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Bats of the Reserva Nacional Allpahuayo-Mishana, northeastern Peru, with notes on community structure

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An inventory of the bat fauna at the Reserva Nacional Allpahuayo-Mishana documented 63 species. Coupled with previous records, this becomes the second most species-rich site for bats in Peru, with 65 species. Reproductively, there was a peak in activity in the early rainy season (October–December) that steadily declined to a low in the late rainy or early dry season (May–June). The community was dominated by *Carollia perspicillata* in terms of relative abundance and biomass. Most species were frugivores (28) or insectivores (26), but frugivores were predominant in the community based on cumulative abundance and biomass. The bat fauna was sampled to 85–91% completion based on extrapolations of local species richness. Nonetheless, only 56% of the regional species pool was captured locally. The fauna was compositionally similar to that of other western Amazonian sites. Although the Reserva Nacional Allpahuayo-Mishana enjoys a relatively high protected status, this has yet to be translated into sustained conservation. As a hotspot of biodiversity in Peru, it deserves protection at the highest possible level.

Key words: Chiroptera, Peru, inventory, species richness, community structure, abundance, biomass, dominance, feeding guild, conservation, reproduction

INTRODUCTION

The Chiroptera is the second most species-rich order of mammals after Rodentia, comprising 17 families, 177 genera, and 925 species (Koopman, 1993). Like most mammal taxa, bat species richness peaks in tropical regions (Findley, 1993; Willig *et al.*, 2003) regardless of spatial scale (e.g., Willig and Selcer, 1989; Willig and Sandlin, 1991; Willig and Lyons, 1998; Lyons and Willig, 2002), with records of up to 175 species from a single country (Indonesia — Mickleburgh *et al.*, 2002). In the New

World tropics, the richest bat fauna has been reported from Colombia, with 170 species (Rodríguez-Mahecha *et al.*, 1995). However, twelve of those species are not represented by voucher specimens and their occurrences are inferred from distributional records from bordering countries. As such, Peru ranks second in the Neotropics, with eight families, 61 genera, and 158 species (Pacheco *et al.*, 1995), of these, six species were documented recently, including *Centronycteris maximiliani* (Hice and Solari, 2002), *Micronycteris matses* (Simmons *et al.*, 2002), *Eumops maurus* (Montambault,

2002), and *Micronycteris brosetti*, *Cynomops paranus*, and *Eptesicus chiriquinus* (Simmons and Voss, 1998). Because all 158 Peruvian species are represented by voucher specimens, the country is tied with Colombia as the most species-rich bat fauna in the New World based on documented records of occurrence.

A summary of geographic variation in bat diversity within Peru can be seen from the works of Tuttle (1970), Koopman (1978), and Pacheco *et al.* (1995). Regional studies include Ceballos (1968), who compiled a list of bats from the Departments of Loreto and Ucayali based on museum specimens and literature reports. The most species (74) from one site within Peru are reported from Manu National Park in southern Peru (Patterson *et al.*, 1996). Woodman *et al.* (1991) collected 44 species in Cuzco Amazónico, which also is in southern Peru. Balta, in central Peru, has been relatively well inventoried for bats, with 56 species (Simmons and Voss, 1998). In the Department of Loreto in northeastern Peru, 63 species are reported from Jenaro Herrera (Ascorra *et al.*, 1991, 1993; Solari *et al.*, 1999) and 57 from Nuevo San Juan (Fleck *et al.*, 2002).

Herein, we present data from an inventory of bats from the Reserva Nacional Allpahuayo-Mishana (RNAM), Department of Loreto, northeastern Peru. Limited sampling of bats in RNAM have been previously published: Davis and Dixon (1976) sampled bats for nine nights (33 net nights, 346.5 net hours) in Mishana, located on the northern border of RNAM, where they captured 25 species; and López-Wong (2002) sampled bats throughout forested areas of the reserve, especially in white sand forests, where she captured 31 species after 2268 net hours. We update the list of species and present reproductive, habitat, and roosting information about species from RNAM.

Neotropical bat communities can be examined from taxonomic and functional perspectives. These emphasize different aspects of community composition and should be used in concert to more fully understand bat community structure. However, these perspectives can be based on either relative abundance or biomass. Whereas several studies examine bat community composition based on abundance (e.g., Pirlot, 1964; Fleming *et al.*, 1972; Willig, 1986; Lim and Engstrom, 2001a; Patterson *et al.*, 2003), only two studies do so based on biomass (Pirlot, 1964; Lim and Engstrom, 2001a). Because larger animals are likely to have a greater impact on available resources than smaller animals, assessing community structure based on biomass has the potential to illuminate biologically meaningful patterns in community structure that might not be apparent when based on abundance. We examine the community structure at RNAM from taxonomic and functional perspectives based on both relative abundance and biomass.

MATERIALS AND METHODS

Study Area

Research was conducted at RNAM (03°58'S, 73°25'W), a 57,667 ha national reserve, located 25 km southwest of Iquitos, Department of Loreto, northeastern Peru. Most bats were collected near the southern border of the reserve several hundred meters from the road, or near Mishana, a small village on the northern border of the reserve on the Río Nanay. Elevation is 120 m a.s.l. at both sites. The climate is tropical with a mean annual temperature of 26°C. Average rainfall is ≈2,800 mm per year, with a slightly drier season from June to September (Johnson, 1976).

The reserve is located in the Humid Tropical Forest Botanical Province of the Holdridge System (Tosi, 1960), and mostly comprises non-flooded forest habitats or terra firme. However, areas of flooded forest exist along the Río Nanay (the northern border of RNAM) and many kinds of disturbed habitats are present throughout the area. Typical forested habitats include white sand forest (varillal), moriche palm

(*Mauritia flexuosa*) swamps (aguajales), flooded forest (igapó), and upland forest (monte alto). Other undisturbed habitats include marshes and ponds. Disturbed areas can be divided into two major classes: those recovering from disturbance and those subject to active use by humans. Successional areas primarily include dense stands of cecropia (*Cecropia* spp.), shrubby areas (chamizal) dominated by *Pachira brevipes*, grassy areas, and various serial stages of succession. Places that are used by humans include poultry ranges, fish farms, cultivated fields (mostly manioc and sugar cane), pasture, orchards, stands of the pijuayo palm (*Bactris gasipaes*), culverts, and dwellings. The last three were used as roosts by bats.

Inventory Methods

Specimens were collected from September 2001 to March 2002 and from May to June 2002, as well as on seven days (3 in January, 1 in April, and 3 in November) in 1998. Three methods were employed to sample bat communities. Standard ground-level mist-netting was conducted to sample the forest understorey. An average of ten 12 × 2.6 m mist-nets were deployed each night. These were placed over streams and other bodies of water, in clearings in the forest and in undisturbed forest, across trails, in and around houses, and near roosts. Nets were opened before dusk (about 18:00) and closed at 01:00 hours. Nets were checked and bats removed approximately every 30 minutes. To better sample bats flying in the canopy or subcanopy, elevated mist-netting (≈15–20 m off the ground) was conducted concurrently with ground-level netting. We only deployed one or two subcanopy nets on any night because of time constraints. We also looked for roosting bats in culverts, fallen and hollow trees, armadillo burrows, walls and roofs of houses, and under leaves.

Data Analysis

Local species richness was estimated by extrapolation using several nonparametric methods based on sampling intensity and empirical species abundance distribution (see Colwell and Coddington, 1994). Records for only 61 species were used for these estimates, as two species were not documented during this study, and two were collected after June 2002. Extrapolation methods can be divided into those based on individuals or time. The first type includes CHAO1 (Chao, 1984), which is based on the number of rare species in a sample, called singletons and doubletons (i.e., those species represented by either

1 or 2 individuals). This estimate of species richness (S_1^*) based on CHAO1 is given by:

$$S_1^* = S_{\text{obs}} + (a^2/2b)$$

where S_{obs} is the observed number of species, a is the number of singletons, and b is the number of doubletons.

The other three methods are based on time and use unicates and duplicates (i.e., those species captured on only 1 or 2 sampling dates). The estimate of species richness (S_2^*) based on CHAO2 (Chao, 1984) is the simplest to calculate:

$$S_2^* = S_{\text{obs}} + (L^2/2M)$$

where L is the number of unicates and M is the number of duplicates. An estimate of species richness (S_3^*) based on the first order jackknife method (JACK1) uses only the number of unicates and is given by:

$$S_3^* = S_{\text{obs}} + L(n - 1/n)$$

where n is the number of samples. The second order jackknife estimate (JACK2) of species richness (S_4^*) uses unicates and duplicates, and is calculated as:

$$S_4^* = S_{\text{obs}} + [\{L(2n - 3)/n\} - \{M(n - 2)^2/n(n - 1)\}].$$

The bat fauna at RNAM was compared to that of 18 other neotropical sites. More specifically, pairwise similarities were quantified with Jaccard's index (J_{ij} ; Janson and Vegelius, 1981), in which $J_{ij} = C_{ij}/T_{ij}$ (C_{ij} is the number of species common to locations i and j , and T_{ij} is the number of unique species in a combined sample). Species lists were based on published compilations of faunas from several sources (see footnotes of Table 3 for specific sources), with corrections for recent taxonomic changes. Results were clustered with an unweighted pair-wise group method (UPGMA) using arithmetic averages (program UPGMA in MatLab 5.3). Inter-site distances were obtained from Microsoft Encarta Virtual Globe 1998. Correlation between faunal similarity and geographic proximity was analyzed with a Mantel test (program MANTEL in MatLab 5.3; Smouse *et al.*, 1986).

Feeding guilds can be defined in a number of ways for bats (Patterson *et al.*, 2003). Relatively few insectivorous species were captured during this study, so subdividing this guild into several types of insectivores was not useful from an analytical perspective. Because of this, we used the relatively simple guild delineations of Wetterer *et al.* (2000) to construct niche matrices.

Most captured individuals were prepared as museum specimens, but many individuals of the most common species were released at the end of each netting session because of limits imposed by collecting

permits. Specimens are deposited at the Museo de Historia Natural of the Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru. Tissue and blood samples are deposited at the University of Texas Medical Branch, Galveston, Texas (UTMB). We follow the taxonomy of Koopman (1993) as modified by Simmons and Voss (1998), Wetterer *et al.* (2000), and Lee *et al.* (2002), except in recognizing the genus *Dermanura* and the species binomial *Mesophylla macconnelli* (Baker *et al.*, 2000).

RESULTS

Species Diversity

Based on 2,257 net hours, 1,937 bats were captured representing 63 species and six families (Appendix). Two additional species have been reported from RNAM, *Cormura brevirostris* and *Vampyrodes caraccioli*, which increases bat richness to 65 species. We report 23 new records for RNAM (Appendix) and three new records for the Department of Loreto (*Chiroderma salvini*, *Lasiurus ega*, and *Molossops teminckii*).

In six nights (56 net hours) of netting in the subcanopy, we collected eighteen individuals representing eight species: *Saccopteryx leptura* (1 ♂), *Phyllostomus hastatus* (3 ♂♂, 2 ♀♀), *Carollia perspicillata* (3 ♂♂, 1 ♀), *Rhinophylla pumilio* (1 ♂), *Artibeus lituratus* (1 ♂, 1 ♀), *A. obscurus* (2 ♀♀), *A. planirostris* (2 ♀♀), and *Dermanura gnoma* (1 ♂). All but one of these species (*S. leptura*) also were captured in ground-level nets. None of the bats captured in the subcanopy were molossids or vespertilionids.

Although less time (approximately 25 hours) was spent searching for putative roosts than netting in the subcanopy, 38 individuals representing ten species were collected. Several species were captured in houses, including *Rhynchonycteris naso* (1 ♂, 1 ♀), *Lophostoma brasiliense* (1 ♀), *Lasiurus ega* (1 ♀), *Eptesicus brasiliense* (1 ♂, 2 ♀♀), *Molossus rufus* (5 ♀♀), and

M. molossus (3 ♂♂, 6 ♀♀). Various types of hollow trees, especially pijuayo palms, harbored a number of species including *Phyllostomus hastatus* (7 ♂♂), *Mimon crenulatum* (3 ♂♂) and *Tonatia saurophila* (3 ♂♂). *Saccopteryx bilineata* (2 ♂♂, 2 ♀♀) was captured in other kinds of hollow trees. On one night we netted a culvert under the Iquitos — Nauta highway at km 62 and captured nearly all the bats (182) roosting in it, representing seventeen species: *Phylloderma stenops* (1 ♂), *Trachops cirrhosus* (2 ♂♂, 1 ♀), *Glossophaga soricina* (2 ♂♂, 2 ♀♀), *Carollia brevicauda* (46 ♂♂, 43 ♀♀), *C. castanea* (1 ♂), *C. perspicillata* (35 ♂♂, 27 ♀♀), *Rhinophylla fischeriae* (1 ♂, 1 ♀), *R. pumilio* (1 ♀), *Artibeus obscurus* (1 ♂, 2 ♀♀), *Dermanura anderseni* (2 ♂♂, 1 ♀), *Platyrrhinus brachycephalus* (2 ♂♂), *P. helleri* (1 ♂), *Sturnira lilium* (1 ♂, 1 ♀), *S. tildae* (2 ♂♂, 1 ♀), *Uroderma bilobatum* (1 ♂), *Vampyressa bidens* (1 ♀), and *V. pusilla* (1 ♂, 1 ♀).

Reproductive Patterns

Annual reproductive activity cannot be estimated accurately because only a few captures were recorded in some months. Nonetheless, for the 27 species for which females were captured, a seasonal pattern of reproduction was apparent, with few individuals of any species being pregnant or lactating in May (2%) or June (6%). No data were available from July or August, but the proportion of pregnant or lactating individuals increased in September (50%), and was nearly 100% from October to December. It remained relatively high (31 to 46%) from January to March, but at a lower level than the previous quarter (Table 1).

The species with the most reproductive information compiled was *C. perspicillata*, which was captured in eight months of the year. Pregnant or lactating individuals were recorded during seven of those months.

TABLE 1. Reproductive condition of females from the Reserva Nacional Allpahuayo-Mishana, Loreto, Peru. No data are available for April, July, or August. Hyphenated numerical sequences represent, in order, number pregnant, number lactating, total number captured. If only one number appears, it is the total number of captured individuals, of which none were pregnant or lactating. Empty cells indicate that no individuals were captured in a particular month

Species	January	February	March	May	June	September	October	November	December
<i>Noctilio albiventris</i>					2-1-5				
<i>Carollia brevicauda</i>	4-0-5	4-0-6	2	52	10			0-1-2	
<i>C. perspicillata</i>	8	3-0-8	12-1-44	2-2-168	0-1-153	1-0-4		7-0-10	3-2-5
<i>Rhinophylla fischeriae</i>			1-0-1	3	1				
<i>R. pumilio</i>			0-1-7	1-0-29	0-1-7				
<i>Desmodus rotundus</i>			1	2	2-0-3				
<i>Glossophaga soricina</i>	0-1-2		1	0-1-22	0-1-4			0-1-1	
<i>Mimon crenulatum</i>		1-0-2	2			0-1-1			
<i>Phyllostomus discolor</i>					0-1-1				
<i>P. hastatus</i>	1		0-1-1	2	4				
<i>Artibeus lituratus</i>			2-4-14	12	0-2-10		0-1-1		
<i>A. obscurus</i>			3-1-6	20	6			1-0-1	2-0-2
<i>A. planirostris</i>		1	1-0-9	10	4		2-0-2		0-1-1
<i>Chiroderma salvini</i>			1-0-1					1-0-1	
<i>C. trinitatum</i>		1-0-1		3					
<i>Dermanura cinerea</i>			1-0-1	1					
<i>D. gnomia</i>			1-0-1	8	2			2-0-4	2-0-2
<i>Mesophylla macconnelli</i>			1-0-1	7	1				
<i>Platyrrhinus helleri</i>				2	1		1-0-1	0-3-4	
<i>Sturnira lilium</i>			1-0-2	0-1-23	0-1-14		2-0-2	23-1-27	
<i>S. magna</i>			1		0-1-7				
<i>S. tildae</i>		1		0-1-8	0-1-3				
<i>Uroderma bilobatum</i>				3	3		1-0-1	1-1-2	
<i>Vampyressa bidens</i>		3-0-7		11			1-0-1	0-3-3	
<i>V. brocki</i>			1-0-1	6			2-0-2		
<i>V. pusilla</i>		1-0-1	1-0-2	5	2		6-0-7	1-15-19	
<i>Molossus molossus</i>		1	1		4	1-0-1	1	1	1

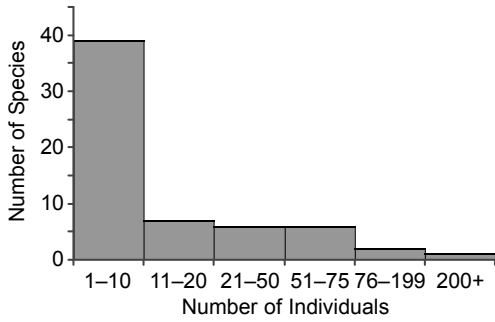


FIG. 1. Histogram of the number of species in each of a number of abundance categories from rare to common

Although sample size was small, all five females captured in December were reproductively active. In contrast, over 100 females were captured in May and June, but reproductive activity was minimal (Table 1). This suggests that most parturition occurs during the wet season.

Community Structure

The distribution of the number of individuals captured per species was highly

right-skewed, with 64% (39 of 61) of the species captured ten or fewer times (Fig. 1). In contrast, only nine species (15%) were captured more than 50 times and three (5%) more than 100 times. The abundance distribution of bat species also was highly skewed and the bat assemblage was dominated by *C. perspicillata* (Fig. 2). This species was five times more abundant than the next most abundant species, *C. breviceauda*. Only one other species, *S. lilium*, accounted for more than 5% of captured individuals. The twenty most abundant species accounted for 90% of captured individuals. The four most abundant species were frugivorous, and all were small to medium-sized species (i.e., 9.0 to 25.0 g).

In terms of biomass, *C. perspicillata* remained the dominant species (Fig. 3), but comprised a smaller percentage of the total biomass than it did the total number of individuals. One of the top five species was an insectivore and the remaining species were frugivores. Four of the five dominant species were large bats (i.e., 35.0 to

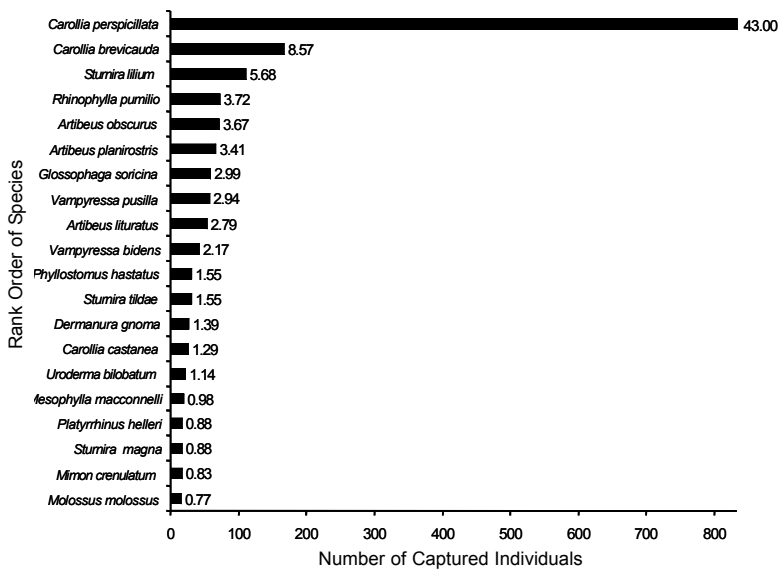


FIG. 2. Bar diagram of the 20 most dominant species of bats at the Reserva Nacional Allpahuayo-Mishana based on number of captured individuals. Numerical values to the right of each bar are percents of all individuals ($n = 1,937$)

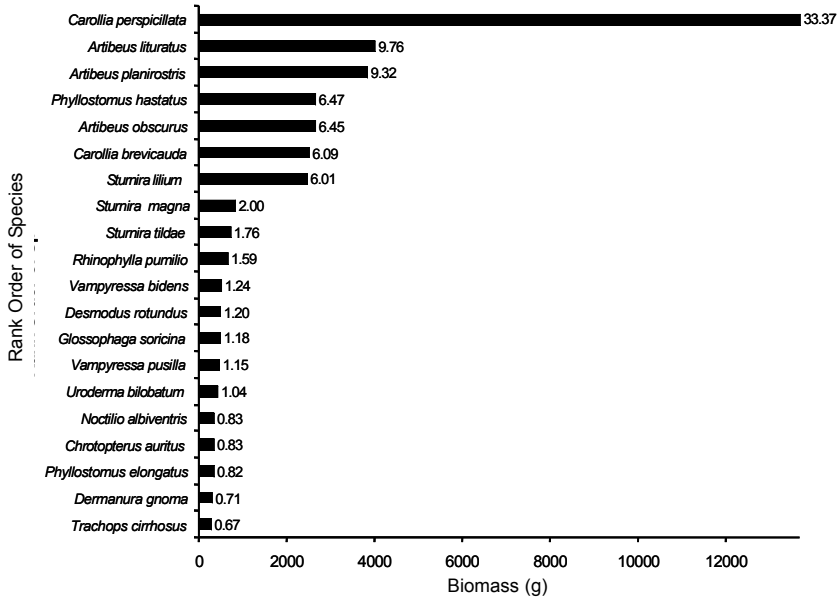


FIG. 3. Bar diagram of the 20 most dominant species of bats at the Reserva Nacional Allpahuayo-Mishana based on biomass. Numerical values to the right of each bar are percents of total cumulative biomass (41,012 g)

90.0 g) in the genera *Artibeus* and *Phyllostomus*.

Most species were frugivorous (28) or insectivorous (26), with a small number of species in each of the other three guilds (Fig. 4A). Frugivores dominated the community in terms of abundance, accounting for 88% of all captures, whereas insectivores represented only 7% of the captures (Fig. 4B). Frugivore dominance diminished only slightly (84%) when abundance was weighted by biomass, and insectivores increased slightly (12% — Fig. 4C)

Estimates of local species richness ranged from 67 (CHAO 1 and 2) to 72 species (JACK 1 and 2) indicating the local fauna was sampled to 85–91% completion. In contrast, only 61 of a possible 108 regional species (56%) were documented at the local level (Table 2).

Regional Comparisons

RNAM was most compositionally similar to six other bat faunas from the western

Amazonian subregion (i.e., in decreasing order Jenaro Herrera, Balta, Cuzco Amazónico, Manu, Yasuni, Nuevo San Juan) based on Jaccard’s similarity index and was

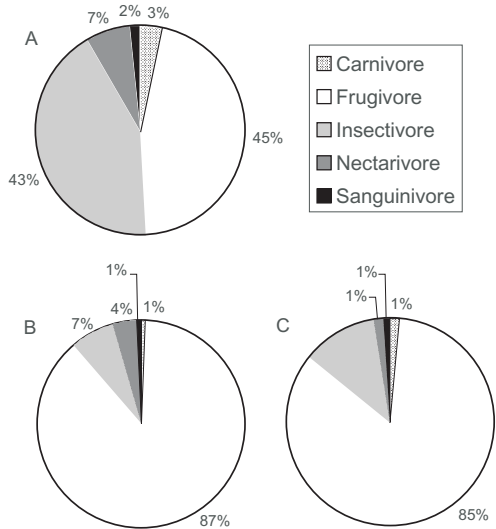


FIG. 4. Bat community structure at the Reserva Nacional Allpahuayo-Mishana by guild based on A — number of species, B — number of individuals, and C — biomass

least similar to that of Montes Azules (Table 3). The dendrogram based on UPGMA clustering (not shown) was topologically similar to other published dendrograms of bat community similarity, with faunas of major geographic regions within the Neotropics clustered together. Geographic proximity and faunal similarity were highly correlated (Mantel test; $r = 0.740$, $P < 0.001$).

DISCUSSION

Carollia perspicillata was the most abundant species at RNAM, representing 51% of all captures in disturbed habitats and 43% in undisturbed forest. This is similar to the pattern in French Guiana, where *C. perspicillata* was more abundant in disturbed habitats than in primary forest (Brosset and Charles-Dominique, 1990). Several rare species of bat were captured in disturbed habitats of RNAM, including *Artibeus concolor*, *Micronycteris minuta*, *Myotis simus*, *Phyloderma stenops*, *Thyroptera tricolor*, *Lophostoma brasiliense*, and *Trinycteris nicefori*. In several cases, rare species were captured within a few meters from the edge of a paved road, suggesting considerable tolerance to human activities and noise.

The seventeen species representing four subfamilies of Phyllostomidae collected from the same culvert represents the highest number of species reported from a single roost (Kunz and Lumsden, 2003). This could be attributed to the size of the culvert (≈ 15 m long) or the presence of two large entrances (≈ 2 m in diameter). *Carollia brevicauda* and *C. perspicillata* comprised 83% of the individuals from the culvert.

The low level of reproductive activity observed in May and June coincides with the dry season in northeastern Peru. Reproductive activity increased as the rainy season began in September and remained

TABLE 2. Bat species that could potentially occur, but were not captured at RNAM

Family Emballonuridae
<i>Centronycteris centralis</i>
<i>Diclidurus albus</i>
<i>Diclidurus ingens</i>
<i>D. scutatus</i>
<i>Peropteryx kappleri</i>
<i>P. macrotis</i>
Family Furipteridae
<i>Furipterus horrens</i>
Family Noctilionidae
<i>Noctilio leporinus</i>
Family Phyllostomidae
Subfamily Desmodontinae
<i>Diphylla ecaudata</i>
<i>Diaemus youngi</i>
Subfamily Glossophaginae
<i>Anoura caudifera</i>
<i>Lichonycteris obscura</i>
<i>Lionycteris spurrelli</i>
Subfamily Phyllostominae
<i>Glyphonycteris daviesi</i>
<i>G. sylvestris</i>
<i>Lampronnycteris brachyotis</i>
<i>Lonchorhina aurita</i>
<i>Lophostoma carrikeri</i>
<i>Macrophyllum macrophyllum</i>
<i>Micronycteris brosetti</i>
<i>M. hirsuta</i>
<i>M. matses</i>
<i>M. schmidtorum</i>
<i>Vampyrum spectrum</i>
Subfamily Stenodermatinae
<i>Enchisthenes hartii</i>
<i>Sphaeronnycteris toxophyllum</i>
Subfamily Thyropteridae
<i>Thyroptera discifera</i>
<i>T. lavalii</i>
Family Vespertilionidae
<i>Lasiurus cinereus</i>
<i>L. blossevillii</i>
Family Molossidae
<i>Cynomops paranus</i>
<i>C. planirostris</i>
<i>Eumops aripendulus</i>
<i>E. bonariensis</i>
<i>E. glaucinus</i>
<i>E. hansae</i>
<i>E. perotis</i>
<i>Molossops abrasus</i>
<i>M. neglectus</i>
<i>Nyctinomops aurispinosus</i>
<i>N. macrotis</i>
<i>N. laticaudatus</i>
<i>Promops nasutus</i>

TABLE 3. Percent faunal similarity (lower left triangle) based on Jaccard's index between all possible pairs of 19 neotropical rainforest bat faunas. Inter-site distances (km) appear in the upper right triangle

Bat fauna	MoA	LSe	BCI	Ima	PSE	Par	Iwo	Ara	Cun	Mus	Xin	JHe	Bal	Man	CAm	NSJ	SJM	Yas	RNAM
MoA ^a		986	1,429	3,385	4,304	4,325	3,748	4,393	3,090	4,046	2,953	3,037	3,641	3,794	4,001	3,076	2,985	2,459	2,963
LSe ^b	43		388	2,452	3,454	3,379	2,857	3,435	2,131	3,057	3,788	2,053	2,652	2,829	2,995	2,114	2,039	1,496	1,991
BCI ^c	40	64		1,989	2,988	3,004	2,383	3,037	1,656	2,596	3,315	1,712	2,320	2,508	2,655	1,765	1,569	1,169	1,627
Ima ^d	31	42	41		939	1,023	460	1,076	649	1,220	1,613	1,983	2,281	2,454	2,428	1,977	618	1,930	1,886
PSE ^e	24	38	34	60		17	645	143	1,431	1,220	1,000	2,566	2,646	2,793	2,670	2,525	1,453	2,689	2,485
Par ^f	29	40	37	61	63		662	136	1,458	1,217	994	2,582	2,714	2,838	2,732	2,535	1,472	2,583	2,501
Iwo ^g	32	36	39	68	54	66		683	780	842	1,141	1,956	2,118	2,277	2,198	1,915	823	2,031	1,869
Ara ^h	26	31	35	64	62	62	55		1,456	1,162	859	2,556	2,636	2,754	2,640	2,503	1,504	2,689	2,476
Cun ⁱ	27	31	35	53	53	44	46	56		993	1,701	1,311	1,643	1,847	1,849	1,280	197	1,274	1,198
Mus ^j	27	33	37	54	51	53	52	53	48		850	1,589	1,465	1,584	1,448	1,476	1,162	1,846	1,491
Xin ^k	25	30	29	46	53	49	45	50	43	48		2,375	2,220	2,284	2,119	2,313	1,833	2,696	2,336
JHe ^l	26	33	37	49	52	50	49	48	41	47	53		643	819	997	74	1,412	560	120
Bal ^m	29	32	35	55	49	44	48	46	43	54	49	59		200	346	585	1,805	1,202	727
Man ⁿ	33	40	43	53	47	43	47	44	48	40	42	56	59		223	771	2,004	1,462	912
CAm ^o	26	31	34	44	48	39	41	42	40	50	47	55	64	55		938	2,009	1,552	1,076
NSJ ^p	26	37	33	46	52	50	47	46	45	45	51	60	47	52	51		1,407	624	147
SJM ^q	32	35	40	56	45	51	59	52	46	46	42	43	46	45	37	42		1,311	1,310
Yas ^r	26	38	36	57	52	53	50	51	47	46	47	55	53	57	51	60	41		498
RNAM^s	28	33	35	54	53	47	53	47	46	50	49	71	66	62	65	61	45	45	62

^a—Montes Azules, Mexico; 64 species; Medellín (1993); ^b—La Selva, Costa Rica; 65 species; Simmons and Voss (1998); ^c—Barro Colorado Island, Panama; 63 species; Simmons and Voss (1998). Although they state that 66 species are present on BCI, there are only 63 presences in the species matrix in appendix 2; ^d—Imataca, Venezuela; 77 species; Lim and Engstrom (2001b); ^e—Piste St.-Élie, French Guiana; 54 species; Simmons and Voss (1998); ^f—Paracou, French Guiana; 78 species; Simmons and Voss (1998); ^g—Iwokrama Forest, Guiana; 86 species; Lim and Engstrom (2001b); ^h—Arataye, French Guiana; 61 species; Voss and Emmons (1996); ⁱ—Cunucunuma, Venezuela; 50 species; Voss and Emmons (1996); ^j—Manaus, Brazil; 52 species; Simmons and Voss (1998); ^k—Xingu, Brazil; 47 species; Voss and Emmons (1996); ^l—Jenaro Herrera, Peru; 63 species; Ascorra *et al.* (1991) as modified by Ascorra *et al.* (1993) and Solari *et al.* (1999); ^m—Balta, Peru; 56 species; Voss and Emmons (1996); ⁿ—Manu, Peru; 74 species; Lim and Engstrom (2001b). We do not include *Anoura cultrata*, *Anoura* sp. nov., *Sturnira erythromis*, *Vampyressa melissa*, *Eptesicus brasiliensis*, or *E. furinalis*, because they were captured above 900 m. We also do not include *Choronomiscus godmani*, as it has never been captured in Peru and is not listed in Patterson *et al.* (1996). We do include *Vampyressa nymphaea* (Patterson *et al.*, 1996); ^o—Cuzco Amazónico, Peru; 44 species; Woodman *et al.* (1991); ^p—Nuevo San Juan, Peru; 57 species; Fleck *et al.* (2002); ^q—San Juan de Manabiate, Venezuela; 71 species; Lim and Engstrom (2001b). We do not include *Anoura latidens* because it is not a lowland rainforest species. This specimen may have been misidentified ^r—Yasuni, Ecuador; 66 species; Lim and Engstrom (2001b); ^s—Reserva Nacional Allpahuayo-Mishana, Peru; 65 species; data presented herein

high until two months before the end of the rainy season (see Table 1). This allowed most parturition to occur during the mid- to late-rainy season, when fruits may be most abundant. This pattern commonly is observed in neotropical phyllostomid frugivorous bats (Willig, 1985a, 1985b).

Although sampling effort was unequal throughout the year, the pattern of reproductive activity for *C. perspicillata* at RNAM corresponded to the pattern at Jenaro Herrera, where pregnant or lactating *C. brevicauda* and *C. perspicillata* were captured in all months even though the proportion of reproductively active individuals was lowest from May to July and highest in the early rainy season (Ascorra *et al.*, 1993). This also is similar to the pattern observed in Panama for *C. perspicillata*, where it was seasonally polyestrous, although peaks in proportion of pregnant individuals occurred in the middle of the dry season and beginning of the rainy season (Fleming *et al.*, 1972).

The bat community at RNAM comprised many rare species and few common species, a pattern typical of neotropical rainforest bat communities (Simmons and Voss, 1998; Lim and Engstrom, 2001a; Stevens and Willig, 2002). It was highly dominated by one species, *C. perspicillata*, which accounted for 43% of all captures. Members of the genus *Carollia* were an important component of the bat community at RNAM, with the three species present comprising 53% of captured individuals. This also was true of several other sites in the Neotropics, with one to three species of *Carollia* among the five most abundant species (Findley, 1993; Simmons and Voss, 1998; Lim and Engstrom, 2001a). Other important genera at RNAM included *Sturnira* (three species in the top 20), *Artibeus* (3), and *Vampyressa* (2). When biomass was examined, the rank order of species changed, with larger bats becoming

more important. However, 15 of the 20 most abundant bat species also were in the top 20 for biomass.

Species richness of frugivorous and insectivorous bats were nearly equal in the community, but frugivores were much more abundant. Although low abundance of insectivores could be attributed partially to a sampling bias, subcanopy nets captured only two insectivorous species (*Saccopteryx leptura* and *Phyllostomus hastatus*). Roosts, with the exception of the large culvert that was netted, yielded exclusively insectivorous species, but not many individuals. We documented only 4 of 17 molossids and 12 of 23 insectivorous phyllostomines that could occur at the site based on geographic range descriptions (see Table 2; Simmons and Voss, 1998; Eisenberg and Redford, 1999). Some insectivorous species are particularly difficult to capture in mist nets because of their characteristic high and fast flight or their ability to avoid mist nets. This makes it difficult to document all insectivorous species present in the area in a manner comparable to data obtained for more easily captured frugivores. Nonetheless, it is possible that low abundances of insectivores recorded at RNAM are representative of low densities or the absence of some insectivorous species. A comparison of guild structure of RNAM to that published for other lowland neotropical rainforest sites could clarify if this low density of insectivores is typical of bat communities in this biome.

The species richness (65) reported from RNAM is typical of neotropical rainforests. As such, it is tied for seventh position in bat species richness in the New World (see footnotes of Table 3 for number of species present at each site). It is the second most species-rich bat fauna in Peru after Manu, which has 74 lowland and 82 total species. Manu enjoys a higher protected status, is much larger (17,000 km² vs. 570 km²), and

is highly heterogeneous in habitat attributes when compared to RNAM.

This survey is as complete as many other surveys of bats conducted in lowland rainforest habitats of South and Central America, although more species could be expected to occur at RNAM based on ecogeographic range data (see Table 2). At Paracou, French Guiana, Voss *et al.* (2001) used the same methods for estimating local species richness as were used for the bat fauna at RNAM. They predicted the bat fauna had been sampled 83–91% completely, although they only encountered 78 of 103 (76%) regional species (see Table 2). Complete inventories of bats are difficult to obtain because many species are not collected easily by traditional methods (e.g., mist netting at ground level). Even if additional methods are employed, including canopy and subcanopy netting, shooting, or searching for roosts, some species may not be obtained (Voss and Emmons, 1996; Simmons and Voss, 1998) because of behavioral characteristics, habit association (e.g., canopy or high flying taxa) or rarity. Moreover, local species richness does not equal regional species richness, especially in tropical regions (Stevens and Willig, 2002). Thus, it is likely that some species that occur in the region simply were not present in the local community at RNAM during the inventory.

Within the New World tropics, faunal similarity and geographic proximity are correlated (Simmons and Voss, 1998). However, this relationship is based only on the presence or absence of species. It is unclear if this spatial correlation is true of community structure when the presence of species is weighted by relative abundance or biomass.

These results clearly demonstrate the high level of species richness of bats in the northwestern Amazon Basin. They also demonstrate our lack of knowledge of even

the most basic natural history and ecological information about neotropical bat species and communities, much less broad-scale patterns in diversity and community structure. Additional inventories are needed to better document patterns in diversity throughout Amazonia, and develop conservation strategies to protect this incredibly diverse region.

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APPENDIX

Bats of the Reserva Nacional Allpahuayo-Mishana, Loreto, Peru. An asterisk (*) indicates a new record for RNAM based on this research. A cross (†) indicates that the species is listed as near threatened by the IUCN (Hutson *et al.*, 2001). All species except *Cormura brevirostris* and *Vampyroides caraccioli* were documented by this study. *Molossops temminckii* and *Promops centralis* were captured subsequent to this field season, so no data are presented, but they are included for completeness. Average mass was not always obtained from the total number of individuals captured, as some individuals were released. Local demographic status: A = abundant, almost always captured; C = common, frequently captured in several habitat types; U = uncommon, infrequently captured (< 10 individuals); R = rare, only 1 individual captured. Feeding guild: C = carnivorous, F = frugivorous, I = insectivorous, N = nectarivorous, S = sanguinivorous. The first letter indicates a species primary feeding guild. Letters in parentheses indicate its secondary feeding guild(s). Dominance values were calculated as the percentage of the total number of individuals captured or total biomass. Habitat association: A = aguajal, C = cecropial, Ch = chamizal, Cu = culvert, F = flooded forest, Fr = farm, G = grassy area, M = marsh, O = orchard, P = primary forest, Pi = pijuayal, Po = pond, S = secondary growth, V = varillal, Vi = village. See text for habitat descriptions. Previous reports: 1 = Davis and Dixon (1976), 2 = Hice and Solari (2002), 3 = Lopez-Wong (2002)

Taxon	Number captured	Average mass (g)	Status	Guild	Dominance — individuals (%)	Dominance — biomass (%)	Habitat	Previous
Emballonuridae								
<i>Centronycteris maximiliani</i>	1	7.0	R	I	0.1	< 0.1	V	2
<i>Cormura brevirostris</i>	na	na	R	I	na	na	S	3
<i>Peropteryx leucoptera</i>	2	7.0	U	I	0.1	0.0	A	3
<i>Rhynchonycteris naso</i> *	3	4.0	U	I	0.2	0.0	Vi	
<i>Saccopteryx bilineata</i> *	8	9.1	U	I	0.4	0.2	P, S, V	
<i>S. leptura</i> *	2	4.8	U	I	0.1	0.0	P	
Noctilionidae								
<i>Noctilio albiventris</i> *	9	37.8	U	I	0.5	0.8	Fr	
Phyllostomidae								
Carollinae								
<i>Carollia brevicauda</i>	166	15.1	A	F(I, N)	8.6	6.1	A, C, Cu, F, G, M, O, P, S, V	1, 3
<i>C. castanea</i>	25	10.3	C	F(I, N)	1.3	0.6	Cu, O, Pi, S, V	1, 3
<i>C. perspicillata</i>	833	16.4	A	F(I, N)	43.0	33.4	All 15 habitats	1, 3
<i>Rhinophylla fischerae</i> †	9	7.4	U	F(I, N)	0.5	0.2	Cu, M, P, S, V	3
<i>R. pumilio</i>	72	9.0	A	F(I, N)	3.7	1.6	A, C, Ch, Cu, F, G, M, O, P, Pi, S	1, 3
Desmodontinae								
<i>Desmodus rotundus</i>	14	35.3	C	S	0.7	1.2	Fr, O, P	1, 3
Glossophaginae								
<i>Choeronycteris minor</i> *	3	8.2	U	N(I, F)	0.2	0.1	P	
<i>Glossophaga soricina</i>	58	8.4	A	N(I, F)	3.0	1.2	A, C, Cu, Fr, O, P, Pi, Po, S	1, 3
<i>Lonchophylla mordax</i> *	3	6.8	R	N(I, F)	0.2	0.1	P, Pi, S	
<i>L. thomasi</i> *	7	6.5	U	N(I, F)	0.4	0.1	C, O, P, S	

APPENDIX. Continued

Taxon	Number captured	Average mass (g)	Status	Guild	Dominance — individuals (%)	Dominance — biomass (%)	Habitat	Previous
Phyllostominae								
<i>Chropterus auritus</i>	4	84.7	U	(I,C,F)	0.2	0.8	P, V	3
<i>Lophostoma brasilense*</i>	3	10.0	U	I(F, N)	0.2	0.1	O, P	
<i>L. silvicolum*</i>	3	32.2	U	I(F, N)	0.2	0.2	C, S	
<i>Miconycteris megalotis</i>	1	5.2	R	I(F)	0.1	0.0	V	3
<i>M. minuta</i>	1	6.5	R	I(F)	0.1	0.0	S	3
<i>Mimon crenulatum</i>	16	12.6	C	I(F, C)	0.8	0.5	A, P, Pi, S	3
<i>Phyloderma stenops</i>	2	59.5	R	I(F, N)	0.1	0.3	Cu, O	1
<i>Phyllostoma discolor</i>	1	40.0	R	I(F, N)	0.1	0.1	S	1
<i>P. elongatus</i>	9	37.3	U	I(F, N)	0.5	0.8	P, S	1, 3
<i>P. hastatus</i>	30	88.5	C	I(F, N)	1.6	6.5	A, C, E, P, S, V	3
<i>Tonatia saurophila</i>	9	24.2	U	I(F, N)	0.5	0.5	A, Ch, F, O, P, Pi	3
<i>Trachops cirrhosus*</i>	9	30.7	U	(I, C, F)	0.5	0.7	C, Cu, P	3
<i>Trinycteris nicefori</i>	1	9.0	R	I(F)	0.1	0.0	S	3
Stenodermatinae								
<i>Artibeus concolor**1</i>	3	21.0	U	F	0.2	0.2	F, Fr	
<i>A. lituratus</i>	54	74.1	A	F(I, N)	2.8	9.8	A, Ch, F, Fr, M, O, P, S	1, 3
<i>A. obscurus†</i>	71	37.3	A	F(I, N)	3.7	6.5	A, Cu, F, M, O, P, Pi, S, V	1, 3
<i>A. planirostris</i>	66	57.9	A	F(I, N)	3.4	9.3	A, Ch, F, Fr, G, O, P, Pi, S, V	1, 3
<i>Chiroderma salvini*</i>	2	28.5	U	F(I, N)	0.1	0.1	P	
<i>C. trinitatum</i>	9	13.9	U	F(I, N)	0.5	0.3	A, Fr, M, P, Pi	1
<i>C. villosus</i>	2	24.0	U	F(I, N)	0.1	0.1	A, Fr	1
<i>Dermanura anderseni*</i>	10	8.9	C	F	0.5	0.2	Cu, M, S	
<i>D. cinerea</i>	3	10.0	U	F	0.2	0.1	M, S	1
<i>D. glauca</i>	6	10.2	U	F	0.3	0.2	A, P	3
<i>D. gnoma</i>	27	10.8	C	F	1.4	0.7	A, C, Fr, G, O, P, S, V	3
<i>Mesophylla macconnelli</i>	19	7.0	C	F(I, N)	1.0	0.3	A, Fr, M, O, P, V	1, 3
<i>Platyrrhinus brachycephalus</i>	8	11.4	U	F(I, N)	0.4	0.2	Cu, Fr, M, Pi, S	1, 3
<i>P. helleri</i>	17	10.9	U	F(I, N)	0.9	0.5	A, Cu, Fr, P, Vi	1, 3
<i>P. infuscus†</i>	3	35.3	U	F(I, N)	0.2	0.3	O, P	3
<i>Sturnira liliium</i>	110	22.4	A	F(I, N)	5.7	6.0	A, Cu, Fr, G, M, O, P, Pi, S	1
<i>S. magna†</i>	17	48.3	C	F(I, N)	0.9	2.0	Fr, P, Pi, S	3
<i>S. tildae</i>	30	24.0	C	F(I, N)	1.6	1.8	A, Cu, F, Fr, G, M, O, P, S	3
<i>Uroderma bilobatum</i>	22	19.4	C	F(I, N)	1.1	1.0	Cu, Fr, M, O, Pi	1, 3

APPENDIX. Continued

Taxon	Number captured	Average mass (g)	Status	Guild	Dominance — individuals (%)	Dominance — biomass (%)	Habitat	Previous
<i>Uroderma magnirostrum</i> *	7	23.7	U	F(L, N)	0.4	0.4	M, O	
<i>Vampyressa bidenst</i> ^t	42	12.1	C	F(L, N)	2.2	1.2	A, Cu, P, V, Vi	1, 3
<i>V. brockii</i> **	14	9.1	C	F(L, N)	0.7	0.3	O, P, Vi	
<i>V. pusilla</i>	57	8.3	A	F(L, N)	2.9	1.2	A, Cu, Fr, M, P, S, Vi	1, 3
<i>Vampyrodes caraccioli</i>	na	na	R	F(L, N)	na	na	Fr, O	1
Thypteridae								
<i>Thyoptera tricolor</i>	1	4.0	R	I	0.1	0.0	S	
Vespertilionidae								
<i>Eptesicus brasiliensis</i> *	3	9.3	U	I	0.2	0.1	Vi	
<i>Lasturus ega</i> *	1	18.0	R	I	0.1	0.0	Vi	
<i>Myotis albescens</i> *	4	6.2	U	I	0.2	0.1	Fr	
<i>M. nigricans</i>	2	5.0	U	I	0.1	0.0	A, Fr	1
<i>M. riparius</i>	2	5.5	U	I	0.1	0.0	S	1
<i>M. simus</i> *	1	4.0	R	I	0.1	0.0	Fr	
Molossidae								
<i>Molossus molossus</i> *	15	14.8	U	I	0.8	0.5	Vi	
<i>M. rufus</i> *	5	44.0	C	I	0.3	0.5	Fr, Vi	
<i>Molossops temminckii</i> *	na	na	R	I	na	na	P	
<i>Promops centralis</i> *	na	na	R	I	na	na	Vi	