Diet, activity and reproduction of bat species (Mammalia, Chiroptera) in Central Amazonia, Brazil

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ABSTRACT. The diet, activity and reproductive patterns of several species of bats were investigated in primary forests of Central Amazon. Between August 1996 and August 1997, using mist nets set both at canopy and understorey levels, 936 bats, belonging to 51 species, 31 genera and 6 families were captured. Fecal samples from 35 species were examined, with four food categories and 25 food items identified. Time of captures indicate a wide variation, but the major part of the species presented a peak of activity around the first hour after sunset. Three reproductive peaks were observed: October-November; January-February; and July-August, but reproductive patterns varied among the families. The structure of the bat fauna in Manaus is similar to other sites in the Amazon and Central America, the main common points being: a) a high diversity of bat species, usually more than 40 species representing 6-8 families; b) 3-4 very common and geographically widespread species; c) most species are represented by a few captures; d) frugivorous species dominate the fauna and insectivorous species are less often captured; and e) most species cluster in 2-3 guilds, dominated by small (≤ 12 g) species.

KEY WORDS. Chiroptera, activity patterns, bats, biodiversity, Amazon Forest, Brazil, diet, guilds, primary forests, reproductive patterns

Bats comprise the second largest order of mammals in number of species and they account for approximately 39% of the mammal species in Neotropical forests (EMMONS & FEER 1997). The diversity of ecological relationships involving bats in Neotropical forests include dispersion of seeds, pollination of flowers, and predation on arthropods and small vertebrates (e.g. VEHRENCAMP *et al.* 1977; SAZIMA & SAZIMA 1978; TUTTLE & RYAN 1981; HEITHAUS 1982; FLEMING 1988; FENTON 1990; GORCHOV *et al.* 1993). Due to their great biomass and diversity of dietary habits, bats play a fundamental role in the maintenance of ecological processes in tropical forests. Frugivorous bats may eat and disperse the seeds of at least 96 genera of 49 families of Neotropical plants (FLEMING 1988), which represent, in some cases, more than 25% of the trees in a given tropical forest (HUMPHREY & BONACCORSO 1979).

In spite of their fundamental ecological role in the neotropics, proportionally little is known about the basics of the majority of the Neotropical bat species, from reproduction to diet to distribution. This is particularly true for the high speciose areas in the Amazon biome (see SIMMONS & VOSS 1998). Brazilian Amazon harbors around 130 species of bats (MARINHO-FILHO & SAZIMA 1998), representing almost

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one-third of the Brazilian mammal fauna but the biology and ecology of just a few species have been studied there (e.g. REIS 1984; MARQUES 1986; GRIBEL & TADDEI 1989; UIEDA & VASCONCELLOS-NETO 1985; MARINHO-FILHO & VASCONCELLOS-NETO 1994; GRIBEL *et al.* 1999). More field data revealing details of the biology, ecology and behavior of amazonian bat species are necessary. Hopefully, this knowledge will be used for understanding how bat species respond to the intense and crescent deforestation process in the Amazon, and also to provide support for conservation actions.

This paper presents biological data collected during a study of vertical stratification of bat communities using small tree fall gaps in primary forests of Central Amazonia (BERNARD 2001). These data will be focused on: a) the diet of the species; b) the time of the activity of the most captured species; c) the reproductive patterns observed; and d) the classification of the species according proposed guilds.

MATERIAL AND METHODS

This study was conducted in Reserves 1501 (Camp 41) and 1401 (Gavião) of Biological Dynamics of Forest Fragments Project (BDFFP). The BDFFP is a joint project between the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Smithsonian Institution. Reserves are located in a non-flooded forest 80 km north of Manaus (2º24'S, 59º43'W and 2º25'S, 59º45'W) at an altitude of 30-125 m above sea level. The region receives between 2200 and 2600 mm of rain annually, with a rainy season from January to May, and a dry season from June to October. Flowering and fruiting peaks occur in the dry and rainy season, respectively (ALENCAR *et al.* 1979).

Bats were captured with mist nets set both in the understory and canopy levels (17 to 30 m high), inside and around 17 small natural tree-fall gaps (70 to 240 m^2). High nets were installed using a rope and pulley system (HUMPHREY *et al.* 1968) and ground nets were tied to poles, with the first shelf at ground level and the last at 2.5 m high. All mist nets used were 12 x 2.5 m, with four shelves.

Mist nets have been used in several studies with bats (see KUNZ 1982). This methodology presents the advantage to permit the monitoring of several species at the same time, and the recording of important data such as age, sex and reproductive status of the captured bats. It also provides a reasonable information about the diversity and abundance of the bat fauna in the studied area. However, it is important to note that mist netting is selective and it tends to misrepresent insectivorous bats, which detect and avoid them more often than frugivorous ones (FLEMING 1986). Furthermore, bats have a good spatial memory and may avoid areas frequently sampled. To minimize this possibility, a 50-days interval between captures at the site sites was respected.

Six sampling sessions were conducted between August 1996 and August 1997 but not between the lunar phases of first quarter and full moon, when the light intensity is higher and bat activity lower. Mist nets were opened at 18:00 h and closed again at 06:00 h of the next morning, and checked at intervals of 20 to 45 minutes. Time of capture of all bats were recorded and grouped in 12 intervals of one hour each. During strong wind and rain all nets were closed.

Captured bats were placed in cloth bags, for one hour, at which time they were identified, measured, and their reproductive status was evaluated. Bat identification was based on an identification key for Amazonian bats (C.O. Handley pers. comm.). The age of each bat captured was estimated by the closure rate of phalangial epiphisis, with all those with open phalanxis classified as juveniles. Were considered to be lactating all females with milk, or large, black and naked nipples. Females were also palpated to determine if large embryos were present.

Cloth bags were checked for feces, which were collected and stored in individual glass vials with 50% glycerin solution for later analysis. Feces were placed in Petri's dishes with water and examined in 10 to 40x stereo-microscopy. The proportion of each component in the feces (i.e. seeds, insects, etc) was estimated by computing their volume in the total volume of the sample. Insect parts, when possible, were identified to the taxonomic order.

Bats of rare species or those with problematic identification were collected and preserved for later identification, others were freed soon after measuring and marking process. Bats collected, together with all bats which died during the marking or measuring process were deposited in the Setor de Coleções Zoológicas at INPA (Manaus, Amazonas, Brazil).

The species recorded were classified using a matrix of guilds, adopting the division proposed by KALKO *et al.* (1996a). These authors classified guilds according habitat use, diet, and feeding mode of each species. Thus, species were classified as users of: (1) uncluttered space, such as the region above the canopy or large open areas; (2) background cluttered space, including forest edges, large gaps, or trails surrounded by forest; and (3) highly cluttered spaces, for species foraging close to the vegetation. Species' foraging mode were classified as: (a) aerial, for bat species catching flying insects on the wing; and (b) gleaning, for bat species that take prey from surfaces (fruit, nectar, pollen, non-flying insects, small vertebrates, and blood). Species were divided according to the most frequent type of food used by them (i.e. insectivores, frugivores, nectarivores, etc) according data from the analysis of the fecal samples from this study and references in the literature (BONACCORSO 1979; FINDLEY 1993; GARDNER 1977; HANDLEY *et al.* 1991; KALKO *et al.* 1996a). The mean weight of each species was used as body size index (Fig. 1).

RESULTS

Between August 1996 and August 1997, 64 nights of sample were performed, and the final capture effort was 3398 mistnet-hours. A total of 936 bats were captured, belonging to 51 species, 31 genera and six families (Tab. I). Three very common species (*Carollia perspicillata* (Linnaeus, 1758), *Artibeus concolor* Peters, 1865 and *Rhinophylla pumilio* Peters, 1865) represented 57,9% of the captures. Twenty-four of the 51 species captured were represented by three or less captures (Tab. I).

Most bats were captured at canopy level: 397 bats, representing 42,41% of the total, resulting in the highest capture index (0,369 bats/mistnet-hour). In ground nets inside gaps 286 bats (30,56% of the total) were captured (0,268 bats/mistnet-hour). Even with the highest effort (1.259 mistnet-hours) captures at ground level

Table I. Division by families and sub-families, classification by guilds, number of captures, and diet of bat species captured in primary forests near Manaus, Brazil. See text for classification into guilds. (**a**) Family/Sub-family: (MOR) Mormoopidae; (VES) Vespertilionidae; (EMB) Emballonuridae; (THY) Thyropteridae; (MOL) Molossidae; (PHY) Phyllostomidae, with sub-families (Phy) Phyllostominae, (Car) Carolliinae, (Glo) Glossophaginae, (Lon) Lonchophyllinae, (Ste) Stenodermatinae, (Des) Desmodontinae. (**b**) Guilds: (1) open space/aerial insectivores; (2) background cluttered/aerial insectivores; (3) highly cluttered/aerial insectivores; (4) highly cluttered/gleaning insectivores; (5) highly cluttered/hematofagous; (6) highly cluttered/frugivores; (7) highly cluttered/nectarivores; (8) highly cluttered/omnivores; (U) understory species; (C) canopy species; (O) opportunistic species; (AC) above canopy species. (**c**) Food resources: (1) unknown; (2) *Vismia* spp.; (3) *Piper* spp.; (4) *Solanum* sp.1; (5) *Solanum* sp.2; (6) *Miconia* spp.; (7) *Trema* spp.; (8) fruit, Crysobalanaceae; (9) *Cecropia* spp.; (10) *Passiflora* spp.; (11) sp. 1; (12) sp. 2; (13) sp.3; (14) sp.4; (15) sp. 5; (16) sp. 6; (17) sp.7; (18) sp. 8; (19) unknown insect; (20) Coleoptera; (21) Hymenoptera; (22) Diptera; (23) Isoptera; (24) Homoptera; (25) Aranida.

Species	Fam/Subfam (a)	Captures	Guild (b)	Food resources (c)	Samples
Carollia perspicillata (Linnaeus, 1758)	PHY/Car	271	6/U	1, 2, 3, 4, 9, 11, 12, 18, 19, 21	102
Artibeus concolor Peters, 1865	PHY/Ste	186	6/C	1, 2	12
Rhinophylla pumilio Peters, 1865	PHY/Car	85	6/U	1, 2, 3, 7, 9, 11, 16, 22	29
Artibeus cinereus (Gervais, 1856)	PHY/Ste	58	6/C	2	5
Artibeus obscurus (Schinz, 1821)	PHY/Ste	36	6/O		
Carollia brevicauda (Schinz, 1821)	PHY/Car	27	6/U	2, 3, 4, 11, 12	10
Artibeus lituratus (Olfers, 1818)	PHY/Ste	26	6/C	1, 2, 14	4
Ametrida centurio Gray, 1847	PHY/Ste	23	6/C		
Artibeus gnomus Handley, 1987	PHY/Ste	22	6/C	17, 19	2
Tonatia saurophila Koopman & Williams, 1951	PHY/Phy	20	4/U	1, 2, 19, 20	12
Tonatia silvicola (d'Orbigny, 1836)	PHY/Phy	17	4/U	2, 3, 19, 20	11
Artibeus jamaicensis Leach, 1821	PHY/Ste	16	6/O		
Pteronotus parnellii (Gray, 1843)	MOR	15	3/U	19, 20, 23, 24	13
Vampyressa bidens (Dobson, 1878)	PHY/Ste	13	6/C	1, 3	3
Phyllostomus elongatus (E. Geoffroy, 1810)	PHY/Phy	9	4/C	20	2
Mimon crenulatum (E. Geoffroy, 1810)	PHY/Phy	9	4/U	19, 20, 21	5
Sturnira lilium (E. Geoffroy, 1810)	PHY/Ste	8	6/O	1, 2, 4, 5	4
Sturnira tildae de la Torre, 1959	PHY/Ste	7	6/O	2, 3, 16	5
Phyllostomus hastatus (Pallas, 1767)	PHY/Phy	7	8/U	18, 20, 21	3
Phylloderma stenops Peters, 1865	PHY/Phy	6	8/U	10, 19, 20	4
Choeroniscus minor (Peters, 1868)	PHY/Glo	6	7/O		
Trachops cirrhosus (Spix, 1823)	PHY/Phy	6	4/U		
Cormura brevirostris (Wagner, 1843)	EMB	5	2/O	20	1
Saccopteryx canescens Thomas, 1901	EMB	5	2/0	19	2
Ectophylla macconnelli (Thomas, 1901)	PHY/Ste	5	6/C	1, 19	1
Chiroderma trinitatum Goodwin, 1958	PHY/Ste	4	6/O	14	3
Phyllostomus discolor Wagner, 1843	PHY/Phy	4	8/O	1, 19	2
Micronycteris hirsuta (Peters, 1869)	PHY/Phy	3	4/U	19	2
Eptesicus brasiliensis (Desmarest, 1819)	VES	3	2/?	19	1
Lonchophylla thomasi J.A. Allen, 1904	PHY/Lon	3	8/O	19	1
Eptesicus chiriquinus Thomas, 1920	VES	2	2/?	20	2
Myotis riparius Handley, 1960	VES	2	2/?	19	1
Molossops abrasus (Temminck 1827)	MOL	2	1/AC		
Saccopteryx leptura (Schreber, 1774)	EMB	2	2/O	19	1

Cont.

Table I. Continued.

Species	Fam/Subfam (a)	Captures	Guild (b)	Food resources (c)	Samples
Saccopteryx bilineata (Temminck, 1838)	EMB	2	2/O	19	1
Thyroptera tricolor Spix, 1823	THY	2	2/U		
Chrotopterus auritus (Peters, 1856)	PHY/Phy	2	8/C	2, 25	2
Desmodus rotundus (E. Geoffroy, 1810)	PHY/Des	2	5/U		
Trinycteris nicefori (Sanborn, 1949)	PHY/Phy	2	4/U	1	2
Glossophaga soricina (Pallas, 1766)	PHY/Glo	2	8/O	19	1
Molossops greenhalli (Goodwin, 1958)	MOL	1	1/AC		
Vampyressa brocki Peterson, 1968	PHY/Ste	1	6/?		
Chiroderma villosum Peters, 1860	PHY/Ste	1	6/C		
Micronycteris megalotis (Gray, 1842)	PHY/Phy	1	4/?		
Uroderma bilobatum Peters, 1866	PHY/Ste	1	6/O		
Diaemus youngi (Jentink, 1893)	PHY/Des	1	5/C		
Tonatia brasiliense (Peters, 1867)	PHY/Phy	1	4/?		
Tonatia schulzi Genoways & Williams, 1980	PHY/Phy	1	4/?	19	1
Centronycteris maximiliani (J. Fischer, 1829)	EMB	1	2/?	19	1
Micronycteris schmidtorum Sanborn, 1935	PHY/Phy	1	4/?	19	1
Glyphonycteris sylvestris Thomas, 1896	PHY/Phy	1	4/?		
Total 51	6/6	936	8/4	25	252

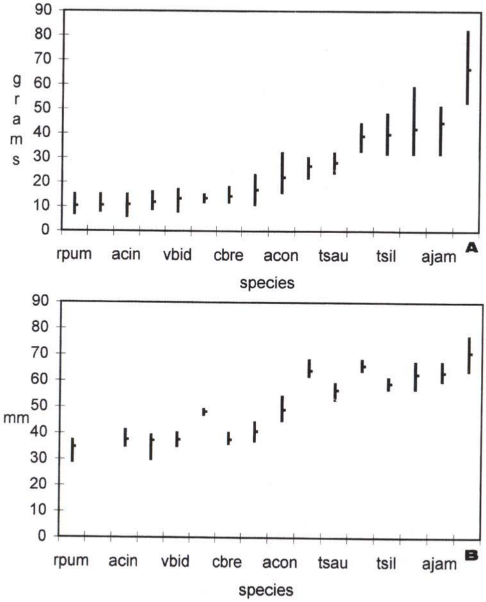

Fig. 1. Mean weight and forearm length of 16 species of bats captured in mist nets set both at canopy and understory levels in primary forest near Manaus, Amazonas, Brazil, between August 1996 and August 1997. (rpum) *Rhinophylla pumilio*, (acen) *Ametrida centurio*, (acin) *Artibeus cinereus*, (agno) *A. gnomus*, (vbid) *Vampyressa bidens*, (mcre) *Mimon crenulatum*, (cbre) *Carollia brevicauda*, (cper) *C. perspicillata*, (acon) *A. concolor*, (ppar) *Pteronotus parnellii*, (tsau) *Tonatia saurophila*, (tsil) *T. silvicola*, (aobs) *A. obscurus*, (ajam) *A. jamaicensis*, (alit) *A. lituratus*.

outside gaps represented just 27,03% of the total (253 bats), with capture index of 0,200 bats/mistnet-hour. A complete analysis of the vertical stratification of bat communities in Central Amazonia, its possible causes, and conservation implications is presented elsewhere (Bernard 2001).

Analyses of 252 fecal samples, from 35 species (Tab. I) revealed 25 items in four categories: seeds, fruits, insects and spiders, and unknown material. Sixteen seed types were observed and eight identified to genera. The others were classified as morpho-species, i.e., sp1, sp2, etc. Among the seeds, *Vismia* spp. (Guttiferae) were the most frequent, being registered in feces of 11 species, and accounting for approximately 83% from *A. concolor*, 55% from *R. pumilio*, and 70% of the samples from *C. perspicillta*. In samples from the later, the mean number of seeds was 30 (n = 70), with extremes of 134 seeds in a unique sample (Tab. II). Seeds of *Piper* spp. (Piperaceae), two species of Solanaceae, *Miconia* spp. (Melastomataceae), *Trema micrantha* (Ulmaceae), *Cecropia* spp. (Cecropiaceae), *Passiflora* spp. (Passifloreaceae), and a large fruit of Chrysobalanaceae were also identified (Tab. I). Insect identification was difficult as consequence of the small size of the fragments found in fecal samples. Most insects were therefore classified as "unknown". Among the identifiable samples, Coleoptera was the most frequent item. Diptera, Hymenoptera, Homoptera, Isoptera, and Arachnida were also identified. In the fecal samples from species of the sub-family Phyllostominae, insects were the most frequent component found, representing 100% of the contents from *Mimon crenulatum* (E. Geoffroy, 1810), *P. elongatus* (E. Geoffroy, 1810), and *M. hirsuta* (Peters, 1869). Seeds of *Vismia* spp. were found in feces of the genus *Tonatia*, however they were always less than 1% of the total volume.

Table II. Temporal distribution of seed of *Vismia* spp. (Guttiferae) in fecal samples from *Carollia perspicillata* (Phyllostomidae), captured in primary forests near Manaus, Brazil, between August 1996 and August 1997.

	Aug	Sep	Oct	Nov	Jan	Feb	Apr	May	Jun	Jul	Aug	Total
Fecal samples	1	2	7	10	4	12	12	2	31	3	16	102
Presence of Vismia spp. (%)	100	100	85	50	50	93	58	0	48	100	100	68
Mean number of seed,	18	3	25	13	70	32	19		40	15	30	30
mim-max	2-4	2-4	3-82	2-34	7-134	3-105	2-50		2-99	5-24	1-81	1-134

Activity patterns for the 16 most abundant species (833 captures) indicate a wide variation in bat species (Fig. 2). The peak of activity of members of the sub-family Carolliinae was the first two hours after sunset, with uniform activity for the rest of the night. In the Phyllostominae, the highest activity seems to also occur the first two hours after sunset, but activity decreases in the middle of the night. Sub-family Stenodermatinae has high species diversity, so there is a wide variation between the time of activity of its species. In the *Artibeus* species, the first two hours after sunset is a time of low activity, followed by a wide variation for each species (Fig. 2).

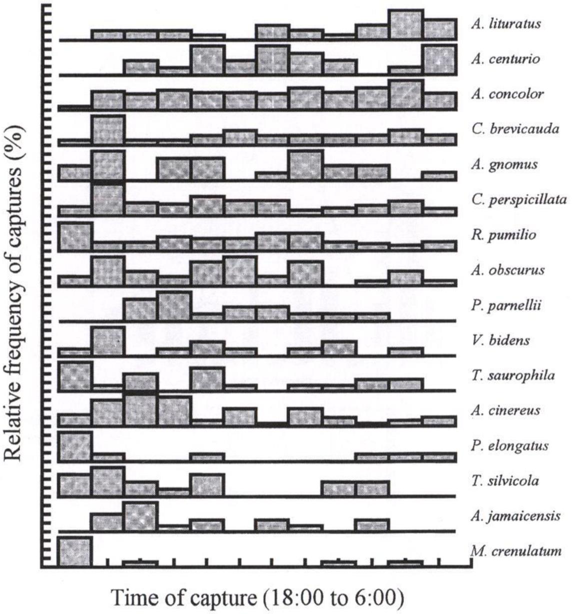

Fig. 2. Time of capture of 16 species of bats in primary forests near Manaus, Brazil, during one-year period (August 1996 to August 1997). Captures, based on mist-netting, were grouped in 12 one-hour intervals, from 18:00 (left) to 6:00 (right). Marks on the Y axis represent 25% intervals.

Pregnant and lactating females of 32 species were captured during the study, but three reproductive peaks were observed: October-November, 1996; January-February, 1997; and July, 1997 (Tab. III). Reproductive periods were coincident with flowering and fruit peaks (Fig. 3)

The guild classification proposed contained 31 of the 51 species recorded by me. Based on items found in the samples in this study, and on the records available in the literature, *Phylloderma stenops* Peter, 1965, *Chrotopterus auritus* (Peters, 1856), *Phyllostomus discolor* Wagner 1843, *Lonchophylla thomasi* J.A. Allen, 1904 and *Glossophaga soricina* (Pallas, 1766) were classified as omnivores. The first two species were considered as, respectively, a frugivore and a carnivore, and the others as nectarivores (KALKO *et al.* 1996a).

The guild matrix obtained has 24 occupied cells (Tab. IV). Guild composed by background cluttered/frugivores was the richest in species (18), followed by highly cluttered/gleaning insectivores, with 12 species. The least represented guild was open space/aerial insectivores, with only two species of molossids. Large size bats (more than 46 g) were represented by just three species (Tab. IV), and small bats (4-9 g) by 13 species. Those were composed by members of the background cluttered/aerial insectivores (seven species), the highly cluttered/gleaning insectivores (three species), and gleaning omnivores and frugivores, with respectively two and one species. The three large size bat species were *Artibeus lituratus* (Olfers, 1818), a frugivore, *C. auritus* and *Phyllostomus hastatus* (Pallas, 1767), both omnivores.

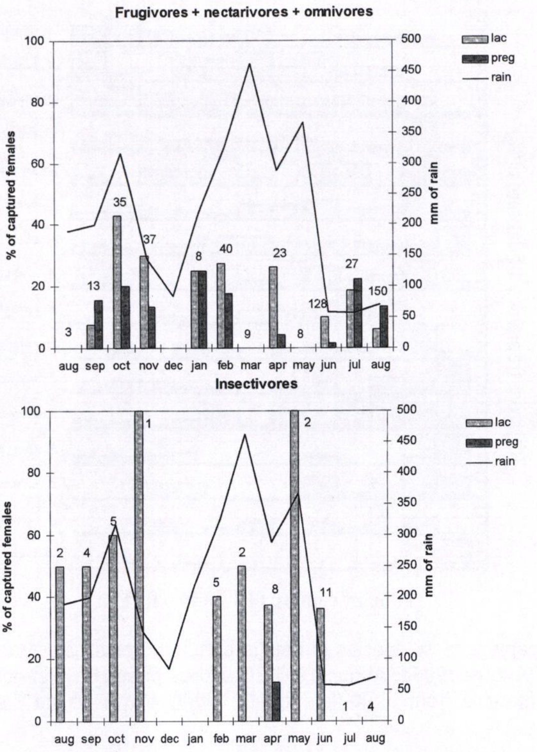

Fig. 3. Amount of rain and the proportion of lactating and pregnant females bats captured in primary forests near Manaus, Brazil. Numbers above bars represents the total of females captured in each month.

Table III. Reproductive status of females of 32 species of bats captured in primary forest near Manaus, Brazil, between August 1996 and August1997. Occurrence of pregnant females are in bold. Number of pregnant females/number of females captured, (L) lactating, (j) juveniles.

	Aug/96	Sep	Oct	Nov	Jan/97	Feb	Mar	Apr	May	Jun	Jul	Aug
Frugivores												
A. centurio			0/1							0/1	0/2 1L	1/9 2L
A. cinereus			3/7 3L	0/9 1L 4j		0/1 1L	0/2	0/1		0/2 1j	1/2	0/3
A. concolor		0/5	0/2 5j	4/5 1L		3/5 2L 1j		0/1		0/12 1L	4/14 2L	8/69 6L
A. gnomus	0/1	0/1	1/6 4L 4j	0/3 1j				0/1		1/4		
A. jamaicensis							0/0 1j	0/2 1L		1/2	0/2 1L	1/6
A. lituratus			0/3 2L			0/1 1L	0/1	0/1				0/4
A. obscurus			1/3	0/4 1L		2/8 3L 1j		1/3	0/1	0/2		
C. brevicauda				0/1 1L		0/1	0/1	0/1 1L		0/5		0/1
C. perspicillata	0/1	0/3 1L	0/6 2L	0/8 5L	1/1	1/12 2L		0/8 1L	0/4	0/88 9L		6/38
C. trinitatum				0/1 1L								
R. pumilio	0/1 1j	0/2 2j	0/4 3L 4j	0/5 1L 2j	1/4	0/7 2L 3j	0/4	0/2 1L	0/3 2j	0/7	0/3 1j	4/15
S. lilium								0/1		0/3 2L		0/2
S. tildae					0/1							0/1 1L
V. bidens				0/0 1j		1/2	0/1	0/1 1L		0/1 1L	0/1	0/1
V. brocki			1/1									

Cont.

Table III. Continued.

	Aug/96	Sep	Oct	Nov	Jan/97	Feb	Mar	Apr	May	Jun	Jul	Aug
Nectarivores												
C. minor		2/2			0/1 1L							
Omnivores												
L. thomasi			0/1 1L									
P. stenops			1/1		0/1 1L	0/1						
P. discolor											1/1	
P. hastatus				1/1		0/1 1L 1j		0/1 1L		0/1		0/1
T. cirrhosus						0/1					0/1 1L	
Insectivores												
E. brasiliensis											0/1	
E. chiriquinus		1/1										
M. crenulatum				1/1		0/2 1L 1j		0/1 1L		0/1		0/1
M. riparius			0/1 1L									
P. elongatus								0/1		0/3 1L		0/2
P. parnellii	0/2 1L	0/2 2L	0/2 2L			0/1 1L		1/3	0/1 1L	0/2 2L		
S. bilineata								0/1 1L				
S. leptura							0/1 1L					
T. saurophila		0/1	0/2	0/1 1L		0/1		0/1 1L	0/1 1L	0/3		0/1
T. silvicola							0/1	0/1	0/0 1j	0/2 1L		

Table IV. Matrix of guilds for 51 species of bats captured with mist nets set both at canopy and understory levels in primary forests near Manaus, Brazil. See text for division into guilds.

Guild	Mean weight (g)							Total
	4-9	10-12	13-17	18-25	26-37	38-46	+46	
Open space/aerial insectivores				1		1		2
Background cluttered/gleaning insectivores	7	2						9
Highly cluttered/aerial insectivores					1			1
Highly cluttered/gleaning insectivores	3	2	2	1	1	3		12
Highly cluttered/hematofagous					1	1		2
Highly cluttered/frugivores	1	5	5	3	1	2	1	18
Highly cluttered/nectarivores		1						1
Highly cluttered/omnivores	2					2	2	6
Total	13	10	7	5	4	9	3	51

DISCUSSION

Diet

As expected, the high speciose bat fauna of Central Amazon showed a directly high diversity of diet items. Family Phyllostomidae, represented by 39 of the 51 recorded species, showed the higher diversity of food items. Sub-families Carolliinae and Stenodermatinae were predominantly frugivores, feeding mainly on the very abundant pioneer species, such as *Vismia* spp., *Piper* spp., *Miconia* spp. and *Cecropia* spp. The presence of insect remains in the feces of species considered as nectarivores, such as *G. soricina* and *L. thomasi* agrees with records from other areas (FLEMING *et al.* 1972; HEITHAUS *et al.* 1975).

Contrary to data from Central America, where *Ficus* spp. (Moraceae) are the most important food resource (e.g. HANDLEY *et al.* 1991; KALKO *et al.* 1996b), in this study *Vismia* spp. was the most often eaten fruit. Associations between plant species considered pioneers and bats are well documented (see FLEMING & ESTRA-

DA 1993). These pioneer plant species are characterized by an opportunistic strategy based mainly on short lifespan, flowering and fruiting at early ages, long periods of fruit availability, and dissemination of a large number of small seeds (CHARLES-DOMINIQUE 1986). Noted, *Vismia* sp. was present in the diet of *C. perspicillata* along all the study period (Tab. II), and the number of seeds present in the samples was high. These values emphasize how important bats are as seed dispersors and provide an indication of the volume of seeds transported by bats in tropical forests (see KALKO *et al.* 1996b).

As pointed by FLEMING (1988), the use of fecal samples as the main technique to document bats' diet, especially frugivorous species, involves potential sources of bias. This technique may underestimates the occurrence of fruits whose seeds are too large to be ingested and some bat species may extract juices from seeds, leaves, and insects, discarding the solid part after chewing them (ZORTEA & MENDES 1993; KUNZ & DIAZ 1995; BERNARD 1997). Consequently, the documentation of these resources will be not complete.

Insectivorous species were represented by those in the families Mormoopidae, Vespertilionidae, Emballonuridae and some species of the sub-family Phyllostominae, being small beetles the most frequent item found in their samples. A single sample from *Pteronotus parnellii* (Gray, 1843) contained seven heads of termites, confirming insectivorous bats may exploit a wide variety of resources.

Determining the diet choice in Neotropical bats is a complex matter, and diet habits may be broader than expected, or even not easily predictable (*e.g.* NORBERG & FENTON 1988; HERRERA *et al.* 1998). Several other factors not observed in this study, such as the abundance and diversity of potential food resources, their nutritional characteristics, and the energetic costs and risks involved may affect bats diet (e.g. DINERSTEIN 1986; FLEMING 1988; NORBERG *et al.* 1993; FENTON 1995). The data presented here provide just a small idea about what resources bats are using, and further studies are definitively necessary to better understand bats' choices and reasons involved.

Time of activity

Flight is an energetically costing activity (NORBERG *et al.* 1993) and it is plausible to expect that differences in chiropteran feeding habits are closely related with their activity patterns. Thus, species feeding on high-energy food, such as blood, meat and insects, should require a shorter foraging time to meet their daily energy requirements than frugivores, which main food is usually high in carbohydrates, low in proteins, and contain a high proportion of indigestible material (*e.g.* FLEMING 1988). In fact, in this study, frugivores species presented a more uniform activity, with shorter intervals between the activity peaks when compared with insectivores (Fig. 3).

At the study sites, *C. perspicillata* was captured through the night, but two peaks of activity were evident: the first one around 19:00h, and the second one at 01:00h. FLEMING (1988), in a long-term study about the biology of *C. perspicillata*, pointed a similar pattern, that may be explained by the species' feeding behavior. Individuals of this species usually leave the day roost at or shortly after the sunset and fly directly to a feeding area. They spend the following time exploiting the local food resources, and may remain in the same area all night or may fly to one or more additional feeding areas during the night, but returning to the day roost between 03:00 and 05:00 h. A bimodal similar pattern was observed in *A. jamaicensis* Leach, 1821 and *P. hastatus* (MORRISON 1978; AUGUST 1981; MCCRAKEN & BRADBURY 1981). An increase in the activity of *A. lituratus* close to dawn is in accordance with other records (ERKERT 1982). Time of capture of *P. parnellii* indicates this species seems to focus its activity at the middle of the night, with absence of activity just after sunset and before dawn.

Species of families Emballonuridae and Vespertilionidae were poorly represented because they are able to detect and avoid mist nets. As a consequence, records of their activity were omitted. However, in the study sites, emballonurids were the first group to fly into gaps, starting before the sunset, and extending their activity to 30-60 minutes after that. They were absent along the night, returning to gaps at the end of dawn. In fact, bimodal activity patterns are characteristic for several insectivorous species (see ERKERT 1982). Surprisingly, emballonurids were observed performing feeding flights as late as 8:00h a.m., under bright sunlight.

It is important to point that other factors such as the sexual and social status of the individual, as well as intra and inter specific competition for food resources may affect the activity pattern of bats. Also, as pointed before, the use of mist nets has an inherent bias, and may not provide a real picture of a bat's activity pattern. One example is *M. crenulatum*. Both in this study as in other sites in the Amazon this species presented one of the most distinct activity pattern: almost all the individuals were captured in the first half-hour after sunset, and just vestigial activity was observed after that. However, in a recent study using radio-transmitters in *M. crenulatum*, those bats tracked were extremely active all along the night, contrary to the picture showed with the exclusive use of mist nets (E. Bernard, unpublished data). Thus, when bat's activity pattern is a crucial element in a given study, more precise techniques, such as radio-telemetry or direct observation, must be used.

Reproduction

Most Neotropical frugivorous bat species tend to produce two offspring per year, one toward the end of the dry season and the other in the middle of the wet season, coinciding with the periods of higher food availability (FLEMING *et al.* 1972; BONACCORSO 1979; DINERSTEIN 1986). Although there is food available in Central Amazonia all year, flowering peaks occur in the dry season, with fruiting peaks in the rainy season (ALENCAR *et al.* 1979). The major part of the bat species registered in the present study had reproductive peaks coincident with these periods (Fig. 3).

Members of the Phyllostomidae family are considered polyestrous with bimodal reproductive activity (FLEMING *et al.* 1972) and in fact January/February and July/August were the reproductive peaks observed for the sub-family Caroliinae. For stenodermatines, the capture of pregnant females in February (*A. concolor* and *A. obscur*us (Schinz, 1821)), June (*A. gnomus* Handley, 1987 and *A. jamaicensis*), and July/August (*A. cinereus* Gervais, 1856 and *A. gnomus*) seems to indicate that the interval between the peaks was shorter, around three to four months. One of the peaks was therefore in October/November, with the others in February and

July/August. Lactating females of *Sturnira lilium* E. Geoffroy, 1810 and *S. tildae* de la Torre, 1959 were recorded in June and August 1997. FLEMING *et al.* (1972), working in Costa Rica and Panamá, recorded for sturnirines the polyestrous bimodal pattern. Thus, June-August may have corresponded to the second peak. Unfortunately, the few samples observed for these species in the beginning of this study did not had permit identification of the first peak.

In tropical forests, the insect abundance generally decreases during the dry season and increases during the rainy season (WILSON 1971; FLEMING *et al.* 1972; CUMMING & BERNARD 1997; RACEY & ENTWISTLE 2000), and, as observed, reproductive periods of bats tend to coincide with periods of higher food abundance. Thus, in Central Amazonia, one may expect an increase in the reproductive activity of insectivores species during January to May. In fact, this pattern was observed in species such as *T. silvicola* (d'Orbigny, 1836), *T. saurophila* Koopman and Williams, 1951, *P. elongatus*, *M. crenulatum*, *Saccopteryx leptura* (Schreber, 1774) and *S. bilineata* (Temminck, 1838).

Identifying reproductive patterns for species of the families Vespertilionidae and Emballonuridae is difficult due to the few captures observed in this study. However, *M. riparius* Handley, 1960 is classified as a seasonally monestrous species (LAVAL & FITCH 1977; MYERS 1977) and the capture of one lactating *M. riparius* female in October and one pregnant female *E. chiriquinus* Thomas, 1920 in September suggests this could be a reproductive period for those species in study area. *S. bilineata* is classified as a seasonally monestrous species (FLEMING *et al.* 1972) and lactating females of two *Saccopteryx* species were captured in March and April.

Pteronotus parnellii is considered a monestrous species (FLEMING *et al.* 1972; LAVAL & FITCH 1977). In the present study there is a gap in the captures of this species in November, December and January. In LAVAL & FITCH's (1977) study, coincidentally, the period of October to December corresponded to the reproductive interval for *P. parnellii*. Females with signs of lactation were recorded in August, September, October of 1996, February, May and June in 1997, and a pregnant female in April 1997. Therefore, a reproductive interval of November to December may be a reasonable estimate.

Community Structure

The structure of the bat fauna in Manaus is similar to other sites in the Amazon and Central America (see SIMMONS & VOSS 1998), the main common points being: a) a high diversity of bat species, usually more than 40 species representing 6-8 families; b) 3-4 very common and geographically widespread species; c) most species are represented by a few captures; d) frugivorous species dominate the fauna and insectivorous species are less often captured; and e) most species cluster in 2-3 guilds, dominated by small (≤ 12 g) species.

The Amazon Basin harbors around 150 species of bats (KOOPMAN 1993) and at sampled sites around Manaus 80 species have been recorded (E.M. Sampaio, pers. comm). Comparing species richness among Neotropical rainforest bat inventories is difficult because of methodological problems, different ecological characteristics, and different intensity of faunal sampling. Data from 14 sites sampled in the Amazon and Central America, where the number of bat species varied between

44 to 78, confirm that the bat species richness in the neotropics is very high (see SIMMONS & VOSS 1998).

The dominance of frugivorous bats in terms of number of individuals and species agrees with similar patterns observed in other sites in the Amazon Basin (*e.g.* HANDLEY 1967, 1976; REIS 1984; BROSSET & CHARLES-DOMINIQUE 1990; SIMMONS & VOSS 1998). However, as pointed by SIMMONS & V*OSS* (1998), it remain unclear if the dominance of frugivores is a real pattern or a sampling bias, i.e., if frugivores really comprises the bulk of the bats in Neotropical forests. Real census data would provide a more precise answer to this question, but such data are not available due to the loggistical problem to count individual bats in a delimited area. In fact, sites with the higher proportion of insectivores were those with long term surveys, or complementary collecting techniques such as elevated mistnetting, regular roost searching, or monitoring echolocation calls (see SIMMONS & VOSS 1998).

In five other studies in the Amazon Basin, *C. perspicillata* was also the most abundant bat species (HANDLEY 1967, 1976; REIS 1984; BROSSET *et al.* 1996; SIMMONS & VOSS 1998). The list of the four most abundant bats species in each of the six studies included 13 widespread species. In two of those studies the seccond most abundant species was represented by species captured at canopy level, *Molossus molossus* and *Artibeus concolor* (respectivelly in SIMMONS & VOSS 1998, and the present study), proving that abundant species may be misrepresented when netting is restricted to understory level (BERNARD 2001 and references therein).

Factors explaining why *C. perspicillata* is so abundant are related with the species' natural history and ecology (including polyestrous bimodal reproduction, low annual mortality rate, medium average life expectancy, broad dietary generalization, optimal food and roost selection; FLEMING 1988). The density of *C. perspicillata* in Guanacaste Province, Costa Rica, was estimated to be from 0.06 to 0.07 individuals per hectare if the bats were uniformly distributed over their foraging range (FLEMING 1988). Considering that *C. perspicillata* are usually clumped, foraging in patches of food plants, their density can be much greater. Similar estimates are very necessary for the most part of the other species presents in the Amazon.

Some of the species represented by ≤ 3 captures were considered as rare not just in Manaus but elsewhere [e.g. *Centronycteris maximiliani* (J. Fischer, 1829), *Tonatia schulzi* Genoways & Williams, 1980 and *Vampyressa brocki* Peterson, 1968]. However, as discussed before, some of the species with low capture rates (especially emballonurids) seems to be actually more abundant at the study sites but not often captured by mist nets. Thus, before labeling a bat species as rare, one should stress the capture possibilities along time, using preferentially more than one technique.

The most occupied cells in the guild matrix contained seven and five species and were formed, respectively, by 4-9 g background cluttered/aerial insectivores and 13-17 g highly cluttered/ frugivores. The cluster of several species in those guilds may be explained by slight differences in morphology and echolocation calls frequencies, which would allow the species to exploit different food resources (e.g. BOGDANOWICZ *et al.* 1999). Is highly like that those small insectivorous species are not using the same resources, but exploiting different insect species (e.g. BOWIE-RAURI *et al.* 1999). Unfortunately, due to the imprecise identification of insect parts present in the sampled feces, important factors such as the size and softness of the preys were not determined. The constant availability of superabundant food resources may also minimize the competition intra-guilds, and this was observed among the 13-17 g frugivores (*C. perspicillata*, *C. brevicauda*, *V. bidens*, *C. trinitatum*, *C. villosum* and *U. bilobatum*). Those species showed a strong preference for fruits of *Vismia* spp., which were very abundant in disturbed areas near the reserves, with fruit available all around the year.

The refinement necessary to better understand how so many species coexist in the same area will just came with more information about the biology, ecology and distribution of the species present in the Amazon. Considering that the bat species inventories in the Brazilian Amazon are restricted to a few isolated points, and the biology and ecology of just a few species have been subject to detailed studies, the perspectives for the bat research in that area are extremely positive. As an example, the savanas and forests near the delta of the Tapajós River in Pará, were just recently surveyed and this site is potentially among the richest in bat species in the neotropics (E. Bernard, unpublished data). And recent studies on the use of different habitats and the bats' response to forest fragmentation and logging are providing crucial information that will aid in the conservation of bats in the Amazon (E.M. Sampaio and N. Saldanha, pers. comm.)

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