

MAMMALIAN DIVERSITY IN
NEOTROPICAL LOWLAND
RAINFORESTS: A PRELIMINARY
ASSESSMENT

ROBERT S. VOSS AND LOUISE H. EMMONS

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ABSTRACT

Information about the magnitude and geographic distribution of mammalian diversity in Neotropical lowland rainforests is important for evaluating research and conservation priorities in Central and South America. Although relevant inventory data are rapidly accumulating in the literature, real site-to-site diversity differences are hard to identify because many confounding factors can affect the size and composition of faunal lists. Herein we assess the available information about Neotropical rainforest mammal diversity and suggest guidelines for future work by reviewing inventory methods, documenting and discussing faunal lists from ten localities, and summarizing geographic range data to predict diversity patterns that can be tested by field and museum research.

All inventory methods are biased because each is suitable for collecting or observing only a fraction of the morphologically and behaviorally diverse mammalian fauna that inhabits Neotropical rainforests. Hence, many methods must be used in combination to census whole communities. Although no combination of methods can be guaranteed to produce complete inventories, the omission or nonintensive application of any of several essential methods probably guarantees incomplete results. We recommend nine methods that, used intensively and in combination, should maximize the efficiency of future inventory fieldwork.

Ten rainforest mammal inventories selected as exemplars illustrate several common problems: sampling effort is highly variable from study to study, species accumulation curves are not asymptotic for any fauna, essential field methods were omitted in every case, and some localities were partially defaunated by hunters prior to inventory. Meaningful diversity comparisons are therefore impossible without a major investment in additional fieldwork at each site.

Geographic range data provide an essential alternative source of diversity estimates. Comparisons of inventory results with geographic expectations (diversity predictions based on range data) suggest that all existing inventories are incomplete, that the degree of incompleteness is inversely cor-

related with inventory duration, and that special methods are required to add elusive species to faunal lists. The range data at hand also suggest several geographic patterns that should be tested with carefully focussed fieldwork. (1) Mammalian diversity in Amazonia is probably greatest in the western subregion (between the Rio Negro and the Rio Madeira, where over 200 species might be sympatric at some localities), least in the Guiana subregion (east of the Negro and north of the Amazon), and intermediate in southeastern Amazonia (east of the Madeira and south of the Amazon). (2) Geographic variation in Amazonian diversity chiefly involves marsupials, bats, primates, and rodents; by contrast, xenarthran, carnivore, and ungulate faunas are remarkably uniform across the entire region. (3) In Central American rainforests, a conspicuous and apparently monotonic diversity gradient extends from eastern Panama (where mammalian diversity is within the range of Amazonian values) to southern Mexico (where mammalian diversity may be less than anywhere else on the rainforested Neotropical mainland). Mammalian diversity in coastal Venezuelan and southeastern Brazilian rainforests is difficult to assess with existing literature and collection resources, but neither region is likely to be as diverse as Amazonia.

Despite a few dissenting voices, the literature of New World mammalogy provides compelling evidence that mammalian diversity, as measured by sympatric species richness, is greatest in lowland tropical rainforests and decreases along gradients of increasing latitude, elevation, and aridity. Thus, the mammalian faunas of western Amazonia are the most diverse of any in the Americas and perhaps in the world. We briefly discuss the generality and causes of observed diversity patterns in terms of contemporary ecology and historical scenarios.

Significant advances in understanding mammalian diversity patterns in Neotropical rainforests will require systematic revisions of many problematic genera and an aggressive program to inventory poorly sampled areas while opportunities to do so yet remain.

RESUMEN

La información sobre la magnitud y distribución geográfica de la diversidad de los mamíferos en la selva neotropical es importante para la evaluación de las prioridades de investigación y conservación en Centro y Sur América. Aunque datos de inventarios relevantes se están acumulando rápidamente en la literatura, reales diferencias de

diversidad, de sitio a sitio, son difíciles de identificar debido a que muchos factores confusos pueden afectar el tamaño y la composición de las listas faunísticas. Aquí, evaluamos la información disponible acerca de la diversidad de mamíferos de la selva húmeda neotropical y sugerimos lineamientos para futuros trabajos, al revisar métodos de

inventario, documentar y discutir listas faunísticas de diez localidades, y al resumir datos de distribución geográfica para predecir patrones de diversidad que pueden ser probados por investigaciones de museo y de campo.

Todos los métodos de inventario son sesgados debido a que cada uno es apropiado para la colección u observación de sólo una fracción de la diversidad morfológica y conductual de la fauna mastozoológica que habita la selva húmeda neotropical. De aquí que, muchos métodos deben ser usados en combinación a censos de comunidades íntegras. Aunque ninguna combinación de métodos puede garantizar el producir inventarios completos, la omisión o aplicación no intensiva de alguno de los varios métodos esenciales probablemente garantiza resultados incompletos. Nosotros recomendamos nueve métodos que, usados intensivamente y en combinación, deben maximizar la eficiencia de futuras exploraciones de campo para inventarios.

Diez inventarios de mamíferos en selvas húmedas seleccionados como ejemplares ilustran varios problemas comunes: el esfuerzo de muestreo es altamente variable de estudio a estudio, las curvas de acumulación de especies no son asíntotas para ninguna fauna, métodos esenciales de campo fueron omitidos en cada caso, y en algunas localidades su fauna fue parcialmente extirpada por cacerías previas al inventario. Comparaciones de diversidad significativas son por ello imposibles sin una inversión mayor de trabajo de campo adicional en cada sitio.

Datos de rangos geográficos proveen una fuente alternativa esencial de estimados de diversidad. Comparaciones de resultados de inventarios con esperados geográficos (predicciones de diversidad basados en datos de rango) sugieren que todos los inventarios existentes son incompletos, que el grado de lo incompleto es inversamente correlacionado con la duración del inventario, y que métodos especiales son requeridos para incluir aquellas especies evasivas en las listas faunísticas. Los datos de rango disponibles también sugieren varios patrones geográficos que deberían ser probados con trabajos de campo cuidadosamente enfocados. (1)

La diversidad de mamíferos en la Amazonía es probablemente superior en la subregión occidental (entre el Río Negro y el Río Madeira, donde más de 200 especies podrían ser simpátricas en algunas localidades), menor en la subregión guyana (al este del Río Negro y norte del Río Amazonas), e intermedia en la Amazonía suroriental (al este del Río Madeira y sur del Río Amazonas). (2) La variación geográfica en la diversidad amazónica principalmente involucra marsupiales, murciélagos, primates, y roedores; en contraste, la fauna de edentados, carnívoros, y ungulados son remarcablemente uniformes a través de toda la región. (3) En las selvas húmedas centroamericanas, una gradiente de diversidad conspicua y aparentemente monotónica se extiende desde Panamá oriental (donde la diversidad de mamíferos es dentro del rango de valores amazónicos) hasta el sur de México (donde la diversidad de mamíferos de la selva húmeda puede ser menor que en cualquier otro lugar del territorio neotropical). La diversidad de mamíferos en las selvas venezolanas costeras y brasileras surorientales es difícil de evaluar con los recursos de literatura y colecciones existentes, pero ninguna de estas regiones es probablemente tan diversa como la Amazonía.

A pesar de unas pocas voces discrepantes, la literatura mastozoológica del Nuevo Mundo provee evidencias concluyentes que la diversidad de mamíferos, medida por la riqueza de especies simpátricas, es superior en la selva baja tropical y decrece a lo largo de gradientes de incremento de latitud, elevación, y aridez. Así, las faunas de mamíferos de la Amazonía occidental son las más diversas comparada a cualquier otra en las Américas y quizás del mundo. Brevemente discutimos la generalidad y causas de los patrones de diversidad observados en términos de ecología contemporánea y escenarios históricos.

Avances significativos en el entendimiento de patrones de diversidad de mamíferos, en las selvas neotropicales, requerirán de revisiones sistemáticas de muchos géneros problemáticos y un programa agresivo para inventariar áreas pobremente muestreadas, mientras que las oportunidades de hacerlo aún existen.

RESUMO

Informações referentes à magnitude e distribuição geográfica da diversidade de mamíferos nas florestas neotropicais são importantes na avaliação de prioridades para a pesquisa e conservação nas Américas do Sul e Central. Apesar do rápido acúmulo de dados provenientes de inventários faunísticos na literatura especializada, diferenças reais de diversidade entre localidades são de difícil constatação, já que muitos fatores podem influen-

ciar o tamanho e a composição de uma lista de fauna. Neste trabalho nós avaliamos as informações existentes sobre a diversidade da fauna de mamíferos em florestas neotropicais e sugerimos diretrizes para trabalhos futuros, através de revisão de métodos de inventariamento, documentação e discussão das listas de fauna de dez localidades nas Américas do Sul e Central, além da compilação de dados de distribuição geográfica

para a predição de padrões de diversidade passíveis de serem testados por pesquisa de campo e consultas às coleções de museus.

Todos os métodos de inventariamento são parciais na medida que cada um é adequado para coleta e/ou observação de apenas uma fração da rica fauna de mamíferos neotropicais, que exibe uma grande diversidade morfológica e comportamental. Consequentemente diferentes métodos devem ser combinados para o censo adequado da comunidade como um todo. Ainda que nenhuma combinação de métodos possa garantir um inventário completo, a omissão e/ou aplicação não intensiva de métodos essenciais provavelmente resultará em um inventário incompleto. Recomendamos nove métodos que, se combinados e intensamente aplicados, deverão maximizar a eficiência de inventariamentos da fauna de mamíferos.

A partir da análise de dez inventários de mamíferos, considerados exemplares, uma série de problemas recorrentes foram identificados: o esforço amostral é altamente variável de estudo para estudo, as curvas de acumulação de espécies não são assintóticas para nenhuma fauna, métodos essenciais para os estudos de campo são constantemente omitidos e, finalmente, alguns dos estudos foram efetivados em localidades parcialmente alteradas por atividades de caça anteriores à realização dos inventários. Cabe-se dizer que, em função do exposto, análises confiáveis em termos de comparações entre padrões de diversidade fazem-se praticamente impossíveis sem que consideráveis investimentos em trabalhos adicionais de campo sejam efetivados para cada um dos sítios acima considerados.

Dados de distribuição geográfica constituem uma alternativa essencial para a elaboração de estimativas de diversidade. Comparações entre resultados de inventários e expectativas geográficas (previsões de diversidade com base em dados de distribuição) sugerem que todos os inventários existentes são incompletos, que os graus de incompletitude estão inversamente correlacionados com a duração dos inventários, e que métodos especiais para inventários são requeridos de maneira a que se possa adicionar espécies raras e de difícil amostragem às listas de fauna. Os dados de distribuição disponíveis no momento também sugerem vários padrões geográficos que deverão ser testados através de trabalhos de campo cuidadosamente direcionados. (1) A diversidade de mamíferos encon-

trada na Amazônia é provavelmente maior na sub-região ocidental (entre os rios Negro e Madeira, onde mais de duzentas espécies podem ser simpátricas em algumas localidades), mais pobre na sub-região das Guianas (leste do rio Negro e norte do rio Amazonas) e intermediária no sudeste da Amazônia (leste do rio Madeira e sul do rio Amazonas). (2) A variação geográfica da diversidade amazônica deve-se principalmente aos marsupiais, quirópteros, primatas, e roedores, ao passo que as faunas de edentados, carnívoros, e ungulados são praticamente as mesmas ao longo de toda a região. (3) Nas florestas da América Central o evidente e aparentemente monótono gradiente de diversidade estende-se desde a parte oriental do Panamá (onde a diversidade de mamíferos apresenta-se em nível equivalente aos encontrados na região amazônica) até o sudeste do México (onde a diversidade de mamíferos de mata tropical pluvial ali existente deve ser menor do que em qualquer outra parte dos neotrópicos continental). A diversidade de mamíferos na região costeira da Venezuela e na região sudeste do Brasil é de difícil avaliação a partir dos dados atualmente disponíveis na literatura e do acervo existente em coleções de museus. No entanto, pode-se afirmar que nenhuma dessas regiões poderá apresentar-se como portadora de índices de diversidade para mamíferos em níveis equivalentes aos existentes na Amazônia.

Apesar de algumas vozes discordantes, a literatura científica relativa aos mamíferos do novo mundo apresenta evidências suficientes de que a diversidade de mamíferos, medida pela riqueza de espécies simpátricas, é maior nas florestas tropicais de terras baixas e decresce com os gradientes de aumento em latitude, altitude, e aridez. Pode-se dizer então que a fauna de mamíferos da Amazônia ocidental é mais diversa que qualquer outra nas Américas e talvez no mundo. Aproveitamos para discutir a abrangência e causas dos padrões de diversidade observados em termos da ecologia contemporânea e de cenários históricos.

Cabe salientar que avanços significativos no entendimento dos padrões de diversidade das florestas tropicais irão requerer revisões sistemáticas dos gêneros mais problemáticos, assim como o estabelecimento de um programa mais agressivo para o inventariamento de áreas pobremente investigadas, enquanto as oportunidades para tal ainda existem.

INTRODUCTION

The accelerating pace of deforestation in humid tropical lowlands worldwide threatens the continued existence of magnificent eco-

systems whose biological diversity is still largely unexplored (Whitmore and Sayer, 1992). Tragically, lowland rainforests are now

only a memory in some regions where they were once extensive (Fonseca, 1985; Por, 1992). Even where large tracts remain uncut, hunting has extirpated populations of key predators and large frugivores along roads and navigable rivers, compromising the long-term survival of natural communities in most accessible areas (Redford, 1992; Terborgh, 1992). Thus, opportunities to inventory the biotas of undisturbed rainforests, and to study the ecology of rainforest species under pristine conditions, are rapidly dwindling.

Assessments of current knowledge about the magnitude and geographic distribution of biological diversity in Neotropical rainforests are urgently needed to evaluate priorities for research and conservation in Central and South America. Much of what can yet be learned from faunal surveys in zoologically unexplored areas and much of what can still be saved by effectively locating protected areas may depend crucially on using information already at hand to maximum advantage. To date, however, progress in reviewing diversity data for Neotropical rainforest organisms has been limited chiefly to trees, butterflies, frogs, squamate reptiles, and birds (e.g., Duellman, 1988; Heyer, 1988; Haffer, 1990; Gentry, 1992; Prance, 1994; Beccaloni and Gaston, 1995; Silva and Sites, 1995).

This report is the first attempt to comprehensively review published and unpublished information about mammalian diversity in Neotropical lowland rainforests. The need for synthesis is now acute because relevant inventory data are rapidly accumulating in the absence of any context for meaningful comparisons (e.g., Fonseca and Kierulff, 1988; George et al., 1988; Mascarenhas and Puerto, 1988; Ochoa et al., 1988; Malcolm, 1990; Woodman et al., 1991; March and Aranda, 1992; Ascorra et al., 1993; Pacheco et al., 1993; Medellín, 1994; Timm, 1994; Hutterer et al., 1995). The essential problem with inventory comparisons, distinguishing real site-to-site diversity differences from sampling artifacts that can affect the size and composition of species lists, has not hitherto been addressed in the mammalogical literature. Alternative sources of diversity data have likewise not been evaluated in studies of the Neotropical rainforest fauna.

Below we define the geographic, ecological,

and taxonomic scope of our review and explain relevant issues of semantics, scale, and taxonomy. We summarize methods for collecting and observing mammals in rainforests, discuss their sampling biases (if known), and suggest an essential core of techniques that should be used in combination to maximize inventory efficiency. We compare species lists from ten Neotropical rainforest localities and discuss the limited conclusions that can be drawn from incomplete data obtained by unstandardized and methodologically biased collecting. We evaluate distributional data from published and unpublished sources and estimate minimal and maximal species counts that could be expected in Central American and Amazonian rainforests. We discuss discrepancies between expected diversity (from distributional data) and observed diversity (from inventories) in terms of sampling artifacts and other limitations of the information at hand. Finally, we summarize diversity patterns within and among Neotropical rainforest regions, contrast mammalian faunas in rainforests with those of other New World biomes, discuss ecological and historical hypotheses proposed to explain relevant diversity phenomena, and conclude with recommendations for future research.

GEOGRAPHIC, ECOLOGICAL, AND TAXONOMIC SCOPE

Lowland tropical rainforests on the Central and South American mainland are distributed in four regions more-or-less isolated from one another by intervening mountain ranges and open vegetation (fig. 1). These regions define the geographic limits of our review and provide a convenient framework for faunal analyses and comparisons.

Trans-Andean rainforests extend from the Mexican state of Veracruz southeastward (chiefly along the Caribbean versant of the Central American isthmus) to northwestern South America. In South America, trans-Andean rainforests extend southward along the Pacific littoral to northwestern Ecuador and eastward across the lower Cauca and Magdalena valleys to the western flanks of the Serranía de Perijá in northern Colombia; an isolated enclave once cloaked the northern

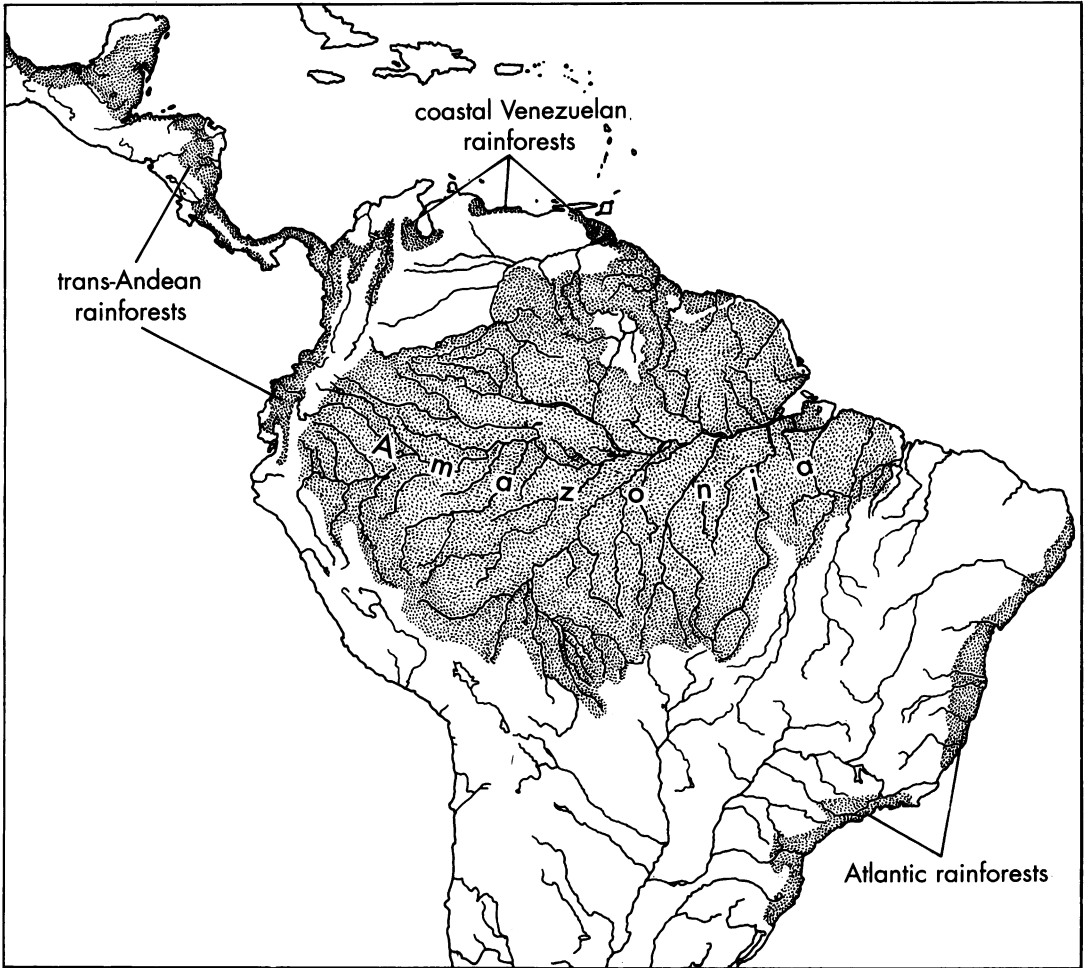


Fig. 1. Distribution of lowland rainforest on the Central and South American mainland (after Prance, 1989, and others). The predominant natural vegetation in shaded regions is rainforest except where local soils and steep climatic gradients (e.g., rainshadows and coastal deserts too small to show on a map of this scale) produce other plant formations. Unshaded areas are mostly covered with montane or xeromorphic vegetation. The nomenclature for rainforested regions and subregions is defined in the accompanying text.

and eastern foothills of the Sierra Nevada de Santa Marta. The wettest of these forests, in western Colombia and northwestern Ecuador, are known as the Chocó (Gentry, 1982b). Deforestation and settlement have been extensive throughout the humid trans-Andean lowlands, but pristine habitat may persist in some remote areas. Trans-Andean rainforests are separated from Amazonian rainforests by the Andes and from coastal Venezuelan rainforests by the Serranía de Perijá and by arid vegetation on the Península de Guajira.

Coastal Venezuelan rainforests occur discontinuously from the Maracaibo Basin eastward to the Orinoco delta. The largest enclave once covered much of the southwestern Maracaibo lowlands, but human intervention throughout northern Venezuela has been extensive (Huber and Alarcon, 1988) and it seems unlikely that any pristine habitat now remains. The lower Orinoco and the llanos separate coastal Venezuelan rainforests from Amazonian habitats to the east and south.

Amazonian rainforests (the hylaea of Humboldt) cover most of the Guianas, the

upper Orinoco catchment, and the Amazon valley itself (Ducke and Black, 1953). We follow Wallace (1854) in recognizing zoogeographic subdivisions of Amazonia defined by the Rio Negro, the Rio Madeira, and the lower Amazon: the *Guiana subregion* (east of the Negro and north of the Amazon), *southeastern Amazonia* (east of the Madeira and south of the Amazon), and *western Amazonia* (west of the Negro and Madeira).¹ A diagonal swath of semiarid vegetation on the Brazilian Shield—caatinga, cerrado, and chaco—separates Amazonia from the humid Atlantic lowlands of southeastern Brazil.

Atlantic rainforests once extended (Por, 1992) along the eponymous coastline of southeastern Brazil from Cabo São Roque (ca. 5°S) to the Rio Taquari (ca. 30°S). Most of the Atlantic littoral region of southeastern Brazil is now completely deforested, however, and the biotas of most (perhaps all) surviving fragments have been impoverished by hunting and selective logging (Fonseca, 1985).

Within these geographic limits, the climax vegetation below about 1000 m elevation and receiving about 2000 mm or more of annual rainfall broadly conforms to Richards' (1952) classic description of "Tropical [nonmontane] Rain forest," for which we use "lowland rainforest" (after Grubb et al., 1963) or simply "rainforest" (without modifiers) as synonyms below. Although plant communities at many localities in the wet Neotropical lowlands exhibit conspicuous floristic and physiognomic variation correlated with seral stage and edaphic conditions (e.g., in riverine floodplains; Puhakka and Kalliola, 1995), few

specimens of Neotropical mammals are accompanied by detailed habitat descriptions and we therefore use "rainforest" to subsume the entire local matrix of natural vegetation characterized by an evergreen canopy of tall trees at inventory sites within the four regions defined above. Not included are savannas (sábanas, campos), shrublands (arbustales, campinas, muri scrub), marshes, and other kinds of open vegetation that may occur on patches of rocky, sandy, or waterlogged soils within otherwise rainforested landscapes (Cooper, 1979; Anderson, 1981; Pires and Prance, 1985). Some mammals found in such nonforest enclaves never enter undisturbed rainforest and exist as paleoclimatically isolated representatives of faunas widespread in other biomes (Voss, 1991).

Although transitions to nonforest habitats (e.g., savannas and shrublands) are often sharply defined, lowland rainforest sometimes forms broad ecotones with montane ("cloud") and deciduous ("dry") forests. We arbitrarily chose 1000 m above sea level to limit our survey of the lowland rainforest fauna, but montane forests can occur at lower elevations on outlying ridges and small cordilleras (the *Massenerhebung* effect; Grubb, 1977). For practical reasons (lack of relevant data from most mammal inventory sites), we ignore subtle phenological distinctions among forests on gradients of decreasing rainfall and include in our survey any with an evergreen canopy whether or not a small number of tree species are seasonally leafless (e.g., the "semideciduous" forest on Barro Colorado Island; Foster and Brokaw, 1982).

The mammalian fauna indigenous to lowland rainforests on the Neotropical mainland (within the geographic and ecological limits defined above) is presently known to include 170 genera in 9 orders and 35 families (excluding humans, domesticated and commensal species, sirenians, and cetaceans; table 1). A simple tabulation of distribution patterns (table 2) indicates that whereas half (85) of these genera occur from Central America or the Chocó to southeastern Brazil, the remainder have more restricted ranges that reveal significant faunal divergence among the four rainforest regions previously identified. Although regional totals for genera (bottom of table 1) hint at geographic differences in

¹ Wallace (1854) also used the upper Amazon (Solimões-Marañón) to partition Amazonia into faunal units, but this river is (arguably) of lesser zoogeographic importance than the Madeira, Negro, and lower Amazon. Wallace's "Ecuador district" and "Peru district," separated by the upper Amazon, are therefore combined in our western Amazonian subregion. His "Guiana district" exactly corresponds to our Guiana subregion and his "Brazil district" to our southeastern Amazonian subregion. Of Wallace's four districts, only Guiana has persisted with essentially the same name and geographic definition in the zoological literature (e.g., Tate, 1939; Hoogmoed, 1979). Wallace's hypothesis that large Amazonian rivers are important zoogeographic boundaries was corroborated by a recent quantitative analysis of primate distributions (Ayres and Clutton-Brock, 1992) but needs to be reevaluated when reliable range maps become available for other taxa.

lineage diversity, our principal concern below is with numbers of species in local faunas.

QUESTIONS OF SEMANTICS AND SCALE

Because biological diversity can be measured in various ways and studied at different ecological and spatial scales, clear statements about these problematic issues are important at the outset to avoid confusion. Following the emerging consensus among ecologists (e.g., Brown, 1988; Schluter and Ricklefs, 1993; May, 1994), we quantify diversity as species richness (number of species). Alternative diversity measures that incorporate information about relative abundance (reviewed by Magurran, 1988) or phylogenetic relationships (Humphries et al., 1995) may be useful for special purposes but require data that are seldom available for comparisons of rainforest mammal faunas.

The ecological and spatial scale of the data reviewed herein is essentially that of biological survey work accomplished by collectors working on foot from a single camp. Within the typical working radius of most rainforest campsites,² a variety of habitats including riparian and terra firme formations, different stages of successional growth (following tree-falls or riverine meanders in pristine terrain), and palm swamps are usually present. Whereas generalist species may occur throughout the entire range of local habitats, other species are habitat specialists confined

to one or a few vegetation types. In the usual absence of ecological information associated with individual specimens and observations, however, distinctions between alpha (within-habitat) and beta (between-habitat) components of local diversity (Whittaker, 1972, 1977) are seldom possible. In effect, sympatry (not syntopy) is the most that can usually be inferred from collections of rainforest mammals with the same locality data, and we use this criterion to define the context of diversity comparisons reported below.

TAXONOMIC PROBLEMS

Most genera of Neotropical rainforest mammals have never been revised, or were last revised many years ago, so species concepts reflected in current taxonomic references (e.g., Wilson and Reeder, 1993) are often little more than conventions sanctioned by long use. Even genera with recent revisions are not free of taxonomic ambiguities, however, as differences among three current classifications of squirrel monkeys, *Saimiri*, eloquently attest (Hershkovitz, 1984; Thorington, 1985; Costello et al., 1993). Especially suspect are some "species" of small marsupials, bats, and rodents whose ranges are currently believed to extend for thousands of kilometers across landscapes divided by major rivers and other zoogeographic barriers (e.g., *Marmosa murina*, *Carollia brevicauda*, *Oryzomys capito*, etc.). In many such cases, close study may reveal morphological and/or molecular discontinuities among taxa currently ignored as obsolete synonyms or subspecies. A recent example is the discovery that *Tonatia bidens*, previously thought to range from Argentina to Mexico, is apparently replaced in the northern Neotropics by *T. saurophila*, a distinct species (Williams et al., 1995).

Although unrevised taxa are a major impediment for assessing faunal complementarity (sensu Colwell and Coddington, 1994), they are less problematic for comparisons of species richness. Usually, sympatric species are easily recognized and can be counted as such even when the nomenclature is in doubt. The few cases known to us in which the current nomenclature obscures sympatric diversity are noted in appendix 1, but future sys-

² For mammalogists laden with traps and other collecting impedimenta, 5 km is about the maximum walking distance from camp that inventory activities usually extend, but a 3 km radius would probably enclose 90% of the collections and observations made at a typical rainforest locality. Assuming a roughly circular dispersion of effort, the area sampled might therefore be estimated as approximately 30–80 km², but survey work at riverside localities is almost always confined to one bank and most collectors use trail systems that are densely reticulated near camp but sparsely developed elsewhere (fig. 3). Hence, the area effectively sampled by inventory work around most rainforest camps is unlikely to exceed about 10 km². Within faunally homogeneous landscapes, however, area per se is unlikely to substantially affect the outcome of rainforest mammal inventory work. The counterexamples cited by Hutterer et al. (1995: 13) confound area with sampling effort (number of collecting localities) and biotic heterogeneity (presence of montane forest), neither of which is a necessary correlate.

TABLE 1
Regional Distribution of Mammalian Genera in Neotropical Lowland Rainforests
(After ranges mapped by Emmons and Feer [1990] except as noted.)

	Rainforested lowland regions ^a					Rainforested lowland regions ^a			
	tr-And	CoVen	Ama	Atl		tr-And	CoVen	Ama	Atl
MARSUPIALIA									
					<i>Tonatia</i>	X	X	X	X
Didelphidae					<i>Trachops</i>	X	X	X	X
<i>Caluromys</i>	X	X	X	X	<i>Vampyrum</i>	X	X	X	
<i>Caluromysiops</i>			X		Glossophaginae				
<i>Chironectes</i>	X	X	X	X	<i>Anoura</i>	X	X	X	X
<i>Didelphis</i>	X	X	X	X	<i>Choeroniscus</i>	X	X	X	X ^h
<i>Glironia</i>			X		<i>Glossophaga</i>	X	X	X	X
<i>Gracilinanus</i>	X ^b	X	X	X	<i>Hylonycteris</i>	X ^d			
<i>Marmosa</i>	X	X	X	X ^c	<i>Lichonycteris</i>	X		X	X ⁱ
<i>Marmosops</i>	X ^d	X ^d	X	X	<i>Lionycteris</i>	X		X	
<i>Metachirus</i>	X	X	X	X	<i>Lonchophylla</i>	X	X	X	X
<i>Micoureus</i>	X	X	X	X	<i>Scleronycteris</i>			X	
<i>Monodelphis</i>	X ^d	X	X	X	Carollinae				
<i>Philander</i>	X	X	X	X	<i>Carollia</i>	X	X	X	X
					<i>Rhinophylla</i>	X		X	X
XENARTHRA									
					Stenodermatinae				
Bradypodidae					<i>Ametrida</i>	X ^j	X	X	
<i>Bradypus</i>	X	X	X	X	<i>Artibeus</i>	X	X	X	X
Megalonychidae					<i>Centurio</i>	X	X		
<i>Choloepus</i>	X	X	X		<i>Chiroderma</i>	X	X	X	X
Dasypodidae					<i>Ectophylla</i>	X			
<i>Cabassous</i>	X	X	X	X	<i>Mesophylla</i>	X	X	X	
<i>Dasytus</i>	X	X	X	X	<i>Platyrrhinus</i>	X	X	X	X
<i>Priodontes</i>		X ^e	X	X ^e	<i>Pygoderma</i> ^k				X
Myrmecophagidae					<i>Sphaeronycteris</i>		X	X	
<i>Cyclopes</i>	X	X	X	X	<i>Sturnira</i>	X	X	X	X
<i>Myrmecophaga</i>	X ^e	X ^e	X	X ^e	<i>Uroderma</i>	X	X	X	X
<i>Tamandua</i>	X	X	X	X	<i>Vampyressa</i>	X	X	X	X
					<i>Vampyrodes</i>	X	X	X	
CHIROPTERA									
					Desmodontinae				
Emballonuridae					<i>Desmodus</i>	X	X	X	X
<i>Balantiopteryx</i>	X				<i>Diaemus</i>	X	X	X	X
<i>Centronycteris</i>	X		X	X	<i>Diphylla</i>	X	X	X	X
<i>Cormura</i>	X	X ^f	X		Natalidae				
<i>Cyttarops</i>	X		X		<i>Natalus</i>	X	X	X	X
<i>Diclidurus</i>	X	X	X	X	Furipteridae				
<i>Peropteryx</i>	X	X	X	X	<i>Furipterus</i> ^l	X		X	X
<i>Rhynchonycteris</i>	X	X	X	X	Thyropteridae				
<i>Saccopteryx</i>	X	X	X	X	<i>Thyroptera</i>	X	X	X	X
Noctilionidae					Vespertilionidae				
<i>Noctilio</i>	X	X	X	X	<i>Antrozous</i> ^m	X			
Mormoopidae					<i>Eptesicus</i>	X	X	X	X
<i>Mormoops</i>	X	X	X		<i>Histiotus</i>	X ^d	X ^d	X ^d	X ^d
<i>Pteronotus</i>	X	X	X	X	<i>Lasiurus</i>	X	X	X	X
Phyllostominae					<i>Myotis</i>	X	X	X	X
<i>Chrotopterus</i>	X	X	X	X	<i>Pipistrellus</i> ^m	X			
<i>Lonchorhina</i>	X	X	X	X	<i>Rhogeessa</i>	X	X	X	X
<i>Macrophyllum</i>	X	X	X	X	Molossidae				
<i>Micronycteris</i>	X	X	X	X	<i>Eumops</i>	X	X	X	X
<i>Mimon</i>	X	X	X	X	<i>Molossops</i>	X	X	X	X
<i>Phylloderma</i>	X	X ^g	X	X	<i>Molossus</i>	X	X	X	X
<i>Phyllostomus</i>	X	X	X	X					

TABLE 1—(Continued)

	Rainforested lowland regions ^a					Rainforested lowland regions ^a			
	tr-And	CoVen	Ama	Atl		tr-And	CoVen	Ama	Atl
<i>Neoplatymops</i>			X		Cervidae				
<i>Nyctinomops</i>	X	X	X	X	<i>Mazama</i>	X	X	X	X
<i>Promops</i>	X	X	X	X	<i>Odocoileus</i> ^a	X	X	X	
PRIMATES					PERISSODACTYLA				
Callitrichidae					Tapiridae				
<i>Callimico</i>			X		<i>Tapirus</i>	X	X	X	X
<i>Callithrix</i>			X	X	RODENTIA				
<i>Cebuella</i>			X		Sciuridae				
<i>Leontopithecus</i>				X	<i>Microsciurus</i>	X		X	
<i>Saguinus</i>	X		X		<i>Sciurillus</i>			X	
Cebidae					<i>Sciurus</i>	X	X	X	X
<i>Alouatta</i>	X	X	X	X	Geomyidae				
<i>Aotus</i>	X	X	X		<i>Orthogeomys</i>	X ^r			
<i>Ateles</i>	X	X	X		Heteromyidae				
<i>Brachyteles</i>				X	<i>Heteromys</i>	X	X		
<i>Cacajao</i>			X		Muridae				
<i>Callicebus</i>			X	X	<i>Abrawayaomys</i>				X ^s
<i>Cebus</i>	X	X	X	X	<i>Akodon</i> ⁱ		X		X
<i>Chiropotes</i>			X		<i>Blarinomys</i>				X
<i>Lagothrix</i> ^a			X		<i>Delomys</i>				X
<i>Pithecia</i>			X		<i>Ichthyomys</i>	X	X ^d	X ^d	
<i>Saimiri</i>	X		X		<i>Isthomys</i>	X ^d			
CARNIVORA					<i>Melanomys</i>	X	X	X ^u	
Canidae					<i>Neacomys</i>	X	X ^d	X	
<i>Atelocynus</i>			X		<i>Nectomys</i>	X	X	X	X
<i>Speothos</i>	X	X	X	X	<i>Neusticomys</i>		X	X	
Felidae					<i>Nyctomys</i>	X			
<i>Herpailurus</i>	X	X	X	X	<i>Oecomys</i>	X	X	X	X
<i>Leopardus</i>	X	X	X	X	<i>Oligoryzomys</i>	X	X	X	X
<i>Panthera</i>	X	X	X	X	<i>Oryzomys</i>	X	X	X	X
<i>Puma</i>	X	X	X	X	<i>Ototylomys</i>	X ^v			
Mustelidae					<i>Oxymycterus</i>			X	X
<i>Conepatus</i>	X	X		X	<i>Peromyscus</i>	X ^w			
<i>Eira</i>	X	X	X	X	<i>Phaenomys</i>				X
<i>Galictis</i>	X	X	X	X	<i>Reithrodontomys</i>	X ^x			
<i>Lontra</i>	X	X	X	X	<i>Rhagomys</i>				X
<i>Mustela</i>	X ^d	X ^d	X		<i>Rheomys</i>	X ^d			
<i>Pteronura</i>			X	X ^e	<i>Rhipidomys</i>	X	X	X	X
Procyonidae					<i>Scolomys</i>			X	
<i>Bassaricyon</i>	X	X	X		<i>Sigmodontomys</i> ^v	X	X		
<i>Bassariscus</i>	X				<i>Tylomys</i>	X			
<i>Nasua</i>	X		X	X	ERETHIZONTIDAE				
<i>Potos</i>	X	X	X	X ^o	<i>Chaetomys</i>				X
<i>Procyon</i>	X	X	X	X	<i>Coendou</i>	X	X	X	X
Ursidae					Dinomyidae				
<i>Tremarctos</i>			X ^p		<i>Dinomys</i>			X	
ARTIODACTYLA					Hydrochaeridae				
Tayassuidae					<i>Hydrochaeris</i>	X	X	X	X
<i>Pecari</i>	X	X	X	X	Dasyproctidae				
<i>Tayassu</i>	X	X	X	X	<i>Dasyprocta</i>	X	X	X	X
					<i>Myoprocta</i>			X	

TABLE 1—(Continued)

	Rainforested lowland regions ^a					Rainforested lowland regions ^a			
	tr-And	CoVen	Ama	Atl		tr-And	CoVen	Ama	Atl
Agoutidae					<i>Lonchothrix</i>			X	
<i>Agouti</i>	X	X	X	X	<i>Mesomys</i>			X	
Echimyidae					<i>Nelomys</i>				X
<i>Dactylomys</i>			X		<i>Proechimys</i>	X	X	X	X
<i>Diplomys</i>	X				LAGOMORPHA				
<i>Echimyis</i>		X	X	X	Leporidae				
<i>Hoplomys</i>	X				<i>Sylvilagus</i>	X	X	X	X
<i>Isotrix</i>			X		Total genera	130	109	138	109
<i>Kannabateomys</i>				X					

^a Abbreviations: tr-And, trans-Andean rainforests of Central America and northwestern South America; CoVen, coastal Venezuelan rainforests; Ama, Amazonian rainforests; Atl, Atlantic rainforests of southeastern Brazil. See figure 1 and accompanying text.

^b Collections of *Gracilinanus* from the Chocó rainforests of western Colombia and Ecuador were mapped by Hershkovitz (1992: fig. 1).

^c The holotype of *Marmosa moreirae* (a putative synonym of *M. murina*) was described from Itatiaya near Rio de Janeiro (Avila-Pires and Gouvêa, 1977). Other Atlantic forest specimens identified as *M. murina* are known from the states of Espírito Santo, Bahia, and Alagoas (M. Mustang, personal commun.).

^d Predominantly in montane forests; lowland records from piedmont landscapes.

^e Possibly now extirpated.

^f *Cormura brevirostris* was reported from northern Venezuela by Handley (1976).

^g Handley (1976) reported collections of *Phylloderma stenops* from the Caribbean littoral of northern Venezuela.

^h *Choeroniscus minor* was reported from the Atlantic rainforest region by Peracchi and Albuquerque (1993).

ⁱ *Lichonycteris obscura* was reported from the Atlantic rainforest region by Taddei and Pedro (1993).

^j *Ametrida centurio* was recently collected on Barro Colorado Island, Panama (Handley et al., 1991).

^k Two specimens of *Pygoderma bilabiatum* said to have been collected in Surinam over a century ago are lost (Husson, 1978); no other Amazonian examples are known, and it seems probable that the record was erroneous.

^l Collections of *Furipterus* are apparently unknown from coastal Venezuelan rainforests.

^m *Antrozous (Bauerus) dubiaquercus* and *Pipistrellus subflavus* were reported from the Lacandon rainforest of Chiapas by Medellín (1993).

ⁿ Isolated populations of woolly monkeys in northern Colombia are apparently restricted to montane forests (Hernández-Camacho and Cooper, 1976; Green, 1976); no trans-Andean lowland records are known.

^o The distribution of *Potos flavus* in the Atlantic rainforest region was summarized by Vieira (1952).

^p Spectacled bears principally inhabit montane habitats, but there is at least one definite lowland rainforest record from eastern Peru (Patton et al., 1982).

^q White-tailed deer principally occur in savannas, scrub, dry forests, montane forests, and riverside vegetation but stray into nearby rainforests; records from Amazonian Venezuela were reported by Tate (1939) and Handley (1976).

^r Species of *Orthogeomys* occur in lowland rainforests from Mexico to northwestern Colombia (Goldman, 1920; Hall and Dalquest, 1963; Coates-Estrada and Estrada, 1986; Greene and Rojas, 1989; Timm et al., 1989; Alberico, 1990).

^s The occurrence of *Abrawayomys* in the Atlantic rainforest of southeastern Brazil was reported by Fonseca and Kierulff (1988) and Stallings (1988).

^t Species of *Akodon* are definitely known to occur in rainforests below 1000 m only in the coastal Venezuela and Atlantic regions (e.g., Handley, 1976; Crespo, 1982; Olmos, 1991). Populations in southern Venezuela (provisionally identified as *A. aerosus* or *A. urichi*) are confined to montane habitats, grassland, or scrub (Tate, 1939; Gardner, 1989; Voss, 1991). To the best of our knowledge, no specimens of *Akodon* have ever been collected in Amazonian lowland rainforest.

^u *Melanomys robustulus* is known only from the Andean piedmont of eastern Ecuador.

^v Species of *Ototylomys* chiefly inhabit dry (deciduous) forests but sometimes occur in ecotones with evergreen formations.

^w *Peromyscus mexicanus* inhabits lowland rainforest in southern Mexico (Hall and Dalquest, 1963; Coates-Estrada and Estrada, 1986; March and Aranda, 1992), but elsewhere this species is apparently restricted to montane forests. Other Central American congeners are either montane or inhabit clearings and semiarid vegetation.

^x Most species of *Reithrodontomys* occur in open vegetation or montane habitats, but *R. darienensis* may be a species of the lowland rainforest edge (Handley, 1966).

^y *Sigmodontomys alfari* occurs in lowland rainforests from Nicaragua to northwestern Ecuador and western Venezuela (Hershkovitz, 1944; Handley, 1966; Fleming, 1970, 1973b).

tematic research may confidently be expected to discover additional examples.

In an ideal world, we would have waited until all the taxonomic problems that might affect the interpretation of our data were solved before attempting this review. Such,

however, is neither a practical nor an ethical option: chainsaws and bulldozers work faster than systematists. Flawed as it is, we offer this preliminary assessment in lieu of the more authoritative monograph we could have written later.

INVENTORY METHODS

Neotropical rainforest mammals range in size from a few grams to hundreds of kilograms and include species differing in diet, habitat, locomotion, social behavior, and circadian activity. Methods and equipment designed to collect or observe members of one family or order are therefore seldom effective for other taxa, and many techniques must be used in combination to census entire faunas. As academic biology programs increasingly emphasize laboratory training, however, few practical details of essential inventory methods are now familiar to any but a small and dwindling number of experienced fieldworkers.

The account that follows is intended both as a reference for future inventory projects and to explain the real complexity of the sampling problem. Without an appreciation for the scope and intensity of fieldwork required to obtain taxonomically comprehensive surveys of rainforest mammal faunas, it is difficult to evaluate the diversity data on which biogeographic comparisons, ecological interpretations, or conservation decisions might be based. Thus, a methodological review is essential background for analyzing currently available inventory results.

Marsupials

Most Neotropical rainforest marsupials are nocturnal and can only be collected or observed by hunting at night or by trapping. Because local populations of some species apparently undergo dramatic fluctuations in density (completely disappearing from study areas in certain seasons or years despite intensive census efforts; see Enders [1935], Atramantowicz [1986], Fleck and Harder [1995]), long-term surveys provide the most reliable diversity data. Some of the larger opossums can be identified without capture by visually conspicuous external characters

(Emmons and Feer, 1990), but definite identifications for all of the smaller species require voucher specimens.

NIGHT HUNTING: A head-mounted light is essential for night hunting because eyeshine is only reflected toward the source of the beam and because the hands must be free to use binoculars, aim a gun, or take notes. Justrite Head Lanterns (Model 1904; Justright Mfg. Co., Mattoon, IL 61938) are inexpensive 6-volt lights with focusable reflectors and belt-mounted battery packs; four alkaline D-cells provide enough power for 8–12 hours of nocturnal observations. While walking slowly (about 0.5 km/hr) and as quietly as possible, the ground, undergrowth, and subcanopy should be scanned with the reflector adjusted to produce a moderately broad beam. When eyeshine is detected, the beam can be narrowed for brighter illumination. If the forest

TABLE 2
**Analysis of Mammalian Generic Distributions in
Neotropical Lowland Rainforest Regions**
(Table entries are counts from table 1.)

Distribution pattern	Genera
Trans-Andean only	16
Coastal Venezuelan only	0
Amazonian only	20
Atlantic only	11
Trans-Andean and Coastal Venezuelan	3
Trans-Andean and Amazonian	5
Trans-Andean and Atlantic	0
Coastal Venezuelan and Amazonian	2
Coastal Venezuelan and Atlantic	1
Amazonian and Atlantic	4
All but Trans-Andean	2
All but Coastal Venezuelan	5
All but Amazonian	1
All but Atlantic	15
All four regions	85
Total	170

is very tall, however, a hand-held 9- or 12-volt light may be necessary to identify animals in the canopy.

Many marsupials are motionless or move slowly when they first appear in the headlight beam, giving ample time for observation or collection, but *Metachirus nudicaudatus* (a terrestrial species) usually flees and the collector must shoot quickly to obtain a specimen. Some small opossums (e.g., *Marmosa murina*) are fast and evasive, but others (e.g., *Marmosops parvidens*) can sometimes be caught by hand. *Chironectes minimus* is seldom encountered except by wading in streams (Beebe, 1923a), following streamside trails, or by waiting quietly in the dark at the water's edge (water opossums splash noisily while foraging). Species of *Caluromys*, *Caluromysiops*, *Glironia*, and *Micoureus* are exclusively arboreal; patient scanning of the canopy and subcanopy is the only way to see them. Arboreal opossums usually turn to face the light (confronting the human observer with two brightly luminous eyes; fig. 2), whereas snakes, frogs, and arboreal rodents (the latter always with dimmer eyeshine) usually do not. Binoculars are essential for identifying animals in the canopy or subcanopy (Zeiss's 10 × 40 model is ideal), but practice is necessary to use binoculars effectively with a head light.

The most versatile weapon for collecting marsupials at night is a 16- or 20-gauge, "double-barreled" (side-by-side or over-and-under) shotgun, with at least one barrel fully choked to deliver a tight pattern of pellets at long range. Number six lead shot (about 2.8 mm diameter) is sometimes necessary to take *Caluromys* in treetops, but number nine shot (about 2 mm diameter) is normally sufficient for all of the larger species at moderate range (20–25 m). For smaller species, "dust" (#12) shot in .22-caliber long-rifle shells or .410-gauge shotgun cartridges can be used in 12-, 16-, or 20-gauge guns fitted with removable "auxes" (auxiliary barrels) made from brass or aluminum rod stock machined to the outside diameter of regular ammunition. The visibility of the front sight can be improved with a dab of white paint.

A well laid-out system of trails is essential for efficient night hunting (and for many other inventory activities; fig. 3). Trails should

traverse all local habitats, such as swamps, seasonally flooded areas, well-drained high ground, tree falls, and successional communities. Selective removal of understory trees along trails can greatly improve the visibility of canopy and subcanopy habitats favored by marsupials and other arboreal mammals (e.g., viny tangles and concentrations of fruit resources).

TRAPPING: The larger nonaquatic marsupials (*Caluromys*, *Didelphis*, *Metachirus*, and *Philander*) can all be taken in wire live traps (fig. 4) baited with banana or ripe plantain; we prefer folding models measuring 145 × 145 × 410 mm (Model 201; Tomahawk Live Trap Co., P.O. Box 323, Tomahawk, WI 54487). Traps for *Caluromys* (and, presumably, for other arboreal opossums such as *Caluromysiops* and *Glironia*) should be placed as high as possible in trees (Malcolm, 1991a). *Chironectes minimus* can be taken in partially submerged, unbaited wire live traps (larger models are more effective) set in shallow, slow-moving streams; rows of vertical stakes (spaced about 2–3 cm apart) should be driven into the streambed from the mouth of the trap to the bank on either side. These sets must be cleaned periodically of leaves and other drifting debris, and several days or a week may be required to obtain results. We have also taken water opossums in live traps set in shallow water beneath undercut banks and baited with pieces of fish or crabs.

Some mouse opossums (e.g., *Marmosa*, *Marmosops*, and *Micoureus*) can be taken in folding aluminum live traps (80 × 90 × 230 mm models are standard; H. B. Sherman Traps Inc., P.O. Box 20267, Tallahassee, FL 32316) baited with banana or ripe plantain, but snap traps are also effective (see the discussion of muroid rodent trapping, below). Traps set for mouse opossums in the forest understory should be placed on top of logs, on lianas, and in tangles of vines; traps set on the ground under sheltering vegetation also take mouse opossums occasionally, especially during the dry season when fruit is scarce. Species of *Monodelphis* (fig. 5) are exclusively terrestrial and some may be at least partially diurnal; they are usually elusive but can sometimes be trapped in hollow logs and other dark cavities on the forest floor (fig. 6).

Lines of pitfall traps set beneath drift fences



Fig. 2. Rainforest marsupials encountered during nocturnal hunting/census. Clockwise from upper left: *Caluromysiops irrupta* (Cocha Cashu, Peru), *Philander opossum* (Cocha Cashu, Peru), *Marmosops parvidens* (Arataye, French Guiana), *Micoureus* sp. (Cocha Cashu, Peru). Note the binocular visage that distinguishes most rainforest marsupials illuminated at night from rodents (which generally show only one eye at a time). Photographed by L. H. Emmons.

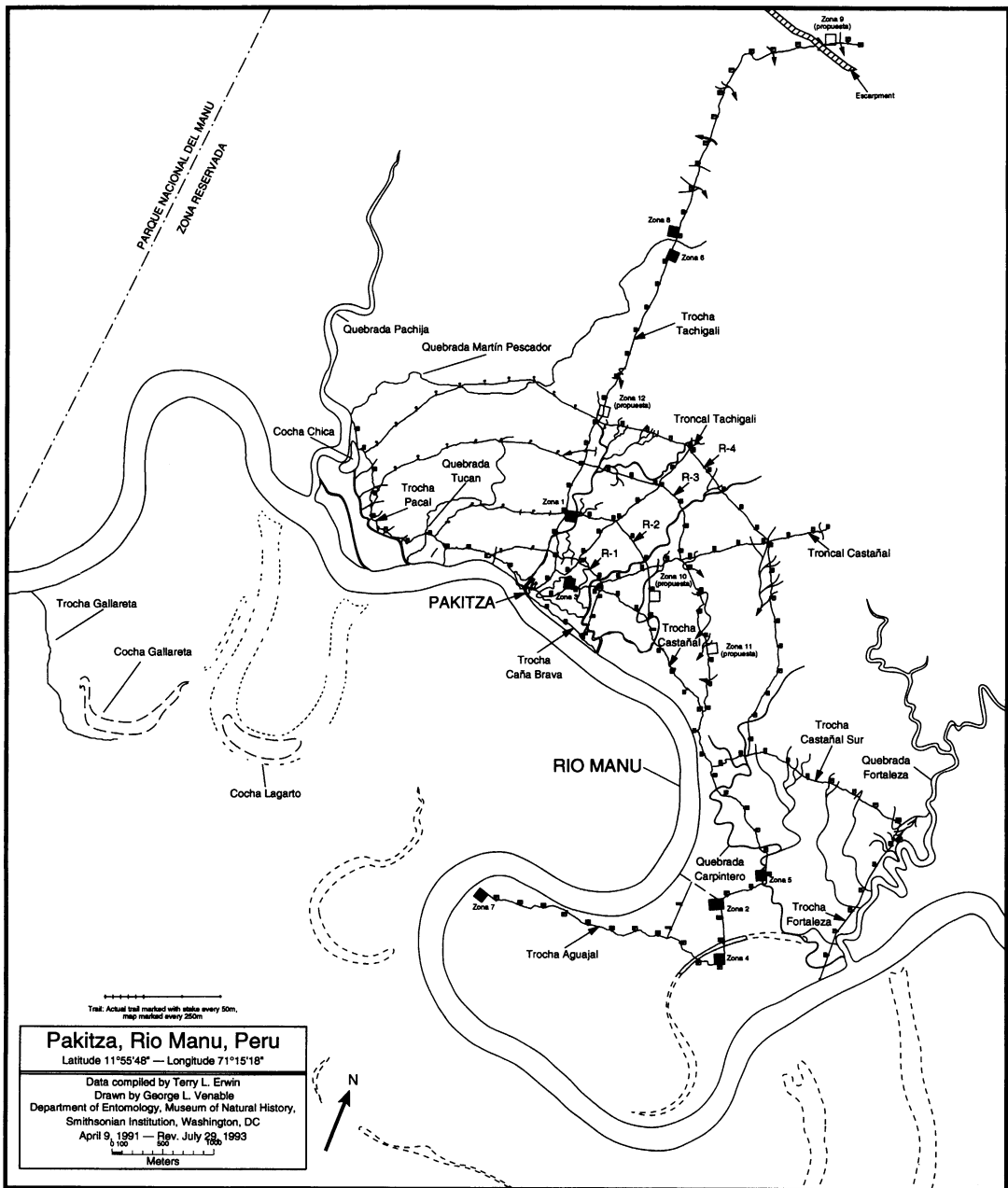


Fig. 3. The trail system at Pakitza, Departamento Madre de Dios, Peru. Trail systems are essential for efficient rainforest inventory work, providing corridors for unobtrusive access through dense vegetation otherwise difficult to sample by trapping, netting, or visual census. At this site (described in appendix 10), the trail system traverses at least 12 distinct habitats within the matrix of pristine rainforest vegetation surrounding a manmade clearing on the left bank of the Río Manu (Erwin, 1990). Courtesy of T. L. Erwin and G. L. Venable.

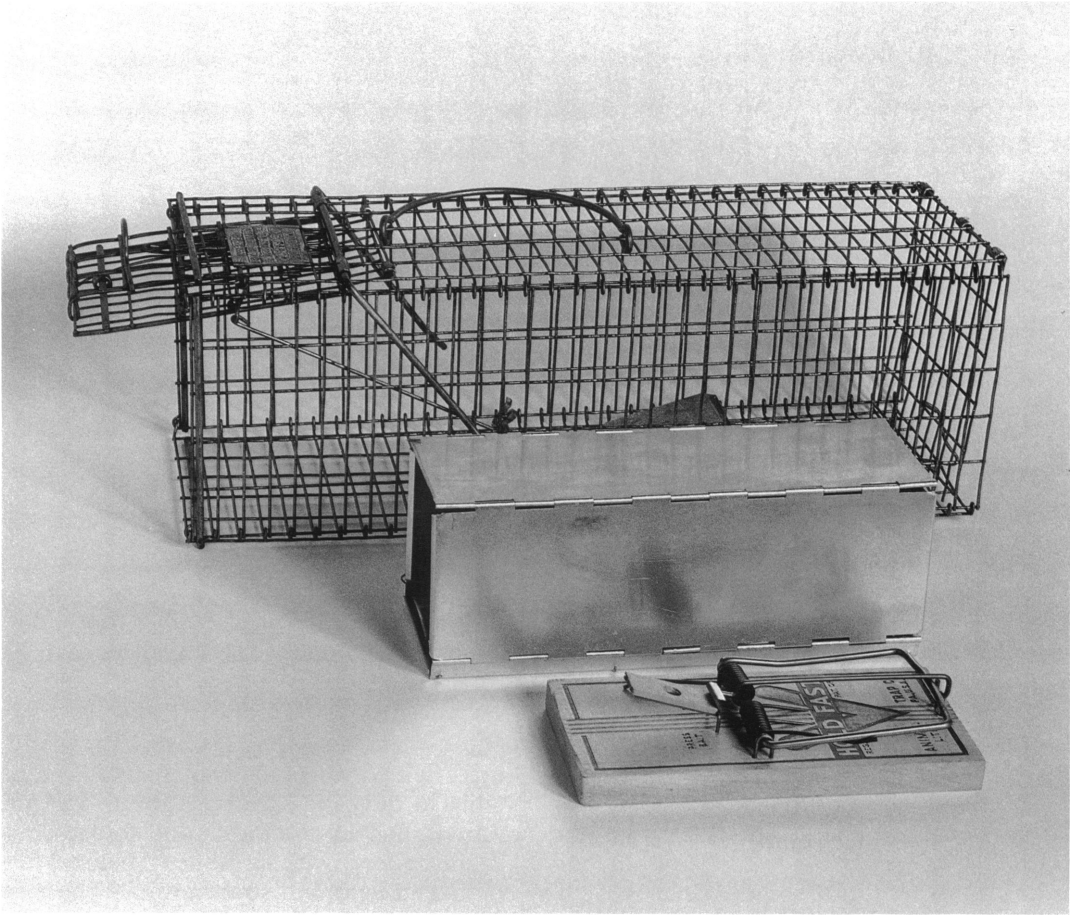


Fig. 4. Three standard traps for rainforest mammal inventory work (from back to front): Tomahawk folding wire live trap, Sherman folding aluminum live trap, and Victor rat trap (with push-down wooden bait pedal).

(fig. 7) are probably essential for collecting small marsupials that are seldom or inconsistently attracted to baited traps (e.g., species of *Gracilinanus* and *Monodelphis*). Buckets for pitfalls should be sunk flush with the soil surface and contain several inches of water (to keep animals from jumping out). Sheet plastic is an inexpensive and easily transported material for drift fences: long strips (ca. 0.5 m wide) can be stapled to vertical stakes for support, and about 5 cm should lie flat on the ground with earth heaped over it to anchor the bottom of the fence; a flap should be cut in the bottom fold of plastic where it passes over each bucket. An effective design for rainforest inventory work uses 16-liter buckets placed every 5 m under a con-

tinuous 50 m drift fence (S. M. Goodman, personal commun.).

XENARTHTRANS

Anteaters (*Cyclopes*, *Myrmecophaga*, and *Tamandua*) are virtually impossible to trap with commercially available equipment³ and

³ But Indians occasionally take them in baited dead-falls and pit traps (e.g., the Yagua described by Fejos, 1943). The traditional hunting and trapping expertise of indigenous rainforest cultures is a valuable source of inventory methods (and natural history data) that merits close study while any opportunities to do so yet remain. Most existing ethnographies (even Fejos' admirable treatise on the Yagua) are frustratingly vague about important zoological details of Indian subsistence technology.



Fig. 5. Elusive and shrewlike in habits, rainforest species of *Monodelphis* (above, *M. brevicaudata*) are seldom collected without special efforts, such as trapping in favored microhabitats (opposite) or constructing drift fences with pitfalls. Photographed by R. S. Voss (near San Ignacio Yuruaní, Edo. Bolívar, Venezuela).

are usually encountered haphazardly. All can be identified without voucher specimens by obvious external characters. Nocturnal and diurnal, *Myrmecophaga tridactyla* is uncommon everywhere and should never be collected. *Cyclopes didactylus* is cryptic and nocturnal but can sometimes be found by carefully inspecting subcanopy vegetation in the daytime (when these animals sleep curled around slender lianas; Montgomery, 1983). Tamanduas rip apart termite nests and dead wood in trees and can often be found by following the sound of falling debris.

Sloths are hard to see and impossible to trap. Three-toed sloths (*Bradypus*) usually stay in the canopy (except to defecate), but two-toed sloths (*Choloepus*) can sometimes be found hanging motionless in the subcanopy or understory at night. In regions where two congeneric sloths are to be expected, confident identifications require voucher specimens. Sloths have thick skin and dense bones; because a careless shot is more likely to injure than kill, collecting specimens should only be attempted with adequate ammunition.

Armadillos are hard to catch with commercially available traps, but their burrows

are often conspicuous and it should be possible to develop effective capture methods. Armadillos are nocturnal and forage noisily in the undergrowth; most flee the direct beam of a head light, but some animals pause momentarily, affording a brief opportunity for collection or observation. Giant armadillos (*Priodontes maximus*) are rare everywhere and should never be collected. Armadillos are prized for their meat throughout Central and South America, so discarded shells and skulls can often be found in piles of kitchen refuse behind native houses.

BATS

Because Neotropical rainforest bat communities are very diverse and include many elusive species (see capture frequency data in LaVal and Fitch, 1977; Bonaccorso, 1979; Handley et al., 1991; Medellín, 1993), major commitments of time and effort are necessary to obtain asymptotic species lists. Tuttle (1976) and Kunz and Kurta (1988) provided excellent general reviews of bat-collecting materials and methods, but we add a few supplementary suggestions for rainforest



Fig. 6. Microhabitat of *Monodelphis brevicaudata* (opposite page) in primary forest near San Ignacio Yuruaní, Edo. Bolívar, Venezuela. Specimens were trapped inside this hollow log and others like it, under piles of dead limbs, and in similar dark refugia carpeted and sheltered by decaying wood. Photographed by R. S. Voss.

work. All bats must be identified with specimens in hand and many cannot be identified without cleaned skeletal material. New taxa are described every year, so vouchers of all species encountered during inventory fieldwork should be preserved to document identifications.

MIST NETS: Mist nets set at ground level (0–3 m) are by far the most effective method for collecting most bats, especially phyllostomids, that forage or travel through the forest understory (fig. 8). Heavyweight (70-denier) nets are standard because they are cheap and durable, but lightweight (50- and 30-denier) mesh is more effective for small-bodied insectivorous species (e.g., emballonurids, *Micronycteris*, vespertilionids). By using large numbers of ground-level nets for many nights in a variety of habitats (e.g., in both well-drained sites and swamps, over streams, across treefalls, beneath fruiting trees, around flowering shrubs and vines, etc.), very large

species lists can eventually be obtained. The pioneering studies of Handley (1967) and Brosset and Charles-Dominique (1990), however, indicate that some rainforest bats (especially molossids) are only active at or above the level of the canopy. Several methods for rigging elevated nets have been described in the literature (e.g., Humphrey et al., 1968; Munn, 1991; Ingle, 1993) and other effective designs can be improvised in the field.

Mist nets are commonly checked for captured bats at half-hour or longer intervals, but this is a bad practice; nets should never be left unattended. Unattended nets are often damaged by large bats attempting to free themselves, by predators (usually opossums) attracted by struggling bats, or by fieldworkers who must cut the mesh to extract badly entangled animals (Tuttle, 1976; Kunz and Kurta, 1988). An additional disadvantage of unattended nets for inventory work is that

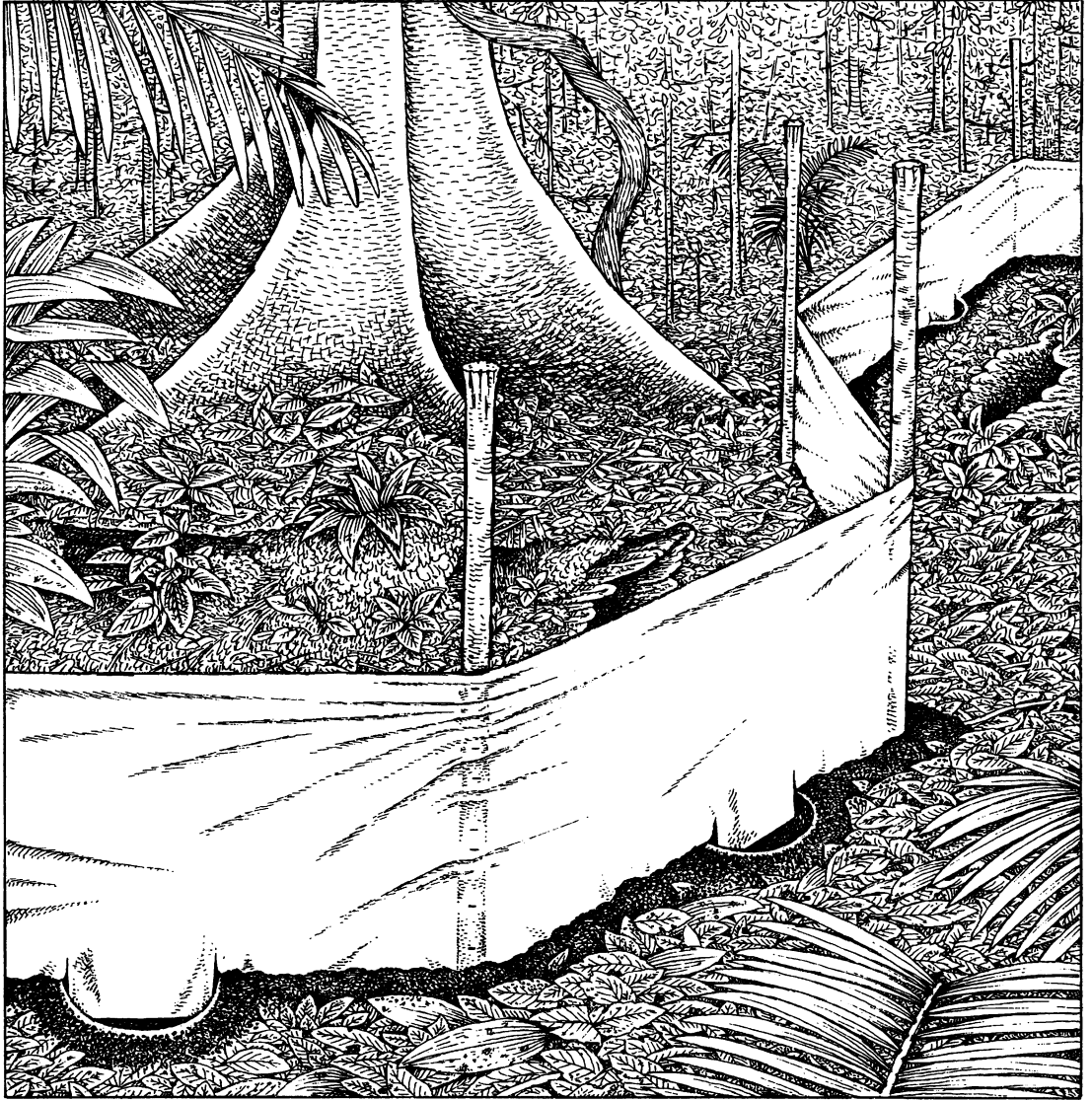


Fig. 7. An inexpensive pitfall-trapping design for rainforest inventory work (after S. M. Goodman, personal commun.). Buckets containing a few inches of water are sunk flush with the soil surface beneath a continuous sheet-plastic drift fence. See text for other construction details.

small insectivorous bats seldom hit the net with enough force to become fully enveloped and will often flutter out again if they are not immediately seized.

COLLECTING AT ROOSTS: Many species of rainforest bats can be collected or observed at their diurnal roosts in buildings, culverts, tunnels, caves, tree cavities, and foliage (Tuttle, 1976; Kunz, 1982; Timm, 1987). Searching for roosts of insectivorous species that

are difficult to catch in mist nets is an essential part of inventory work, but this is time-consuming in undisturbed rainforest where daytime retreats are far from obvious. Emballonurids can be found clinging to inclined tree trunks over streams and rivers (*Rhynchonycteris*), in recesses between buttresses of standing trees (*Saccopteryx*), between buttresses on the undersides of fallen trees (*Cormura*, *Peropteryx*), and in many other dark

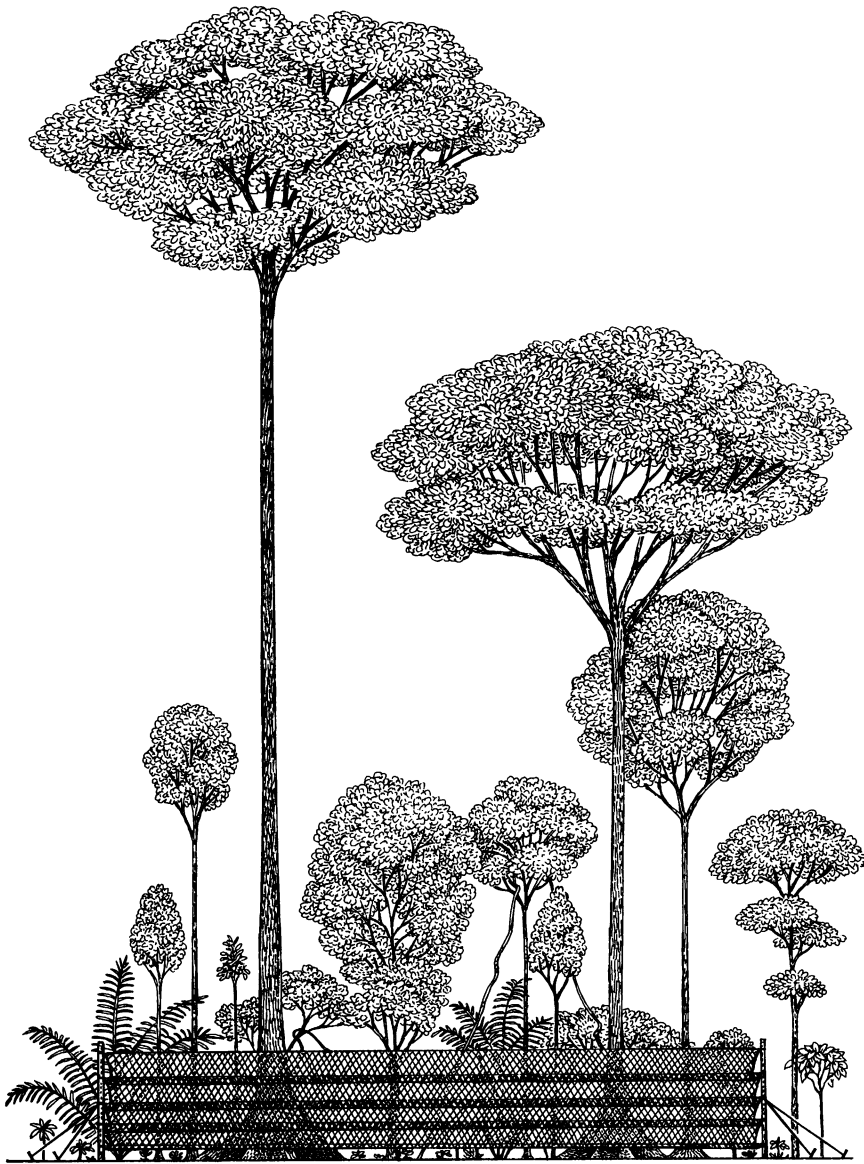


Fig. 8. A standard mist net as deployed to collect bats in the rainforest understory (vegetation profile at Cuzco Amazónico after Duellman and Koechlin, 1991). Such ground-level nets sample less than ten percent of the airspace under a typical rainforest canopy and seldom capture molossids or other high-flying taxa. Elevated nets hoisted into canopy gaps are essential for obtaining more comprehensive inventories of rainforest bat faunas.

cavities and hollows near ground level. *Diclidurine* emballonurids (*Cyttarops* and *Diclidurus*), however, roost in the crowns of palm trees (Romero and Sánchez, 1994; F. Reid, personal commun.), where they can be hard to see. The single species of rainforest furipterid (*Furipterus horrens*) roosts under

the buttresses of fallen trees and in hollow logs. The half-unrolled new leaves of bananas and related genera of large monocots (e.g., *Heliconia* and *Phenakospermum*) should be inspected for roosting colonies of thyropterids, as should scrolled dead leaves hanging from the plant. Roosts at ground level are

often discovered accidentally when one or more bats suddenly fly up from some hidden refuge, but the animals will usually return in a few minutes if the collector is not too close and remains motionless. Information recorded on specimen labels by A. M. Olalla (summarized by Patterson, 1992) suggests that rainforest molossids often roost in tree holes, probably at some distance above the ground; simple climbing equipment (Mori, 1987) might be useful for gaining access to such cavities, beneath which bag traps (e.g., Kunz and Kurta, 1988: fig. 1) could be installed to catch emerging bats.

Roosting bats can sometimes be taken alive with hand-nets and by other methods (Bradbury and Emmons, 1974; Tuttle, 1976), but shooting with a .22-caliber revolver loaded with shot-shells is easier and often more effective. Fallen trees and hollow logs should be searched cautiously because these shelters are also used by large poisonous snakes (e.g., *Bothrops atrox* and *Lachesis muta*).

MISCELLANEOUS METHODS: Harp traps consist of two or more vertical arrays of fine wires or nylon monofilament suspended in frames over an open bag (see Palmeirim and Rodrigues, 1993, for a review of the literature and a lightweight design). Bats that collide with the wires fall into the bag, from which they can be retrieved unharmed. Harp traps have seldom been used in Neotropical rainforests, but LaVal and Fitch (1977) found them to be more effective than mist nets for collecting vespertilionids in Costa Rica.

The Audubon Birdcall (manufactured by R. W. Eddy, Box 0172, Newington, CT 06131) is a small wooden cylinder enclosing a pewter key with a rounded shank. Twisting the key (with a little powdered resin in the cylinder bore) produces a high-pitched squeaking that can be used to attract bats to nets. Under fruiting trees, squeaking often attracts large numbers of *Artibeus* (Handley et al., 1991: see fig. 12.1) and other stenodermatines whose distress calls the noise resembles; prolonged squeaking (anywhere in the forest) also attracts carnivorous species that may be interested in distressed bats as prey (e.g., *Chrotopterus*, *Phyllostomus*, *Tonatia*, *Trachops*, and *Vampyrum*).

Shooting bats on the wing is difficult, but some high-flying species may not be obtain-

able by other means. The Smithsonian Venezuelan Project, for example, collected 69 specimens of four species of *Diclidurus*, all of which were shot in flight over water or clearings (Handley, 1976). The portable electric lights used by entomologists to attract nocturnal insects might be useful for luring such bats within shotgun range if other opportunities for shooting are unavailable (A. L. Gardner, personal commun.).

PRIMATES

All Neotropical primates except night monkeys (*Aotus*) are diurnal and, except where hunted intensively, most are easily seen. Spider monkeys (*Ateles*) and howlers (*Alouatta*) can also be located by their distinctive calls, and some callitrichids (*Cebuella* and *Callithrix*) leave characteristic scars in the bark of trees with edible sap (Coimbra-Filho and Mittermeier, 1978; Ramírez et al., 1978). Most callitrichids and large cebids can be identified by obvious external characters, but species of *Aotus* (sensu Hershkovitz, 1983) and members of the *Callicebus moloch* group (sensu Hershkovitz, 1990) may be difficult or impossible to identify without vouchers. In general, taxonomic problems with Neotropical primates concern geographically differentiated allopatric taxa that some systematists recognize as species while others do not; it is seldom (if ever) difficult to distinguish sympatric species by external characters.

Transect census data obtained by walking trails or scanning shorelines from a boat are standard for studies of primate diversity in Neotropical rainforests (e.g., Branch, 1983; Deffer, 1983; Freese et al., 1982; Peres, 1988). Species accumulation curves from primate inventories at 14 sites in Amazonian Peru and Bolivia (Freese et al., 1982) suggest that new species are seldom found after the first 20 km of walked transect census in areas of high primate density, but longer surveys are indicated if primate density is low. Many small monkeys are habitat specialists (Terborgh, 1985b; Rylands, 1987), so transects should be carefully planned to sample all local vegetation types, especially in western Amazonia where meandering rivers create intricate mosaics of successional growth.

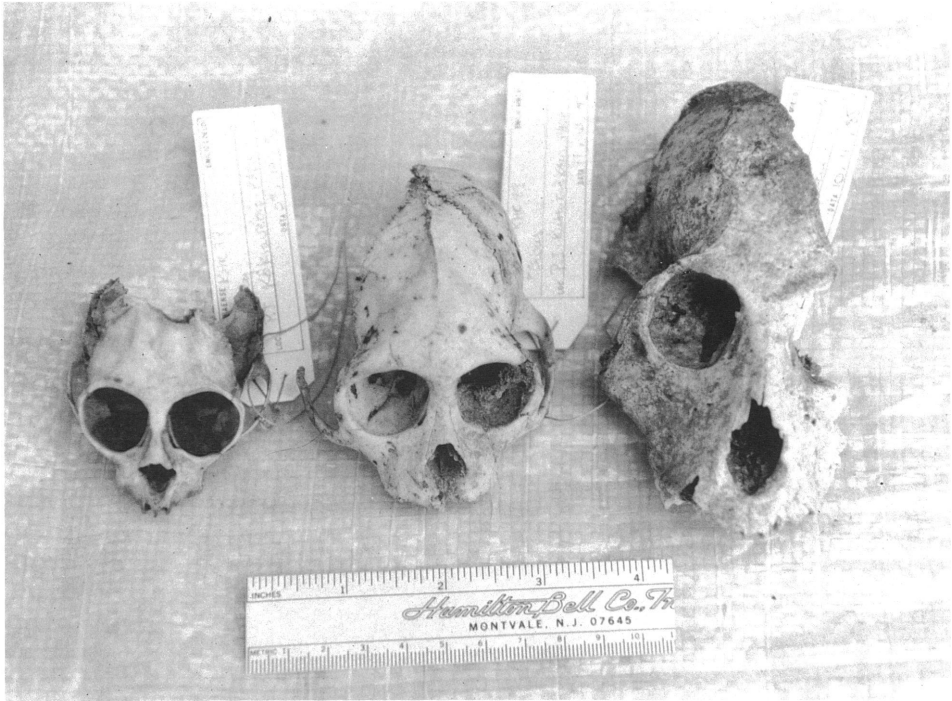


Fig. 9. Monkey skulls discarded behind Kayapó indian houses at Kubenkrakein (Cubencranquém) on the upper Riosinho, Estado de Pará, Brazil. Left to right: *Chiropotes satanas*, *Cebus apella*, *Alouatta belzebul* (specimens in Museu Goeldi). Indigenous rainforest cultures eat a wide variety of terrestrial vertebrates (Redford and Robinson, 1987) and their kitchen middens are a useful source of vouchers that might otherwise be difficult or illegal to collect. Photographed by K. H. Redford.

However, because some species may be seasonal vagrants present only when food is abundant (Peres, 1993), even the best-planned short-term surveys are liable to miss a transient component of local diversity. Hence, year-round (or multiyear) studies provide the most reliable primate inventories.

Although interviews with local inhabitants (if any) can usefully supplement primate census data, second-hand reports of night monkeys (*Aotus*) are often unreliable because kinkajous (*Potos*) and olingos (*Bassaricyon*) are commonly known by the same local names (e.g., *mono de noche*, *macaco da noite*). The local impact of human activities should always be carefully assessed for primate inventory work because well-armed hunters can extirpate populations of large monkeys (especially *Ateles* and *Lagothrix*, universally prized for their meat) even in extensive tracts of primary forest (Freese et al., 1982; Peres, 1990; Redford, 1992; Bodmer, 1995; Ráez-

Luna, 1995). The local history of sylvan yellow fever epidemics, which can decimate populations of some species (Galindo, 1973), is also relevant.

When it is possible to take primate vouchers, each specimen should be treated as if it were the last from that locality (which, because of increasingly onerous legal restrictions on collecting, it might be) and the maximum amount of information and material preserved. The only efficient way to collect monkeys is by shooting, which should never be attempted with inadequate ammunition or at extreme range. Kitchen refuse behind native houses is an alternative source of osteological voucher material (fig. 9).

CARNIVORES

Most carnivores are encountered unpredictably and occur at low densities, so a long time (many years) may be required to obtain



Fig. 10. Tracks of *Leopardus pardalis* on the beach at Cocha Cashu, Peru. Diagnostic features of ocelot pugs include size (those of other sympatric felids are substantially larger or smaller) and the characteristically wider impressions of the forefeet (behind those of the narrower hindfeet in each print-pair). Length of machete (juxtaposed for scale) is 47 cm. Photographed by L. H. Emmons.

a complete inventory. A few species can be lured with imitations of rodent or bird vocalizations (ornithologists using recorded sounds to attract birds see unusual numbers of tayras and coatis). Some rainforest carnivores can be taken in live traps, but this is time-consuming and requires special methods (such as live bait) and equipment (e.g., Emmons, 1988). An extensive literature on commercial fur trapping in north-temperate habitats is perhaps relevant, but we are aware of only a few successful attempts to collect rainforest carnivores with leghold traps. Interviewing local hunters and trappers is probably the most effective way to obtain information about carnivore diversity (but note

that cats and coatis are oversplit in many folk taxonomies; e.g., that of the Aguarunas studied by Patton et al., 1982). Cat skins and teeth are often used as ornaments by indians, and the young of other elusive taxa (e.g., *Speothos*) are sometimes kept as pets, so visits to local villages can provide useful data.

Kinkajous and olingos forage noisily in trees at night and have bright eyeshine, but their vocalizations are similar and both species may be present simultaneously (sometimes with night monkeys) in the same fruiting tree. Olingos are always sympatric with kinkajous (but not vice versa) and, unless a clear view is obtained with a strong light, can only be confidently identified from shot specimens.

Some carnivores leave distinctive sign. Otters can be detected from spraints and slides along river banks, and the larger cats (ocelots, pumas, jaguars) leave distinctive prints (Emmons and Feer, 1990; Aranda, 1994) along trails, riverbanks, and lakeshores (fig. 10). Prints of smaller felids (margays, oncillas, jaguaroundis), however, are hard to distinguish from one another. Scent stations using commercial lures over substrate prepared to preserve tracks have been used to census felid populations in the U.S. (Diefenbach et al., 1994), and this method might also be adapted for rainforest inventory work. Cameras actuated by trip-wires, pressure-sensitive mats, or infrared sensors could also prove useful. Although Griffiths and van Schaik (1993) recently described "camera-trapping" as a novel technique for rainforest mammal surveys, the method was known to Chapman (1927, 1929), whose trip-wired cameras photographed several species of carnivores and ungulates previously undetected on Barro Colorado Island (figs. 11, 12). State-of-the-art camera traps (Karanth, 1995) merit trial use in future Neotropical rainforest inventories.

UNGULATES

Rainforest ungulates are usually encountered by chance unless the local distribution of food (e.g., choice browse, fallen fruit, or mast) and salt licks is known. Tapirs and rainforest deer are diurnal and nocturnal, but rainforest peccaries are exclusively diurnal. Collared peccaries (*Pecari tajacu*) live in small social groups that confine their activities to



Fig. 11. An early camera trap used by F. M. Chapman on Barro Colorado Island (above) and *Puma concolor* photographed with the same apparatus (below). Cups of magnesium powder, mounted on poles beside the camera, were ignited by a battery to provide flash illumination when a trip-wire (almost invisible in the lower photo) was displaced. Pumas were unknown on the island before Chapman's camera-trapping recorded several individuals in the late 1920s, but the insular population is now extinct and only photographs exist as vouchers. Courtesy AMNH Department of Library Services.

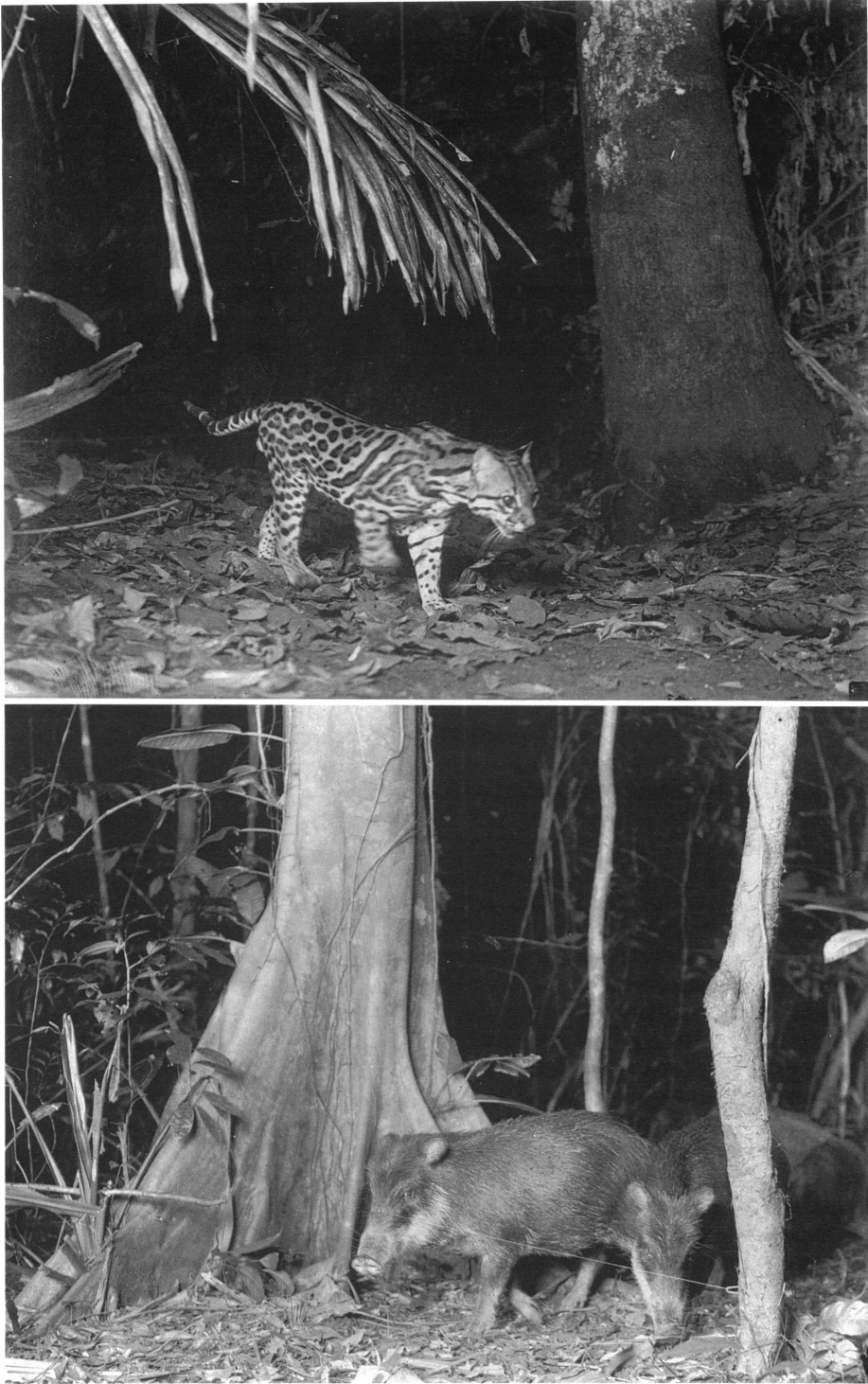


Fig. 12. *Leopardus pardalis* (above) and *Tayassu pecari* (below) camera-trapped by F. M. Chapman on Barro Colorado Island in the 1920s. The local population of white-lipped peccaries that once visited the island is now extinct. Other rainforest mammals that Chapman camera-trapped at this locality included *Didelphis marsupialis*, *Eira barbara*, *Nasua narica*, *Tapirus bairdii*, *Pecari tajacu*, *Dasyprocta punctata*, and *Proechimys semispinosus*.

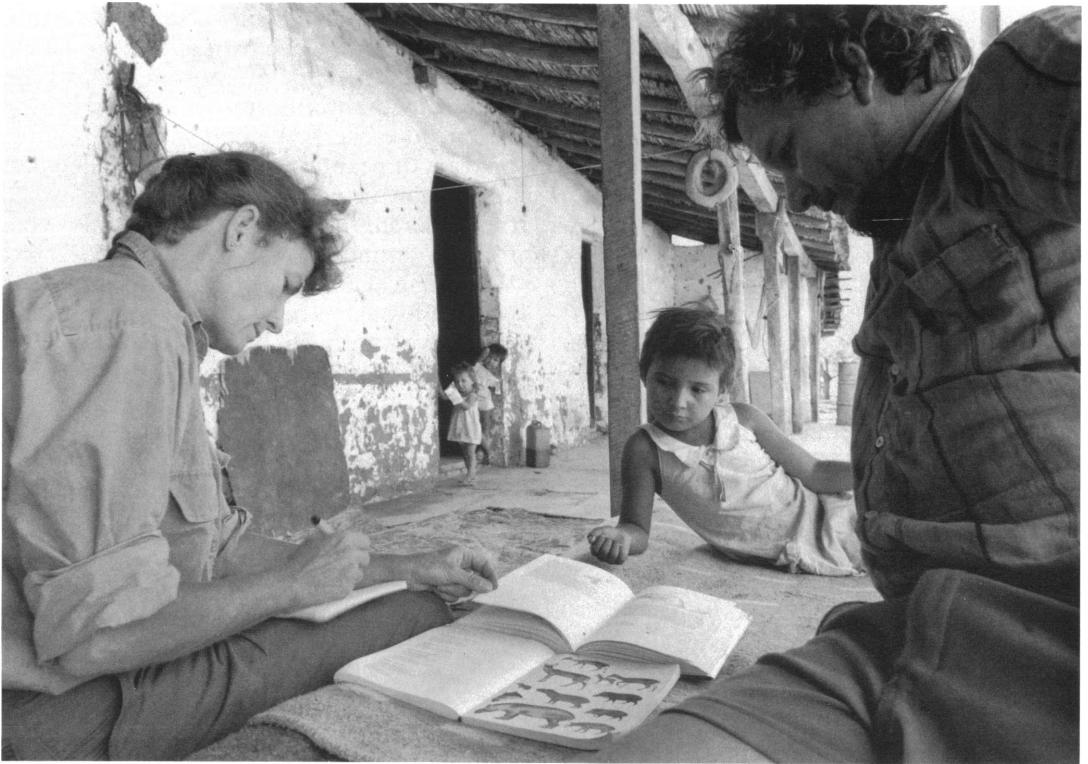


Fig. 13. Interviews are an essential source of information about large mammals easily identified by external characters (edentates, primates, carnivores, ungulates, and some large rodents). Illustrations are useful for discussing diagnostic traits with local informants (Emmons with Bolivian campesinos). Photographed by J. Maier (courtesy of JB Pictures).

the same home range all year; they are usually easy to find even where hunting has reduced local population densities. White-lipped pecararies (*Tayassu pecari*), however, form large herds that may visit local habitats only occasionally; they have been extirpated by overhunting from many regions where they once occurred. Interviews with local hunters (fig. 13) are usually a good source of accurate information about ungulate diversity, and skulls can often be found in piles of kitchen refuse around native houses. The tracks of most species are distinctive and persistent (Emmons and Feer, 1990: appendix D); the presence of tapirs, for example, is most often revealed by the deep spoor they leave in soft ground.

RODENTS AND LAGOMORPHS

SQUIRRELS: All Neotropical squirrels are diurnal and can be located by sight or sound

in the morning when they are most active. Some squirrels are habitat generalists that occur throughout the forest, whereas others prefer viny riverside vegetation or the tangled margins of treefalls. Normally solitary or in pairs, Neotropical squirrels sometimes gather in larger numbers to feed in fruiting trees, especially palms. Distinctive sounds by which squirrels can be located include vocalizations (chatters, chucks, and high-pitched whines are the usual repertoire) and loud gnawing (of hard palm nuts, generally from high exposed perches). It is sometimes possible to take squirrels in baited live traps or in unbaited Conibear traps (Model 110-2; Woodstream Corp., Lititz, PA 17543-0327) tied across frequently travelled limbs or vines, but it is easier to shoot them. Museum specimens are always required for positive identifications.

MUROIDS: Muroid rodent faunas are hard to sample exhaustively in Neotropical rainforests. Intensive trapping programs are the

standard approach, but elusive species can suddenly appear after months or years of work, so completeness is hard to document. Trapping for rainforest rodents is frequently unproductive because of ants, rain, or bright moonlight, but trap success is usually low even in the best of circumstances. Typically, less than ten percent of the traps set on a given night are successful (e.g., Guillotin, 1982; Emmons, 1984; Malcolm, 1988; Barnett and da Cunha, 1994; McClearn et al., 1994; Woodman et al., 1995), and only a few taxa usually account for most captures (fig. 14). Nevertheless, the results of rainforest rodent trapping can be significantly improved by careful attention to equipment, bait, trap placement, and trapline maintenance.

Snap traps and live traps should be used together because exclusive reliance on one kind of trap may produce a biased sample of the fauna (but see Woodman et al., 1996). Although folding Sherman live traps measuring $80 \times 90 \times 230$ mm are standard, longer models may be more effective (Slade et al., 1993). With the trigger lightly set, these traps catch both small mice (e.g., *Neacomys guianae*, with a mean weight of about 10–15 g) and large rats (e.g., *Nectomys squamipes*, to about 300 g). Sherman traps can be baited with rolled oats (a common bait for North American muroids), but oats are often carried away by ants; rolled oats also become sticky when wet, and if traps containing wet oats are not promptly washed out they become moldy and malodorous. Better baits for rainforest trapping are commercial birdseed (killed in a microwave oven to prevent dissemination of exotic weeds), coconut, plantain, or yuca (manioc), which rainforest ants do not carry away and which do not gum up wet traps. Species of *Neacomys*, *Oecomys*, *Oligoryzomys*, and *Oryzomys* readily enter baited Sherman traps, which should be disassembled and thoroughly washed (without soap) after each capture to remove feces and urine.

North American mammalogists often use Museum Specials (designed to kill *Peromyscus*), but these traps are too small to be effective in Neotropical rainforests where most muroids (and all other rodents) are larger. We prefer Victor Holdfast rat traps (Woodstream Corporation, Lititz, PA 17543-0327). Inex-

pensive, lightweight, and versatile, these traps can be set almost anywhere to take an unparalleled diversity of muroid species (including the *Neacomys*-to-*Nectomys* size range described earlier). We bait snap traps with a mixture of peanut butter, raisins, rolled oats, and bacon in 6:2:2:1 proportion by weight (but different formulae including other seeds, fruit, or animal fat may be equally effective; Woodman et al., 1996). These ingredients are passed through a meat grinder several times to ensure thorough mixing and the bait is then packed in one-pint cans for transport to the field; unopened, canned bait keeps for many months without spoiling. To prepare bait for use, a quantity of the canned mixture is scooped into a plastic bag and enough water is added to form a stiff paste (the texture is somewhat oily rather than gummy). Each bait pedal must be thoroughly cleaned of old bait and the fresh bait pressed firmly in place to ensure that it adheres well. Traps should be set to go off at the slightest touch, despite the risk of accidental release by raindrops or falling leaves.

Trap placement is important because muroids are eaten by owls and seldom forage in unprotected situations. Ideal places to set ground-level traps include: among the elevated roots of palms, cecropias, and other trees supported by stilts; beneath low-growing understory plants with large leaves (e.g., *Heliconia*, aroids, and dwarf palms); inside rotting logs; and under all kinds of dead vegetable litter (e.g., palm fronds, dead limbs, buttresses of fallen trees). Snap traps that are not tethered to roots or stems are often carried off by scavengers or by animals that are caught but not killed. A stout piece of braided cotton or nylon cord at least 80 cm long should be tied to each trap through the staple that anchors the retaining bar or through a hole drilled in the wooden platform. In addition to preventing traps from being carried off, tie-cords can be used to bind traps to lianas for elevated sets (figs. 15, 16). Victor rat traps tied to lianas are effective not only for arboreal muroids (*Rhipidomys* and *Oecomys*) but also for mouse opossums (especially *Marmosa* and *Micoureus*) and some echimyids (e.g., *Mesomys*). Even pencil-thin vines can be trapped where they intersect saplings in the understory. Liana traps sheltered by



Fig. 14. Most small rodents collected in rainforest inventories are morphologically unspecialized inhabitants of the forest floor. Species of *Oryzomys* (above, *O. macconnelli*) and *Proechimys* (below, *P. cayennensis*) typically account for the majority of rodents trapped at ground level in well-drained primary forest. Photographed by R. S. Voss (near San Ignacio Yuruaní, Edo. Bolívar, Venezuela; not to the same scale).



Fig. 15. Canopy-dwelling muroids (e.g., *Rhipidomys*) and marsupials (e.g., *Micoureus*) are seldom trapped near ground level unless traps are tied to lianas descending from the treetops, but liana traps may take weeks of daily rebaiting and maintenance to obtain results. Photographed by R. S. Voss (near San Ignacio Yuruaní, Edo. Bolívar, Venezuela).



Fig. 16. Viny tangles are ideal substrates for trapping semiarboreal muroid rodents (e.g., *Oecomys*) and small marsupials (e.g., *Marmosa*, *Marmosops*) that inhabit understory vegetation. Photographed by R. S. Voss (near San Ignacio Yuruaní, Edo. Bolívar, Venezuela).

overhanging vegetation work best. All else being equal, traps set for arboreal species should be set as high as possible, as nearly horizontal as possible, and across the anticipated path of travelling animals (e.g., on lianas that loop from one mass of vegetation to another or that descend from the canopy to the ground). Traplines should remain in place for at least a week to be maximally effective (Woodman et al., 1995), but the useful lifetime of a properly maintained rainforest trapline can be much longer. With daily rebaiting and other minor adjustments as necessary, even three-week-old lines continue to accumulate new species at some localities.

Some muroids with unusual diets or microhabitats can only be collected by special efforts. *Nectomys* and ichthyomyines, for example, usually forage in streams (fig. 17). Whereas *Nectomys* can be taken in snap traps or live traps set on the banks (especially across small runways leading from the water to dense bordering vegetation), ichthyomyines are seldom taken anywhere but in the streambed itself (Stirton, 1944; Voss, 1988). Victor rat traps or small Tomahawk live traps placed in or near shallow water under overhanging banks and baited with small freshwater crabs are probably effective sets for most lowland ichthyomyine species.

Rain and ants are major nuisances, but their impact on trapping can be minimized by scheduling. Although trapping is always easier in the dry season when traps are less often sprung and bait is seldom soaked by rain, some workers report maximal trap success in the wet season (Woodman et al., 1995). To minimize the time when bait and specimens are vulnerable to ants, traplines should be rebaited as late as possible in the afternoon and checked at dawn. Note, however, that a few rainforest muroids (e.g., some akodonts and *Melanomys*) are diurnal.

Specimens in the hand are always required for identification of rainforest muroids even to genus, and most species cannot be definitely identified without cleaned skulls. For this reason, and because trap-shy species may not be captured until more aggressive species are removed (Woodman et al., 1996), mark-and-release trapping programs are generally unsuitable for rainforest inventory work.

PORCUPINES: Neotropical porcupines (*Coendou*) are nocturnal, arboreal, and silent, habits that are doubtless responsible for their scarcity in museum collections and their absence from many faunal inventories. Porcupines have dim eyeshine and move slowly through the canopy and subcanopy. Night hunting (see Marsupials) for porcupines is often unproductive: we have sometimes spent weeks hunting every night in apparently suitable habitat before seeing any, but at other localities they are common. We know of no effective method to trap porcupines, but they can sometimes be extracted from their malodorous dens in hollow trees (Miles et al., 1981; Janzen, 1983a; Ochoa et al., 1993). Specimens are required for unambiguous identification of all South American species.

LARGE TERRESTRIAL CAVIOMORPHS: Pacas (*Agouti paca*) are nocturnal but their eyeshine is very bright and they are easily observed or collected by hunting at night. They can be encountered anywhere in the forest, but favor streamsides, old treefalls, swampy areas with dense undergrowth, and the neighborhood of fruiting trees. Superficially similar in appearance, pacaranas (*Dinomys branickii*) are rarely observed or collected and their habits are unknown. Pacas and pacaranas are sympatric in western Amazonia, and records of the latter should be documented by voucher specimens if possible (pacaranas are protected by law in some countries).

Agoutis (*Dasyprocta*) and acouchis (*Myoprocta*) are most often encountered in the early morning or late afternoon. These nervous, cursorial rodents feed on fallen seeds and fruits and are attracted to masting or fruiting trees beneath which they can be observed from blinds, shot, or live-trapped. Specimens are necessary to document specific identifications of both agoutis and acouchis in many parts of South America.

ECHIMYIDS: Terrestrial echimyids (*Proechimys* and *Hoplomys*) are among the most abundant mammals in Neotropical rainforests and can easily be caught in live traps baited with bananas, plantains, yuca (manioc), corn, peanuts, coconut, or local mast; some animals will squeeze themselves into 80 × 90 × 230 mm Sherman traps, but larger Shermans or Tomahawks are a better choice. All terrestrial echimyids are strictly noctur-



Fig. 17. Habitat of *Nectomys squamipes* and *Neusticomys venezuelae* near San Ignacio Yuruani, Edo. Bolívar, Venezuela. Rainforest streams harbor a distinctive fauna of semiaquatic mammals, which are seldom collected unless traps are specially set for them. Photographed by R. S. Voss.



Fig. 18. *Dactylomys dactylinus*, a folivorous echimyid rodent that barks from elevated perches at night, in subcanopy vegetation near Cocha Cashu, Peru. Arboreal echimyids, most of which are silent and elusive, can be found by nocturnal searching in suitable habitats, but their dim eyeshine is difficult to detect and successful hunts require intense concentration. Photographed by L. H. Emmons.

nal, but some species of *Proechimys* can be found during the day by looking in hollow logs with a light. Except in Central America, two to five species of *Proechimys* are usually sympatric and museum specimens are always required for positive identification.

Observing or collecting other rainforest echimyids, all of which are arboreal, requires a substantial commitment of time and effort. Night hunting (see Marsupials) is the most effective collecting method, but most arboreal echimyids have very dim eyeshine and finding them requires intense concentration. Species of *Dactylomys* and *Kannabateomys* can be located by their loud calls from dense clumps of bamboo or masses of tangled vines in the canopy and subcanopy (fig. 18). Other echimyids seldom vocalize, but their presence is sometimes betrayed by falling bits of gnawed rinds or husks as they forage overhead. Strenuous programs of arboreal trapping (Kierulff et al., 1991; Malcolm, 1991a)

are the only other means by which most climbing echimyid species can be collected. *Mesomys hispidus* is exceptional because it is commonly active in understory vegetation near the ground, especially in treefall gaps; it can be caught in traps set on low branches or lianas. Specimens are required for positive identification of all arboreal echimyids that lack bold external markings.

RABBITS: The single species of Neotropical rainforest rabbit (*Sylvilagus brasiliensis*) is usually observed or collected by hunting at night, but specimens have also been trapped in Tomahawks set in native gardens and baited with yuca (J. L. Patton, personal commun.).

SUMMARY

Although no combination of methods can be guaranteed to produce complete inventories of rainforest mammal faunas, the

omission or nonintensive application of any of several essential methods probably guarantees incomplete results. There are no effective substitutes for conventional trapping, diurnal and nocturnal hunting (or sight-census), and mist-netting (at ground level and in the canopy). In the hands of experienced personnel using suitable equipment, these methods alone might eventually produce complete species lists, but other techniques are more

effective for rare and elusive species (table 3). Tree-trapping (above 10 m), pitfall-trapping, interviews with local residents, and searching for bat roosts are likely to dramatically improve the efficiency of short-term inventories (i.e., projects of less than several decades) and should be standard practice. Unfortunately, no inventory project to date has used a full complement of these methods.

INVENTORY RESULTS FROM TEN LOCALITIES

Although hundreds of zoological expeditions have collected mammals in the rainforested Neotropical lowlands, large species lists are available from only a few localities. We compiled data for this review from sites where experienced personnel worked intensively for at least several person-months and preserved voucher specimens to corroborate identifications of problematic taxa (chiefly marsupials, bats, and rodents; see above). To avoid inflating estimates of sympatric diversity with allopatric species, we required collections and observations obtained from closely circumscribed areas (\leq ca. 10 km radius) within faunistically uniform landscapes (undivided by known zoogeographic barriers). Finally, we sought inventories for which local rainforest habitats have been described in the literature, in unpublished theses, or in fieldnotes, as providing a richer basis for ecological inference than species lists accompanied only by geographic information.

Ten inventories that satisfy these criteria (fig. 19, table 4) range in latitude from 10°26'N (at La Selva) to 12°33'S (at Cuzco Amazónico), and in elevation from near sea level (at Kartabo) to 370 m (at Cocha Cashu/Pakitza). Average annual temperatures are almost uniform within these geographic and altitudinal limits, but the amount and seasonality of precipitation is quite variable: La Selva, with almost 4 m of annual rainfall and no distinct dry season, is at one climatic extreme, whereas Cocha Cashu/Pakitza, with only 2 m of annual rainfall and five dry months, is at the other. Despite phenological and floristic differences described or referenced in appendices 2–11, however, vegetation at all sites

conforms to the classic physiognomy of lowland tropical rainforest (Richards, 1952).

The sampling periods over which these inventories were made range from about two calendar months (for intensive collecting expeditions at the Cunucunuma and Xingu localities) to many years (for observations by resident researchers at Barro Colorado, La Selva, Arataye, and Cocha Cashu/Pakitza).

TABLE 3
Summary of Essential Methods for Neotropical Rainforest Mammal Inventories
(See text for detailed explanations.)

Method	Target taxa
Conventional trapping ^a	Marsupials and small rodents
Tree trapping ^b	Arboreal marsupials and rodents
Pitfall trapping	Small marsupials and rodents
Diurnal hunting/census	Primates, squirrels, and other diurnal species
Nocturnal hunting/census	Nonvolant nocturnal species
Interviews	Xenarthrans, primates, carnivores, ungulates, and large rodents
Ground-level mist-netting	Understory bats
Canopy mist-netting	Molossids and other high-flying bats
Searching for roosts	Many bats, but especially small insectivorous species

^a With traps suitable for species weighing 10–500 g, placed 0–3 m above ground.

^b At least 10 m above ground, preferably higher.

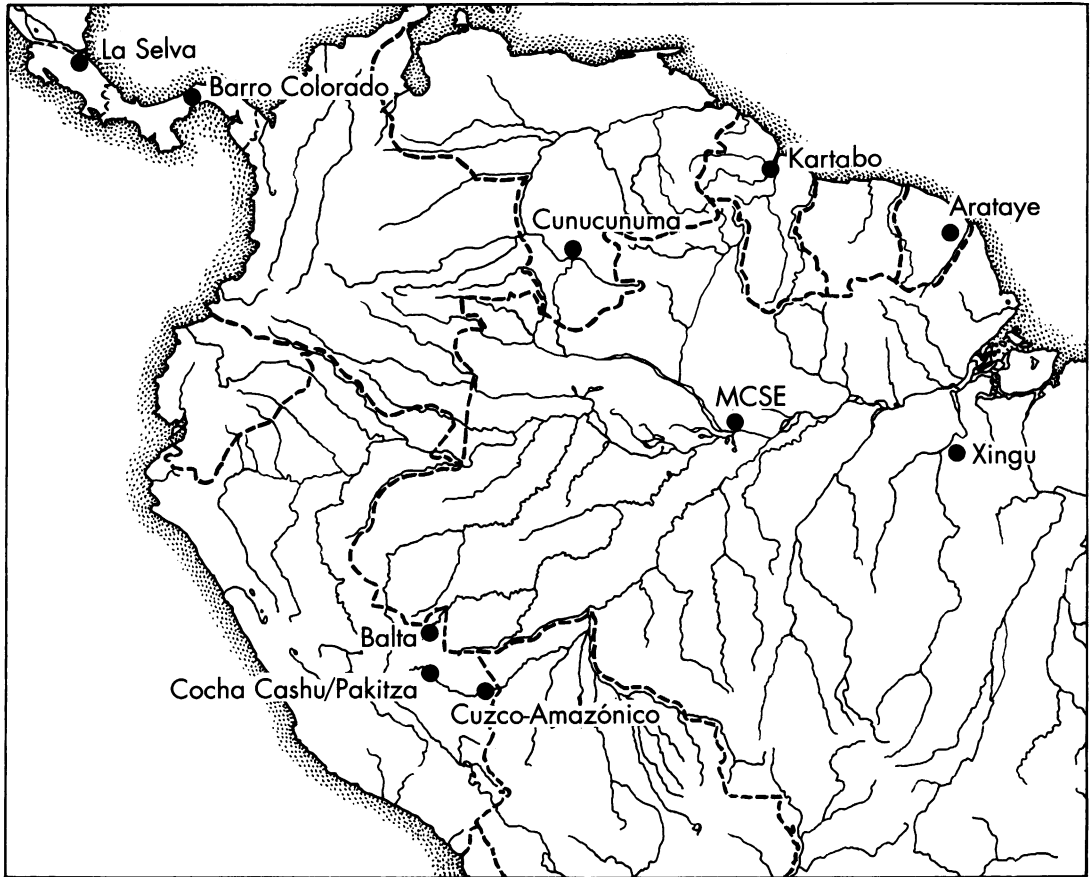


Fig. 19. Ten rainforest mammal inventory sites. See table 4 and appendices 2–11 for geographic coordinates and other information.

Unfortunately, the bat fauna at Kartabo was not sampled with mist nets and no effort was made to collect bats on the MCSE Reserves, so useful inventory data from those places are restricted to nonvolant species.

Lists of mammals collected or observed (in appendices 2–11) can be reduced to species counts for a preliminary overview (table 5). Bats are far the most speciose order at every locality where they were sampled effectively, representing 56% of the total number of mammalian species known at both of the two Central American localities and only a little less (43–54%) at South American study sites. Rodents are consistently next in ordinal diversity, but account for a highly variable fraction (26–48%) of the nonvolant species. Marsupials, xenarthrans, primates, and carnivores each represent 10% or more of the spe-

cies in some nonvolant faunas, whereas the ungulate orders and lagomorphs are usually less diverse.

Despite such broad similarities in relative ordinal diversity, differences in the actual numbers of species recorded are conspicuous and invite explanation. What factors are responsible for the unusual poverty of carnivores observed at the Xingu site, for example, or for the very diverse primate fauna at Cocha Cashu/Pakitza? Why are some localities (e.g., La Selva and Barro Colorado) apparently so rich in bats by comparison with others (e.g., Xingu and Cuzco Amazónico)? Is the observed variation in total mammalian diversity (93–139 species) among localities correlated with some variable aspect of the physical or biotic environment (e.g., precipitation, soil chemistry, primary productivity,

TABLE 4
Ten Neotropical Lowland Rainforest Localities

Locality ^a	Country	Latitude	Elevation ^b	Rainfall ^c	Sampling period ^d
La Selva	Costa Rica	10°26'N	90 m	3950 mm	34 years
Barro Colorado	Panama	9°09'N	90 m	2600 mm	71 years
Kartabo	Guyana	6°23'N	10 m	2550 mm	5 years
Arataye	French Guiana	4°03'N	125 m	ca. 2750 mm	17 years
Cunucunuma	Venezuela	3°39'N	150 m	unknown	<1 year
MCSE Reserves	Brazil	2°30'S	80 m	ca. 2200 mm	6 years
Xingu	Brazil	3°39'S	110 m	unknown	<1 year
Balta	Peru	10°08'S	300 m	unknown	3 years
Cocha Cashu/Pakitza	Peru	11°54'S	370 m	ca. 2000 mm	21 years
Cuzco Amazónico	Peru	12°33'S	200 m	2400 mm	2 years

^a Described in appendices 2–11.

^b Midpoint, rounded to nearest 10 m.

^c Annual average, rounded to nearest 50 mm. Approximations (“ca.”) are based on very limited local records or data from distant weather stations (see appendices).

^d Approximate interval over which inventory data were obtained. Expeditions made in different years are counted as years. Research stations continuously occupied by observers potentially contributing to faunal lists are attributed a sampling period equivalent to the total interval of their operation (to 1994).

habitat complexity), or does it reflect biogeographic history (e.g., isolation in Pleistocene refugia)?

For inventory results like these to sustain valid ecological or historical interpretation, the potentially confounding effects of sampling require close scrutiny. As should be clear from the preceding methodological review, Neotropical rainforest mammal communities are hard to census exhaustively. Disparate species counts obtained by local faunal surveys could therefore result from unequal

effort, from different methods, or from other variable circumstances of inventory fieldwork, rather than (or in addition to) real site-to-site differences in diversity. Several independent lines of evidence suggest that the data at hand are not free of such artifacts.

First, it is noteworthy that the three localities with the least diverse faunas (Cunucunuma, Xingu, and Cuzco Amazónico) were each sampled for two years or less, whereas four of the five most diverse localities (La Selva, Barro Colorado, Arataye, and Cocha

TABLE 5
Numbers of Mammalian Species Observed or Collected at Ten Neotropical Localities^a

	Marsupials	Xenarthrans	Bats	Primates	Carnivores	Ungulates ^b	Rodents	Lagomorphs	Totals
La Selva	5	7	65	4	14	5	16	1	117
Barro Colorado	6	6	64	4	13	5	14	1	113
Kartabo	7	9	—	6	13	5	20	0	[60] ^c
Arataye	9	8	61	7	11	5	21	0	122
Cunucunuma	8	7	50	7	7	3	11	0	93
MCSE Reserves	9	8	—	6	8	5	17	0	[53] ^c
Xingu	8	4	47	7	2	3	23	1	95
Balta	11	9	56	10	15	4	24	1	130
Cocha Cashu/Pakitza	12	7	60	13	14	5	27	1	139
Cuzco Amazónico	9	5	44	7	11	4	22	1	103

^a Described in appendices 2–11.

^b Perissodactyls and artiodactyls.

^c Nonvolant species only.

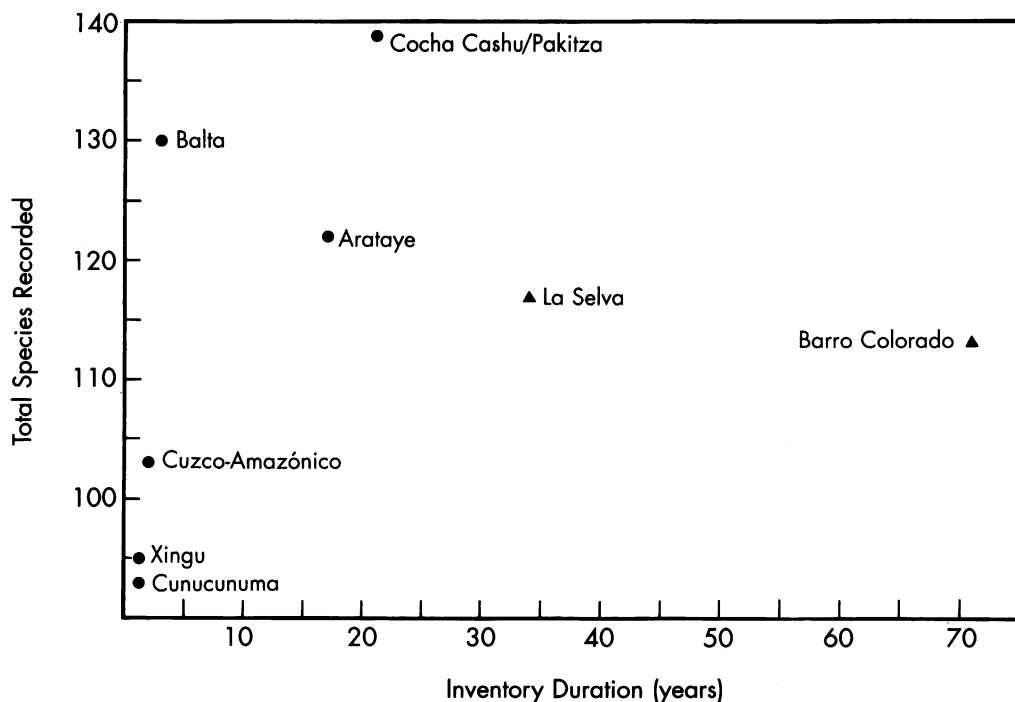


Fig. 20. Number of species recorded versus inventory duration at eight Neotropical rainforest localities; only faunal surveys that included bats are shown (see tables 4 and 5 for data). Amazonian localities are represented by dots, Central American localities by triangles.

Cashu/Pakitza) are field stations with long histories of inventory work. Although the correlation between sampling period (in years, the only coarse measure of effort available for all sites; see table 4, footnote *d*) and total number of species is not statistically significant when all eight Central American and Amazonian inventories with complete data (including bats) are analyzed together ($r = 0.24$, $df = 6$, $p = 0.56$), the two Central American points are conspicuous outliers from the central tendency among Amazonian sites (fig. 20). If the correlation between sampling period and total number of species is recalculated excluding La Selva and Barro Colorado, the coefficient is stronger, but still not statistically significant ($r = 0.76$, $df = 4$, $p = 0.08$). The principal outlier in the Amazonian data is the short-term inventory at Balta, where inventory personnel were substantially assisted by local indian hunters (appendix 9); without Balta, the correlation between sampling period and total species among Amazonian inventories is highly significant ($r = 0.97$, $df = 3$, $p < 0.01$).

Second, although species accumulation curves from the Cunucunuma, Xingu, and Balta sites (fig. 21) and from Cuzco Amazónico (Duellman and Koechlin, 1991: fig. 23) all show species discovery rates decreasing with time, none documents a convincing asymptotic value for species richness: new species were added in the last few days of each inventory. Although not strictly comparable, historical accumulations of mammal records at Barro Colorado (fig. 22) and at La Selva (Timm, 1994: fig. 18.2) likewise fail to show well-defined asymptotes. Unfortunately, no graphs of sampling results are available to assess inventory completeness at the other localities.

Third, inventory methods (insofar as known) differed among these projects, none of which employed a full complement of essential techniques (table 6). Only the Balta inventory, for example, is known to have included methodical interviews with indigenous hunters (A. L. Gardner, personal commun.); only the MCSE inventory included intensive trapping above 10 m in trees (Mal-

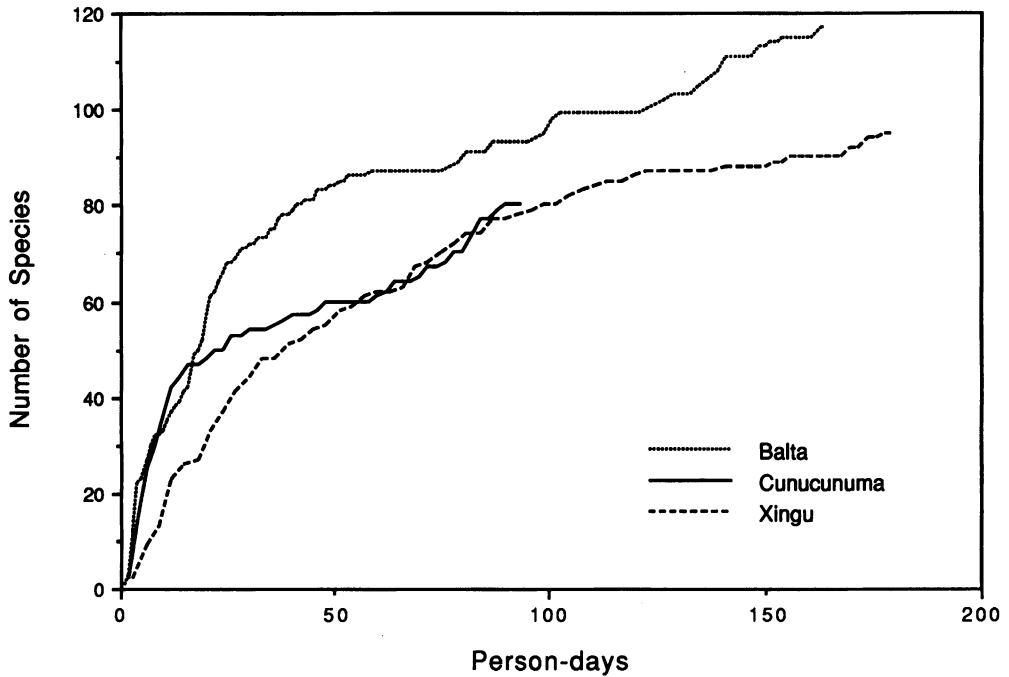


Fig. 21. Species accumulation curves reconstructed from specimen records and fieldnotes for three inventory sites. Person-days were calculated by multiplying the number of collectors by the number of productive field days (excluding dates with no mammals observed or collected). The Río Cunucunuma curve represents collecting at Culebra ("Belén") by M. D. Tuttle and F. L. Harder from 30 December 1966 to 21 February 1967, but omits two sight records for which dates are unavailable and does not include specimens purchased from Yekuanas at nearby Acanaña (see appendix 6). The Río Xingu curve represents collections and sight records by USNM personnel near their base camp (50–54 km SSW Altamira) from 13 August to 23 October 1986; collections at other sites up- and down-river are excluded (see appendix 8). The Balta curve represents collections made by A. L. Gardner and J. L. Patton from 1966 to 1971, but omits miscellaneous specimens obtained at the same locality by other researchers not continuously engaged in mammal inventory work (see appendix 9).

colm, 1991a); and only the Arataye inventory included mist-netting in canopy gaps (Brosset and Charles-Dominique, 1990). Even such widely used techniques as conventional trapping and ground-level mist-netting differed in aspects of equipment and application from site to site.

Finally, the larger fauna may not have been equally accessible to inventory personnel at all localities. Hunters are known (or may be presumed) to have visited many inventory sites prior to faunal survey work and may have extirpated or reduced local populations of some species (e.g., on the lower Río Xingu; appendix 8). By contrast, the faunas at Arataye and Cocha Cashu/Pakitza are believed to be pristine.

Thus, it seems probable that none of these

inventories is complete, and that the degree of incompleteness varies from locality to locality. Meaningful faunal comparisons cannot be based on such partial and uneven data. Ideally, fieldwork should be continued, using the full range of methods described in the preceding chapter, until asymptotic species lists are obtained at each locality, but more timely alternatives also merit consideration.

One way to compare inventories differing in completeness is to standardize them at some common level of sampling effort. Thus, at least 94 person-days of collecting were spent at each site represented in figure 21, which effort produced 93 species at Balta, 80 species on the Río Cunucunuma, and 78 species on the Río Xingu; apparently, the same exertion produced only about 60 species at Cuzco

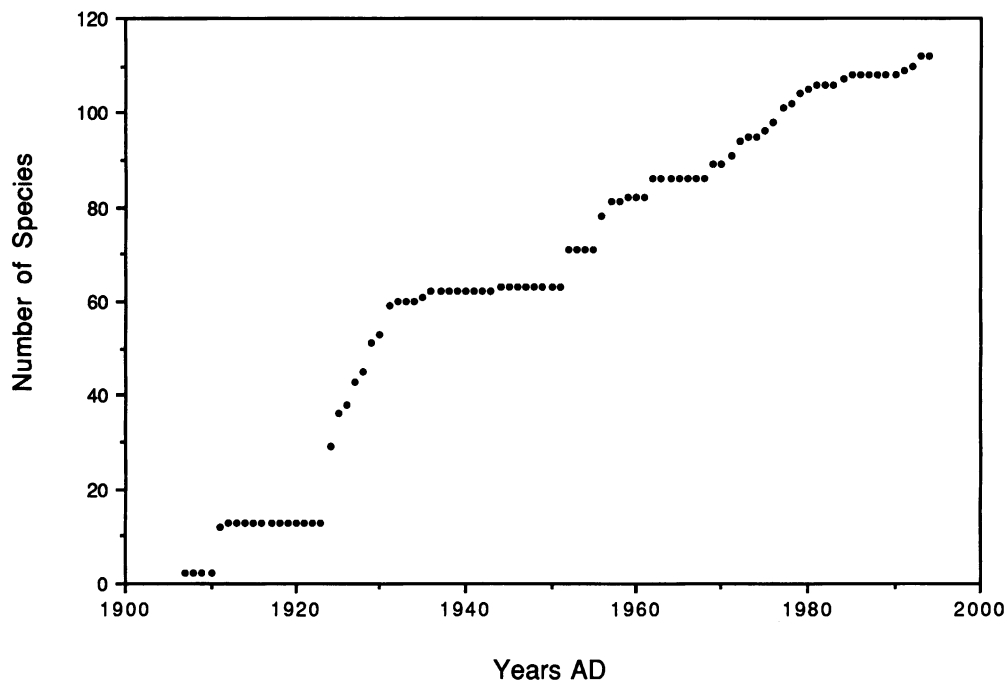


Fig. 22. Historical accumulation of species records from Barro Colorado Island and surrounding mainland localities (see appendix 3 for geographic limits). Insofar as possible, plotted dates are of actual events (collections or observations), not publications; for example, observations reported by Allee (1926) were made in 1924. Dates of first record were obtained from vouchers deposited in museum collections (AMNH, FMNH, MCZ, MSB, UMA, UMMZ, USNM), personal communications (from C. O. Handley, Jr., W. J. Smith, and R. W. Thorington, Jr.), unpublished fieldnotes (of C. B. Koford; in MVZ archives), and the literature (Allee, 1926; Chapman, 1927, 1929, 1933; Enders, 1930, 1935; Hall and Jackson, 1953; Ingles, 1953; Glanz, 1982). No definite date of first record could be determined for *Leopardus wiedii*, which is not represented in this plot.

The history of faunal sampling on or near Barro Colorado Island explains much of the obvious irregularity in species accumulation over time. The first significant collections in the area were made by E. A. Goldman from 1911 to 1912 during the Smithsonian Institution's biological survey of the Canal Zone (Goldman, 1920). Eleven years of inactivity were followed by a productive decade of observations and collections (1923–1932) after a field station was built and the island declared a biological reserve (Allee, 1926; Chapman, 1927; Enders, 1935). The first use of mist nets to collect bats on the island in 1952 (Hall and Jackson, 1953) and the residence of Carl B. Koford (1956–1957) each resulted in several new records that are conspicuous in a long interval (1933–1968) otherwise characterized by stasis. Most subsequent records (from 1969–1985) accumulated as mist nets were used with increasing frequency and expertise to study the bat fauna, but some recent discoveries (1991–1993) reflect the use of new technologies (night vision scopes and ultrasonic microphones).

Amazónico (Duellman and Koechlin, 1991: fig. 23). Although there is some suggestion of real site-to-site diversity differences in these effort-adjusted results, problems for interpretation remain.

Standardizing inventories only by effort does not take into account differences in methods (table 6), scheduling (e.g., rainy versus dry season visits), personnel (with disparate skills, energy, and experience), and

other factors (e.g., selective defaunation by local hunters) that cannot be removed by any subsequent manipulation of the data. Therefore, the large species list produced by 94 person-days of effort at Balta could owe as much to unique circumstances of fieldwork there as to high local diversity. Since most of the inventory data at hand were obtained by ad hoc collecting, meaningful standardization after the fact is essentially impossible.

TABLE 6
Sampling Methods Used at Ten Inventory Sites

Methods ^a	Inventories ^b									
	LaSe	BaCo	Kart	Arat	Cunu	MCSE	Xing	Balt	CC/P	CuAm
Conventional trapping	some	yes	?	yes	some	yes	yes	yes	yes	yes
Tree trapping	no	some	?	no	no	yes	no	no	some	no
Pitfall trapping	no	no	some	no	no	no	no	no	no	some
Diurnal hunting/census ^c	some	yes	yes	yes	some	yes	yes	yes	yes	some
Nocturnal hunting/census ^c	some	yes	?	yes	some	yes	yes	some	yes	some
Interviews ^d	no	no	no	no	no	no	no	yes	no	no
Ground-level netting	yes	yes	—	yes	yes	—	yes	yes	yes	yes
Canopy netting	no	no	—	yes	no	—	no	no	some	no
Searching for roosts	yes	some	—	yes	some	—	some	some	some	some

^a See table 3 and accompanying text for explanations.

^b See appendices 2–11 for more detailed descriptions of methods. Abbreviations: LaSe, La Selva (Costa Rica); BaCo, Barro Colorado (Panama); Kart, Kartabo (Guyana); Arat, Arataye (French Guiana); Cunu, Cunucunuma (Venezuela); MCSE, MCSE Reserves (Brazil); Xing, Rio Xingu (Brazil); Balt, Balta (Peru); CC/P, Cocha Cashu/Pakitzta (Peru); CuAm, Cuzco Amazónico (Peru).

^c Haphazard observations by personnel primarily engaged in other activities are recorded as "some."

^d Explicitly cited as a source of unvouchered records.

Another way to compare incomplete inventories is to estimate species richness by extrapolation. Of the several methods available (usefully reviewed by Colwell and Coddington, 1994), extrapolating species accumulation curves requires the simplest data and minimal assumptions. Only the presence or absence of new species for each collecting day (the only sampling unit available for analysis in our data) need be recorded, but each day's collections must be assumed to represent an unbiased sample from the same underlying pool of species throughout the temporal course and spatial extent of the inventory. Unfortunately, ad hoc collecting in rainforests is unlikely to obtain unbiased daily samples from the same pool of mammalian species for many reasons, among which the most obvious are the following: (1) personnel devoted to one activity (bat-netting, for example) on a given date cannot be simultaneously engaged with equal efficiency in others (e.g., nocturnal hunting for arboreal marsupials and rodents); (2) most (possibly all) species are unevenly distributed among rainforest habitats (understory, canopy, treefalls, river banks, etc.) and are therefore not equally accessible to collectors who cannot effectively sample all habitats on a daily schedule; and (3) seasonal and year-to-year differences in juvenile recruitment, mortality, habitat use, and other demographic phenomena (abun-

dantly documented in the literature: e.g., by Enders, 1935; Fleming, 1971; Atramentowicz, 1986; Peres, 1993) will inevitably produce many temporal patterns of collecting bias.

Because other methods for estimating species richness by extrapolation require unavailable data or inappropriate assumptions,⁴ we are forced to conclude that mean-

⁴ Methods for estimating species richness that fit parametric models of relative abundance to sampling results (e.g., the negative binomial, lognormal, and log-series distributions; see Pielou, 1975; Magurran, 1988; Colwell and Coddington, 1994) require more-or-less accurate counts of individuals for each species captured or observed. However, common species are often discarded or ignored in faunal surveys after sufficient series for taxonomic study have been preserved, so specimen counts in most of the collections at hand probably underestimate the relative abundance of *Didelphis*, *Carollia*, *Proechimys*, and other abundant or easily collected taxa. Some nonparametric estimators (reviewed by Colwell and Coddington, 1994) only require frequency data for the rarest species, but locally common mammals may be rare as specimens because they are difficult to preserve (e.g., armadillos, porcupines) and/or taxonomically uninteresting (most ungulates), so most collections are unlikely to provide meaningful frequency data for any range of abundance classes. Other methods for estimating diversity (reviewed by Hammond, 1994) use taxonomic ratios in well-known reference faunas to estimate species richness at localities where only one or a few taxa have been adequately surveyed. The requisite assumption, that taxon ratios remain approximately constant, is obviously inappropriate for this preliminary review.

ingful comparisons of these inventories are impossible without a major investment in additional fieldwork at each site. In the meantime, the only alternative for assessing Neotropical rainforest mammal diversity is indirect estimation based on geographic range data. The following section synthesizes information from published and unpublished sources to develop preliminary hypotheses

about the magnitude and geographic distribution of diversity for different groups of rainforest mammals. Hypotheses are not a substitute for fieldwork, but they are essential for planning geographically and taxonomically focussed sampling that is likely to be far more productive than the haphazard accumulation of incomplete data hitherto available for analysis.

INFERENCES FROM GEOGRAPHIC RANGE DATA

If every species were uniformly distributed within accurately known geographic limits, local diversity could be assessed simply by listing all those taxa whose mapped ranges in authoritative monographs overlap the site of interest. Unfortunately, nonuniform distributions, taxonomic problems, and sparse geographic sampling complicate the interpretation of range data for most (if not all) faunal studies. Valid inferences about mammalian diversity in Neotropical rainforests require careful evaluation of these and other problems with the range data at hand.

Animals may not occur everywhere within their known geographic limits if they are restricted to special habitats, if they are excluded from local communities by competitors or predators, if crucial resources are locally absent, or if they are patchily distributed for historical reasons. When these are common phenomena, geographic expectations (predictions based on range maps) will tend to overestimate local diversity. Although diversity predictions informed by natural history data and knowledge of local habitats are presumably more accurate than inferences from range maps alone, the ecological requirements of many Neotropical rainforest mammals are unknown.

Taxonomic problems can bias geographic expectations in the opposite direction, that is, to underestimate local diversity. Many Neotropical rainforest mammals originally described as distinct species in the late 19th and early 20th centuries were subsequently swept into synonymy by taxonomists who did not appreciate the subtle characters by which reproductively isolated congeners may differ. As a consequence, current species concepts and range data in standard references

may conceal some sympatric diversity, especially for genera lacking modern revisions (relevant examples are listed in appendix 1). Correcting for this source of bias requires familiarity with the taxonomic literature of problematic groups and an awareness of current research results.

Sparse sampling of geographic distributions can also bias map-based diversity predictions. Because estimated range size increases with collection frequency (Colwell and Hurtt, 1994), very rare (or elusive) species usually have larger distributions than available specimen records suggest. Mammal lists predicted from range overlap are therefore prone to underestimate local diversity for higher taxa with many rare (or undescribed) species, especially within regions that themselves remain poorly sampled. Amazonian marsupial, bat, and rodent faunas are clearly problematic in this respect.

Finally, locality records for all but the commonest species are usually clustered around major population centers (e.g., Belém, Manaus, Iquitos), along roads and navigable rivers, and in areas long accessible to North American and European zoologists (e.g., Central America and the Guianas). Although this is a general problem for distributional analyses of rainforest organisms (Heyer, 1988; Nelson et al., 1990; Oren and Albuquerque, 1991), uneven geographic sampling is exacerbated by behavioral and morphological traits that make many rainforest mammals especially hard to collect (e.g., nocturnality, arboreality, lack of audible vocalizations, lack of conspicuous coloration, small body size). Extrapolating from known specimen records to probable distributions at any geographic scale is therefore a matter of judgement based

on natural history information and known historical patterns of collecting bias.

For all the reasons mentioned above, a discursive taxon-by-taxon evaluation is the only effective way to extract meaningful diversity estimates from the incomplete and heterogeneous range data available for Neotropical rainforest mammals. In the absence of reliable published maps for many species, we extensively consulted museum collections, manuscript revisions, and unpublished geographic records compiled by taxonomic specialists (see Acknowledgments); evidence for significant revisions of ranges mapped in standard references (e.g., Mammalian Species accounts; Hall, 1981; Emmons and Feer, 1990) is cited where appropriate below (also see footnotes to table 1). Whenever possible, we compare geographic expectations with inventory results to assess discrepancies between expected and observed diversity; such comparisons afford considerable scope for interpretation in terms of sampling artifacts and the ecological or anthropological circumstances of inventory fieldwork.

This review of the geographic evidence is necessarily limited to Amazonia and Central America, from which areas large collections and an extensive literature are available for analysis. Mammalian diversity in the trans-Andean rainforests of northwestern South America, in the Venezuelan coastal rainforests, and in the Atlantic rainforests of southeastern Brazil cannot be comparably evaluated because collections from those biomes are generally inadequate and the relevant literature sparse (see Discussion). Extending this preliminary assessment to other Neotropical rainforest regions should be a priority for future researchers with access to appropriate collection resources and a more comprehensive literature.

MARSUPIALS

AMAZONIA: The marsupial genera *Caluromys*, *Didelphis*, *Marmosa*, *Marmosops*, *Metachirus*, *Micoureus*, *Monodelphis*, and *Philander* are widespread, eurytopic, and probably ubiquitous in Amazonian rainforests despite the lack of records from some areas that remain poorly collected. Although

Chironectes is also widely distributed,⁵ water opossums may be absent from some central Amazonian stream systems inhabited by the voracious caiman *Paleosuchus trigonatus* (W. E. Magnusson, in litt.).

Whereas *Chironectes* and *Metachirus* are monotypic, sympatric congeners of *Caluromys*, *Didelphis*, *Marmosops*, *Micoureus*, *Monodelphis*, and *Philander* have been reported at least occasionally from Amazonian rainforests: (1) *Caluromys lanatus* and *C. philander* are sympatric in some parts of the Guiana region (Handley, 1976; Malcolm, 1990; Emmons, 1993b), but elsewhere in Amazonia these species are apparently allopatric. (2) *Didelphis marsupialis* and *D. imperfecta*⁶ occur sympatrically in southern Venezuela (Handley, 1976), in the Guianas (Julien-Laferrrière, 1991; M. D. Engstrom, personal commun.), and perhaps in adjacent parts of northernmost Brazil, but *D. marsupialis* apparently occurs allopatrically throughout the rest of Amazonia. (3) Two species of *Marmosa* are apparently sympatric in northern Surinam (where *M. murina* and *M. lepida* have been taken at adjacent localities; Husson, 1978) and three may be sympatric in western Amazonia (where the ranges of *M. murina*, *M. lepida*, and *M. rubra* overlap), but only *M. murina* is known to occur in southeastern Amazonia and most of the Guiana subregion. (4) Two or three species of *Marmosops* are probably sympatric throughout western Amazonia (where the ranges of *M. noctivagus*, *M. impavidus*, *M. parvidens*, and perhaps other species overlap; Musturangi, 1995), and two may occur sympatrically in parts of southeastern Amazonia (if the ranges of *M. noctivagus* and *M. par-*

⁵ Published range maps for *Chironectes minimus* (Marshall, 1978; Emmons and Feer, 1990) show no records between disjunct populations along the Andean piedmont, the Guianan coastal watershed, and the lower Tocantins, but recent collections from southern Venezuela (Pérez-Hernández et al., 1994) and one from the lower Tapajós (George et al., 1988) suggest that much of this enormous geographic hiatus is an artifact of inadequate sampling.

⁶ *Didelphis imperfecta* appears to be the correct name (M. D. Engstrom, personal commun.) for the animal identified as *Didelphis* "sp. A" by Handley (1976) and as *Didelphis "albiventris"* by Julien-Laferrrière (1991).

videns overlap west of the Tapajós), but only *M. parvidens* is known from lowland Guianan habitats. (5) Two species of *Micoureus* are known to occur sympatrically at several widely separated sites in western Amazonia (Hutterer et al., 1995; J. L. Patton, in litt.), but elsewhere the genus is apparently represented by allopatric species. (6) *Monodelphis breviceaudata* and *M. emiliae* have been taken sympatrically at several rainforested localities south of the Amazon spanning almost the entire longitudinal extent of the basin from headwaters to delta, and three species could be expected in southwestern Peru (where *M. adusta* has also been reported from the lowlands; Woodman et al., 1991), but only *M. breviceaudata* apparently occurs in Guianan rainforests. (7) Two species of *Philander* occur sympatrically in parts of eastern Peru and western Brazil south of the Amazon (appendix 9; Fleck and Harder, 1995; Hutterer et al., 1995; J. L. Patton, in litt.), but elsewhere the genus is only represented by allopatric forms.

The geographic limits of other Amazonian marsupial genera are poorly documented. Collections of *Gracilinanus* mapped by Hershkovitz (1992) include few Amazonian localities, but a specimen of *G. emiliae* from Surinam (Husson, 1978; not cited by Hershkovitz) and recently identified material from Pakitza (appendix 10) and Balta (appendix 9) suggest that these diminutive opossums are widespread in the region. The monotypic genera *Caluromysiops* and *Glironia* are each known from fewer than a dozen specimens collected at widely scattered localities in western Amazonia, but *Caluromysiops* is also known from a marginal southeastern Amazonian record (Vivo and Gomès, 1989) and *Glironia* from a marginal Guianan locality (Silva and Langguth, 1989).

Marsupial faunas throughout Amazonia therefore probably consist of at least eight sympatric species (one each of the ubiquitous genera identified above), a very conservative estimate that might not be exceeded in some parts of the Guiana subregion (e.g., near Manaus, where *Chironectes* is unknown and only one species of *Didelphis* occurs). Most Amazonian rainforests, however, probably have more species; overlapping geographic ranges suggest that 14–17 might occur sympatrically

throughout much of western Amazonia. Twelve species (at Cocha Cashu/Pakitza, appendix 10), however, is the maximum diversity yet documented anywhere in the region.

CENTRAL AMERICA: *Caluromys*, *Chironectes*, *Didelphis*, *Marmosa*, *Metachirus*, and *Philander* are probably ubiquitous in the rainforested lowlands from southern Mexico to Panama.⁷ *Chironectes* and *Metachirus* are monotypic, only a single species each of *Caluromys* and *Philander* occur in the region, and no Central American rainforest locality is definitely known to have more than a single species of *Marmosa*, but two species of *Didelphis* occur sympatrically from southern Mexico to Nicaragua (Gardner, 1973; Coates-Estrada and Estrada, 1986; March and Aranda, 1992).

Members of other Central American marsupial genera have more restricted distributions: (1) *Micoureus alstoni* is known from Costa Rica to Belize and another congener⁸ occurs in Panama from the Colombian frontier to Bocas del Toro; both are infrequently collected. (2) *Marmosops invicta* occurs below 1000 m elevation in Panama, but perhaps only in submontane forests (Handley, 1966). (3) *Monodelphis adusta* has only been collected in extreme eastern Panama, where a species of *Gracilinanus* probably occurs as well (a specimen resembling *G. agilis* was reported from a locality near the Panamanian border in northwestern Colombia by Hershkovitz, 1992).

Marsupial diversity in Central American rainforests is therefore likely to range from an expected minimum of seven species in southern Mexico to an expected maximum of ten in eastern Panama. The most diverse Central American marsupial fauna yet documented by inventory results, however, is only eight species (USNM specimens from Tacarcuna Village, Provincia Darién, Panama).

⁷ *Metachirus*, previously known only as far north as Nicaragua (Hall, 1981; Emmons and Feer, 1990), was recently reported from Chiapas, Mexico (Medellín et al., 1992).

⁸ Resembling *M. phaea* according to Handley (1966 and personal commun.). This taxon is currently considered a junior synonym of *M. regina* (Wilson and Reeder, 1993) but may be distinct.

XENARTHTRANS

AMAZONIA: At least nine species of xenarthrans are probably present everywhere in Amazonia, consisting of one species each of *Bradypus*, *Choloepus*, *Cabassous*, *Priodontes*, *Cyclopes*, *Myrmecophaga*, and *Tamandua*, and two species of *Dasypus*.⁹ Although this expected diversity has only been documented by inventory results from Kartabo (appendix 4), Balta (appendix 9), Panguana (Hutterer et al., 1995), and the lower Tocantins (Mascarenhas and Puerto, 1988), some taxa are always rare (e.g., *Priodontes*, *Myrmecophaga*) and others are elusive (*Cabassous*, *Cyclopes*), so xenarthran inventories are hard to complete. Slightly higher counts might be anticipated in western Amazonia, where *Choloepus didactylus* and *C. hoffmanni* both occur (but perhaps not sympatrically), and along both banks of the lower Amazon, where the ranges of *Bradypus tridactylus* and *B. variegatus* overlap (Wetzel and Avila-Pires, 1980).

CENTRAL AMERICA: The genera *Bradypus*, *Choloepus*, *Cabassous*, *Dasypus*, *Cyclopes*, *Myrmecophaga*, and *Tamandua* are (or were historically) each represented by a single species in eastern Central America, but xenarthran diversity decreases with distance from the Colombian frontier: the range of *Choloepus* extends just to Nicaragua, that of *Bradypus* to Honduras, and that of *Myrmecophaga* (historically at least) to Belize (Hall, 1981). Thus, only four species (*Cyclopes didactylus*, *Tamandua mexicana*, *Dasypus novemcinctus*, and *Cabassous centralis*) are known to occur in Mexican rainforests.¹⁰ The maximum expected xenarthran diversity in Central American rainforest faunas (seven species) has been documented by inventory results only at La Selva (appendix 2).

⁹ *Dasypus kappleri* and *D. novemcinctus*. Two additional armadillos known from scattered Amazonian collections, *Dasypus septemcinctus* and *Euphractus sexcinctus*, are probably restricted to enclaves of savanna vegetation (Wetzel and Mondolfi, 1979; Wetzel, 1982; Redford and Wetzel, 1985); neither has been definitely recorded from undisturbed rainforest far from open vegetation.

¹⁰ Recent observations and collections from Guatemala and Chiapas (Cuarón et al., 1989) significantly extend the known range of *Cabassous centralis* beyond the northern limits mapped by Hall (1981).

BATS

AMAZONIA: Mist nets have been widely used to collect bats for just a few decades, and Amazonian bat distributions are therefore still very incompletely documented. Nevertheless, even the sparse range data currently available suggest that between 90 and 110 sympatric species could be expected throughout the region.¹¹ At least 69 species are widespread and possibly ubiquitous (table 7), so only a minor fraction of any Amazonian bat inventory is likely to reflect local ecological conditions or subregional faunal differences. Because some bats seldom (or never) roost in tree cavities and foliage, bat diversity is probably highest in the vicinity of rocky outcrops and caves, which are seldom encountered in the floodplain landscapes of central Amazonia. A distinctive "paramontane" fauna (Koopman, 1984) may contribute an additional increment to local diversity near the base of the Andes.

Available species counts of bats from Amazonian faunal surveys (table 8) are considerably less than those expected from geographic range data. Although some inventory projects have reported stenoderminine diversities that approach geographic expectations (e.g., 19–21 species at Jenaro Herrera, Balta, and Cocha Cashu/Pakitza), most other bat taxa are conspicuously underrepresented in these data. Whereas most Amazonian localities should have 10–12 species of emballonurids, 20–22 species of phyllostomines, 6–8 species of glossophagines, 7 or 8 species of vespertilionids, and 10–12 species of molossids, such numbers are rare in pub-

¹¹ We arrived at this estimate by counting the number of rainforest bats expected at ten Amazonian localities: the eight inventory sites described in appendices 4–11 plus Belém and Iquitos. These localities span virtually the entire length and breadth of the hylaea and appear representative of the range of ecological conditions and zoogeographic gradients likely to affect bat diversity in the region. Our counts are conservative because they exclude cave-roosting taxa (e.g., *Lonchorhina* spp., except at localities adjacent to large rock formations) and species of uncertain ecological provenance whose collection localities are clustered near enclaves of nonforest vegetation (e.g., *Eumops bonariensis*). Additionally, many Amazonian bats probably have larger distributions than suggested by available locality records, so lists of expected species based on range overlap may underestimate local diversity.

TABLE 7
Widespread Species of Amazonian Bats^a

Emballonuridae
<i>Cormura brevirostris</i>
<i>Peropteryx leucoptera</i>
<i>Peropteryx macrotis</i>
<i>Rhynchonycteris naso</i>
<i>Saccopteryx bilineata</i>
<i>Saccopteryx canescens</i>
<i>Saccopteryx leptura</i>
Noctilionidae
<i>Noctilio albiventris</i>
<i>Noctilio leporinus</i>
Mormoopidae
<i>Pteronotus parnellii</i>
Phyllostominae
<i>Chrotopterus auritus</i>
<i>Macrophyllum macrophyllum</i>
<i>Micronycteris megalotis</i>
<i>Micronycteris minuta</i>
<i>Micronycteris nicefori</i>
<i>Mimon crenulatum</i>
<i>Phylloderma stenops</i>
<i>Phyllostomus discolor</i>
<i>Phyllostomus elongatus</i>
<i>Phyllostomus hastatus</i>
<i>Tonatia brasiliensis</i>
<i>Tonatia carrikeri</i>
<i>Tonatia saurophila</i>
<i>Tonatia silvicola</i>
<i>Trachops cirrhosus</i>
<i>Vampyrus spectrum</i>
Glossophaginae
<i>Anoura caudifera</i>
<i>Choeroniscus minor</i>
<i>Glossophaga soricina</i>
<i>Lichonycteris obscura</i>
<i>Lionycteris spurrelli</i>
<i>Lonchophylla thomasi</i>
Carollinae
<i>Carollia brevicauda</i>
<i>Carollia perspicillata</i>
<i>Rhinophylla pumilio</i>
Stenodermatinae
<i>Artibeus (Artibeus) jamaicensis</i>
<i>Artibeus (A.) lituratus</i>
<i>Artibeus (A.) obscurus</i>
<i>Artibeus (Dermanura) gnomus</i>
<i>Artibeus (Koopmania) concolor</i>
<i>Chiroderma trinitatum</i>
<i>Chiroderma villosus</i>
<i>Mesophylla macconnelli</i>
<i>Platyrrhinus helleri</i>

TABLE 7—(Continued)

<i>Sturnira lilium</i>
<i>Sturnira tildae</i>
<i>Uroderma bilobatum</i>
<i>Uroderma magnirostrum</i>
<i>Vampyressa bidens</i>
<i>Vampyrodes caraccioli</i>
Desmodontinae
<i>Desmodus rotundus</i>
<i>Diaemus youngi</i>
Furipteridae
<i>Furipterus horrens</i>
Thyropteridae
<i>Thyroptera discifera</i>
<i>Thyroptera tricolor</i>
Vespertilionidae
<i>Eptesicus furinalis</i>
<i>Lasiurus blossevillii</i>
<i>Lasiurus ega</i>
<i>Myotis albescentis</i>
<i>Myotis nigricans</i>
<i>Myotis riparius</i>
Molossidae
<i>Eumops auripendulus</i>
<i>Eumops hansae</i>
<i>Eumops perotis</i>
<i>Molossops abrasus</i>
<i>Molossops planirostris</i>
<i>Molossus ater</i>
<i>Molossus molossus</i>
<i>Nyctinomops laticaudatus</i>

^a Species that could be expected to occur in rainforests throughout Amazonia. At least 12 additional species represented by scattered Amazonian records might eventually prove to be equally widespread: *Centronycteris maximiliani*, *Dididurus albus*, *D. scutatus*, *Peropteryx kappleri*, *Micronycteris brachyotis*, *M. daviesi*, *M. hirsuta*, *M. microtis*, *M. schmidtorum*, *M. sylvestris*, *Pro-mops centralis*, and *P. nasutus*.

lished inventory results. Conceivably, local communities of sympatric bats may be assembled from larger source faunas according to unknown ecological rules, but sampling inadequacy provides a more compelling explanation: the greatest discrepancies between geographic expectations and inventory results are for insectivorous taxa that are notoriously difficult to capture in mist nets.

At least seven species of emballonurids in four genera are widespread and possibly

TABLE 8
Taxonomic Distribution of Bat Diversity at 11 Lowland Rainforest Localities
(Table entries are numbers of species present.)

	Bat families and subfamilies ^a													Total species
	Phyllostomidae													
	Emb	Noc	Mor	Phy	Glo	Car	Ste	Des	Nat	Fur	Thy	Ves	Mol	
CENTRAL AMERICA														
Chajul ^b	3	1	2	13	2	2	11	3	1	0	1	8	3	50
La Selva ^c	8	2	2	19	6	3	13	1	0	1	1	7	2	65
Barro Colorado ^d	7	2	2	16	3	3	16	1	0	0	2	6	6	64
AMAZONIA														
St. Elie ^e	6	0	0	17	5	2	15	1	0	1	1	4	2	54
Arataye ^f	5	0	1	18	6	3	18	1	0	0	1	2	6	61
Cunucunuma ^g	5	1	1	10	4	3	17	1	0	1	1	3	3	50
Xingu ^h	5	1	1	13	4	3	14	2	0	1	0	2	1	47
Jenaro Herrera ⁱ	5	1	0	15	5	5	19	1	0	1	1	5	4	62
Balta ^j	3	1	0	11	5	4	19	1	0	0	1	8	3	56
Cocha Cashu/Pakitza ^k	3	2	0	14	5	4	21	2	0	1	1	5	2	60
Cuzco Amazónico ^l	4	1	0	9	3	4	15	1	0	0	1	5	1	44

^a Abbreviations: Emb, Emballonuridae; Noc, Noctilionidae; Mor, Mormoopidae; Phy, Phyllostominae; Glo, Glossophaginae; Car, Carollinae; Ste, Stenodermatinae; Des, Desmodontinae; Nat, Natalidae; Fur, Furipteridae; Thy, Thyropteridae; Ves, Vespertilionidae; Mol, Molossidae.

^b Medellín (1993). Chajul (16°06'N, 90°57'W; 150 m elevation) is a research station in the Lacandon rainforest of Chiapas, Mexico.

^c Appendix 2.

^d Appendix 3.

^e Brosset and Charles-Dominique (1990); Masson and Cosson (1992). St. Elie (5°18'N, 53°04'W; near sea level) is a field station in the coastal rainforest of French Guiana. Species collected at Petit Saut (30 km to the SE) are not included in these counts.

^f Appendix 5.

^g Appendix 6.

^h Appendix 8.

ⁱ Ascorra et al. (1993). Jenaro Herrera (4°55'S, 73°45'W; 150 m elevation) is a field station about 140 km SSW of Iquitos, Peru.

^j Appendix 9.

^k Appendix 10.

^l Appendix 11.

ubiquitous in Amazonian rainforests (table 7); species of a fifth genus, *Diclidurus*, are seldom collected, but at least one is probably also present in every local fauna. *Centronycteris*, *Cormura*, *Cyttarops*, and *Rhynchonycteris* are monotypic, but three species each of *Peropteryx* and *Saccopteryx* are often sympatric and as many as four species of *Diclidurus* can occur together. Although the highest documented local diversity of emballonurids in Amazonia is 11 species,¹² as many

as 14 could be expected at some localities.

Noctilionids and mormoopids are minor components of Amazonian bat diversity. Both known species of noctilionids are sympatric throughout the region, but *Pteronotus parnellii* is the only mormoopid that may be

were obtained within a 30 km radius (op. cit.: p. 83) that included savanna vegetation as well as rainforest. Findley (1993: table 4.9) erroneously counted 78 species from San Juan in Handley's report by omitting *Carollia brevicauda* and including seven names ("*Saccopteryx* sp.," "*Glossophaga* sp.," "*Carollia* sp.," "*Chiroderma* sp.," "*Sturnira* sp.," "*Uroderma* sp.," and "*Molossus* sp.") used for incompletely identified material lost or discarded by SVP collectors.

¹² At San Juan Manapiare, an important collecting site of the Smithsonian Venezuelan Project (SVP). Handley (1976) listed 72 species of bats from San Juan, but these

ubiquitous (other *Pteronotus* species are possibly restricted to the vicinity of caves). Only a few examples of sympatry among Amazonian mormoopids have been reported: Ochoa et al. (1988) encountered *Pteronotus davyi*, *P. parnellii*, and *P. personatus* in the Serranía de los Pijiguaos of Amazonian Venezuela; Marques (1985) collected *P. parnellii* and *P. personatus* on the lower Rio Tapajós; and Emmons (1993b) reported *P. gymnotus* and *P. parnellii* from the western Kanuku Mountains of Guyana.

Phyllostomines are very speciose in all Neotropical rainforests. At least 16 species are widespread and possibly ubiquitous in Amazonia (table 7) and up to 25 could occur at some localities. To date, however, the maximum documented diversity of sympatric phyllostomines is only 18 species (at Arataye, appendix 5). Five phyllostomine genera (*Chrotopterus*, *Macrophyllum*, *Phyllostoma*, *Trachops*, *Vampyrus*) are monotypic, and congeners of another (*Lonchorhina*) are apparently never sympatric, but three genera (*Micronycteris*, *Phyllostomus*, *Tonatia*) are consistently more speciose in well-sampled local faunas. Seven species of *Micronycteris* were collected near San Juan Manapiare (Handley, 1976) and five are known from sympatry at St. Elie (Brosset and Charles-Dominique, 1990) and the Serranía de los Pijiguaos (Ochoa et al., 1988), but at least nine could be expected throughout much of the region (N. B. Simmons, personal commun.). Three species of *Phyllostomus* and four of *Tonatia* are probably ubiquitous (table 7) and an additional species of each genus could be expected at some localities.

Glossophagines form a small but characteristic component of Neotropical rainforest bat communities. At least six species in as many genera are widespread and possibly ubiquitous in Amazonia (table 7). Three genera (*Lichonycteris*, *Lionycteris*, *Scleronycteris*) are monotypic, but *Anoura*, *Choeroniscus*, *Glossophaga*, and *Lonchophylla* are represented by sympatric congeners at various Amazonian collection localities. The maximum known sympatric diversity of Amazonian glossophagines is six species (at Arataye, appendix 5), but eight or nine could be expected throughout much of western Amazonia.

Carollinae are easy to catch with ground-level mist nets, and most inventory projects probably obtain complete lists of local species. *Carollia perspicillata* and *Rhinophylla pumilio* are widespread and probably ubiquitous in the region. *Carollia brevicauda* is also widespread, but this species is apparently absent at two localities with intensively sampled understory bat faunas: St. Elie (Brosset and Charles-Dominique, 1990) and the lower Rio Xingu (appendix 8). Carollinae are most speciose in western Amazonia, where the greatest known sympatric diversity—five species (Patton et al., 1982; Webster and Jones, 1984; Ascorra et al., 1993)—corresponds to the expected maximum.

Stenodermatines are very speciose in all Neotropical rainforests. Ten genera occur in Amazonia (table 1), where 15 species are widespread and possibly ubiquitous (table 7). Although overlapping geographic ranges suggest that 20 or more stenodermatine species could be expected throughout much of the region, such numbers have seldom been documented by inventory results (table 8). Sympatric congeners of Amazonian stenodermatines are the rule rather than the exception; only *Ametrida*, *Mesophylla*, *Sphaeronycteris*, and *Vampyrodes* are monotypic. Three species of giant *Artibeus* (subgenus *Artibeus*: *jamaicensis*, *lituratus*, and *obscurus*) are apparently ubiquitous in the region and a fourth (*A. amplus*) occurs sympatrically in Guyana and southern Venezuela (e.g., on the Río Cunucunuma, appendix 6). At least two species of dwarf *Artibeus* (subgenus *Dermanura*) are probably present in local faunas throughout the region, and three or four can occur sympatrically in western Amazonia (e.g., at Cocha Cashu/Pakitza, appendix 10). Two species each of *Chiroderma*, *Sturnira*, and *Uroderma* are widespread (table 7), but three species each of *Chiroderma* and *Sturnira* could be expected near the base of the Andes. At least one species each of *Platyrrhinus* and *Vampyressa* are widespread, but as many as three *Platyrrhinus* and four *Vampyressa* are known from some local faunas.

Vampires (Desmodontinae) are not abundant in undisturbed rainforest, where many inventory projects collect only *Desmodus rotundus*. Overlapping geographic ranges suggest that all three living species could occur

at many localities but, to the best of our knowledge, *Diaemus youngi* and *Diphylla ecaudata* have only been collected sympatrically at a single Amazonian locality (Panguana Biological Station, Peru; Hutterer et al., 1995).

Natalids, furipterids, and thyropterids are inconspicuous elements of Amazonian bat faunas. Natalids (*Natalus stramineus* and *N. tumidirostris* both occur in the region but perhaps not sympatrically) are probably restricted to the vicinity of caves. The single known species of rainforest furipterid (*Furipterus horrens*) probably occurs throughout Amazonia but is seldom recorded by inventory projects unless a special search is made for roosts. Two thyropterids (*Thyroptera discifera* and *T. tricolor*) range throughout Amazonia but are rarely collected at the same locality; a third species, *T. lavalii*, occurs sympatrically with *T. tricolor* in northeastern Peru (Pine, 1993) and eastern Ecuador (M. D. Engstrom, personal commun.).

Vespertilionids are probably represented by at least seven species in all Amazonian faunas and nine could be expected at some localities, but eight (at Balta, appendix 9) is the most yet reported from sympatry. Three species of *Myotis* and two of *Lasiurus* are widespread and possibly ubiquitous (table 7). Two species of *Eptesicus* (one of which is always *E. furinalis*) are to be expected in local faunas throughout the region and three are known from at least one Amazonian locality (Ochoa et al., 1993). *Histiotus* and *Rhogeessa* are only known in Amazonia from a few ecologically marginal or geographically peripheral localities.

Molossids are perhaps the least known component of Amazonian mammal diversity because most species forage at great heights and are only collected when they descend to drink (from rivers and roadside puddles), when their roosts are discovered (in buildings and tree cavities), or when nets are hoisted into canopy gaps. At least three species of *Eumops*, two each of *Molossops* and *Molossus*, and one *Nyctinomops* are widespread and possibly ubiquitous in the region (table 7). Many Amazonian localities could have 12–14 sympatric rainforest molossids, but a large list (15 species) from the eastern Kanuku Mountains of Guyana (Emmons, 1993b) in-

cludes species that are probably associated with nearby savanna habitats (e.g., *Eumops bonariensis*). Six species (at Arataye, appendix 5) is the most yet recorded from any exclusively forested Amazonian locality.

CENTRAL AMERICA: All of the bat families known from Amazonia are also present in Central American rainforests, and generic-level diversity is closely comparable between the two regions (table 1). Geographic range data (Alvarez-Castañeda and Alvarez, 1991; Hall, 1981; Jones et al., 1988; McCarthy et al., 1993) suggest that approximately the same species richness expected at most Amazonian localities could also obtain in eastern Panama, where about 100 bat species probably occur in lowland rainforest, but a steady attrition occurs from the Colombian frontier northward along the Central American isthmus. Thus, five species are not known to occur beyond Panama (*Lionycteris spurrelli*, *Lonchophylla thomasi*, *Platyrrhinus dorsalis*, *Lasiurus egregius*, *Molossops planirostris*), another six appear to drop out in Costa Rica (*Anoura cultrata*, *Lonchophylla mordax*, *Chiroderma trinitatum*, *Platyrrhinus vittatus*, *Furipterus horrens*, *Lasiurus castaneus*), six more in Nicaragua (*Cormura brevirostris*, *Cyttarops alecto*, *Lonchophylla robusta*, *Mesophylla macconnelli*, *Vampyressa nymphaea*, *Thyroptera discifera*), and ten in Honduras or Belize (*Micronycteris daviesi*, *M. hirsuta*, *M. minuta*, *M. nicefori*, *Tonatia silvicola*, *Phyllostomus hastatus*, *Carollia castanea*, *Ectophylla alba*, *Myotis riparius*, *Molossus bondae*). Because most of these are not replaced by Central American endemics (which chiefly inhabit montane or semiarid habitats), only about 80 species of bats are expected to occur in the lowland rainforests of southern Mexico (Medellín, 1993).

PRIMATES

AMAZONIA: Of the 14 primate genera that occur in Amazonian rainforests (table 1), only *Alouatta* and *Cebus* appear to be genuinely ubiquitous. The geographic range of *Saimiri* probably includes all of Amazonia, but squirrel monkeys are often absent from extensive tracts of upland forest far from rivers and lakes. Although *Ateles* may once have been ubiquitous in Amazonia (except, perhaps, east

of the Xingu and south of the Amazon; see Martins et al., 1988), spider monkeys are vulnerable to overhunting and are now absent from many areas that lack sufficient historical records to document the diversity of unexploited primate faunas. Other Amazonian monkeys have more restricted distributions that result in considerable geographic variation in expected species richness. Primate inventories from 13 Amazonian localities (appendix 12) illustrate several noteworthy taxonomic and geographic patterns.

Two species of *Cebus* are sympatric throughout most of Amazonia, and two species each of *Saguinus* and *Callicebus* are sympatric at many western Amazonian localities, but species in other genera are usually allopatric. Site-to-site variation in Amazonian primate diversity therefore chiefly involves the presence or absence of genera, each with a distinctive ecological role in local faunas (Izawa, 1975; Mittermeier and van Roosmalen, 1981; Terborgh, 1985b; Soini, 1986; Rylands, 1987; Peres, 1993).

A marked east-to-west gradient of increasing primate diversity in Amazonian forests is apparent from both range data and inventory results. Only seven genera (*Saguinus*, *Alouatta*, *Ateles*, *Cebus*, *Chiropotes*, *Pithecia*, *Saimiri*) are widely distributed in the Guiana subregion, where some upland localities may have as few as six species¹³ (e.g., the MCSE reserves, appendix 7) and where the maximum known sympatric diversity is eight (e.g., at the Raleighvallen-Voltzberg Nature Reserve, appendix 12). Primate faunas are slightly more diverse in southeastern Amazonia, where eight genera are widespread (*Callithrix*, *Saguinus*, *Alouatta*, *Aotus*, *Callicebus*, *Cebus*, *Chiropotes*, *Saimiri*), but the maximum richness yet documented anywhere east of the Xingu is still only eight species (at Anilzinho, appendix 12).

By contrast, 13 genera are widely distrib-

uted in western Amazonia (where only *Chiropotes* is absent). Within this subregion, expected primate diversity ranges from a minimum of 9 species (between the Guaviare and Apaporis in Colombia; Hernández-Camacho and Defler, 1983: fig. 2) to a maximum of 14 (between the Ucayali and Purus).¹⁴ Very high species counts have been reported from both white-water floodplain forest (e.g., 13 species at Cocha Cashu, appendix 10; 14 species at Lago da Fortuna, appendix 12) and terra firme forest drained by black-water streams (e.g., 13 species at SM-1, appendix 12).

In general, species lists from primate inventory projects conform closely to geographic expectations except where monkey populations have been heavily hunted and/or where census data were obtained from a restricted range of local habitats. Because many small species prefer the dense, tangled vegetation of swamps, riverbanks, lakeshores, and the margins of treefall gaps (Terborgh, 1985b; Rylands, 1987), uninterrupted tracts of tall forest may lack a full complement of local species. Flooded forests (várzea and igapó) may have fewer primate species than adjacent terra firme growth (Peres, 1988, 1993), but explicit comparisons of primate faunas from different forest types at the same locality are seldom published and much remains to be learned about the alpha and beta components of local primate diversity in Amazonia.

CENTRAL AMERICA: Six genera (*Saguinus*, *Alouatta*, *Aotus*, *Ateles*, *Cebus*, *Saimiri*) are known from Central America, but primate diversity decreases with distance from the Colombian frontier: the ranges of *Saguinus* and *Aotus* extend no further than Costa Rica, *Cebus* occurs only as far north as Honduras, and *Saimiri* has a presumably relictual distribution on the Pacific coast of western Panama and eastern Costa Rica. Thus, only *Alouatta* and *Ateles* occur in Mexican rainforests. Range data suggest that five species occurred together historically throughout most of eastern and central Panama, although inventory results to document this expected di-

¹³ Even lower diversity might be expected in the Amazonian forests of eastern Venezuela if the distributional data published by Bodini and Pérez-Hernández (1987) are not simply artifacts of inadequate collecting. The extremely depauperate primate fauna of eastern Marajó Island (Peres, 1989) inhabits gallery forest surrounded by savannas, an ecological landscape not included in this review.

¹⁴ Higher expectations (15 species between the Javari and the Juruá according to Rylands, 1987) are not yet indicated by published range data.

versity are apparently lacking (reports of five species from Barro Colorado [Glanz, 1982, 1990] included an introduced population of *Ateles geoffroyi*; see appendix 3). Higher species counts alleged to obtain in western Panama (six according to Eisenberg, 1979) are, to the best of our knowledge, undocumented by inventory results and are not expected from known distributions.

CARNIVORES

AMAZONIA: Geographic range data suggest that at least 11 carnivore species are ubiquitous in Amazonian rainforests. This widespread fauna includes one canid (*Speothos venaticus*¹⁵), five cats (*Herpailurus yaguarondi*, *Leopardus pardalis*, *Leopardus wiedii*, *Panthera onca*, *Puma concolor*), three mustelids (*Eira barbara*, *Galictis vittata*, *Lontra longicaudis*), and two procyonids (*Nasua nasua*, *Potos flavus*). Crab-eating raccoons (*Procyon cancrivorus*) range throughout the region but may be absent from upland sites that lack riparian or lakeshore habitats. Although the range of giant otters (*Pteronura brasiliensis*) probably once encompassed all of Amazonia, these animals have been extirpated throughout large areas that lack historical records and are likewise absent from uplands without large rivers or lakes.

Other carnivores have less extensive distributions in Amazonian rainforests: (1) The oncilla (*Leopardus tigrinus*) occurs along the outskirts of the hylaea in savannas and montane habitats but is sometimes found in adjacent lowland forest. (2) The small-eared dog

(*Atelocynus microtis*) is widespread in western and southeastern Amazonia (where it is sympatric with *Speothos venaticus*; Peres, 1991), but no records are known from the Guiana subregion. (3) Olingos (*Bassaricyon gabbii*) are widespread in western Amazonia and occur marginally in the Guiana subregion (between the Orinoco and the Essequibo),¹⁶ but records are apparently unknown from southeastern Amazonia. (4) The Amazonian weasel (*Mustela africana*) is known from scattered localities in western and southeastern Amazonia from the Andean piedmont to Belém, but no collections or sightings have been reported from the Guiana subregion. (5) The spectacled bear (*Tremarctos ornatus*) is principally montane but also occurs in lowland rainforest near the base of the Andes in extreme western Amazonia (Patton et al., 1982).

As a consequence of these restricted distributions, communities of sympatric carnivores are probably most diverse in western Amazonia, where up to 18 species might be expected, and least in the Guianas, where as few as 11 species may occur at some upland localities. Because many species are elusive, most rainforest carnivore inventories are incomplete. Fifteen species (at Balta, appendix 9) is the highest diversity yet documented anywhere in Amazonia.

CENTRAL AMERICA: At least ten species of carnivores are probably ubiquitous in the rainforested lowlands from eastern Panama to southern Mexico; these include five cats (*Herpailurus yaguarondi*, *Leopardus pardalis*, *L. wiedii*, *Panthera onca*, *Puma concolor*), three mustelids (*Eira barbara*, *Galictis vittata*, *Lontra longicaudis*), and two procyonids (*Nasua narica*, *Potos flavus*). Skunks (*Coonopatus striatus*) and weasels (*Mustela frenata*) may also occur throughout the region, but both are rare (or elusive) in lowland rainforests and collection records are widely scattered.

¹⁵ Historical records from Belém (Pine, 1973) and recent observations from the lower Tapajós (George et al., 1988) significantly extend the known range of *Speothos venaticus* beyond the limits mapped by Emmons and Feer (1990: map 111) and it now seems likely that the bush dog ranges throughout the hylaea. By contrast, the widespread fox *Cerdocyon thous* is not a rainforest species; it occurs in savanna landscapes north and south of the hylaea, in some isolated savanna enclaves, and in cleared areas around human settlements. Its presence in a few Amazonian inventories (e.g., Pine, 1973; George et al., 1988; Mascarenhas and Puerto, 1988; Ochoa and Sánchez, 1988) is always correlated with proximity to savanna landscapes or with the occurrence of other nonforest taxa (e.g., *Euphractus* and *Bolomys*) that provide independent evidence of nonforest vegetation in the sampled area.

¹⁶ One historical record from "Bastrica" on the Essequibo River (possibly Bartica, on the left bank; see appendix 4) and recently collected material from eastern Venezuela (Bisbal, 1989) document the presence of olingos in the western Guiana subregion where none were previously believed to exist (Emmons and Feer, 1990: map 115).

Other carnivores known or expected to occur in Central American rainforests¹⁷ have limited distributions in the region (Hall, 1981). The bush dog (*Speothos venaticus*) is definitely known in Central America from only two Panamanian collections (AMNH and USNM specimens from Veraguas and Darién), but unvouchered reports from the former Canal Zone, Bocas del Toro, and Chiriquí (Handley, 1966) suggest that it is (or was historically) widespread in the republic and may yet be found in remote parts of eastern Costa Rica. The oncilla (*Leopardus tigrinus*) has only been collected in Central America at four Costa Rican localities, just one of which is in the lowlands (Gardner, 1971). Olingos (*Bassaricyon gabbii*) extend northward into Central America only to Nicaragua, and crab-eating raccoons (*Procyon cancrivorus*) only to eastern Costa Rica. Northern raccoons (*Procyon lotor*) extend as far southward as central Panama, where Goldman (1920) documented sympatry with *P. cancrivorus*. The ecological distribution of Sumichrast's cacomistle (*Bassariscus sumichrasti*) may vary geographically; whereas the species inhabits lowland rainforest in southern Mexico and Belize (Coates-Estrada and Estrada, 1986; March and Aranda, 1992; Emmons, 1993a), all Costa Rican and most Panamanian records are montane (Goodwin, 1946; Handley, 1966; but see Enders, 1935).

Rainforest carnivore diversity is therefore not highly variable in Central America, ranging only from an expected maximum of 15 species in easternmost Panama to an expected minimum of 14 in southern Mexico. Fourteen species, the most yet documented in sympatry, have been reported from La Selva (appendix 2) and two study sites in southern Mexico (Coates-Estrada and Estrada, 1986; March and Aranda, 1992).

UNGULATES

AMAZONIA: Two species of peccary (*Pecari tajacu*, *Tayassu pecari*), two brocket deer (*Mazama americana*, *M. gouazoupira*), and

Tapirus terrestris are probably ubiquitous in Amazonia. White-tailed deer (*Odocoileus virginianus*) and marsh deer (*Blastocerus dichotomus*), occasionally reported from rainforested sites near the northern and southern limits of the hylaea, respectively, are the only other ungulates known from the region.¹⁸ In heavily hunted local faunas, brockets are elusive and white-lipped peccaries (*T. pecari*) and tapirs may be extirpated, so short-term surveys based near human settlements often obtain incomplete ungulate inventories. Nevertheless, the maximum expected ungulate diversity in Amazonian rainforests (five species) has been reported from numerous localities (e.g., appendices 4, 5, 7, 10).

CENTRAL AMERICA: The same two species of peccaries and one of the brockets (*Mazama americana*) found throughout Amazonia are (or were) also ubiquitous in Central American rainforests, as is (was) Baird's tapir (*Tapirus bairdii*). Gray brockets (*Mazama gouazoupira*) are present on the Pearl Archipelago (in the Gulf of Panama) but not on the Central American mainland. Although white-tailed deer (*Odocoileus virginianus*) favor open vegetation, dry forests, secondary growth, and clearings (Goldman, 1920; Leopold, 1959; Hall and Dalquest, 1963; Janzen, 1983b), this species is occasionally recorded from rainforested sites as well (e.g., appendix 2). Thus, four or five ungulate species could be expected in all Central American rainforest faunas, but white-lipped peccaries and tapirs may now be extirpated throughout most of the region. Complete rainforest ungulate inventories have been reported from many localities in the region (e.g., appendices 2, 3; Coates-Estrada and Estrada, 1986; March and Aranda, 1992).

RODENTS AND LAGOMORPHS

AMAZONIA: The systematics of Amazonian rodents are still poorly understood. Although it is usually easy to sort out sympatric species,

¹⁷ Two nonforest canids (*Canis latrans* and *Urocyon cinereoargenteus*) sometimes invade cleared areas in otherwise rainforested Central American landscapes (Hall and Dalquest, 1963; Coates-Estrada and Estrada, 1986; March and Aranda, 1992).

¹⁸ Records of white-tailed deer along the northern fringes of Amazonia (Tate, 1939; Handley, 1976) and rare reports of marsh deer from riparian habitats in southeastern Peru (e.g., at Cuzco Amazónico, appendix 11) may represent wandering individuals from nearby savannas. Neither species is apparently known from rainforest localities far removed from open vegetation.

TABLE 9
Taxonomic Distribution of Rodent Diversity at 14 Lowland Rainforest Localities
(Table entries are numbers of species present.)

	Rodent families ^a										Total species
	Sci	Geo	Het	Mur	Ere	Din	Hyd	Das	Ago	Ech	
CENTRAL AMERICA											
Los Tuxtlas ^b	2	1	1	4	1	0	0	1	1	0	11
La Selva ^c	3	1	1	6	1	0	0	1	1	2	16
Fort Sherman ^d	1	0	1	5	1	0	0	1	1	3	13
Barro Colorado ^e	2	0	1	5	1	0	1	1	1	2	14
Tacarcuna Village ^f	3	1	1	9	0	0	0	1	1	2	18
AMAZONIA											
Kartabo ^g	2	0	0	11	1	0	1	2	1	2	20
Arataye ^h	2	0	0	9	1	0	1	2	1	5	21
Cunucunuma ⁱ	1	0	0	4	1	0	0	2	1	2	11
MCSE Reserves ^j	1	0	0	7	1	0	0	2	1	5	17
Xingu ^k	1	0	0	10	1	0	1	2	1	7	23
Huampami ^l	3	0	0	7	1	1	1	2	1	3	19
Balta ^m	2	0	0	10	1	1	1	2	1	6	24
Cocha Cashu/Pakitza ⁿ	3	0	0	11	1	1	1	2	1	7	27
Cuzco Amazónico ^o	2	0	0	11	1	0	0	2	1	5	22

^a Abbreviations: Sci, Sciuridae; Geo, Geomyidae; Het, Heteromyidae; Mur, Muridae (excluding introduced species); Ere, Erethizontidae; Din, Dinomyidae; Hyd, Hydrochaeridae; Das, Dasyproctidae; Ago, Agoutidae; Ech, Echimyidae.

^b Coates-Estrada and Estrada (1986). Los Tuxtlas (18°35'N, 95°06'W; 150–530 m elevation) is a field station in the Mexican state of Veracruz.

^c Appendix 2.

^d Fleming (1970). Fort Sherman (9°20'N, 79°57'W; 5 m elevation) is a military reservation in the Caribbean littoral of central Panama (formerly in the Canal Zone).

^e Appendix 3.

^f Handley (1966) and USNM collections. Tacarcuna Village (8°05'N, 77°17'W; 554–923 m elevation), former site of the Tacarcuna Yellow Fever Station, is located in the foothills of the massif of Cerros Tacarcuna and Malí in Provincia Darién, Panama (Galindo and Rodaniche, 1964; Fairchild and Handley, 1966).

^g Appendix 4.

^h Appendix 5.

ⁱ Appendix 6.

^j Appendix 7.

^k Appendix 8.

^l Patton et al. (1982). Huampami (ca. 4°28'S, 78°10'W; 210 m elevation) is an Aguaruna village on the lower Río Cenepa in Departamento Amazonas, Peru.

^m Appendix 9.

ⁿ Appendix 10.

^o Appendix 11.

comparisons of samples obtained from distant localities commonly present difficulties of synonymy that can only be solved by revisionary studies. Unfortunately, no modern revisions are available to document the morphological and geographic limits of most Amazonian species of squirrels, muroids, porcupines, dasyproctids, and echimyids, so current taxonomic usage and our remarks on distribution can only be regarded as provi-

sional for these important groups. Amazonian rodent faunas probably consist of at least 21–24 sympatric species in the Guiana sub-region, but higher counts could be expected everywhere else. Although as many as 38–40 species might occur together at some western Amazonian localities, currently available inventory results do not approach such numbers (table 9).

Sciurids are a minor and inconspicuous

component of rodent faunas in the Guiana region and southeastern Amazonia, where no more than two or three species probably occur sympatrically and only members of the *Sciurus aestuans* group are commonly collected. Western Amazonia has a more diverse squirrel fauna, however; as many as five species could be sympatric between the Marañón and the Javari in northeastern Peru (M. de Vivo, personal commun.). Because the smaller Amazonian squirrels (*Microsciurus* and *Sciurillus*) are elusive, few modern collecting expeditions¹⁹ obtain complete inventories of squirrel faunas; the maximum number represented in published results is only three species (e.g., at Huampami, Patton et al., 1982; and Cocha Cashu/Pakitza, appendix 10).

The Amazonian rainforest muroid fauna consists of six apparently ubiquitous genera and a few others with restricted geographic ranges.²⁰ At least one species each of *Neacomys*, *Nectomys*, *Oligoryzomys*, and *Rhipidomys*, four species of *Oecomys*, and three species of *Oryzomys* are probably present in local faunas throughout the region. No more than a single species each of *Nectomys*, *Oligoryzomys*, and *Rhipidomys* are apparently known from any Amazonian locality, but two species of *Neacomys* are sympatric in parts of western Amazonia (Lawrence, 1941). As many as five Amazonian species of *Oecomys* and four of *Oryzomys* are known to occur sympatrically (e.g., appendices 4, 9). Amazonian ichthyomyines are difficult to collect and their distributions are poorly known, but one species of *Neusticomys* may be present in local faunas throughout the region (despite the absence of any published records from Brazil) and *Ichthyomys stolzmanni* occurs along the Andean piedmont of Ecuador and

Peru. The akodont genus *Oxymycterus* and the oryzomyine genus *Scolomys* have extensive but sparsely sampled Amazonian distributions (Hershkovitz, 1994; Patton and Silva, 1995); neither is apparently represented by more than a single species in any local fauna. *Melanomys robustulus*, an oryzomyine, is known only from the Andean piedmont of southeastern Ecuador. Muroid faunas therefore probably consist of at least 11 sympatric species throughout the region, but up to 16 could be expected in much of western Amazonia. To date, however, the highest documented diversity of muroids in any local Amazonian fauna is only 11 species (e.g., appendices 4, 10, 11).

Prehensile-tailed porcupines (*Coendou*) are probably ubiquitous in Amazonian forests. Large numbers are recovered during rescue operations when forests are flooded by hydroelectric dams (Walsh and Gannon, 1967; Mascarenhas and Puerto, 1988), but many inventory projects fail to detect any. A few published sources (e.g., Walsh and Gannon, 1967; George et al., 1988; Handley and Pine, 1992) and numerous unpublished collections suggest that two species are sympatric at many localities.

At least three species of large terrestrial caenomorphs are present in all Amazonian forests, and five could be expected along the Andean piedmont. Pacas (*Agouti paca*) are ubiquitous, as are agoutis (*Dasyprocta*) and acouchis (*Myoprocta*). Although several species of *Dasyprocta* and two of *Myoprocta* are currently recognized, neither genus is apparently represented by more than a single species in any local fauna. Capybaras (*Hydrochaeris hydrochaeris*) are found throughout Amazonia but may be absent from upland terrain away from large rivers, marshes, and lakes (e.g., the MCSE Reserves, appendix 7). Pacaranas (*Dinomys branickii*) occur in the Amazonian lowlands of Bolivia and Peru, but most northern records of this species are from montane or submontane habitats.

Amazonian echimyids include one genus of terrestrial species and five genera of arboreal species. Terrestrial spiny rats (*Proechimys*) are abundant and ubiquitous, with seven species groups represented in the Amazonian fauna (Patton, 1987). Two species of *Proechimys* are probably sympatric through-

¹⁹ Prior to the widespread use of mist nets, ornithological collectors hunting birds with shotguns also obtained large series of squirrels, which are active at the same time of day in the same subcanopy and understory habitats. Most large series of Neotropical rainforest squirrels therefore date from 1890–1940, when many gun-toting bird collectors were employed by European and American museums.

²⁰ Four muroid genera occasionally reported from Amazonian localities are restricted to enclaves of non-forest habitats (e.g., marshes, savannas, and manmade clearings): *Bolomys*, *Holochilus*, *Sigmodon*, and *Zygodontomys*.

out the Guiana subregion, three can be found sympatrically in southeastern Amazonia (e.g., on the Rio Xingu, appendix 8), and as many as four or five occur together at some western Amazonian localities (e.g., at Balta, appendix 9; and Cocha Cashu/Pakitza, appendix 10). Arboreal echimyids (*Dactylomys*, *Echimy*s, *Isothrix*, *Lonchothrix*, and *Mesomys*) are seldom collected. At least one species each of *Echimy*s (including *Makalata*) and *Mesomys* are probably present everywhere in the region, despite the absence of records of either genus from many poorly sampled areas. *Dactylomys* and *Isothrix*, each represented by single species in local faunas, may be absent from most of the Guiana subregion but are probably ubiquitous elsewhere in Amazonia. Five species of arboreal echimyids are known from several historical collecting localities along the south bank of the Amazon (six are expected between the Tapajós and the Xingu), and as many as seven might be sympatric near the base of the Andes in northern Peru. Therefore, 10–12 echimyid species could occur together at some localities in western Amazonia, but the most yet documented from sympatry in our lists or in the literature is seven (e.g., appendices 8, 10).

The single species of lowland rainforest rabbit, *Sylvilagus brasiliensis*, is widespread but perhaps patchily distributed in western and southeastern Amazonia. In the Guiana subregion, *S. brasiliensis* is known from so few localities that its distribution is impossible to evaluate with any certainty.²¹

CENTRAL AMERICA: Central American rainforest rodent faunas range from an expected maximum of about 22 species in east-

ern Panama to an expected minimum of about 13 in southern Mexico. The most yet documented by published inventory results anywhere in the region is 18 species (at Tacarcuna Village, table 8).

Squirrels of the genus *Sciurus* are ubiquitous in Central American rainforests, and dwarf squirrels (*Microsciurus*) occur from the Colombian frontier to Nicaragua. At least two sciurid species are probably sympatric throughout the region, and three occur together at several Costa Rican and Panamanian localities (e.g., at La Selva, appendix 2; and Barro Colorado, appendix 3).

Geomyoids (geomyids and heteromyids) are a small but distinctive component of trans-Andean rainforest faunas. Pocket gophers (*Orthogeomys*) occur in lowland rainforests from southern Mexico to Colombia, but their distribution is apparently discontinuous (e.g., gophers are apparently absent in central Panama) and local faunas never have more than one species. Pocketmice of the genus *Heteromys* are ubiquitous in the humid Central American lowlands, but apparently no more than one rainforest species is ever present locally.

Most Central American rodents are muroids, ten genera of which (*Ichthyomys*, *Melanomys*, *Neacomys*, *Nyctomys*, *Oecomys*, *Oligoryzomys*, *Oryzomys*, *Peromyscus*, *Sigmodontomys*, *Tylomys*) are known to inhabit lowland rainforests in the region. Three others (*Isthmomys*, *Rheomys*, *Rhipidomys*) are usually collected in montane (cloud) forests but sometimes occur below 1000 m in foothills. Another genus (*Ototylomys*) inhabits dry (deciduous) forests but is sometimes found in ecotones with evergreen formations. Muroid diversity is highest near the Colombian frontier, where as many as 12 species could be sympatric, but three extend no further into Central America than central Panama (*Ichthyomys tweedii*, *Neacomys pictus*, *Oecomys bicolor*), two extend only as far as Costa Rica (*Oecomys trinitatis*, *Oryzomys talamancae*), and three reach their northernmost limit in Honduras (*Melanomys caliginosus*, *Oryzomys bolivaris*, *Sigmodontomys alfari*). Because most endemic species of Central American muroids are restricted to montane or semiarid habitats, the lowland rainforest faunas of northern Central America are improv-

²¹ Dramatic differences between recently published range maps for *Sylvilagus brasiliensis* (Hoogmoed, 1983; Emmons and Feer, 1990) exemplify the ambiguities of geographic interpretation when distributions are sparsely sampled and collection records are unpublished or widely scattered in the literature. Whereas collections from the lower Xingu (appendix 8) and Belém (Pine, 1973) suggest that the species is more widely distributed in southeastern Amazonia than indicated on Hoogmoed's map (which is unshaded along the south bank of the Amazon east of the Tapajós), we are aware of only one record from Amazonian Venezuela (in Handley, 1976), one from the "mouth of Rio Negro" (Hershkovitz, 1950), and a few from western Surinam (Hoogmoed, 1983) to justify continuous shading across the entire western Guiana subregion (including Guyana, where no rabbits have yet been observed or collected).

erished by these losses. Thus, only six species (*Nyctomys sumichrasti*, *Oligoryzomys fulvescens*, *Oryzomys alfaroi*, *O. melanotis*, *Peromyscus mexicanus*, *Tylomys nudicaudatus*) are definitely known to inhabit lowland rainforest in southern Mexico (Hall and Dalquest, 1963).

The caviomorph fauna of Central American rainforests is not diverse. One species each of porcupines (*Coendou*) and agoutis (*Dasyprocta*) and the paca (*Agouti paca*) are present in intact rainforest faunas throughout

the region, but capybaras (*Hydrochaeris hydrochaeris*) occur only from central Panama to the Colombian frontier. Two terrestrial echimyids (*Proechimys semispinosus* and *Hoplomys gymnurus*) range northward from South America as far as Honduras, and one arboreal species (*Diplomys labilis*) extends to central Panama.

The rabbit *Sylvilagus brasiliensis* is probably ubiquitous in Central American rainforests.

DISCUSSION

SOURCES OF DIVERSITY INFORMATION

Each of the two principal sources of diversity estimates reviewed above has unique advantages and disadvantages. Inventory results (observations and collections obtained by local faunal surveys) have the outstanding advantage of concreteness: assuming correct identifications, the listed species from an inventory are definitely known to have occurred together at a particular place and time. However, inventory results are strongly biased (underestimating true diversity) because species lists always increase with additional sampling effort up to an asymptote. Biologically informative inventory comparisons therefore require either (1) asymptotic lists, (2) results that can be meaningfully standardized at a common level of sampling effort, or (3) statistically defensible extrapolations. Unfortunately, no Neotropical rainforest mammal inventory has yet produced a demonstrably asymptotic species list, and methodological differences among existing inventories preclude valid standardization or extrapolation. Additionally, inventory data are available from so few localities that comparisons even of complete lists would be of limited use for documenting geographic patterns (e.g., by mapping diversity isopleths), testing hypotheses of ecological or historical causality, etc. Other sources of faunal information are therefore essential.

Distributional data (e.g., range maps) provide an alternative source of diversity estimates, but geographic expectations (species lists predicted from range overlap) are subject

to several sources of uncertainty. Among others, geographic expectations might consistently overestimate sympatric diversity if many species are patchily distributed within their known range limits, or underestimate diversity if many taxa are unrevised, undescribed, or rarely collected. Hence, diversity estimation from range data requires much supplementary information (e.g., about natural history, systematics, and historical patterns of collecting bias) to minimize inaccuracy.

Comparisons of inventory results with geographic expectations reveal wide discordance at most Neotropical rainforest localities (table 10, fig. 23). Among eight sites where total faunas (including bats) were censused, observed and expected species counts are not even significantly correlated ($r = 0.16$, $df = 6$, $p = 0.70$). The largest discrepancies, however, are associated with three short-term inventories (Cunucunuma, Xingu, and Cuzco Amazónico), suggesting that sampling is a confounding factor. Indeed, the number of "missing" species (those expected but not observed at each site) is negatively correlated with inventory duration ($r = -0.76$, $df = 6$, $p = 0.03$) despite one conspicuously outlying data point (fig. 24). The outlier, Barro Colorado, has many more "missing" species than would be expected from the central tendency among other inventories, probably because most fieldwork at that locality has been confined to a faunally impoverished island (see Comments in appendix 3). Without Barro Colorado, the negative correlation between "missing" species and sampling duration is much stronger ($r = -0.90$, $df = 5$, $p < 0.01$).

TABLE 10
Observed and Expected Species of Rainforest Mammals at Ten Neotropical Inventory Localities

Locality ^a	Years of sampling ^b	Total species ^c			Nonvolant species		
		Observed ^d	Expected ^e	Difference ^f	Observed ^d	Expected ^e	Difference ^f
La Selva	34	117	138	21	52	55	3
Barro Colorado	71	113	144	31	49	60	11
Kartabo	5	—	—	—	60	71	11
Arataye	17	122	165	43	61	70	9
Cunucunuma	<1	93	177	84	43	72	29
MCSE Reserves	6	—	—	—	53	67	14
Xingu	<1	95	163	68	48	74	26
Balta	3	130	185	55	74	92	18
Cocha Cashu/Pakitzá	21	139	187	48	79	93	14
Cuzco Amazónico	2	103	187	84	59	93	34

^a See appendices 2–11.

^b See table 4, footnote *d*.

^c Including bats.

^d Inventory results; see table 5.

^e From geographic range data (appendix 1 explains criteria for listing expected species at each locality).

^f “Missing” species (expected minus observed); see Comments in appendices 2–11.

Thus, lists of observed species tend to converge on expected lists as inventories are prolonged, at least where local faunas remain essentially intact.

The hypothesis that incomplete sampling accounts for much of the discordance between inventory results and geographic expectations gains additional credence when behavioral and other traits of “missing” species are considered. At localities where inventory fieldwork was very brief (i.e., about two years or less), lists of “missing” rainforest mammals (see Comments in appendices 2–11) include many common, morphologically distinctive, and easily captured (or observed) understory taxa; adding such species to inventories is just a matter of time. By contrast, most “missing” rainforest mammals at longer-term inventory sites are usually either notoriously elusive (e.g., canopy-dwelling marsupials, high-flying bats, semiaquatic rodents) or hard for nonspecialists to identify (and therefore likely to be unrecognized in sparsely vouchered mark-and-release surveys); adding these taxa to inventories requires special methods and large voucher collections identified by taxonomic experts.

Although diversity estimates from distributional data have yet to be rigorously tested against the results of any intensive, meth-

odologically complete inventory (a future research priority), we conjecture that the expected species counts in table 10 are probably within about 10% of true diversity at each locality. For example, real species richness at Balta is unlikely to be much less than about 166 species or much more than about 204 species; correspondingly, inventory results from Balta are perhaps 64–78% complete. For comparison, the Cunucunuma inventory is probably about 48–58% complete and the La Selva inventory 77–94% complete. Without additional fieldwork, however, such numbers can only serve as rough indications of the current limits of plausible inference.

DIVERSITY IN AMAZONIAN RAINFORESTS

The diversity information reviewed herein strongly supports Emmons' (1984) suggestion that Amazonian rainforest mammal faunas are most diverse in the western subregion, where over 200 species could occur sympatrically if the loci of maximal ordinal diversity roughly coincide (table 11). By contrast, Amazonian mammal faunas are probably least diverse in the Guianan subregion, where only about 150 species might be sym-

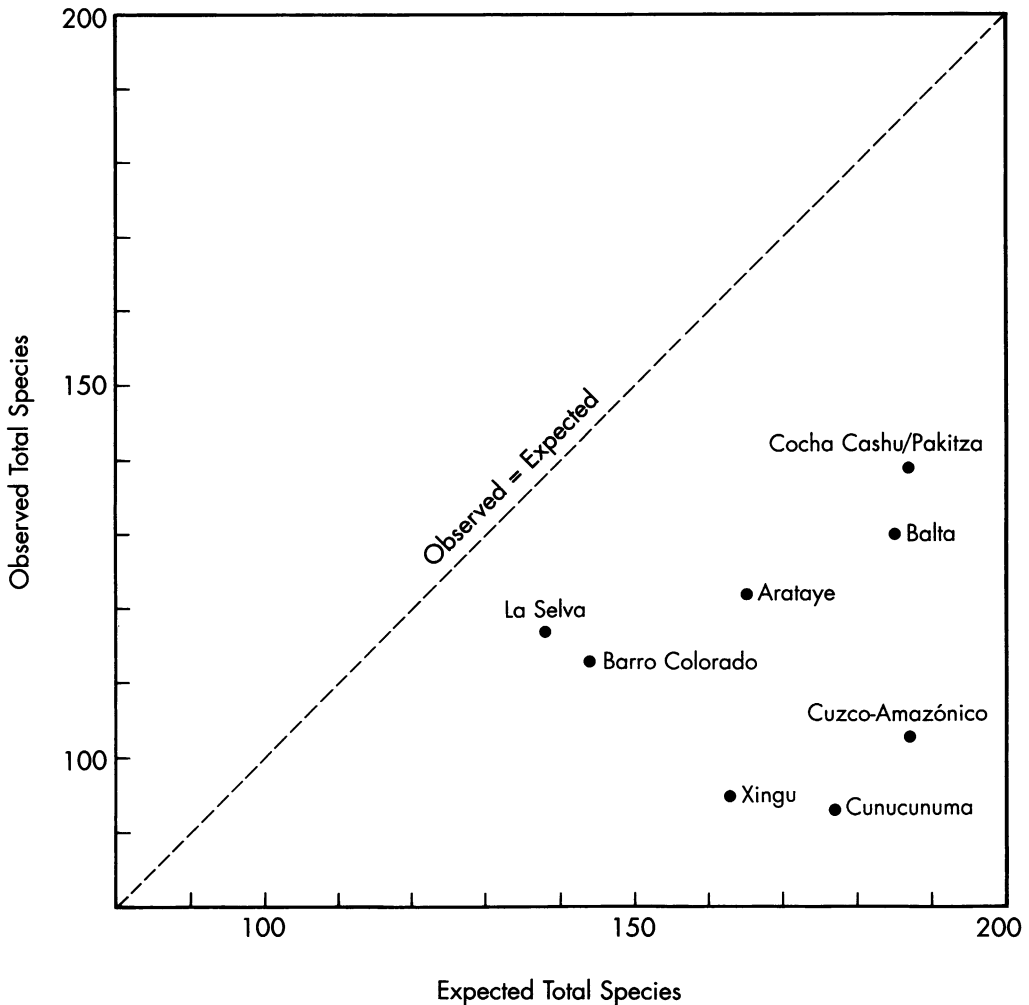


Fig. 23. Observed versus expected total species richness (including bats) at eight Neotropical rainforest localities (from data in table 10). The vertical distance of each point from the dashed diagonal is proportional to the number of "missing" species (those expected but not observed) at each inventory site.

patric at some upland sites away from large rivers or lakes. Rainforest mammal faunas in southeastern Amazonia are very poorly sampled (except in the vicinity of Belém), but the data at hand suggest that diversity in this area is neither as low as in the Guiana subregion nor as high as in western Amazonia.²² The

distributional phenomena responsible for these subregional differences merit discussion.

A striking aspect of Amazonian mammal faunas is their higher-taxonomic uniformity across thousands of kilometers. Of the 33

²² Pine's (1973: 47) prediction that future work "... will probably show Belém to have a larger mammalian fauna than any other locality on earth" is implausible. The fauna of Belém is conspicuously depauperate in primates and rodents and there is no realistic prospect that more collecting in the area will yield enough

additional records to rival western Amazonian diversity. Excluding five nonforest mammals (*Dasypus septemcinctus*, *Euphractus sexcinctus*, *Bolomys lasiurus*, *Holochilus sciureus*, *Cerdocyon thous*), two cetaceans, one manatee, and three introduced muroids, Pine's list is reduced to only 61 nonvolant rainforest species, almost 40% less than could be expected at some western Amazonian localities.

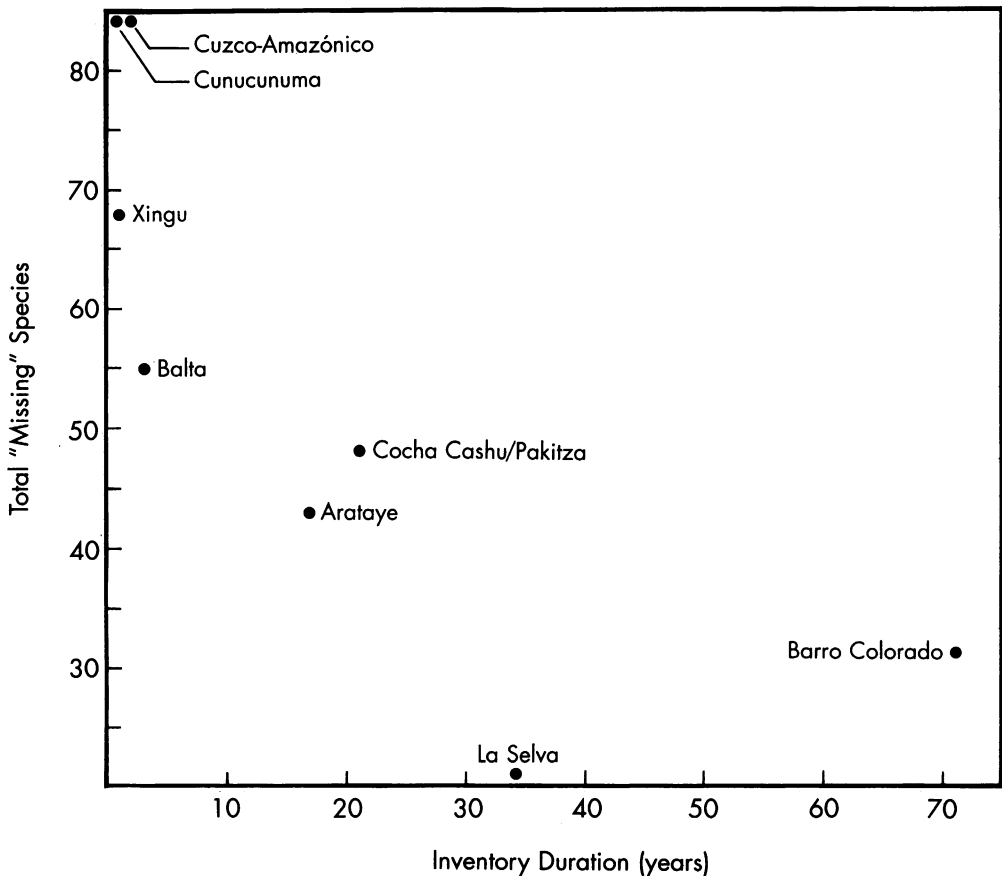


Fig. 24. "Missing" species (those expected but not observed) versus inventory duration at eight Neotropical rainforest localities where total mammal faunas (including bats) were sampled (from data in table 10).

mammalian families known from Amazonian rainforests (table 1), 28 range throughout the region. Of the five that do not, one (*Dinomyidae*) is monotypic, two (*Ursidae* and *Natalidae*, represented by one and two species, respectively) have peripheral distributions, another (*Callitrichidae*) is absent only in the Orinoco catchment, and the last (*Leporidae*, represented by a single species) is apparently absent only in the easternmost Guianas. Most geographic variation in Amazonian mammal diversity therefore involves lower taxonomic categories. Because different factors affect interpretations of distributional data for nonvolant mammals on the one hand and bats on the other, it is useful to consider these two faunal elements separately.

Most genera of nonvolant Amazonian

rainforest mammals are very widespread: over two-thirds (57 of the 82 listed in table 1) are probably found in suitable habitats throughout most of the region. Among 25 genera with restricted Amazonian distributions, however, subregional diversity differences are clear (table 12): 17 are widely distributed in western Amazonia, 12 in southeastern Amazonia, and only 1 in the Guiana subregion. Additionally, widespread genera with geographic variation in numbers of sympatric species are usually more diverse in western Amazonia than elsewhere (table 13). The elevated diversity of western Amazonian nonvolant faunas is therefore attributable to both high generic and congeneric richness.

Geographic expectations (tables 11, 12, 13) and some inventory results also support Emmons' (1984) observation that three mam-

TABLE 11
Expected Minimal and Maximal Rainforest Mammal Diversity in Central America and Amazonia^a

	Species expected	
	Minimum	Maximum
CENTRAL AMERICA ^b		
Marsupials	7 (SM, B)	10 (EP)
Xenarthrans	4 (SM)	7 (P, CR, N)
Bats	ca. 80 (SM)	ca. 100 (EP)
Primates	2 (SM)	5 (EP)
Carnivores	14 (SM)	15 (EP)
Ungulates	5	5
Rodents	13 (SM)	22 (EP)
Lagomorphs	1	1
Totals	ca. 126 (SM)	ca. 165 (EP)
AMAZONIA ^c		
Marsupials	8 (G)	17 (W)
Xenarthrans	9 (G)	10 (W, LA)
Bats	ca. 90 (G, SE)	ca. 110 (W)
Primates	6 (G)	14 (W)
Carnivores	11 (G)	18 (W)
Ungulates	5	5
Rodents	21 (G)	40 (W)
Lagomorphs	0 (G)	1 (G, W, SE)
Totals	ca. 150 (G)	ca. 215 (W)

^a From geographic range data. Summing minimal and maximal expectations over orders assumes geographic congruence of ordinal diversity patterns. To evaluate this assumption, we provide abbreviated geographic information following each estimate, but the scale of resolution is necessarily very coarse.

^b Abbreviations: B, Belize; CR, Costa Rica; EP, eastern Panama; N, Nicaragua; P, Panama; SM, southern Mexico.

^c Abbreviations: G, Guiana subregion; SE, Southeastern Amazonia; LA, banks of lower Amazon; W, Western Amazonia.

malian orders—Marsupialia, Primates, and Rodentia—account for most diversity differences among nonvolant Amazonian faunas. Geographic variation in primate diversity is especially striking (numbers of local monkey species differ at least twofold in some comparisons of Guianan and western Amazonian inventories), but distributional data suggest that comparable subregional diversity differences could be expected for Amazonian rodents and marsupials. By contrast, rainforest xenarthran and ungulate species richness appears to be almost invariant across Amazonia, and expected subregional differences in rainforest carnivore faunas involve just a few species.

Within Amazonian subregions, some site-to-site faunal differences are obviously correlated with the proximity of rivers and lakes. Large bodies of water are clearly important

for semiaquatic species (e.g., *Pteronura brasiliensis*, *Hydrochaeris hydrochaeris*), but they also create habitats for terrestrial and arboreal species that favor tangled edges, swampy ground, seasonally flooded forests, canebrakes, or other common features of fluvial landscapes (e.g., *Cebuella pygmaea*, *Cacajao* spp., *Callicebus* spp., *Saimiri sciureus*, *Procyon cancrivorus*, *Oligoryzomys* spp., *Dactylomys dactylinus*, some *Proechimys* spp., *Sylvilagus brasiliensis*). All else being equal, inventory sites that include both riparian and terra firme habitats are therefore likely to have more diverse mammalian communities than upland sites within otherwise faunally homogeneous landscapes.

Because distributional data for Amazonian bats are still so fragmentary, geographic range limits are difficult to distinguish from collecting artifacts. Locality records for many

TABLE 12
Genera of Nonvolant Rainforest Mammals with
Restricted Distributions in Amazonia

	Amazonian distribution ^a		
	WA	G	SE
<i>Caluromysiops</i>	X		(X)
<i>Glironia</i>	X	(X)	
<i>Callimico</i>	X		
<i>Callithrix</i>			X
<i>Callicebus</i>	X	(X)	X
<i>Cebuella</i>	X		
<i>Aotus</i>	X	(X)	X
<i>Cacajao</i>	X	(X)	
<i>Chiropotes</i>		X	X
<i>Lagothrix</i>	X		X
<i>Atelocynus</i>	X		X
<i>Mustela</i>	X		X
<i>Bassaricyon</i>	X	(X)	
<i>Tremarctos</i>	(X)		
<i>Odocoileus</i>		(X)	
<i>Microsciurus</i>	X		
<i>Ichthyomys</i>	(X)		
<i>Melanomys</i>	(X)		
<i>Oxymycterus</i>	(X)		X
<i>Scolomys</i>	X		
<i>Dinomys</i>	X		
<i>Dactylomys</i>	X	(X)	X
<i>Isothrix</i>	X	(X)	X
<i>Lonchothrix</i>			X
<i>Sylvilagus</i>	X	(X)	X

^a Abbreviations: WA, western Amazonia; G, Guiana subregion; SE, southeastern Amazonia. See Introduction for geographic definitions. Parentheses indicate marginal or very restricted occurrence.

insectivorous taxa, for example, are clustered in areas long accessible to professional zoologists (e.g., the Guianas), around often-visited cities (e.g., Belém), or near the campsites of unusually skilled collectors (e.g., SVP stations in southern Venezuela; Handley, 1976). By contrast, Amazonian locality records for frugivorous phyllostomids (carollines and stenodermatines) are generally more numerous and provide somewhat less problematic data for diversity estimates. Although inventory results and geographic expectations both suggest higher diversity for frugivorous phyllostomids in western Amazonia than elsewhere, subregional diversity differences may be less marked for bats than for primates, marsupials, and rodents. Roost diversity (e.g., the proximity of caves and rock outcrops) is

TABLE 13
Genera of Nonvolant Amazonian Rainforest
Mammals with Geographic Variation in Species
Richness

	Subregion(s) of highest richness
<i>Caluromys</i>	Guiana
<i>Didelphis</i>	Guiana
<i>Marmosa</i>	W Amazonia ^a
<i>Marmosops</i>	W Amazonia
<i>Micoureus</i>	W Amazonia
<i>Monodelphis</i>	W Amazonia ^a
<i>Philander</i>	W Amazonia
<i>Bradypus</i>	Guiana and SE Amazonia (banks of lower Amazon)
<i>Choloepus</i>	W Amazonia ^a
<i>Saguinus</i>	W Amazonia, Guiana (extreme S)
<i>Callicebus</i>	W Amazonia
<i>Cebus</i>	Parts of all three subregions
<i>Sciurus</i>	W Amazonia
<i>Neacomys</i>	W Amazonia
<i>Oecomys</i>	?Guiana ^a
<i>Oryzomys</i>	W Amazonia
<i>Coendou</i>	Parts of all three subregions
<i>Echimys</i>	W Amazonia ^a
<i>Proechimys</i>	W Amazonia

^a Expected from geographic range overlap; not yet documented by sympatric collections.

perhaps the single most important factor affecting bat species richness at Amazonian localities, but obtaining credible inventory data to test this or any other conjecture about Amazonian bat faunas remains an outstanding challenge for future research.

DIVERSITY IN CENTRAL AMERICAN RAINFORESTS

A gradient of decreasing diversity along the Central American isthmus from the Colombian frontier to southern Mexico is evident for rainforest marsupials, edentates, bats, primates, and rodents, but not for carnivores or ungulates. This pattern results from the incremental loss of species with predominantly South American distributions, most of which are not replaced by Central American endemics. As a consequence, rainforest mammal faunas in southern Mexico, where local diversity is unlikely to exceed 125 species (table 11), are perhaps the least diverse of any in Central or South America. By contrast, expected mammalian diversity in the Darién

lowlands of eastern Panama (about 165 species) is within the range of Amazonian values.

Although neither long-term inventories nor reliable range maps are available to estimate total mammalian diversity in the contiguous Chocó lowlands of western Colombia and northwestern Ecuador, the primate data summarized by Hernández-Camacho and Defler (1983: fig. 2) suggest a gradient of decreasing richness from north to south in this poorly sampled area. The unimpressive number of small marsupial and rodent species (seven) captured during an eight-month trapping study in very wet forest at Bajo Calima (González and Alberico, 1993) likewise hints that Chocoan mammal faunas are not exceptionally diverse. If these two studies are not completely misleading, then mammalian species richness in trans-Andean rainforests is probably maximal near the Panamanian-Colombian frontier, i.e., at the southern extreme of the Central American gradient.

DIVERSITY IN OTHER NEOTROPICAL RAINFOREST REGIONS

Mammalian faunas in the rainforested coastal lowlands of northern Venezuela have not been sampled by any long-term inventory, and extensive anthropogenic disturbance preceded modern collecting in the region (see gazetteer entries in Handley, 1976). Because little (if any) pristine lowland habitat now remains in northern Venezuela (Huber and Alarcon, 1982), the diversity of intact rainforest faunas there may never be known. Lacking any substantial inventory results, we compiled collection records from the once-extensive rainforests of the western Maracaibo basin as the best available substitute (appendix 13). Although this list (with only 85 species) is almost certainly incomplete, the absence of some taxa that are easily collected or observed in Central American and/or Amazonian rainforests (e.g., *Rhinophylla*, Callitrichidae, *Nasua*) surely reflects faunal impoverishment rather than sampling artifacts. This impression is also supported by comparing species richness among faunal samples obtained by identical methods in coastal Venezuelan and Amazonian rainforest (fig. 25). Altogether, the information at hand suggests that mammalian communities

in coastal Venezuelan rainforests are (or were historically) not highly diverse, except by comparison with the faunas of adjoining savannas, deserts, and montane forests.

Mammalian diversity in the Atlantic rainforests of southeastern Brazil is also poorly documented. Most published faunal surveys from this general area are from montane sites (e.g., Davis, 1945; Carvalho, 1965; Avila-Pires and Gouvêa, 1977) and/or subtropical latitudes (Crespo, 1982; Olmos, 1991; Bergallo, 1994). The largest mammalian inventory we have seen from any tropical lowland rainforest in southeastern Brazil contains only 60 species (Stallings et al., 1991) and is obviously very incomplete.²³ Because generic diversity in the region is low (table 1) and because the few local species lists at hand do not suggest any compensatory increase in numbers of sympatric congeners, it seems unlikely that any Atlantic rainforest mammal fauna approaches the richness of even the poorest Amazonian rainforest site.

COMPARISONS WITH OTHER BIOMES

A comprehensive synthesis of inventory and distributional data from other New World biomes is beyond the scope of our review, but information previously summarized in the literature provides compelling evidence that sympatric mammalian diversity is highest in lowland tropical rainforests and declines along gradients of increasing latitude, elevation, and aridity. A brief synopsis of the principal research results supporting this conclusion is necessary in order to evaluate a few

²³ Excluding one introduced muroid (*Rattus rattus*) and several nonforest taxa (*Euphractus sexcinctus*, *Cerdocyon thous*, *Calomys laucha*, *Cavia* sp.), Stallings et al.'s (1991) inventory from Parque Florestal Estadual do Rio Doce actually contains no more than 55 species that could possibly be classified as rainforest mammals. Although the forest understory at this locality was intensively censused by trapping (a total effort of over 64,300 trap-nights captured 1067 individual marsupials and small rodents; op. cit.), most animals trapped in the park were released (Fonseca and Kierulff, 1988; Stallings, 1988), so some hard-to-identify species probably went unrecognized. By contrast, the absence of arboreal echimyids suggests that canopy habitats were not effectively sampled. Only 103 individual bats were captured in 84 net-hours and the listed species represent just 12 of the 46 genera known to occur in the Atlantic rainforest region.

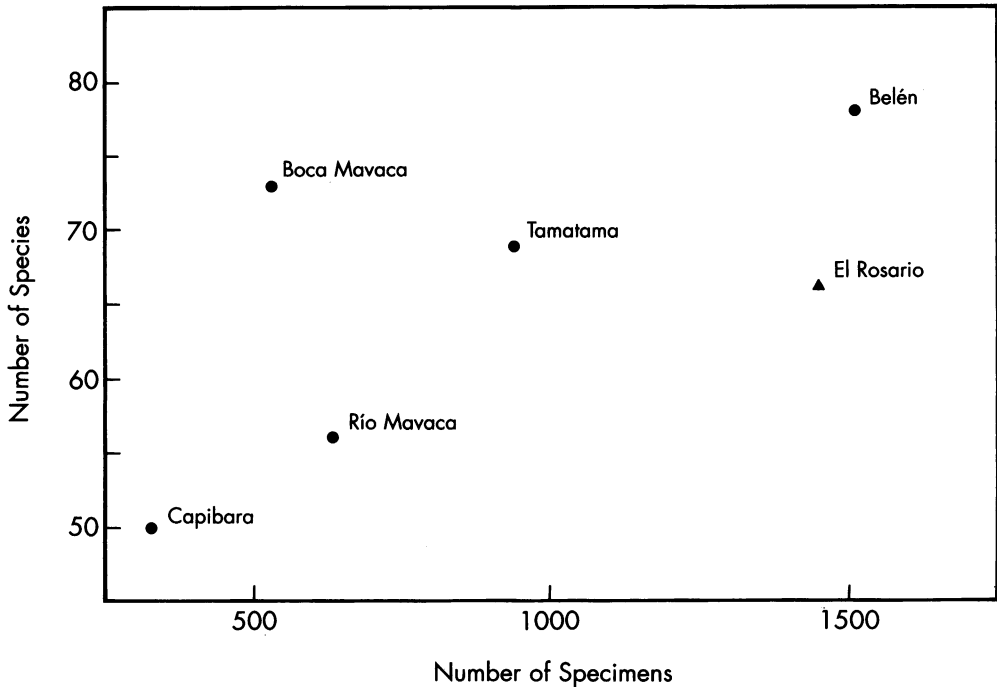


Fig. 25. Numbers of rainforest mammal species versus numbers of specimens collected by Smithsonian Venezuelan Project (SVP) field crews at six Venezuelan localities (data from Handley, 1976). Amazonian rainforest collections (dots) contain more species per specimen than the single available coastal rainforest sample (triangle), suggesting greater diversity in the former region. Although the field team that worked at El Rosario was different from the team that sampled the Amazonian sites, all SVP field crews were identically equipped and followed identical collecting instructions (Handley, personal commun.).

published studies with apparently contradictory results.

LATITUDE: In a pioneering quantitative analysis of mammalian zoogeography in North America, Simpson (1964) counted species in map quadrats measuring 150×150 miles and drew isopleths of "species density" to illustrate how this quantity covaries with latitude, longitude, and topography. Although not all the mammals in each of Simpson's 22,500-square-mile sampling units are likely to occur together, species density obviously sets an upper bound on sympatric diversity, an upper bound that was shown to increase from less than 40 in Alaska and northern Canada to over 160 in Central America (op. cit.: fig. 1).²⁴ Unfortunately,

most subsequent studies of species density gradients (e.g., Wilson, 1974; McCoy and Connor, 1980; Willig and Selcer, 1989; Willig and Sandlin, 1991; Kaufman, 1995) have analyzed latitudinal effects using statistical methods that are inappropriate for spatially autocorrelated data (Pagel et al., 1991), so calculated regression coefficients and associated significance tests are probably biased (Odland, 1988). However, the temperate-to-

cally underestimated species density at lower latitudes. Whereas mammal faunas in Canada and the United States were reasonably well known by 1959, subsequent collecting has added many new species to the known fauna of Central America. Using updated distributional data (in Hall [1981] and other recent publications), we determined that a 150×150 mile quadrat in eastern Panama (centered at about $8^{\circ}30'N$, $78^{\circ}15'W$) would overlap the geographic ranges of at least 183 species of indigenous, nonaquatic, noninsular mammals, a 12% increase over the highest species density reported by Simpson.

²⁴ The latitudinal gradient is actually steeper than these numbers imply because Simpson's data, based on range maps compiled by Hall and Kelson (1959), systemati-

tropical gradient on both American continents (Kaufman, 1995) is sufficiently obvious from simple scatterplots of species density versus latitude (e.g., Willig and Selcer, 1989: figs. 2–4) that statistical tests to prove the point are superfluous.

Both Wilson (1974), who reanalyzed Simpson's distributional data, and Fleming (1973a), who compared inventory results from North and Central American forests, concluded that nonvolant mammal diversity is essentially unaffected by latitude; according to this interpretation, the conspicuous temperate-to-tropical increase in mammalian species documented by Simpson is largely or exclusively due to bats. Recent studies of species density gradients (e.g., Pagel et al., 1991; Kaufman, 1995) have not supported Wilson's (1974) analytic results, however, and Fleming's (1973a) inventory comparisons are not convincing in the light of subsequent field research. The only tropical sites included in Fleming's data were two Panamanian localities, each sampled by ground-level mist-netting and trapping for just one year (Fleming, 1970, 1971, 1972; Fleming et al., 1972). Although perhaps the best Central American inventories available at the time, methodological considerations and long-term sampling results reviewed herein suggest that Fleming's Panamanian lists are grossly incomplete, perhaps representing no more than 50% of the fauna at each site. In another review of faunal surveys from temperate and tropical habitats, Lacher and Mares (1986) likewise purported to find no evidence for latitudinal trends in nonvolant mammal diversity, but their data are too heterogeneous to support any useful conclusions.²⁵ In fact,

²⁵ Lacher and Mares (1986) claimed that, "Our analysis of species richness is based upon on-site censuses rather than an examination of distribution maps" (op. cit.: 129), but some of their "sites" are large political units (e.g., Malleco Province, Chile; 14,277 km² according to Greer, 1965) and some of their data are, in fact, based on distributional assumptions. For example, their mammal list from a temperate rainforest "site" (western Oregon) was originally compiled from range maps, not census results (Harris et al., 1982). Compounding the difficulty of interpreting such motley information, Lacher and Mares gave only perfunctory attention to sampling effort and none to sampling methods, both of which are crucial problems for any study based (at least in part) on census data. In effect, the faunal studies represented in

no list of sympatric mammals from any temperate locality known to us contains as many nonvolant species as even the least complete tropical rainforest inventory analyzed in this report (i.e., 43 species on the Río Cunucunuma; table 10).

To briefly summarize ordinal diversity data from many sources, lowland rainforests in Central America and tropical South America are conspicuously richer in sympatric marsupials, edentates, bats, and primates than are any habitats at temperate latitudes in the New World. By contrast, latitudinal trends in ungulate and carnivore diversity are less obvious, while insectivore and lagomorph diversities are maximal at middle latitudes in North America. Rodent diversity is likewise high in some mid-latitude habitats (e.g., 17 species on the Cave Creek Bajada in southeastern Arizona; Brown and Zeng, 1989), but no temperate rodent fauna apparently exceeds the diversity documented at many Amazonian rainforest localities (20–27 species; table 9), where even higher numbers could still be expected.

ELEVATION: Except where disturbed by man, forest vegetation on wet tropical mountains dwindles in stature with increasing elevation, to be replaced above treeline by mossy thickets, grasslands, and sphagnum bogs (Richards, 1952; Grubb, 1977). Faunal survey results from southeastern Peru (Pacheco et al., 1993) provide the best available information about mammalian diversity along this habitat gradient (fig. 26). Based on extensive collections and observations in the Río Madre de Dios watershed from 365 to 3450 m, these data illustrate a conspicuous, monotonic decline in diversity of both bats and nonvolant mammals with increasing elevation along the continuously forested part of the transect; above 3000 m, however, nonvolant mammal diversity increases by admixture of grassland species where elfin forest and puna are intermingled at treeline (see Terborgh, 1971, for a description of vegetation along a similar transect in the Apurimac Valley). Although census effort was unevenly

their scatterplots of species richness against latitude (Lacher and Mares, 1986: figs. 1, 2) are incommensurable in methodology, completeness, and spatial scale, providing no basis for meaningful inference.

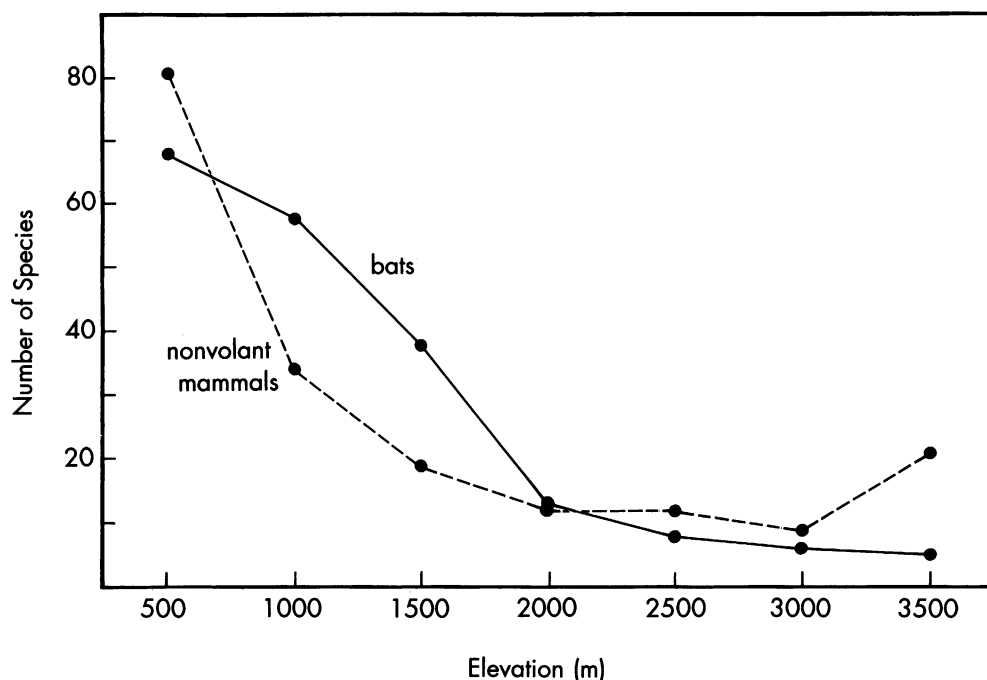


Fig. 26. Diversity of bats and nonvolant mammals along an elevational transect from lowland rainforest to treeline in southeastern Peru. To estimate diversity at each elevational interval (≤ 500 m, 500–1000 m, 1000–1500 m, 1500–2000 m, 2000–2500 m, 2500–3000 m, ≥ 3000 m), species were assumed to be continuously distributed between their known upper and lower limits in the Rio Madre de Dios watershed (Pacheco et al., 1993).

distributed among sampling sites (the middle elevations especially need more work; V. Pacheco, personal commun.), the percentage change in diversity between opposite ends of the transect is unlikely to be substantially affected by future collecting. Whereas distributional data reviewed herein suggest that at least 42 additional species could be expected below 500 m, only about 18 more species are likely to occur between 3000 and 3500 m (based on information in Grimwood, 1969; Graham, 1983; Cadle and Patton, 1988; Pacheco et al., 1993). Thus, the observed decline in mammalian species richness (from 149 species below 500 m to 26 species above 3000 m) and the expected decline (about 191 to 44 species over the same interval) both suggest a net loss of approximately 80% from lowland rainforest to treeline.

Comparable sampling along elevational transects is not available to document mammalian diversity gradients in other mountainous parts of the New World tropics, but

scattered inventory data suggest similar trends: the largest species lists from montane habitats are consistently from foothill sites (e.g., 92 species at 1100 m in eastern Ecuador; Rageot and Albuja, 1994) and the smallest are from much higher elevations (e.g., 20 species at 2800–3300 m in Costa Rica; Wilson, 1983). Distributional data (e.g., Graham, 1983; Hernández-Camacho and Defler, 1983; Bisbal, 1989) are also suggestive: most mammals that occur in lowland rainforest are not known from elevations much above 1500 m and are not replaced by montane forest endemics. Muroid rodents are a notable exception to this trend because many species and genera are endemic to montane habitats, from which available inventory data suggest no consistent elevational decline in muroid diversity (Cadle and Patton, 1988; Voss, 1988: table 43). Although some higher taxa present in montane forests are altogether absent in adjacent lowland habitats (e.g., Caenolestidae, Soricidae), none is very speciose.

ARIDITY: As annual rainfall decreases and dry seasons become increasingly severe along climatic transects in the tropical lowlands, evergreen forests are replaced by deciduous forests, shrublands, and savannas. The minimum annual rainfall necessary to support tropical rainforest is usually estimated to be about 2000 mm, but xeromorphic vegetation can occur on highly permeable soils (which do not retain moisture) in wetter climates, and evergreen forests can extend for hundreds of miles as gallery formations along streams and rivers in regions that receive substantially less precipitation (Richards, 1952; Eiten, 1972; Sarmiento and Monasterio, 1975). Thus, rainfall alone does not completely determine aridity gradients as these affect tropical vegetation and the fauna that inhabits it.

Because the transition from evergreen forest to drier plant formations is intricately associated with local topography and soils, faunal comparisons among biomes delimited on large-scale vegetation maps are often misleading. Mares (1992), for example, used a crude map of continental vegetation (op. cit.: fig. 1) to define the mammal faunas of South American "macrohabitats." Comparing species lists from rainforests and "drylands," he concluded (1) that "drylands" have more species than rainforests, and (2) that rainforests have few endemic species. Yet mammalogists working in the cerrado, the most extensive "dryland" (*sensu* Mares) in tropical South America, have consistently emphasized that evergreen gallery formations, riparian extensions of neighboring Amazonian and Atlantic rainforests, harbor the most speciose mammalian communities in landscapes otherwise covered by faunally depauperate xeromorphic vegetation (Fonseca and Redford, 1984; Alho et al., 1986; Mares et al., 1986; Redford and Fonseca, 1986; Nitikman and Mares, 1987). Such relevant complexities are obscured in Mares' (1992) simplistic and biased analysis.²⁶

²⁶ Although Mares (1992) counted species in "macrohabitats" measuring 10^4 – 10^7 km², not local faunas, his results are frequently cited in contexts that suggest implications for diversity phenomena at other scales. Thus, a recent review of species diversity gradients (Rosenzweig, 1992: 716) cited Mares (1992) to the effect that mammals are most diverse "in arid areas at horse lati-

In fact, no published inventory from any locality in the five principal "drylands" bordering Amazonia (llanos, caatinga, cerrado, pantanal, and chaco) has recorded numbers of sympatric mammals equivalent to those routinely collected or observed with comparable effort at rainforested sites. Instead, the largest existing lists from tropical South American "drylands" (table 14) are consistent with the generalization previously suggested by bat and primate studies (e.g., LaVal and Fitch, 1977; Eisenberg, 1979; Humphrey and Bonaccorso, 1979; Freese et al., 1982; Bourlière, 1985; Fleming, 1986; Reed and Fleagle, 1995) that arid habitats support less diverse mammalian faunas than rainforest. Only a few unspeciose taxa appear to achieve their maximal sympatric diversity in tropical "dryland" habitat mosaics (e.g., dasypodids, canids, and cervids in the cerrado and pantanal; see species lists in Redford [1983] and Schaller [1983]).

GENERALITY AND CAUSES OF OBSERVED DIVERSITY PATTERNS

The data reviewed herein suggest that mammalian communities in western Amazonia are more diverse than those found anywhere else in the Americas and perhaps in the world.²⁷ Extraordinarily high diversity may be a general property of the western Am-

tudes," an astonishing misstatement. Likewise, an article on mammalian community structure in Amazonian Peru (Woodman et al., 1995) considered rainforest mammal diversity as "the subject of current controversy," citing Mares (1992) and subsequent rejoinders. Yet Mares' "macrohabitat" classification is transparently biased, lumping together such disparate nonforest ecosystems as the llanos, caatinga, cerrado, chaco, pampas, páramo, puna, and coastal deserts into a single "drylands" unit for which no faunistic or floristic precedent exists (Chesser and Hackett, 1992). That such a biogeographic gerrymander, extending from the Caribbean to the Straits of Magellan, includes more mammalian species than the Amazonian rainforest is neither surprising nor consequential (except as a tactic to influence research funding priorities; Mares, 1992: 979).

²⁷ A review of Old World inventory data is beyond the scope of this report, but we are not aware of any species lists from African or Asian rainforests that exceed those reported from western Amazonia. The largest appear to be 122 species from a well-studied site in Gabon, and 103 species from an incompletely surveyed locality in Borneo (references in Emmons, 1995: table II).

azonian biota, however, and not a peculiarly mammalian phenomenon: globally maximal diversities have been claimed for western Amazonian communities of birds (Terborgh, 1985a; Robinson and Terborgh, 1990), frogs (Duellman, 1978), odonates (Paulson, 1985), butterflies (Lamas, 1994), robberflies (Fisher, 1985), carabid beetles (Erwin, 1990), ants (Verhaag, 1990), and trees (Gentry, 1988). However, whereas a gradient of generally decreasing diversity from west to east across the hylaea seems reasonably well supported for vertebrates (Duellman, 1988; Haffer, 1990; this report), the data from Amazonian insect and plant surveys are still too sparse to conclude anything other than that species richness at some western Amazonian localities is very high.

The extraordinary diversity of western Amazonian vertebrate communities has been variously attributed to climatic, edaphic, and geomorphological factors.²⁸ Amphibian diversity in the Neotropical lowlands is positively correlated with annual rainfall (Duellman, 1988), which in Amazonia is highest along the northwestern margin of the basin near the base of the Andes and generally decreases to the east and south (Salati, 1985). Some localities in southwestern Amazonia that barely receive the minimum precipitation necessary to sustain rainforest vegetation, however, are the most diverse yet known for birds and mammals (e.g., Cocha Cashu/Pakitza). Consequently, ornithologists and mammalogists have emphasized other environmental factors to explain high diversity for their groups in western Amazonia.

Most western Amazonian study sites are located in the floodplains of meandering white-water rivers that periodically replenish local soils (by lateral channel erosion and deposition) with nutrient-rich sediments weathered from the Andes (e.g., appendix 10). In addition, meandering rivers create complex habitat mosaics of successional vegetation in western Amazonian floodplains (Salo et al., 1986; Puhakka et al., 1992; Puhakka

TABLE 14
Mammalian Diversity at Four Neotropical
"Dryland" Inventory Sites

Site	Rainfall ^b	Biome	Number of species ^a		
			Bats	Non-vol- ant	To- tal
Masaguaral ^c	1450 mm	llanos	42	29	71
El Frio ^d	1400 mm	llanos	34	29	63
Exu ^e	<700 mm	caatinga	35	20	55
Acurizal ^f	1100 mm	pantanal	21	43	64

^a Excluding introduced and aquatic mammals.

^b Annual average, rounded to nearest 50 mm.

^c At 8°34'N, 67°35'W in Estado Guárico, Venezuela; climatic data and habitat information from Troth (1979); mammal list from Eisenberg et al. (1979).

^d At 7°45'N, 68°55'W in Estado Apure, Venezuela; all data from Ibáñez (1981).

^e At 7°31'S, 39°43'W in Estado do Pernambuco, Brazil; annual rainfall estimated from monthly means graphed by Streilein (1982). Our species counts are primarily based on Mares et al.'s (1981) list of mammals from Município Exu (within 21 km radius of Exu), but we include additional bats subsequently identified from Exu material by Williams et al. (1995) and Simmons (1996). Lacher and Mares (1986) reported higher diversity at an unspecified caatinga locality, but their cited sources (all of which describe fieldwork at Exu) do not account for the numbers of species they list (op. cit.: table 3).

^f At 17°45'S, 57°37'W in Estado do Mato Grosso, Brazil; all data from Schaller (1983).

and Kalliola, 1995). Comparably fertile and ecologically heterogeneous landscapes are uncommon in the Guiana subregion and southeastern Amazonia, where nutrient-impo-
verished soils weathered in situ from ancient geological shields are drained by non-meandering black- or clear-water rivers.

Whereas ornithologists have generally emphasized habitat mosaicism in discussing the extraordinary avian diversity of western Amazonian floodplain forests (Terborgh, 1985a; Robinson and Terborgh, 1990), few rainforest mammals exhibit the obvious habitat specializations commonly seen in tropical birds. Although the proximity of different vegetation types is demonstrably important for maintaining mammalian diversity in the seasonal floodplain landscapes of southwestern Amazonia, the crucial factor is perhaps not habitat diversity per se but the temporal con-

²⁸ Historical factors have also been invoked, but in the absence of compelling independent evidence for Pleistocene scenarios (e.g., about the location, duration, and size of putative forest refugia), causal hypotheses are more appropriately based on tangible facts about modern environments.

tinuity of primary production among habitats with asynchronous peaks of fruiting and masting (Janson and Emmons, 1990). If the year-long availability of plant resources is the primary ecological factor regulating mammalian diversity in Neotropical rainforests (Emmons, 1984), and if soil fertility and rainfall jointly determine rainforest primary production (Gentry and Emmons, 1987), then mammalian diversity is probably highest in the ever-wet floodplain forests of northwestern Amazonia (i.e., in southeastern Colombia, eastern Ecuador, northeastern Peru, and adjacent parts of Brazil), not in the seasonal southwestern part of the basin where most inventory work has been done to date.

The other major geographic pattern in our results, of decreasing diversity in Central American lowland rainforests from eastern Panama to southern Mexico, has also been reported for birds (Haffer, 1975, 1987), frogs (Duellman, 1988), and vascular plants (Gentry, 1982a). For amphibians and plants, the Central American diversity gradient is continued southward into the contiguous Chocóan rainforests of Colombia and Ecuador, where the maximal trans-Andean diversity of these groups is probably located (Gentry, 1982a, 1982b; Lynch, 1979). For birds, however, trans-Andean diversity is apparently highest in eastern Panama (Haffer, 1975). The scant data at hand suggest that mammals may follow the avian rather than the amphibian-plant diversity pattern in trans-Andean rainforests.

Central American lowland rainforest plant communities show greater taxonomic resemblance to floras widely distributed in lowland South America than to adjacent montane floras, whose affinities are clearly North American (Gentry, 1982a). The northward decrease in lowland rainforest plant diversity could therefore be explained as the attenuation with distance of an invading Gondwanan flora spreading northward after the closure of the last Pliocene seaway separating Central and South America; alternatively, lowland rainforest plants might have spread northward from a Chocó refugium at a much later date if moist lowland floras in Central America were obliterated by drought during Quaternary glaciations (op. cit.). The first explanation is inapplicable to mammals (because

the rainforest fauna is not Gondwanan in origin), but postglacial dispersion from South America is at least a superficially plausible scenario. On the other hand, Central American rainforest diversity gradients could simply reflect global latitudinal trends or peninsular effects caused by immigration-extinction equilibria (MacArthur and Wilson, 1967) in a biota narrowly bounded at several points by coastlines, mountains, and xeromorphic vegetation. Unfortunately, critical data are not available to discriminate among these nonexclusive alternatives.

DIRECTIONS FOR FUTURE RESEARCH

This review has identified several outstanding problems with the information currently available to assess the magnitude and geographic distribution of mammalian diversity in Neotropical rainforests: (1) the biological limits of many species are problematic in the absence of relevant systematic revisions, (2) geographic distributions are uncertain because most collecting has been concentrated in a few historically accessible areas, and (3) existing inventories are all obviously incomplete and methodologically biased. The following directions for museum and field research are therefore compelling priorities.

REVISIONARY SYSTEMATICS: The lack of modern systematic revisions for dozens of rainforest mammal genera is a major research impediment. Reliable field identifications to species are impossible for many unrevised genera, and even vouchered identifications are problematic if (as is often the case) diagnostic characters have not been adequately described in the primary literature. Although valid estimates of species richness can be based on provisional identifications from competent sorting of specimens collected in sympatry (e.g., "*Marmosops* cf. *impavidus*," "*Oryzomys* sp. A," etc.), such equivocations are not useful for studying other diversity phenomena of crucial interest to researchers and conservationists. For example, measures of biotic distinctness (such as complementarity; Colwell and Coddington, 1994) require decisions about the systematic status of allopatric taxa that can only come from re-

visionary studies. Systematic revisions are also important as authoritative compilations of locality data, the absence of which was a major problem even for the limited goals of this review.

Few (if any) genera of Neotropical rainforest mammals are wholly free of taxonomic problems, but some are much worse than others. The most egregious examples of which we are aware include *Marmosa*, *Marmosops*, *Micoureus*, *Monodelphis*, *Philander*, *Micronycteris*, *Choeroniscus*, *Platyrrhinus*, *Molossus*, *Aotus*, *Microsciurus*, *Sciurus*, *Neacomys*, *Nectomys*, *Oecomys*, *Oryzomys*, *Rhipidomys*, *Coendou*, *Dasyprocta*, *Myoprocta*, *Echimy*s, *Mesomys*, and *Proechimys*. Although descriptions of new species always contribute useful information about biological diversity, what is crucially needed for these genera at this stage of Neotropical mammalogy are comprehensive revisions to convincingly document the biological and geographic limits of the species they are already known to contain. Until such monographs become available, the empirical basis for much diversity research on rainforest mammals will remain unsatisfactory.

SHORT-TERM COLLECTING: Museum collections are the bedrock on which revisionary monographs, field guides, range maps, and other essential resources for biodiversity research are fundamentally based. Yet existing collection resources are inadequate for the urgent task of revising species, illustrating characters for field identification, documenting habitat associations, and mapping geographic distributions. Old specimens are often faded, damaged, incomplete, poorly labelled, and otherwise unsatisfactory, but collecting expeditions to obtain fresh material with better data are now uncommon. Tight research budgets, bureaucratic restrictions on fieldwork, changing fashions in research, and lack of trained personnel are all implicated in the decline of collecting even as the need for more biological survey work has become increasingly apparent.

There is an important role for short-term collecting expeditions in providing crucial diversity data for research and conservation objectives. Many rainforested areas remain essentially unexplored for mammals, either because they were historically inaccessible

(e.g., the headwaters of unnavigable rivers, the territories of hostile indians, etc.) or because they were only visited briefly by collectors using inefficient or biased methods many years ago. The most important of these geographic lacunae should be targeted by an aggressive program of short-term collecting expeditions before habitat destruction makes moot the absence of relevant information for ecologists, biogeographers, and land-use planners.

The usefulness of brief collecting (i.e., by expeditions resident at a single site for several months or less) can be maximized by focusing on taxa known to respond to ecological or zoogeographic gradients and ignoring faunally uninformative groups. In Amazonia, for example, short expeditions should focus on collecting marsupials, primates, bats, and rodents (see above). Suitably documented by records of methods, effort, and habitats, such taxonomically focussed collecting can provide a valid basis for extrapolating diversity trends across vast landscapes from which exhaustive inventories will probably never be available.

EXHAUSTIVE INVENTORIES: Complete (or nearly complete) species lists are indispensable for understanding the ecological organization of sympatric communities, for documenting biogeographic gradients, and as standards for calibrating rapid assessment protocols, to mention just a few applications. Obtaining such lists, however, will inevitably be time-consuming and expensive, so exhaustive inventory projects must be carefully planned.

Planning rainforest inventory fieldwork to obtain mammalian species lists of any specified degree of completeness from scratch (i.e., at previously unworked sites) is difficult because no inventory to date has used a complete array of essential methods (table 3). The best information at hand (from the Cunucunuma, Xingu, and Balta inventories) suggests that 12–15 person-weeks of intensive work by experienced personnel using conventional methods (ground-level trapping and mist-netting plus hunting) may be sufficient to obtain 50% of the expected fauna, but we have no basis for estimating what effort with supplementary methods might be required to achieve, say, 90% completeness. Because the

logistics of obtaining reasonably complete inventory data may largely determine how much we can expect to learn about biogeographic gradients and other diversity phenomena in the near future, research to explore the feasibility of exhaustive sampling is an urgent priority. Projects with this objective should employ all of the methods listed in table 3 to evaluate their merits, alone or in combination, for future work. Heuristic "stop rules" (Collwell and Coddington, 1994: 111) suggest that sampling should continue until all species are represented by multiple specimens or observations.

Perhaps the easiest way to obtain complete species lists is by renewed inventory efforts at the sites selected as exemplars in this review (table 4, fig. 19). New work at those localities should address the methodological deficiencies of earlier surveys (table 6) and focus on detecting the species listed as "missing" for each (see Comments in appendices 2–11). Expected species that remain undetected after enough additional work has been done to discount sampling (or historical extinctions) as plausible explanations may provide evidence for ecological processes that assemble sympatric communities from larger source faunas, or suggest refinements in the criteria used to predict local diversity from range data.

Existing inventory sites, however, are not ideally dispersed to test hypotheses about biogeographic diversity gradients. For example, La Selva and Barro Colorado redundantly sample the eastern Central American

rainforest biota, Arataye and Kartabo are both located in the coastal Guianas, and three sites (Balta, Cocha Cashu/Pakitza, and Cuzco Amazónico) are tightly clustered in southwestern Amazonia. Also, some of these sites no longer have intact faunas, and restrictions on collecting at others preclude adequately vouchered identifications of problematic taxa.

New sites for exhaustive inventories are therefore needed. Although site selection must be guided by practical considerations (accessibility, land ownership, infrastructure, etc.), the primary criterion should be to provide diversity information relevant to well-defined research and conservation objectives. Priority areas from a biogeographic perspective include: (1) any substantial tracts of rainforest with intact faunas in Nicaragua and Honduras (a crucial sampling gap, acutely threatened by development, between established inventory sites in Costa Rica and Chiapas); (2) the Chocoan rainforests of western Colombia and northwestern Ecuador (still perhaps pristine in remote areas and virtually unsampled except by methodologically limited short-term collecting); (3) western Amazonian rainforests north of the Solimões-Marañón (still very extensive but not well sampled for mammals anywhere); (4) southeastern Amazonian rainforests (also very extensive but not well sampled except near Belém, where intact faunas can no longer be expected); and (5) any large surviving fragments of Atlantic rainforest in southeastern Brazil (the least known and most threatened rainforest region in the Neotropics).

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APPENDIX 1

Introduction to the Appendices

The following appendices document the results of mammal inventory work at ten localities in the lowland rainforests of Central and South America. For each locality, we provide essential geographic data (latitude, longitude, elevation above sea level, and compass bearings and distances from prominent landmarks or settlements); we summarize information about local habitats and cite references (if any) that can be consulted for more detailed ecological accounts; we describe the duration of inventory work, explain the inventory methods used (insofar as known), and identify inventory personnel; we list the species collected or observed, indicate where voucher specimens (if any) are deposited, and note emended identifications (for lists previously published elsewhere); finally, we comment on inventory completeness and list species that could still be expected based on their known geographic and ecological distribution.

Obviously, unvouchered field identifications are only as reliable as the fieldworkers who recorded them. Furthermore, it is impossible to guarantee that all vouchered identifications are correct because we could not undertake personally to examine thousands of specimens representing hundreds of species in museums scattered across three continents. We investigated many problematic records, however, and took the following steps to determine correct identifications: (1) We borrowed voucher specimens and examined them ourselves or submitted them to systematists with special expertise. (2) We consulted fieldnotes to determine the observational basis for unvouchered identifications. (3) In the absence of vouchers and fieldnotes, we contacted inventory participants or other project personnel for additional corroborative details. These procedures were sufficient to resolve many problems, but equivocal identifications remain. Whereas names of uncertain application are indicated by the interpolation “cf.,” names not so marked imply conformance with current usage (Wilson and Reeder, 1993; except as noted below).

Our lists exclude aquatic mammals, introduced species, and species that do not occur in undisturbed rainforest but which inhabit savanna enclaves, clearings, and roadsides in otherwise for-

ested areas (e.g., *Liomys adspersus*, *Sigmodon hispidus*, *Zygodontomys brevicauda* on Barro Colorado Island). However, animals collected or observed in buildings, clearings, secondary growth, and other manmade habitats are included if the species is known elsewhere from undisturbed rainforest.

In compiling lists of unrecorded species expected at each locality we applied two criteria. A rainforest species is listed as expected at a given locality if (1) the locality is enclosed by or adjoins an outline connecting marginal records of the species' known range; and (2) the habitat(s) required by the species can reasonably be expected to occur in the immediate area (within a few kilometers), whether or not such habitats were visited by inventory personnel. Because elusive animals generally have larger ranges than available collection records suggest, we tried to correct for this bias with more expansive expectations for rarer species. We were conservative in applying the second criterion: for example, by excluding cave-roosting bats from lists of expected species at localities where caves are unknown. Similarly, species that usually inhabit riverine forest or lakeshore habitats are not listed as expected at upland sites.

Classificatory conventions (nomenclature and taxonomic sequence) in these lists follow Wilson and Reeder (1993) with the following exceptions. (1) We retain the traditional usage of Marsupialia because alternative ordinal-level classifications of metatherians are irrelevant for the Neotropical rainforest species treated herein. (2) We follow Handley (1976), Brosset and Charles-Dominique (1990), and Simmons (1996) in recognizing *Micronycteris megalotis* and *M. microtis* as distinct species documented by sympatric collections from several Amazonian localities. (3) We recognize *Tonatia bidens* and *T. saurophila* as distinct species following Williams et al. (1995). (4) We use Glossophaginae to include lonchophyllines because recent phylogenetic analyses suggest that all nectarivorous phyllostomids form a monophyletic group (Baker et al., 1989; N. B. Simmons and A. L. Peffley, personal commun.) and it is convenient to retain a single name for them in faunal lists and ecological analyses. (5) We follow the species-level

revision of *Artibeus* (*Artibeus*) by Marques (1993) and the species-level taxonomy of *Artibeus* (*Dermanura*) by Handley (1987). (6) We follow Handley (1976), Brosset and Charles-Dominique (1991), and Ochoa et al. (1993) in recognizing *Eptesicus andinus* and *E. brasiliensis* as distinct species distinguished by trenchant character differences maintained in sympatry. (7) We accept the prima facie interpretation of recent biochemical studies (Baker et al., 1988; Morales and Bickham, 1995) that suggest species-level differentiation between Neotropical red bats (*Lasiurus blossevillii*) and northern red bats (*L. borealis*). (8) We follow Dolan (1989) and Handley et al. (1991) in recognizing *Molossus coibensis* and *M. molossus* as distinct species documented by sympatric collections from at least two Panamanian localities. (9) We agree with Handley and Pine (1992) that *Sphiggurus* is indistinguishable from *Coendou*. (10) We retain *Myoprocta* cf. *acouchy* for the red acouchy and *M.* cf. *pratti* for the green acouchy rather than Husson's (1978) inadequately justified alternative taxonomy. (11) We use *Echimyus didelphoides* instead of *Makalata armata* following Emmons (1993c). (12) We refer all named forms of *Mesomys* to *M. hispidus* pending revision of the genus (Emmons, 1994).

The following abbreviations are employed for museum collections where voucher specimens are deposited: AMNH, American Museum of Natural History (New York); BMNH, British Museum of Natural History (London); CIMNH, College of

Idaho Museum of Natural History (Caldwell); FMNH, Field Museum of Natural History (Chicago); INPA, Instituto Nacional de Pesquisas da Amazônia (Manaus); KU, Museum of Natural History, University of Kansas (Lawrence); LACM, Los Angeles County Museum of Natural History (Los Angeles); LSU, Louisiana State University Museum of Zoology (Baton Rouge); MARNR, Ministerio de Agricultura y de los Recursos Naturales Renovables (Maracay); MCZ, Museum of Comparative Zoology at Harvard University (Cambridge); MHNLS, Museo de Historia Natural La Salle (Caracas); MIZA, Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela (Maracay); MNCR, Museo Nacional de Costa Rica (San José); MNHN, Muséum National d'Histoire Naturelle (Paris); MSB, Museum of Southwestern Biology, University of New Mexico (Albuquerque); MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (Lima); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley); MZUSP, Museu de Zoologia, Universidade de São Paulo (São Paulo); UCV, Museo de Biología, Universidad Central de Venezuela (Caracas); ULA, Colección de Vertebrados, Universidad de los Andes (Mérida); UMA, University of Massachusetts Museum of Zoology (Amherst); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); USNM, National Museum of Natural History (Washington, D.C.).

APPENDIX 2

Rainforest Mammals of La Selva and Vicinity

The La Selva Biological Station (10°26'N, 83°59'W) is located at the confluence of the Río Sarapiquí and the Río Puerto Viejo in the Caribbean watershed of Provincia Heredia, Costa Rica (maps in Slud, 1960; Hartshorn, 1983; McDade and Hartshorn, 1994). Owned and operated by the Organization for Tropical Studies (OTS), La Selva includes level and hilly terrain from about 35 to 150 m elevation. Upland soils are derived from in situ weathering of ancient lava flows, but bedrock at lower elevations is overlain by old alluvial terraces and by recent alluvium that is sometimes flooded (Hartshorn, 1983; Sollins et al., 1994). The average annual rainfall is 3962 mm; although some months are consistently wetter than others, none receives an average precipitation of less than 150 mm (Sanford et al., 1994). Nearly two-thirds of the 1536 ha currently held by OTS is covered by undisturbed or selectively logged primary forest (Hammel, 1990; MacDade and Hartshorn, 1994), but the original 730 ha reserve wherein most of

the mammalian faunal inventory efforts were carried out in the 1960s and 1970s is about 90% primary forest (Hartshorn, 1983). Swamps, secondary forests, abandoned pastures, and cacao (*Theobroma cacao*) and pejibaye palm (*Bactris gasipaes*) plantations make up the remainder of the La Selva property. The average height of the primary forest canopy on well-drained terrain is 30–35 m, with scattered emergents reaching 40–55 m; palms are unusually abundant in the understory and subcanopy (Hartshorn, 1983; Hartshorn and Hammel, 1994). Floristic information and comparisons with plant inventories from other Neotropical lowland rainforests are reported by Hammel (1990), Gentry (1990), and Hartshorn and Hammel (1994). Excellent photographs of forest habitats at La Selva were published by Slud (1960).

Observations and collections of mammals at La Selva began when the property was privately owned: the earliest published records date from

1960 (Timm et al., 1989). Bats were intensively surveyed from 1973 to 1974 with mist nets (on 34 nights) and harp traps (76 nights) set at ground level across trails, but some species were taken by hand from their roosts in hollow logs and trees (LaVal and Fitch, 1977). Subsequent bat-netting during OTS courses taught at the station has also contributed significantly to the inventory (Timm et al., 1989; Wilson, 1990), and the understory vegetation has been repeatedly searched for foliage-roosting species (Timm, 1987; Brooke, 1990). Small nonvolant mammals were only trapped systematically on 94 nights from August 1970 to July 1972, when an unspecified number of National live traps (similar in size and design to Tomahawk traps) were baited with corn kernels and placed on the ground in a 4.8 ha grid (Fleming, 1973b). Subsequent knowledge of the nonvolant fauna has accumulated through sightings recorded in a log book (Timm et al., 1989; Wilson, 1990).

The following inventory includes species known from La Selva and nearby Puerto Viejo (3 km N) listed by Timm et al. (1989) and Timm (1994); information about voucher specimens was extracted from Timm et al. (1989). The nomenclature has been updated to conform with current usage (Wilson and Reeder, 1993; but see exceptions noted in appendix 1).

MARSUPIALIA [5 spp.]

Didelphidae

- Caluromys derbianus* (FMNH)
- Chironectes minimus* (UMMZ)
- Didelphis marsupialis*
- Marmosa mexicana* (KU, LACM)
- Philander opossum* (UMMZ)

XENARTHRA [7 spp.]

Bradypodidae

- Bradypus variegatus* (UMMZ)

Megalonychidae

- Choloepus hoffmanni*

Dasypodidae

- Cabassous centralis*
- Dasypus novemcinctus*

Myrmecophagidae

- Cyclopes didactylus*
- Myrmecophaga tridactyla*
- Tamandua mexicana*

CHIROPTERA [65 spp.]

Emballonuridae

- Centronycteris maximiliani* (KU)
- Cormura brevirostris*
- Cyttarops alecto* (LACM)
- Diclidurus albus*
- Peropteryx kappleri* (MSB)
- Rhynchonycteris naso* (MSB)
- Saccopteryx bilineata* (KU, LACM, MSB, UMMZ)
- Saccopteryx leptura* (UMMZ)

Noctilionidae

- Noctilio albiventris* (UMMZ)
- Noctilio leporinus*

Mormoopidae

- Pteronotus davyi* (KU)
- Pteronotus parnellii* (KU, MSB)

Phyllostominae

- Chrotopterus auritus*
- Macrophyllum macrophyllum* (MSB)
- Micronycteris brachyotis*
- Micronycteris daviesi* (KU, MSB)
- Micronycteris hirsuta* (MSB)
- Micronycteris microtis* (KU, LACM, MSB, UMMZ)
- Micronycteris minuta*
- Micronycteris nicefori* (KU)
- Micronycteris schmidtorum*
- Mimon cozumelae* (MSB)
- Mimon crenulatum* (MSB)
- Phylloderma stenops* (KU)
- Phyllostomus discolor*
- Phyllostomus hastatus* (LACM)
- Tonatia brasiliensis* (KU)
- Tonatia saurophila* (KU, MSB)
- Tonatia silvicola*
- Trachops cirrhosus* (MSB)
- Vampyrus spectrum* (KU, MSB)

Glossophaginae

- Choeroniscus godmani*
- Glossophaga commissarisi* (KU, MSB, UMMZ)
- Glossophaga soricina* (KU)
- Hylonycteris underwoodi* (LACM, MSB)
- Lichonycteris obscura* (LACM)
- Lonchophylla robusta* (MSB)

Caroliinae

- Carollia brevicauda* (KU, MSB)
- Carollia castanea* (FMNH, KU, LACM, MSB, UMMZ)
- Carollia perspicillata* (KU, LACM, MSB, UMMZ)

Stenodermatinae

- Artibeus (Artibeus) jamaicensis* (KU, LACM, UMMZ)
- Artibeus (A.) lituratus* (KU, LACM, MSB)
- Artibeus (Dermanura) phaeotis* (KU, MSB)
- Artibeus (D.) watsoni* (FMNH, KU, LACM, MSB, UMMZ)
- Chiroderma villosus* (KU, LACM, UMMZ)
- Ectophylla alba* (KU, LACM, MSB, UMMZ)
- Platyrrhinus helleri* (KU, LACM)
- Sturnira lilium* (UMMZ)
- Sturnira ludovici* (KU)
- Uroderma bilobatum* (FMNH, LACM, MSB, UMMZ)
- Vampyressa nymphaea* (FMNH)
- Vampyressa pusilla* (FMNH, KU, MSB)
- Vampyrodes caraccioli* (KU, MSB)

Desmodontinae
Desmodus rotundus (LACM)
 Furipteridae
Furipterus horrens (KU)
 Thyropteridae
Thyroptera tricolor (LACM)
 Vespertilionidae
Eptesicus andinus
Eptesicus furinalis
Myotis albescens (KU, LACM)
Myotis elegans (KU)
Myotis nigricans (KU, LACM)
Myotis riparius (KU)
Rhogeessa tumida
 Molossidae
Molossus bondae
Molossus sinaloae (KU, UMMZ)
 PRIMATES [4 spp.]
 Cebidae
Alouatta palliata
Aotus cf. lemurinus
Ateles geoffroyi
Cebus capucinus
 CARNIVORA [14 spp.]
 Felidae
Herpailurus yaguarondi
Leopardus pardalis
Leopardus wiedii
Panthera onca
Puma concolor
 Mustelidae
Conepatus semistriatus
Eira barbara
Galictis vittata
Lontra longicaudis
Mustela frenata
 Procyonidae
Bassaricyon gabbii (UMMZ)
Nasua narica
Potos flavus (MVZ)
Procyon lotor
 PERISSODACTYLA [1 sp.]
 Tapiridae
Tapirus bairdii
 ARTIODACTYLA [4 spp.]
 Tayassuidae
Pecari tajacu
Tayassu pecari
 Cervidae
Mazama americana
Odocoileus virginianus
 RODENTIA [16 spp.]
 Sciuridae
Microsciurus alfari (UMMZ)
Sciurus granatensis (UMMZ)
Sciurus variegatoides

Geomyidae
Orthogeomys cherriei
 Heteromyidae
Heteromys desmarestianus (KU, LACM, UMMZ)
 Muridae
Nyctomys sumichrasti (KU, MSB)
Melanomys caliginosus (UMMZ)
Oligoryzomys fulvescens (KU)
Oryzomys bolivaris (UMMZ)
Sigmodontomys alfari (UMMZ)
Tylomys watsoni
 Erethizontidae
Coendou mexicanus (MNCR)
 Dasyproctidae
Dasyprocta punctata
 Agoutidae
Agouti paca
 Echimyidae
Hoplomys gymnurus (KU, UMMZ)
Proechimys semispinosus (KU, UMMZ)
 LAGOMORPHA [1 sp.]
 Leporidae
Sylvilagus brasiliensis (UMMZ)

Comments: The continuous presence of resident and visiting researchers at La Selva for over three decades is probably responsible for the apparently complete roster of large mammals. Among the smaller nonvolant fauna, however, at least two marsupials (*Metachirus nudicaudatus*, *Micoureus alstoni*) and one rodent (*Oryzomys talamancae*) could still be expected; their absence from the current list is possibly due to the lack of any intensive trapping efforts since Fleming's (1973b) methodologically limited survey.²⁹ A conservative list of expected bats (excluding cave-roosting species, the proximity of suitable roosts for which is unknown) includes many high-flying species, for which appropriate capture methods have apparently never been used at La Selva: *Peropteryx macrotis*, *Micronycteris sylvestris*, *Artibeus hartii*, *Centurio senex*, *Mesophylla macconnelli*, *Diaemus youngi*, *Diphylla ecaudata*, *Thyroptera discifera*, *Lasiurus blossevillii*, *Lasiurus castaneus*, *Lasiurus ega*, *Eumops auripendulus*, *Eumops hansae*, *Molossops greenhalli*, *Nyctinomops laticaudatus*, *Promops centralis*, *Molossus ater*, *Molossus molossus* (18 total).

²⁹ Because *Oryzomys talamancae* is superficially similar to *O. bolivaris*, it might have gone unrecognized among the animals released in Fleming's (1973b) live-trapping study; only a few specimens of *Oryzomys* taken in removal lines located away from the live-trapping grid were apparently preserved as vouchers.

APPENDIX 3

Rainforest Mammals of Barro Colorado Island and Vicinity

Barro Colorado Island (BCI; 9°09'N, 79°51'W) was isolated from the Panamanian mainland sometime between 1910 and 1914 as the impounded waters of the Río Chagres rose to form Gatun Lake, part of the Panama Canal system; the island was declared a reserve in 1923 and since 1946 has been administered by the Smithsonian Institution (Leigh, 1982; Leigh and Wright, 1990). BCI is a 1500 ha hilltop that rises 137 m above the lake, or about 162 m above sea level. From a central plateau with nutrient-impoverished oxisols weathered from andesitic basalt, steep slopes dissected by narrow ravines descend through a variety of sedimentary formations to the shoreline (Dietrich et al., 1982; Leigh and Wright, 1990). Annual rainfall is about 2600 mm, 90% of which occurs from May to December (Dietrich et al., 1982; Rand and Rand, 1982). The island is almost entirely covered with evergreen forest,³⁰ about half of which is perhaps about a century old; the remainder has probably been undisturbed for at least 200–400 years and possibly much longer (Enders, 1935; Foster and Brokaw, 1982; Leigh and Wright, 1990). Clearings now account for less than 1% of the island's area (Foster and Hubbell, 1990) but were formerly more extensive (Enders, 1935). Canopy trees in the older forest are mostly between 30 and 40 m tall, with occasional emergents to almost 50 m (Foster and Brokaw, 1982). Floristic studies of the forest on BCI were reviewed by Foster and Hubbell (1990), and photographs are provided in Croat's (1978) magnificent monograph.

Although earlier collections and observations were made by W. C. Allee, T. Barbour, F. M. Chapman, J. Van Tyne, J. Zetek, and others, mammalian faunal studies on BCI effectively began with R. K. Enders' surveys from 1929 to 1937 (Enders, 1930, 1935, 1939). Enders trapped (at ground level) and hunted (in the daytime and at night) to collect voucher material, but most subsequent studies of the nonvolant fauna (e.g., Eisenberg and Thorington, 1973; Glanz, 1982, 1990; Wright et al., 1994) have relied on sight-census methods. Mist nets were used by mammalogists on BCI as early as 1952 (Hall and Jackson, 1953)

and have since been deployed intensively together with harp traps to sample the understory bat community (Bonaccorso, 1979; Handley et al., 1991). Enders (1935) and others also collected bats by hand in hollow trees, buildings, and foliage. Recently, the BCI bat fauna has been censused with night vision scopes and ultrasonic microphones (E. Kalko and C. O. Handley, Jr., personal commun.). Despite this varied and prolonged history of inventory work, the known fauna of the island is obviously an incomplete sample of the rainforest mammals of the central Chagres valley (see Comments, below). We have, therefore, expanded the geographic scope of the inventory to include collections from mainland localities in the Barro Colorado Nature Monument (BCNM; map in Leigh and Wright, 1990), one adjacent island, and three historical collecting stations inundated by Gatun Lake (none are more than 5 km from BCI): Bohio (= Bohio Soldado, 9°10'N, 79°51'W; now submerged); Bohio Peninsula (9°12'N, 79°50'W); Buena Vista Peninsula (9°11'N, 79°50'W); Frijoles (9°10'N, 79°48'W); Orchid Island (9°11'N, 79°51'W); San Pablo (9°06'N, 79°48'W; now submerged); and Tabernilla (= Tavernilla, 9°07'N, 79°49'W; now submerged).

The list below incorporates a number of substantive changes from recent compilations of the BCI fauna by Glanz (1982, 1990) and Handley et al. (1991) as follow. (1) Four species of bats recently detected on the island are included (*Diclidurus albus*, *Peropteryx* sp., *Lasiurus* sp., *Natalus stramineus*; E. Kalko and C. O. Handley, Jr., personal commun.) as are four others collected on the adjacent mainland or at localities now submerged beneath Gatun Lake (see above; *Tonatia brasiliensis*, *Eptesicus furinalis*, *Eumops auripendulus*, *Molossus sinaloae*). (2) *Ateles geoffroyi* is omitted because there are no specimens or historical records to prove that indigenous populations of spider monkeys occurred in the vicinity of BCI; the group now inhabiting the island is descended from animals introduced in the early 1960s (Eisenberg and Kuehn, 1966). (3) *Galictis vittata* is included on the basis of an unambiguous but hitherto unpublished sighting in 1959 by W. J. Smith (personal commun.). (4) Enders' (1935) sighting of *Bassariscus sumichrasti* on nearby Orchid Island (see above) is included because no other identification is plausible despite the absence of museum specimens from any locality in central Panama. (5) *Procyon lotor*, listed as a member of the Barro Colorado fauna by Eisenberg and Thorington (1973) and by Glanz (1990), is excluded; the orig-

³⁰ Barro Colorado Island occupies an ecotone between the wetter evergreen forests of the Caribbean coast and the drier semideciduous forests of the Pacific coast (see Fleming, 1971, for relevant descriptions of forest habitats and phenology at either end of this gradient). Most of the trees in the Barro Colorado forest are evergreen; only a small fraction are even facultatively deciduous (Foster and Brokaw, 1982).

inal observation was equivocal (J. F. Eisenberg, in litt.) and no other local sightings of the species have been reported. (6) Three nonforest rodents that Enders (1935) collected only in clearings are excluded (*Liomys adspersus*, *Sigmodon hispidus*, *Zygodontomys brevicauda*) as are two nonnative muroids (*Mus musculus*, *Rattus rattus*). (7) One rodent (*Tylomys panamensis*) reported by Eisenberg and Thorington (1973) but omitted from subsequent lists (Glanz, 1982, 1990) is included because the unique sighting was unambiguous (Thorington, personal commun.).

MARSUPIALIA [6 spp.]

Didelphidae

- Caluromys derbianus* (USNM)
- Chironectes minimus*
- Didelphis marsupialis* (UMMZ, USNM)
- Marmosa robinsoni* (FMNH, UMMZ, USNM)
- Metachirus nudicaudatus* (USNM)
- Philander opossum* (USNM)

XENARTHRA [6 spp.]

Bradypodidae

- Bradypus variegatus* (FMNH, MSB, UMMZ, USNM)

Megalonychidae

- Choloepus hoffmanni* (FMNH, MSB, USNM)

Dasypodidae

- Cabassous centralis* (photo: Ingles, 1954)
- Dasypus novemcinctus* (UMMZ)

Myrmecophagidae

- Cyclopes didactylus* (FMNH, MCZ, UMMZ)
- Tamandua mexicana* (FMNH, UMMZ)

CHIROPTERA [64 spp.]

Emballonuridae

- Centronycteris maximiliani* (USNM)
- Cormura brevirostris* (AMNH, USNM)
- Diclidurus albus* (recorded calls)
- Peropteryx* sp. (recorded calls)
- Rhynchonycteris naso* (USNM)
- Saccopteryx bilineata* (AMNH, ANSP, MSB, UMMZ, USNM)
- Saccopteryx leptura* (UMMZ)

Noctilionidae

- Noctilio albiventris* (USNM)
- Noctilio leporinus*

Mormoopidae

- Pteronotus gymnonotus* (MSB, USNM)
- Pteronotus parnellii* (MSB, UMMZ, USNM)

Phyllostominae

- Chrotopterus auritus*
- Macrophyllum macrophyllum* (MSB, USNM)
- Micronycteris brachyotis* (MSB, USNM)
- Micronycteris hirsuta* (MSB, USNM)
- Micronycteris microtis* (AMNH, FMNH, MSB, UMMZ, USNM)
- Micronycteris nicefori* (USNM)

- Micronycteris schmidtorum* (USNM)
- Mimon crenulatum* (USNM)
- Phylloderma stenops* (USNM)
- Phyllostomus discolor* (UMMZ, USNM)
- Phyllostomus hastatus* (USNM)
- Tonatia brasiliensis* (USNM)
- Tonatia saurophila* (MSB, USNM)
- Tonatia silvicola* (MSB, USNM)
- Trachops cirrhosus* (MSB, USNM)
- Vampyrum spectrum* (USNM)

Glossophaginae

- Glossophaga commissarisi* (FMNH, USNM)
- Glossophaga soricina* (AMNH, USNM)
- Lonchophylla robusta* (USNM)

Caroliinae

- Carollia brevicauda* (MCZ)
- Carollia castanea* (MSB, USNM)
- Carollia perspicillata* (AMNH, ANSP, MSB, UMMZ, USNM)

Stenodermatinae

- Ametrida centurio* (USNM)
- Artibeus (Artibeus) jamaicensis* (AMNH, UMMZ, USNM)
- Artibeus (A.) lituratus* (USNM)
- Artibeus (Dermanura) phaeotis* (MSB, USNM)
- Artibeus (D.) watsoni* (AMNH, USNM)
- Artibeus (Enchisthenes) hartii* (USNM)
- Centurio senex* (USNM)
- Chiroderma villosum* (MSB, USNM)
- Mesophylla macconnelli*
- Platyrrhinus helleri* (MSB, USNM)
- Sturnira luisi* (USNM)
- Uroderma bilobatum* (USNM)
- Uroderma magnirostrum* (USNM)
- Vampyressa nymphaea* (USNM)
- Vampyressa pusilla* (MSB, USNM)
- Vampyrodes caraccioli* (AMNH, MSB, USNM)

Desmodontinae

- Desmodus rotundus* (MSB, USNM)

Natalidae

- Natalus stramineus*

Thyropteridae

- Thyroptera discifera* (USNM)
- Thyroptera tricolor* (MCZ, USNM)

Vespertilionidae

- Eptesicus furinalis* (USNM)
- Lasiurus* sp. (recorded calls)
- Myotis albescens* (MSB, UMMZ, USNM)
- Myotis nigricans* (AMNH, ANSP, MCZ, MSB, UMMZ, USNM)
- Rhogeessa tumida* (USNM)

Molossidae

- Eumops auripendulus* (USNM)
- Molossus bondae* (USNM)
- Molossus coibensis* (FMNH, MSB, USNM)
- Molossus molossus* (USNM)

Molossus sinaloae (UMA)
Nyctinomops laticaudatus (MSB)
PRIMATES [4 spp.]
 Callitrichidae
Saguinus oedipus (UMMZ, USNM)
 Cebidae
Alouatta palliata (MSB, USNM)
Aotus lemurinus (USNM)
Cebus capucinus (USNM)
CARNIVORA [13 spp.]
 Felidae
Herpailurus yaguarondi
Leopardus pardalis (UMMZ, USNM)
Leopardus wiedii
Panthera onca
Puma concolor (photos: Chapman, 1927, 1929)
 Mustelidae
Eira barbara (UMMZ, USNM)
Galictis vittata
Lontra longicaudis
 Procyonidae
Bassaricyon gabbii
Bassariscus sumichrasti
Nasua narica (FMNH, UMMZ, USNM)
Potos flavus (MCZ, UMMZ, USNM)
Procyon cancrivorus
PERISSODACTYLA [1 sp.]
 Tapiridae
Tapirus bairdii (photos: Chapman, 1927, 1929)
ARTIODACTYLA [4 spp.]
 Tayassuidae
Pecari tajacu (UMMZ, USNM)
Tayassu pecari (photos: Chapman, 1927, 1929)
 Cervidae
Mazama americana
Odocoileus virginianus
RODENTIA [14 spp.]
 Sciuridae
Microsciurus alfari (UMMZ)
Sciurus granatensis (FMNH, UMMZ, USNM)
 Heteromyidae
Heteromys desmarestianus (FMNH, MCZ, UMMZ)
 Muridae
Oecomys bicolor (UMMZ)
Oecomys trinitatis (UMMZ)
Oligoryzomys fulvescens (USNM)
Oryzomys talamancae (FMNH, MSB, UMMZ, USNM)
Tylomys panamensis
 Erethizontidae
Coendou rothschildi (UMMZ, USNM)
 Hydrochaeridae
Hydrochaeris hydrochaeris (USNM)
 Dasyproctidae
Dasyprocta punctata (UMMZ, USNM)

Agoutidae
Agouti paca (UMMZ)
 Echimyidae
Diplomys labilis
Proechimys semispinosus (FMNH, MSB, UMMZ, USNM)
LAGOMORPHA [1 sp.]
 Leporidae
Sylvilagus brasiliensis (USNM)

Comments: Although BCI and its immediate environs have been visited by scores of competent collectors and observers since 1911 (the date of E. A. Goldman's first visit), several circumstances are probably responsible for the surprising number of unrecorded species expected in the area (below). First, most faunal survey work has been done on the island itself, an isolated hilltop that lacks swamps, large permanent streams, tangled riparian growth, and other habitats normally present at rainforest localities with more varied topography. Numerous mammalian extinctions have been documented on BCI (Glanz, 1990), and extinctions of unrecorded species have doubtless also occurred. Thus, the island's mammal fauna is probably impoverished for the same reasons (reduced habitat diversity plus extinctions) believed responsible for the conspicuously depauperate insular avifauna (Willis, 1974; Karr, 1982, 1990). Second, some essential sampling methods have seldom been used and others have never been attempted. For example, there have been no effective trapping programs on the island (or elsewhere, to our knowledge, within the BCNM) since Enders' early survey,³¹ and the canopy has never been effectively netted for bats (C. O. Handley, Jr., in litt.). Finally, local rainforest habitats were far from pristine when faunal sampling was initiated by Goldman in 1911: French efforts to excavate an interoceanic canal had begun 30 years before (McCullough, 1977), and subsequent construction along the entire route was probably accompanied by more-or-less persistent hunting, with predictably dire consequences for vulnerable elements of the larger fauna.

Unrecorded nonvolant mammals expected to occur (or to have occurred historically) in the vicinity of Barro Colorado Island include one marsupial (*Micoureus* cf. *phaea*), three large species probably long extirpated from the area (*Myrme-*

³¹ A recent trapping study (McClearn et al., 1994) on Gigante Peninsula (a mainland locality just a few hundred meters from BCI) used a diversity of traps set from ground level to 20 m above the ground in trees. Although 2212 trap-nights were logged in this project and trap success was average for Neotropical rainforest surveys, only five species of mammals were recorded (of about 21 potentially catchable with the bait and equipment used).

cophaga tridactyla, *Ateles geoffroyi*, *Speothos venaticus*), three carnivores (*Procyon lotor*, *Conepatus semistriatus*, *Mustela frenata*), and four rodents (*Ichthyomys tweedii*, *Nyctomys sumichrasti*, *Sigmodontomys alfari*, *Hoplomys gymnurus*). A conservative list of expected bats (excluding cave-roosting species, the proximity of suitable roosts for which is unknown) includes some understory species that may be extinct on the island as well as high-flying taxa for which appropriate collecting efforts have never been made: *Cyttarops alecto*, *Peropteryx* sp. (recorded calls could be those of *P.*

kappleri or *P. macrotis*, both of which are expected), *Micronycteris daviesi*, *Micronycteris minuta*, *Micronycteris sylvestris*, *Lichonycteris obscura*, *Choeroniscus godmani*, *Sturnira lilium*, *Diaemus youngi*, *Diphylla ecuadata*, *Furipterus horrens*, *Eptesicus andinus*, *Lasiurus* spp. (recorded calls could be those of *L. blossevillii*, *L. ega*, or *L. egregius*, all of which could be expected), *Myotis riparius*, *Eumops hansae*, *Molossops greenhalli*, *Molossops planirostris*, *Promops centralis*, and *Molossus ater* (20 total).

APPENDIX 4

Nonvolant Rainforest Mammals of Kartabo and Vicinity

The British Guiana Tropical Research Station at Kartabo, Guyana, was founded by the New York Zoological Society (NYZS) in 1916 and operated until 1924 as a base for five expeditions, each of about seven months duration, that collected zoological specimens and recorded ecological data over the entire annual climatic cycle (Osborn, 1925). The following description of the physical and biotic environment at Kartabo is mostly abstracted from Beebe's (1925) summary report, which contains photographs of local habitats. Popular accounts of field research at or near Kartabo (Beebe, 1918, 1921, 1923b) include additional photographs but little text of any biological substance.

The laboratories and surrounding research area at Kartabo occupied the apex of land (Kartabu Point on recent maps; 6°23'N, 58°41'W) between the Cuyuni (a black-water river) and the Mazaruni (with clear water), about 10 km upstream from the confluence of the latter with the Essequibo and approximately 72 km from the coast (maps in Anthony, 1921; Beebe, 1925). The gently undulating local terrain averages about 9–15 m above sea level; local soils are sands and clays weathered from an underlying granitic bedrock. Twenty years of records from two weather stations only 5 km downstream from Kartabo document a local average annual rainfall of 2550 mm, of which slightly over half falls during five "wet" months (January, May, June, July, and December), but no month receives an average rainfall of less than 100 mm. Except for a narrow zone of littoral growth along the river banks (including mangroves between the tide marks), the local vegetation at the time of the NYZS expeditions consisted of tall, well-drained primary rainforest, old secondary growth, and palm swamps. No explicit measurements of canopy height in the primary forest were published, but many remarks imply that 100 ft (ca. 30 m) was an average value with emergents not uncommonly to 150 ft (ca. 45 m).

Mammals reported from the vicinity of Kartabo by Anthony (1921) and Beebe (1925) were collected or observed within about a 3 mile (4.8 km) radius. About 700 specimens of nonvolant species were shot or trapped by Beebe or by the Akawaio hunters he employed; at least a few rodents were taken in pitfalls, but other methodological details are unknown. Unfortunately, the trivial numbers of bats obtained are inadequate for faunal comparisons.³² Localities other than Kartabo written on Beebe's specimen labels are "Bartica" (6°24'N, 58°37'W), "Kalacoon" (6°24'N, 58°39'W), and "Penal Settlement" (with the same coordinates as Kalacoon, but on the opposite bank of the Mazaruni). All of the vouchered identifications cited below are represented by specimens from Kartabo except *Cyclopes didactylus*, *Potos flavus*, *Procyon cancrivorus*, and *Oecomys roberti*, which were taken at the other localities mentioned above; the last (from Bartica) was not collected by Beebe. The holotype of *Bassaricyon beddardi* may have been collected at Bartica (Tate, 1939), but the locality given in the original description (Pocock, 1921) was spelled "Bastrica" and, in the absence of other specimens, we omit the species from the present list.

Our emendations of previously published inventories of the Kartabo fauna (Anthony, 1921; Beebe, 1925) include two species recently discovered among AMNH voucher specimens from the project (*Caluromys philander*, *Neusticomys venezuelae*) and one (*Oecomys roberti*) from previously unreported BMNH material (G. G. Musser, personal commun.). A few corrected identifications and numerous nomenclatural changes are also incorporated (see Wilson and Reeder, 1993, for obsolete synonyms).

³² Hill's (1964) list of 31 bat species from a forest reserve 24–27 mi SSE Kartabo appears to be the closest geographic sample of chiropteran diversity.

MARSUPIALIA [7 spp.]

Didelphidae

- Caluromys philander* (AMNH)
- Chironectes minimus*
- Didelphis marsupialis* (AMNH)
- Marmosa murina* (AMNH)
- Metachirus nudicaudatus* (AMNH)
- Micoureus demerarae* (AMNH)
- Monodelphis brevicaudata* (AMNH)

XENARTHRA [9 spp.]

Bradyrodidae

- Bradypus tridactylus* (AMNH)

Megalonychidae

- Choloepus didactylus* (AMNH)

Dasypodidae

- Cabassous unicinctus* (AMNH)
- Dasypus kappleri* (AMNH)
- Dasypus novemcinctus* (AMNH)
- Priodontes maximus* (AMNH)

Myrmecophagidae

- Cyclopes didactylus* (AMNH)
- Myrmecophaga tridactyla* (AMNH)
- Tamandua tetradactyla* (AMNH)

PRIMATES [6 spp.]

Callitrichidae

- Saguinus midas* (AMNH)

Cebidae

- Alouatta seniculus* (AMNH)
- Ateles paniscus*
- Cebus olivaceus* (AMNH)
- Pithecia pithecia* (AMNH)
- Saimiri sciureus* (AMNH)

CARNIVORA [13 spp.]

Canidae

- Speothos venaticus*

Felidae

- Herpailurus yagouaroundi* (AMNH)
- Leopardus pardalis* (AMNH)
- Leopardus wiedii* (AMNH)
- Panthera onca* (AMNH)
- Puma concolor*

Mustelidae

- Eira barbara* (AMNH)
- Galictis vittata*
- Lontra longicaudis* (AMNH)
- Pteronura brasiliensis*

Procyonidae

- Nasua nasua* (AMNH)
- Potos flavus* (AMNH)
- Procyon cancrivorus* (AMNH)

PERISSODACTYLA [1 sp.]

Tapiridae

- Tapirus terrestris* (AMNH)

ARTIODACTYLA [4 spp.]

Tayassuidae

- Pecari tajacu* (AMNH)
- Tayassu pecari* (AMNH)

Cervidae

- Mazama americana* (AMNH)
- Mazama gouazoubira* (AMNH)

RODENTIA [20 spp.]

Sciuridae

- Sciurillus pusillus*
- Sciurus aestuans* (AMNH)

Muridae

- Neacomys guianae* (AMNH)
- Nectomys squamipes* (AMNH)
- Neusticomys venezuelae* (AMNH)
- Oecomys bicolor* (AMNH)
- Oecomys paricola* (AMNH)
- Oecomys rex* (AMNH)
- Oecomys roberti* (BMNH)
- Oecomys rutilus* (AMNH)
- Oryzomys capito* (AMNH)
- Oryzomys macconnelli* (AMNH)
- Rhipidomys nitela* (AMNH)

Erethizontidae

- Coendou melanurus* (AMNH)

Hydrochaeridae

- Hydrochaeris hydrochaeris* (AMNH)

Dasypodidae

- Dasypoda leporina* (AMNH)
- Myopoda acouchy* (AMNH)

Agoutidae

- Agouti paca* (AMNH)

Echimyidae

- Echimyus didelphoides* (AMNH)
- Proechimyus cuvieri* (AMNH)

Comments: Most of the unrecorded nonvolant species expected at Kartabo are small and/or arboreal, Beebe's Akawaio hunters having obtained virtually all of the anticipated larger fauna. Species that could yet be expected include at least three more marsupials (*Didelphis imperfecta*, *Marmosops parvidens*, *Philander opossum*), one primate (*Chiropotes satanas*), one carnivore (*Bassaricyon gabbii*), and six rodents (*Oecomys trinitatis*, *Oligoryzomys fulvescens*, *Oryzomys yunganus*, *Coendou prehensilis*, *Mesomys hispidus*, *Proechimyus cayennensis*). No plausible explanation can be given for the absence of these taxa in Beebe's collections because essential details of his inventory methods are unknown.

A conservative tabulation of expected bats for Kartabo (omitting cave-roosting taxa for which suitable refugia are probably absent) includes 96 species.

APPENDIX 5

Rainforest Mammals of the Lower Arataye

Crique Arataye, a tributary of the Approuague, drains a large and virtually uninhabited black-water catchment in the lowlands of east-central French Guiana. Two localities in the lower Arataye basin (both on the left side of the river) have been the foci of long-term ecological studies by mammalogists from the Muséum National d'Histoire Naturelle (MNHN): Les Nouragues (4°05'N, 52°40'W; ca. 210 m elevation) and Saut Pararé (4°02'N, 52°42'W; ca. 40 m). Both field stations are in pristine evergreen forest far removed from resident human populations (there are no roads or villages in a radius of about 50 km; Brosset and Charles-Dominique, 1990). Fifteen years of weather records from Régina (about 70 km NE of Saut Pararé) document an average annual rainfall of 3700 mm (Dubost, 1988), but mean annual rainfall at Les Nouragues from 1988 to 1989 was only 2750 mm (Sarhou and Grimaldi, 1992). Adjacent to the field station at Les Nouragues is a high (ca. 400 m) granitic formation with caves, fissured cliffs, and a skirting talus of large boulders (Brosset and Charles-Dominique, 1990). The forest understory is very open and the canopy has an average height of about 30 m, with occasional emergents to 40 m (Guillotin, 1982). The locally dominant families of trees are Burseraceae, Chrysobalanaceae, Lecythidaceae, and Mimosaceae (Guillotin, 1982; Dubost, 1988), which (with Sapotaceae) are also the most important tree families cataloged in an extensive botanical survey near Saül, about 70 km to the southwest (Mori and Boom, 1987).

The list below includes published records (Guillotin, 1982; Guillotin and Petter, 1984; Dubost, 1988; Brosset and Charles-Dominique, 1990; Julien-Laferrère, 1991; Guillotin et al., 1994) and data from unpublished collections and observations (by P. Charles-Dominique, G. Dubost, L. H. Emmons, and M. Guillotin). Brosset and Charles-Dominique's (1990) inventory of the bat fauna, one of the most complete available from any Neotropical locality, was accomplished over 11 years (1979–1990); with subsequent fieldwork, a total of 2119 bat captures have been recorded at Les Nouragues (P. Charles-Dominique, in litt.). Although most bats were taken in mist nets (set at ground level and in canopy gaps 20–30 m above the ground), additional species were discovered by searching for roosts in foliage, hollow trees, caves, and heaps of boulders. Research on nonvolant mammals began in 1977 at Saut Pararé, where Guillotin (1982) and Julien-Laferrère (1991) used live traps (Tomahawks and Shermans) and snap traps set at or near ground level to sample the rodent and marsupial fauna. Emmons trapped and

hunted at night to collect nonvolant species and used mist nets (at ground level) to collect bats; her collections and observations were made on the right bank of the Arataye about 5 km downstream from Saut Pararé from 24 September to 22 October 1984, and from 30 June to 30 July 1988.

Our list incorporates numerous nomenclatural changes from the literature cited above (see Wilson and Reeder, 1993, for obsolete synonyms).

MARSUPIALIA [9 spp.]

Didelphidae

- Caluromys philander* (MNHN)
- Chironectes minimus*
- Didelphis marsupialis* (MNHN)
- Marmosa murina* (MNHN, USNM)
- Marmosops parvidens* (MNHN, USNM)
- Metachirus nudicaudatus* (MNHN, USNM)
- Micoureus demerarae* (MNHN, USNM)
- Monodelphis brevicaudata* (MNHN, USNM)
- Philander opossum* (MNHN)

XENARTHRA [8 spp.]

Bradyrodidae

- Bradypus tridactylus*

Megalonychidae

- Choloepus didactylus*

Dasypodidae

- Dasypus kappleri*
- Dasypus novemcinctus*
- Priodontes maximus*

Myrmecophagidae

- Cyclopes didactylus*
- Myrmecophaga tridactyla*
- Tamandua tetradactyla*

CHIROPTERA [61 spp.]

Emballonuridae

- Cormura brevirostris* (MNHN)
- Diclidurus scutatus* (MNHN)
- Peropteryx macrotis* (MNHN)
- Saccopteryx bilineata* (MNHN)
- Saccopteryx leptura* (MNHN)

Mormoopidae

- Pteronotus parnellii* (MNHN)

Phyllostominae

- Chrotopterus auritus* (USNM)
- Lonchorhina cf. marinkellei* (MNHN)
- Macrophyllum macrophyllum*
- Micronycteris megalotis* (MNHN)
- Micronycteris nicefori* (MNHN)
- Micronycteris sylvestris* (MNHN)
- Mimon bennettii*
- Mimon crenulatum* (MNHN)
- Phylloderma stenops* (USNM)
- Phyllostomus discolor* (MNHN)
- Phyllostomus elongatus* (MNHN, USNM)

- Phyllostomus hastatus* (USNM)
Phyllostomus latifolius (MNHN)
Tonatia saurophila (USNM)
Tonatia schulzi
Tonatia silvicola
Trachops cirrhosus (MNHN, USNM)
Vampyrum spectrum (MNHN)
- Glossophaginae**
- Anoura caudifera* (MNHN)
Anoura geoffroyi (MNHN)
Choeroniscus intermedius (MNHN)
Glossophaga soricina (USNM)
Lionycteris spurrelli (MNHN)
Lonchophylla thomasi (MNHN)
- Caroliinae**
- Carollia brevicauda* (MNHN, USNM)
Carollia perspicillata (MNHN, USNM)
Rhinophylla pumilio (MNHN, USNM)
- Stenodermatinae**
- Ametrida centurio* (MNHN)
Artibeus (Artibeus) jamaicensis (MNHN)
Artibeus (A.) lituratus (MNHN)
Artibeus (A.) obscurus (MNHN, USNM)
Artibeus (Dermanura) gnomus (MNHN)
Artibeus (Koopmania) concolor (MNHN)
Chiroderma trinitatum (MNHN)
Chiroderma villosus (MNHN)
Mesophylla macconnelli (MNHN)
Platyrrhinus helleri (MNHN)
Platyrrhinus lineatus (MNHN)
Sturnira lilium (MNHN)
Sturnira tildae (MNHN, USNM)
Uroderma bilobatum (MNHN)
Vampyressa bidens (MNHN)
Vampyressa brocki (MNHN)
Vampyressa cf. melissa (MNHN)
Vampyressa pusilla (MNHN)
- Desmodontinae**
- Desmodus rotundus* (MNHN)
- Thyropteridae**
- Thyroptera tricolor*
- Vespertilionidae**
- Myotis nigricans* (MNHN)
Myotis riparius (MNHN)
- Molossidae**
- Eumops hansae* (MNHN)
Molossops greenhalli (MNHN)
Molossops planirostris (MNHN)
Molossus ater
Molossus molossus
Nyctinomops laticaudatus (MNHN)
- PRIMATES [7 spp.]**
- Callitrichidae**
- Saguinus midas*
- Cebidae**
- Alouatta seniculus*
Ateles paniscus
Cebus apella
Cebus olivaceus
Pithecia pithecia
Saimiri sciureus
- CARNIVORA [11 spp.]**
- Canidae**
- Speothos venaticus*
- Felidae**
- Herpailurus yaguarondi*
Leopardus pardalis
Leopardus wiedii
Panthera onca
Puma concolor
- Mustelidae**
- Eira barbara*
Galictis vittata
Lontra longicaudis
- Procyonidae**
- Nasua nasua*
Potos flavus
- PERISSODACTYLA [1 sp.]**
- Tapiridae**
- Tapirus terrestris*
- ARTIODACTYLA [4 spp.]**
- Tayassuidae**
- Pecari tajacu*
Tayassu pecari
- Cervidae**
- Mazama americana*
Mazama gouazoubira
- RODENTIA [21 spp.]**
- Sciuridae**
- Sciurillus pusillus* (MNHN, USNM)
Sciurus aestuans (MNHN, USNM)
- Muridae**
- Neacomys guianae* (MNHN)
Nectomys squamipes (MNHN)
Oecomys paricola (MNHN)
Oecomys rex (MNHN)
Oligoryzomys fulvescens (MNHN, USNM)
Oryzomys capito (MNHN, USNM)
Oryzomys macconnelli (MNHN, USNM)
Oryzomys yunganus (MNHN)
Rhipidomys leucodactylus (MNHN)
- Erethizontidae**
- Coendou prehensilis*
- Hydrochaeridae**
- Hydrochaeris hydrochaeris*
- Dasyproctidae**
- Dasyprocta leporina*
Myoprocta acouchy
- Agoutidae**
- Agouti paca*
- Echimyidae**
- Echimys chrysurus* (MNHN)
Echimys didelphoides (MNHN)
Mesomys hispidus (USNM)
Proechimys cayennensis (MNHN, USNM)
Proechimys cuvieri (MNHN, USNM)

Comments: The long residence of mammalogists at this pristine locality is doubtless responsible for the small number of nonvolant species yet expected to occur in the area; these include only one marsupial (*Didelphis imperfecta*), one xenarthran (*Cabassous unicinctus*), one carnivore (*Procyon cancrivorus*), and six rodents (*Neusticomys oya-pocki*, *Oecomys bicolor*, *Oecomys roberti*, *Oecomys rutilus*, *Oecomys trinitatis*, *Coendou melanurus*). A substantial number of unrecorded bats, however, are also expected (suitable roosts for cavernicolous species are present at Les Nouragues); most are high-flying species or small understory insectivores: *Centronycteris maximiliani*, *Cyttarops alecto*, *Peropteryx kappleri*, *Peropteryx leu-*

coptera, *Rhynchonycteris naso*, *Saccopteryx canescens*, *Noctilio albiventris*, *Noctilio leporinus*, *Pteronotus personatus*, *Micronycteris brachyotis*, *Micronycteris daviesi*, *Micronycteris hirsuta*, *Micronycteris microtis*, *Micronycteris minuta*, *Micronycteris schmidtorum*, *Tonatia brasiliensis*, *Tonatia carrikeri*, *Lichonycteris obscura*, *Artibeus cinereus*, *Vampyroides caraccioli*, *Diaemus youngi*, *Natalus stramineus*, *Furipterus horrens*, *Thyroptera discifera*, *Eptesicus andinus*, *Eptesicus furinalis*, *Lasiurus blossevillii*, *Lasiurus ega*, *Lasiurus egregius*, *Myotis albesens*, *Eumops auripendulus*, *Eumops perotis*, *Molossops abrasus*, *Promops centralis* (34 total).

APPENDIX 6

Rainforest Mammals of the Río Cunucunuma

The Río Cunucunuma, a black-water tributary of the upper Orinoco, drains an undulating valley bordered by high, cliff-sided, sandstone mountains of the Guiana Shield. M. D. Tuttle and F. L. Harder, field collectors working for the Smithsonian Venezuelan Project (SVP), visited the Yekuana (Maquiritare) indian village of Culebra (= "Belén"; 3°39'N, 65°46'W) at 150 m elevation on the left bank of the Río Cunucunuma,³³ where they collected 1506 mammals from 30 December 1966 to 21 February 1967 (Handley, 1976). Tuttle and Harder also trained Yekuanas from the nearby village of Acanaña (about 13 km SSW of Culebra) to collect and preserve specimens; 80 mammals obtained by these native collectors are also part of the SVP material reported herein. Tuttle's unpublished fieldnotes (in the USNM Division of Mammals archives) provide the basis for the following description of the local environment and collecting methods.

The Río Cunucunuma valley near Culebra is about 4 km wide, bordered to the south by Cerro Duida and to the north by Cerro Guachamacari; Cerro Marahuaca lies about 5 km to the east. Except for garden plots and secondary growth around the village, and a small patch of natural savanna at the base of Cerro Duida, the local vegetation is

undisturbed evergreen forest with a canopy estimated to be 18–37 m tall (photographs in Delascio, 1993). Local forest streams were described by Tuttle as being either clear or "red," the latter presumably tannin-stained rather than clouded by eroded soil (which would be unlikely in an almost pristine, forested catchment).

Bats were collected intensively with ground-level mist nets and harp traps, and by searching for roosts, activities that are described by the bulk of Tuttle's fieldnotes. Small nonvolant species were taken in banana-baited National and Rinker live traps set on the ground, or in Museum Specials (baited with bananas or sardines) in trees (Handley, in litt.). Steel leg-hold traps, set for carnivores, were baited with skinned carcasses of birds or monkeys. Monkeys and most other larger mammals were shot. The methods employed by the Yekuana collectors at Acanaña were not recorded.

The list below includes all of the species reported from "Belén" and Acanaña by Handley (1976) except *Zygodontomys brevicauda*, a nonforest murid rodent that was only collected in the savanna, gardens, and houses; we also include *Chironectes minimus* and *Priodontes maximus*, whose distinctive prints were observed by Tuttle. New collections from Culebra by Venezuelan researchers have produced several additional species: *Ametrida centurio* and *Artibeus lituratus* (Guerrero et al., 1989), *Phyllostomus hastatus* (Guerrero, in litt.), and *Scleronycteris ega* (Ochoa et al., 1993). Other emendments are a few corrected identifications and several purely nomenclatural changes (see Wilson and Reeder, 1993, for obsolete synonyms).

MARSUPIALIA [8 spp.]

Didelphidae

Caluromys lanatus (MARNR, USNM)

³³ According to Delascio (1993) and R. Guerrero (in litt.), this village is properly known as Culebra (in Spanish) or Mawadianejödo (in Yekuana). "Belén" was apparently used only by American missionaries living at Culebra in the 1960s, presumably those who hosted Tuttle and Harder. Delascio (1993) gives the coordinates of Culebra as 3°40'N, 65°45'W; the elevation as 220 m; and the estimated annual rainfall as 2000–3000 mm. The isohyets mapped by Snow (1976: fig. 10), however, suggest an average annual rainfall of about 3500 mm.

- Caluromys philander* (MARNR, USNM)
Chironectes minimus
Didelphis marsupialis (MARNR, USNM)
Marmosa murina (USNM)
Micoureus demerarae (USNM)
Monodelphis brevicaudata (MARNR, USNM)
Philander andersoni (MARNR, USNM)
- XENARTHRA** [7 spp.]
- Megalonychidae**
Choloepus didactylus (MARNR, USNM)
- Dasypodidae**
Dasyus kappleri (USNM)
Dasyus novemcinctus (MARNR, USNM)
Prionotes maximus
- Myrmecophagidae**
Cyclopes didactylus (USNM)
Myrmecophaga tridactyla (MARNR, USNM)
Tamandua tetradactyla (MARNR, USNM)
- CHIROPTERA** [50 spp.]
- Emballonuridae**
Cormura brevirostris (MARNR, USNM)
Peropteryx macrotis (MARNR, USNM)
Rhynchonycteris naso (MARNR, USNM)
Saccopteryx bilineata (MARNR, USNM)
Saccopteryx leptura (MARNR, USNM)
- Noctilionidae**
Noctilio leporinus (MARNR, USNM)
- Mormoopidae**
Pteronotus parnellii (USNM)
- Phyllostominae**
Chrotopterus auritus (MARNR, USNM)
Lonchorhina sp. (USNM)
Macrophyllum macrophyllum (USNM)
Micronycteris megalotis (MARNR, USNM)
Micronycteris microtis (MARNR, USNM)
Micronycteris schmidtorum (MARNR, USNM)
Phylloderma stenops (MARNR, USNM)
Phyllostomus elongatus (USNM)
Phyllostomus hastatus (UCV)
Tonatia silvicola (MARNR, USNM)
- Glossophaginae**
Anoura caudifera (MARNR, USNM)
Glossophaga soricina (MARNR, USNM)
Lionycteris spurrelli (USNM)
Scleronycteris ega (MHNLS)
- Carollinae**
Carollia brevicauda (MARNR, USNM)
Carollia perspicillata (MARNR, USNM)
Rhinophylla pumilio (MARNR, MIZA, USNM)
- Stenodermatinae**
Ametrida centurio (MIZA)
Artibeus (Artibeus) amplus (MARNR, USNM)
Artibeus (A.) jamaicensis (MARNR, USNM)
Artibeus (A.) lituratus (UCV, ULA)
Artibeus (A.) obscurus (MARNR, USNM)
Artibeus (Dermanura) glaucus (USNM)
Artibeus (D.) gnomus (MARNR, USNM)
- Artibeus (Koopmania) concolor* (MARNR, USNM)
Chiroderma trinitatum (MARNR, USNM)
Chiroderma villosum (MARNR, USNM)
Mesophylla macconnelli (MARNR, USNM)
Platyrrhinus helleri (MARNR, USNM)
Sturnira lilium (MARNR, USNM)
Sturnira tildae (MARNR, USNM)
Uroderma bilobatum (MARNR, USNM)
Vampyressa bidens (MARNR, USNM)
Vampyrodes caraccioli (MARNR, USNM)
- Desmodontinae**
Desmodus rotundus (MARNR, USNM)
- Furipteridae**
Furipterus horrens (USNM)
- Thyropteridae**
Thyroptera tricolor (USNM)
- Vespertilionidae**
Eptesicus brasiliensis (USNM)
Myotis albescentis (MARNR, USNM)
Myotis nigricans (USNM)
- Molossidae**
Molossus ater (MARNR, USNM)
Molossus molossus (USNM)
Nyctinomops laticaudatus (MARNR, USNM)
- PRIMATES** [7 spp.]
- Cebidae**
Alouatta seniculus (MARNR, USNM)
Aotus trivirgatus (MARNR, USNM)
Callicebus torquatus (MARNR, USNM)
Cebus olivaceus (MARNR, USNM)
Chiropotes satanas (MARNR, USNM)
Pithecia pithecia
Saimiri sciureus (MARNR, USNM)
- CARNIVORA** [7 spp.]
- Felidae**
Leopardus pardalis (MARNR, USNM)
Leopardus wiedii (MARNR, USNM)
Panthera onca (MARNR, USNM)
- Mustelidae**
Eira barbara (USNM)
Lontra longicaudis (USNM)
- Procyonidae**
Nasua nasua (USNM)
Potos flavus (MARNR, USNM)
- PERISSODACTYLA** [1 sp.]
- Tapiridae**
Tapirus terrestris (USNM)
- ARTIODACTYLA** [2 spp.]
- Tayassuidae**
Tayassu pecari (USNM)
- Cervidae**
Mazama americana (USNM)
- RODENTIA** [11 spp.]
- Sciuridae**
Sciurus igniventris (MARNR, USNM)
- Muridae**
Nectomys squamipes (MARNR, USNM)
Oecomys bicolor (MARNR, USNM)

Oecomys concolor (MARNR, USNM)

Rhipidomys leucodactylus (USNM)

Erethizontidae

Coendou prehensilis (MARNR, USNM)

Dasyproctidae

Dasyprocta cf. *fuliginosa* (MARNR, USNM)

Myoprocta cf. *pratti* (USNM)

Agoutidae

Agouti paca (MARNR, USNM)

Echimyidae

Mesomys cf. *hispidus* (MARNR, USNM)

Proechimys cf. *cayennensis* (MARNR, USNM)

Comments: The brief duration of sustained fieldwork at this locality is reflected in a very long list of unrecorded mammals expected to occur in the area. Among the nonvolant fauna, these include three marsupials (*Didelphis imperfecta*, *Marmosops parvidens*, *Metachirus nudicaudatus*), two xenarthrans (*Bradypus variegatus*, *Cabassous unicinctus*), two primates (*Ateles belzebuth*, *Cebus apella*), six carnivores (*Speothos venaticus*, *Herpailurus yagouaroundi*, *Puma concolor*, *Galictis vittata*, *Bassaricyon gabbii*, *Procyon cancrivorus*), two ungulates (*Pecari tajacu*, *Mazama gouazoubira*), and 14 rodents (*Sciurus gilvularis*, *Neacomys guianae*, *Neusticomys venezuelae*, *Oecomys roberti*, *Oecomys trinitatis*, *Oligoryzomys fulvescens*, *Oryzomys capito*, *Oryzomys macconnelli*, *Oryzomys yunganus*, *Coendou melanurus*, *Hydrochaeris hydrochaeris*, *Echimys didelphoides*, *Isothrix bis-triata*, *Proechimys amphichoricus*). The list of bats

yet to be expected is also extensive, especially given the likely presence of suitable refugia for cave- and fissure-roosting species in the cliff-sided mountains nearby; although many are elusive small-bodied insectivores or high-flying taxa (for which no special collecting efforts were apparently made), some are easily netted understory species: *Centronycteris maximiliani*, *Cyttarops alecto*, *Di-clidurus albus*, *Diclidurus ingens*, *Diclidurus isabellus*, *Diclidurus scutatus*, *Peropteryx kappleri*, *Peropteryx leucoptera*, *Saccopteryx canescens*, *Noctilio albiventris*, *Pteronotus davyi*, *Pteronotus gymnonotus*, *Pteronotus personatus*, *Micronycteris brachyotis*, *Micronycteris daviesi*, *Micronycteris hirsuta*, *Micronycteris minuta*, *Micronycteris nicefori*, *Micronycteris sylvestris*, *Mimon bennettii*, *Mimon crenulatum*, *Phyllostomus discolor*, *Phyllostomus latifolius*, *Tonatia brasiliensis*, *Tonatia carrikeri*, *Tonatia saurophila*, *Trachops cirrhosus*, *Vampyrus spectrum*, *Anoura geoffroyi*, *Choeroniscus godmani*, *Choeroniscus minor*, *Lichonycteris obscura*, *Lonchophylla thomasi*, *Carollia castanea*, *Artibeus hartii*, *Platyrrhinus brachycephalus*, *Sphaeronycteris toxophyllum*, *Uroderma magnirostrum*, *Vampyressa brocki*, *Vampyressa pusilla*, *Diaemus youngi*, *Natalus tumidirostris*, *Thyroptera discifera*, *Eptesicus furinalis*, *Lasiurus blossevillei*, *Lasiurus ega*, *Myotis riparius*, *Eumops auripendulus*, *Eumops hansae*, *Eumops perotis*, *Molossops abrasus*, *Molossops planirostris*, *Neoplatymops mattogrossensis*, *Promops centralis*, *Promops nasutus* (55 total).

APPENDIX 7

Nonvolant Rainforest Mammals of the MCSE Reserves

The Minimum Critical Size of Ecosystems (MCSE) reserves (ca. 2°30'S, 60°W) are located from 60 to 90 km north of Manaus at an elevation of about 80 m in the Brazilian state of Amazonas; the reserves are part of the Distrito Agropecuario, which comprises approximately 500,000 ha of relatively undisturbed upland forests currently under development by the Manaus Free Trade Zone Authority, SUFRAMA (Lovejoy and Bierregaard, 1990; Rankin de Mérona et al., 1992). The local climate is presumably similar to that of Manaus, where the annual average rainfall is about 2200 mm and where monthly mean rainfall is less than 100 mm during a dry season that extends from July through September (Lovejoy and Bierregaard, 1990). The MCSE reserves occupy hilly terrain drained by small black-water streams; hillside soils are predominantly aluminum-rich clays (red-yellow podzols and yellow latosols), but low-lying areas have sandy soil (Rankin de Mérona et al., 1992). Because the reserves are far removed from

major rivers and associated riparian formations, the local forests are exclusively terra firme growth. The understory vegetation, dominated by small trees and seedling palms (op. cit.), appears very open by comparison with other Amazonian localities (Emmons, 1984; Gentry and Emmons, 1987). The canopy has an average height of 30–37 m, with occasional emergents to over 50 m (Lovejoy and Bierregaard, 1990). Preliminary botanical inventories of the upland forests north of Manaus are described by Prance (1990) and Rankin de Mérona et al. (1992); Gentry (1990) discusses floristic comparisons with other Neotropical rainforests.

Hunting pressure on the mammalian fauna of the MCSE reserves is light and restricted to roadsides; within most of the continuously forested areas sampled by Emmons (1984) and Malcolm (1988, 1990, 1991a, 1991b), the fauna appears to be essentially unaffected by human activities. Malcolm's (1990) summary report provides detailed

descriptions of his live-trapping and nocturnal sight census methods from 1983 to 1987; his work was exemplary for the systematic use of arboreal traps, which were set at an average height of almost 15 m. Adding Malcolm's (1990) records of trapping and census to those from Emmons' (1984) survey (which was carried out in 1982), mammal inventory efforts on the MCSE reserves total about 45,000 trap-nights and 416 km of walked transect census. Unfortunately, most trapped animals were released and sighted animals were not collected; thus, only a small number of vouchers are available to document field identifications.

Bats have not been systematically sampled in the MCSE reserves. Reis and Peracchi (1987) reported 52 species from the vicinity of Manaus, but their collections are too geographically and ecologically heterogeneous to be included here.

Our list below differs from Malcolm's (1990) by including two new records (*Leopardus pardalis*, *Oecomys rex*), a few corrected identifications, and some purely nomenclatural changes (see Wilson and Reeder, 1993, for obsolete synonyms). Voucher specimens (at INPA and USNM) are either labelled with the project initials MCSE (or PDBFF, for Projeto Dinamica Biologica de Fragmentos Florestais) or with the names of fazendas and experimental plots mapped by Lovejoy and Bierregaard (1990) and Rankin de Mérona et al (1992).

MARSUPIALIA [9 spp.]

Didephidae

- Caluromys lanatus* (INPA)
- Caluromys philander* (INPA, USNM)
- Didelphis marsupialis* (INPA)
- Marmosa murina* (INPA, USNM)
- Marmosops parvidens* (INPA, USNM)
- Metachirus nudicaudatus* (INPA, USNM)
- Micoureus demerarae* (INPA, USNM)
- Monodelphis brevicaudata* (INPA, USNM)
- Philander opossum* (INPA)

XENARTHRA [8 spp.]

Bradypodidae

- Bradypus tridactylus*

Megalonychidae

- Choloepus didactylus*

Dasypodidae

- Dasypus kappleri*
- Dasypus novemcinctus*
- Priodontes maximus*

Myrmecophagidae

- Cyclopes didactylus*
- Myrmecophaga tridactyla*
- Tamandua tetradactyla*

PRIMATES [6 spp.]

Callitrichidae

- Saguinus midas*

Cebidae

- Alouatta seniculus*

Ateles paniscus

Cebus apella

Chiropotes satanas

Pithecia pithecia

CARNIVORA [8 spp.]

Canidae

- Speothos venaticus*

Felidae

- Leopardus pardalis*
- Panthera onca*
- Puma concolor*

Mustelidae

- Eira barbara*
- Lontra longicaudis*

Procyonidae

- Nasua nasua*
- Potos flavus*

PERISSODACTYLA [1 sp.]

Tapiridae

- Tapirus terrestris*

ARTIODACTYLA [4 spp.]

Tayassuidae

- Pecari tajacu*
- Tayassu pecari*

Cervidae

- Mazama americana*
- Mazama gouazoubira*

RODENTIA [17 spp.]

Sciuridae

- Sciurus gilvularis*

Muridae

- Neacomys guianae* (INPA, USNM)
- Oecomys bicolor* (INPA, USNM)
- Oecomys paricola* (INPA, USNM)
- Oecomys rex* (INPA)
- Oryzomys capito* (INPA, USNM)
- Oryzomys macconnelli* (INPA, USNM)
- Rhipidomys nitela* (INPA, USNM)

Erethizontidae

- Coendou prehensilis*

Dasyproctidae

- Myoprocta cf. acouchy*
- Dasyprocta leporina*

Agoutidae

- Agouti paca*

Echimyidae

- Echimys cf. chrysurus* (INPA)
- Isothrix pagurus* (INPA)
- Mesomys cf. hispidus* (INPA)
- Proechimys cuvieri* (INPA, USNM)
- Proechimys cf. cayennensis* (INPA, USNM)

Comments: Despite colossal trapping and sight census efforts at this locality, a few nonvolant mammals are still to be expected. A conservative list (excluding species restricted to riverine and lakeshore habitats) includes one marsupial (*Chironectes minimus*), one armadillo (*Cabassous unicinctus*), one primate (*Cebus olivaceus*), three car-

nivores (*Herpailurus yagouaroundi*, *Leopardus wiedii*, *Galictis vittata*), and eight rodents (*Nectomys squamipes*, *Oecomys concolor*, *Oecomys roberti*, *Oecomys trinitatis*, *Oligoryzomys fulvescens*, *Oryzomys yunganus*, *Coendou melanurus*, *Echimys didelphoides*). Some of these species are elusive, and others favor habitats that were perhaps not effectively sampled by trapping and census (e.g., small streams, swampy growth, secondary vegetation). The expected species of *Oecomys* and *Ory-*

zomys are hard for nonspecialists to identify in the field, so some or all of them may have been captured and released unrecognized. Only the absence of *Cebus olivaceus* lacks a plausible methodological explanation.

A conservative list of expected bats (excluding cave-roosting species, suitable refugia for which are probably not locally available) includes 91 species.

APPENDIX 8

Rainforest Mammals of the Lower Rio Xingu

Mammals were intensively collected on the lower Rio Xingu (a clear-water river) in 1986 as part of an attempt to evaluate the biological impact of a proposed hydroelectric construction project. Four experienced fieldworkers from the Smithsonian Institution and the U.S. Fish and Wildlife Service (M. D. Carleton, L. H. Emmons, L. K. Gordon, and D. E. Wilson) participated in the inventory at various intervals from 13 August through 23 October, for a total of 180 collector-days of effort. The following account is abstracted verbatim from an unpublished summary report:

The principal area censused was on the east [right] bank of the Rio Xingu, upriver from the proposed dam site near Altamira. The base camp itself [at 110 m elevation] was located 52 km SSW Altamira (3°39'S, 52°22'W) and served as the focus for field work within a 3–5 km radius, including up- and downriver localities and the large island (Ilha Jabuti) opposite the base camp, which were reached by boat. Short-term visits of one or two days were made to the Iriri camp (85 km SW Altamira, 3°50'S, 52°40'W) near the confluence of the Rio Iriri and Rio Xingu, as well as to two cave sites situated 9 and 17 km south of Altamira.

The dominant vegetation in the area surveyed can be categorized as tropical evergreen rainforest. Within this broad formation, several more or less distinctive vegetational complexes were sampled: seasonally flooded forest (várzea) near the banks and on the islands;³⁴ unflooded forest (terra firme) on upper, better drained slopes; palm swamps, both with and without a dense herbaceous understory; and viny forest, usually with a relatively low canopy and often intermixed with close stands of bamboo. The distinctiveness of these plant associations and their intergradation seemed dependent on local edaphic factors and drainage patterns. In addition to primary forest habitats, some collecting was carried out in areas modified through human activities, including active and abandoned banana groves, orchards, overgrown fields, and buildings.

³⁴ In Prance's (1979) now-standard terminology for Amazonian flooded forests, those periodically inundated by clear-water rivers like the Xingu are properly called seasonal igapó.

Mammal specimens were collected by kill-trapping (Museum Specials, rat traps, Conibears), live-trapping (Shermans, Nationals), shooting (night and day hunting), and mist-netting. Since the survey was intended to document as much of the mammal fauna as feasible, collecting efforts were aimed at sampling a variety of habitats with sustained removal trapping and netting. . . .

Although much of the region consists of primary forest, the area surveyed has clearly been subjected to subsistence hunting by seringueiros and local farmers. The lack of sign for many large carnivores and the apparent rarity of mammals such as deer, tapir, and capybara probably reflects this hunting pressure.

It is relevant to note that, although many arboreal rats and marsupials were shot, no traps were placed high (> 3 m above the ground) in trees. All bats were collected by mist-netting at ground level (ca. 0–3 m) with the exception of a few taken by hand from their diurnal roosts.

In the list provided below, we include only the species collected or observed around the base camp (50–54 km SSW Altamira, including Ilha Jabuti). Voucher specimens from this project deposited at MZUSP may have been relabelled with the place-name "Cachoeira do Espelho."

MARSUPIALIA [8 spp.]

Didelphidae

Caluromys philander (MZUSP, USNM)

Didelphis marsupialis (MZUSP, USNM)

Marmosa murina (MZUSP, USNM)

Marmosops parvidens (MZUSP, USNM)

Metachirus nudicaudatus (MZUSP, USNM)

Micoureus demerarae (MZUSP, USNM)

Monodelphis brevicaudata (MZUSP, USNM)

Philander opossum (MZUSP, USNM)

XENARTHRA [4 spp.]

Bradypodidae

Bradypus variegatus (MZUSP)

Megalonychidae

Choloepus didactylus (MZUSP)

Dasypodidae

Dasypus novemcinctus (MZUSP, USNM)

- Myrmecophagidae
Tamandua tetradactyla (MZUSP)
 CHIROPTERA [47 spp.]
 Emballonuridae
Peropteryx macrotis (MZUSP, USNM)
Rhynchonycteris naso (MZUSP, USNM)
Saccopteryx bilineata (MZUSP, USNM)
Saccopteryx canescens (MZUSP)
Saccopteryx leptura (MZUSP, USNM)
 Noctilionidae
Noctilio albiventris (MZUSP, USNM)
 Mormoopidae
Pteronotus parnellii (MZUSP, USNM)
 Phyllostominae
Chrotopterus auritus (MZUSP, USNM)
Macrophyllum macrophyllum (MZUSP)
Micronycteris daviesi (MZUSP)
Micronycteris cf. megalotis (MZUSP)
Micronycteris nicefori (MZUSP, USNM)
Micronycteris sylvestris (MZUSP)
Phyllostomus discolor (MZUSP)
Phyllostomus elongatus (MZUSP, USNM)
Phyllostomus hastatus (MZUSP, USNM)
Tonatia brasiliensis (MZUSP)
Tonatia saurophila (MZUSP)
Tonatia silvicola (MZUSP, USNM)
Trachops cirrhosus (MZUSP, USNM)
 Glossophaginae
Anoura caudifera (MZUSP, USNM)
Choeroniscus minor (MZUSP, USNM)
Glossophaga soricina (MZUSP, USNM)
Lonchophylla thomasi (MZUSP, USNM)
 Carollinae
Carollia perspicillata (MZUSP, USNM)
Rhinophylla fischeriae (MZUSP, USNM)
Rhinophylla pumilio (MZUSP)
 Stenodermatinae
Artibeus (Artibeus) jamaicensis (MZUSP, USNM)
Artibeus (A.) lituratus (MZUSP, USNM)
Artibeus (A.) obscurus (MZUSP, USNM)
Artibeus (Dermanura) cinereus (MZUSP, USNM)
Artibeus (D.) gnomus (MZUSP, USNM)
Artibeus (Koopmania) concolor (MZUSP, USNM)
Chiroderma villosum (MZUSP)
Mesophylla macconnelli (MZUSP, USNM)
Platyrrhinus helleri (MZUSP, USNM)
Sturnira lilium (MZUSP, USNM)
Sturnira tildae (MZUSP, USNM)
Uroderma bilobatum (MZUSP, USNM)
Uroderma magnirostrum (MZUSP, USNM)
Vampyressa brocki (MZUSP, USNM)
 Desmodontinae
Desmodus rotundus (MZUSP, USNM)
Diphylla ecaudata (USNM)
- Furipteridae
Furipterus horrens (MZUSP, USNM)
 Vespertilionidae
Myotis albescentis (MZUSP, USNM)
Myotis riparius (MZUSP, USNM)
 Molossidae
Neoplatymops mattogrossensis (MZUSP)
 PRIMATES [7 spp.]
 Callitrichidae
Saguinus midas (MZUSP, USNM)
 Cebidae
Alouatta belzebul (USNM)
Aotus infulatus (MZUSP)
Callicebus moloch
Cebus apella (MZUSP)
Chiropotes satanas (MZUSP, USNM)
Saimiri sciureus
 CARNIVORA [2 spp.]
 Procyonidae
Nasua nasua (MZUSP)
Potos flavus (MZUSP)
 PERISSODACTYLA [1 sp.]
 Tapiridae
Tapirus terrestris
 ARTIODACTYLA [2 spp.]
 Tayassuidae
Pecari tajacu
 Cervidae
Mazama americana
 RODENTIA [23 spp.]
 Sciuridae
Sciurus gilvularis (MZUSP, USNM)
 Muridae
Neacomys guianae (MZUSP, USNM)
Nectomys squamipes (MZUSP)
Oecomys bicolor (MZUSP, USNM)
Oecomys paricola (MZUSP, USNM)
Oecomys roberti (MZUSP, USNM)
Oecomys trinitatis (USNM)
Oryzomys capito (MZUSP, USNM)
Oryzomys nitidus (MZUSP, USNM)
Oxymycterus amazonicus (MZUSP)
Rhipidomys mastacalis (MZUSP, USNM)
 Erethizontidae
Coendou prehensilis (MZUSP, USNM)
 Hydrochaeridae
Hydrochaeris hydrochaeris
 Dasyproctidae
Dasyprocta leporina (MZUSP, USNM)
Myoprocta acouchy
 Agoutidae
Agouti paca (MZUSP, USNM)
 Echimyidae
Dactylomys dactylinus (MZUSP, USNM)
Echimys chrysurus (MZUSP, USNM)
Echimys didelphoides (MZUSP, USNM)
Mesomys hispidus (MZUSP, USNM)

Proechimys cuvieri (MZUSP, USNM)

Proechimys goeldii (MZUSP, USNM)

Proechimys oris (MZUSP, USNM)

LAGOMORPHA [1 sp.]

Leporidae

Sylvilagus brasiliensis (MZUSP, USNM)

Comments: The brief duration of inventory work and the local impact of subsistence hunting are doubtless responsible for the long list of mammals that could yet be expected at this locality. Among the nonvolant fauna these include two marsupials (*Chironectes minimus*, *Monodelphis emiliae*), five xenarthrans (*Cabassous unicinctus*, *Dasylops kappleri*, *Priodontes maximus*, *Cyclops didactylus*, *Myrmecophaga tridactyla*), one primate³⁵ (*Calithrix argentata*), 12 carnivores (*Atelocynus microtis*, *Speothos venaticus*, *Herpailurus yagouaroni*, *Leopardus pardalis*, *Leopardus wiedii*, *Panth-*

³⁵ The distribution of primates between the Xingu and Tocantins was recently reviewed by Ferrari and Lopes Ferrari (1990) who provided additional records of *Calithrix argentata* to supplement the single collection locality previously known from this area (Hershkovitz, 1977). Although the type locality of *Ateles belzebuth marginatus* was restricted by Kellogg and Goldman (1944) to Cametá (on the left bank of the lower Tocantins), no specimens or modern sightings are apparently known from anywhere east of the Xingu and the historical occurrence of spider monkeys in the area seems doubtful (Martins et al., 1988).

era onca, *Puma concolor*, *Eira barbara*, *Galictis vittata*, *Lontra longicaudis*, *Mustela africana*, *Procyon cancrivorus*), two ungulates (*Tayassu pecari*, *Mazama gouazoubira*), and four rodents (*Oligoryzomys microtis*, *Oryzomys yunganus*, *Coendou koopmani*, *Echimys grandis*). The list of expected bats (excluding cave-roosting species, suitable refugia for which may be locally unavailable) predictably includes many high-flying species (for which no appropriate collecting methods were used) but also a large number of elusive understory insectivores: *Centronycteris maximiliani*, *Coromura brevirostris*, *Cyttarops alecto*, *Diclidurus albus*, *Diclidurus scutatus*, *Peropteryx kappleri*, *Peropteryx leucoptera*, *Noctilio leporinus*, *Micronycteris brachyotis*, *Micronycteris hirsuta*, *Micronycteris microtis*, *Micronycteris minuta*, *Micronycteris schmidtorum*, *Mimon crenulatum*, *Phylloderma stenops*, *Tonatia carrikeri*, *Vampyrus spectrum*, *Lichonycteris obscura*, *Lionycteris spurrelli*, *Carollia brevicauda*, *Ametrida centurio*, *Chiroderma trinitatum*, *Sphaeronycteris toxophyllum*, *Vampyressa bidens*, *Vampyrodes caraccioli*, *Diaemus youngi*, *Thyroptera discifera*, *Thyroptera tricolor*, *Eptesicus brasiliensis*, *Eptesicus furinalis*, *Lasiurus blossevillii*, *Lasiurus ega*, *Myotis nigricans*, *Myotis simus*, *Eumops auripendulus*, *Eumops hansae*, *Eumops perotis*, *Molossops abrasus*, *Molossops planirostris*, *Molossus ater*, *Molossus molossus*, *Nyctinomops laticaudatus* (42 total).

APPENDIX 9

Rainforest Mammals of Balta

The Cashinahua indian village of Balta (10°08'S, 71°13'W; ca. 300 m elevation), in Departamento Ucayali (formerly Loreto), Peru, was visited by field biologists from Louisiana State University (and elsewhere), who made extensive collections of local birds and mammals from 1963 to 1971. Except as noted, the following account of the physical and biotic environment is abstracted from O'Neill's (1974) dissertation on the avifauna.

Balta sits in the level floodplain of the Río Curanja (a white-water tributary of the Río Alto Purús), but smaller streams (known to the Cashinahua as the Inuya and Xumuya) drain a landscape of rolling hills that rise on either hand only a few hundred meters back from the riverbanks. The local climate is characterized by a prolonged dry season from mid-April or early May to the end of September or mid-October; austral cold fronts accompanied by dense mists typically occur several times in the course of each dry season. Judging from the isohyets mapped by Ratisbona (1976: fig.

8), local rainfall probably totals about 2000 mm annually. Both the floodplain and the hilly interfluvium are covered with very tall primary forest; some trees are leafless in the dry season but most retain foliage throughout the year and the canopy as a whole is always green and leafy (O'Neill, in litt.). Floodplain soils (composed of mixed sands and clays) are poorly drained, with pools of standing water during the rainy season. The dense undergrowth of the floodplain forest is characterized by abundant *Heliconia* and large, spiny, terrestrial bromeliads. Forest growth on well-drained hillsides differs by having an open understory with many palms and bamboo but almost no *Heliconia* or terrestrial bromeliads. Nonforest habitats near Balta are mostly limited to dense riverside canebrakes and herbaceous secondary growth in recently abandoned clearings. Local streams have predominantly sandy bottoms (O'Neill, in litt.).

A few mammal specimens were obtained at Balta by O'Neill and other ornithologists from 1963

to 1971, but intensive collecting by A. L. Gardner (June–August 1966, June–August 1968, March–April 1971) and J. L. Patton (June–August 1968) produced most of the vouchers cited below. Small mammals were trapped on the ground with Shermans and homemade wire live traps, steel leghold traps were set for carnivores, bats were collected with ground-level mist nets (a few were also taken by hand from roosts in tree cavities), and some hunting was done at night (Patton, in litt.). Mist nets were in short supply in 1966, however, so bat netting was initially limited; furthermore, collecting was concentrated in the floodplain forest and little effort was made to sample the surrounding hilly country (Gardner, personal commun.). Many specimens were donated by Cashinahua hunters, interviews with whom elicited unequivocal descriptions of several unvouchered species.

Our list includes several corrected identifications and numerous nomenclatural changes from previously published records (e.g., Gardner, 1976; Gardner and Carter, 1972; Gardner and Patton, 1972; Musser and Gardner, 1974; Patton and Gardner, 1972; see Wilson and Reeder, 1993, for obsolete synonyms). The taxonomy of Balta *Proechimys* followed herein is Patton's (1987), but the specimens he referred to the *cuvieri* group (op. cit.) are listed below as an undescribed species.

MARSUPIALIA [11 spp.]

Didelphidae

- Caluromys lanatus* (LSU)
- Chironectes minimus* (LSU)
- Didelphis marsupialis* (LSU)
- Gracilinanus agilis* (LSU)
- Marmosa murina* (LSU, MVZ)
- Marmosops noctivagus* (LSU, MVZ)
- Marmosops parvidens* (LSU)
- Metachirus nudicaudatus* (LSU, MVZ)
- Micoureus regina* (LSU, MVZ)
- Philander mcilhennyi* (LSU, MVZ)
- Philander opossum* (LSU, MVZ)

XENARTHRA [9 spp.]

Bradypodidae

- Bradypus variegatus* (LSU, MVZ)

Megalonychidae

- Choloepus* cf. *hoffmanni*

Dasypodidae

- Cabassous unicinctus*
- Dasypus kappleri* (LSU)
- Dasypus novemcinctus* (LSU)
- Prionomys maximus* (LSU)

Myrmecophagidae

- Cyclopes didactylus* (LSU)
- Myrmecophaga tridactyla* (LSU)
- Tamandua tetradactyla* (LSU)

CHIROPTERA [56 spp.]

Emballonuridae

- Rhynchonycteris naso* (LSU, MVZ)

Saccopteryx bilineata (LSU)

Saccopteryx leptura (LSU)

Noctilionidae

Noctilio albiventris (LSU, MVZ)

Phyllostominae

- Macrophyllum macrophyllum* (LSU, MVZ)
- Micronycteris megalotis* (LSU)
- Micronycteris nicefori* (LSU)
- Mimon crenulatum* (LSU, MVZ)
- Phyllostomus elongatus* (LSU, MVZ)
- Phyllostomus hastatus* (LSU, MVZ)
- Tonatia brasiliensis* (LSU)
- Tonatia carrikeri* (LSU)
- Tonatia saurophila* (LSU)
- Tonatia silvicola* (LSU)
- Trachops cirrhosus* (LSU, MVZ)

Glossophaginae

- Anoura caudifera* (LSU, MVZ)
- Anoura geoffroyi* (LSU)
- Choeroniscus intermedius* (LSU)
- Glossophaga soricina* (LSU, MVZ)
- Lonchophylla thomasi* (LSU, MVZ)

Carollinae

- Carollia brevicauda* (LSU, MVZ)
- Carollia castanea* (LSU, MVZ)
- Carollia perspicillata* (LSU, MVZ)
- Rhinophylla pusillum* (LSU, MVZ)

Stenodermatinae

- Artibeus (Artibeus) jamaicensis* (LSU, MVZ)
- Artibeus (A.) lituratus* (LSU, MVZ)
- Artibeus (A.) obscurus* (LSU, MVZ)
- Artibeus (Dermanura) anderseni* (LSU, MVZ)
- Artibeus (D.) cinereus* (LSU)
- Artibeus (Koopmania) concolor* (LSU)
- Chiroderma trinitatum* (LSU)
- Chiroderma villosum* (LSU, MVZ)
- Mesophylla macconnelli* (LSU)
- Platyrrhinus brachycephalus* (LSU)
- Platyrrhinus helleri* (LSU, MVZ)
- Platyrrhinus infuscus* (LSU)
- Sturnira lilium* (LSU, MVZ)
- Sturnira tildae* (LSU, MVZ)
- Uroderma bilobatum* (LSU, MVZ)
- Uroderma magnirostrum* (LSU, MVZ)
- Vampyressa bidens* (LSU, MVZ)
- Vampyressa pusilla* (LSU)
- Vampyroides caraccioli* (LSU)

Desmodontinae

- Desmodus rotundus* (LSU, MVZ)

Thyropteridae

- Thyroptera tricolor* (LSU)

Vespertilionidae

- Eptesicus brasiliensis* (LSU, MVZ)
- Eptesicus furinalis* (LSU, MVZ)
- Lasiurus blossevillii* (LSU, MVZ)
- Lasiurus ega* (LSU)
- Myotis albescens* (LSU, MSB)
- Myotis nigricans* (LSU, MSB)

Myotis riparius (LSU)
Myotis simus (LSU, MSB)
 Molossidae
Molossops abrasus (LSU)
Molossops greenhalli (LSU)
Molossus molossus (LSU, MVZ)
 PRIMATES [10 spp.]
 Callitrichidae
Saguinus imperator (LSU, MVZ)
 Cebidae
Alouatta seniculus (LSU, MVZ)
Aotus nigriceps (LSU)
Ateles chamek (LSU)
Callicebus cupreus (LSU, MVZ)
Cebus albifrons (LSU, MVZ)
Cebus apella (LSU)
Lagothrix lagotricha
Pithecia monachus (LSU)
Saimiri sciureus (LSU)
 CARNIVORA [15 spp.]
 Canidae
Atelocynus microtis (LSU, MVZ)
Speothos venaticus
 Felidae
Herpailurus yaguarondi (LSU)
Leopardus pardalis (LSU)
Leopardus wiedii (LSU)
Panthera onca
Puma concolor
 Mustelidae
Eira barbara (LSU, MVZ)
Galictis vittata (LSU)
Lontra longicaudis (LSU)
Pteronura brasiliensis
 Procyonidae
Bassaricyon gabbii (LSU)
Nasua nasua (LSU)
Potos flavus (LSU)
Procyon cancrivorus (LSU)
 PERISSODACTYLA [1 sp.]
 Tapiridae
Tapirus terrestris (LSU)
 ARTIODACTYLA [3 spp.]
 Tayassuidae
Pecari tajacu (LSU)
Tayassu pecari (LSU)
 Cervidae
Mazama americana (LSU, MVZ)
 RODENTIA [24 spp.]
 Sciuridae
Sciurus ignitus (LSU, MVZ)
Sciurus spadiceus (LSU, MVZ)
 Muridae
Neomys spinosus (LSU, MVZ)
Nectomys squamipes (LSU, MVZ)
Neusticomys peruviansis (LSU)
Oecomys bicolor (LSU, MVZ)
Oecomys superans (LSU, MVZ)

Oligoryzomys microtis (LSU, MVZ)
Oryzomys capito (LSU, MVZ)
Oryzomys macconnelli (LSU)
Oryzomys nitidus (LSU, MVZ)
Oryzomys yunganus (LSU, MVZ)
 Erethizontidae
Coendou cf. bicolor (LSU)
 Hydrochaeridae
Hydrochaeris hydrochaeris (LSU)
 Dinomyidae
Dinomys branickii (LSU)
 Dasyproctidae
Dasyprocta variegata (LSU, MVZ)
Myoprocta pratti (LSU, MVZ)
 Agoutidae
Agouti paca (LSU)
 Echimyidae
Dactylomys dactylinus (LSU)
Mesomys hispidus (LSU)
Proechimys breviceauda (LSU, MVZ)
Proechimys simonsi (LSU, MVZ)
Proechimys steerei (LSU)
Proechimys sp. nov. (LSU)
 LAGOMORPHA [1 sp.]
 Leporidae
Sylvilagus brasiliensis (LSU)

Comments: Although Balta was visited on three separate occasions by experienced collectors whose efforts were supplemented by those of Cashinahua hunters, a substantial number of nonvolant species could still be expected. These include five marsupials (*Caluromysiops irrupta*, *Glironia venusta*, *Marmosa lepida*, *Monodelphis brevicaudata*, *Monodelphis emiliae*), three primates (*Callimico goeldii*, *Cebuella pygmaea*, *Saguinus fuscicollis*), one carnivore (*Mustela africana*), one ungulate (*Mazama gouazoupira*), and eight rodents (*Microsciurus flaviventer*, *Oecomys concolor*, *Oecomys roberti*, *Oecomys trinitatis*, *Rhipidomys cf. couesi*, *Echimys didelphoides*, *Echimys occasius*, *Isothrix bistrata*). Most of these species are either (1) nocturnal and arboreal (no traps were placed high in trees), (2) always elusive (e.g., *Monodelphis* spp., *Mustela africana*, *Microsciurus flaviventer*), or (3) restricted to special habitats that may be locally absent (e.g., *Cebuella pygmaea*, *Callimico goeldii*); only the absences of *Mazama gouazoupira* and *Saguinus fuscicollis* lack plausible explanations.³⁶

³⁶ Balta occupies a conspicuous lacuna in the known range of *Saguinus fuscicollis* between the upper Purus and the headwaters of the Juruá (Hershkovitz, 1977: fig. X.24), but this area remains largely unexplored for primates (op. cit.: 636). Although Gardner and Patton's extensive collections from Balta provide compelling evidence that the species may be locally absent, we list it as expected to maintain consistency with the criteria used to infer the potential occurrence of other taxa.

Most bats that could yet be expected at Balta (excluding cave-roosting forms, which may lack suitable roosts nearby) are high-flying species (for which no special capture methods were used) or elusive understory insectivores: *Centronycteris maximiliani*, *Cormura brevirostris*, *Diclidurus albus*, *Peropteryx kappleri*, *Peropteryx leucoptera*, *Peropteryx macrotis*, *Saccopteryx canescens*, *Nocilio leporinus*, *Pteronotus parnellii*, *Chrotopterus auritus*, *Micronycteris daviesi*, *Micronycteris hirsuta*, *Micronycteris minuta*, *Micronycteris schmid-*

torum, *Micronycteris sylvestris*, *Phylloderma stenops*, *Phyllostomus discolor*, *Vampyrus spectrum*, *Glossophaga comissarisi*, *Lichonycteris obscura*, *Lionycteris spurrelli*, *Artibeus gnomus*, *Artibeus hartii*, *Sphaeronycteris toxophyllum*, *Sturnira magna*, *Diaemus youngi*, *Diphylla ecaudata*, *Furipterus horrens*, *Thyroptera discifera*, *Eumops auripendulus*, *Eumops hansae*, *Eumops perotis*, *Molossops planirostris*, *Molossus ater*, *Nyctinomops laticaudatus*, *Promops centralis*, *Promops nasutus* (37 total).

APPENDIX 10

Rainforest Mammals of Cocha Cashu and Pakitza

The Cocha Cashu Biological Station (11°54'S, 71°22'W) is situated at about 380 m elevation on the left bank of the Río Manu, a white-water tributary of the Río Alto Madre de Dios, in Departamento Madre de Dios, Peru; the station lies within Parque Nacional Manu, a 15,320 km² reserve created in 1973 to protect the pristine forests of the Río Manu catchment. The 10 km² study area surrounding the station is in the floodplain or meander belt of the Río Manu; local soils are nutrient-rich alluvial silts and sand replenished on the order of every 500–1000 years by lateral channel erosion and redeposition (Terborgh, 1990). Four years of weather records suggest an annual rainfall average slightly in excess of 2000 mm, most of which occurs from November to May; during the dry season, from June to October, monthly rainfall is usually less than 100 mm (op. cit.). Fluvial processes are responsible for an extraordinary variety of habitats around Cocha Cashu, including seasonal swamps and a successional series of plant communities from canebrakes and thickets of a few quickly growing tree species behind the river beach to mature evergreen forest on well-drained soils (Terborgh, 1983; Gentry and Terborgh, 1990). The mature forest has an open understory and a canopy 25–30 m tall, with many emergent trees to 50 m or more; palms and large stranglers are unusually abundant, perhaps a consequence of the rich alluvial soils (Gentry and Terborgh, 1990). Floristic surveys of the Río Manu floodplain forests and botanical comparisons with other Neotropical study sites are summarized by Foster (1990).

Knowledge of the mammal fauna at Cocha Cashu has accumulated through the observations of numerous researchers resident at the biological station since 1973. Perhaps because the area has not been visited by commercial or subsistence hunters for over 20 years, many large mammals (notably primates and cats) occur at much higher densities than elsewhere in Amazonia and are consequently easier to observe (Terborgh et al., 1984;

Janson and Emmons, 1990). The roster of larger mammals is the product of hundreds of hours of diurnal and nocturnal sight-surveys by various personnel over many years; a species accumulation curve for the first 160 hours (116 km) of nocturnal transect census was illustrated by Emmons (1984). Marsupials and rodents were live-trapped (using 5 × 5 × 16 in. Tomahawks), marked, and released by Emmons at intervals during both dry and rainy seasons from 1978 to 1984; a total of 5803 trap-nights were recorded. Some identifications are tentative in the absence of voucher specimens (which cannot be collected in the park).

Discrepancies and omissions in previously published lists of mammals from Cocha Cashu have been corrected below. Our list omits four species that Terborgh et al. (1984) considered hypothetical at Cocha Cashu (*Philander andersoni*, *Dasyurus kappleri*, *Speothos venaticus*, *Leopardus tigrinus*), but *Atelocynus microtis*, *Galictis vittata*, *Herpailurus yaguarondi*, and *Dinomys branickii*, originally listed as hypothetical (op. cit.), have recently been confirmed by specimens or sightings (Pacheco et al., 1993). We omit *Chironectes minimus*, originally listed by Terborgh et al. (1984) on the basis of an old sight record that cannot be corroborated and has never been duplicated. However, we include *Microsciurus* cf. *flaviventer* (listed by Terborgh et al., 1984, but not in subsequent lists) because a specimen of this distinctive squirrel was photographed before release. *Sciurus sanborni* (also listed by Terborgh et al., 1984) is not a valid species (M. de Vivo, personal commun.). Records of *Vampyressa nymphaea* from Cocha Cashu (Terborgh et al., 1984) and nearby Pakitza (Pacheco et al., 1993) were based on misidentifications (no Peruvian specimens of this species are known; V. Pacheco, in litt.).

An important supplement to the largely unvouchered inventory from Cocha Cashu is provided by recent collections and observations at Pakitza (11°57'S, 71°17'W; ca. 360 m elevation), a guard station located just outside Parque Na-

cional Manu, about 21 km ESE of Cocha Cashu, and on the same (left) bank of the Río Manu (maps and local habitat descriptions in Erwin, 1990). Because Pakitza is at approximately the same elevation as Cocha Cashu and because there are no known zoogeographic barriers between them, we combine inventory data from the two sites below.

Inventory methods used at Pakitza were described by Ascorra et al. (1996) and by Pacheco and Vivar (1996). Bats were collected on four visits (from 1987 to 1992) totalling 72 days; several distinct habitats (primary high-ground forest, forest streams, forest edges around a clearing, riverside early-successional thickets, and open shorelines) were sampled with mist nets for one to ten nights on each visit. Most nets were located in the understory (0–5 m above the ground) but some were raised to subcanopy level (over 20 m); a few bats were also collected from diurnal roosts. Small non-volant mammals were trapped at Pakitza on four visits (from 1989 to 1992) in both dry and rainy seasons; an average of four weeks were devoted to trapping on each visit, for a total of 12,673 trap-nights. Trap stations were spaced at 12–15 m intervals along trails traversing different local habitats (e.g., dissected alluvial terrace forest, upper floodplain forest, old alluvial terraces with bamboo, hardwood swamp forest; see Erwin, 1990, for descriptions). Two to six traps (Shermans and Victors, variously baited) were set at each station, usually including at least one Sherman-Victor pair on the ground and another on elevated substrates (e.g., lianas, logs, etc.); a few traps were set as high as 5–7 m above the ground. Trap success was very low, about 1% averaged across all habitats and both seasons.

Our list of the combined faunas of Cocha Cashu and Pakitza includes all of the taxa reported from the latter site by Ascorra et al. (1991) and Pacheco et al. (1993) plus *Micronycteris schmidtorum* (recently identified from a specimen collected at Pakitza; Simmons, 1996). The deer tentatively identified as *Blastocerus dichotomus* from an unvouchered sighting on Quebrada Picaflor, about 2 km SE Pakitza (Pacheco and Vivar, 1996), however, is omitted as a probable nonforest vagrant.

MARSUPIALIA [12 spp.]

Didelphidae

- Caluromys lanatus*
- Caluromyslops irrupita*
- Didelphis marsupialis*
- Glirionia venusta*
- Gracilinanus agilis* (MUSM)
- Marmosa murina* (MUSM)
- Marmosops noctivagus* (MUSM)
- Marmosops parvidens* (MUSM)
- Metachirus nudicaudatus* (MUSM)
- Micoureus regina* (MUSM)

Monodelphis brevicaudata (MUSM)

Philander opossum (MUSM)

XENARTHRA [7 spp.]

Bradypodidae

Bradypus variegatus

Megalonychidae

Choloepus hoffmanni (USNM)

Dasyopodidae

Dasyopus novemcinctus

Prionodontes maximus

Myrmecophagidae

Cyclopes didactylus

Myrmecophaga tridactyla

Tamandua tetradactyla

CHIROPTERA [60 spp.]

Emballonuridae

Rhynchonycteris naso (MUSM)

Saccopteryx bilineata (MUSM)

Saccopteryx leptura (MUSM)

Noctilionidae

Noctilio albiventris (MUSM, USNM)

Noctilio leporinus (MUSM)

Phyllostominae

Chrotopterus auritus (MUSM)

Macrophyllum macrophyllum (MUSM, USNM)

Micronycteris cf. megalotis (MUSM)

Micronycteris minuta (MUSM)

Micronycteris schmidtorum (MUSM)

Mimon crenulatum (MUSM)

Phylloderma stenops (MUSM)

Phyllostomus elongatus (MUSM, USNM)

Phyllostomus hastatus (MUSM, USNM)

Tonatia brasiliensis (MUSM, USNM)

Tonatia saurophila (MUSM)

Tonatia silvicola (MUSM)

Trachops cirrhosus (MUSM, USNM)

Vampyrus spectrum (MUSM)

Glossophaginae

Anoura caudifera (MUSM, USNM)

Choeroniscus minor (MUSM, USNM)

Glossophaga commissarisi (MUSM)

Glossophaga soricina (MUSM, USNM)

Lonchophylla thomasi (MUSM)

Carollinae

Carollia brevicauda (MUSM, USNM)

Carollia castanea (MUSM, USNM)

Carollia perspicillata (MUSM, USNM)

Rhinophylla pumilio (MUSM)

Stenodermatinae

Artibeus (Artibeus) jamaicensis (MUSM, USNM)

Artibeus (A.) lituratus (MUSM, USNM)

Artibeus (A.) obscurus (MUSM, USNM)

Artibeus (Dermanura) anderseni (MUSM, USNM)

Artibeus (D.) cinereus (MUSM)

Artibeus (D.) glaucus (MUSM)

Artibeus (D.) gnomus (USNM)

Chiroderma trinitatum (MUSM)
Chiroderma villosum (MUSM, USNM)
Mesophylla macconnelli (MUSM, USNM)
Platyrrhinus brachycephalus (MUSM)
Platyrrhinus helleri (MUSM)
Platyrrhinus infuscus (MUSM, USNM)
Sphaeronycteris toxophyllum
Sturnira lilium (MUSM)
Sturnira tildae (MUSM, USNM)
Uroderma bilobatum (MUSM, USNM)
Uroderma magnirostrum (MUSM, USNM)
Vampyressa bidens (MUSM)
Vampyressa pusilla (MUSM)
Vampyrodes caraccioli (MUSM, USNM)
Desmodontinae
Desmodus rotundus (MUSM, USNM)
Diphylla ecaudata (MUSM)
Furipteridae
Furipterus horrens (MUSM)
Thyropteridae
Thyroptera tricolor (MUSM, USNM)
Vespertilionidae
Lasiurus ega (MUSM)
Myotis albescens (MUSM, USNM)
Myotis nigricans (MUSM)
Myotis cf. riparius (MUSM)
Myotis simus (MUSM)
Molossidae
Molossus molossus (MUSM)
Nyctinomops laticaudatus (MUSM)
PRIMATES [13 spp.]
Callitrichidae
Callimico goeldii
Cebuella pygmaea
Saguinus fuscicollis
Saguinus imperator
Cebidae
Alouatta seniculus
Aotus nigriceps
Ateles chamek
Callicebus brunneus
Cebus albifrons
Cebus apella
Lagothrix lagotricha
Pithecia irrorata
Saimiri boliviensis
CARNIVORA [14 spp.]
Canidae
Atelocynus microtis
Felidae
Herpailurus yaguarondi
Leopardus pardalis
Leopardus wiedii
Panthera onca
Puma concolor
Mustelidae
Eira barbara
Galictis vittata

Lontra longicaudis
Pteronura brasiliensis
Procyonidae
Bassaricyon gabbii
Nasua nasua
Potos flavus
Procyon cancrivorus
PERISSODACTYLA [1 sp.]
Tapiridae
Tapirus terrestris
ARTIODACTYLA [4 spp.]
Tayassuidae
Pecari tajacu
Tayassu pecari
Cervidae
Mazama americana
Mazama gouazoupira
RODENTIA [27 spp.]
Sciuridae
Microsciurus cf. flaviventer
Sciurus ignitus
Sciurus spadiceus
Muridae
Neacomys spinosus (MUSM)
Nectomys squamipes (MUSM)
Neusticomys peruviansis (MUSM)
Oecomys bicolor (MUSM, USNM)
Oecomys superans (MUSM, USNM)
Oligoryzomys microtis (MUSM, USNM)
Oryzomys capito (MUSM, USNM)
Oryzomys macconnelli
Oryzomys nitidus (MUSM)
Oxymycterus sp.
Rhipidomys cf. couesi (MUSM, USNM)
Erethizontidae
Coendou cf. bicolor
Dinomyidae
Dinomys branickii (USNM)
Hydrochaeridae
Hydrochaeris hydrochaeris
Dasyproctidae
Dasyprocta variegata
Myoprocta pratti (USNM)
Agoutidae
Agouti paca
Echimyidae
Dactylomys dactylinus
Echimys cf. occasius
Mesomys hispidus (MUSM)
Proechimys brevicauda (MUSM, USNM)
Proechimys simonsi (MUSM, USNM)
Proechimys steerei (MUSM, USNM)
Proechimys sp. nov. (MUSM)
LAGOMORPHA [1 sp.]
Leporidae
Sylvilagus brasiliensis

Comments: The long duration of field research at Cocha Cashu and the intensity of recent trap-

ping efforts at Pakitza are probably responsible for the modest list of expected nonvolant species, which consist only of four marsupials (*Chironectes minimus*, *Marmosa lepida*, *Monodelphis adusta*, *Monodelphis emiliae*), two xenarthrans (*Cabassous unicinctus*, *Dasyurus kappleri*), two carnivores (*Speothos venaticus*, *Mustela africana*), and six rodents (*Oecomys concolor*, *Oecomys roberti*, *Oecomys trinitatis*, *Oryzomys yunganus*, *Echimys didelphoides*, *Isothrix bistrata*). By contrast, many bats (even excluding cave-roosting species that may lack suitable roosts in the area) are still to be expected; most are elusive understory insectivores or high-flying species: *Centronycteris maximiliani*, *Cormura brevirostris*, *Diclidurus albus*, *Per-*

opteryx kappleri, *Peropteryx leucoptera*, *Peropteryx macrotis*, *Saccopteryx canescens*, *Pteronotus parnellii*, *Micronycteris daviesi*, *Micronycteris hirsuta*, *Micronycteris nicefori*, *Micronycteris sylvestris*, *Phyllostomus discolor*, *Tonatia carrikeri*, *Anoura geoffroyi*, *Lichonycteris obscura*, *Lionycteris spurrelli*, *Artibeus hartii*, *Artibeus concolor*, *Chiroderma salvini*, *Sturnira magna*, *Diaemus youngi*, *Thyroptera discifera*, *Eptesicus brasiliensis*, *Eptesicus furinalis*, *Lasiurus blossevillii*, *Eumops auripendulus*, *Eumops hansae*, *Eumops perotis*, *Molossops abrasus*, *Molossops planirostris*, *Molossus ater*, *Promops centralis*, *Promops nasutus* (34 total).

APPENDIX 11

Rainforest Mammals of Cuzco Amazónico

The Reserva Cuzco Amazónico (12°33'S, 69°03'W) is situated on the left bank of the white-water Río Madre de Dios at an elevation of about 200 m in Departamento Madre de Dios, Peru. Established in 1979 and privately managed for ecotourism and research, the reserve comprises 10,000 ha of relatively undisturbed forest on alluvial soils (see Duellman and Koechlin, 1991, from which the remainder of this paragraph is abstracted). Eighteen years of weather records from Puerto Maldonado, about 15 km WSW of Cuzco Amazónico, document an annual average rainfall of 2387 mm and a dry season from June through August (when monthly means are less than 100 mm). The forest is predominantly evergreen, with an average canopy height of 30 m and emergents to 40 m or more; lianas are unusually abundant by comparison with other Amazonian sites and large bamboos are apparently absent. Areas of the forest seasonally inundated by accumulated rainfall (not by riverine flooding) have a generally more open understory than forest growth on well-drained sites; canebrakes and *Cecropia* thickets line the riverbanks (op. cit.: figs. 6–11).

Although mammals were collected sporadically at Cuzco Amazónico from 1979 to 1984 by various personnel, systematic efforts to inventory the fauna were restricted to two expeditions in 1989 and 1990 by Woodman et al. (1991, 1995). Most of the nonvolant small mammals they reported were taken in Sherman live traps and Victor rat traps set at 20 m intervals along four 500 m trails. One pair of Sherman and Victor traps was set on the ground and another on elevated substrates (e.g., logs and lianas; to about 3 m above the ground) at each trap station. Each trapline was maintained for 12 consecutive days, on both rainy and dry season visits, for a total of 9600 trap-nights; this

effort obtained 505 specimens of small marsupials and rodents, for an overall success rate of about five percent. Tomahawk traps for larger species were set at 100 m intervals along the same trails. A few specimens of small marsupials and rodents were taken in pitfalls. Squirrels, agoutis, and other large mammals were collected by hunting. Most bats were taken in ground-level mist nets (erected along trails, in clearings, and over streams), but some were collected at roosts. Although sightings of large mammals were also recorded, poaching on the reserve may have reduced or extirpated local populations of some primates and ungulates (R. M. Timm, personal commun.). According to Woodman et al. (1991), the canopy fauna was not effectively sampled by any of these methods.

Ongoing studies of the collections from Cuzco Amazónico have revised several identifications in Woodman et al.'s (1991) preliminary report (R. M. Timm, personal commun.), and other names have been emended below to conform with current taxonomy (see Wilson and Reeder, 1993, for obsolete synonyms). Two additional species (*Tayassu pecari* and *Mazama americana*) have recently been sighted at Cuzco Amazónico and a few records from nearby Lago Sandoval are also included in our list. The large deer previously identified as *Odocoileus virginianus* (Woodman et al., 1991) is here omitted; the animal is now believed to be *Blastocerus dichotomus* (R. M. Timm, personal commun.), a nonforest species probably straying from the nearby Pampas del Heath.

MARSUPIALIA [9 spp.]

Didelphidae

Caluromys lanatus (KU, MVZ)

Didelphis marsupialis (CIMNH, KU, MUSM, MVZ)

Marmosa murina (KU, MUSM, MVZ)
Marmosops noctivagus (CIMNH, KU, MUSM, MVZ)
Marmosops parvidens (KU, MUSM, MVZ)
Metachirus nudicaudatus (CIMNH, KU, MUSM, MVZ)
Micoureus regina (CIMNH, KU, MUSM, MVZ)
Monodelphis adusta (MUSM)
Philander opossum (CIMNH, KU, MUSM, MVZ)

XENARTHRA [5 spp.]

Bradypodidae
Bradypus variegatus (KU)
Megalonychidae
Choloepus hoffmanni (MUSM)
Dasypodidae
Dasybus novemcinctus (MUSM)
Myrmecophagidae
Myrmecophaga tridactyla
Tamandua tetradactyla

CHIROPTERA [44 spp.]

Emballonuridae
Peropteryx leucoptera (KU, MUSM)
Rhynchonycteris naso
Saccopteryx bilineata (KU, MUSM, MVZ)
Saccopteryx leptura (MVZ)
Noctilionidae
Noctilio albiventris (KU, MUSM)
Phyllostominae
Chrotopterus auritus (MVZ)
Micronycteris cf. megalotis (KU)
Micronycteris minuta (KU, MVZ)
Mimon crenulatum (KU, MVZ)
Phyllostomus elongatus (KU, MUSM, MVZ)
Phyllostomus hastatus (KU, MUSM, MVZ)
Tonatia silvicola (KU, MUSM, MVZ)
Trachops cirrhosus (KU, MUSM, MVZ)
Vampyrum spectrum (MVZ)

Glossophaginae
Choeroniscus minor (KU, MUSM)
Glossophaga soricina (KU, MUSM, MVZ)
Lonchophylla thomasi (KU, MUSM)

Caroliinae
Carollia brevicauda (KU, MUSM, MVZ)
Carollia castanea (KU, MUSM, MVZ)
Carollia perspicillata (KU, MUSM, MVZ)
Rhinophylla pumilio (KU, MUSM, MVZ)

Stenodermatinae
Artibeus (Artibeus) jamaicensis (CIMNH, KU, MUSM, MVZ)
Artibeus (A.) lituratus (KU, MUSM, MVZ)
Artibeus (A.) obscurus (KU, MUSM, MVZ)
Artibeus (Dermanura) anderseni (KU, MUSM, MVZ)
Artibeus (D.) cinereus (MUSM)
Chiroderma salvini (KU, MVZ)
Chiroderma villosum (KU, MVZ)
Mesophylla macconnelli (KU, MUSM, MVZ)

Platyrrhinus helleri (KU, MUSM, MVZ)
Platyrrhinus infuscus (MUSM, MVZ)
Sturnira lilium (KU, MUSM, MVZ)
Sturnira tildae (KU, MUSM)
Uroderma bilobatum (KU, MUSM, MVZ)
Uroderma magnirostrum (MUSM)
Vampyressa pusilla (KU, MUSM, MVZ)

Desmodontinae

Desmodus rotundus (KU, MUSM, MVZ)

Thyropteridae

Thyroptera tricolor (KU, MVZ)

Vespertilionidae

Eptesicus brasiliensis (KU, MVZ)
Lasiurus ega (MVZ)
Myotis albescens (MVZ)
Myotis nigricans (KU, MUSM)
Myotis riparius (MUSM, MVZ)

Molossidae

Molossus molossus (KU, MUSM)

PRIMATES [7 spp.]

Callitrichidae
Saguinus fuscicollis
Cebidae
Alouatta seniculus
Aotus nigriceps
Cebus albifrons
Cebus apella
Lagothrix lagotricha
Saimiri boliviensis

CARNIVORA [11 spp.]

Canidae
Atelocynus microtis
Felidae
Herpailurus yaguarondi
Leopardus pardalis (MUSM)
Panthera onca
Puma concolor
Mustelidae
Eira barbara
Galictis vittata
Lontra longicaudis
Mustela sp.
Pteronura brasiliensis

Procyonidae

Potos flavus

PERISSODACTYLA [1 sp.]

Tapiridae
Tapirus terrestris

ARTIODACTYLA [3 spp.]

Tayassuidae
Pecari tajacu
Tayassu pecari (MUSM)

Cervidae

Mazama americana

RODENTIA [22 spp.]

Sciuridae
Sciurus ignitus (KU, MUSM)
Sciurus spadiceus (CIMNH, KU, MUSM, MVZ)

Muridae

Neacomys spinosus (KU, MUSM, MVZ)
Neacomys cf. *tenuipes* (KU)
Nectomys squamipes (KU, MUSM)
Oecomys bicolor (KU, MUSM)
Oecomys roberti (KU, MUSM)
Oecomys superans (KU, MUSM)
Oligoryzomys microtis (KU, MUSM)
Oryzomys capito (KU, MUSM, MVZ)
Oryzomys nitidus (KU, MUSM, MVZ)
Oryzomys yunganus (KU, MUSM)
Rhipidomys cf. *couesi* (KU, MUSM, MVZ)

Erethizontidae

Coendou cf. *bicolor* (KU)

Dasyproctidae

Dasyprocta variegata (KU, MUSM)
Myoprocta pratti (MVZ)

Agoutidae

Agouti *paca*

Echimyidae

Isothrix bistrata (KU)
Mesomys hispidus (KU, MUSM, MVZ)
Proechimys brevicauda (KU, MUSM, MVZ)
Proechimys simonsi (KU, MUSM, MVZ)
Proechimys steerei (KU, MUSM, MVZ)

LAGOMORPHA [1 sp.]**Leporidae**

Sylvilagus brasiliensis

Comments: The long list of expected nonvolant species for this inventory probably reflects the brief duration of intensive sampling, the lack of effective trapping or hunting for canopy species, and perhaps the local impact of poaching; included are seven marsupials (*Caluromys* *irrupta*, *Chironectes* *minimus*, *Glironia* *venusta*, *Gracilinanus* *agilis*, *Marmosa* *lepida*, *Monodelphis* *brevicauda*, *Monodelphis* *emiliae*), four xenarthrans (*Cabassous* *unicinctus*, *Dasyprocta* *kappleri*, *Priodontes* *maximus*, *Cyclopes* *didactylus*), six primates (*Cal-*

limico *goeldii*, *Cebuella* *pygmaea*, *Saguinus* *imperator*, *Ateles* *chamek*, *Callicebus* *brunneus*, *Pithecia* *irrorata*), five carnivores (*Speothos* *venaticus*, *Leopardus* *wiedii*, *Bassaricyon* *gabbii*, *Nasua* *nasua*, *Procyon* *cancrivorus*), one ungulate (*Mazama* *gouazoupira*), and 11 rodents (*Microsciurus* *flaviventer*, *Neusticomys* *peruviansis*, *Oecomys* *concolor*, *Oecomys* *trinitatis*, *Oryzomys* *macconnelli*, *Dinomys* *branickii*, *Hydrochaeris* *hydrochaeris*, *Dactylomys* *dactylinus*, *Echimys* *didelphoides*, *Echimys* *occasius*, *Proechimys* sp. nov.).

Whereas the long list of expected bats (excluding cave-roosting species for which suitable roosts may be locally absent) is predictably dominated by small-bodied understory insectivores and high-flying species, the absence of many species in other categories probably reflects brief sampling rather than elusiveness per se: *Centronycteris* *maximiliani*, *Cormura* *brevirostris*, *Diclidurus* *albus*, *Peropteryx* *kappleri*, *Peropteryx* *macrotis*, *Saccopteryx* *canescens*, *Noctilio* *leporinus*, *Pteronotus* *parnellii*, *Macrophyllum* *macrophyllum*, *Micronycteris* *daviesi*, *Micronycteris* *hirsuta*, *Micronycteris* *nicefori*, *Micronycteris* *schmidtorum*, *Micronycteris* *sylvestris*, *Phylloderma* *stenops*, *Phyllostomus* *discolor*, *Tonatia* *brasiliensis*, *Tonatia* *carrikeri*, *Tonatia* *saurophila*, *Anoura* *caudifera*, *Anoura* *geoffroyi*, *Glossophaga* *commissarisi*, *Lichonycteris* *obscura*, *Lionycteris* *spurrelli*, *Artibeus* *glauca*, *Artibeus* *gnomus*, *Artibeus* *hartii*, *Artibeus* *concolor*, *Chiroderma* *trinitatum*, *Platyrrhinus* *brachycephalus*, *Sphaeronycteris* *toxophyllum*, *Sturnira* *magna*, *Vampyressa* *bidens*, *Vampyrodes* *caraccioli*, *Diaemus* *youngi*, *Diphylla* *ecaadata*, *Furipterus* *horrens*, *Thyroptera* *discifera*, *Eptesicus* *furinalis*, *Lasiurus* *blossevillii*, *Myotis* *simus*, *Eumops* *auripendulus*, *Eumops* *hansae*, *Eumops* *perotis*, *Molossops* *abrasus*, *Molossops* *planirostris*, *Molossus* *ater*, *Nyctinomops* *laticaudatus*, *Promops* *centralis*, *Promops* *nasutus* (50 total).

APPENDIX 12**Amazonian Primate Inventories**

This appendix summarizes primate inventory results from 13 Amazonian localities to supplement information from whole-faunal surveys in appendices 2–11. For each site listed below, we provide basic geographic data, an abbreviated ecological description, and a list of species (revised as necessary to conform with current taxonomic usage). Voucher specimens are infrequently collected in primate surveys, but we mention where any are deposited, if known. Localities are listed alphabetically.

1. **Brazil, Acre, São Domingos** (between upper

Rio Purus and Rio Iaco; 8°55'S, 68°20'W). Primary terra firme forest with light selective logging; hydrology not described, annual rainfall unknown; inventory data obtained from 26 km of walked transect census (Peres, 1988).

Callitrichidae

Callimico goeldii
Saguinus imperator
Saguinus fuscicollis

Cebidae

Alouatta seniculus
Aotus cf. *nigriceps*

Ateles cf. chamek
Callicebus cupreus
Cebus albifrons
Cebus apella
Saimiri boliviensis

2. **Brazil, Amazonas, Igarapé-Açu** (left bank of lower Rio Urucú; 4°30'S, 64°29'W). Pristine, uninhabited terra firme forest on undulating terrain producing clear-water streams; annual rainfall unknown; inventory data obtained from 51 km of walked transect census (Peres, 1988).

Callitrichidae

Saguinus fuscicollis
Saguinus mystax

Cebidae

Alouatta seniculus
Aotus cf. nigriceps
Callicebus cupreus
Callicebus torquatus
Cebus albifrons
Cebus apella
Lagothrix lagotricha
Pithecia albicans

3. **Brazil, Amazonas, Lago da Fortuna** (left bank of Rio Juruá; 5°05'S, 67°10'W). Primary terra firme forest, floodplain forest, and várzea near an oxbow lake of white-water Juruá; annual rainfall unknown; inventory data obtained from 40 km of transect census by foot and canoe (Peres, 1988).

Callitrichidae

Cebuella pygmaea
Saguinus fuscicollis
Saguinus mystax

Cebidae

Alouatta seniculus
Aotus cf. nigriceps
Ateles cf. chamek
Cacajao calvus
Callicebus cupreus
Callicebus torquatus
Cebus albifrons
Cebus apella
Lagothrix lagotricha
Pithecia irrorata
Saimiri sciureus

4. **Brazil, Amazonas, Rio Ipixuna** (left bank; ca. 7°31'S, 63°22'W). Primary, disturbed and secondary terra firme forest and igapó; hydrology and rainfall not described; inventory data obtained from seven-day census and interviews (Ferrari and Lopes, 1992). Voucher specimens collected in the course of this survey are deposited in the Museu Paraense Emílio Goeldi (Belém).

Callitrichidae

Saguinus fuscicollis
Saguinus labiatus

Cebidae

Alouatta seniculus

Aotus sp.
Ateles sp.
Callicebus caligatus
Cebus albifrons
Cebus apella
Lagothrix lagotricha
Pithecia sp.
Saimiri cf. madeirae

5. **Brazil, Amazonas, SM-1** (oil-drilling site between Rio Urucú and Rio Coari; 4°50'S, 65°16'W). Tall, pristine terra firme forest on undulating terrain (93% of 900 ha study plot), plus some creek-side forest and palm swamps on waterlogged soils near black-water stream (also igapó forest 4 km distant on right bank of black-water Urucú); annual rainfall ca. 3250 mm; inventory data from 34 km of walked transect census for preliminary survey (Peres, 1988) followed by 398 days of observations over 20 consecutive months for study of community ecology (Peres, 1993).

Callitrichidae

Cebuella pygmaea
Saguinus fuscicollis
Saguinus mystax

Cebidae

Alouatta seniculus
Aotus cf. nigriceps
Ateles cf. chamek
Callicebus cupreus
Callicebus torquatus
Cebus albifrons
Cebus apella
Lagothrix lagotricha
Pithecia albicans
Saimiri sp.

6. **Brazil, Pará, Anilzinho** (between Rio Tocantins and Rio Xingu; 3°21'S, 49°52'W). Primary, disturbed, and secondary terra firme forest, also "riverine" forest; hydrology and rainfall not described; inventory data obtained from five-day survey (40 km walked) and interviews (Ferrari and Lopes, 1990).

Callitrichidae

Callithrix argentata
Saguinus midas

Cebidae

Alouatta belzebul
Aotus cf. infulatus
Callicebus moloch
Cebus apella
Chiropotes satanas
Saimiri sciureus

7. **Brazil, Pará, Rio Tapajós** (left bank; ca. 4°30'S, 57°W). Tall primary and secondary terra firme forest, low liana forest, and "várzea" (= seasonal igapó sensu France [1979] because the Tapajós has clear water); annual rainfall ca. 1750 mm; inventory data obtained from ca. 15-month study of habitat use (Branch, 1983).

Callitrichidae

Callithrix humeralifer

Cebidae

*Alouatta belzebul**Aotus cf. nigriceps**Ateles cf. marginatus**Callicebus hoffmannsi**Cebus albifrons**Cebus apella**Chiropotes albinasus**Pithecia irrorata**Saimiri sciureus*

8. **Colombia**, Amazonas, Río Mirití-Paraná (study site on right bank, ca. 18 airline km WNW of confluence with left bank of lower Caquetá at ca. 1°11'S, 70°02'W). Mostly pristine forests on hilly terrain drained by black-water river (only 30–60 m wide near study area) and streams; annual precipitation believed to exceed 3500 mm; inventory data from 48-day census along 18 km of trails; local Yucuna indians also interviewed (Defler, 1983). Voucher specimens collected in the course of this project are deposited in the zoological collections of INDERENA (Bogotá).

Callitrichidae

Saguinus inustus

Cebidae

*Alouatta seniculus**Aotus cf. vociferans**Callicebus torquatus**Cebus albifrons**Cebus apella**Lagothrix lagothricha**Saimiri sciureus*

9. **Colombia**, Caquetá, Río Peneya (left-bank tributary of middle Caquetá; study sites located ca. 30–40 km upstream from mouth at 0°07'S, 74°22'W). Uninhabited, pristine rainforest, but no details of local vegetation, hydrology, or rainfall provided; inventory data from 17-month study of feeding ecology and social behavior; apparently identical primate faunas on both banks (Izawa, 1975, 1976).

Callitrichidae

Saguinus fuscicollis

Cebidae

*Alouatta seniculus**Aotus cf. vociferans**Ateles cf. belzebul**Cebus albifrons**Cebus apella**Lagothrix lagothricha**Pithecia monachus**Saimiri sciureus*

10. **Peru**, Loreto, Río Ampiyacu (surveys centered at ca. 3°10'S, 71°50'W). Floodplain forest (with some selective logging) seasonally inundated by mixed (black and white) water, and undisturbed high-ground (terra firme) forest producing mostly

black water; annual rainfall unknown; inventory data obtained from 29 km of transect census and interviews; apparently identical primate faunas on both banks (Freese et al., 1982).

Callitrichidae

*Cebuella pygmaea**Saguinus nigricollis*

Cebidae

*Alouatta seniculus**Aotus cf. vociferans**Callicebus torquatus**Cebus albifrons**Cebus apella**Lagothrix lagothricha**Pithecia monachus**Saimiri sciureus*

11. **Peru**, Loreto, Río Orosa (average coordinates of survey ca. 3°34'S, 72°14'W). Floodplain forest (with selective logging) seasonally inundated by mixed (black and white) water, and undisturbed high-ground (terra firme) forest producing mostly black water; annual rainfall unknown; inventory data obtained from 22 km of transect census and interviews; apparently identical primate faunas on both banks (Freese et al., 1982). Collections from "Orosa" in the AMNH include specimens of *Saguinus mystax* in addition to 9 of the 12 species listed below.

Callitrichidae

*Cebuella pygmaea**Saguinus fuscicollis*

Cebidae

*Alouatta seniculus**Aotus cf. nancymai**Ateles cf. chamek**Cacajao calvus**Callicebus cupreus*³⁷*Cebus albifrons**Cebus apella**Lagothrix lagothricha**Pithecia monachus**Saimiri sciureus*

12. **Peru**, Loreto, Río Samiria (ca. 5°00'S, 74°35'W). Mostly undisturbed floodplain forest (seasonally inundated by black water), and palm

³⁷ Five specimens of titis from "Orosa" in the AMNH were listed by Hershkovitz (1990: 62) as examples of *Callicebus cupreus* and six others as *C. caligatus* (op. cit.: 66). However, the AMNH has only six specimens of *Callicebus* from Orosa, not eleven; the skin characters of this series (AMNH 73703–73708) match those described (op. cit.: 61) for *C. cupreus cupreus*. The report of two sympatric members of the *moloch* group of titis at Orosa was an error caused by inadvertently listing both original and revised identifications of the same series among the specimens examined (Hershkovitz, in litt.). Thus, *Callicebus cupreus* is presumably the correct identification for the monkeys Freese et al. (1982) reported as *C. moloch*.

swamps; annual rainfall unknown; inventory data obtained from 55 km of transect census and interviews; apparently identical primate faunas on both banks (Freese et al., 1982). (The same fauna was studied for 12 months at nearby Cahuana [5°26'S, 74°34'W] on the Río Pacaya, another black-water river; Soini, 1986.)

Callitrichidae

Cebuella pygmaea
Saguinus fuscicollis

Cebidae

Alouatta seniculus
Aotus cf. nancymai
Ateles cf. chamek
Cebus albifrons
Cebus apella
Lagothrix lagotricha
Pithecia monachus
Saimiri sciureus

13. **Surinam, Saramacca, Raleighvallen-Voltzberg Nature Reserve** (ca. 4°40'N, 56°10'W). Undisturbed habitats, predominantly tall forest on well-drained terrain; swamp and liana forest also present, but no riparian formations; hydrology and rainfall unknown; inventory data obtained from 147 days of observations on feeding ecology, habitat use, and social behavior (Mittermeier and van Roosmalen, 1981).

Callitrichidae

Saguinus midas

Cebidae

Alouatta seniculus
Ateles paniscus
Cebus apella
Cebus olivaceus
Chiropotes satanas
Pithecia pithecia
Saimiri sciureus

APPENDIX 13

Rainforest Mammals of the Maracaibo Basin, Venezuela

Collections from the southwestern Maracaibo Basin provide the best sample of mammalian diversity currently available for any rainforest enclave in the Caribbean lowlands of northern Venezuela. No ecologically detailed description of rainforest vegetation in the area is apparently available, but brief accounts of mammalian habitats were published by Pirlot (1963), Handley (1976; see Gazetteer entry for El Rosario), and Voss (1991: 69–70). Local precipitation probably ranges from 2000 to 3500 mm annually (Snow, 1976).

Besides rainforest, the Maracaibo Basin includes open vegetation (e.g., savannas and thornscrub, chiefly in the northern and eastern sectors; Huber and Alarcon, 1988) and some expeditions to the area worked from the lowlands to 2000 m above sea level in the bordering Serranía de Perijá (e.g., Mendez, 1953), so close attention to locality data is necessary to compile an ecologically homogeneous inventory. Because nonforest mammals have invaded cleared land at formerly rainforested localities, some manmade ecotones (e.g., abandoned orchards and overgrown garden plots) now support mixed faunas.

Our list includes records originally published by Osgood (1912), Pirlot (1963, 1967), Handley (1976), Bisbal (1989), and Voss (1991: table 24). However, Pirlot's (1967) dubious record of *Choronycteris mexicana* is omitted (see Koopman, 1993). Records of nonforest species (*Cerdocyon thous*, *Holochilus sciureus*, *Sigmodon hispidus*, *Zygodontomys brevicauda*, *Sylvilagus floridanus*) are also excluded. Specimens collected at the following localities in the Venezuelan states of Zulia

and Táchira are cited as vouchers: El Rosario (ca. 9°09'N, 72°36'W; 24–125 m); Encontrados (9°03'N, 72°14'W; 10 m); Kasmera (9°59'N, 72°43'W; ca. 270 m); Las Mesas (8°10'N, 72°10'W; 300–460 m); Misión Tukuko (= "El Tukuko" and "Tukuko"; 9°50'N, 72°52'W; 200–400 m); Río Catatumbo (miscellaneous localities near Encontrados); San Carlos del Zulia (9°01'N, 71°55'W; 10 m). Although these localities span almost 500 m of altitude and two degrees of latitude, all of the species listed below could reasonably be expected to occur in sympatry.

MARSUPIALIA [6 spp.]

Didelphidae

Caluromys lanatus (USNM)
Didelphis marsupialis (MARNR, USNM)
Marmosa murina (MARNR, MHNLS, USNM)
Metachirus nudicaudatus (MARNR, MHNLS, USNM)
Monodelphis brevicaudata (MHNLS, USNM)
Philander opossum (MARNR, USNM)

XENARTHRA [4 spp.]

Bradypodidae

Bradypus variegatus (MARNR, USNM)

Megalonychidae

Choloepus hoffmanni (USNM)

Dasypodidae

Dasypus novemcinctus (MARNR, MHNLS, USNM)

Myrmecophagidae

Tamandua mexicana (MARNR, MHNLS, USNM)

CHIROPTERA [47 spp.]

Emballonuridae

- Diclidurus albus* (MARNR, USNM)
Peropteryx macrotis (MARNR, USNM)
Rhynchonycteris naso (MARNR, USNM)
Saccopteryx bilineata (MARNR, USNM)
Saccopteryx canescens (USNM)
Saccopteryx leptura (USNM)

Noctilionidae

- Noctilio albiventris* (MARNR, USNM)
Noctilio leporinus (MARNR, USNM)

Phyllostominae

- Chrotopterus auritus* (USNM)
Lonchorhina aurita (MARNR, USNM)
Macrophyllum macrophyllum (AMNH, MARNR, USNM)
Micronycteris homezi
Micronycteris megalotis (MARNR, USNM)
Micronycteris microtis (USNM)
Micronycteris minuta (USNM)
Micronycteris nicefori (USNM)
Mimon crenulatum (MARNR, USNM)
Phyllostomus discolor (AMNH, MARNR, USNM)
Phyllostomus hastatus (AMNH, MARNR, USNM)
Tonatia brasiliensis (USNM)
Tonatia saurophila (USNM)
Tonatia silvicola (USNM)
Trachops cirrhosus (MARNR, USNM)
Vampyrus spectrum (FMNH)

Glossophaginae

- Anoura geoffroyi* (USNM)
Glossophaga soricina (AMNH, MARNR, USNM)
Lonchopylla robusta (MARNR, USNM)

Carollinae

- Carollia brevicauda* (MARNR, USNM)
Carollia castanea (MARNR, USNM)
Carollia perspicillata (AMNH, MARNR, USNM)

Stenodermatinae

- Artibeus (Artibeus) amplus* (MARNR, USNM)
Artibeus (A.) jamaicensis (AMNH, MARNR, USNM)
Artibeus (A.) lituratus (AMNH, MARNR, USNM)
Artibeus (Dermanura) glaucus (USNM)
Centurio senex (MARNR, USNM)
Chiroderma villosus (MARNR, USNM)
Platyrrhinus helleri (AMNH, MARNR, USNM)
Sphaeronycteris toxophyllum (USNM)
Sturmira lilium (AMNH, MARNR, USNM)
Uroderma bilobatum (AMNH, MARNR, USNM)
Uroderma magnirostrum (MARNR, USNM)

Desmodontinae

- Desmodus rotundus* (MARNR, USNM)
Diaemus youngi (USNM)

Vespertilionidae

- Eptesicus andinus* (MARNR, USNM)
Lasiurus blossevillii (USNM)
Myotis albescens (USNM)
Rhogeessa tumida (MARNR, USNM)

PRIMATES [4 spp.]

Cebidae

- Alouatta seniculus* (MARNR, USNM)
Aotus lemurinus (MARNR, MHNLS, USNM)
Ateles belzebuth (MARNR, USNM)
Cebus albifrons (MARNR, MHNLS, USNM)

CARNIVORA [11 spp.]

Felidae

- Herpailurus yaguarondi* (Bisbal, 1989)
Leopardus pardalis (USNM)
Panthera onca (USNM)
Puma concolor (MARNR, USNM)

Mustelidae

- Conepatus semistriatus* (USNM)
Eira barbara (MARNR, USNM)
Galictis vittata (Handley, 1976)
Lontra longicaudis (MARNR, USNM)

Procyonidae

- Bassaricyon gabbii* (MHNLS)
Potos flavus (MARNR, MHNLS, USNM)
Procyon cancrivorus (MARNR)

ARTIODACTYLA [1 sp.]

Cervidae

- Mazama americana* (USNM)

RODENTIA [13 spp.]

Sciuridae

- Sciurus granatensis* (MARNR, MHNLS, USNM)

Heteromyidae

- Heteromys anomalus* (MARNR, MHNLS, USNM)

Muridae

- Melanomys caliginosus* (MHNLS, USNM)
Nectomys squamipes (MARNR, MHNLS, USNM)
Oecomys trinitatis (MHNLS, USNM)
Oryzomys talamancae (MHNLS, USNM)
Sigmodontomys alfari (MHNLS)
Rhipidomys venezuelae (MHNLS, USNM)

Erethizontidae

- Coendou prehensilis* (MARNR, USNM)
Coendou pruinus (MHNLS, USNM)

Dasyproctidae

- Dasyprocta variegata* (MARNR, MHNLS, USNM)

Agoutidae

- Agouti paca* (MARNR, MHNLS, USNM)

Echimyidae

- Proechimys poliopus* (MARNR, MHNLS, USNM)

