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Mammal Diversity and Conservation in the Selva Lacandona, Chiapas, Mexico

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Abstract: *The Selva Lacandona region of Chiapas, Mexico, has high biodiversity, represents the last large portion of tropical rainforest in México, and faces imminent destruction. Through fieldwork and literature searches I found a total of 112 mammal species (including 17 Middle-American endemics) on the Lacandona's 331,200 ha Montes Azules Biosphere Reserve. This inventory plus those from eight additional Neotropical localities show local mammal species richness in the Neotropics to be in the range of 70–116 species. Richness is primarily correlated with the amount of annual rainfall, but within rainforest areas species richness is probably not correlated with rainfall, latitude, altitude, or area size. Rather, above a certain limit of rainfall and below a critical level of latitude and altitude, mammal species richness seem to reach an asymptotic maximum. Areas covered with tropical rainforest and with a well-known, relatively intact fauna have about 112–116 mammal species. In the Montes Azules Reserve most mammals (57%) are bats. The most heavily occupied feeding guilds are frugivores/herbivores and insectivores/omnivores. Large species and carnivores appear most vulnerable to local extinction. Montes Azules (and thus the Selva Lacandona) is especially noteworthy because (1) it contains a greater proportion of species facing conservation problems than expected from a random draw of Mexican mammals; (2) it is probably the most diverse ecosystem in Mexico; (3) many species sustain their only Mexican populations in this area; and (4) it is the largest remnant of tropical rainforest in Mexico and is part of the largest expanse of that vegetation type in Central America.*

Diversidad de mamíferos y conservación en la Selva Locandona, Chiapas, México

Resumen: *La región de la Selva Lacandona de Chiapas, México, posee altos niveles de biodiversidad, representa la última porción grande de bosque tropical perennifolio, y enfrenta una destrucción inminente. Por medio de trabajo de campo y búsquedas de literatura, se documentó la presencia de un total de 112 especies de mamíferos (incluyendo a 17 endémicos de Mesoamérica) representando la Reserva de la Biosfera de Montes Azules (1/5 de la Lacandona; 331,200 ha). Este inventario más los de ocho localidades adicionales en el Neotrópico mostraron que la riqueza específica local de los mamíferos tiende a contener entre 70 y 116 especies. La riqueza está correlacionada con la precipitación anual, pero en sitios de bosque tropical lluvioso la riqueza específica probablemente no está correlacionada con la precipitación, latitud, altitud, o tamaño del área. Al parecer, por encima de cierto límite de precipitación y por debajo de cierto nivel de altitud y latitud, la riqueza específica de los mamíferos parece alcanzar un máximo asintótico. Las áreas cubiertas con bosque tropical perennifolio y con una fauna bien conocida e intacta, tienen de 112 a 116 especies. En Montes Azules la mayoría de los mamíferos (57%) son murciélagos. Los gremios de alimentación con mayor número de especies incluyen a los frugívoros/herbívoros, y a los insectívoros/omnívoros. Las especies grandes y las carnívoras son las más vulnerables a la extinción local. La importancia de la Reserva de Montes Azules (y por lo tanto de la Selva Lacandona) radica en que (1) contiene una proporción mayor de especies que enfrentan problemas de conservación que la esperada en una muestra al azar de la fauna Mexicana; (2) es probablemente el ecosistema más diverso de México; (3) muchas especies poseen su única población Mexicana en esta región; y (4) es el mayor remanente de bosque tropical perennifolio en México y forma parte del mayor macizo de este tipo de vegetación en Mesoamérica.*

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Introduction

Tropical forests are widely known to be much more species-rich than most other ecosystems (Bourlière 1983; Connell 1978; Gentry 1986; MacArthur 1972; Wilson 1988), but there are still few relatively complete species inventories of that habitat. Surveys and species inventories for geographical areas in the tropics are one of the most urgent research priorities for conservation biology in order to adequately protect natural resources in areas with high biodiversity, high endemism, or facing imminent destruction (Soulé & Kohm 1989). The region of the Selva Lacandona, Chiapas, Mexico, clearly fits the first and third of these criteria, and there is a moderate level of endemism in groups such as plants, vertebrates, and invertebrates.

The Selva Lacandona is critically threatened by imminent human destruction. This is the largest remaining piece of tropical rainforest in Mexico. Of the original 1,500,000 ha of the Lacandona (Gobierno del Estado de Chiapas et al. 1992), currently only about 500,000 ha remain covered with forest. The forested portion is still connected with the Guatemalan Petén by a corridor running from Bonampak to the Yaxchilán archaeological site on the Usumacinta river, the border with Guatemala. Over three-fifths of the forested area are within the Montes Azules Biosphere Reserve. Primary threats to the ecosystem come from three sources (Medellín 1991, 1992): high growth rate of human populations, oil exploitation, and flora and fauna extraction for disorganized commercial and subsistence purposes.

Given the geographic position of the Selva Lacandona relatively few endemic species and genera would be expected. An example of a plant (and monotypic family) endemic to Lacandona is *Lacandonia schismatica* (Lacandoniaceae; Martínez & Ramos 1989). The possibility of finding new endemic species, particularly of plants and arthropods, is almost certain. The core of the Reserve has not been studied in any significant detail for any group.

The only Mexican tropical rainforest that has been subjected to detailed ecological studies is the National University of Mexico's Los Tuxtlas Tropical Biology Station in southern Veracruz. This site has produced detailed information on the biology and ecology of tropical Mexican mammals (Estrada & Coates-Estrada 1986; Navarro 1982; Sánchez-Cordero in press), but the inventory (89 species) is still incomplete.

This paper introduces and analyzes the inventory of mammal species in the Selva Lacandona (as represented by the Montes Azules Biosphere Reserve). The objectives are to present a local mammal inventory, near completion after 10 years of work, and to analyze this inventory from four perspectives: (1) diversity as indicated by mammal species richness in Montes Azules compared with other Neotropical rainforest areas and with other local Mexican inventories; (2) roles played in the ecosystem by these mammals; (3) conservation status of all species; and (4) role of the Montes Azules Biosphere Reserve in protecting endangered species of Mexican mammals.

Study Site

The Selva Lacandona (Fig. 1) is located in eastern Chiapas, Mexico, and includes a triangular projection into Guatemala. It encompasses about 1.5 million hectares. The primary vegetation type is lowland tropical rainforest (Medellín 1992). The forested area of the Selva has been reduced by two-thirds in 40 years; only 500,000 ha remain. Currently the Montes Azules Biosphere Reserve, (one-fifth [3310 km^2] of the total surface of the Selva Lacandona and 0.16% of the total Mexican territory) contains the majority of remaining forest in the region; about 90% of its 331,200 ha are forested (Gobierno del Estado de Chiapas 1992; Medellín 1991, 1992). The inventory was primarily based in this Reserve.

The mammal fauna of Chiapas is one of the richest in Mexico (Alvarez del Toro 1991; Alvarez-C. & Alvarez 1991). The few biological studies published from the Selva Lacandona, primarily focused on the Montes Azules Biosphere Reserve (Medellín 1992), indicate that the region is inhabited by at least 345 species of birds (migratory + resident) and 800 species of diurnal butterflies, roughly 33 and 44%, respectively, of the Mexican species. Vascular plant species richness has been estimated at about 4000 species, or 15–20% of the total for Mexico (E. Martínez personal communication). Most of these lists are still preliminary and are expected to grow as further surveys are completed.

Methods

Data Collection

Little research on the mammals of the Lacandona appears in the literature. The first paper dealing with mammals is that of Burnett and Lyman (1957), which lists 17 species. Other mammal studies in the area examined the Lacandon Indian use of wildlife (March 1987) and natural history of the paca (Aguirre & Fey 1981; Gallina 1981). Two publications focus on the large mammal species at the state level. Alvarez del Toro (1991) deals with the larger species, but treats only 21 species of rodents and 20 species of bats in Chiapas. A guide to the mammals of Chiapas (Aranda & March 1987) treats mice and bats in one page for each group. Cuarón et al. (1989) reported a species of armadillo from the Lacandona that was previously unknown in Mexico.

I have studied bat diversity of the southern Montes Azules Reserve around Chajul for over 10 years (Medel-

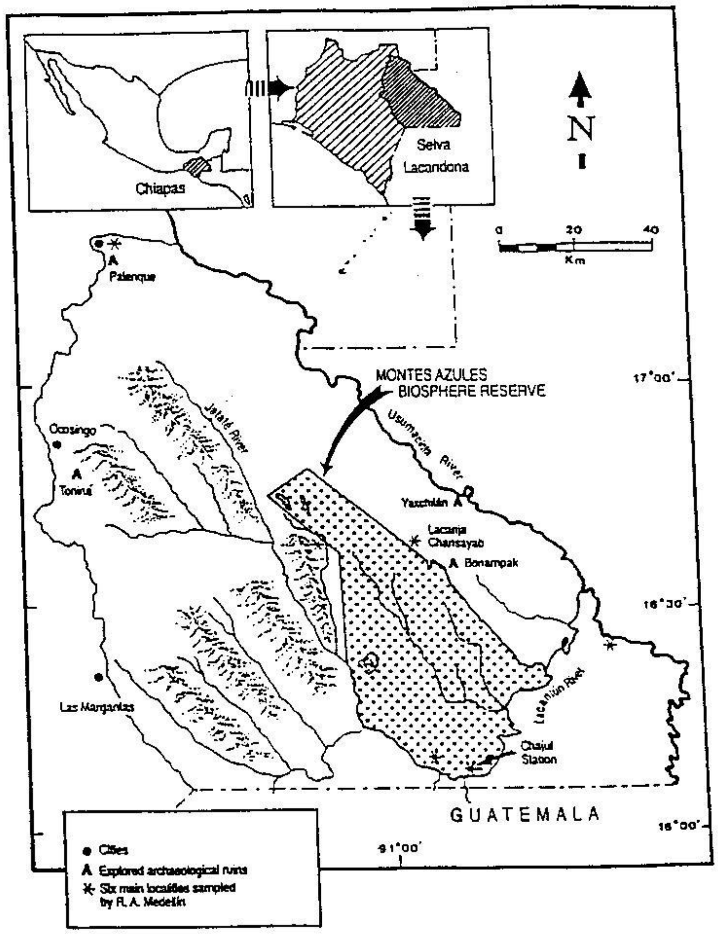

Figure 1. Geographic position of the Selva Lacandona, Chiapas, in southern Mexico.

lín 1983, 1986, in press; Medellín et al. 1992*a*). In addition, I have visited other localities in the Reserve and Lacandona, and my colleagues from the Instituto Nacional de Antropología e Historia have been working on the small mammals in the Yaxchilán archeological site (J. Arroyo-Cabrales, personal communication). During six years of intermittent work in the Lacandona (1981–86), I carried out surveys for the Mammal Collection, Instituto de Biología, UNAM, and later for an environmental impact project.

Bats were captured with hand nets, by hand (in roosts), and with mist nets. Small and medium-sized mammals were sampled with the help of Sherman and Tomahawk traps. Large mammals were recorded by collecting entire animals, skins, skulls, and other portions of specimens in the field and by purchasing them from local inhabitants. Tracks and scats were recorded and a visual survey is ongoing at the Chajul Tropical Biology Station. A systematic trapping, marking, and releasing program was conducted at eight sites near the Chajul

Tropical Biology Station during 1990 and 1991 to examine the effects of abandoned agricultural fields on the mammal community (Medellín 1992).

Analyses and Comparisons

I compared the Montes Azules mammal inventory with that of eight other localities in the Neotropics for which entire mammal faunas are relatively well-known (Table 1): Chamela in Jalisco, Mexico; La Selva Biological Station, Costa Rica; Barro Colorado Island, Panama; Guatopo National Park and Fundo Pecuarió Masaguaral, Venezuela; Manu National Park and Cuzco Amazónico, Peru; and Belém, Para, Brazil. Some problems are evident. The areas range in size from very small and entirely isolated (1500 ha for Barro Colorado Island; Leigh & Wright 1990) to large (15,320 km^2 for Manu; Terborgh et al. 1984). Some have virtually no altitudinal variation (e.g., Masaguaral, Belém), whereas Guatopo and Montes Azules have a wide range.

A key difficulty in these analyses is the assignment of an area to the inventory. Mammals move widely within regions and among habitats, which prevents researchers from calculating species–area relationships, except on a political, much larger scale, such as states or countries. I used inventories from lowland regions, but included one midelevation locality (1000 m above sea level). The six localities in this study are in the Reserve or within 20 km of its limits, except for Palenque, which was included because it is part of the Lacandona region, although all species recorded from there were also recorded in the Reserve localities.

To examine the patterns of species richness and their allocation per mammal order I ran a stepwise multiple regression where independent variables were mean latitude of the site, mean annual rainfall, mean altitude, and altitudinal range. I first ran a stepwise multiple regression analysis on all sites and then removed those not covered by tropical rainforest (Chamela and Masaguaral). I did this to assess the effects of the predictive variables by controlling for vegetation type. For example, I expected the initial analysis to yield some correlation of mammal species richness with rainfall, which was expected to disappear or weaken when the nonrainforest localities were removed. Different measures of species richness (dependent variable) were given by total number of mammal species, species of bats, rodents, carnivores, marsupials, and xenarthrans.

Mammal species from the Montes Azules Reserve were assigned to categories relevant to their biology and conservation status. These variables were diet, body mass, spatial habits, temporal habits, and endangerment status (see Table 2). Categories of endangerment status were assigned following the classification proposed by Ceballos and Navarro (1991) for nonvolant species, and the classification of Medellín and Arita (in press) for bats. These categories include "out of danger," "fragile," "threatened," and "endangered," and as used here they are applicable only to the Mexican populations of each species. This means that in some cases the species may not be endangered worldwide, but only in Mexico.

In most cases tests of allocation of particular groups to guilds, status, or cells in the matrix of spatial and temporal habits, diet categories, and body mass were prevented by the large number of empty cells that did not allow the use of categorical models to analyze these patterns. In cases where sample size in the smallest cell was equal to or greater than 3 I used a G-test of goodness of fit with Williams' correction for samples of less than 200 (Sokal & Rohlf 1981). To test whether Montes Azules offers shelter to a greater proportion of species facing conservation problems than expected by chance, I calculated the expected frequencies from the frequencies observed in the nonmarine, nonvolant mammal fauna of Mexico as reported by Ceballos and Navarro (1991) and those reported by Medellín and Arita (in press) for bats. To examine the distribution of species

Table 1. Neotropical locations used in the diversity comparison and the independent variables used for the stepwise analysis.

Location	*Latitude*	*Average Rainfall (mm/yr)*	*Average Altitude (M above sea level)*	*Altitude Range*
Chamela	19.5°	748	250	500
Mts. Azules	16.5°	2,500	300	1,650
La Selva	10.5°	3,994	85	100
Barro Colorado	9.15°	2,656	100	165
Guatopo	10.0°	1,500	700	1,250
Masaguaral	8.5°	1,500	68	15
Cuzco Amazónico	12.5°	2,387	200	50
Manu	12.0°	2,028	380	300
Belém	1.0°	2,337	50	50

Data are from Chamela, Ceballos and Miranda (1986); Selva Lacandona, this study and Gobierno del Estado. de Chiapas (1992); La Selva, Clark (1990); Barro Colorado, Leigh and Wright (1990); Guatopo and Masaguaral, Eisenberg et al. (1979) and Troth (1979); Cuzco Amazónico, Duellman and Koechlin (1991); Manu, Terborgh (1990) and Ascorra et al. (1991a); Belém, Hammond (1992).

Table 2. List of mammal species found in the Montes Azules Biosphere Reserve, Selva Lacandona, Chiapas, Mexico.

Species	*Diet*[b]	*Mass*[c]	*Space*[d]	*Time*[e]	*Status*[f]
Marsupialia					
*Caluromys derbianus**	F/O	M	Ar	No	Co
*Chironectes minimus**	C	M	T	No	Th
*Didelphis marsupialis**	F/O	L	Sc	No	Co
*Didelphis virginiana**	F/O	L	Sc	No	Co
*Marmosa mexicana**	I/O	S	Ar	No	Co
*Metachirus nudicaudatus**	F/O	M	Sc	No	En
*Philander opossum**	F/O	M	Sc	No	Co
Chiroptera					
Balantiopteryx io	I/O	S	Vo	No	Th
Balantiopteryx plicata	I/O	S	Vo	No	Co
*Peropteryx kappleri**	I/O	S	Vo	No	Fr
Peropteryx macrotis	I/O	S	Vo	No	Fr
*Rhynchonycteris naso**	I/O	S	Vo	No	Th
*Saccopteryx bilineata**	I/O	S	Vo	No	Fr
Noctilio albiventris	I/O	S	Vo	No	Co
*Noctilio leporinus**	C	S	Vo	No	Co
*Mormoops megalophylla**	I/O	S	Vo	No	Co
*Pteronotus davyii**	I/O	S	Vo	No	Co
Pteronotus gymnonotus	I/O	S	Vo	No	Th
*Pteronotus parnellii**	I/O	S	Vo	No	Co
*Chrotopterus auritus**	C	S	Vo	No	Th
*Lonchorhina aurita**	I/O	S	Vo	No	Fr
Macrotus waterhousii	I/O	S	Vo	No	Co
*Macrophyllum macrophyllum**	I/O	S	Vo	No	Fr
*Micronycteris brachyotis**	I/O	S	Vo	No	Fr
*Micronycteris megalotis**	I/O	S	Vo	No	Co
Micronycteris schmidtorum	I/O	S	Vo	No	Fr
*Mimon cozumelae**	I/O	S	Vo	No	Fr
*Mimon crenulatum**	I/O	S	Vo	No	En
*Phyllostomus discolor**	F/O	S	Vo	No	Co
*Phyllostomus stenops**	F/O	S	Vo	No	Th
*Tonatia evotis**	I/O	S	Vo	No	Th
*Tonatia brasiliensis**	I/O	S	Vo	No	Fr
*Tonatia bidens**	I/O	S	Vo	No	En
*Trachops cirrhosus**	C	S	Vo	No	Fr
*Glossophaga commissarisi**	P	S	Vo	No	Co
*Glossophaga soricina**	P	S	Vo	No	Co
*Hylonycteris underwoodi**	P	S	Vo	No	Fr
*Carollia brevicauda**	F/H	S	Vo	No	Co
*Carollia perspicillata**	F/H	S	Vo	No	Co
*Artibeus jamaicensis**	F/H	S	Vo	No	Co
*Artibeus lituratus**	F/H	S	Vo	No	Co
*Centurio senex**	F/H	S	Vo	No	Co
*Chiroderma salvini**	F/H	S	Vo	No	Co
*Chiroderma villosum**	F/H	S	Vo	No	Fr
*Dermanura azteca**	F/H	S	Vo	No	Co
*Dermanura phaeotis**	F/H	S	Vo	No	Co
*Dermanura watsoni**	F/H	S	Vo	No	Co
*Platyrrhinus helleri**	F/H	S	Vo	No	Co
*Sturnira lilium**	F/H	S	Vo	No	Co
*Sturnira ludovici**	F/H	S	Vo	No	Co
*Uroderma bilobatum**	F/H	S	Vo	No	Co
*Vampyressa pusilla**	F/H	S	Vo	No	Fr
*Vampyrodes major**	F/H	S	Vo	No	Fr
*Desmodus rotundus**	B	S	Vo	No	Co
*Diaemus youngi**	B	S	Vo	No	Th
*Diphylla ecaudata**	B	S	Vo	No	Co
*Natalus stramineus**	I/O	S	Vo	No	Co
*Thyroptera tricolor**	I/O	S	Vo	No	Th
*Eptesicus furinalis**	I/O	S	Vo	No	Co
*Lasiurus borealis**	I/O	S	Vo	No	Co
*Lasiurus ega**	I/O	S	Vo	No	Co

Table 2. Continued.

Species[a]	Diet[b]	Mass[c]	Space[d]	Time[e]	Status[f]
*Myotis albescens**	I/O	S	Vo	No	Fr
*Myotis elegans**	I/O	S	Vo	No	Co
*Myotis fortidens**	I/O	S	Vo	No	Co
*Myotis keaysi**	I/O	S	Vo	No	Co
*Pipistrellus subflavus**	I/O	S	Vo	No	Co
*Bauerus dubiaquercus**	I/O	S	Vo	No	Th
*Eumops hansae**	I/O	S	Vo	No	En
*Molossops greenhalli**	I/O	S	Vo	No	Fr
*Molossus ater**	I/O	S	Vo	No	Co
*Molossus molossus**	I/O	S	Vo	No	Co
Primates					
*Alouatta pigra**	F/H	L	Ar	Di	En
*Ateles geoffroyi**	F/H	L	Ar	Di	En
Xenarthra					
*Cyclopes didactylus**	I/O	M	Ar	No	Th
*Tamandua mexicana**	I/O	L	Sc	Di	Th
Cabassous centralis	I/O	L	T	No	En
*Dasypus novemcinctus**	I/O	L	T	Di	Co
Carnivora					
*Urocyon cinereoargenteus**	C	L	T	Di	Co
*Felis onca**	C	VL	Sc	Di	En
*Felis concolor**	C	VL	T	Di	Th
*Felis pardalis**	C	VL	Sc	No	En
*Felis wiedii**	C	L	Sc	No	En
*Felis yagouaroundi**	C	L	T	Di	Th
*Lutra longicaudis**	C	L	T	Di	Th
*Conepatus semistriatus**	F/O	L	T	No	Co
*Eira barbara**	C	L	Sc	Di	En
*Potos flavus**	F/O	L	Ar	No	Fr
*Procyon lotor**	F/O	L	T	No	Co
*Nasua nasua**	F/O	L	Sc	Di	Co
Perissodactyla					
*Tapirus bairdii**	F/H	VL	T	Di	En
Artiodactyla					
*Tayassu tajacu**	F/H	VL	T	Di	Fr
*Tayassu pecari**	F/H	VL	T	Di	En
*Mazama americana**	H/G	VL	T	Di	Th
*Odocoileus virginianus**	H/G	VL	T	Di	Fr
Rodentia					
*Sciurus aureogaster**	GN	M	Ar	Di	Co
*Sciurus deppei**	GN	M	Ar	Di	Co
*Sciurus yucatanensis**	GN	M	Ar	No	Co
*Orthogeomys hispidus**	H/G	M	T	Di	Co
*Heteromys desmarestianus**	GN	S	T	No	Co
*Nyctomys sumichrasti**	GN	S	Ar	No	Co
*Oryzomys palustris**	GN	S	T	No	Co
*Oryzomys alfaroi**	GN	S	T	No	Co
*Oryzomys melanotis**	GN	S	T	No	Co
*Oryzomys fulvescens**	GN	S	T	No	Co
*Ototylomys phyllotis**	GN	S	Sc	No	Co
*Peromyscus mexicanus**	GN	S	T	No	Co
*Sigmodon hispidus**	H/G	S	T	Di	Co
*Tylomys nudicaudus**	GN	M	Ar	No	Co
*Sphiggurus mexicanus**	F/H	L	Ar	No	Th
*Dasyprocta punctata**	F/H	L	T	Di	Th
*Agouti paca**	F/H	L	T	No	Th
Lagomorpha					
*Sylvilagus brasiliensis**	H/G	M	T	No	Co

[a] *Order, family, and subfamily arrangement follows that of Wilson and Reeder (1993). Species marked with an asterisk are those recorded by the author.*

[b] *Diet categories were modified from Eisenberg and Thorington (1973) and Robinson and Redford (1986) with data from many areas in tropical America: herbivore/grazer (H/G), at least 50% of diet is leaves; granivore (GN) at least 50% of diet is seeds; pollinivore (P), at least 50% of diet is pollen and nectar; frugivore/herbivore (F/H), at least 50% of diet is fruits, remainder mostly plant matter; frugivore/omnivore (F/O),*

at least 50% of diet is fruits, remainder mostly animal matter; insectivore/omnivore (I/O), at least 50% of diet is insects; carnivore (C), at least 50% of diet is flesh of vertebrates; sanguivore (B), diet composed of vertebrate blood.

[c] *Body mass categories were assigned on a logarithmic scale and the data came from adult animals in the field and from Robinson and Redford (1986): small (S), <100 grams; medium (M), >100 g, <1000 g; large (L) >1000 g, <10,000 g; very large (VL), >10,000 g.*

[d] *Spatial habits refer to where the species spends most of its active time: primarily terrestrial (T); scansorial (Sc); primarily arboreal (Ar); volant (Vo).*

[e] *Temporal habits refer to time of day when species is active: nocturnal (No); at least partially diurnal (Di).*

[f] *Endangerment status categories follow Ceballos and Navarro (1991) for nonvolant species and Medellín and Arita (in press) for bats: Common, out of all danger (Co); Fragile (Fr); Threatened (Th); Endangered (En).*

by conservation status among levels of biological categories I calculated the expected distributions from the proportions observed in the mammal fauna at Montes Azules and not those for all of Mexico.

Results

One hundred and twelve mammal species have been recorded in the Montes Azules Biosphere Reserve. My field work accounted for 103 species, 97 of which I found in the vicinity of the Chajul Tropical Biology Station. The others I found were in four additional lowland rainforest localities and one midelevation (1000 m) locality (Table 2, Fig. 1). Field work by other researchers working at Lacanjá-Chansayab and the Yaxchilán ruins have reported many species, among which are nine additional ones (J. Arroyo-Cabrales personal communication) not yet detected by me. Ceballos and Navarro (1991) reported a total of 449 species of native Mexican mammals. Recent additions to the national fauna include those by Medellín et al. (1992a: one opossum and one bat) and J. Arroyo-Cabrales' (personal communication) collection of another bat species in Yaxchilán, Selva Lacandona for a total of 452 Mexican mammal species. Therefore, the mammal fauna of the Lacandona represents 25% of the Mexican total.

In Montes Azules there are 7 species of marsupials (all but one of the total for Mexico), 64 species of bats (48% of the 133 Mexican species), and 2 of the 3 species of primates (there is some anecdotal evidence that the third primate species [*Alouatta palliata*] may be present in the northwest). All 4 Mexican xenarthrans have been reported from the region, 1 lagomorph out of 14 Mexican species, 17 (7.7%) rodents out of 220 species, and 12 carnivores (34.3%) out of 35 Mexican species. The only Mexican perissodactyl, the tapir, is well-represented, and four of the nine Mexican artiodactyl species are there. Rodents, carnivores, and bats are the groups most likely to increase in species numbers through additional surveys. All the orders of nonmarine mammals and 27 of the 33 Mexican families are present in the region. If we relate these numbers to the land area of the Montes Azules Reserve (0.16% of the Republic of Mexico), it is evident that this is one of the most important biodiversity sites (measured by species richness) in the country.

The 112 species of mammals within the Montes Azules Biosphere Reserve represent a typical Neotropical mammal fauna (Tables 2 and 3). Cuzco Amazónico, Perú, seems to be notably richer in mammal species than the other areas (Table 3). Considering faunal composition by mammalian order (Table 3; Appendix) there

Table 3. Faunal richness and composition by mammalian order (marsupials, bats, primates, xenarthrans, lagomorphs, rodents, carnivores, perissodactyls, and artiodactyls) in nine localities in the Neotropics.

	Order*										
Location	*Mars*	*Bats*	*Prim*	*Eden*	*Lag*	*Rode*	*Carn*	*Peri*	*Arti*	*Total*	*Reference*
Chamela	2/3	33/49	0/0	1/1	1/1	16/24	15/22	0/0	2/3	67	Ceballos & Miranda 1986
Mts Azules	7/6	64/57	2/2	4/4	1/1	17/15	12/11	1/1	4/4	112	This paper
La Selva	5/4	65/56	4/3	6/5	1/1	16/14	14/12	1/1	4/3	116	Timm 1994
B. Colorado	6/6	56/59	5/5	6/6	1/1	11/12	6/6	1/1	3/3	95	Glanz 1990; Handley et al. 1991
Guatopo	7/10	29/42	3/4	5/7	1/1	13/18	8/12	1/1	2/3	69	Eisenberg et al. 1979
Masaguaral	2/3	41/59	2/3	3/4	1/1	11/15	8/11	0/0	2/3	70	Eisenberg et al. 1979
Cuzco	10/7	54/40	13/10	9/7	1/1	26/19	15/11	1/1	5/4	134	Woodman et al. 1991
Manu	8/7	44/39	13/11	7/6	1/1	24/21	12/11	1/1	4/4	114	Janson & Emmons 1990; Ascorra et al. 1991a
Belém	9/8	46/41	6/5	10/9	1/1	18/16	17/15	1/1	4/4	112	Ascorra et al. 1991b; Eger 1977; Handley 1967; McCarthy & Handley 1987; Mok et al. 1982; Peterson 1965; Pine 1973; Thomas 1913; McCarthy 1993.

* *The number of species is separated by a diagonal from the percentage of the total that each group represents.*

markable similarity between La Selva, Costa Rica, ontes Azules. The appendix lists the species in-ies for each of the nine localities.

cies richness of a given site is affected by many nmental and geographic factors; notable among are rainfall (directly correlated with primary pro-vity), latitude, and altitude. Thus, comparisons d be made among localities that exhibit similar ll, latitude, and altitude, or at least areas that are n well-defined limits that characterize their physi-phy (e.g., within dry tropical deciduous forests, in lowland rainforests, within deserts). Because the localities include sites as small as Barro Colorado d (1500 ha) and as large as the Montes Azules Re-e (331,200 ha) with a wide range in between and use all these had very similar numbers of mammal ies, the size of the area seems not to be an impor-factor in species richness.

n the stepwise analysis, total mammalian species ness was correlated with rainfall (mammal species 59.77 + rainfall) × 0.02; $r = 0.69$; $p = 0.04$), as s bat species richness (bat species = (22.18 + rain-) × 0.01; $r = 0.86$; $p = 0.003$). Xenarthrans showed ompound model where latitude had a negative effect d rain had a positive effect (xenarthran species = 28 + (latitude × −0.31) + (rainfall × 0.01); r = 79; $p = 0.14$). No other group showed any significant ends.

When I removed the localities not covered with trop-al rainforest (Chamela and Masaguaral) the correlation ith rainfall disappeared, as expected. The only signifi-nt model (at the multiple regression critical level of α 0.15) for total mammal species richness was a nega-e correlation with altitude (mammal species = 25.8 + altitude) × −0.07; $r = 0.71$, $p < 0.15$); how-er, this seemed biased. Bats were correlated with rain-ll (bat species = (18.07 + rainfall) × 0.013; $r = 0.82$, < 0.05). Xenarthra species richness correlated nega-vely with altitude range (xenarthra species = (8.41 + altitude range) × −0.003; $r = 0.87$, $p < 0.01$). No other model was significant for any other group.

Other regional (not by state) Mexican mammal inventories do not reach the richness levels (112 species) of Montes Azules; among the richest inventories are the Chamela Reserve with 67 species (Ceballos & Miranda 1986), Los Tuxtlas with 89 (Estrada & Coates-Estrada 1986), the Valley of Mexico with 87 (Ceballos & Galindo 1984), and la Angostura, Chiapas with 74 (Alvarez et al. 1984).

Bats are major contributors to mammal species richness in the Neotropics (Eisenberg 1989; Wilson 1990). In Montes Azules, La Selva, and Barro Colorado bats account for over 50% of the mammal species. Four localities (Montes Azules, La Selva, Manu, and Belém) show a remarkably similar number of mammalian species, but their values in the predictive variables (diet, mass, habits in space and time, and status) vary widely.

Sixty-six percent of the mammals in Montes Azules are smaller than 100 g, whereas only 8 (7.1%) are larger than 10 kg (Table 4). This is mainly due to bats, all of which fall in size category 1. If we remove bats, the richest spatial habits group is the terrestrial species, with 25 species. Of the remaining 23 species, 11 are scansorial and 12 are arboreal. The terrestrial species are more or less evenly distributed among size categories, the scansorial species are primarily intermediate in size with some large species, and the arboreal species are intermediate in size with few large species, indicating a negative size trend when progressively analyzing the spatial layers of the forest from the bottom up. The most heavily occupied cells in the matrix of diet/habits/size are those occupied by frugivorous/herbivorous bats (16 species) and by insectivorous/omnivorous bats (37 species).

Nearly half of the mammal species in Montes Azules interact directly with plants in a variety of ways, including herbivorous/grazer and granivorous species (e.g., deer, mice), seed dispersers (e.g., tapir, many bats), and

Table 4. Allocation of mammal species recorded from Montes Azules Biosphere Reserve to cells in four variables of their biology.

	Spatial Resource[a]																
	Terrestrial (T) Size				*Scansorial (Sc) Size*				*Arboreal (Ar) Size*				*Volant (Vo) Size*				
Diet	*S*	*M*	*L*	*VL*	*S*	*M*	*L*	*VL*	*S*	*M*	*L*	*VL*	*S*	*M*	*L*	*VL*	*Total*
H/G	0/1	1/1		0/2													5
GN	6/0				1/0				1/0	1/3							12
P													3/0				3
F/H			1/1	0/3							1/2		16/0				24
F/O			2/0			2/0	2/1			1/0	1/0		2/0				11
I/O			1/1				0/1		1/0	1/0			37/0				42
C		1/0	0/3	0/1			1/1	1/1					3/0				12
B													3/0				3
Total	7	3	9	6	1	2	6	2	2	6	4	0	64				112

[a] *The numbers in each cell indicate species that are nocturnal/at least partially diurnal. Abbreviations are defined in the footnote of Table 2.*

pollinators (e.g., *Caluromys, Glossophaga* spp.). The other half of the mammal species feed mostly on insects or vertebrates.

In Montes Azules there are no sloths or spiny rats (Echimyidae). Several species of primates (at least *Saimiri* and *Cebus*) in addition to several species of bats that occupy similar habitats in nearby regions are also absent. All these species are present in nearby rainforests to the south, but seem to reach their northern distributional limit between the parallels 9–10 north, on the border of Panamá–Costa Rica and southern Nicaragua. On the basis of species distribution, habitat affinities, and the habitats present in the Lacandona, there are at least 24 species that are expected (but not recorded) in the region. Among them are: two shrews (*Cryptotis parva* and *C. nigrescens*), several bats (*Centronycteris maximiliani, Diclidurus albus, Pteronotus personatus, Micronycteris sylvestris, Vampyrum spectrum, Choeroniscus godmani, Dermanura tolteca, D. hartii, Lasiurus cinereus, Eumops auripendulus, E. nanus, Promops centralis,* and *Molossus pretiosus*), several mice (*Otonyctomys hatti, Reithrodontomys mexicanus, Peromyscus boylii, P. oaxacensis, Neotoma mexicana*) plus the long-tailed weasel (*Mustela frenata*), the grison (*Galictis vittata*), the striped skunk (*Spilogale putorius*), and the tropical ringtail (*Bassariscus sumichrasti*). From reports of some local inhabitants, possibly the mantled howler monkey (*Alouatta palliata*) reaches the western edge of the Lacandona, but no hard evidence is yet available. Two species that frequently are benefitted by human activity are expected to show up in the near future: a cottontail (*Sylvilagus floridanus*) and the coyote (*Canis latrans*).

The mammal fauna of the Lacandona includes several species that in Mexico have been reported only from this area, including *Metachirus nudicaudatus, Tonatia bidens,* and *Cabassous centralis.* Additionally, six species of bats reach Mexico only in the fringe of rainforest near the border with Guatemala: *Micronycteris schmidtorum, Macrophyllum macrophyllum, Tonatia evotis, Mimon crenulatum, Phyllostomus stenops,* and *Eumops hansae.* Other than the data presented here the most recent collection of most of these species was about 30 years ago in Campeche and Tabasco (Lay 1962; Jones 1964). The Gulf flatlands of these states have since undergone drastic environmental modifications.

Endemics for Middle America (as defined by Hershkovitz 1958) that are present here include 17 species, of which 7 (denoted by an asterisk) are endemic to the Central American Core, the area between the Isthmus of Tehuantepec and Panama: two marsupials (*Caluromys derbianus, Marmosa mexicana*), five bats (*Balantiopteryx io**, *Tonatia evotis**, *Mimon cozumelae, Dermanura watsoni, Myotis elegans*), the black howler monkey (*A. pigra**), three squirrels (*Sciurus yucatanensis**, *S. deppei**, *S. aureogaster*), a pocket gopher (*Orthogeomys hispidus*), four mice (*Heteromys desmarestianus, Tylomys nudicaudus**, *Ototylomys phyllotis**, and *Peromyscus mexicanus*), and the porcupine (*Sphiggurus mexicanus*).

Assignment to a status category must be based not only on population densities and distributional range, which are correlated in Neotropical mammals (Arita et al. 1990), but also on more immediate factors such as hunting pressure, economic impact (pests, pets, etc.), body mass, and feeding and migratory habits, which expose a given species to habitat destruction in at least two separate geographic areas. A certain degree of autocorrelation will be unavoidable when attempting to produce a list of endangered species by categorical ordination; for example, carnivores, which sustain lower population densities (Eisenberg & Thorington 1973; Robinson & Redford 1986), tend to be large-bodied. These two factors interact in this case to make this group more susceptible to endangerment.

The goodness-of-fit test examining whether the distribution of species among the four status categories was different between the fauna of Mexico and that of Montes Azules (Williams' corrected $G = 5.48$; d.f. $= 3$) was not significant. However, when I grouped together the categories of species at risk (fragile + threatened + endangered) I found that there are more species facing conservation problems in the Montes Azules Reserve than expected from a random sample of the Mexican mammal fauna (Williams' corrected $G = 5.09$; $p < 0.025$; d.f. $= 1$). Statuses of mammal species from Montes Azules are listed in Table 5. All large species face conservation problems, and carnivores tend to be in the same situation ($G = 7.07$; $p < 0.01$).

Discussion

Based on the local Mexican mammal inventories available the Montes Azules Biosphere Reserve (represent-

Table 5. Conservation status of 112 species of mammals from Montes Azules, Selva Lacandona, by order.

Order	*Out of Danger*	*Fragile*	*Threatened*	*Endangered*
Marsupialia	5	0	1	1
Chiroptera	36	16	9	3
Primates	0	0	0	2
Xenarthra	1	0	2	1
Lagomorpha	1	0	0	0
Rodentia	14	0	3	0
Carnivora	4	1	3	4
Perissodactyla	0	0	0	1
Artiodactyla	0	2	1	1
Total	61	19	19	13
Total for Mexico	307	65	35	45

These status levels are applicable only in Mexico. Allocation is based on the categories by Ceballos and Navarro (1991) and Medellín and Arita (in press).

g the Selva Lacandona) is the richest region in mammal species. Comparing it with other localities in the humid Neotropics, Montes Azules is as rich as most other localities; only Cuzco Amazónico, Peru, has more species.

Mammal species richness increases with decreasing latitude, from the temperate regions toward the tropics (Pagel et al. 1991; McCoy & Connor 1980; Simpson 1964; Wilson 1974). However, I did not find such a trend. All of the localities I used are within the tropics and are primarily at low altitudes. This suggests that although latitudinal gradients exist at scales that encompass tropical and temperate zones, the trend is not detectable within the lowland tropics.

The two localities not covered with tropical rainforest are responsible for the correlation with rainfall. Within rainforest habitats there is no correlation between species richness and rainfall. In those habitats mammal species richness may be inversely related to altitude. However, the pattern is not clear. There is only one locality (Guatopo) at 700 m above sea level, all the others are below 380. The Guatopo data point seems to drive the regression. It is striking that there are 4 localities for which the species number is very similar, ranging from 112 in Montes Azules to 116 in La Selva. This similarity greatly reduces the significance of the regressions because the four localities represent a wide range of variation in latitude, altitudinal range, and rainfall. This suggests that mammal species richness in localities sharing a vegetation type (tropical rainforest) and a climate pattern (hot humid) is high and relatively stable. The similarities in mammal species richness among localities that vary in rainfall, latitude, and altitude seem to indicate an asymptotic maximum (around 110–120) of mammal species-packing in areas where rainfall is at least 2000 mm a year, altitude is at most 380 m, and latitude is at most 16.5 degrees.

These results suggest that comparisons should be kept within particular ranges in altitude and among areas with a similar range of microhabitats. However, there are virtually no inventories for such narrowly defined regions, and these results are indicative of the high diversity and asymptotic nature of mammal faunas in tropical rainforests. Area effects seem futile if we consider that this analysis included very small areas (e.g., Barro Colorado) and very large ones (e.g., Montes Azules Reserve), covering a wide range of area size. In all areas species richnesses remained very similar; evidently there is no correlation between the size of these areas and the number of species that inhabit them.

Most mammal species reached their distribution limits before the Pleistocene or shortly thereafter, and mammal distribution in the Neotropics follows a decreasing gradient (Hershkovitz 1958; Savage 1974). Medellín et al. (1992*b*) reported that the distribution of at least 10 species of bats reach their northern limits in Panamá–Costa Rica, significantly reducing the total number of bats found north of this region. We have argued that this depauperation suggests a biogeographic boundary comparable to Hershkovitz's (1958) Middle American Province of the Brazilian Subregion, but one that shifted to Panama–Costa Rica, about four degrees toward the west.

The mammal fauna at Lacandona lacks some groups that can be remarkably abundant and/or widespread in other areas of Middle America and the rest of the Neotropics (e.g., Echimyidae, sloths, *Cebus*, *Saimiri*, several bats). An ecological explanation for the absence of these species in Chiapas is not immediately evident; there is no apparent habitat discontinuity that would prevent their northward extension (as attested by the multitude of species associated biogeographically with the Brazilian subregion that have successfully colonized the Mexican wet tropics). There is only a geographic bottleneck along the lowland rainforest in the northern coast of Honduras (Hershkovitz 1969).

Temperature appears to at least partially limit the distribution of animals (McNab 1973; Brown & Gibson 1983; Root 1988; Bozinovic & Rosenmann 1989). The winter's constantly cloudy/hazy, cold spells ("nortes") that characterize southern Mexico's weather pattern may be a partial explanation for the absence of at least some of these species. The sloths, for example, have very low basal metabolic rates (McNab 1982) and behave like a near-ectothermic mammal, requiring daily exposure to direct sunlight to increase digestive efficiency (Montgomery & Sunquist 1978; Eisenberg 1983). Thus, nortes probably prevent them from reaching into northern Central America and southern Mexico.

The echimyids are terrestrial and scansorial rats feeding on fruits, insects, seeds, and fungi (Eisenberg 1989). In northern Middle America there are a series of scansorial and arboreal (*Ototylomys phyllotis*, *Tylomys* spp., *Nyctomys sumichrasti*, and *Otonyctomys hatti*) and terrestrial (at least *Peromyscus mexicanus* and *Oryzomys* spp.) rats and mice whose niches would seemingly overlap at least partially with those of the missing echimyids. However, many of these species co-occur at a local scale with *P. semispinosus* and *Hoplomys gymnurus* in Costa Rica (McPherson 1985). Additionally, the high biomass of these echimyids (Fleming 1971) indicate that whenever they are present they are fairly successful, being one of the most abundant mammal species. If their niche overlapped with that of the other mouse and rat species, we would expect that in the absence of echimyids the other mice would increase in biomass to reach the levels reported in localities where the two occur together. However, biomass levels reported by Fleming (1971) are hardly ever approximated by all the other mice combined in localities where no echimyids exist, and then only under depaupered, isolated conditions (e.g., Los Tuxtlas, Veracruz, Dirzo & Miranda 1991; Sánchez-Cordero 1993). This suggests that some environmental factor, perhaps a niche variable, is the cause of the echimyids' absence in southern Mexico.

The northern coast of Honduras is probably a key region to investigate the northward attenuation of mammal faunas. In particular, plant and animal inventories should be carefully developed on both sides of the rainforest bottleneck in the region of the Patuca River in the northeast and the region of the Ulua River basin, next to Guatemala. Comparing these two inventories and identifying and evaluating the discrepancies might help explain the faunal crease observed to the north.

Even with the missing species, the fauna of Montes Azules stands as very diverse in Mexico, comparable to Amazonian faunas. These analyses suggest that within the lowland Neotropical rainforest, differences in species richness are probably not related to limitations of rainfall, latitude, and altitude. Rather, above a certain limit of rainfall and below a critical level of latitude and altitude, mammal species richness seems to reach an asymptotic maximum. This observation should be reexamined once more complete mammal inventories are available for the Neotropical rainforest.

Herbivorous vertebrates affect the forest vegetation in many ways, from specific selective pressures to structural characteristics. A significant influence of herbivorous mammals on forest structure and species composition has been suggested by Dirzo and Miranda (1991). They found that where the large herbivorous species had been hunted out in the past 20 years (Los Tuxtlas) damage to seedling and sapling foliage was zero and seedling density was 53 per m^2. In contrast, in an area with an intact mammal fauna (Montes Azules) this damage accounts for 27% of the leaves of seedlings and saplings, and seedling density was 23 per m^2. Of their 20 1-m^2 plots 14 had one dominant species, and there was an average of 2.3 species per plot in Los Tuxtlas. Only 2 showed dominance in Montes Azules, and the plots contained an average of 6.7 species. The Shannon–Wiener value in Los Tuxtlas was 1.07 and 3.71 in Montes Azules.

Additionally, Putz et al. (1990) examined the forest composition in small islands where seed predators and herbivores have been absent for 75 years in Panama. They found lower diversity levels in the large trees, and the same few dominant tree species dominated understory and herbaceous layers. Dominants in these islands are mammal-preferred, large-seeded species.

Similarly, if the species occupying the top of the trophic pyramid are absent, frugivores, granivores, and herbivores become unnaturally abundant and forest structure will change accordingly, with either a thinned undergrowth or undergrowth dominated by species not predated upon by vertebrates. For example, De Steven and Putz (1984) evaluated seed predation and recruitment of a tree species favored by mammals (*Dipteryx panamensis*). Predation on *Dipteryx* seeds and seedlings on Barro Colorado (where seed predators have low predation pressures) was much greater than on the mainland (where predation by humans and other carnivores is strong), which resulted in decreased recruitment of seedlings into saplings and saplings into trees. Although some experimental work remains to be done to ascertain the process outlined here, it is intuitively clear that herbivorous mammals determine to an important extent the diversity and structure of tropical forests.

The analysis of conservation status has some problems of autocorrelation. Ceballos and Navarro (1991), whose classification is employed here, used a series of traits of each species to assign endangerment points. For example, carnivorous species received one point, while large species received up to six points. Endangered species were those with at least 11 points, threatened species had 9 or 10 points, and fragile species were those with 8 points. Below that level species were considered out of danger. It is evident from my results that all large species face conservation problems and that being a carnivore affects the probability of being endangered at least in part due to the classification method. Arita et al. (1990) found the same. Carnivores in general live at lower densities and need larger habitat areas than species in other trophic levels (Eisenberg 1980; Robinson & Redford 1986; Redford & Robinson 1991). Thus, carnivores tend to be endangered. Similarly, large species live at lower densities (Eisenberg 1980; Robinson & Redford 1986) and are the most sought-after animals for hunting. In three studies on hunting in South America 21 of 24, 13 of 15, and 20 of 22 mammal species weigh over 1 kg (Vickers 1991; Ayres et al. 1991; Mittermeier 1991, respectively), whereas the vast majority of the Neotropical mammals weigh less than 1 kg. Redford (1992) has also shown that it is the larger species that suffer the greatest hunting pressure. All this implies that large species indeed are more susceptible to endangerment.

A greater proportion of species face conservation problems in the Montes Azules Biosphere Reserve than expected from a random draw of the Mexican fauna. It is imperative to conserve this area as we would be protecting a significantly greater number of fragile, threatened, and endangered species than in other portions of Mexico. The Selva Lacandona (together with its extensions into Peten and Calakmul) contains one of the last viable populations of jaguars, white-lipped peccaries, and tapirs in Middle America. The outstanding species richness of Lacandona strengthens the importance of conserving the region. The fact that at least nine species are represented in Mexico only in the Lacandona adds patrimony value to it and further reinforces the need to protect the region.

The urgency and significance of conserving the Selva

Lacandona is clearly evident by the large number of species of different groups that inhabit it. This point is further emphasized since: (1) Montes Azules (and thus Lacandona) contains a greater number of species facing conservation problems than expected by chance alone; (2) it is the most species-rich ecosystem in Mexico; (3) many species are represented in Mexico by their populations in Lacandona; and (4) it is the largest remnant of the tropical rainforest ecosystem in Mexico and part of the largest expanse of this vegetation type in Middle America. Conservation of the Lacandona represents one of our last chances to explore, test, and apply sustainable development practices in one of the most diverse ecosystems of the world.

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Appendix. Mammal species inventory of nine neotropical locations.

	Chamela	*Mts Azules*	*La Selva, C.R.*	*Barro Colorado*	*Guatopo*	*Masaguaral*	*Cuzco Amaz.*	*Manu*	*Belem*
Marsupilla									
Caluromys derbianus		X	X	X					
Caluromys lanatus							X	X	
Caluromys philander					X				X
Caluromysiops irrupta								X	
Glironia sp.								X	
Chironectes minimus		X	X	X	X		X		X
Didelphis marsupialis		X	X	X	X	X	X	X	X
Didelphis virginiana	X	X							
Marmosa canescens	X								
Marmosa fuscata					X				
Marmosa mexicana		X	X						
Marmosa murina					X		X		X
Marmosa robinsoni				X		X			
Marmosops noctivagus							X	X	
Marmosops parvidens							X		X
Metachirus nudicaudatus		X		X			X	X	X
Micoureus cinerea					X			X	X
Micoureus regina							X		
Monodelphis adusta							X		
Monodelphis americana									X
Monodelphis brevicaudata					X				
Philander andersoni							X		
Philander opossum		X	X	X				X	X
Chiroptera									
Balantiopteryx io		X							
Balantiopteryx plicata	X	X							
Centronycteris maximiliani			X	X					X
Cormura brevirostris			X	X					X
Cyttarops alecto			X						
Diclidurus albus	X		X						
Peropteryx kappleri		X	X						X
Peropteryx leucoptera							X		
Peropteryx macrotis		X							
Rhynchonycteris naso		X	X	X		X	X		X
Saccopteryx bilineata	X	X	X	X	X	X	X		
Saccopteryx canescens						X			
Saccopteryx leptura			X	X	X	X	X	X	
Noctilio albiventris		X	X	X		X	X	X	

Appendix continued

	Chamela	Mts Azules	La Selva, C.R.	Barro Colorado	Guatopo	Masaguaral	Cuzco Amaz.	Manu	Belem
Noctilio leporinus	X	X	X	X		X	X		
Mormoops megalophylla	X	X							
Pteronotus davyi	X	X	X		X				
Pteronotus gymnonotus		X		X					
Pteronotus parnellii	X	X	X	X	X				
Pteronotus personatus	X								
Chrotopterus auritus		X	X	X			X	X	
Lonchorhina aurita		X							
Macrophyllum macrophyllum		X	X	X			X	X	
Macrotus waterhousii		X							
Micronycteris brachyotis		X	X	X					
Micronycteris daviesi			X						
Micronycteris hirsuta			X	X					
Micronycteris megalotis	X	X	X	X		X	X	X	
Micronycteris minuta			X			X	X	X	X
Micronycteris nicefori			X	X		X			X
Micronycteris schmidtorum		X	X	X					
Micronycteris sylvestris									X
Mimon crenulatum		X	X	X		X	X	X	
Mimon cozumelae		X	X						
Phyllostomus discolor		X	X	X	X	X			X
Phyllostomus elongatus						X	X	X	X
Phyllostomus hastatus			X	X	X	X	X	X	X
Phyllostomus stenops		X	X	X			X	X	X
Tonatia bidens		X	X	X			X	X	X
Tonatia brasiliense		X	X			X		X	
Tonatia carrikeri									X
Tonatia evotis		X							
Tonatia silvicola			X	X			X	X	X
Trachops cirrhosus		X	X	X		X	X	X	X
Vampyrum spectrum			X	X		X	X	X	
Lionycteris spurrelli							X		X
Lonchophylla mordax									X
Lonchophylla robusta			X	X					
Lonchophylla thomasi							X		
Anoura caudifer					X		X	X	
Choeroniscus godmani	X		X						
Choeroniscus minor							X	X	X
Glossophaga commissarisi	X	X	X	X					
Glossophaga longirostris						X			
Glossophaga soricina	X	X	X	X	X	X	X	X	X
Hylonycteris underwoodi		X	X						
Leptonycteris curasoae	X								
Lichonycteris obscura			X						
Musonycteris harrisoni	X								
Carollia brevicauda		X	X	X			X	X	
Carollia castanea			X	X			X	X	
Carollia perspicillata		X	X	X	X	X	X	X	X
Carollia subrufa	X								X
Rhinophylla pumilio							X	X	X
Rhinophylla sp									X
Ametrida centurio				X	X	X			X
Artibeus jamaicensis	X	X	X	X	X	X		X	X
Artibeus lituratus	X	X	X	X	X		X	X	X
Artibeus obscurus							X	X	
Artibeus planirostris							X		
Centurio senex	X	X		X					
Chiroderma salvini	X	X					X		
Chiroderma trinitatum					X				X
Chiroderma villosum		X	X	X			X	X	X
Dermanura anderseni								X	
Dermanura azteca		X							
Dermanura cinerea					X		X	X	X
Dermanura glauca								X	
Dermanura gnoma								X	X
Dermanura hartii				X			X		
Dermanura phaeotis	X	X	X	X	X				