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Richness, Complementarity, and Community Structure of Amazonian Mammal Faunas: Results from Multiyear Inventories in French Guiana and Peru

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ABSTRACT

Mammal faunas from northern French Guiana (in northeastern Amazonia) and the Yavarí-Ucayali interfluve (in southwestern Amazonia) are the first Amazonian mammal faunas to be comprehensively described in terms of taxonomic composition and community structure. Bats are the most speciose group in each fauna, followed in order of decreasing species richness by rodents, didelphimorphians, carnivorans, xenarthrans or primates, and ungulates. A total of 180 species are known from northern French Guiana and 199 species from the Yavarí-Ucayali interfluve, but an additional 25 species are possibly missing ("pseudoabsent") from the Yavarí-Ucayali interfluvial inventory; therefore, the increment by which species richness in northeastern Peru exceeds that of northern French Guiana is on the order of 10–25%. Complementarity (dissimilarity) between these faunas is high (79%–89%) for opossums, primates, and rodents, but complementarity is substantially lower for other groups (especially bats, carnivorans, and ungulates), suggesting taxonomic differences in geographic filtering. Most species in both faunas are nocturnal, as might be expected from the abundance of bats, but even among nonflying mammals nocturnal species outnumber diurnal species by about 2:1. Approximately equal numbers of nonflying species in both faunas are arboreal or terrestrial, whereas much smaller numbers are scansorial or semiaquatic; with one possible exception, none is fossorial. Despite such behavioral similarities, these faunas differ in trophic composition and guild membership: substantially more primary consumers are present in the Yavarí-Ucayali interfluve than in northern French Guiana, whereas numbers of secondary consumers and omnivores are similar. Higher primary productivity in western Amazonia, a geomorphologically dynamic landscape with fertile soils and phenologically diverse habitats, could explain faunal differences in both species richness and trophic structure.

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INTRODUCTION

Accurate information about mammalian diversity and community ecology in Neotropical rainforests is important for both research and conservation agendas, but it is hard to obtain. Taxonomically comprehensive inventories require time and intensive effort with multiple methods to detect the presence of elusive species differing in size, diel activity, substrate use, and diet (Voss and Emmons, 1996; Sampaio et al., 2003; Munari et al., 2011; Palmeirim et al., 2019). Additionally, because small mammals (opossums, bats, and rodents) are often difficult to identify in the field, species lists can be problematic if specimens are unavailable to voucher dubious occurrence records. Lastly, sites where inventory fieldwork is logistically feasible have often been partially defaunated by hunting or habitat fragmentation (Voss and Emmons, 1996; Bogoni et al., 2022).

For Amazonia, by far the largest Neotropical rainforest biome, we still lack basic knowledge about sympatric species richness and site-to-site faunal differences. Although richness and turnover can be estimated from stacked range maps (Tognelli and Kelt, 2004), the accuracy of stacked-map estimates cannot be properly assessed without inventory-based ground-truthing. Even so-called expert range maps are likely to be unreliable for small mammals, especially in Amazonia where new species and large range extensions are still routinely reported.

In addition to such Linnaean (taxonomic) and Wallacian (biogeographic) shortfalls (Hortal et al., 2015), our understanding of mammalian diversity in Amazonia is handicapped by the lack of ecobehavioral trait data for many species. As a result, no taxonomically comprehensive analysis of ecological community structure exists for any Amazonian mammal fauna, despite useful attempts that have been made for various faunal subsets (e.g., Janson and Emmons, 1990; Peres, 1999; Kalko and Handley, 2001; Haugaasen and Peres, 2005). Important new sources of natural history information are now available from camera-trapping studies (Gómez et al., 2005; Blake et al., 2012; Gregory et al., 2022) and ethnographic interviews (Voss and Fleck, 2011; Fleck and Voss, 2016), but these data have yet to be combined in any general synthesis of Amazonian mammal community structure.

This report is based on the results of long-term faunal research programs in French Guiana and Peru, results that now provide sufficient materials for assessing the taxonomic and ecological dimensions of mammalian diversity and community structure at opposite biogeographic poles of Amazonia. Importantly, large numbers of specimens were collected in both regions, and taxonomic analyses of those specimens have been summarized in monographs that document species identifications for taxa previously neglected or deemed intractable by many faunal researchers. Although some species remain data deficient, this report also incorporates natural history information from camera-trap surveys, traditional autecological and dietary studies, and ethnographic sources to provide preliminary but taxonomically inclusive analyses of community structure in both regions.

MATERIALS AND METHODS

Species Lists

Most previous discussions of Amazonian mammal diversity have been based on species lists from single-site inventories, but single-site inventories have the key disadvantage of incompleteness.

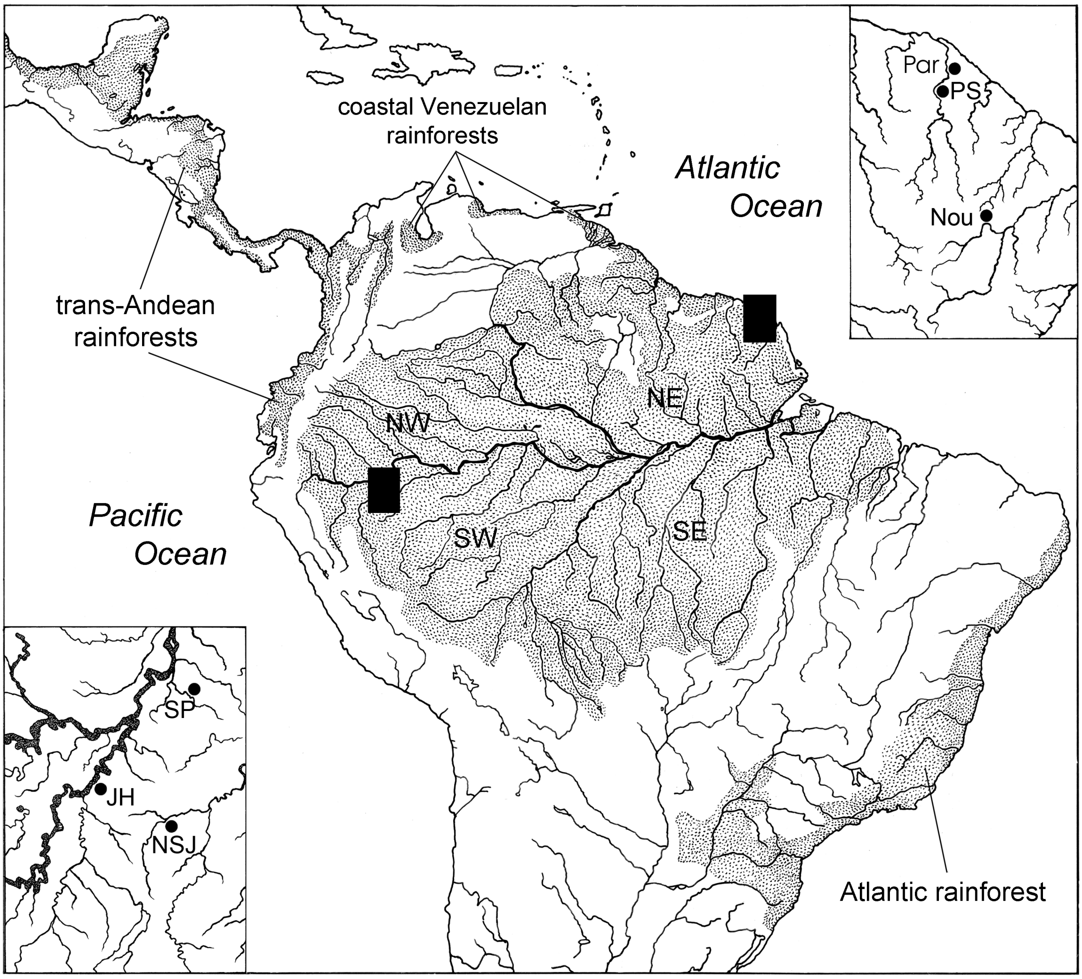

FIG. 1. Four Neotropical rainforest biomes (stippled) separated by montane or nonforest vegetation. Primary intercardinal directions (NE, NW, SE, SW) label quadrants of Amazonia defined by the Amazon, Negro, and Madeira rivers (after Wallace, 1854). Insets show the location of important faunal inventory sites in northern French Guiana (in NE Amazonia: **Par**, Paracou; **PS**, Petit Saut; **Nou**, Nouragues) and the Yavarí-Ucayali interfluve (in SW Amazonia: **SP**, San Pedro; **JH**, Jenaro Herrera; **NSJ**, Nuevo San Juan).

Among other evidence of inventory incompleteness, graphs of species accumulation from single-site inventories are never convincingly asymptotic, and long lists of "missing" species (unobserved species with geographic ranges that overlap the site) are dominated by behaviorally elusive taxa (Voss and Emmons, 1996). Therefore, a more meaningful basis for faunal inference can be had by combining lists from multiple localities within biogeographically homogeneous regions. Such regional lists include species that are potentially sympatric, although not necessarily syntopic.

I compiled species lists from the published results of inventory projects and ecological research at rainforested sites in northern French Guiana and the Yavarí-Ucayali interfluve of northeastern Peru (fig. 1). These regions lack internal dispersal barriers, and they occupy opposite quadrants of Amazonia as traditionally recognized by biogeographers (Wallace, 1854). Whereas northern French Guiana is in northeastern Amazonia (north of the lower Amazon and east of the Rio Negro), the Yavarí-Ucayali interfluve is in southwestern Amazonia (south of the upper Amazon and west of the Rio Madeira).

Northern French Guiana: An overseas department of France, French Guiana lies between the Maroni and Oyapock rivers, which have their headwaters in the remote Tumuc Humac Mountains along the Brazilian border and discharge into the Atlantic Ocean. Other rivers in the department are substantially smaller, have their headwaters in the central highlands (<900 m above sea level), and none is known to limit the distribution of any terrestrial vertebrate. Except for coastal swamps and savannas, low scrub associated with rocky soil on isolated hilltops, a few urban areas, and small agricultural clearings, the department is uniformly covered by tall, closed-canopy, evergreen forest. Physiognomic and floristic descriptions of local rainforest habitats were reported by Mori and Boom (1987), Sabatier (1993), and Poncy et al. (2001). Isohyets based on weather records from 1961 to 1990 suggest that most of this region receives at least 2700 mm of rainfall annually (Freycon et al., 2010).

Faunal data are available from multiyear inventory sites, ecological research stations, and other localities in the northern part of the department (within 100 km of the Atlantic coast), from the right bank of the Maroni to the left bank of the Oyapock. The largest species lists were obtained from Paracou (5.28°N, 52.92°W), a forestry research station where AMNH research teams worked for several years to inventory the entire mammalian fauna (Simmons and Voss, 1998; Voss et al., 2001); Petit Saut (5.07°N, 53.05°W), where thousands of mammals were rescued from rising water behind a newly constructed hydroelectric dam (Vié, 1999); and Nouragues (4.09°N, 52.68°W), an ecological field station where French researchers have studied mammals and their biotic interactions for several decades (Charles-Dominique, 2001; Feer and Charles-Dominique, 2001). Although local populations of some game species may have been depleted by hunting at Paracou, the fauna at Petit Saut was remote from human disturbance prior to dam construction, and the Nouragues site is pristine.

The mammals listed in appendices 1 and 2 include all the rainforest species reported by Simmons and Voss (1998), Vié (1999), Feer and Charles-Dominique (2001), Voss et al. (2001), Catzeflis et al. (2013), Moratelli et al. (2015), Pavan et al. (2018), and Alexandre and Thoisy (2023). Not included in these lists are seven species associated with coastal savannas rather than rainforest (*Cryptonanus* sp., *Natalus tumidirostris*, *Odocoileus virginiana*, *Holochilus nanus*, *Oligoryzomys* sp., *Sigmodon alstoni*, and *Zygodontomys brevicauda*). Voucher specimens that document taxonomic identifications of mammals from northern French Guiana are at the American Museum of Natural History (AMNH, New York) and the Muséum National d'Histoire Naturelle (MNHN, Paris).

Yavarí-Ucayali Interfluve: The Río Yavarí and the Río Ucayali are right-bank tributaries of the upper Amazon, and the region they delimit is part of Loreto department in northeastern Peru (Voss and Fleck, 2011). All the streams that drain the interfluvial interior are small, have their headwaters in low hills (<200 m above sea level), and are not known to limit the distribution of any terrestrial vertebrate. Except for river beaches, small patches of peatland savanna, and agricultural clearings around several villages, the entire landscape is covered with tall, closed-canopy evergreen forest. Physiognomic and floristic descriptions of local rainforest habitats were reported by Fine et al. (2006), Lopez-Parodi and Freitas (1990), and Pitman et al. (2003). Annual average rainfall throughout the region is thought to be at least 2500 mm (Marengo, 1983).

Information about mammals of the Yavarí-Ucayali interfluve is primarily available from three sites where multiyear faunal inventory projects and/or long-term ecological studies have been carried out: Jenaro Herrera (4.92°S, 73.67°W), a forestry research station on the right bank of the lower Ucayali; Nuevo San Juan (5.25°S, 73.17°W), a Matses Indian village on the Río Gálvez (a left-bank tributary of the Yavarí); and San Pedro (4.33°S, 73.20°W), a ribereño village on the Quebrada Blanco (a tributary of the Río Tahuayo, which is a right-bank tributary of the Amazon). Ecological research, faunal inventory efforts, and historical collecting activities at these and other sites in the Yavarí-Ucayali interfluve were summarized by Voss and Fleck (2011) and Velazco et al. (2021). Species lists from the Yavarí-Ucayali interfluve (appendices 3, 4) were compiled from faunal monographs that treated the regional primates (Voss and Fleck, 2011); xenarthrans, carnivorans, and ungulates (Voss and Fleck, 2017); didelphimorphians (Voss et al., 2019); bats (Velazco et al., 2021); and rodents (Voss et al., 2024). Not included in these lists are two rodent species (*Holochilus nanus* and *Oligoryzomys microtis*) that are restricted to open (grassy or marshy) vegetation along river beaches. Voucher specimens that document taxonomic identifications of species from the Yavarí-Ucayali interfluve are at the AMNH and the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM, Lima).

NOMENCLATURE: Scientific names in the source literature cited above have been updated to conform with current usage as summarized by Catzeflis et al. (2013, 2016), Pavan et al. (2018), and Velazco et al. (2021) for bats; Patton et al. (2015), Salazar-Bravo et al. (2023), and Voss et al. (2024) for rodents; Voss (2022) for opossums; Miranda et al. (2018) for pygmy anteaters (*Cyclopes*); Acosta et al. (2020) for tayassuids; and Morales-Donoso (2023) for cervids. To conserve long-standing binomial usage (Teta, 2019), I treat *Sapajus* (tufted capuchins) as a subgenus of *Cebus*, *Cebuella* (pygmy marmosets) as a subgenus of *Callithrix*, *Leontocebus* (a clade of tamarins) as a subgenus of *Saguinus*, *Plecturocebus* (a clade of titi monkeys) as a subgenus of *Callicebus*, and *Neogale* as a subgenus of *Mustela*. As discussed by Voss and Fleck (2011), Lima et al. (2018), and Martins et al. (2023), there seems to be no compelling evidence for more than a single Amazonian species of tufted capuchins (*Cebus apella*). Although analyses of mitochondrial DNA have revealed numerous haplogroups of Amazonian squirrel monkeys (Lynch Alfaro et al., 2015), multiple lines of evidence suggest that all represent a single species (*Saimiri sciureus*).

COMPLEMENTARITY: The dissimilarity (D) between two species lists, X and Y, can be quantified as the number of species unique to one or the other as a fraction of the species in both. In set notation,

$$D = (|X \cup Y| - |X \cap Y|) \div |X \cup Y|,$$

where the brackets for absolute value indicate the number of elements (species) in the corresponding union or intersection. This quantity, which Colwell and Coddington (1994) called complementarity, can vary from zero (for two identical lists) to 1 (for two lists with no species in common). As noted by Levandowski and Winter (1971), *D* is the one-complement of Jaccard's familiar index of similarity. Because decimal fractions are awkward to discuss in running text, complementarity values are commonly multiplied by 100 and described as percentages.

Although complementarity is a straightforward measure of faunal difference when computed from complete species lists, incomplete faunal sampling tends to overestimate complementarity by inflating the number of unique species (Colwell and Coddington, 1994). Faunal sampling completeness at Paracou was discussed by Simmons and Voss (1998) and Voss et al. (2001), who concluded that numerous species of bats and several species of nonflying mammals remained undetected there, but almost all the missing species they discussed have either been discovered at Paracou by subsequent researchers or are known from adjacent research sites (e.g., Petit Saut and Nouragues), such that the species lists from northern French Guiana (appendices 1, 2) are plausibly complete. Faunal sampling in the Yavarí-Ucayali interfluve (reviewed by Voss and Fleck, 2011, 2017; Voss et al., 2019, 2024; Velazco et al., 2021) is thought to be nearly complete, with the important exception of high-flying insectivorous bats (molossids, diclidurine emballonurids, and *Lasiurus* spp.), which were ineffectively and haphazardly sampled for methodological reasons, and cave-roosting bats, which might occur in rocky outcrops of the remote and very incompletely surveyed Sierra del Divisor.

I computed complementarity between whole-faunal lists from northern French Guiana and the Yavarí-Ucayali interfluve and for selected taxonomic groups (opossums, xenarthrans, bats, primates, carnivorans, ungulates, and rodents) that were sampled in both regions. Acknowledging the probable undersampling of high-flying insectivorous and cave-roosting bats in the Yavarí-Ucayali interfluve, I also computed complementarity between subsets of the bat fauna by excluding species in those categories.

Missing species: Species with geographic ranges that overlap a region but were not observed there are candidate "missing" species (sensu Voss and Emmons, 1996) or "pseudo-absences" (sensu Bogoni et al., 2022). As explained above, the French Guianan species lists for nonflying mammals and bats are believed to be complete, or nearly so, because they include all the species with geographic ranges that overlap the region; however, this criterion might be unreliable for a coastal area, beyond which no species of terrestrial mammal can occur. The species potentially missing from the Yavarí-Ucayali fauna were discussed by Voss et al. (2019: appendix 4), Velazco et al. (2021: appendix 2), and Voss et al. (2024: appendix 5); they include 3 opossums, 18 bats, and 4 rodents. Because the criterion of geographic overlap might bias the comparison of coastal and interior faunas, I provide comparisons of northern French Guiana with the observed fauna from the Yavarí-Ucayali interfluve and with the "expected" fauna (including candidate missing species) of the latter region.

Body Mass and Ecobehavioral Traits

Body mass: I extracted mass data from the faunal monographs cited above and from other literature (e.g., Richard-Hansen et al., 1999), but I consulted specimen labels or fieldnotes for a few species without published sources of mass data. Insofar as possible, tabulated masses in appendices 1–4 are means of nonpregnant adults (for sexually monomorphic species) or midpoints of male and female means (for size-dimorphic species); for a few species, however, I used the midpoint of the range of values reported by Emmons (1997) for samples of unknown sex composition. Whenever possible, I used mass data of regional origin to allow for geographic variation; however, when regional data were unavailable or were based on excessively small samples, I used data pooled from geographically heterogeneous sources. Masses of nonvolant mammals are rounded to the nearest gram (g), but masses of large mammals were often recorded at coarser intervals (e.g., to the nearest 20 g by Richard-Hansen et al., 1999), and only kilograms (kg) are recorded in the literature for very large species. I rounded bat masses to the nearest 0.1 g following the prevailing custom among bat researchers (e.g., Simmons and Voss, 1998; Velazco et al., 2021). Mass data are unavailable for just two mammals treated in this report (*Mustela africana* and *Coendou ichillus*).

Ecobehavioral traits: Information about diel activity (nocturnal, diurnal, cathemeral) and substrate use (arboreal, semiaquatic, scansorial, terrestrial) for nonflying species were obtained from camera-trap surveys (e.g., Gómez et al., 2005; Blake et al., 2012; Bowler et al., 2017; Gregory et al., 2022), conventional trapping studies (e.g., Malcolm, 1991; Patton et al., 2000), direct-observational studies (e.g., Emmons, 1981; Dubost, 1988; Soini and Soini, 1992), interviews with indigenous Amazonians (Voss and Fleck, 2011, 2017; Voss et al., 2024), and fieldnotes. In reviewing fieldnotes, specimens recovered at dawn from traps baited in the late afternoon of the previous day were assumed to have been caught at night. Because game species are known to shift their diel activity near human communities (Mendes et al., 2020), I tabulated activity from the results of camera-trap surveys at remote, unhunted sites whenever possible.

I compiled dietary information for bats from studies that summarized results of fecal analyses or that reviewed such results from previous research (e.g., Giannini and Kalko, 2004, 2005; Delaval et al., 2005; Pellón et al., 2023), and I assumed that species for which such data are lacking have diets resembling those of congeners with known diets (e.g., that unstudied *Saccopteryx gymnura* trophically resembles well-studied *S. bilineata* and *S. leptura*). Additionally, dietarily unstudied species belonging to clades that are morphologically specialized for nectarivory (glossophagines and lonchophyllines) were assumed to be nectarivores. In general, phyllostomids are readily divisible into primarily phytophagous or animalivorous species, but published evidence suggests that *Lampronycteris brachyotis*, *Trinycteris nicefori*, and species of *Phyllostomus* consume substantial quantities of fruit and/or nectar in addition to arthropods (Delaval et al., 2005; Giannini and Kalko, 2005; Pellón et al., 2003) and should be classified as omnivores.

Trophic-Guild Membership

Community structure is often discussed in terms of species membership in trophic guilds: sets of species that use the same food resource in similar ways. Unfortunately, many species lack sufficiently detailed information to consistently distinguish (for example) frugivore-granivores from granivore-frugivores—just two among other possible permutations of phytophagous species with mixed diets. Therefore, I defined trophic guilds of nonflying mammals by cross-classifying species by diel activity (diurnal, nocturnal, cathemeral), substrate use (arboreal, terrestrial, scansorial, semiaquatic), and trophic level (primary consumers, secondary consumers, and omnivores). Only a few of the 36 resulting categories (diurnal arboreal primary consumers, nocturnal terrestrial secondary consumers, etc.) are useful for faunal comparisons because some categories are unoccupied—for example, there are no diurnal arboreal secondary consumers in either fauna—whereas other categories (e.g., diurnal semiaquatic secondary consumers) are occupied by the same species throughout Amazonia.

I recognize the following bat trophic guilds: aerial insectivores, gleaning animalivores (including piscivores), gleaning frugivores, gleaning nectarivores, gleaning omnivores, and gleaning sanguivores. More or less the same ecobehavioral categories are widely recognized by Neotropical bat researchers, although there are minor disagreements about species membership. Among other occasionally disputed taxa, I classify *Lampronycteris brachyotis* and *Trinycteris nicefori* as omnivores and *Phylloderma stenops* as a frugivore based on dietary data summarized by Giannini and Kalko (2005: appendix), and I classify species of *Thyroptera*—formerly considered aerial insectivores (e.g., by Sampaio et al., 2003)—as gleaning animalivores because they appear to mostly eat nonflying arthropods (Dechmann et al., 2006).

RESULTS AND DISCUSSION

Richness and Taxonomic Composition

The observed rainforest mammal faunas of northern French Guiana and the Yavarí-Ucayali interfluve consist of 180 and 199 species, respectively (table 1). The same major groups—opossums, xenarthrans, bats, primates, carnivorans, ungulates, and rodents—are present in both faunas, and the most speciose groups are represented in roughly equivalent proportions: bats are by far the most species-rich ordinal-level clade in each fauna, followed by rodents, opossums, and carnivorans. The same Linnaean families are also present in both faunas (appendices 1–4), with two exceptions: Mormoopidae (present in northern French Guiana but not in the Yavarí-Ucayali interfluve) and Dinomyidae (present in the Yavarí-Ucayali interfluve but not in northern French Guiana). Despite such higher-taxonomic resemblances, there are noteworthy faunal differences in numbers of species. Primates and rodents, in particular, are more speciose in the Yavarí-Ucayali interfluve than in northern French Guiana. Adding missing species to the expected fauna of the Yavarí-Ucayali interfluve (in the rightmost column of table 1) does not affect the diversity ranking of groups but increases the percent representation of bats.

The higher species richness of the Yavarí-Ucayali interfluve by comparison with northern French Guiana—an increment of about 10% based on observed species, but almost 25% if based on expected species)—is consistent with the gradient of increasing species richness from

TABLE 1. Taxonomic composition of Amazonian rainforest mammal faunas in northern French Guiana (NFG) and the Yavarí-Ucayali interfluve (YUI).

	Numbers of species (% of fauna)		
	NFG	YUI (observed)	YUI (expected)[a]
Didelphimorphia	15 (8%)	19 (10%)	22 (10%)
Xenarthra[b]	9 (5%)	9 (5%)	9 (4%)
Chiroptera	103 (57%)	98 (49%)	116 (52%)
Primates	7 (4%)	14 (7%)	14 (6%)
Carnivora	14 (8%)	16 (8%)	16 (7%)
Ungulates[c]	5 (3%)	5 (3%)	5 (2%)
Rodents	27 (15%)	38 (19%)	42 (19%)
TOTALS	180	199	224

[a] Including unobserved species of opossums, rodents, and bats with geographic ranges that overlap the Yavarí-Ucayali interfluve (see Materials and Methods).

[b] Cingulata and Pilosa.

[c] Perissodactyla and terrestrial Artiodactyla.

eastern to western Amazonia that Voss and Emmons (1996) hypothesized from geographic range data. Richness contours subsequently generated by computerized stacking of range maps have illustrated this hypothetical gradient for nonflying mammals (Tognelli and Kelt, 2004: fig. 1a) and for various subsets of the nonflying fauna (Fergnani and Ruggiero, 2015: fig. 4). The species lists reported here for northern French Guiana and the Yavarí-Ucayali interfluve—based on fieldwork, specimen collection, and taxonomic analysis—provide empirical confirmation of this predicted gradient and establish a plausible range (180–224 species) to bracket diversity expectations within other faunally homogeneous Amazonian regions.

Complementarity

Complementarity between the observed faunas of northern French Guiana and the Yavarí-Ucayali interfluve is 56% (table 2): over half the total species present in these faunas occur in one region or the other, but not in both. Such a large fraction is perhaps unsurprising for faunas that are separated by almost 2500 km, but complementarity values computed for different groups suggest wide taxonomic divergence in geographic filtering. Complementarity is notably high (79%–89%) for opossums, primates, and rodents, only a few species of which are common to both faunas. By contrast, complementarity is much lower (0%–24%) for ungulates and carnivorans, many species of which are found throughout Amazonia. Bat complementarity (42%) is probably biased by incomplete sampling of high-flying insectivorous and cave-roosting species in the Yavarí-Ucayali interfluve (see Methods); for the well-sampled subset of these bat faunas, complementarity is only 32%. Thus, the dissimilarity between these bat faunas seems to be substantially less than the faunal dissimilarities observed for opossums, primates, and rodents. Two possible explanations merit consideration.

TABLE 2. Complementarity between rainforest mammal faunas in northern French Guiana and the Yavarí-Ucayali interfluve.

	Complementarity
Observed faunas (all groups)	0.56
Didelphimorphia	0.79
Xenarthra	0.62
Chiroptera	0.42
Chiroptera (subset)[a]	0.32
Primates	0.89
Carnivora	0.24
Ungulates	0.00
Rodents	0.82

[a] Minus high-flying aerial insectivores and cave-roosting species.

First, complementarity estimates are sensitive to taxonomic resolution. The complementarity values recovered in this analysis for marsupials, primates, and rodents are higher than those that would have been estimated just 30 years ago, when (for example) *Marmosa constantiae* was not distinguished from *M. demerarae*, *Alouatta seniculus* was not distinguished from *A. macconnelli*, and *Hylaeamys perenensis* was not distinguished from *H. megacephalus*. If bats were taxonomically neglected by comparison with those groups, bat faunas might exhibit lower complementarity as a consequence.

Second, it is possible that different landscape features or ecological factors limit the distribution of opossums, primates, and rodents on the one hand and bats on the other. The obvious limiting landscape features in Amazonia are large rivers, which have often been identified as dispersal barriers for primates (Ayres and Clutton-Brock, 1992; Fordham et al., 2020; Mouthé et al., 2022) and sometimes also for opossums (Rocha et al., 2015; Voss et al., 2019) and rodents (da Silva et al., 2017; Saldanha et al., 2019; Voss et al., 2024). By contrast, rivers are seldom suggested as distributional limits for Amazonian bats (the unique exception seems to be *Carollia benkeithi*; Solari and Baker, 2006), and riverine barriers do not explain geographic patterns of Amazonian bat endemism or community composition (Silva et al., 2022). Of course, these alternative explanations for the lower faunal complementarity of bats on the one hand versus opossums, primates, and rodents on the other are not mutually exclusive: bats could be both taxonomically neglected and unaffected by riverine barriers. However, the revisionary taxonomy of Neotropical bats is an active research field—a recent monograph (Velazco et al., 2021) cited 99 publications on this topic in the interval from 2000 to 2020—and numerous analyses of molecular data seem to support the conspecificity of geographically remote Amazonian bat populations. A relevant example is Silva et al.'s (2023) genetic survey of *Rhinophylla pumilio*, a small (ca. 9–10 g) understory frugivore, which exhibits <2% sequence divergence in protein-coding mitochondrial genes among populations scattered throughout Amazonia (on opposite banks of the Amazon and of all its major tributaries). Although cryptic diversity doubtless exists within some currently recognized species (e.g., *Myotis riparius*; Novaes et al., 2023), most

TABLE 3. Body mass statistics for rainforest mammals in northern French Guiana (NFG) and the Yavarí-Ucayali interfluve (YUI).

	NFG	YUI[a]
NONFLYING SPECIES		
N[b]	77	99
1st quartile	102 g	123 g
Median	1035 g	602 g
3rd quartile	6000 g	5645 g
Range	12 g–177 kg	12 g–126 kg
Skewness	4.8	4.4
BATS		
N[b]	103	98
1st quartile	8.1 g	8.6 g
Median	13.0 g	11.1 g
3rd quartile	23.6 g	21.8 g
Range	3.4–145.5 g	3.5–170.0 g
Skewness	3.6	4.1

[a] Observed species.

[b] Number of species from which mass data are available.

evidence suggests that Amazonian bats tend to have substantially larger geographic distributions than small and medium-size nonflying Amazonian mammals, consistent with the complementarity values reported here.

Size Distributions

Mammalian size distributions have long been scrutinized for evidence of ecological patterns and processes (e.g., by Hutchinson and MacArthur, 1959; Brown and Nicoletto, 1991; Rodríguez, 1999; Bakker and Kelt, 2000). To date, most studies have focused on mass data from nonflying mammals, which are not affected by the physics of flight and echolocation that constrain body size among bats (Norberg and Rayner, 1987; Barclay and Brigham, 1991; Jones, 1999). Rather than ignoring body size in bats, we analyze those data separately.

Nonflying species: Nonflying rainforest mammals in both northern French Guiana and the Yavarí-Ucayali interfluve vary in mass by four orders of magnitude (table 3), but only a few species in each fauna—giant armadillo (*Priodontes maximus*), giant anteater (*Myrmecophaga tridactyla*), giant otter (*Pteronura brasiliensis*), puma (*Puma concolor*), jaguar (*Panthera onca*), peccaries (*Pecari tajacu*, *Tayassu pecari*), deer (*Mazama americana*, *Passalites nemorivagus*), tapir (*Tapirus terrestris*), pacarana (*Dinomys branickii*), and capybara (*Hydrochoerus hydrochaeris*)—exceed 10 kg. Most nonflying mammals are smaller; 75% of the species in both faunas are less than about 6 kg. However, the median mass of nonflying mammals in the Yavarí-Ucayali interfluve (602 g) is substantially less than the median mass in northern French

TABLE 4. Descriptive statistics for $\log_2$-transformed masses of nonflying rainforest mammals in northern French Guiana (NFG), the Yavarí-Ucayali interfluve (YUI), and seven other Amazonian faunas.

		Log_2-grams				
	N[a]	Median	Minimum	Maximum	IQ range[b]	Skewness
NFG	77	10.0	3.6	17.4	5.9	0.01
YUI	99	9.2	3.6	16.9	5.6	0.14
Other faunas[c]	67–92	9.3–10.3	3.3–4.1	17.7	4.5–5.9	-0.05–0.17

[a] Number of species with mass data.

[b] Interquartile range.

[c] Ranges (minimum–maximum) from seven well-sampled faunas (Balta, Cocha Cashu, Cunucunuma, Cuzco Amazónico, Kartabo, MCSE Reserves, and Xingu) analyzed by Bakker and Kelt (2000: table 2).

Guiana (1035 g), a difference that is explained by the higher richness of small rodents and opossums in the former region.

Descriptive statistics of $\log_2$-transformed mass data (the usual currency of mammalian size-distributional comparisons) from northern French Guiana and the Yavarí-Ucayali interfluve closely resemble values previously reported for other Amazonian faunas (table 4). Consistent with Bakker and Kelt's (2000) results, the medians for both regions are higher than the medians that those authors reported for the entire South American fauna (7.5 $\log_2$ g) and for the Neotropical lowland rainforest biome (8.5 $\log_2$ g), whereas the regional interquartile ranges are larger than the corresponding continental (4.0 $\log_2$ g) and biome (4.5 $\log_2$ g) values. As interpreted by Bakker and Kelt (2000), such results illustrate the scale dependence of mammalian size distributions: medians and interquartile ranges both increase for mass data sequentially compiled from continents, biomes, and smaller regions of uniform habitat. Brown and Nicoletto (1991) suggested several hypotheses that might explain such scaling, but none are uniquely supported or convincingly refuted by data from Amazonian faunas.

Graphs of rank-ordered log-mass data (cenograms) are often used by paleontologists seeking ecological patterns in Recent faunas to interpret fossil data (Rodríguez, 1999; but see Alroy, 2000). Cenograms of nonflying mammals from northern French Guiana and the Yavarí-Ucayali interfluve are smoothly continuous arrays (fig. 2). Neither has any obvious gaps or abrupt changes of slope, consistent with results previously obtained by graphing mass data for other faunas from warm, humid environments (Legendre, 1986; Gingerich, 1989; Croft, 2001). In particular, both faunas include numerous species in the mass interval from 1 to 10 kg (ca. 10–13 $\log_2$ g), which other researchers have alleged is suboptimal for mammals (Smith and Lyons, 2011).

BATS: By contrast with sympatric nonflying mammals, bats from both regions range in mass by only two orders of magnitude (table 3). No bat in either fauna—even the largest nonpregnant specimens of the spectral bat (*Vampyrum spectrum*)—is known to exceed 200 g. The median mass of bats in both regions is in the range of 11–13 g, and the first and third quartiles of mass in both faunas are nearly the same.

Mass data for Amazonian bats have not previously been analyzed by descriptive statistics or graphing, so the literature provides no basis for relevant comparisons. In fact, few Amazo-

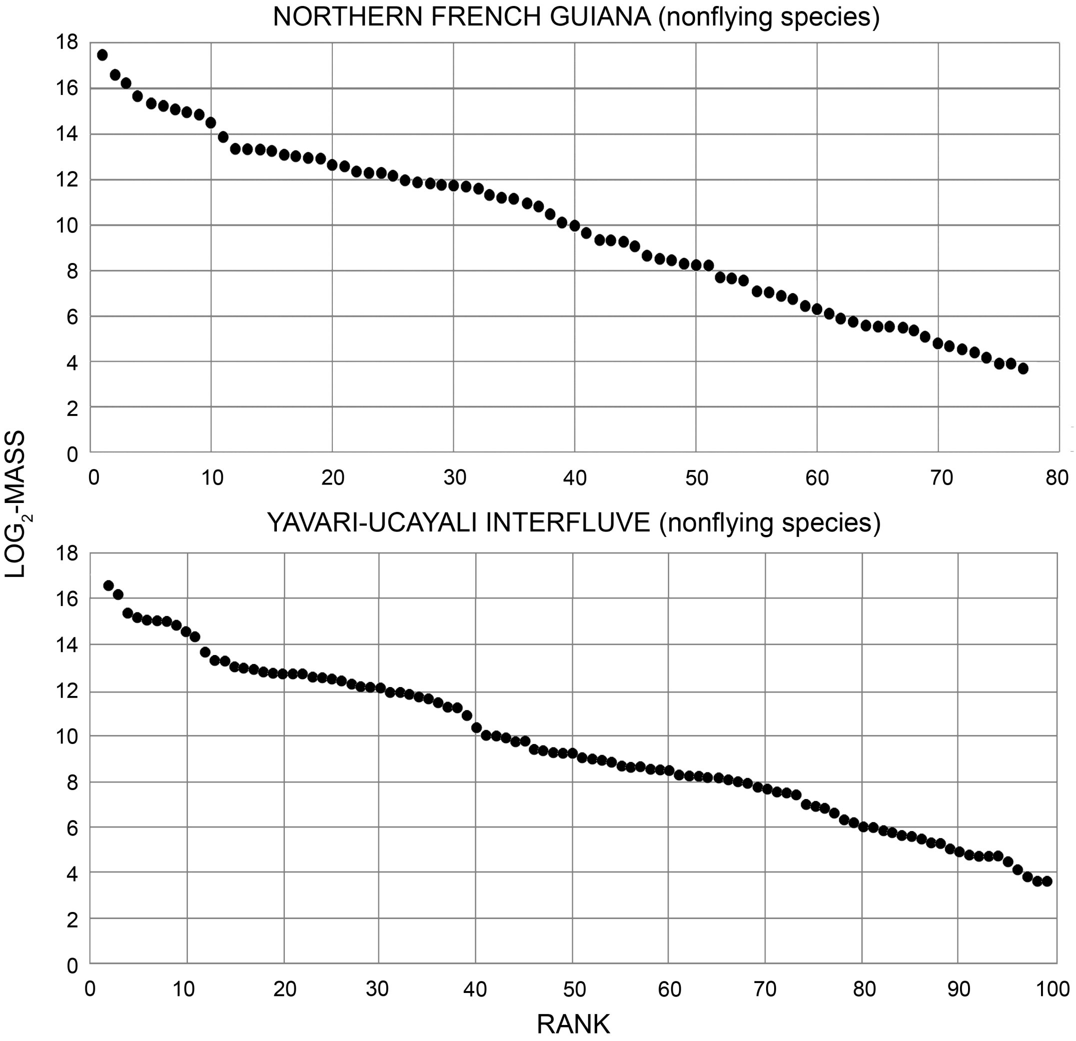

FIG. 2. Cenograms of nonflying mammals from two Amazonian faunas.

nian bat researchers have compiled mass data suitable for comparative analyses, with the noteworthy exceptions of Lim and Engstrom's (2001) inventory of Iwokrama Forest (in Guyana) and Hice et al.'s (2004) inventory of the Allpahuayo-Mishana Reserve (in Peru). Despite smaller sample sizes, descriptive statistics of central tendency, dispersion, and skewness for log-mass data from both of those inventories are similar to those from northern French Guiana and the Yavarí-Ucayali interfluve (table 5). Cenograms for Iwokrama and Allpahuayo-Mishana (not shown) are also similar to those from northern French Guiana and the Yavarí-Ucayali interfluve (fig. 3), which show a steep decline in rank-ordered masses among the largest bats, followed by a gradual and almost linear decrease among the smaller species, without any conspicuous gaps. Consistent with theoretical expectations that echolocation constrains the maximum size of aerial hawkers (Barclay and Brigham, 1991; Jones, 1999), the largest bats in

TABLE 5. Descriptive statistics for $\log_2$-transformed masses of rainforest bats in northern French Guiana (NFG), the Yavarí-Ucayali interfluve (YUI), Iwokrama Forest (IF), and the Reserva Nacional Allpahuayo-Mishana (RNAM).

	N[a]	Log_2-grams				Skewness
		Median	Minimum	Maximum	IQ range[b]	
NFG	103	3.7	1.8	7.2	1.5	0.35
YUI	98	3.5	1.8	7.4	1.3	0.67
IF[c]	73	3.6	2.0	7.1	1.6	0.66
RNAM[d]	61	3.5	2.0	6.5	1.8	0.44

[a] Number of species with mass data.
[b] Interquartile range.
[c] Upper Demerara-Berbice, Guyana. Mass data from Lim and Engstrom (2001).
[d] Loreto, Peru. Mass data from Hice et al. (2004).

these faunas are all gleaning species (e.g., *Vampyrum spectrum*, *Chrotopterus auritus*, *Phyllostomus* spp., and *Artibeus lituratus*).

Diel Activity

The overwhelming majority of rainforest mammals in northern French Guiana and the Yavarí-Ucayali interfluve are nocturnal (table 6). This result is, of course, strongly influenced by bat richness, but even among nonflying mammals nocturnal species are more numerous than diurnal species by a ratio of about 2:1 in both regions. Only a few species are cathemeral (active both by day and by night); of these, most are large terrestrial forms—e.g., giant anteater, jaguar, puma, red brocket (*Mazama americana*)—but three-toed sloths (*Bradypus* spp.) are noteworthy exceptions.

To my knowledge, these are the first Neotropical rainforest faunas to be comprehensively scored for diel activity, but the results do not challenge conventional expectations about trait frequencies. The therian common ancestor is believed to have been nocturnal (Gerkema et al., 2013; Maor et al., 2017), and nocturnality predominates among Recent mammals, especially at low latitudes (Bennie et al., 2014). Most Amazonian species are perhaps nocturnal by direct inheritance from a common therian ancestor, but night monkeys (*Aotus* spp.) acquired this behavior by evolutionary reversal (Santini et al., 2015).

Substrate Use

Communitywide patterns of substrate use are also similar in northern French Guiana and the Yavarí-Ucayali interfluve (table 6), and not only because bats are so numerous in each fauna. Among nonflying mammals, most species are either arboreal (e.g., monkeys, squirrels, sloths, porcupines) or terrestrial (e.g., armadillos, large cats, ungulates, dasyproctid rodents, *Proechimys* spp.), with roughly equivalent numbers in both categories. Many fewer species in each fauna are scansorial, a somewhat heterogeneous category that includes species that travel

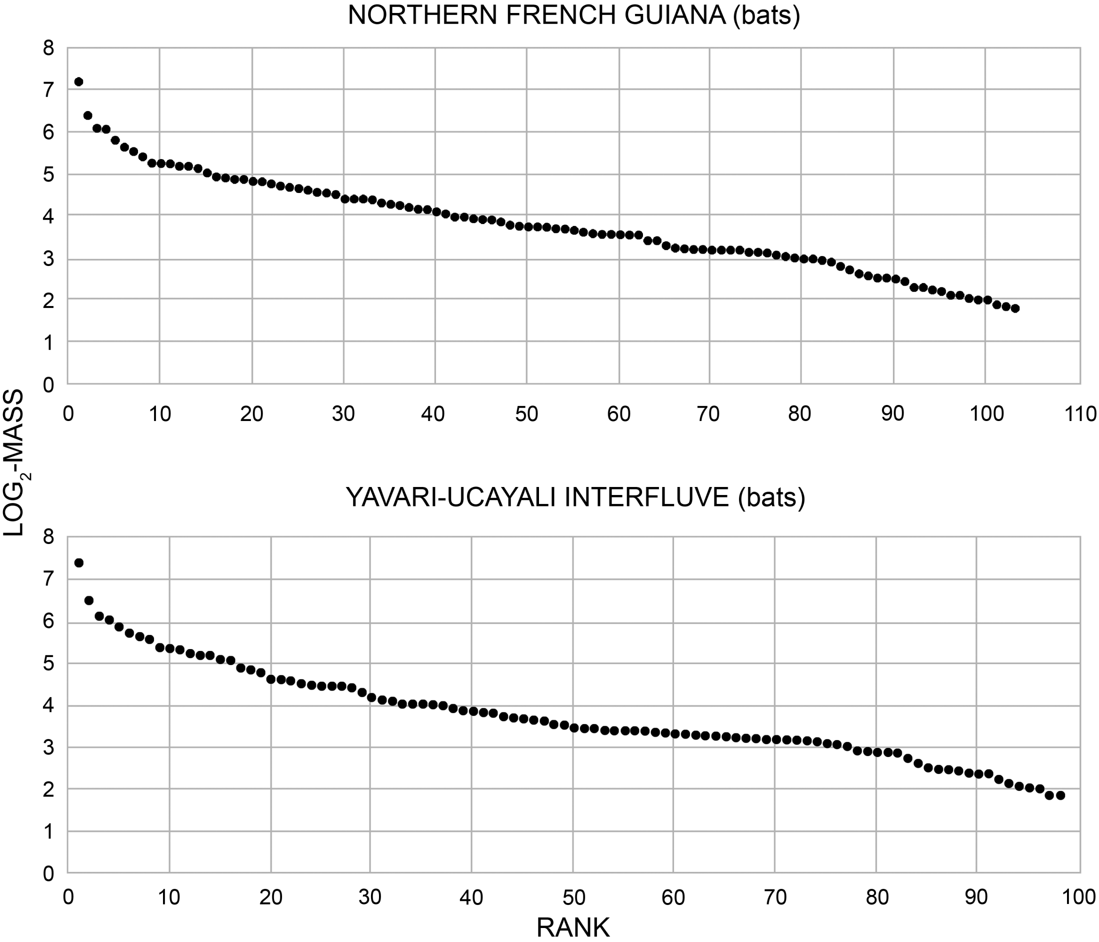

FIG. 3. Cenograms of bats from two Amazonian faunas.

on the ground but often climb into the canopy or subcanopy (e.g., *Didelphis marsupialis*, *Tamandua tetradactyla*, *Eira barbara*, *Leopardus wiedii*) and others that climb in understory vegetation but often descend to the ground (e.g., *Marmosops* spp., *Oecomys* spp.). Still smaller numbers of species in each fauna are semiaquatic (e.g., *Chironectes minimus*, *Nectomys* spp., *Lontra longicaudis*, *Pteronura brasiliensis*, *Hydrochoerus hydrochaeris*). Remarkably, no Amazonian mammal is definitely known to be fossorial, although indigenous reports of such behavior for the armadillo *Cabassous unicinctus* are noteworthy (Voss and Fleck, 2017). Adding missing species to the expected fauna of the Yavarí-Ucayali interfluve brings the proportional representation of several groups (aerial, arboreal, terrestrial) somewhat closer to the percentages observed in northern French Guiana but leaves the proportional representation of others (scansorial, semiaquatic) unchanged.

As for diel activity, these are the first Neotropical rainforest faunas to be comprehensively scored for substrate use. The predominance of aerial species in both faunas follows from the high

TABLE 6. Ecobehavioral traits of rainforest mammals in northern French Guiana (NFG) and the Yavarí-Ucayali interfluve (YUI).

	Numbers of species (% of fauna)		
	NFG	YUI (observed)	YUI (expected)[a]
ACTIVITY			
Diurnal	20 (11%)	32 (16%)	32 (14%)
Nocturnal	152 (84%)	158 (80%)	184 (82%)
Cathemeral	8 (4%)	8 (4%)	8 (4%)
SUBSTRATE			
Aerial	103 (58%)	98 (49%)	116 (52%)
Arboreal	28 (16%)	39 (20%)	42 (19%)
Scansorial	11 (6%)	13 (7%)	15 (7%)
Terrestrial	31 (17%)	41 (21%)	42 (19%)
Semiaquatic	6 (3%)	7 (4%)	8 (4%)
TROPHIC LEVEL			
Primary consumers	65 (37%)	89 (47%)	94 (44%)
Secondary consumers	97 (55%)	85 (45%)	104 (48%)
Omnivores	14 (8%)	17 (9%)	18 (8%)

[a] Including unobserved species of opossums, rodents, and bats with geographic ranges that closely overlap the Yavarí-Ucayali interfluve (see Materials and Methods).

species richness of bats and requires no other explanation, but the nearly equivalent numbers of arboreal and terrestrial species seem counterintuitive. Most edible primary production (e.g., of leaves, flowers, fruit, and seeds) occurs in the canopy, so it would be reasonable to think that more primary consumers would be arboreal than terrestrial, and that predatory species would pursue them in the treetops. Three observations are probably sufficient to explain why this is not the case. First, a substantial fraction of canopy fruit and seed production eventually falls to the forest floor, where it is accessible to terrestrial frugivores and granivores (Smythe, 1986; Feer et al., 2001). Second, carnivorous mammals large enough to prey on monkeys, sloths, porcupines, and other arboreal primary consumers are too heavy to hunt effectively in trees (although jaguars sometimes do so in flooded forest; Ramalho et al., 2021); instead, the usual predators of arboreal primary consumers are eagles (e.g., *Harpia harpyja*; Miranda, 2018). Lastly, the forest floor is a rich source of soil invertebrates and detritus-feeding arthropods (Penny and Arias, 1982; Fragoso and Lavelle, 1992), both of which are fodder for mammalian secondary consumers and omnivores (e.g., armadillos and terrestrial opossums; Fleck and Voss, 2016; Voss and Jansa, 2020).

Trophic Level and Guild Membership

By contrast with faunal similarities in diel activity and substrate use, trophic comparisons reveal substantial divergence in relative numbers of primary versus secondary consumers (table

TABLE 7. Membership in six guilds of nonflying rainforest mammals in northern French Guiana (NFG) and the Yavarí-Ucayali interfluve (YUI).

	Numbers of species		
	NFG	YUI (observed)	YUI (expected)[a]
Diurnal arboreal primary consumers	6	11	11
Diurnal terrestrial primary consumers	5	5	5
Nocturnal arboreal primary consumers	11	12	14
Nocturnal terrestrial primary consumers	6	10	10
Nocturnal arboreal secondary consumers	5	6	7
Nocturnal terrestrial secondary consumers	9	8	8

[a] Including unobserved species of opossums, rodents, and bats with geographic ranges that closely overlap the Yavarí-Ucayali interfluve (see Materials and Methods).

6). Whereas secondary consumers are more numerous than primary consumers in the observed fauna of northern French Guiana, primary consumers outnumber secondary consumers in the observed fauna of the Yavarí-Ucayali interfluve. Only a handful of species (<10%) in each fauna are omnivores. Including missing species (many of which are insectivorous bats) to the expected fauna of the Yavarí-Ucayali interfluve reverses the relative numbers of primary versus secondary consumers, suggesting that at least some of the proportional difference between the observed faunas is an artifact of incomplete sampling. However, the increase in primary consumers from northern French Guiana (65 species observed) to the Yavarí-Ucayali interfluve (94 species expected) amounts to a 45% difference, whereas the increase in secondary consumers (97 species observed in northern French Guiana versus 104 species expected in the Yavarí-Ucayali interfluve) amounts to only a 7% difference. Therefore, whether the observed or the expected fauna of the Yavarí-Ucayali interfluve is accepted as a valid basis for comparison, the disparate allocation of species to trophic categories is substantial.

The six most populated trophic guilds of nonflying mammals in northern French Guiana and the Yavarí-Ucayali interfluve are permutations of diurnal/nocturnal, arboreal/terrestrial, and primary/secondary consumers (table 7). Of these, four are occupied by the same or similar numbers of species in each fauna, but there are >80% more diurnal-arboreal primary consumers and almost 70% more nocturnal-terrestrial primary consumers in the Yavarí-Ucayali interfluve than there are in northern French Guiana. Including expected species in the Yavarí-Ucayali interfluvial fauna also reveals a modest potential increase in the number of nocturnal-arboreal primary consumers.

The same or similar numbers of species populate most bat trophic guilds in northern French Guiana and the Yavarí-Ucayali interfluve, with two conspicuous exceptions (table 8). Far fewer aerial insectivores are known to occur in the Yavarí-Ucayali interfluve than in northern French Guiana, but, as noted previously, this deficit is probably the result of undersampling high-flying and cave-roosting taxa; including candidate missing species in the expected fauna of the Yavarí-Ucayali interfluve suggests that it hosts almost the same number of aerial insectivores as northern French Guiana. By contrast, there are almost 50% more frugivorous bats in

TABLE 8. Membership in six guilds of rainforest bats in northern French Guiana (NFG) and the Yavarí-Ucayali interfluve (YUI).

	Numbers of species		
	NFG	YUI (observed)	YUI (expected)[a]
Aerial insectivores	42	27	40
Gleaning animalivores	23	22	24
Gleaning frugivores	23	34	34
Gleaning nectarivores	7	8	10
Gleaning sanguivores	2	2	3
Gleaning omnivores	6	5	5

[a] Including unobserved species of opossums, rodents, and bats with geographic ranges that closely overlap the Yavarí-Ucayali interfluve (see Materials and Methods).

the Yavarí-Ucayali interfluve than there are in northern French Guiana, and this large increment cannot plausibly be explained by sampling bias (see below).

Given the higher-taxonomic (ordinal and family-level) similarity of faunas from northern French Guiana and the Yavarí-Ucayali interfluve, these differences in trophic structure necessarily reflect regional differences in generic composition and congeneric species richness. Of the 16 genera present in the Yavarí-Ucayali interfluve that do not occur in northern French Guiana, 11 are primary consumers (*Enchisthenes*, *Sphaeronycteris*, *Vampyressa*, *Aotus*, *Cacajao*, *Callicebus*, *Lagothrix*, *Bassaricyon*, *Dinomys*, *Dactylomys*, *Toromys*), whereas of the 10 genera present in northern French Guiana but not observed in the Yavarí-Ucayali interfluve, only 4 are primary consumers (*Lichonycteris*, *Ametrida*, *Rhipidomys*, *Echimys*). More impressively, the 13 shared genera of primary consumers that differ in richness between these faunas include 45 species in the Yavarí-Ucayali interfluve but only 28 species in northern French Guiana (table 9), and a two-tailed sign test indicates that the median species richness in shared genera of primary consumers differs significantly between these faunas ($p = 0.02$).

Such trophic disparities cannot be explained by sampling incompleteness because primary consumers are among the easiest species to observe in rainforest faunas using standard inventory methods (Voss and Emmons, 1996). Most frugivorous bats, even those that forage in the canopy, are readily captured in ground-level mistnets; frugivorous and folivorous monkeys are large, noisy, and diurnal; ungulates and large terrestrial rodents leave visible spoor; and most small terrestrial rodents can be taken in commercially available traps with standard kinds of bait. Canopy-dwelling nocturnal rodents are exceptions (silent, hard to see, and hard to trap), but geographic range data suggest that none were missed in northern French Guiana.

A Common Cause for Faunal Differences

As we have seen, mammal faunas from northern French Guiana and the Yavarí-Ucayali interfluve are similar in many respects—including higher-taxonomic composition, size distri-

TABLE 9. Shared genera of primary consumers that differ in numbers of observed species in northern French Guiana (NFG) and the Yavarí-Ucayali interfluve (YUI).

	Observed species		
	NFG	YUI	Difference[a]
CHIROPTERA			
Carollia	2	3	+
Anoura	2	1	–
Glossophaga	1	2	+
Hsunycteris	1	3	+
Rhinophylla	1	2	+
Artibeus	6	9	+
Platyrrhinus	3	5	+
Sturnira	2	3	+
Uroderma	1	2	+
RODENTIA			
Sciurus	1	4	+
Oecomys	4	5	+
Rhipidomys	2	0	–
Proechimys	2	6	+
Totals:	28	45	

[a] Sign of the remainder obtained by subtracting the number of species in northern French Guiana from the number of species in the Yavarí-Ucayali interfluve.

bution, diel activity, and substrate use—but differ in species richness and trophic structure. Although such differences are logically independent (faunas can presumably differ in species richness but not in trophic structure, and vice versa), they might have a common cause in Amazonia. The observed increase in primary consumers from northern French Guiana to the Yavarí-Ucayali interfluve (24 species; table 6) is more than sufficient to account for the observed increase in species richness (19 species; table 1), whereas the expected increase in primary consumers (29 species) accounts for almost two-thirds of the expected increase in species richness (44 species). These numbers suggest that the east-to-west gradient of increasing species richness of Amazonian mammal faunas (Voss and Emmons, 1996; Peres, 1999) could be largely explained by the surplus of primary consumers in western Amazonia. This hypothesis seems to be supported by stacked range maps, which show conspicuous east-to-west increases in species density for clades with many primary consumers (caviomorph rodents, primates) but no equivalent increases for clades with numerous secondary consumers (xenarthrans, carnivorans; Fergnani and Ruggiero, 2015: fig. 4).

Geographic variation in mammalian species richness has often been attributed to environmental differences in primary productivity (Emmons, 1984; Voss and Emmons, 1996; Kay et al., 1997; Tognelli and Kelt, 2004; Peres, 2008). In Amazonia, the results of several studies suggest that primary production is limited by soil fertility (Malhi et al., 2004; Aragão et al., 2009; Cunha et al., 2022) and covaries geographically with soil fertility and climate (Quesada et al., 2012). In effect, forests growing on fertile soils in regions with abundant rainfall throughout the year tend to be more productive than those growing on nutrient-impoverished soils in regions with less abundant or more seasonally distributed rainfall. There are no consistent differences in rainfall amount or seasonality between eastern and western Amazonia (Salati and Marques, 1984; Sombroek, 2001), but western Amazonian soils are younger (recently weathered from the Andes) and generally more fertile than eastern Amazonian soils (weathered in situ from ancient geological shields; Hammond, 2005a; Quesada et al., 2010). Although upland soils everywhere in Amazonia tend to be highly weathered and nutrient poor, the Acrisols and Ferralsols that blanket most of eastern Amazonia are among the most nutrient-deficient soils to be found anywhere in the rainforested Neotropics, whereas the Fluvisols that occur in the floodplains of western Amazonian rivers are among the most fertile. Maps of soil phosphorous content—the single most consistent predictor of Amazonian primary productivity—show a clear trend of increase from east to west (Quesada et al., 2010: fig. 2b). Therefore, although direct measurements of edible primary production (bark, leaves, green stems, flowers, fruits, and seeds) are unavailable for relevant comparisons, it seems probable that, averaged across the landscape, the rainforest vegetation of western Amazonia is substantially more productive than that of eastern Amazonia.

Habitat mosaicism may be another factor contributing to the primary productivity of western Amazonia, a geomorphologically dynamic landscape where rivers meandering across broad sedimentary floodplains create a variety of riparian formations with phenological schedules that are out of phase with those of adjacent terra firme forests; such offset phenologies sustain yearlong primary production, even in regions with pronounced annual dry seasons (Terborgh, 1983; Diaz-Martin et al., 2014; Haugaasen and Peres, 2007). By contrast, eastern Amazonia is a geomorphologically static landscape where most rivers, closely constrained in their courses by structural features of the underlying geology, do not have equivalently broad floodplains, and the regional vegetation (except where interrupted by savannas) consists almost entirely of terra firme forest (Hammond, 2005b).

Despite multiple alternative mechanisms by which higher primary productivity might result in higher animal species richness (Evans et al., 2005; Storch et al., 2018), it follows from the inefficiency of energy transfer between trophic levels that any positive effects should be stronger for primary consumers than for secondary consumers (Wright, 1983). In terms of diversification processes, differences in primary production seem unlikely to affect speciation rates, but they could affect extinction rates if consumer population densities are higher in more productive regions, and if larger populations are less likely to go extinct. Because such an effect would be substantially stronger for primary consumers than for secondary consumers, one plausible scenario is that, even if speciation rates were constant across an extensive biome like Amazonia, a gradient of primary productivity could result in geographic variation in both species richness and trophic structure as more species of primary consumers than secondary consumers accumulate in highly productive regions. Given the east-to-west gradients in soil chemistry and geomorphology described above, such a scenario could explain faunal differences not just between northern French

Guiana and the Yavarí-Ucayali interfluve, but across the much larger Amazonian landscapes within which these exemplar faunas are embedded.

Intercontinental Comparisons: Two Caveats

Are rainforest mammal faunas on different continents similarly species rich and ecologically structured? Numerous researchers have addressed this question with a variety of data and approaches (e.g., Bourlière, 1973, 1983; Dubost, 1987; Emmons, 1995; Rovero et al., 2020; Tejada et al., 2020; Tanshi et al., 2022). Inevitably, the data provided in this report (appendices 1–4) will be used for intercontinental comparisons, but two caveats are in order. First, no African or Asian rainforest fauna has been inventoried as intensively, nor has any been as thoroughly analyzed taxonomically, as the Amazonian faunas treated here. Although the biases introduced by incomplete faunal sampling and inadequate taxonomic analysis cannot be predicted with certainty, they probably include underestimates of species richness for behaviorally and morphologically cryptic taxa such as bats, eulipotyphlans, and muroid rodents.

The second caveat concerns the end-Pleistocene anthropogenic extinction of megafaunal species, which was severe in South America but not in Africa or tropical Asia (Sandom et al., 2014; Smith et al., 2018). Assessing the impact of such extinctions for Amazonian faunas is difficult because the relevant geological record is sparse. However, Lujanian (latest Pleistocene) fossils from southwestern Amazonia include the gomphotheriid proboscidean *Notiomastodon platensis* (ca. 6300 kg); the ground sloth *Eremotherium laurillardi* (ca. 3500 kg); the toxodontid notoungulates *Trigodonops lopesi* (ca. 1900 kg) and *Toxodon platensis* (ca. 1800 kg); the camelid *Palaeolama major* (ca. 280 kg); and the pampatheriid armadillo *Holmesina rondoniensis* (ca. 120 kg). All these species were herbivores, and stable-isotopic data ($\delta^{13}C$, $\delta^{18}O$) reported by Asevedo et al. (2021) suggest that they could have browsed on understory foliage, a feeding niche that is conspicuously underpopulated in modern Amazonian faunas. Whether these or other extinct taxa were sympatric with the species currently found in northern French Guiana and the Yavarí-Ucayali interfluve is unknown, but it seems certain that the faunas of both regions were taxonomically and ecologically depleted by humans within the last few thousand years.

In summary, meaningful intercontinental comparisons of rainforest mammal faunas are simply not possible without (1) substantial investments of research effort to complete African and Asian inventories, and (2) without taking into account the probable effects of end-Pleistocene extinctions. Both are worthy endeavors because intercontinental comparisons could lead to novel insights about mammalian ecology and evolution in the most biologically diverse landscapes on the planet.

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APPENDIX 1

Nonflying Mammals from Northern French Guiana

Species[a]	Weight	Activity[b]	Substrate[c]	Diet[d]	TL[e]	Guild[f]
Caluromys philander	332	N	Ar	Fr, N, In	P	NArP
Chironectes minimus	605	N	SAq	Fi, In	S	NSAqS
Didelphis imperfecta	770	N	T	V, In, Fr	S	NTS
Didelphis marsupialis	1346	N	Sc	V, In, Fr	S	NScS
Glironia venusta	126	N	Ar	?	?	
Gracilinanus emiliae	12	N	Ar	In, Fr	S	NArS
Hyladelphys kalinowskii	17	N	Ar	?	?	
Marmosa demerarae	102	N	Ar	In, Fr	S	NArS
Marmosa lepida	22	N	Ar	In, Fr	S	NArS
Marmosa murina	50	N	Ar	In, Fr	S	NArS
Marmosops parvidens	24	N	Sc	In	S	NScS
Marmosops pinheiroi	26	N	Sc	In	S	NScS
Metachirus nudicaudatus	385	N	T	In	S	NTS
Monodelphis touan	82	D	T	In	S	DTS
Philander opossum	590	N	T	V, In, Fr	S	NTS
Cabassous unicinctus	3440	N	T	In	S	NTS
Priodontes maximus	33185	N	T	In	S	NTS
Dasypus kappleri	9910	N	T	In	S	NTS
Dasypus novemcinctus	5030	N	T	In	S	NTS
Bradypus tridactylus	4620	C	Ar	L	P	CArP
Choloepus didactylus	7890	N	Ar	L, Fr	P	NArP
Cyclopes didactylus	296	N	Ar	In	S	NArS
Myrmecophaga tridactyla	30650	C	T	In	S	CTS
Tamandua tetradactyla	4800	N	Sc	In	S	NScS
Alouatta macconnelli	7700	D	Ar	Fr, L	P	DArP
Ateles paniscus	9500	D	Ar	Fr	P	DArP
Cebus apella	3000	D	Ar	Fr, In	P	DArP
Cebus olivaceus	3200	D	Ar	Fr, In	P	DArP
Saguinus midas	500	D	Ar	In, Fr	O	DArO
Saimiri sciureus	1035	D	Ar	Fr, In	O	DArO
Pithecia pithecia	1700	D	Ar	Fr, S	P	DArP
Speothos venaticus	6000	C	T	V	S	CTS
Leopardus pardalis	9500	N	T	V	S	NTS
Leopardus tigrinus	2450	N	?	V	S	N?S
Leopardus wiedii	3260	N	Sc	V	S	NScS
Panthera onca	94500	C	T	V	S	CTS
Puma concolor	74500	C	T	V	S	CTS
Puma yagouaroundi	8240	D	T	V	S	DTS
Eira barbara	3750	D	Sc	Fr, V	O	DScO
Galictis vittata	2273	C	T	V	S	CTS
Lontra longicaudis	9875	D	SAq	Fi, In	S	DSAqS
Pteronura brasiliensis	29000	D	SAq	Fi, In	S	DSAqS
Nasua nasua	3105	D	Sc	Fr, In, V	O	DScO

APPENDIX 1 *continued*

Species[a]	Weight	Activity[b]	Substrate[c]	Diet[d]	TL[e]	Guild[f]
Potos flavus	2200	N	Ar	Fr	P	NArP
Procyon cancrivorus	5800	N	T	Fr, In, V	O	NTO
Tapirus terrestris	177200	N	T	L, Fr	P	NTP
Dicotyles tajacu	22100	D	T	Fr, S, In	P	DTP
Tayassu pecari	37100	D	T	Fr, S, In	P	DTP
Mazama americana	40250	C	T	Fr, S, L	P	CTP
Passalites nemorivagus	14270	D	T	Fr, S, L	P	DTP
Sciurillus pusillus	44	D	Ar	?	?	
Sciurus aestuans	189	D	Ar	Fr, S	P	DArP
Daptomys oyapocki	45	N	SAq	In	S	NSAqS
Euryoryzomys macconnelli	75	N	T	?	?	
Hylaeamys megacephalus	42	N	T	Fr, In	P	NTP
Hylaeamys yunganus	39	N	T	Fr, In	P	NTP
Neacomys dubosti	14	N	T	I, Fr	O	NTO
Neacomys paracou	14	N	T	I, Fr	O	NTO
Nectomys rattus	180	N	SAq	Fr, S, In, V	O	NSAqO
Oecomys auyantepui	43	N	Sc	Fr, S	P	NScP
Oecomys bicolor	32	N	Sc	Fr, S	P	NScP
Oecomys rex	65	N	Sc	Fr, S	P	NScP
Oecomys rutilus	20	N	Sc	Fr, S	P	NScP
Rhipidomys leucodactylus	125	N	Ar	Fr, S	P	NArP
Rhipidomys nitela	56	N	Ar	Fr, S	P	NArP
Coendou melanurus	1900	N	Ar	B, L	P	NArP
Coendou longicaudatus	3600	N	Ar	S, Fr, B	P	NArP
Hydrochoerus hydrochaeris	50000	C	SAq	L	P	CSAqP
Cuniculus paca	7500	N	T	Fr, S	P	NTP
Dasyprocta leporina	4370	D	T	Fr, S	P	DTP
Myoprocta acouchy	960	D	T	Fr, S	P	DTP
Echimys chrysurus	610	N	Ar	Fr, L	P	NArP
Isothrix sinnamariensis	280	N	Ar	?	P	NArP
Makalata didelphoides	280	N	Ar	Fr, S	P	NArP
Mesomys hispidus	112	N	Ar	Fr, In, L	P	NArP
Proechimys cuvieri	343	N	T	S, Fr, Fu	P	NTP
Proechimys guyannensis	191	N	T	S, Fr, Fu	P	NTP

[a] Taxonomic sequencing by order and family follows Wilson and Reeder (2005), but confamilial species are listed in alphabetical order.

[b] C = cathemeral, D = diurnal, N = nocturnal.

[c] Ar = arboreal, SAq = semiaquatic, Sc = scansorial, T = terrestrial.

[d] B = bark, Cr = crustaceans, Fi = fish, Fr = fruit, Fu = fungus, In = invertebrates, L = leaves, N = nectar, S = seeds, V = vertebrates.

[e] Trophic level: P = primary consumer, S = secondary consumer.

[f] See text.

APPENDIX 2

BATS FROM NORTHERN FRENCH GUIANA

Species[a]	Weight	Diet[b]	TL[c]	Guild
Centronycteris maximiliani	4.5	In	S	aerial insectivore
Cormura brevirostris	8.5	In	S	aerial insectivore
Cyttarops alecto	6.8	In	S	aerial insectivore
Diclidurus albus	20.5	In	S	aerial insectivore
Diclidurus ingens	30.0	In	S	aerial insectivore
Diclidurus scutatus	12.0	In	S	aerial insectivore
Peropteryx kappleri	8.2	In	S	aerial insectivore
Peropteryx leucoptera	4.8	In	S	aerial insectivore
Peropteryx macrotis	6.4	In	S	aerial insectivore
Peropteryx trinitatis	4.2	In	S	aerial insectivore
Rhynchonycteris naso	4.0	In	S	aerial insectivore
Saccopteryx bilineata	8.9	In	S	aerial insectivore
Saccopteryx canescens	3.9	In	S	aerial insectivore
Saccopteryx gymnura	3.4	In	S	aerial insectivore
Saccopteryx leptura	4.6	In	S	aerial insectivore
Ametrida centurio	9.2	Fr	P	gleaning frugivore
Anoura caudifer	8.9	N	P	gleaning nectarivore
Anoura geoffroyi	14.7	N	P	gleaning nectarivore
Artibeus cinereus	11.4	Fr	P	gleaning frugivore
Artibeus concolor	17.5	Fr	P	gleaning frugivore
Artibeus gnomus	9.6	Fr	P	gleaning frugivore
Artibeus lituratus	65.9	Fr	P	gleaning frugivore
Artibeus obscurus	35.8	Fr	P	gleaning frugivore
Artibeus planirostris	55.2	Fr	P	gleaning frugivore
Carollia brevicauda	11.4	Fr	P	gleaning frugivore
Carollia perspicillata	15.4	Fr	P	gleaning frugivore
Chiroderma trinitatum	13.1	Fr	P	gleaning frugivore
Chiroderma villosum	23.2	Fr	P	gleaning frugivore
Choeroniscus minor	8.9	N	P	gleaning nectarivore
Chrotopterus auritus	67.2	V	S	gleaning animalivore
Desmodus rotundus	28.7	Bl	S	gleaning sanguivore
Diaemus youngi	27.8	Bl	S	gleaning sanguivore
Gardnerycteris crenulata	11.6	In	S	gleaning animalivore
Glossophaga soricina	9.0	N, In, Fr	P	gleaning nectarivore
Glyphonycteris daviesi	18.7	In	S	gleaning animalivore
Glyphonycteris sylvestris	7.7	In, N	S	gleaning animalivore

APPENDIX 2 *continued*

Species[a]	Weight	Diet[b]	TL[c]	Guild
Hsunycteris thomasi	7.3	N, Fr	P	gleaning nectarivore
Lampronycteris brachyotis	41.9	Fr, In, N	O	gleaning omnivore
Lichonycteris obscura	10.4	N	P	gleaning nectarivore
Lionycteris spurrelli	8.6	N	P	gleaning nectarivore
Lonchorhina inusitata	16.8	In	S	gleaning animalivore
Lophostoma brasiliense	9.0	In	S	gleaning animalivore
Lophostoma carrikeri	20.8	In	S	gleaning animalivore
Lophostoma schulzi	19.0	In	S	gleaning animalivore
Lophostoma silvicolum	35.8	In	S	gleaning animalivore
Macrophyllum macrophyllum	7.5	In	S	gleaning animalivore
Mesophylla macconnelli	8.0	Fr	P	gleaning frugivore
Micronycteris brosseti	4.8	In	S	gleaning animalivore
Micronycteris hirsuta	12.3	In	S	gleaning animalivore
Micronycteris megalotis	5.5	In	S	gleaning animalivore
Micronycteris microtis	5.6	In	S	gleaning animalivore
Micronycteris minuta	6.0	In	S	gleaning animalivore
Micronycteris schmidtorum	5.8	In	S	gleaning animalivore
Mimon bennettii	20.8	In	S	gleaning animalivore
Phylloderma stenops	45.6	Fr, In	P	gleaning frugivore
Phyllostomus discolor	34.4	In, N, Fr	O	gleaning omnivore
Phyllostomus elongatus	37.7	In, N, Fr	O	gleaning omnivore
Phyllostomus hastatus	82.8	In, N, Fr	O	gleaning omnivore
Phyllostomus latifolius	27.7	In, N	O	gleaning omnivore
Platyrrhinus brachycephalus	15.0	Fr	P	gleaning frugivore
Platyrrhinus fusciventris	15.4	Fr	P	gleaning frugivore
Platyrrhinus incarum	12.6	Fr	P	gleaning frugivore
Rhinophylla pumilio	8.9	Fr	P	gleaning frugivore
Sturnira giannae	19.5	Fr	P	gleaning frugivore
Sturnira tildae	22.4	Fr	P	gleaning frugivore
Tonatia maresi	26.6	In	S	gleaning animalivore
Trachops cirrhosus	37.2	V, In	S	gleaning animalivore
Trinycteris nicefori	7.8	In, Fr	O	gleaning omnivore
Uroderma bilobatum	17.4	Fr	P	gleaning frugivore
Vampyriscus bidens	11.5	Fr	P	gleaning frugivore
Vampyriscus brocki	9.1	Fr	P	gleaning frugivore
Vampyrodes caraccioli	32.0	Fr	P	gleaning frugivore
Vampyrum spectrum	145.5	V	S	gleaning animalivore
Pteronotus alitonus	20.8	In	S	aerial insectivore

APPENDIX 2 *continued*

Species[a]	Weight	Diet[b]	TL[c]	Guild
Pteronotus gymnonotus	13.5	In	S	aerial insectivore
Pteronotus personatus	10.4	In	S	aerial insectivore
Pteronotus rubiginosus	24.7	In	S	aerial insectivore
Noctilio albiventris	25.8	In	S	aerial insectivore
Noctilio leporinus	49.0	Fi, In	S	gleaning animalivore
Furipterus horrens	3.6	In	S	aerial insectivore
Thyroptera discifera	3.5	In	S	gleaning animalivore
Thyroptera tricolor	3.9	In	S	gleaning animalivore
Eumops auripendulus	29.4	In	S	aerial insectivore
Eumops hansae	13.2	In	S	aerial insectivore
Eumops maurus	24.0	In	S	aerial insectivore
Cynomops abrasus	28.7	In	S	aerial insectivore
Cynomops greenhalli	18.0	In	S	aerial insectivore
Cynomops paranus	16.2	In	S	aerial insectivore
Cynomops planirostris	13.0	In	S	aerial insectivore
Molossus coibensis	14.8	In	S	aerial insectivore
Molossus molossus	14.2	In	S	aerial insectivore
Molossus rufus	37.4	In	S	aerial insectivore
Molossus sinaloae	25.2	In	S	aerial insectivore
Nyctinomops laticaudatus	11.7	In	S	aerial insectivore
Promops centralis	22.9	In	S	aerial insectivore
Eptesicus chiriquinus	11.6	In	S	aerial insectivore
Eptesicus furinalis	8.6	In	S	aerial insectivore
Lasiurus blossevillii	7.7	In	S	aerial insectivore
Lasiurus ega	12.7	In	S	aerial insectivore
Lasiurus egregius	13.1	In	S	aerial insectivore
Myotis albescens	5.3	In	S	aerial insectivore
Myotis nigricans	4.2	In	S	aerial insectivore
Myotis riparius	5.6	In	S	aerial insectivore

[a] Taxonomic sequencing by family follows Wilson and Reeder (2005), but confamilial species are listed in alphabetical order.
[b] Bl = blood, Fi = fish, Fr = fruit, In = insects, N = nectar, V = vertebrates.
[c] Trophic level: P = primary consumer, S = secondary consumer.

APPENDIX 3

Nonflying Mammals from the Yavarí-Ucayali Interfluve

Species[a]	Weight	Activity[b]	Substrate[c]	Diet[d]	TL[e]	Guild[f]
Caluromys lanatus	280	N	Ar	Fr, N, In	P	NArP
Chironectes minimus	605	N	Saq	Fi, Cr	S	NSaqS
Didelphis marsupialis	961	N	Sar	V, In, Fr	S	NSarS
Glironia venusta	126	N	Ar	?	?	
Gracilinanus emiliae	12	N	Ar	In, Fr	S	NArS
Hyladelphys kalinowskii	17	N	Ar	?	?	
Marmosa constantiae	168	N	Ar	In, Fr	S	NArS
Marmosa lepida	22	N	Ar	In, Fr	S	NArS
Marmosa macrotarsus	120	N	Ar	In, Fr	S	NArS
Marmosa rutteri	184	N	Ar	In, Fr	S	NArS
Marmosops bishopi	27	N	Sc	In, Fr	S	NScS
Marmosops noctivagus	72	N	Sc	In, Fr	S	NScS
Marmosops soinii	38	N	Sc	In, Fr	S	NScS
Metachirus myosuros	356	N	T	In	S	NTS
Monodelphis emiliae	47	D	T	In	S	DTS
Monodelphis handleyi	48	D	T	In	S	DTS
Monodelphis peruviana	26	D	T	In	S	DTS
Philander mcilhennyi	484	N	T	V, In, Fr	S	NTS
Philander pebas	408	N	T	V, In, Fr	S	NTS
Cabassous unicinctus	3440	N	T	In	S	NTS
Priodontes maximus	33185	N	T	In	S	NTS
Dasypus novemcinctus	4430	N	T	In	S	NTS
Dasypus pastasae	8274	N	T	In	S	NTS
Bradypus variegatus	4340	C	Ar	L	P	CArP
Choloepus hoffmanni	7900	N	Ar	L, Fr	P	NArP
Cyclopes ida	286	N	Ar	In	S	NArS
Myrmecophaga tridactyla	32000	C	T	In	S	CTS
Tamandua tetradactyla	6660	N	Sc	In	S	NScS
Alouatta seniculus	7020	D	Ar	Fr, L	P	DArP
Ateles belzebuth	6800	D	Ar	Fr	P	DArP
Lagothrix lagothricha	5790	D	Ar	Fr, L	P	DArP
Callimico goeldii	505	D	Ar	In, Fr, Fu	O	DArO
Callithrix pygmaea	114	D	Ar	Ex, In	O	DArO
Cebus albifrons	2880	D	Ar	Fr, In	P	DArP
Cebus apella	3855	D	Ar	Fr, In, S	P	DArP
Saguinus fuscicollis	397	D	Ar	Fr, In	O	DArO

APPENDIX 3 *continued*

Species[a]	Weight	Activity[b]	Substrate[c]	Diet[d]	TL[e]	Guild[f]
Saguinus mystax	602	D	Ar	Fr, In	O	DArO
Saimiri sciureus	1035	D	Ar	Fr, In	O	DArO
Aotus nancymaae	882	N	Ar	Fr, In	P	NArP
Cacajao calvus	3167	D	Ar	S, Fr	P	DArP
Callicebus cupreus	1031	D	Ar	Fr, L	P	DArP
Pithecia monachus	2472	D	Ar	S, Fr, L	P	DArP
Atelocynus microtis	7750	D	T	V	S	DTS
Speothos venaticus	6000	C	T	V	S	CTS
Leopardus pardalis	10000	N	T	V	S	NTS
Leopardus wiedii	6000	N	Sc	V	S	NScS
Panthera onca	94500	C	T	V	S	CTS
Puma concolor	74500	C	T	V	S	CTS
Puma yagouaroundi	6750	D	T	V	S	DTS
Eira barbara	4850	D	Sc	Fr, V	O	DScO
Galictis vittata	1880	C	T	V	S	CTS
Lontra longicaudis	9875	D	SAq	Fi, Cr	S	DSAqS
Mustela africana	?	?	?	V	S	
Pteronura brasiliensis	29000	D	SAq	Fi, Cr	S	DSAqS
Bassaricyon alleni	1336	N	Ar	Fr, In	P	NArP
Nasua nasua	3653	D	Sc	In, Fr	O	DScO
Potos flavus	2420	N	Ar	Fr, In	P	NArP
Procyon cancrivorus	4550	N	T	Fr, In, V	O	NTO
Tapirus terrestris	125800	N	T	L, Fr	P	NTP
Dicotyles tajacu	20430	D	T	Fr, S, In	P	DTP
Tayassu pecari	41000	D	T	Fr, S, In	P	DTP
Mazama americana	36000	C	T	Fr, S, L	P	CTP
Passalites nemorivagus	24000	D	T	Fr, S, L	P	DTP
Sciurillus pusillus	44	D	Ar	?	?	
Sciurus pachecoi	251	D	Ar	S, Fr	P	DArP
Sciurus pyrrhinus	680	D	Ar	S, Fr	P	DArP
Sciurus spadiceus	614	D	Ar	S, Fr	P	DArP
Sciurus flaviventer	96	D	Ar	?	?	
Amphinectomys savamis	201	N	SAq	?	?	
Euryoryzomys macconnelli	79	N	T	?	?	
Hylaeamys perenensis	64	N	T	Fr, In	P	NTP
Hylaeamys yunganus	57	N	T	Fr, In	P	NTP
Neacomys aletheia	14	N	T	In, Fr	O	NTO
Neacomys musseri	12	N	T	In, Fr	O	NTO

APPENDIX 3 *continued*

Species[a]	Weight	Activity[b]	Substrate[c]	Diet[d]	TL[e]	Guild[f]
Nectomys apicalis	268	N	SAq	Fr, S, In, V	O	NSAqO
Nectomys rattus	239	N	SAq	Fr, S, In, V	O	NSAqO
Oecomys bicolor	32	N	Sc	Fr, S	P	NScP
Oecomys nanus	26	N	Sc	Fr, S	P	NScP
Oecomys makampi	39	N	Sc	Fr, S	P	NScP
Oecomys galvez	62	N	Sc	Fr, S	P	NScP
Oecomys roberti	54	N	Sc	Fr, S	P	NScP
Scolomys melanops	26	N	T	?	?	
Scolomys ucayalensis	30	N	T	?	?	
Coendou ichillus	?	N	Ar	?	P	NArP
Coendou longicaudatus	3893	N	Ar	S, Fr, B	P	NArP
Dinomys branickii	13000	N	T	L, Tu	P	NTP
Hydrochoerus hydrochaeris	33710	C	SAq	L	P	CSAqP
Cuniculus paca	6710	N	T	Fr, S	P	NTP
Dasyprocta fuliginosa	5500	D	T	Fr, S	P	DTP
Myoprocta pratti	880	D	T	Fr, S	P	DTP
Dactylomys dactylinus	650	N	Ar	L	P	NArP
Isothrix bistriata	399	N	Ar	?	P	NArP
Makalata "species 5"	295	N	Ar	Fr, S	P	NArP
Mesomys hispidus	216	N	Ar	Fr, In, L	P	NArP
Proechimys brevicauda	307	N	T	S, Fr, Fu	P	NTP
Proechimys cuvieri	356	N	T	S, Fr, Fu	P	NTP
Proechimys kulinae	180	N	T	S, Fr, Fu	P	NTP
Proechimys quadruplicatus	370	N	T	S, Fr, Fu	P	NTP
Proechimys simonsi	297	N	T	S, Fr, Fu	P	NTP
Proechimys steerei	532	N	T	S, Fr, Fu	P	NTP
Toromys rhipidurus	455	N	Ar	?	P	NArP

[a] Taxonomic sequencing by order and family follows Wilson and Reeder (2005), but confamilial species are listed in alphabetical order.

[b] C = cathemeral, D = diurnal, N = nocturnal.

[c] Ar = arboreal, SAq = semiaquatic, Sc = scansorial, T = terrestrial.

[d] B = bark, Cr = crustaceans, Fi = fish, Fr = fruit, Fu = fungus, In = insects/invertebrates, L = leaves, N = nectar, S = seeds, V = vertebrates.

[e] Trophic level: P = primary consumer, S = secondary consumer.

[f] See text.

APPENDIX 4

Bats from the Yavarí-Ucayali Interfluve

Species[a]	Weight	Diet[b]	TL[c]	Guild
Cormura brevirostris	8.8	In	S	aerial insectivore
Cyttarops alecto	5.6	In	S	aerial insectivore
Diclidurus isabella	16.0	In	S	aerial insectivore
Peropteryx kappleri	8.9	In	S	aerial insectivore
Peropteryx leucoptera	8.2	In	S	aerial insectivore
Peropteryx macrotis	5.1	In	S	aerial insectivore
Peropteryx pallidoptera	6.0	In	S	aerial insectivore
Rhynchonycteris naso	4.0	In	S	aerial insectivore
Saccopteryx bilineata	10.2	In	S	aerial insectivore
Saccopteryx canescens	3.9	In	S	aerial insectivore
Saccopteryx leptura	5.4	In	S	aerial insectivore
Anoura caudifer	10.3	N	P	gleaning nectarivore
Artibeus anderseni	9.8	Fr	P	gleaning frugivore
Artibeus bogotensis	10.0	Fr	P	gleaning frugivore
Artibeus cinereus	9.4	Fr	P	gleaning frugivore
Artibeus concolor	19.5	Fr	P	gleaning frugivore
Artibeus glaucus	10.7	Fr	P	gleaning frugivore
Artibeus gnomus	10.8	Fr	P	gleaning frugivore
Artibeus lituratus	70.3	Fr	P	gleaning frugivore
Artibeus obscurus	36.2	Fr	P	gleaning frugivore
Artibeus planirostris	57.9	Fr	P	gleaning frugivore
Carollia benkeithi	10.3	Fr	P	gleaning frugivore
Carollia brevicauda	14.4	Fr	P	gleaning frugivore
Carollia perspicillata	17.2	Fr	P	gleaning frugivore
Chiroderma trinitatum	14.2	Fr	P	gleaning frugivore
Chiroderma villosum	21.6	Fr	P	gleaning frugivore
Choeroniscus minor	9.2	N	P	gleaning nectarivore
Chrotopterus auritus	65.7	V	S	gleaning animalivore
Desmodus rotundus	33.0	Bl	S	gleaning sanguivore
Diphylla ecaudata	28.5	Bl	S	gleaning sanguivore
Enchisthenes hartii	16.0	Fr	P	gleaning frugivore
Gardnerycteris crenulata	14.0	In	S	gleaning animalivore
Glossophaga bakeri	8.8	N	P	gleaning nectarivore
Glossophaga soricina	9.0	N, In, Fr	P	gleaning nectarivore
Glyphonycteris daviesi	24.2	In	S	gleaning animalivore
Glyphonycteris sylvestris	10.2	In, N	S	gleaning animalivore

APPENDIX 4 *continued*

Species[a]	Weight	Diet[b]	TL[c]	Guild
Hsunycteris dashe	9.8	N	P	gleaning nectarivore
Hsunycteris pattoni	7.2	N	P	gleaning nectarivore
Hsunycteris thomasi	7.3	N, Fr	P	gleaning nectarivore
Lampronycteris brachyotis	13.8	Fr, In, N	O	gleaning omnivore
Lionycteris spurrelli	8.6	N	P	gleaning nectarivore
Lophostoma brasiliense	9.5	In	S	gleaning animalivore
Lophostoma carrikeri	22.0	In	S	gleaning animalivore
Lophostoma silvicolum	21.8	In	S	gleaning animalivore
Macrophyllum macrophyllum	8.9	In	S	gleaning animalivore
Mesophylla macconnelli	7.1	Fr	P	gleaning frugivore
Micronycteris brosseti	5.0	In	S	gleaning animalivore
Micronycteris hirsuta	16.0	In	S	gleaning animalivore
Micronycteris matses	10.7	In	S	gleaning animalivore
Micronycteris megalotis	6.5	In	S	gleaning animalivore
Micronycteris microtis	7.2	In	S	gleaning animalivore
Micronycteris minuta	8.0	In	S	gleaning animalivore
Phylloderma stenops	52.3	Fr, In	P	gleaning frugivore
Phyllostomus discolor	33.7	In, N, Fr	O	gleaning omnivore
Phyllostomus elongatus	37.5	In, N, Fr	O	gleaning omnivore
Phyllostomus hastatus	90.7	In, N, Fr	O	gleaning omnivore
Platyrrhinus angustirostris	15.0	Fr	P	gleaning frugivore
Platyrrhinus brachycephalus	12.9	Fr	P	gleaning frugivore
Platyrrhinus fusciventris	17.0	Fr	P	gleaning frugivore
Platyrrhinus incarum	11.4	Fr	P	gleaning frugivore
Platyrrhinus infuscus	46.5	Fr	P	gleaning frugivore
Rhinophylla fischerae	7.4	Fr	P	gleaning frugivore
Rhinophylla pumilio	9.6	Fr	P	gleaning frugivore
Sphaeronycteris toxophyllum	18.0	Fr	P	gleaning frugivore
Sturnira giannae	21.2	Fr	P	gleaning frugivore
Sturnira magna	41.2	Fr	P	gleaning frugivore
Sturnira tildae	24.0	Fr	P	gleaning frugivore
Tonatia maresi	27.0	In	S	gleaning animalivore
Trachops cirrhosus	35.9	V, In	S	gleaning animalivore
Trinycteris nicefori	8.7	In, Fr	O	gleaning omnivore
Uroderma bilobatum	21.8	Fr	P	gleaning frugivore
Uroderma magnirostrum	23.7	Fr	P	gleaning frugivore
Vampyressa thyone	8.3	Fr	P	gleaning frugivore
Vampyriscus bidens	12.1	Fr	P	gleaning frugivore

APPENDIX 4 *continued*

Species[a]	Weight	Diet[b]	TL[c]	Guild
Vampyriscus brocki	9.1	Fr	P	gleaning frugivore
Vampyrodes caraccioli	29.5	Fr	P	gleaning frugivore
Vampyrum spectrum	170.0	V	S	gleaning animalivore
Noctilio albiventris	40.4	In	S	aerial insectivore
Noctilio leporinus	49.0	Fi, In	S	gleaning animalivore
Furipterus horrens	4.1	In	S	aerial insectivore
Thyroptera discifera	3.5	In	S	gleaning animalivore
Thyroptera lavali	5.0	In	S	gleaning animalivore
Thyroptera tricolor	4.6	In	S	gleaning animalivore
Thyroptera wynneae	3.5	In	S	gleaning animalivore
Cynomops planirostris	12.5	In	S	aerial insectivore
Eumops hansae	11.5	In	S	aerial insectivore
Molossops neglectus	12.3	In	S	aerial insectivore
Molossus coibensis	15.6	In	S	aerial insectivore
Molossus molossus	15.9	In	S	aerial insectivore
Molossus rufus	39.4	In	S	aerial insectivore
Promops centralis	22.5	In	S	aerial insectivore
Eptesicus brasiliensis	10.0	In	S	aerial insectivore
Eptesicus furinalis	9.5	In	S	aerial insectivore
Lasiurus ega	12.7	In	S	aerial insectivore
Myotis albescens	5.3	In	S	aerial insectivore
Myotis nigricans	4.3	In	S	aerial insectivore
Myotis riparius	5.4	In	S	aerial insectivore
Myotis simus	10.3	In	S	aerial insectivore

[a] Taxonomic sequencing by family follows Wilson and Reeder (2005), but confamilial species are listed in alphabetical order.

[b] Bl = blood, Fi = fish, Fr = fruit, In = insects, N = nectar, V = vertebrates.

[c] Trophic level: P = primary consumer, S = secondary consumer.

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