-living species that form monospecific flocks

For parrots, we did not have a long-term dataset of flyover observations to estimate group size, as did Terborgh *et al.* (1990). Therefore, we simply used half of the maximum number of perched or fly-over individuals in a single group detected during the study period. This probably gave a conservative estimate of bird density because multiple groups probably used the study plot and a single group likely uses an area greater than the 100 ha plot. As in other studies, we did not know the true spatial extent of parrot movements except that they are very large relative to the size of the plot. We did not observe seasonal changes in group size for parrots, although we did for caciques (*Caccicus haemorrhous*). For caciques, therefore, we used the half of the maximum number of individuals seen in a group each month during the study period and took the average of these counts. Again, because multiple groups used our study plot, this estimate is probably conservative. For trumpeters (*Psophia crepitans*), two groups used the plot, although neither group's large (58-88 ha at Cocha Cashu, Sherman 1995) home range fell exclusively within the plot. Trumpeter groups do not roost in the same location each night, and split up into subgroups during the day (E. I. Johnson, *personal observation*), making it difficult to estimate group size. On two occasions, we encountered the roost of one group and conservatively counted these birds. Assuming each group used half the plot and that group size was similar between groups, we used this count to estimate the number of individuals in the plot.

#### Lekking species

*Tyrannetes virescens*, *Pipra erythrocephala*, *Lipaugus vociferans*, and *Phoenicircus carnifex* form "exploded" leks in which males are separated by a few meters or more, depending on the species, and sing, often throughout the day, to attract females. These are species that are not regularly mist-netted because they rarely descend to the understory, thus other estimation techniques are needed to determine the number of birds in the plot. We followed the approach used by Terborgh *et al.* (1990) and counted the number of singing males at lek sites and multiplied by three to estimate the number of individuals in the 100 ha plot.

*Phaethornis* spp. and *Perissocephalus tricolor* also form exploded leks. Although no leks were located within our 100 ha plot, both species had lekking arenas < 200 m from the plot edge; therefore foraging and probably nesting regularly occurred within our study plot. *Perissocephalus* is a very large and vocal omnivore, thus we simply used the maximum number of birds counted during a spot-map day, which ended up to be half of the number of males observed lekking near the study plot. *Phaethornis* spp. occasionally fell into mist-nets and were frequently detected on the study plot, but neither sampling technique provided us with an accurate count of individuals. We did not estimate the size of the leks nearby, but through personal experience, we assumed that at least 10 males sing at leks, thus we estimated the equivalent of half of 20 adult birds in the lek use the study plot. Both of these estimates are likely conservative because it is probable that several other leks were located close enough to the study plot that individuals from those leks regularly used our plot.

### Biomass

We determined the biomass of each species by multiplying density by mass. Bird masses were determined using the long-term BDFFP mist-netting database of nearly 60,000 captures of 186 species (P. C. Stouffer *unpublished data*). For species without data from Manaus, we used the Handbook of the Birds of the World series (del Hoyo *et al.* 1992-2010), Birds of Venezuela (Hilty 2003), and Terborgh *et al.* (1990).

### Foraging guild

Each species was categorized in a foraging guild, based on its dietary preference and foraging mode, following Terborgh *et al.* (1990), Thiollay (1994), English (1998), and Robinson *et al.* (2000). For some species, authors disagreed in their classification, requiring us to review the recent literature (del Hoyo *et al.* 1992-2010, Hilty 2003) before assigning guilds. Ambiguity in classification mostly comes from the difficulty in assigning guilds to large-bodied species that generally eat fruit, but at least occasionally destroy seeds or eat animal material (*e.g.*, tinamous). Our goal here was not to reclassify species, but to provide as much consistency as possible with previous studies.

### Territory size

Like Terborgh *et al.* (1990), we used a minimum convex polygon (MCP) approach to estimate territory

size, and we only calculated territory size for species that hold typical territories. For these species, we estimated territory size by using ArcMap v 9.2 (ESRI, Redlands, California) to divide the proportion of the plot occupied by the number of territories determined through spot-mapping. Home range estimates were modified by radio-telemetry data for a few species (*see Species richness and density estimations: Radio-telemetry* and Stouffer 2007). This MCP approach to territory size estimation is conservative because it does not consider territory overlap, and probably underestimates occupancy in some cases (Anich *et al.* 2009). Although space use by territorial birds could be more completely described by methods other than MCP, we used this method to maintain consistency with previous studies.

## RESULTS

### Modifying the Manaus core species list

Cohn-Haft *et al.* (1997) listed 394 species for the BDFFP in an area of about 500 km<sup>2</sup>. In general, we considered species that they defined as common (“c”), uncommon (“u”), and rare (“r”) in primary forest (“habitat 1”) as core *terra firme* species. Unlike Cohn-Haft *et al.* (1997), we did not consider accidental (“x”) species as part of the core avifauna. Even though some of these species have been detected in primary *terra firme* forest at the BDFFP, most are associated with other forested habitat types not found in the immediate area (*e.g.*, *igapó*, *várzea*, or *campinarana*); these species probably disperse through *terra firme* forest in search of suitable habitat. We also eliminated *Vireo olivaceus* because the resident subspecies inhabits second growth (boreal migrants occupy primary forest). We added *Cymbilaimus lineatus*, *Pheugopedius coraya*, and *Phaeothlypis rivularis* to the core avifauna list because they are regular in appropriate microhabitat (tree-fall gaps or small streams) within *terra firme* forest. We also added *Piculus chrysochloros* to the core list based on our results here and its presence in other PDBFF plots. We subtracted one species, *Icterus chryscephalus*, because it is now considered conspecific with *I. cayanensis* (D’Horta *et al.* 2008). We also add two previously overlooked resident *terra firme* species not listed by Cohn-Haft *et al.* (1997), *Touit huetti* and *Hemitriccus josephinae* (Johnson *et al.* 2010), making 236 species in the final list of core *terra firme* birds at the BDFFP.

### Community composition

We detected 228 species with a total of 5581 individual detections and mist-net captures within the boundaries of the 100 ha *terra firme* forest plot (Appendix). We

**TABLE 1:** Core *terra firme* species that were not detected in the 100 ha community survey near Manaus, Brazil. Group 1: core *terra firme* species that may have been present on the plot, but were not detected. Group 2: core *terra firme* species that have very large home ranges and were not detected in the plot. Group 3: core *terra firme* species not found in the study plot, are considered rare (Cohn-Haft *et al.* 1997), and are not likely present in every 100 ha patch of forest near Manaus, Brazil.

Group 1	Group 2	Group 3
<i>Harpagus bidentatus</i>	<i>Accipiter bicolor</i>	<i>Tigrisoma lineatum</i>
<i>Discosura longicauda</i>	<i>Morphnus gujanensis</i>	<i>Leucopternis melanopus</i>
	<i>Harpia harpyja</i>	<i>Daptrius ater</i>
	<i>Haematoderus militaris</i>	<i>Aramides cajaneus</i>
		<i>Nyctibius aethereus</i>
		<i>Chloroceryle aenea</i>
		<i>Streptoprocne zonaris</i>
		<i>Panyptila cayannensis</i>
		<i>Anthracoceros nigricollis</i>
		<i>Topaza pella</i>
		<i>Celeus torquatus</i>
		<i>Synallaxis rutilans</i>
		<i>Sclerurus caudacutus</i>
		<i>Hylophylax naevius</i>
		<i>Hylopezus macularius</i>
		<i>Hemitriccus josephinae</i>
		<i>Rhynchocyclus olivaceus</i>
		<i>Tyrannopsis sulphurea</i>
		<i>Cyanicterus cyanicterus</i>
		<i>Euphonia minuta</i>

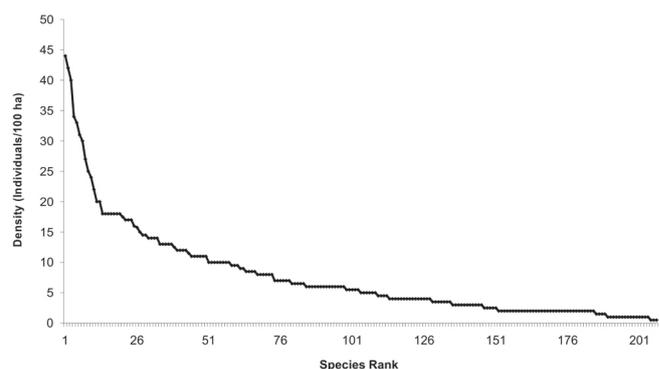
determined 207 of the 236 (88%) core forest species to be resident in this 100 ha area of forest, representing 155 genera in 43 families. Of the 21 other species we detected in the plot, 15 were vagrants not actually residing in our plot and six were migrants. Three of the 15 vagrants, *Falco rufifigularis*, *Chaetura chapmani*, and *Icterus cayannensis* were core forest species not considered resident in our plot. The other twelve vagrants were non-core species associated with habitats not found within the 100 ha plot. Migrants were a relatively small portion of the avifauna. We detected two passage migrants, *Elanoides forficatus* and *Ictinia plumbea*, and four other migrant species, *Coccyzus euleri*, *Legatus leucophaius*, *Vireo olivaceus*, and *Vireo altiloquus* that probably spent their non-breeding season in our plot. Although non-breeding migrants can be difficult to detect, our results suggest that these species represent a small portion of the forest interior avifauna, at least from June through November.

We divided the 26 absent core forest species into three groups (Table 1): group 1) two species that may have been present in low densities, but were not detected (*i.e.*, species not thought to be extraordinarily rare, but that have low detection probabilities); group 2) four species that have extremely large territories (> 50 ha) and low detection probabilities; and group 3) 20 species that have reasonable detection probabilities, but are probably too rare to be found in every 100 ha patch of *terra firme* forest. Nine of the 20 group 3 species were easily detected during brief surveys in nearby continuous forest sites, suggesting that these species should have been detected if they were present in our intensively-surveyed 100 ha plot. The species in group 3 belong to a variety of

guilds including carnivores, omnivores, insectivores, nectarivores, and frugivores. They also occupy a variety of microhabitats including mature forest, disturbed forest, and aquatic systems, and inhabit a variety of forest strata from terrestrial to canopy. In other words, there was no discernable pattern for their absence from our plot other than their distinct rarity.

### Species density distribution

The community was characterized by few abundant species and many species with  $\leq 2$  individuals/100 ha, hereafter called rare species (Figure 1). Of 207 resident species in the plot, 13 (6%) had densities of  $\geq 20$  individuals on the plot, but 55 (27%) had densities of  $\leq 2$  individuals/100 ha. Because some rare species had territories that were not entirely within the plot, these 55



**FIGURE 1:** Rank abundance of species in the 100 ha plot.

**TABLE 2:** Species richness, density (individuals/100 ha), and biomass (g) by foraging guild for core species. Also shown are summaries and proportional richness, density, and biomass by broad guilds (in parentheses).

Guild	Species richness	Density	Biomass
I, A, S (arboreal sallying insectivore)	43	341	9047
I, A, G (arboreal gleaning insectivore)	27	290	4497
I, T, G (terrestrial gleaning insectivore)	12	74	2969
I, B, S (bark surface insectivore)	10	99	2627
I, B, I (bark interior insectivore)	7	40	2473
I, A, DL (arboreal dead-leaf searching insectivore)	5	43	848
I, AF (obligate ant-following insectivore)	3	74	2061
I, Aer. (aerial insectivore)	2	11	443
I, T, S (terrestrial sallying insectivore)	2	8	211
Insectivore total	111 (54%)	979 (62%)	25178 (21%)
O (omnivore)	32 (15%)	220 (14%)	9001 (7%)
F, A (arboreal frugivore)	21	255	29561
F, T (terrestrial frugivore)	3	18	17829
Frugivore total	24 (12%)	272 (17%)	47390 (39%)
G, A (arboreal granivore)	12	30	13887
G, T (terrestrial granivore)	5	19	10702
Granivore total	17 (8%)	49 (3%)	24589 (20%)
R, D (diurnal raptor)	8	11	4889
R, N (nocturnal raptor)	5	14	4076
Raptor total	13 (6%)	25 (2%)	8965 (7%)
N (nectarivore)	7 (3%)	36 (2%)	179 (0.1%)
Carr. (carrion)	2 (1%)	3 (0.2%)	6675 (5%)
Aq. (aquatic)	1 (0.5%)	2 (0.1%)	104 (< 0.1%)
Total	207	1584	122080
Total excluding large-bodied taxa*	166	1461	57529

\* Excluding Tinamidae, Cracidae, Odontophoridae, Cathartidae, Psittacidae, Accipitridae, Falconidae, Strigidae, Nyctibiidae, and Ramphastidae.

rare species accounted for only 90 individuals in the plot. The median density across all species was five individuals in the plot. The most abundant species, the lekking frugivore *Lipaugus vociferans*, had 44 individuals in the plot. The second most abundant species was an obligate ant-follower, *Pithys albifrons*. The third and fourth most abundant species were also lekking frugivores, *Pipra pipra* and *Tyrannetes virescens*. Not until the fifth and sixth most-abundant species did we find typical territorial species: *Glyphorhynchus spirurus* with 16.5 territories and *Hemitriccus zosterops* with 15.5 territories on the plot.

### Mass distribution

About 60% of species in the plot weighed 8-64 g, with 22% in the 8-16 g range (Figure 2). About 10% of species were in the 4-8 g range and in the 64-128 g range. Collectively, < 20% of species were larger than 128 g.

### Biomass distribution

The estimated biomass of the bird community of Manaus was about 122,000 g (Table 2). The greatest

contribution to biomass came from frugivores, which included only 12% of species, but included relatively common, large-bodied species like tinamous, cracids, and toucans. Conversely, although insectivores accounted for 54% of species and 62% of individuals, these relatively small-bodied species accounted for only 21% of biomass. The 55 rare species summed to about 28000 g/100 ha, slightly more than the total for insectivores (some species were rare and insectivores, thus appearing in both lists). Because it is difficult to accurately estimate the abundance of large species, we made a second estimate of biomass without Tinamidae, Cracidae, Odontophoridae, Cathartidae, Psittacidae, Accipitridae, Falconidae, Strigidae, Nyctibiidae, and Ramphastidae. This second estimate omits the species that make the greatest contribution to biomass, but includes the most accurate information for the species with the greatest number of individuals, those in the 4-64 g range.

### Guild structure

Based on detailed guild classifications, the most species-rich foraging guild was arboreal sallying insectivores (43 species), followed by omnivores (32 species), arboreal

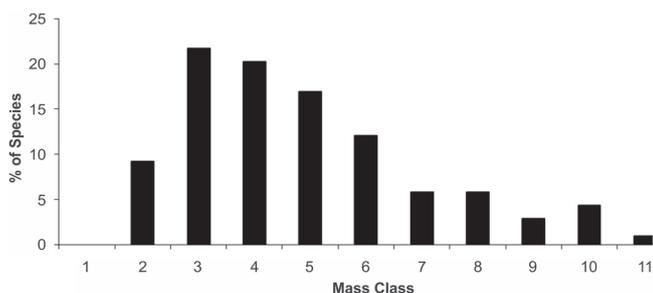
gleaning insectivores (27 species), and arboreal frugivores (21 species; Table 2). No other narrow guild was represented by more than 12 species. These species-rich guilds also had the highest densities of individuals. Despite their large contribution to richness and density, the small-bodied species in the insectivore guilds contributed relatively less to biomass than did granivores and frugivores; the three species of terrestrial frugivores contributed more biomass than the 70 species of arboreal gleaning insectivores and arboreal sallying insectivores.

### Territory size

We estimated the territory size of 103 species, or 50% of the core species (Figure 3). The most-represented size class was between 8.1-16.0 ha, which included > 40% of species. It became increasingly difficult to estimate territory size for species with territories larger than about 40 ha, as these often extended well outside the plot. For species with smaller territories, which were the most accurately sampled, our data clearly show very few species to have territories smaller than 4 ha. Species with the smallest territories were all small-bodied insectivores (*Pheugopedius coraya*, *Cercomacra cinerescens*, *Lophotriccus vitiensis*, *Platyrrhynchus coronatus*, and *Hemitriccus zosterops*).

## DISCUSSION

We are confident that our results represent the plot we surveyed as accurately as possible, and provide a basis for comparison with the few other studies from elsewhere in the Amazon or with other whole-community inventories. Our estimates of density, territory size, and biomass for the small insectivores that make up the majority of species should be robust and useful in any comparative context. Our MARK-based population estimates for two extremely common species that do not hold typical territories, *Pithys albifrons* and *Pipra pipra*, improve upon the

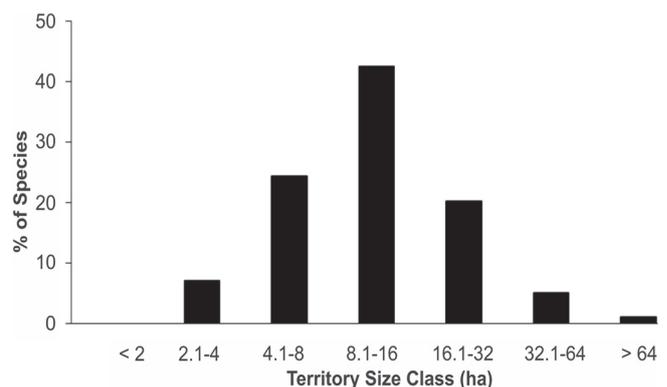


**FIGURE 2:** Proportion of species in body size categories on a log<sub>2</sub> scale (1: 2-4 g; 2: 4-8 g; 3: 8-16 g; 4: 16-32 g; 5: 32-64 g; 6: 64-128 g; 7: 128-256 g; 8: 256-512 g; 9: 512-1024 g; 10: 1024-2048 g; 11: 2048-4096 g).

methods typically used to survey these important species, and our extensive use of radiotagged birds improves the accuracy of territory size estimates (Stouffer 2007). The trail system in our plot, which gave access within 50 m of every point in the plot, allowed us to sample all parts of the plot repeatedly and to map detected birds accurately. Despite these advantages, we recognize biases that become especially important in species-rich communities that include large, wide-ranging species. Simply put, any estimates of density, territory size, and biomass become increasingly inaccurate as body size and territory size increase. Terborgh *et al.* (1990) recognized the importance of surveying a large plot to account for the patchiness and large territories of many species, but even 100 ha provides only a rough guess for species like parrots, swifts, swallows, large icterids, and large raptors that inevitably use much more than 100 ha.

We also emphasize the importance of identifying the core forest avifauna, especially before attempting comparisons among sites. This point was also made by Cohn-Haft *et al.* (1997), who suggested that the apparently greater species richness in western Amazonian forests was inflated by beta diversity (species most associated with other habitats). Questions about community assembly or conservation value cannot be appropriately answered until the resident avifauna can be distinguished from birds in passage from other habitats. Just tallying up the number of species detected does not represent diversity in an ecologically meaningful way, especially in the absence of information on spatial scale, sampling effort, or habitats surveyed (Remsen 1994).

At our site, non-breeding migrants apparently make up a trivial portion of the forest avifauna, although some migrants can be quite common in non-forest habitats (Stotz *et al.* 1992, Cohn-Haft *et al.* 1997). This is a marked contrast to the extensive use of Central American rainforests by North American migrants (*e.g.*, Robinson *et al.* 2000). The lack of elevational relief in the central Amazon also precludes use of these forests by altitudinal migrants, also an important component of diversity in



**FIGURE 3:** Proportion of species in territory size categories.

some Neotropical forest avifaunas (e.g., Loiselle and Blake 1991; see also da Silva 1993, Alves 2007). At the same time, we caution that our sampling ended before peak density of post-breeding migrants from North America. Long-term mist net sampling through the boreal winter has also shown a very low density of migrants in forest understory (just *Catharus* thrushes), but we have no quantitative surveys of migrants using other strata.

### Richness and rarity

The 100 ha plot near Manaus was characterized by high richness and low density (Table 2, Figure 1). Core species richness was slightly less than reported for Peru, Ecuador, or French Guiana (207 vs. 218-228; Terborgh *et al.* 1990, Thiollay 1994, English 1998). The rank-abundance curve showed a high degree of evenness, with few common species, similar to the curve calculated for Peru (Terborgh *et al.* 1990). Even so, the Manaus community had a lower median density and a higher proportion of rare species (those with  $\leq 2$  individuals/100 ha) than Peru, Ecuador, or French Guiana (Terborgh *et al.* 1990, Thiollay 1994, English 1998).

Based on comparison with Terborgh *et al.* (1990), territory sizes were slightly larger in Manaus; the most common size class at Cocha Cashu was 5-8 ha. Comparison with non-Amazonian Neotropical forests provides a striking illustration of the large territories of Amazonian birds. In a Panamanian rainforest, over 60% of species had territories smaller than 4.1 ha, compared to fewer than 10% in Manaus or Peru. Studies of subsets of the avifauna have also commonly shown territories in the 5 ha or smaller range in other Neotropical forests (e.g., Duca *et al.* 2006, Kikuchi 2009).

Species present at Amazonian sites examined so far tend to be quite similar among sites, especially at the genus and family levels (Blake 2007). Of the 155 genera resident in Manaus, 90% are also resident in French Guiana. Even Peru, which is separated from Manaus by several biogeographical barriers (Haffer 1969, Cracraft and Prum 1988), contains 71% of the Manaus genera. Some clades are restricted geographically, such as the absence of Rhinocryptidae in lowlands north of the Amazon. In addition to this pattern, however, some taxa that are generally rare throughout the Amazon are missing from both our plot and the Manaus region, although they were recorded in 100 ha plot surveys elsewhere in the Amazon (Terborgh *et al.* 1990, Thiollay 1994, English 1998, Blake 2007). These absences include some notably large-bodied taxa, such as *Pipile*, *Neomorphus*, and *Xiphocolaptes*.

Interestingly, only 88% of the core forest avifauna was resident in our 100 ha plot, compared to 99% in Peru (Terborgh *et al.* 1990). This suggests that the Manaus community is even more patchy than the Peru

community. In French Guiana, Thiollay (1994) found about 77% of the possible local species in his 100 plot. These results suggest that rarity, or local heterogeneity, is a more important component of central and eastern Amazonian communities than in western Amazonia, although more comparisons among local plots will be necessary to confirm this generalization.

One may argue that we missed species because our sampling effort was less than Terborgh *et al.* (1990). We conducted brief surveys of three other 100 ha continuous forest plots during the study period, and in those plots we found 12 of the 26 core species that were absent from our focal plot. Based on this and our extensive experience in the area, we conclude that many of the absent species are readily detectable even with low sampling effort and should have been detected in our study plot if they had been resident. Another potential problem from reduced sampling could be overlooking territories. We believe this problem is minimal because spot-mapping allowed us to detect most territories many times, and even the weakest-voiced species were detectable using our trail system. Overlooked territories would most likely belong to relatively difficult-to-detect species with large territories that only partially overlap the plot. Examples probably include *Harpia harpyja* and *Cyanicterus cyanicterus*, two core species observed within about 2 km of the plot. Territories of many species, especially less common ones, appear and disappear among years (Stouffer 2007). Certainly our cumulative list of species resident on the plot would increase over time (e.g., Blake 2007), but this does not necessarily mean species were overlooked in our survey.

### Foraging guild structure and biomass

Guild patterns were generally similar to results from other Amazonian studies, particularly for guild contributions to species richness and biomass. In brief, insectivores dominate species richness and number of individuals, but frugivores and granivores (seed predators) dominate biomass. Results so far suggest that arboreal and terrestrial frugivore biomass is reduced in Manaus compared to other Amazonian sites (Terborgh *et al.* 1990, Thiollay 1994, English 1998). This conforms to phenological surveys showing reduced fruit resources on the nutrient-poor Guianan Shield (Gentry and Emmons 1987). It remains to be resolved how productivity patterns across the Amazon influence species richness, biomass partitioning across guilds by trophic level, or relative abundance of large- and small-bodied species (e.g., Stouffer 2007). Growing evidence does show reduced consumer biomass in the central Amazon for various taxa (Emmons 1984, Peres and Dolman 2000, Radtke *et al.* 2007).

### Local variation

Amazonian forests can show local habitat heterogeneity and changes in bird communities due to edaphic and topographic features or microdisturbances (Robinson and Terborgh 1995, Tuomisto *et al.* 2003, Blake 2007). Many species within our 100 ha plot responded to local changes in microhabitat. In some closely-related species pairs, one was found on plateaus and the other was in *baixios* (low, wet areas near streams). For example, we found *Hemitriccus zosterops* primarily in plateaus while *Lophotriccus vitiuosus* was restricted to *baixios* along the small stream that bisected our plot. We also saw this dichotomy in *Formicarius*; *F. colma* was found on plateaus and slopes while *F. analis* was more concentrated in *baixios*. *Formicarius* spp. densities were roughly equal in our plot, but in a nearby 100 ha plot, Stouffer (2007) found about four times as many *F. colma* as *F. analis* in a plot that contained a smaller proportion of *baixios*. The high density of *Hypocnemis cantator*, a gap specialist, was clearly related to the many gaps created by recent storms. Cintra and Cancelli (2008) found that the presence of *Willisornis poecilinotus* territories at the Ducke Reserve, between Manaus and the BDFFP, was highly correlated with increased leaf litter depth, lower elevation, and increased distance from streams. These examples emphasize that local variations in habitat influences bird density at 100 ha scales. No one has yet replicated community-wide density estimates at a local scale, although Blake (2007) and Blake and Loiselle (2009) surveyed two neighboring 100 ha plots in lowland Ecuador and considered differences in the number of detections and mist-net captures to reflect differences in local habitat availability. As predicted, there were local differences in detection rates for many species, although plots were highly similar in species richness and composition.

### Conservation considerations

This study confirms three generalizations about Amazonian bird communities relevant to conservation. First, densities of individual species are low. Supporting populations of any given size will require more area than in other systems (*e.g.*, Stratford and Robinson 2005). Second, most of the avian biomass in these forests is in frugivores and granivores, which are the species most likely to be affected by hunting (*e.g.*, Peres and Palacios 2007). To the extent that these relatively few species are responsible for both seed dispersal and seed predation, they may have considerable effect on tree communities or forest dynamics (*e.g.*, Cramer *et al.* 2007, Terborgh *et al.* 2008). Third, and probably most obviously, these forests are home to fantastic levels of diversity. This observation leads to important unanswered questions. How

is this diversity maintained? For example, how can it be possible for a single 100 ha plot to support 43 species of sallying insectivores? As the Amazon is altered, will it be possible to maintain diversity at this scale? We hope that data like ours, from a site with minimal anthropogenic effects, will be especially useful in evaluating the extent to which secondary or disturbed forests support Amazonian biodiversity (Gardner *et al.* 2007, Chazdon *et al.* 2009). We also encourage other researchers to sample in ways that can lead to absolute measures of diversity, density, and biomass to facilitate whole-community comparisons.

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APPENDIX

Species detected on our study plot, including guild classification (*see* Table 2 for codes), mass classification (*see* Figure 2 for codes), number of spot map detections, number of mist net captures, proportion of the plot occupied, mass/individual (g), total biomass on the plot (g), territory size (ha), number of territorial pairs on the plot, and number of individuals on the plot (Density). + indicates species detected but not considered resident on the plot.

Family (number of resident species)	Species	Guild	Mass class	Det.	Capt.	Occ.	Mass	Biomass	Terr. size	Pairs	Density
Tinamidae (3)	<i>Tinamus major</i>	G, T	10	33	0	95	1112.3	6673.5	31.7	3	6
	<i>Crypturellus soui</i>	+	+	1	0		206.5				+
	<i>Crypturellus variegatus</i>	G, T	8	55	0	95	382.3	3058.0	23.8	4	8
	<i>Crypturellus brevirostris</i>	G, T	8	20	0	35	400.0	600.0	46.7	0.75	1.5
Cracidae (3)	<i>Penelope marail</i>	F, A	9	49	0	100	892.5	5355.0	33.3	3	6
	<i>Penelope jacquacu</i>	F, A	10	2	0		1500.0	750.0		0.25	0.5
	<i>Ortalis motmot</i>	+	+	2	0		502.5				+
	<i>Crax alector</i>	F, T	11	3	0		3106.3	4659.4		0.75	1.5
Odontophoridae (1)	<i>Odontophorus gujanensis</i>	G, T	8	2	0		322.3	322.3			1
Cathartidae (2)	<i>Cathartes melambrotus</i>	Carr.	10	13	0		1650.0	4950.0			3
	<i>Sarcoramphus papa</i>	Carr.	11	4	0		3375.0	6750.0			2
Accipitridae (4)	<i>Elanoides forficatus</i>	+	+	2	0		375.0				+
	<i>Ictinia plumbea</i>	+	+	1	0		242.3				+
	<i>Accipiter superciliosus</i>	R, D	6	0	1		99.8	99.8			1
	<i>Leucopternis albicollis</i>	R, D	8	1	0		480.0	240.0		0.25	0.5
	<i>Buteogallus urubitinga</i>	R, D	10	4	0		1462.0	1462.0		0.5	1
	<i>Spizaetus tyrannus</i>	+	+	1	0		1005.0				+
	<i>Spizaetus ornatus</i>	R, D	10	5	0		1151.7	575.8		0.25	0.5
Falconidae (5)	<i>Micrastur ruficollis</i>	R, D	7	8	0		197.6	197.6		0.5	1
	<i>Micrastur gilvicollis</i>	R, D	7	27	0		211.4	739.9		1.75	3.5
	<i>Micrastur mirandollei</i>	R, D	8	4	0		478.0	956.0		1	2
	<i>Micrastur semitorquatus</i>	R, D	9	2	0		617.5	617.5		0.5	1
	<i>Ibycater americanus</i>	O	9	9	0		595.0	1785.0		0.75	3
	<i>Falco rufifigularis</i>	+	+	1	0		168.8				+
Psophidae (1)	<i>Psophia crepitans</i>	F, T	10	9	0	75	1250.0	12500.0	75.0		10
Eurypyidae (0)	<i>Eurypyga helias</i>	+	+	1	0		188.5				+
Columbidae (3)	<i>Patagioenas plumbea</i>	F, A	7	90	0	95	201.5	3022.5	12.7	7.5	15
	<i>Patagioenas subvinacea</i>	F, A	7	8	0		172.0	519.8		1.75	3.5
	<i>Geotrygon montana</i>	F, T	6	10	6		111.6	669.6			6
Psittacidae (12)	<i>Ara ararauna</i>	G, A	10	11	0		1187.5	1187.5			1
	<i>Ara macao</i>	G, A	10	2	0		1105.0	1105.0			1
	<i>Ara chloropterus</i>	G, A	10	11	0		1379.0	5516.0			4
	<i>Brotogeris chrysoptera</i>	G, A	5	37	0		63.5	190.5			3
	<i>Touit huetii</i>	G, A	5	5	0		60.0	60.0			1
	<i>Touit purpuratus</i>	G, A	5	16	0		60.0	60.0			1
	<i>Pyrilia caica</i>	G, A	7	30	0		132.0	528.0			4
	<i>Pionus menstruus</i>	G, A	7	25	0		252.0	504.0			2
	<i>Pionus fuscus</i>	G, A	7	25	0		204.0	408.0			2
	<i>Amazona autumnalis</i>	G, A	8	16	0		399.5	2397.0			6
	<i>Amazona farinosa</i>	G, A	9	25	0		650.5	1301.0			2
	<i>Deroytus accipitrinus</i>	G, A	7	19	0		245.0	612.5			2.5
Cuculidae (1)	<i>Piaya melanogaster</i>	I, A, G	6	24	0	30	102.0	561.0	10.9	2.75	5.5
	<i>Coccyzus euleri</i>	+	+	2	0		61.0				+
Strigidae (5)	<i>Megascops watsonii</i>	R, N	7	3	0		136.5	546.0		2	4
	<i>Lophostrix cristata</i>	R, N	8	1	0		500.0	1000.0		1	2
	<i>Pulsatrix perspicillata</i>	R, N	9	1	0		785.0	1570.0		1	2
	<i>Ciccaba huhula</i>	R, N	8	1	0		370.0	740.0		1	2
	<i>Glaucidium hardyi</i>	R, N	5	15	0		55.0	110.0		1	2
Nyctibiidae (2)	<i>Nyctibius leucopterus</i>	I, A, S	6	2	0		81.0	162.0		1	2
	<i>Nyctibius bracteatus</i>	I, A, S	5	3	0		52.0	104.0		1	2
Caprimulgidae (2)	<i>Lurocalis semitorquatus</i>	I, Aer	6	9	0		82.8	331.0		2	4
	<i>Nyctidromus albicollis</i>	+	+	4	0		66.0			1	+

Family (number of resident species)	Species	Guild	Mass class	Det.	Capt.	Occ.	Mass	Biomass	Terr. size	Pairs	Density
Apodidae (1)	<i>Caprimulgus nigrescens</i>	I, T, S	5	4	0		39.0	156.0		2	4
	<i>Chaetura spinicaudus</i>	I, Aer.	3	22	0		16.0	112.0			7
	<i>Chaetura chapmani</i>	+	+	1	0		22.0				+
	<i>Tachornis squamata</i>	+	+	1	0		11.0				+
Trochilidae (7)	<i>Florisuga mellivora</i>	N	2	3	1		6.3	12.6		1	2
	<i>Phaethornis bourcieri</i>	N	2	35	6		4.2	42.0			10
	<i>Phaethornis superciliosus</i>	N	2	18	2		5.5	55.0			10
	<i>Heliothryx auritus</i>	N	2	5	0		4.8	19.2		2	4
	<i>Campylopterus largipennis</i>	N	3	10	0		8.2	16.4		1	2
	<i>Thalurania furcata</i>	N	2	13	4		4.3	25.5		3	6
	<i>Hylocharis sapphirina</i>	N	2	2	0		4.1	8.2		1	2
Trogonidae (4)	<i>Trogon melanurus</i>	O	6	33	0	45	87.0	391.5	20.0	2.25	4.5
	<i>Trogon viridis</i>	O	6	59	1	70	84.0	672.0	17.5	4	8
	<i>Trogon violaceus</i>	O	5	38	0	45	47.5	403.8	10.6	4.25	8.5
	<i>Trogon rufus</i>	O	5	33	1	40	49.9	324.4	12.3	3.25	6.5
Alcedinidae (1)	<i>Chloroceryle inda</i>	Aq.	5	1	0		51.9	103.8		1	2
Momotidae (1)	<i>Momotus momota</i>	I, A, S	6	52	5	60	122.2	1343.7	10.9 <sup>†</sup>	5.5	11
Galbulidae (3)	<i>Galbula albirostris</i>	I, A, S	4	21	3	25	17.8	142.4	6.3	4	8
	<i>Galbula leucogastra</i>	+	+	1	0		16.5				+
	<i>Galbula dea</i>	I, A, S	4	64	0	80	29.5	280.3	16.8	4.75	9.5
	<i>Jacamerops aureus</i>	I, A, S	6	16	0	75	69.0	275.9	37.5	2	4
Bucconidae (7)	<i>Notharchus macrorhynchos</i>	I, A, S	6	5	0		93.5	187.0		1	2
	<i>Notharchus tectus</i>	I, A, S	4	3	0		31.8	127.0		2	4
	<i>Bucco tamatia</i>	I, A, S	5	39	0	50	34.3	394.5	8.7	5.75	11.5
	<i>Bucco capensis</i>	I, A, S	5	9	0		52.1	182.4		1.75	3.5
	<i>Malacoptila fusca</i>	I, A, S	5	3	5		44.2	265.2	4.1 <sup>†</sup>	3	6
	<i>Nonnula rubecula</i>	I, A, S	4	1	0		18.5	18.5		1	2
	<i>Monasa atra</i>	I, A, S	6	18	0	20	88.0	1056.0	6.7	3	12
Capitonidae (1)	<i>Capito niger</i>	O	5	20	0	42	56.5	395.5	12.0	3.5	7
Ramphastidae (4)	<i>Ramphastos tucanus</i>	F, A	9	82	0	95	607.5	7897.5	29.2	3.25	13
	<i>Ramphastos vitellinus</i>	F, A	8	22	0	60	370.0	2960.0	30.0	2	8
	<i>Selenidera culik</i>	F, A	7	13	0		147.0	441.0		1.5	3
	<i>Pteroglossus viridis</i>	F, A	7	3	0		136.0	136.0		0.5	1
Picidae (7)	<i>Picumnus exilis</i>	I, B, I	3	14	0	20	9.3	78.6	4.7	4.25	8.5
	<i>Melanerpes cruentatus</i>	+	+	8	0		56.0				+
	<i>Veniliornis cassini</i>	I, B, I	4	15	0	15	31.0	155.0	6.0	2.5	5
	<i>Piculus flavigula</i>	I, B, I	5	22	0	75	53.5	695.5	11.5	6.5	13
	<i>Piculus chrysochloros</i>	I, B, I	6	5	0		76.5	153.0		1	2
	<i>Celeus undatus</i>	I, B, I	6	32	0	70	65.0	422.5	21.5	3.25	6.5
	<i>Celeus elegans</i>	I, B, I	7	1	0		134.7	134.7		0.5	1
	<i>Dryocopus lineatus</i>	+	+	4	0		205.0				+
	<i>Campephilus rubricollis</i>	I, B, I	7	48	0	75	208.5	834.0	35.6	2	4
Furnariidae (8)	<i>Sclerurus mexicanus</i>	I, T, G	4	9	2		24.6	49.2	25.5 <sup>†</sup>	1	2
	<i>Sclerurus rufigularis</i>	I, T, G	4	13	4	30	21.2	74.2	17.1 <sup>†</sup>	1.75	3.5
	<i>Philydor erythrocerum</i>	I, A, DL	4	20	0	80	23.8	333.2	11.4	7	14
	<i>Philydor pyrrhodes</i>	I, A, DL	4	2	0		30.1	60.2		1	2
	<i>Automolus infuscatus</i>	I, A, DL	5	28	4	37	34.8	243.8	10.6	3.5	7
	<i>Automolus rubiginosus</i>	I, A, DL	5	3	1	10	36.4	54.6	13.3	0.75	1.5
	<i>Xenops milleri</i>	I, B, S	3	6	0		12.5	56.3		2.25	4.5
	<i>Xenops minutus</i>	I, B, S	3	23	10	60	12.2	109.8	13.3	4.5	9
	Dendrocolaptinae (13)	<i>Certhiasomus stictolaemus</i>	I, B, S	4	6	8	45	12.9	135.2	12.0	3.5
<i>Dendrocincla fuliginosa</i>		I, A, S	5	28	8	80	37.4	355.7	16.8	4.75	9.5
<i>Dendrocincla merula</i>		I, AF	5	4	17		53.1	637.2			12
<i>Deconychura longicauda</i>		I, B, S	4	21	2	45	29.1	174.6	15.0	3	6
<i>Sittasomus griseicapillus</i>		I, B, S	3	57	2	55	14.3	42.9	36.7	1.5	3
<i>Glyphorhynchus spirurus</i>		I, B, S	3	92	43	85	13.6	448.8	5.2 <sup>†</sup>	16.5	33
<i>Dendrexetastes rufigula</i>		I, A, G	6	15	0	11	70.3	140.5	11.0	1	2
<i>Hylexetastes perrotii</i>		I, B, S	6	37	4	55	114.2	628.1	20.0	2.75	5.5
<i>Dendrocolaptes certhia</i>		I, A, S	6	46	2	60	66.9	468.3	17.1	3.5	7
<i>Dendrocolaptes picumnus</i>		I, A, S	6	17	0	40	78.5	157.0	40.0	1	2

Family (number of resident species)	Species	Guild	Mass class	Det.	Capt.	Occ.	Mass	Biomass	Terr. size	Pairs	Density
	<i>Xiphorhynchus pardalotus</i>	I, B, S	5	147	14	95	37.7	678.6	10.6 <sup>†</sup>	9	18
	<i>Lepidocolaptes albolineatus</i>	I, B, S	4	23	0	60	26.7	266.9	12.0	5	10
	<i>Campylorhynchus procurvoides</i>	I, B, S	5	28	0	36	34.3	102.9	24.0	1.5	3
Thamnophilidae (22)	<i>Cymbilaimus lineatus</i>	I, A, G	5	41	0	55	34.6	346.0	11.0	5	10
	<i>Frederickena viridis</i>	I, A, G	6	7	3	29	67.1	167.8	29.0 <sup>†</sup>	1.25	2.5
	<i>Thamnophilus murinus</i>	I, A, G	4	100	2	70	17.7	442.5	5.6	12.5	25
	<i>Thamnomanes ardesiacus</i>	I, A, S	4	41	25	95	18.1	289.6	10.6	9	18
	<i>Thamnomanes caesioides</i>	I, A, S	4	53	14	95	17.5	280.0	10.6	9	18
	<i>Epinecrophylla gutturalis</i>	I, A, DL	3	24	24	95	8.7	139.2	10.6	9	18
	<i>Myrmotherula brachyura</i>	I, A, G	2	30	0	30	7.0	77.0	5.5	5.5	11
	<i>Myrmotherula guttata</i>	I, A, G	3	1	1		10.3	20.6		1	2
	<i>Myrmotherula axillaris</i>	I, A, G	2	51	12	80	7.6	136.8	8.9	9	18
	<i>Myrmotherula longipennis</i>	I, A, G	3	21	11	95	8.4	134.4	11.9	9	18
	<i>Myrmotherula menetriesii</i>	I, A, G	3	25	4	95	8.1	129.6	11.9	9	18
	<i>Herpilochmus dorsimaculatus</i>	I, A, G	3	89	0	80	10.0	200.0	8.0	10	20
	<i>Hypocnemis cantator</i>	I, A, G	3	100	12	60	11.8	354.0	4.0 <sup>†</sup>	15	30
	<i>Terenura spodioptila</i>	I, A, G	2	23	0	40	7.0	70.0	8.0	5	10
	<i>Cercomacra cinerascens</i>	I, A, G	4	72	0	25	18.0	261.0	3.4	7.25	14.5
	<i>Percnastota rufifrons</i>	I, T, G	4	65	13	45	28.9	462.4	5.6 <sup>†</sup>	8	16
	<i>Schistocichla leucostigma</i>	I, A, G	4	9	0		24.4	48.8		1	2
	<i>Myrmeciza ferruginea</i>	I, T, G	4	69	7	70	24.6	418.2	7.1 <sup>†</sup>	8.5	17
	<i>Myrmornis torquata</i>	I, T, G	5	1	1		44.3	44.3			1
	<i>Pithys albifrons</i>	I, AF	4	15	84		20.1	844.2			42
	<i>Gymnopithys rufigula</i>	I, AF	4	20	48		29.0	580.0			20
	<i>Willisornis poecilinotus</i>	I, A, S	4	42	42	75	16.8	453.6	5.6	13.5	27
Formicariidae (2)	<i>Formicarius colma</i>	I, T, G	5	55	9	50	46.2	508.2	7.3 <sup>†</sup>	5.5	11
	<i>Formicarius analis</i>	I, T, G	5	49	0	30	62.7	344.9	11.5 <sup>†</sup>	2.75	5.5
Grallariidae (2)	<i>Grallaria varia</i>	I, T, G	6	25	0	35	120.1	780.7	9.2	3.25	6.5
	<i>Myrmothera campanisona</i>	I, T, G	5	17	0	8	49.9	99.8	8.0	1	2
Conopophagidae (1)	<i>Conopophaga aurita</i>	I, T, G	4	4			23.6	47.2	6.3 <sup>†</sup>	1	2
Tyrannidae (25)	<i>Tyrannulus elatus</i>	O	2	12	0	10	7.3	25.4	5.7	1.75	3.5
	<i>Myiopagis gaimardii</i>	I, A, S	3	37	0	35	12.5	156.3	5.6	6.25	12.5
	<i>Myiopagis caniceps</i>	I, A, S	3	12	0	15	10.5	52.5	6.0	2.5	5
	<i>Ornithion inermis</i>	I, A, G	2	9	0	10	7.0	21.0	6.7	1.5	3
	<i>Corythopsis torquatus</i>	I, T, S	3	16	0	16	15.9	95.1	5.7 <sup>†</sup>	1.75	3.5
	<i>Zimmerius acer</i>	O	2	65	0	70	7.8	131.8	8.2	8.5	17
	<i>Phylloscartes virescens</i>	I, A, S	2	24	0	30	8.0	64.0	7.5	4	8
	<i>Mionectes macconnelli</i>	O	3	22	19		12.3	270.6			22
	<i>Myiornis ecaudatus</i>	I, A, S	2	3	0		4.2	25.2		3	6
	<i>Lophotriccus vitiosus</i>	I, A, S	2	65	0	25	7.3	94.3	3.8	6.5	13
	<i>Hemitriccus zosterops</i>	I, A, S	3	175	0	60	8.4	260.4	3.9	15.5	31
	<i>Todirostrum pictum</i>	I, A, S	2	14	0		7.0	28.0		2	4
	<i>Tolmomyias assimilis</i>	I, A, S	3	62	0	80	15.3	266.9	9.1	8.75	17.5
	<i>Tolmomyias poliocephalus</i>	I, A, S	3	26	0	15	11.0	55.0	6.0	2.5	5
	<i>Platyrrinchus saturatus</i>	I, A, S	3	2	9		10.3	51.5		2.5	5
	<i>Platyrrinchus coronatus</i>	I, A, S	3	25	1	18	8.6	81.7	3.8	4.75	9.5
	<i>Platyrrinchus platyrhynchus</i>	I, A, S	3	27	1	15	11.9	71.4	5.0	3	6
	<i>Onychorhynchus coronatus</i>	I, A, S	3	0	2		14.4	14.4	37.2 <sup>†</sup>	0.5	1
	<i>Myiobius barbatus</i>	I, A, S	3	19	7		10.4	124.8		6	12
	<i>Terenotriccus erythrurus</i>	I, A, S	2	32	3	20	6.6	56.1	4.7	4.25	8.5
	<i>Legatus leucophaeus</i>	+	+	1	0		24.5				+
	<i>Conopias parvus</i>	I, A, S	4	35	0	55	21.0	189.0	12.2	4.5	9
	<i>Rhytipterna simplex</i>	I, A, S	5	63	0	80	33.5	368.5	14.5	5.5	11
	<i>Sirystes sibilator</i>	I, A, S	5	16	0	20	34.9	52.3	26.7	0.75	1.5
	<i>Ramphotrigon ruficauda</i>	I, A, S	4	8	0		18.7	46.8		1.25	2.5
	<i>Attila spadiceus</i>	I, A, S	5	20	0	24	33.3	99.9	16.0	1.5	3
Cotingidae (5)	<i>Phoenicircus carnifex</i>	F, A	6	25	1		91.2	547.2			6
	<i>Cotinga cayana</i>	F, A	6	2	0		64.3	128.5		1	2

Family (number of resident species)	Species	Guild	Mass class	Det.	Capt.	Occ.	Mass	Biomass	Terr. size	Pairs	Density	
Pipridae (5)	<i>Lipaugus vociferans</i>	F, A	6	97	0		73.8	3247.2			44	
	<i>Xipholena punicea</i>	F, A	6	13	0		66.5	299.3		2.25	4.5	
	<i>Perissocephalus tricolor</i>	F, A	8	30	0		339.0	2712.0			8	
	<i>Tyrannetes virescens</i>	F, A	2	58	0		7.3	246.5		17	34	
	<i>Corapipo gutturalis</i>	F, A	3	40	13		8.1	194.4			24	
	<i>Lepidothrix serena</i>	F, A	3	21	5		10.5	105.0			10	
Tityridae (6)	<i>Pipra pipra</i>	F, A	3	45	35		11.9	476.0			40	
	<i>Pipra erythrocephala</i>	F, A	3	22	2		11.7	152.1			13	
	<i>Tityra cayana</i>	O	6	10	0		69.0	207.0		1.5	3	
	<i>Schiffornis turdina</i>	F, A	5	59	7	45	33.6	184.8	16.4	2.75	5.5	
	<i>Laniocera hypopyrra</i>	O	5	4	0		47.7	95.4		1	2	
	<i>Pachyramphus marginatus</i>	I, A, S	4	26	0	25	18.0	90.0	10.0	2.5	5	
Vireonidae (4)	<i>Pachyramphus surinamus</i>	I, A, S	4	6	0		20.0	40.0		1	2	
	<i>Pachyramphus minor</i>	I, A, S	5	1	0		37.0	74.0		1	2	
	<i>Insertae sedis (1)</i>	<i>Piprites chloris</i>	I, A, G	4	47	0	70	18.0	234.0	10.8	6.5	13
	<i>Cyclarhis gujanensis</i>	+	+	3	0		28.0				+	
	<i>Vireolanius leucotis</i>	I, A, G	4	42	0	65	26.0	286.0	11.8	5.5	11	
	<i>Vireo olivaceus</i>	+	+	4	0		15.5				+	
	<i>Vireo altiloquus</i>	+	+	1	0		19.0				+	
	<i>Hylophilus thoracicus</i>	I, A, G	3	11	0		12.5	25.0		1	2	
	<i>Hylophilus muscicapinus</i>	I, A, G	3	63	0	95	11.0	187.0	11.2	8.5	17	
	<i>Hylophilus ochraceiceps</i>	I, A, G	3	21	8	60	10.0	140.0	8.6	7	14	
	Troglodytidae (3)	<i>Microcerculus bambla</i>	I, T, G	4	12	2		16.5	49.5		1.5	3
		<i>Pheugopedius coraya</i>	I, A, G	4	32	1	10	16.6	107.9	3.1	3.25	6.5
		<i>Cyborhinus arada</i>	I, T, G	4	19	14	40	20.1	90.5	20.0 <sup>†</sup>	2.25	4.5
Poliptilidae (3)	<i>Microbates collaris</i>	I, A, G	3	33	14	20	10.7	107.0	4.0	5	10	
	<i>Ramphocaenus melanurus</i>	I, A, G	3	73	0	75	9.1	127.4	10.7	7	14	
	<i>Poliptila guianensis</i>	I, A, G	2	6	0		5.2	15.6		1.5	3	
Turdidae (1)	<i>Turdus albicollis</i>	O	5	34	4	75	49.2	270.6	27.3	2.75	5.5	
Thraupidae (16)	<i>Lamprospiza melanoleuca</i>	O	5	15	0	30	39.0	136.5	17.1	1.75	3.5	
	<i>Tachyphonus cristatus</i>	O	4	18	0	35	19.5	165.8	8.2	4.25	8.5	
	<i>Tachyphonus surinamus</i>	O	4	31	8		20.5	287.0		7	14	
	<i>Lanio fulvus</i>	I, A, S	4	2	0		25.9	51.8		1	2	
	<i>Ramphocelus carbo</i>	+	+	1	0		24.5				+	
	<i>Thraupis episcopus</i>	+	+	1	0		35.0				+	
	<i>Tangara varia</i>	O	3	28	0		10.0	70.0		3.5	7	
	<i>Tangara punctata</i>	O	3	7	2		13.5	81.0		3	6	
	<i>Tangara chilensis</i>	O	4	7	0		24.0	96.0		2	4	
	<i>Tangara velia</i>	O	4	7	0		21.0	52.5		1.25	2.5	
	<i>Tangara gyrola</i>	O	4	4	0		19.5	78.0		2	4	
	<i>Dacnis lineata</i>	O	3	9	0		13.0	52.0		2	4	
	<i>Dacnis cayana</i>	O	3	4	0		13.0	52.0		2	4	
	<i>Cyanerpes nitidus</i>	O	3	10	0		9.0	54.0		3	6	
	<i>Cyanerpes caeruleus</i>	O	3	5	0		16.0	96.0		3	6	
	<i>Cyanerpes cyaneus</i>	O	3	4	0		14.0	84.0		3	6	
<i>Chlorophanes spiza</i>	O	4	14	0		16.2	81.0		2.5	5		
<i>Hemithraupis flavicollis</i>	I, A, G	4	12	0		17.0	110.5		3.25	6.5		
Incertae sedis (2)	<i>Coereba flaveola</i>	O	3	32	0	50	9.3	111.6	8.3	6	12	
	<i>Salinator grossus</i>	O	5	19	0	20	44.7	134.1	13.3	1.5	3	
Emberizidae (1)	<i>Arremon taciturnus</i>	G, T	4	4	0		24.3	48.6		1	2	
Cardinalidae (2)	<i>Caryothraustes canadensis</i>	O	5	38	0	60	33.0	519.8	11.4	5.25	15.75	
	<i>Cyanocompsa cyanooides</i>	O	4	9	2	21	26.1	52.2	21.0	1	2	
Parulidae (1)	<i>Phaeothlypis rivularis</i>	I, A, G	3	1	0		12.5	12.5		0.5	1	
Icteridae (2)	<i>Psarocolius viridis</i>	O	8	9	0		300.0	600.0			2	
	<i>Cacicus haemorrhous</i>	O	6	26	0		84.5	1225.3			14.5	
	<i>Icterus cayanensis</i>	+	+	3	0		42.0				+	
Fringillidae (2)	<i>Euphonia chrysopasta</i>	F, A	3	5	0		15.0	37.5		1.25	2.5	
	<i>Euphonia cayanensis</i>	F, A	3	23	0	55	13.5	148.5	10.0	5.5	11	

† territory sizes were adjusted by radio-telemetry estimates.