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A Biodiversity Assessment of Bats (Chiroptera) in a Tropical Lowland Rainforest of Central Amazonia, Including Methodological and Conservation Considerations

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Abstract

In our study of bat diversity in the Amazon Basin, we captured bats in undisturbed continuous forest and in forest fragments at the Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil, from January 1996 until July 1999. We recorded 72 species of bats in a sample of more than 7700 individuals caught during 29,900 mistnet hours in terra-firme forest. Species accumulation curves and mathematical estimates of species numbers based on the number of species captured with standardized methodology suggest that we sampled about 95% of the entire expected bat fauna of the area, including aerial insectivorous bats. Our results are similar to those of other mistnetting inventories of Amazonian bat assemblages in terms of species composition and number of species per bat family. Some species considered widespread in Central Amazonia and expected at our study site were not recorded. We interpret their absence as effects of sampling bias and of local ecological conditions. We know from acoustic monitoring (i.e., identification of bats by their echolocation calls) that our mistnet data are incomplete for aerial insectivorous species. We conclude that the development of comprehensive inventories of key vertebrate taxa such as bats derived from a combination of several standardized sampling procedures is essential to develop meaningful, conservation-oriented plans for land-use and management of protected areas.

Resumo

Em nosso estudo sobre diversidade de morcegos na Bacia Amazônica, nós capturamos morcegos em floresta contínua não perturbada e em fragmentos florestais no Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF), próximo à Manaus, Brazil, de Janeiro de 1996 até Julho de 1999. Nós registramos 72 espécies de morcegos capturando cerca de 7700 indivíduos em 29,900 horas de captura em áreas de terra-firme. As curvas de acumulação e modelos matemáticos baseados no número de espécies capturadas com metodologia estandartizada indicam que nós registramos cerca de 95% da fauna esperada para a área, incluindo as capturas de espécies de morcegos aéreos insetívoros. Nossos resultados são equivalentes a outros inventários baseados em redes de captura de morcegos na Amazônia, em termos de composição de espécies e em número de espécies para cada família de morcegos. Algumas espécies consideradas como uniformemente distribuídas na região Amazônica e que deveriam também ocorrer na nossa área de estudo não foram coletadas. Nós interpretamos a ausência de espécies esperadas como um efeito de limitações na metodologia e devido a condições ecológicas locais. Sabemos por monitoramento acústico (identificação de morcegos através dos sinais de ecolocação), que nossos dados de redes de captura estão incompletos para morcegos insetívoros aéreos. Nós concluímos que o desenvolvimento de inventários de grupos

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chave, como morcegos, com a combinação de vários métodos de amostragem estandardizados é essencial para o desenvolvimento de planos conservationistas significativos no uso da terra e no controle de áreas protegidas.

Keywords: Chiroptera, inventories, mistnets, sampling methods, conservation, Central Amazonia.

Introduction

Mammalian diversity in the region of the Brazilian Amazon is very high with about 320 species currently recognized (Fonseca et al., 1996; Voss & Emmons, 1996; Emmons & Feer, 1997). Bats (Chiroptera) account for around 40% of this diversity (see Koopman, 1993; Marinho-Filho & Sazima, 1998). Overall, the region of the Brazilian Amazon, along with the Guyana region (Brosset et al., 1996; Simmons & Voss, 1998; Cosson et al., 1999; Lim & Engstrom, 2001), holds one of the most diverse bat faunas in the Neotropics (e.g., Mok et al., 1982; dos Reis & Peracchi, 1987; Hutterer et al., 1995; Voss & Emmons, 1996; Bernard & Fenton, 2002).

Because of the global biodiversity crisis, caused mainly by anthropogenic habitat destruction and degradation, the search for answers to the questions: 'Which species rely on undisturbed forests' and 'Which species readily adapt to disturbed habitats?' is becoming increasingly important. In this context, detailed studies on the diversity of local species assemblages are crucial, particularly in forests that are seriously affected by the continuing increase of the human population and consequent urbanization and land conversion processes (Dale et al., 1994; Ferreira & Laurance, 1996; Granjon et al., 1996; Whitmore, 1997; Gascon & Lovejoy, 1998; Laurance et al., 1998). Studies on diversity related to conservation issues are needed to develop and apply efficient management programs to preserve and maintain the remaining diversity. However, our knowledge of species diversity is still poor for many taxa. Faunal inventories in the Amazon Basin continue to uncover new species even in well-studied groups such as primates (Ferrari & Lopes, 1992; Mittermeier et al., 1992; Queiroz, 1992; van Roosmalen et al., 1998).

There is increasing evidence that Neotropical bat assemblages are strongly affected by habitat alterations. A common result is the loss of rarer and specialized species and an increase in abundance of a few generalists (Fenton et al., 1992; Simmons & Voss, 1998; Cosson et al., 1999). However, we cannot be sure yet about the overall effects of habitat alterations on bats because most inventories of bat faunas are limited to few sites and to mistnetting at ground level. Adding other methods such as mistnetting in higher forest strata result in a more complete list of species present (e. g., Simmons & Voss, 1998; Kalko & Handley, 2001; Bernard, 2001).

To increase our knowledge about the bats in the Amazon Basin we applied canopy- and ground-level mistnets to inventory bat assemblages near Manaus, Brazil, in the area of the Biological Dynamics of Forest Fragments Project, BDFFP (Bierregaard et al., 1997). Here, we pool the data of two projects that were conducted in parallel at the BDFFP to give a first overview of local species composition. Mistnetting during a period of more than three years revealed new records for some bat species and new information on the distribution patterns of others. To evaluate the quality of our inventory data, we applied the concept of species accumulation curves (Gotelli & Graves, 1996) and species richness estimators (Colwell & Coddington, 1996) and discuss differences between number of recorded and expected species. Detailed analysis of the individual projects are given in subsequent publications (e.g., Bernard, 2001; Berhard & Fenton, 2002).

Materials and methods

Study area

The Biological Dynamics of Forest Fragments Project (BDFFP; Fig. 1), formerly the Minimum Critical Size of Ecosystems project, MCSE (Lovejoy & Bierregaard, 1990), is a cooperative project between the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Smithsonian Institution, Washington, D. C. (USA), represented by the Smithsonian Tropical Research Institute (STRI) in Panamá. The research area is located 80 km north of Manaus (2°24′S, 59°43′W, 2°25′S, 59°45′W; Lovejoy & Bierregaard, 1990). The predominant habitat in this region of the Amazon Basin is unflooded, lowland primary forest (terra-firme). The soils are well-drained, nutrient-poor, yellowish latosols (Chauvel, 1983). The BDFFP area receives between 2200 and 2600 mm of annual precipitation that mostly falls during the rainy season from January to May. The dry season usually extends from June to December. Canopy height is between 30 and 37 m with emergent trees reaching 50 m. The dominant trees belong to the families Chrysobalanaceae, Lecythidaceae, Sapotaceae, Leguminosae, Burseraceae, and Bombacaceae (Gentry, 1990; Prance, 1990; Rankin-De-Merona et al., 1992). The ground level is dominated by palms (Scariot, 1999) of the genera *Astrocaryum*, *Attalea*, and *Bactris*. Flowering and fruiting peaks usually occur in the dry and rainy season, respectively (Rankin-De-Merona et al., 1992).

Mistnetting of bats

We set mistnets at ground level and in the canopy following standardized procedures. Project 1 (Effects of forest fragmentation on bat assemblages) spanned three and a half years (January 1996–June 1999), covering three consecutive rainy and dry seasons. Project 2 (Vertical stratification of bats) ran for one year, from August 1996 to August 1997. We avoided sampling during third-quarter and full moon when light intensity is usually high and bat activity is mostly low

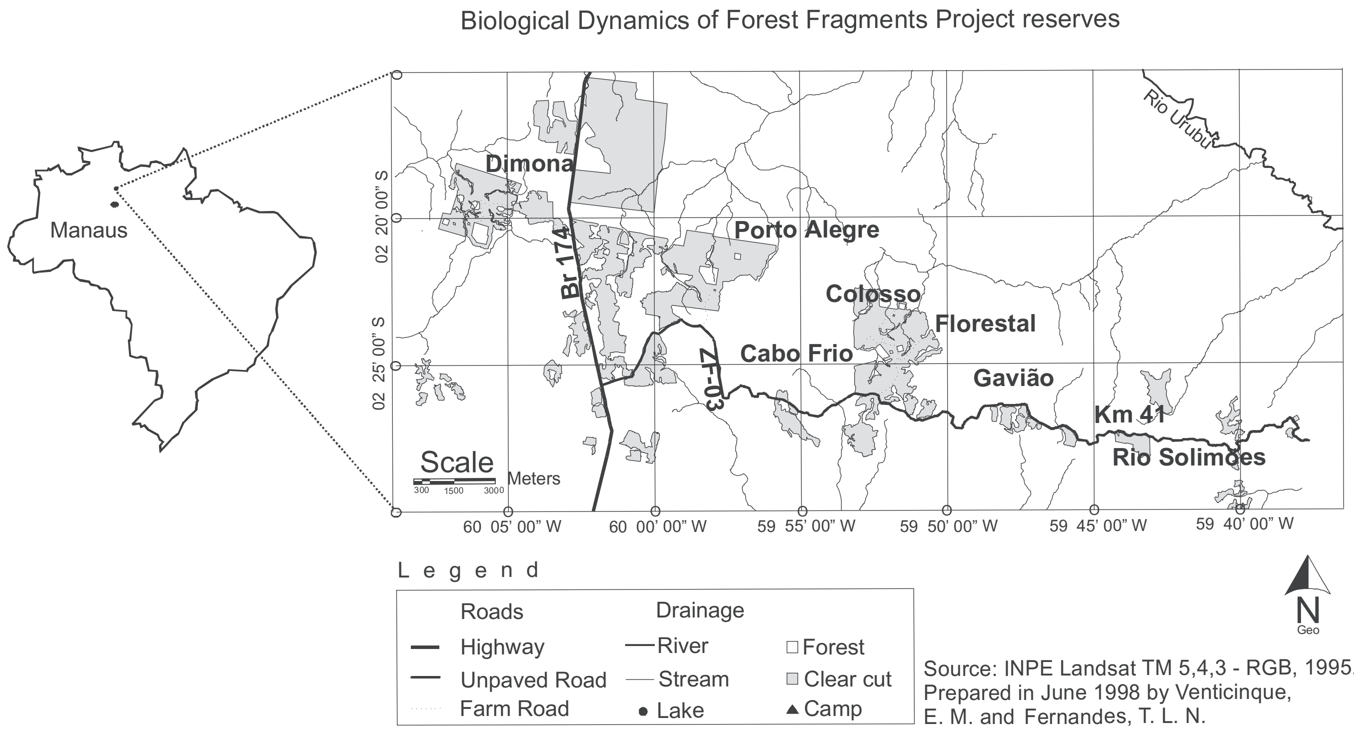

Fig. 1. Experimental area of the Biological Dynamics of Forest Fragmentation Project, about 90 km north from Manaus, Amazonian, Brazil. Map obtained by BDFFP office. Used with permission of the authors.

(Crespo et al., 1972; Morrison, 1978). All mistnets were 12 m long and 2.5 m high, with four shelves and mesh dimensions of 1.5–3 × 1.5–3 cm. We calculated capture effort for each sampling area in mistnet hours. One mistnet hour (mnh) corresponds to one 12-m mistnet open for one hour. Ground nets were tied to poles, with the first shelf string at ground level. Canopy nets were set in treefall gaps by using a pulley system following the technique described by Humphrey et al. (1968), a system successfully applied in previous bat studies (Handley, 1967; Kalko & Handley, 2001). After capture, we removed bats from the mistnets and placed them temporarily in soft cloth bags. Bats were identified using a dichotomous key for the bats of the Amazon Basin developed by Handley, Sampaio, and Kalko (unpublished). The taxonomy used herein follows Koopman (1993), with the exception of *Anoura caudifer, Artibeus* (*Koopmania*) *concolor, Eptesicus chiriquinus, Glyphonycteris daviesi*, *Glyphonycteris sylvestris, Lampronycteris brachyotis*, and *Trinycteris nicefori* that follow the classification of Simmons & Voss (1998) and the subdivision of the genus *Tonatia* into *Lophostoma* and *Tonatia* proposed by Lee et al. (2002). With the exception of rare species or species whose identification was problematic, all bats were released at the respective capture sites. Bats collected for further identification and a few individuals that died during handling were fixed in 10% formaldehyde and preserved in 70% alcohol as voucher specimens (Handley, 1988). Vouchers (n = 124) were sent for identification to the National Museum of Natural History (NMNH), Washington, DC (USA) and were subsequently deposited in the INPA collection in Manaus for further reference (Table 1).

Project 1

In Project 1, we collected bats with mistnets set at ground level in a variety of habitat types. We sampled bats on standardized transects in three replicates each of 1 and 10 ha forest fragments (Colosso, Dimona, and Porto Alegre) and in three replicates each of 1 and 10 ha plots embedded in continuous forest (Cabo Frio, Florestal, and km 41) resulting in a total of 12 study sites (Fig. 1). The transects design was adapted to the existing trail system which consisted of parallel lanes crossing the fragments or plots in N–S direction. Seven 12-m mistnets were set. The capture effort for each replica was about 150 mnh per mistnet night. In addition to the transects, we repeatedly collected bats with ground mistnets in three different pasture areas, in secondary growth composed of *Vismia* sp. and *Cecropia* sp., and at three forest edges, penetrating up to 400 m into continuous forest. We opened the nets from 18:00 until 24:00 and patrolled them at 20-minute intervals. The total capture effort in project 1 amounted to 28,000 mnh. In addition to the transects, we occasionally set nets in the BDFFP area across streams or near water and in front of potential bat roosts. We also netted outside the BDFFP near the road ZF2 leading to silvicultural research sites of EMBRAPA (Brazilian Agricultural Research Corporation) and at the entrances of caves near the village of Presidente Figueiredo about 100 km

Table 1. Specimens collected during the field work and deposited at the mammal collection of the Zoological Museum at INPA, Manaus (Dr. Maria Nazareth Pereira da Silva, curator). The data given are: INPA number, species, locality[1], collector[2], and date.

INPA 2493, *Lasiurus* cf. *castaneus*, 'PDBFF, km 41', C. O. H., 26.01.96; INPA 2494, *Lasiurus* cf. *castaneus*, 'PDBFF, km 41', C. O. H., 26.01.96; INPA 2495, *Centronycteris maximiliani*, 'PDBFF, CO', E. M. S., 16.02.96; INPA 2496, *Phyllostomus latifolius*, Pres. Fig., C. O. H., 19.11.97; INPA 2497, *Phyllostomus latifolius*, Pres. Fig., C. O. H., 19.11.97; INPA 2498, *Lionycteris spurrelli*, 'PDBFF, GA', E. B., 12.04.97; INPA 2499, *Micronycteris microtis*, 'PDBFF, GA', E. B., 07.02.97; INPA 2500, *Trinycteris nicefori*, 'PDBFF, GA', E. B., 13.02.97; INPA 2501, *Micronycteris schmidtorum*, 'PDBFF, GA', E. B., 06.08.97; INPA 2502, *Centronycteris maximiliani*, 'PDBFF, GA', E. B., 30.04.97; INPA 2503, *Cynomops abrasus*, 'PDBFF, km 41', E. B., 01.02.97; INPA 2504, *Peropteryx leucopterus*, 'PDBFF, FLO', E. M. S., 26.08.97; INPA 2505, *Carollia brevicauda*, 'PDBFF, FLO', E. M. S., 13.06.97; INPA 2506, *Choeroniscus minor*, 'PDBFF, FLO', E. M. S., 26.08.97; INPA 2507, *Trinycteris nicefori,* 'PDBFF, FLO', E. M. S., 26.08.97; INPA 2508, *Myotis riparius*, 'PDBFF, CO', E. M. S., 18.06.97; INPA 2509, *Myotis riparius*, 'PDBFF, GA', E. M. S., 24.01.97; INPA 2510, *Eptesicus chiriquinus*, 'PDBFF, km 41', E. M. S., 04.02.97; INPA 2536, *Ametrida centurio*, 'PDBFF, GA', E. B., 09.08.97; INPA 2537, *Artibeus gnomus*, 'PDBFF, km 41', E. B., 31.10.96; INPA 2538, *Vampyressa brocki*, 'PDBFF, km 41', E. B., 31.10.96; INPA 2539, *Eptesicus chiriquinus*, 'PDBFF, km 41', E. B., 30.01.97; INPA 2540, *Lophostoma schulzi*, 'PDBFF, GA', E. B., 06.08.97; INPA 2541, *Centronycteris maximiliani*, 'PDBFF, DI', E. M. S., 23.09.97; INPA 2542, *Cormura brevirostris*, 'PDBFF, CO', E. M. S., 21.11.97; INPA 2543, *Saccopteryx leptura*, 'PDBFF, CO', E. M. S., 21.11.97; INPA 2544, *Molossus molossus*, 'PDBFF, DI', E. M. S., 05.10.97; INPA 2545, *Glyphonycteris sylvestris*, 'PDBFF, FLO', E. M. S., 04.11.97; INPA 2546, *Lophostoma schulzi*, 'PDBFF, km 41', E. M. S., 26.10.96; INPA 2547, *Platyrrhinus helleri*, 'PDBFF, PA', E. M. S., 03.12.97; INPA 2548, *Myotis nigricans*, 'PDBFF, PA', E. M. S., 14.10.97; INPA 2549, *Myotis riparius*, 'PDBFF, km 41', E. M. S., 28.10.96; INPA 2571, *Choeroniscus minor*, 'PDBFF, DI', E. M. S., 15.01.98; INPA 2572, *Saccopteryx leptura*, 'PDBFF, km 41', E. M. S., 27.01.98; INPA 2573, *Myotis* sp., 'PDBFF, CO', E. M. S., 06.02.98; INPA 2574, *Trinycteris nicefori*, 'PDBFF, PA', E. M. S., 09.02.98; INPA 2575, *Centronycteris maximiliani*, 'PDBFF, FLO', E. M. S., 09.03.98; INPA 2576, *Molossus molossus*, ZF3 km 18, E. M. S.; INPA 2577, *Choeroniscus minor*, 'PDBFF, FLO', E. M. S., 08.03.98; INPA 2578, *Glyphonycteris daviesi*, 'PDBFF, DI', E. M. S., 18.02.98; INPA 2579, *Micronycteris minuta*, 'PDBFF, FLO', E. M. S., 09.03.98; INPA 2622, *Carollia perspicillata*, 'PDBFF, PA', E. M. S., 06.03.96; INPA 2623, *Carollia perspicillata*, 'PDBFF, PA', E. M. S., 06.03.96; INPA 2624, *Pteronotus parnellii*, 'PDBFF, km 41', E. M. S., 20.03.96; INPA 2625, *Glyphonycteris daviesi*, 'PDBFF, km 41', E. M. S., 24.03.96; INPA 2626, *Carollia brevicauda*, 'PDBFF, PA', E. M. S., 12.10.96; INPA 2627, *Carollia perspicillata*, 'PDBFF, PA', E. M. S., 12.10.96; INPA 2628, *Peropteryx macrotis*, Pres. Fig., E. M. S., 20.11.96; INPA 2629, *Carollia perspicillata*, 'PDBFF, CO', E. M. S., 06.12.96; INPA 2630, *Carollia perspicillata*, 'PDBFF, CO', E. M. S., 07.12.96; INPA 2631, *Micronycteris minuta*, Silv. Treat., E. M. S.; INPA 2632, *Ametrida centurio*, 'PDBFF, DI', E. M. S., 02.08.97; INPA 2633, *Ametrida centurio*, 'PDBFF, DI', E. M. S., 02.08.97; INPA 2634, *Pteronotus parnellii*, 'PDBFF, PA', E. M. S., 05.08.97; INPA 2635, *Carollia perspicillata*, 'PDBFF, DI', E. M. S., 07.10.97; INPA 2636, *Sturnira tildae*, 'PDBFF, PA', E. M. S., 09.10.97; INPA 2637, *Carollia perspicillata*, 'PDBFF, CO', E. M. S., 22.11.97; INPA 2638, *Carollia brevicauda*, 'PDBFF, DI', E. M. S., 14.01.98; INPA 2639, *Carollia perspicillata*, 'PDBFF, CO', E. M. S., 06.02.98; INPA 2640, *Mimon crenulatum*, 'PDBFF, DI', E. M. S., 18.02.98; INPA 2641, *Lonchophylla thomasi*, 'PDBFF, FLO', E. M. S., 31.05.97; INPA 2642, *Carollia perspicillata*, 'PDBFF, CO', E. M. S., 18.06.97; INPA 2643, *Thyroptera tricolor*, 'PDBFF, DI', E. M. S., 24.09.97; INPA 2644, *Carollia perspicillata*, 'PDBFF, PA', E. M. S., 02.12.97; INPA 2645, *Carollia brevicauda*, 'PDBFF, km 41', E. M. S., 12.04.98; INPA 2646, *Artibeus jamaicensis*, 'PDBFF, km 41', E. M. S., 13.04.98; INPA 2647, *Carollia perspicillata*, 'PDBFF, PA', E. M. S., 14.04.98; INPA 2648, *Saccopteryx* cf. *canescens*, 'PDBFF, DI', E. M. S., 16.04.98; INPA 2649, *Uroderma* cf. *magnirostrum*, 'PDBFF, DI', E. M. S., 16.04.98; INPA 2650, *Cormura brevirostris*, 'PDBFF, km 41', E. M. S., 12.04.98; INPA 2651, *Glyphonycteris sylvestris*, 'PDBFF, CO', E. M. S., 05.05.98; INPA 2652, *Tonatia saurophila*, 'PDBFF, km 41', E. M. S., 24.05.98; INPA 2653, *Centronycteris maximiliani*, 'PDBFF, km 41', E. M. S., 25.05.98; INPA 2654, *Artibeus jamaicensis*, 'PDBFF, km 41', E. B., 31.08.96; INPA 2655, *Cormura brevirostris*, 'PDBFF, km 41', E. B., 03.09.96; INPA 2656, *Koopmania concolor*, 'PDBFF, km 41', E. B., 05.09.96; INPA 2657, *Myotis* sp., 'PDBFF, GA', E. B., 04.10.96; INPA 2658, *Molossops greenhalli*, 'PDBFF, GA', E. B., 01.09.96; INPA 2659, *Eptesicus andinus*, 'PDBFF, km 41', E. B., 03.09.96; INPA 2688, *Artibeus cinereus*, 'PDBFF, DI', B. R.-H, 31.08.98; INPA 2691, *Carollia perspicillata*, 'PDBFF, FLO', B. R.-H, 23.04.98; INPA 2692, *Platyrrhinus helleri*, 'PDBFF, DI', B. R.-H, 04.08.98; INPA 2693, *Cormura brevirostris*, 'PDBFF, DI', B. R.-H, 05.08.98; INPA 2694, *Rhynchonycteris naso*, Silv. Treat., E. M. S., 29.08.98; INPA 2695, *Phylloderma stenops*, 'PDBFF, DI', B. R.-H, 14.09.98; INPA 2696, *Choeroniscus* cf. *minor*, 'PDBFF, FLO', B. R.-H, 15.09.98; INPA 2697, *Lonchophylla thomasi*, JAU, B. R.-H, 06.09.98; INPA 2698, *Myotis riparius*, JAU, B. R.-H, 07.09.98; INPA 2699, *Cormura brevirostris*, JAU, B. R.-H, 07.09.98; INPA 2700, *Trachops cirrhosus*, JAU, B. R.-H, 07.09.98; INPA 2701, *Vampyrum spectrum*, 'PDBFF, CF', B. R.-H, 24.09.98; INPA 2702, *Trachops cirrhosus*, 'PDBFF, CF', B. R.-H, 25.09.98; INPA 2703, *Thyroptera discifera*, 'PDBFF, CF', B. R.-H, 26.09.98; INPA 2704, *Thyroptera discifera*, 'PDBFF, CF', B. R.-H, 26.09.98; INPA 2705, *Myotis* sp., 'PDBFF, CF', B. R.-H, 26.09.98; INPA 2706, *Phylloderma stenops*, 'PDBFF, CF', B. R.-H, 26.09.98; INPA 2707, *Ametrida centurio*, 'PDBFF, PA', B. R.-H, 13.10.98; INPA 2708, *Vampyressa bidens*, 'PDBFF, PA', B. R.-H, 13.10.98; INPA 2709, *Phylloderma stenops*, 'PDBFF, CO', B. R.-H, 16.10.98; INPA 2710, *Artibeus cinereus*, 'PDBFF, CO', B. R.-H, 16.10.98; INPA 2711, *Carollia brevicauda*, 'PDBFF, CO', B. R.-H, 16.10.98; INPA 2712, *Lophostoma brasiliense*, 'PDBFF, CO', B. R.-H, 17.10.98; INPA 2723, *Ametrida centurio*, 'PDBFF, DI', B. R.-H, 04.11.98; INPA 2724, *Trachops cirrhosus*, 'PDBFF, CF', B. R.-H, 17.11.98; INPA 2725, *Trinycteris nicefori*, 'PDBFF, CF', B. R.-H, 18.11.98; INPA 2726, *Sturnira lilium*, 'PDBFF, PA', B. R.-H, 15.12.98; INPA 2727, *Platyrrhinus helleri*, 'PDBFF, PA', B. R.-H, 15.12.98; INPA 2728, *Desmodus rotundus*, 'PDBFF, DI', B. R.-H, 26.11.98; INPA 2729, *Artibeus jamaicensis*, 'PDBFF, DI', B. R.-H, 26.11.98; INPA 2839, *Platyrrhinus helleri*, 'PDBFF, CO', E. B., 17.01.99; INPA 2840, *Saccopteryx canescens*, 'PDBFF, DI', E. B., 20.01.99; INPA 2841, *Molossus molossus*, 'PDBFF, DI', E. B., 21.01.99; INPA 2842, *Molossus molossus*, 'PDBFF, DI', E. B., 21.01.99; INPA 2843, *Artibeus anderseni*, 'PDBFF, CO', E. B., 02.02.99; INPA 2844, *Carollia perspicillata*, 'PDBFF, GA', E. B., 03.02.99; INPA 2845, *Glyphonycteris daviesi*, 'PDBFF, GA', E. B., 03.02.99; INPA 2846, *Lonchophylla thomasi*, 'PDBFF, CF', E. B., 20.03.99; INPA 2847, *Rhinophylla pumilio*, 'PDBFF, CO', E. B., 09.04.99; INPA 2848, *Uroderma bilobatum*, 'PDBFF, CO', E. B., 11.04.99; INPA 2849, *Platyrrhinus* cf. *helleri*, 'PDBFF, CO', E. B., 11.04.99; INPA 2850, *Myotis nigricans*, 'PDBFF, PA', E. B., 19.05.99; INPA 2851, *Carollia* cf. *castanea*, 'PDBFF, CF', E. B., 05.06.99; INPA 2852, *Carollia perspicillata*, 'PDBFF, CF', E. B., 05.06.99; INPA 2853, *Artibeus obscurus*, 'PDBFF, CF', E. B., 05.06.99.

[1] Reserves: CF = Cabo Frio reserves, CO = Colosso reserves, DI = Dimona reserves, FLO = Florestal reserve, GA = Gaviao reserve, PA = Porto Alegre reserves, Pres. Fig = Presidente Figueiredo, Silv. Treat = Silvicultural Treatment.
[2] Collector(s): B. R.-H = Bernal Rodriguez C. O. H. = Charles O. Handley, Jr., E. B. = Enrico Bernard, and E. M. S. = Erica Sampaio. Cf. = to confirm, *Myotis* sp. = *M. riparius* o. *nigricans*.

north of the BDFFP. Capture effort at the additional sites varied from 30 to 100 mnh per night. The additional species that we collected outside the BDFFP areas are listed but they are not included in the evaluation of the completeness of our samples.

Project 2

Ground and high nets (height 17 to 30 m) were set inside 17 small tree-fall gaps in undisturbed forest (Gavião, km 41; Fig.1). Additionally, ground-level mistnets were placed in the forest near gaps. Sampling took place for 12 hours per night. The mistnets were opened at 18:00 and checked at intervals of 20 to 45 minutes. Each gap was sampled five times at 50 day intervals during the study period (August 1996–August 1997). Because the number of mistnets used in each gap differed, total capture effort per gap varied between 114–322 mnh. Total capture effort of project 2 encompassed 3398.5 mnh (Bernard, 2001; Bernard & Fenton, 2002).

Species accumulation curve

To qualitatively assess the completeness of our data, we pooled the data from both projects and plotted the number of newly recorded species against the number of individuals captured (Fig. 2a). We randomized the data of the species accumulation curves to minimize the effect of order in which the nights and hence the species captured accumulated on the x-axis (see Colwell & Coddington, 1996). For the number of sampled individuals (x-axis) we excluded all subsequent recaptures at a given capture site. We applied parametric and non-parametric estimators to our data (Chao, 1984; Bunge & Fitzpatrick, 1993; Colwell & Coddington, 1996) to quantify sampling completeness and to estimate the minimum capture effort necessary to achieve a satisfactory result of local species richness (>90% of the expected species).

Guild classification

We classified all bats captured in this study into guilds following Kalko (1997) and Schnitzler and Kalko (1998). Each guild consists of species foraging in similar ways in similar habitats for similar foods (Root, 1967).

Complementarity

In order to estimate the number of species common to both projects and at both levels (ground and canopy) we calculated the index of complementarity U/S_{total} as described in Colwell and Coddington (1996):
Where U is the number of unshared species or

$$\text{Uniques} = S_1 + S_2 - 2 * \text{Shared species}$$
$$\text{and } S_{total} = S_1 + S_2 - \text{Shared species}$$

(S_1 = number of species in project 1; S_2 = number of species in project 2).

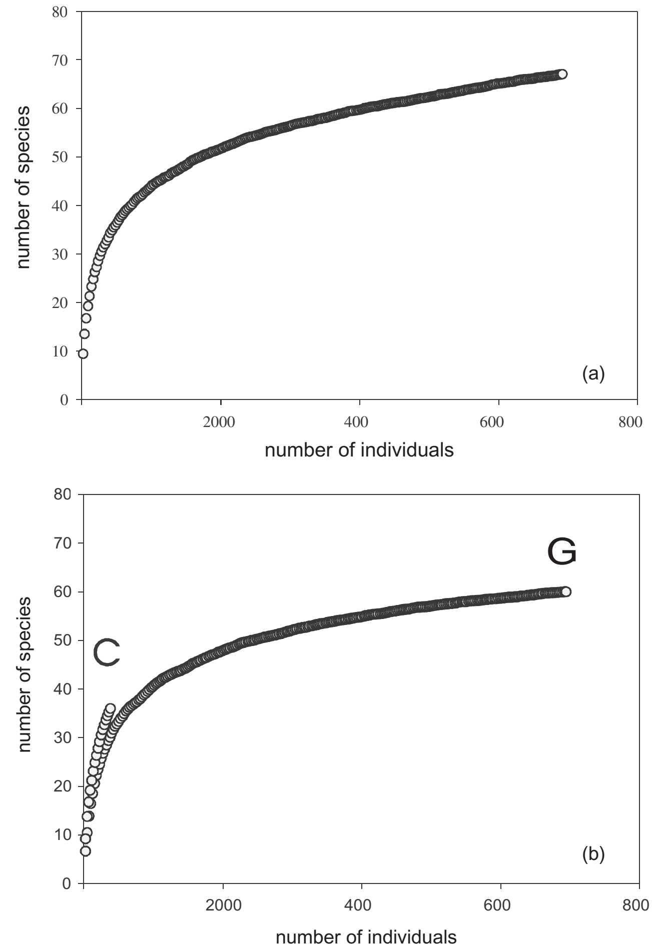

Fig. 2. Species accumulation curves (randomized × 100) of the bats sampled with mistnets at the BDFFP project near Manaus, Brazil. (a) Data of both projects pooled; (b) data presented separately for canopy- (C) and ground-level (G) mistnets.

Results

The bat fauna of the BDFFP

Pooling both ground and canopy netting data sets, we documented six of the nine families of bats expected to occur in the area of Central Amazonia (Koopman, 1993; Voss & Emmons, 1996; Emmons & Feer, 1997; Marinho-Filho & Sazima, 1998). We did not sample members of three families (Noctilionidae, Natalidae, and Furipteridae) within the BDFFP (but see results on species caught outside the BDFFP). In project 1 (forest fragmentation) more than 6700 bats were caught in about 26,500 mnh (Table 2). We obtained 61 species with confirmed identifications representing 39 genera and six families. The pooled capture rate per sample area averaged 0.16 bats/mnh. The most common species in the forest fragments was *Carollia perspicillata* (52% of all captures), followed by *Rhinophylla pumilio* (9%), and *Artibeus obscurus* (7.6%). This pattern differed for the plots in continuous forest. There, *Rhinophylla pumilio* was the most

Table 2. Summary of both projects including ground- and canopy-level mistnetting. Mnh = mistnet hour (one 12-m mistnet open for one hour).

Localities	Nights (*N*)	Mnh	No. of ind.	No. of recaptures	Families (*N*)	Genera (*N*)	Species (*N*)
Project 1 (fragmentation)							
Reserve km 41	39	4,011	507	41 (8%)	5	24	43
Florestal	28	3,876	991	49 (4.9%)	5	25	38
Cabo Frio	18	2,583	473	12 (2.5%)	5	20	32
Dimona	31	3,613	572	41 (7.1%)	5	20	31
Porto Alegre	39	3,696	1013	100 (9.8%)	4	23	37
Colosso	35	3,822	1037	91 (8.7%)	4	24	44
Forest edges	22	3,511	516	60 (11.6%)	5	20	28
Secondary growth	38	1,419	1671	133 (8%)	5	24	44
Total	250	26,531	6780	527 (8.2%)	6	34	61
Project 2 (vertical stratification)							
Reserve km 41	34	1,738.50	271	2 (0.7%)	5	22	33
Gavião	30	1,680.50	665	7 (1.05%)	6	32	48
Total	64	3,419.00	936	9 (0.9%)	6	32	52
Ground vs. canopy mistnets							
Ground mistnets	294	28,875	7333		6	38	62
Canopy mistnets	20	1,075	383		5	24	36
Pooled data	314	29,950	7716		6	40	67

common species with 10% of total captures followed by *Pteronotus parnellii* (5%). We achieved a recapture rate of about 8–10% for most areas with the exception of the plots in continuous forest (Cabo Frio, Florestal) with lower recapture rates (2.5% and 4.9%) (Table 2).

Project 2 (vertical stratification) accumulated a total of 936 individuals in about 3400 mnh representing 52 species in 32 genera and six families (Table 2). Of those, 37 species were recorded in the canopy nets. As in the ground-nets set in the forest fragments, three frugivorous species made up more than half (57.9%) of all captures. *Carollia perspicillata* had the highest capture rate followed by *Artibeus (Koopmania) concolor*, and *Rhinophylla pumilio*. Pooling the data from project 1 and 2 revealed that five species (*Micronycteris schmidtorum, Chiroderma villosum, Vampyressa brocki, Diaemus youngi*, and *Molossops (Cynomops) abrasus* were exclusively captured in canopy nets (Table 3). Each of these species was represented only by one individual.

Overall, nets in the canopy showed a higher average capture rate per sampling effort (0.36 bats/mnh) than the ground-level mistnets in project 2 (0.26 bats/mnh) and in project 1 (0.16 bats/mnh). Recapture rates in the canopy were much lower than in the groundnets of project 1 and 2, ranging from 0.7 to 1.05 bats/mnh (Table 2).

Species recorded outside the BDFFP area

At the silvicultural research site (ZF2), our brief netting sessions yielded two *Furipterus horrens* (Furipteridae) and one *Rhynchonycteris naso* (Emballonuridae). In Presidente Figueiredo, we caught *Peropteryx kappleri* and *P. macrotis* (Emballonuridae) and the rare *Phyllostomus latifolius* (Phyllostominae). The two specimens of *P. latifolius* are clearly distinct in forearm length and cranial measurements from the similar-looking, syntopic *P. elongatus*.

Species accumulation curve

We sampled a total of 67 species with standardized ground and canopy mistnets. This corresponds to more than 90% of the number of species (63–78) predicted by most of the selected species-richness estimators (Table 4). We therefore consider our sample as a satisfactory approximation of the total number of species. Based on our species accumulation curve (Fig. 2a), we conclude that about 2000 captures of individuals are needed to reach the 75% mark, and that more than 6700 captures of individuals are required to reach about 95% of the expected number of species. Adding the five species to our list that we captured outside the BDFFP area brings the total number of species up to 72.

Table 3. Species list of bats captured with ground and canopy mistnets between January 1996 and July 1999 in the area of the BDFFP near Manaus, Brazil. See Table 4 for description of feeding guilds.

	Project 1	Project 2				
	Ground mistnets	Ground mistnets	Canopy mistnets	New occurrence	Conservation status	Guild
Emballonuridae						
Centronycteris maximiliani	x	–	x	*	(–)	II
Cormura brevirostris	x	x	x		(–)	II
Peropteryx leucoptera	x	–	–		(–)	II
Saccopteryx bilineata	x	x	x		(–)	I
Saccopteryx canescens	x	–	x		(–)	II
Saccopteryx leptura	x	–	x		(–)	II
Mormoopidae						
Pteronotus gymnonotus	x	–	–	(*)	(–)	II
Pteronotus parnellii	x	x	–		(–)	III
Phyllostomidae-Phyllostominae						
Chrotopterus auritus	x	x	–		(±)	V
Glyphonycteris daviesi	x	–	–	*	(±)	IV
Glyphonycteris sylvestris	x	x	–		(±)	IV
Lampronycteris brachyotis	x	–	–		(–)	IV
Lophostoma brasiliense	x	x	–		(–)	IV
Lophostoma carrikeri	x	–	–		(±)	IV
Lophostoma schulzi	x	x	–		(±)	IV
Lophostoma silvicola	x	x	x		(–)	IV
Micronycteris hirsuta	x	x	–		(–)	IV
Micronycteris megalotis	x	x	–		(–)	IV
Micronycteris microtis		x			(–)	IV
Micronycteris minuta	x	–	–		(±)	IV
Micronycteris schmidtorum	–	–	x		(–)	IV
Mimon crenulatum	x	x	x		(–)	IV
Phylloderma stenops	x	x	x		(±)	VIIIb
Phyllostomus discolor	x	–	x		(–)	X
Phyllostomus elongatus	x	x	–		(–)	X
Phyllostomus hastatus	x	–	x		(–)	X
Tonatia saurophila	x	x	x		(–)	IV
Trachops cirrhosus	x	x	–		(–)	V
Trinycteris nicefori	x	x	–		(–)	IV
Vampyrum spectrum	x	–	–		(+)	V
Glossophaginae						
Anoura caudifer	x	–	–		(–)	IX
Choeroniscus minor	x	x	x		(–)	IX
Glossophaga soricina	x	–	x		(–)	IX
Lonchophyllinae						
Lionycteris spurrelli	x		x		(±)	IX
Lonchopylla thomasi	x	x	–		(±)	IX
Carollinae						
Carollia brevicauda	x	x	–		(–)	VIIIb
Carollia perspicillata	x	x	x		(–)	VIIIb
Rhinophylla pumilio	x	x	x		(–)	VIIIb
Stenodermatinae						
Ametrida centurio	x	x	x		(–)	VIIIb
Artibeus cinereus	x	x	x		(–)	VIIIa
Artibeus (Koopmania) concolor	x	x	x		(–)	VIIIa
Artibeus gnomus	x	x	x		(–)	VIIIa
Artibeus jamaicensis	x	x	x		(–)	VIIIa
Artibeus lituratus	x	x	x		(–)	VIIIa

Table 3. *Continued*

	Project 1 Ground mistnets	Project 2 Ground mistnets	Project 2 Canopy mistnets	New occurrence	Conservation status	Guild
Artibeus obscurus	x	x	x		(–)	VIIIa
Chiroderma trinitatum	x	x	x		(–)	VIIIa
Chiroderma villosum	–	–	x		(–)	VIIIa
Ectophylla macconnelli	x	x	x		(–)	VIIIb
Platyrrhinus helleri	x	–	–		(–)	VIIIa
Sturnira lilium	x	x	x		(–)	VIIIb
Sturnira tildae	x	x	x		(–)	VIIIb
Uroderma bilobatum	x	–	x		(–)	VIIIb
Vampyressa bidens	x	–	x		(–)	VIIIa
Vampyressa brocki			x			
Desmodontinae						
Desmodus rotundus	x	x	–		(–)	VI
Diaemus youngi	–	–	x		(–)	VI
Thyropteridae						
Thyroptera discifera	x	–	–	*	(–)	II
Thyroptera tricolor	x	x	–		(–)	II
Vespertilionidae						
Eptesicus chiriquinus	x	x	x		(–)	II
Lasiurus castaneus	(x)	–	–	*	(–)	II
Myotis albescens	x	–	–		(–)	II
Myotis nigricans	x	–	–		(–)	II
Myotis riparius	x	x	–		(–)	II
Molossidae						
Molossops (Cynomops) abrasus	–	–	x		(–)	I
Molossops (Cynomops) greenhalli	x	–	x		(–)	I
Molossus bondae	x	–	–		(–)	I
Molossus molossus	x	–	–		(–)	I
		37	36			
Total number of species				67		
Project 1	61					
Project 2	52					
Ground mistnetting	62					
Canopy mistnetting	36					
Complementarity indices						
Project 1 × Project 2	0.29					
Ground × canopy mistnetting	0.51					

* = Species that have not been previously reported in the literature for the Manaus area; x = captured and identified species; (x) = preliminary identification; * new occurrence for the area with voucher specimen. All voucher specimens are deposited and listed at INPA, Manaus (see Table 1). (*) = New occurrence without voucher specimen. Conservation status (–) = stable; (±) = potentially vulnerable; (+) = vulnerable (Aguiar & Taddei, 1995; Wilson, 1996). Complementarity indices follow Colwell and Coddington (1996).

Complementarity of ground and canopy mistnetting

The estimated completeness of the bat fauna was lower for the canopy mistnets (between 73 and 85%) than for the ground-level mistnets, which actually exceeded the respective estimates (>100%; Table 4). The complementarity of species captured between both projects was 0.29. Project 1 yielded 17 unique species in contrast to five species that were taken only in the canopy nets. Complementarity between both netting placements (ground vs. canopy) was 0.51 with 31 species that were exclusively captured in ground-level mistnets (Table 3).

Because the collecting effort in project 1 (forest fragmentation) was much higher than in project 2 (vertical

Table 4. Results of selected species richness estimators for the expected number of species sampled during both projects ($N = 7716$ individuals) at the BDFFP in ground ($N = 62$ species) and canopy ($N = 36$ species) mistnets. SD = standard deviation; ACE = Incidence Coverage Estimator; Jack1 = Jacknife 1 estimator; MMMean = Michaelis–Menten Mean estimator.

Estimators*	Pooled data all mistnets	SD	% complete	Ground mistnets	SD	% complete	Canopy mistnets	SD	% complete
ACE	72.7	0.4	93	56.3	0.2	110	45.1	2.5	78
Chao1	70	4	97	56.0	0.3	110	41	4.2	85
Jack1	79	4.5	86	60	2.4	103	48.2	2.9	73
Bootstrap	72		94	58.4		106	41.8		83
MMMean	63.2		>100	55.4		111	42		83

*Estimates: http://viceroy.eeb.uconn.edu/estimates, R. K. Colwell (1999).

Table 5. Guild structure of the bat fauna sampled in the BDFFP area based on ground and canopy mistnetting.

Guilds		Expected	Observed	New occurrences
I	Uncluttered space aerial insectivores	23	5	
II	Background cluttered space aerial insectivores*	24	13	4
III	Highly cluttered space aerial insectivores	1	1	
IV	Highly cluttered space gleaning insectivores	17	15	4
V	Highly cluttered space gleaning carnivores	3	3	
VI	Highly cluttered space gleaning piscivores	1	0	
VII	Highly cluttered space gleaning sanguivores	3	2	
VIIIa	Highly cluttered space gleaning canopy frugivores	20	12	1
VIIIb	Highly cluttered space gleaning shrub frugivores	10	9	
IX	Highly cluttered space gleaning nectarivores	11	5	
X	Highly cluttered space gleaning omnivores	4	3	1
Total		117	67	10

The classification follows the bat guilds proposed by Kalko (1997) and Schnitzler and Kalko (1998). *Natalus stramineus* is included in guild II because of its foraging behaviour close to vegetation where it captures insects in flight (Kalko, pers. obs.). The expected number of species is based on a list for bats proposed by Marinho-Filho and Sazima (1998) for the Brazilian Amazon region. The new occurrences are included in the total number of observed species.

stratification), both on a nightly basis and as a whole, direct comparison of species composition and patterns of relative abundance between ground level and canopy strata is difficult. Nevertheless, we observed different trends in the preference of either canopy or ground level between and within guilds. Gleaning insectivorous bats, both in number of species and individuals, as well as *Pteronotus parnellii* (highly cluttered space aerial insectivore), were mainly caught in ground-level mistnets (Table 3). Of the two members of the blood-feeding guild, *Desmodus rotundus* was sampled exclusively at ground level and *Diaemus youngi* only in the canopy.

Discussion

Species accumulation curves

Although the use of species accumulation curves in inventory studies of bats was initiated only recently, we consider it an essential tool to assess the quality of inventory data (see Kalko et al., 1996a; Longino & Colwell, 1997; Moreno & Halffter, 2000). The shape of the curves indicates how well a local bat fauna has been sampled. In case the curve is nearing an asymptote, most species that can be adequately sampled with a certain method have been recorded. Overall, our samples confirm the high numbers of New World leaf-nosed bats (Phyllostomidae) and *Pteronotus parnellii* (Mormoopidae) that are dominant components of bats in Neotropical lowland forests. Both are well-sampled with mistnets (e.g., Fenton et al., 1992; Kalko, 1997, 1998). Because our curve closely approached the plateau of the expected number of species as determined by species-richness estimators (Colwell & Coddington, 1996), we conclude that we captured most of the local bat fauna (Fig. 2a).

Based on pooled data from various local inventories in the Amazon Basin, the expected total number of species for the Amazon Basin is about 117 on a regional scale (Marinho-Filho & Sazima, 1998). Up to now none of the mistnetting bat inventories reported for this area (e.g., Mok et al., 1982; dos Reis & Peracchi, 1987; Hutterer et al., 1995; Voss &

Emmons, 1996; Marinho-Filho & Sazima, 1998), including our results, have yet reached or have come close to this number of species. Although the results of the studies are based on well-sampled communities, some species are still underrepresented or lacking, particularly aerial insectivores. This bias is inherent to the exclusive use of mistnets (Voss & Emmons, 1996; Kalko, 1998; Simmons & Voss, 1998) because aerial insectivorous bats forage mainly in spaces that are difficult or impossible to sample with mistnets. Additional investigations are needed to reduce this bias such as the identification of aerial insectivores by their echolocation calls (e.g., Kalko, 1998; Kuenzi & Morrison, 1998; O'Farrell & Gannon, 1999; O'Farrell & Miller, 1999).

Comparison of canopy- and ground-level mistnets

The species accumulation curves of both projects give a first impression of the complementarity between the placement of the mistnets at ground and at canopy level (Longino & Colwell, 1997; Kalko & Handley, 2001; Fig. 2b). Because both projects were located in the same area, comparison of project 1 and 2 showed rather low overall species complementarity (<30%) that is high similarity of species composition whereas the comparison between ground and canopy mistnetting revealed higher complementarity (>50%), in other words less similarity. One reason for the lower similarity between canopy and ground mistnets is unequal capture effort. Capture effort was almost 30 times higher for the ground-level nets (projects 1 and 2 combined) than for the canopy nets (28,000 vs. 1000 mnh). This leads to a higher probability to capture more species at ground-level than in the canopy.

Another reason is the differential use of space. Our studies confirm trends in vertical stratification found in Neotropical bats (Handley, 1967; Simmons & Voss, 1998; Kalko & Handley, 2001; Lim & Engstrom, 2001). However, although some bats do show differential use of forest strata, vertical stratification may not be as strict in bats as it is in other species such as birds (see Kalko & Handley, 2001; Bernard, 2001). For instance, most forest bats are not limited to a particular forest level even though some species might forage more frequently in particular strata. Kalko & Handley (2001) argue that the classification of bats into 'ground' or 'canopy' bats is still premature due to low sample size and insufficient information on the diet, behavior, and sensorial flexibility of many species.

In our study, only a few species were captured exclusively in canopy nets, as, for example, one individual each of *Diaemus youngi* and one of the 'mostly fig-eating' bat, *Vampyressa brocki.* Although *D. youngi* seems to be rarely collected with other vampire species (Hutterer et al., 1995), the absence or low capture rates of this species might to some degree be due to a capture bias because of fewer canopy nets compared with the ground nets. *Diaemus youngi* is a bird-blood specialists and probably feeds mainly on birds roosting in the canopy (Uieda, 1992). It was also captured exclusively in canopy nets in a study at Belém (Kalko & Handley, 2001). Frugivorous bats that are known to feed mainly on canopy trees such as *Artibeus concolor* (Kalko & Handley, 2001) were well represented in our canopy mistnets. Comparing both mistnetting levels, we observed more species of aerial insectivorous bats in our canopy samples which is the stratum frequently used by these bats as foraging areas. Overall, the combination of canopy- and ground-level mistnets produced a higher number of species per mistnet hour than either placement alone (Fig. 2a, b).

Comparisons with other inventories

Overall we documented 72 species of 43 genera from 117 species predicted for the greater Amazon region (Marinho-Filho & Sazima, 1998; Table 3). We recorded 10 species new for the area, but already known from other locations in the Amazon Basin (dos Reis & Schubart, 1979; Mok et al., 1982; dos Reis & Guillaumet, 1983; dos Reis, 1984; dos Reis & Peracchi, 1987; Emmons & Feer, 1997; Marinho-Filho & Sazima, 1998). These species include *Centronycteris maximiliani*, *Glyphonycteris daviesi, Micronycteris hirsuta*, *Micronycteris microtis*, *Phyllostomus latifolius*, *Trinycteris nicefori*, *Vampyressa brocki*, *Lasiurus* cf. *castaneus*, *Thyroptera discifera*, and *Pteronotus gymnonotus.* The results compare well with other studies in the Amazon region and in the adjacent Guyanas, all of which document an impressively high species richness of bats. Currently, the highest numbers of species recorded locally in those areas encompass 86 species at Iwokrama Forest in Central Guyana (Lim & Engstrom, 2001), 78 species at Paracou, French Guyana (Simmons & Voss, 1998) and 72 species at Altér do Chão, Central Amazonia, Brazil (Bernard & Fenton, 2002).

None of the inventories, however, is close to completeness. This applies also for our study as revealed by a comparison of the number of recorded species with the number of species based on information on distribution patterns in the current literature (e.g., dos Reis & Schubart, 1979; Mok et al., 1982; dos Reis & Guillaumet, 1983; dos Reis, 1984; dos Reis & Peracchi, 1987; Emmons & Feer, 1997; Marinho-Filho & Sazima, 1998; Bernard & Fenton, 2002). Interestingly, the proportional composition of species in each family is similar to earlier inventories in the Amazon Basin and the Guyanas. Probably, the expected number of species is too high because it includes all species recorded in previous inventories, which were scattered over a huge area. Furthermore, some of the species may not occur in the area of the BDFFP because they are patchily distributed in the Amazon Basin or do not find the appropriate ecological requirements there such as rocky outcrops for cave-roosting bats.

With the capture of approximately 3000 individuals we reached about 90% of the expected species richness. This compares well to the Paracou Project in French Guyana (Simmons & Voss, 1998) where over 1500 bats bats were sampled with ground-level mistnets in about 2500 mnh (24,957 net-meter-hours (nmh)/12 m mistnets) resulting in a total of 78 species with 65 species sampled in ground-level and 39 species in canopy nets. Lim and Engstrom (2001) caught 2117 bats representing 73 species in Guyana with a capture effort of about 1660 mnh (495,136 m^2/h; one 12-m net approximates 300 m^2). Bernard & Fenton (2002) documented 72 species of bats with a capture effort of 6116 mnh over 102 nights with more than 3900 individuals at a highly diverse savanna-forest site in Brazil (Altér do Chão, Pará). In Mexico, Moreno and Halffter (2000) netted 20 nights (3853 nmh, or about 320 mnh) in different habitat types to obtain about 90% of the expected fauna with ground-level mistnets. One of the long-term bat projects on Barro Colorado Island (BCI) in Panamá (Kalko et al., 1996a) spanned more than 10 years and included more than 48,000 captures/recaptures. An average of 30 net nights was needed to compile 30 species. After additional years of sampling including other methods (canopy netting, acoustic monitoring, roost search) the number of species recorded for BCI has recently reached 72 (E. Kalko, pers. comm.), which is similar to the species richness in our study when we include our captures of areas adjacent to the BDFFP.

In all studies, a large proportion of the bat fauna has already been recorded during the first few samples. Most of the less common species accumulated gradually in the course of the study. After capturing about 70% of the total number of species for a given locality, the increase in species accumulation usually slows down drastically. Even though in most Neotropical bat inventories a relatively large number of species (between 70 to 80% of the total number of species ultimately recorded in the respective projects) are captured within 30 nights or in about 1000 mnh or with a capture effort of about 1000 individuals, an intense and committed capture effort is necessary to go beyond the more common species and to also include rare species.

Unsampled species

In our study, we caught only nine out of the 14 expected emballonurids, six out of the nine expected vespertilionids and four out of the 16 expected molossids. The most remarkable captures of aerial insectivores were the rare *Centronycteris maximiliani* and *Lasiurus* cf. *castaneus*, resulting in substantial range extensions for both species (e. g., Masson & Cosson, 1992; Simmons & Handley, 1998). Based on our extensive echolocation call recordings of aerial insectivorous bats in the BDFFP area and subsequent species identification we expect an additional 10–15 species bringing the total number of bats in the area to 82–87 species. Details about the results of the echolocation call analysis will be published elsewhere.

In our mistnetting study at the BDFFP, we missed several families and species which are considered to be widespread in the Central Amazon Basin (dos Reis & Schubart, 1979; Mok et al., 1982; dos Reis & Perracchi, 1987; Koopman, 1993; Emmons & Feer, 1997), in particular Noctilionidae, and Natalidae. The absence of noctilionids and *Macrophyllum macrophyllum* (Phyllostominae) in our mistnet data may be correlated with the almost complete absence of large rivers and other large water bodies in our study area. *Noctilio leporinus* is well known for its fish-eating habits and *N. albiventris* mainly for its insect-eating habits (e.g., Hooper & Brown, 1968; Hood & Pitocchelli, 1983). Both species of *Noctilio* forage predominantly over water surfaces (e.g., Hood & Jones, 1984; Schnitzler et al., 1994; Kalko et al., 1998). We recorded both species frequently and in large numbers over the Amazon as well as the Branco and Madeira river. *Macrophyllum macrophyllum* is the only phyllostomid known to forage regularly over water. This is reflected in its diet that includes, among other foods, water striders (Hemiptera, Gerridae; Gardner, 1977). Adding those species to our list in addition to the species identified by echolocation brings the total number of bats to 85–90 species.

Some bat species prefer or require caves as roost sites. Hence, the lack of caves in the BDFFP area may explain the absence of *Natalus stramineus* (Natalidae). The absence of moormopids such as *P. personatus* which is also known to roost predominantly in caves (Kalko et al., 1996a; Voss & Emmons, 1996), might also be in part due to sampling bias. *Pteronotus personatus* forages mostly at forest edges and in gaps (Table 4), and is usually not well sampled by ground mistnets. However, we recorded the characteristic echolocation calls of this species frequently at the BDFFP. Interestingly, its congener, *Pteronotus parnellii* is the only mormoopid that is well sampled with mistnets (Kalko et al., 1996a; Bernard et al., 2001; Bernard & Fenton, 2002). This is probably mainly linked to its foraging habits because it frequently forages along man-made trails inside the forest, as documented by ultrasound monitoring. At Presidente Figueiredo, where we netted bats at cave entrances, the capture effort was too low (two nights) to permit comprehensive conclusions about the bat fauna roosting in those caves. The species we caught included *Pteronotus parnellii, Phyllostomus latifolius*, and *Carollia perspicillata*.

Although frugivorous bats are well represented in our samples (Table 4), our inventory did not record some species of the genera *Platyrrhinus*, and *Vampyressa*, and the nectarivorous bats *Lichonycteris degener* and *Scleronycteris ega* that are expected to occur in the area (dos Reis & Peracchi, 1987; Kalko et al., 1996a; Voss & Emmons, 1996; Moreno & Halffter, 2000). The distribution and abundance of frugivorous and nectarivorous bats is tightly associated with the temporal and spatial availability of certain fruits and flowers (Fleming, 1986a; Marinho-Filho, 1991). In particular, species such as figs (Moraceae, *Ficus* spp.) have keystone functions for frugivorous bats and other frugivores in part because of their year-long fruiting within populations and the asynchronous fruiting of individuals (Handley et al., 1991; Kalko et al., 1996b; Korine et al., 2000). In contrast to the BDFFP area, frugivorous bats of the genera *Artibeus, Platyrrhinus*, and *Vampyressa* are common on BCI, Panamá, and other localities where figs are abundant (Handley et al., 1991). This discrepancy may be mainly due to the nutrient-poor latosols of Manaus region (Chauvel, 1983) that produce a distinctive local flora where poor-soil specialist trees predominate. Many bat-dispersed fruits, such as *Piper* and *Ficus* require richer soils (Gentry, 1990). The low abundance of fig trees in the Manaus area is likely to be one of the main reasons for our low capture rates or absence of canopy frugivores considered to be mainly fig-eaters (e.g. *Artibeus jamaicensis, A. lituratus, Vampyrodes carracioli, Vampyressa pusilla, Platyrrhinus brachycephalus*, and *P. infuscus*; see Handley et al., 1991; Galetti & Morellato, 1994; Kalko et al., 1996b; Bernhard & Fenton, 2002).

The most common species we encountered in our mist-netting samples were ground story frugivores equivalent to the 'highly-cluttered-space ground-level frugivorous bats' described by Kalko (1997) and Schnitzler and Kalko (1998). For instance, *Carollia perspicillata* was the most abundant species in this guild in the BDFFP area and contributed to more than half (52%) of all captures. In contrast to *C. perspicillata* and *C. brevicauda*, which are both widespread, common, and often occur sympatrically in the Amazon Basin, *C. castanea*, was not represented in our samples. To date, the nearest capture of *C. castanea* has been in Acre, Rio Branco, in the western Brazilian Amazon (Uieda, 1980). In Panamá, *Carollia castanea* and *C. perspicillata* overlap in habitat use and certain dietary resources (Thies et al., 1998). Both species eat *Piper* fruits but *C. castanea* is clearly a *Piper* specialist and may be thus strongly limited by the availability of these plants. *Carollia perspicillata* and *C. brevicauda* have broader food preferences and fecal analysis indicates that in the BDFFP both species feed almost exclusively on fruits of *Vismia* sp., a common secondary shrub (Sampaio, pers. obs.). The dominance of *Carollia* in the BDFFP area conforms well to similar results of bat assemblages in Altér do Chão, Central Brazil (Bernhard & Fenton, 2001) and in French Guyana (Simmons & Voss, 1998).

We also did not find *Rhinophylla fischerae*, which has been recorded from southern Venezuela (Gardner, 1988), and was described from the upper Amazon (Ucayali) of Perú (Carter, 1966), and is expected to occur elsewhere in the Amazon Basin (Marinho-Filho & Sazima, 1998). It is relatively common in Altér do Chão, along the Tapajós river (Bernard et al., 2001) but appears to be rare in most bat surveys conducted thus far. Probably, essential ecological requirements of this species are not met in our study area. Ecological limitations may also play a role in the rareness of other phyllostomids in our samples where we captured less than five individuals in 13 species.

Diversity and conservation of Amazonian lowland bats

Our Central Amazonian bat inventory reveals a high number of coexisting species. If we add to our current data base about 15 species of aerial insectivores which we missed in our mist-netting inventory but whose presence has been confirmed by ultrasound recordings (Sampaio & Kalko, unpublished), and four bat species that are considered to be widespread in Amazonia but that were also absent in our samples, leads to a total of 91 species. This result compares favorably with the high bat diversity documented for other Neotropical localities (Handley, 1967; McNab, 1971; Mok et al., 1982; dos Reis, 1984; Fleming, 1986b; Willig, 1986; dos Reis & Peracchi, 1987; Brosset & Charles-Dominique, 1990; Findley, 1993; Voss & Emmons, 1996; Kalko & Handley, 2001; Bernard & Fenton, 2002). However, none of the inventories is close to completeness and in most cases we do not fully understand why certain species are absent. We recognize the urgency in acquiring a better understanding of the biology and demographics of Amazon bat assemblages. This knowledge is necessary for developing strategies for conserving habitats and their associated fauna. For instance, we captured nine species in our study that are considered as 'potentially endangered' in their range and one species (*Vampyrum spectrum*) that is already included in the official Brazilian list of threatened bat species (Aguiar & Taddei, 1995; Wilson, 1996). The reason for the 'rarity' of *V. spectrum* may be related to its trophic position as a top predator.

Aguiar and Taddei (1995) used rarity of species and the degree of endemism of species to define their vulnerability to habitat changes such as fragmentation and isolation. When is a species considered to be rare? Are species truly rare or simply difficult to be captured or recorded? Answers to these questions will help us to determine which species become rare due to habitat changes that limit or prevent the natural maintenance of their populations. Methodological biases in our sampling techniques may result in the characterization of a species as either 'rare' or 'common' when the opposite may be true. For example, species that are 'rare' or 'absent' in mistnet surveys, (e.g., *Diclidurus* spp. or *Peropteryx* spp.) are frequently recorded in ultrasound monitoring.

Furthermore, designating bat species as endangered or threatened requires a thorough understanding of their natural history, especially of the underlying ecological factors determining population density and size (Brussard, 1991). This includes for instance lack of adaptability to habitat changes, low dispersal capacities, and dietary spezializations, foraging habits, and roosting behavior. Furthermore, it is arguable that rare species are always more prone to extinction than more abundant and widespread species (Terborgh & Winter, 1980; McIntyire, 1992).

Distribution and occurrence data of many taxa, in particular bats, are still meager and are often difficult to interpret and evaluate due to the lack of standardized methodology. Consequently, data of species richness and relative abundance in inventories for many species are still insufficient to be taken as indicators of rarity and vulnerability to extinction. An adequate understanding of the role of bats as indicator species and as providers of critical ecosystem services (e.g., pollinators, seed dispersal agents, control of insect populations), requires considerably more study of the community organization and ecology of bats across a range of different sites and habits than is available to date.

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