Mammalian Diversity and Matses Ethnomammalogy in Amazonian Peru Part 1: Primates

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Source: Bulletin of the American Museum of Natural History, 2011(351) : 1-81

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/351.1

MAMMALIAN DIVERSITY AND MATSES ETHNOMAMMALOGY IN AMAZONIAN PERU

PART 1: PRIMATES

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 351, 81 pp., 3 figures, 25 tables
Issued April 29, 2011

ISSN 0003-0090

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ABSTRACT

This report is the first installment of a monographic study of mammalian diversity and ethnomammalogy in a sparsely inhabited rainforest region between the Yavarí and Ucayali rivers in northeastern Peru. Our study is based on several large collections of mammals (totaling about 3500 specimens) made at various localities in this region between 1926 and 2003, and on our long-term ethnobiological and linguistic fieldwork with the Matses, a Panoan-speaking group of indigenous Amazonians who still obtain most of their dietary protein by hunting mammals. Our primary objectives are to document the species richness of the regional fauna through taxonomic analysis of collected specimens, and to assess the detail and accuracy of Matses knowledge of mammalian natural history by linguistic analysis of recorded interviews.

The regional primate fauna is definitely known to consist of at least 14 species documented by collected specimens and/or repeated sightings of taxa with visually conspicuous diagnostic traits. This fauna includes three atelids (*Alouatta seniculus*, *Ateles belzebuth*, *Lagothrix lagothricha*), eight cebids (*Aotus nancymaae*, *Callimico goeldii*, *Callithrix pygmaea*, *Cebus albifrons*, *Cebus apella*, *Saguinus fuscicollis*, *Saguinus mystax*, *Saimiri sciureus*), and three pitheciids (*Cacajao calvus*, *Callicebus cupreus*, *Pithecia monachus*). All 14 species are known to occur sympatrically at one inventory site, but Goeldi's monkey (*Callimico goeldii*) is rare and uakaris (*Cacajao calvus*) seem to be patchily distributed, so some local faunas may have only 12 or even fewer species. This regional fauna is unique because neighboring interfluvial regions lack some species that are present in the Yavarí-Ucayali interfluve, and because some species that are present in neighboring interfluvial regions are not known to occur between the Yavarí and the Ucayali.

Matses knowledge about primate natural history is clearly correlated with size and cultural importance. For example, information obtained from standardized interviews about spider monkeys (*Ateles belzebuth*, a large game species) can be parsed into 86 observations about its ecology and/or behavior, whereas interviews about pygmy marmosets (*Callithrix pygmaea*, a small nongame species) contain only nine observations on these topics. Item-by-item comparisons of Matses observations about spider monkeys with the published results of scientific field research suggests that the Matses are generally accurate observers of primate natural history, a conclusion that is additionally supported by comparing community patterns of resource use compiled from our interview data with community-ecological studies of primate faunas in the scientific literature. Most exceptions (discrepancies between Matses observations and the scientific literature) can be explained by cultural inattention to small nongame species.

Although these results suggest that archiving native Amazonian knowledge about mammalian natural history might be a cost-effective alternative to lengthy fieldwork for some research objectives, there are significant linguistic barriers than can inhibit effective cross-cultural communication. Among the Matses, these include a surprisingly large number of zoologically redundant names (synonyms and hyponyms). Relevant primate examples are discussed in substantive detail.

INTRODUCTION

South of the Amazon and west of the Rio Madeira is one of the largest remaining tracts of intact lowland rain forest on the planet. To an observer rising in a small plane from one of the few dirt airstrips scratched in the green hide of forest that still stretches from horizon to horizon, the landscape seems static and monotonous, but the geological reality is not. Writhing like enormous snakes within the broad confines of their meander belts, great white-water rivers with catchment basins larger than many European countries annually deposit and rework millions of tons of nutrient-rich sediments weathered from the Andes, building new land on alternate banks while eroding old land from the opposite shores. Oxbow lakes and palm swamps mark the location of extinct river channels in the same floodplain landscapes, whose complexity and dynamic nature are now apparent from satellite imagery. Between the river floodplains, however, and comprising by far the most extensive habitat in southwestern Amazonia, are vast hilly wedges of unbroken upland forest. Dissected by small streams too narrow even for canoe travel, the roadless interiors of many of these interfluvial regions remain largely inaccessible and biologically unexplored.

The mammalian fauna that inhabits this richly textured terrain is the product of unique historical events (Simpson, 1969, 1980; Patterson and Pascual, 1972; Marshall and Sempere, 1993; Flynn and Wyss, 1998). Separated by open seaways from other landmasses throughout much of the Tertiary, South America was an island continent where a few founding clades (marsupials, xenarthrans, archaic "ungulates") and early overwater colonists (primates, caviomorph rodents) radiated in isolation from neighboring faunas in North America and Antarctica. Then, beginning in the late Miocene, but accelerating dramatically after the Panamanian landbridge emerged in the Pliocene, a flood of immigrant taxa—proboscideans, carnivores, deer, peccaries, tapirs, lagomorphs, and cricetid rodents—mingled with the old endemic elements and, briefly, resulted in what was perhaps the most diverse continental fauna that has ever existed. Although mammalian diversity in South America was subsequently winnowed by Pleistocene extinctions, the causes of which are still controversial (Vrba, 1993; Lessa and Fariña, 1996; Webb and Rancey, 1996; Lessa et al., 1997), Amazonian lowland rainforests still support globally maximal numbers of sympatric mammalian species (Voss and Emmons, 1996).

Scientific knowledge of Amazonian mammals began with the 18th century "Viagem Filosófica" of Alexandre Rodrigues Ferreira, and continued in fits and starts with notable 19th-century contributions from Humboldt, Spix, Natterer, Tschudi, and d'Orbigny (Hershkovitz, 1987a). Professional collectors in the early 20th century contributed much additional material for museum taxonomists to work with, but reliable information about the natural history of Amazonian mammals was not forthcoming until the advent of long-term field studies in the last few decades (e.g., Terborgh, 1983; Dubost, 1988; Emmons, 1988; Bodmer, 1990). Unfortunately, only a handful of species in a few local faunas have been studied in depth.

There are, however, other sources of information about the natural history of Amazonian mammals, information that resides in the collective knowledge of indigenous cultures. Native Amazonians hunt monkeys, ungulates, xenarthrans, rodents, and other mammals for dietary protein (Vickers, 1984; Milton, 1991; Cormier, 2007); they often keep young mammals as household pets (Erikson, 2000); they use mammalian hides, teeth, and claws as ornaments; they keep a watchful eye out for dangerous felids; and they have abundant opportunities to observe many other species of little or no cultural importance. People whose very lives depend on close observation of the natural world can be presumed to know a great deal about the fauna that surrounds them, but the extent of what they know has seldom been assayed.

This study, the result of a multiyear collaboration between a systematic mammalogist (Voss) and an anthropological linguist (Fleck), has two main objectives. The first is to document the taxonomic diversity of an intact mammalian fauna in a sparsely populated region of western Amazonia, and the second is to document the ethnomammalogical knowledge of the people who live there. Below we introduce the geographic and anthropological context of our study, review previous fieldwork that has contributed to what is currently known about the local fauna, and report the results of our taxonomic and ethnobiological research on primates. The taxonomy and ethnobiology of nonprimate mammals will be treated in subsequent reports.

The Yavarí-Ucayali Interfluvial Region

The area encompassed by our study is bounded by four rivers—the Yavarí, the Ucayali, the Tapiche, and the Amazon—in the Peruvian department of Loreto (figs. 1, 2). For brevity, we will refer to this region as the Yavarí-Ucayali interfluve to distinguish it from neighboring regions delimited by other Amazonian tributaries.[1] Most of this region consists of densely forested hills, usually less

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[1] Note that the Yavarí is known as the Javari in Brazil and that the Brazilian spelling often appears on English-language maps. The Yavarí-Ucayali interfluve includes parts of three Peruvian administrative districts (provincias)—Mariscal Ramón Castilla, Maynas, and Requena—that sometimes appear on specimen labels.

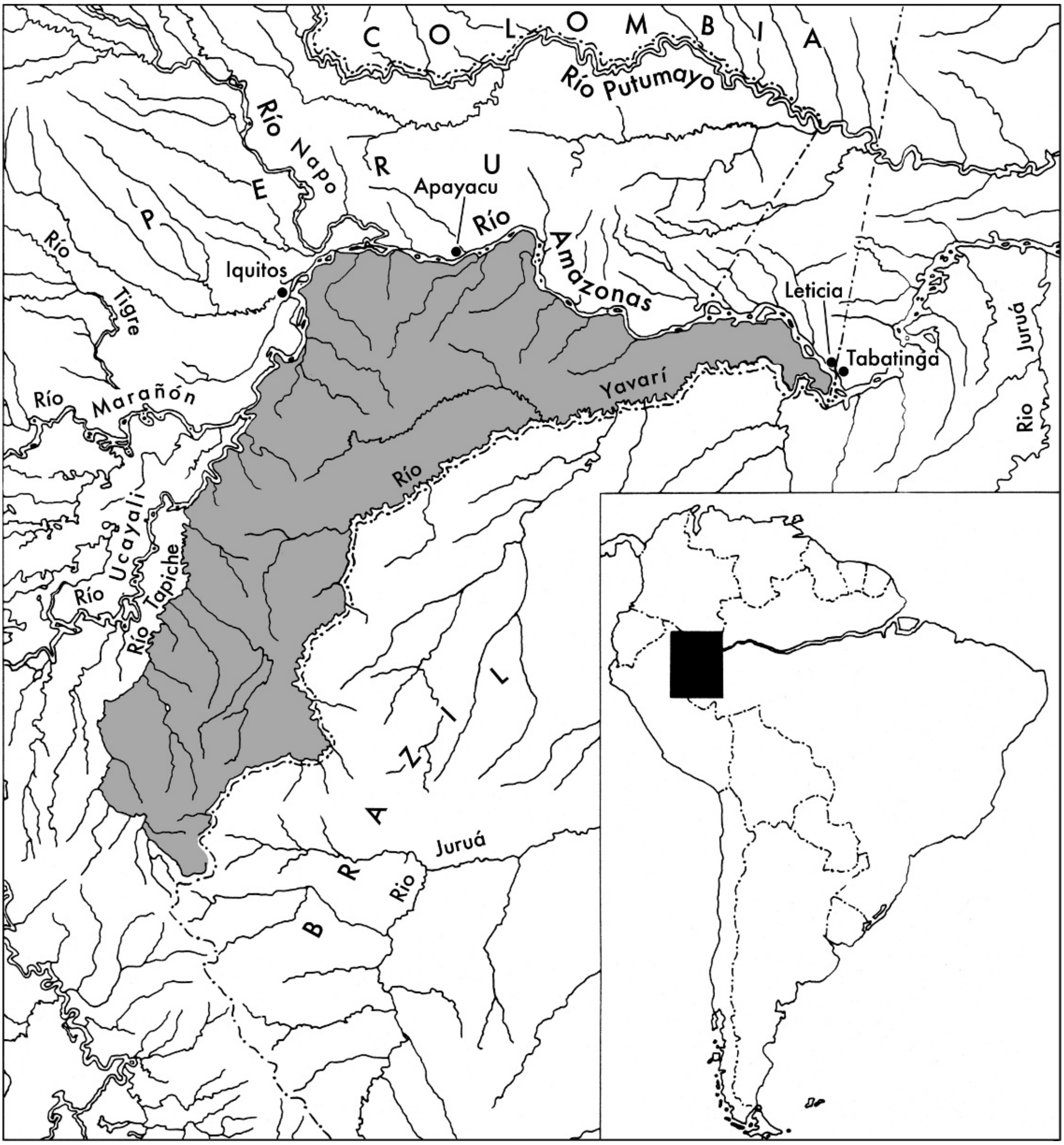

Fig. 1. The Yavarí-Ucayali interfluve (shaded) in relation to surrounding geographical features of western Amazonia.

than 200 m above sea level, that are drained by small clear-water, black-water, or mixed-water (dark but turbid) streams. The Ucayali and the Amazon, however, are huge, sediment-laden, white-water rivers with broad floodplains characterized by ridge-and-swale topography (Lamotte, 1990; Puhakka et al., 1992), and the Tapiche drains an extensive low-lying flood basin in the western part of the region (Kalliola et al., 1993). Local soils—weathered from Miocene lacustrine deposits of the Pebas Formation (Hoorn, 1993; Wesselingh et al., 2002) and from more recently deposited fluvial sediments—include a wide variety of variously colored clays, sandy clay loams, and sandy loams, but there are also extensive areas of white quartz sand along the upper Río Blanco (a right-bank

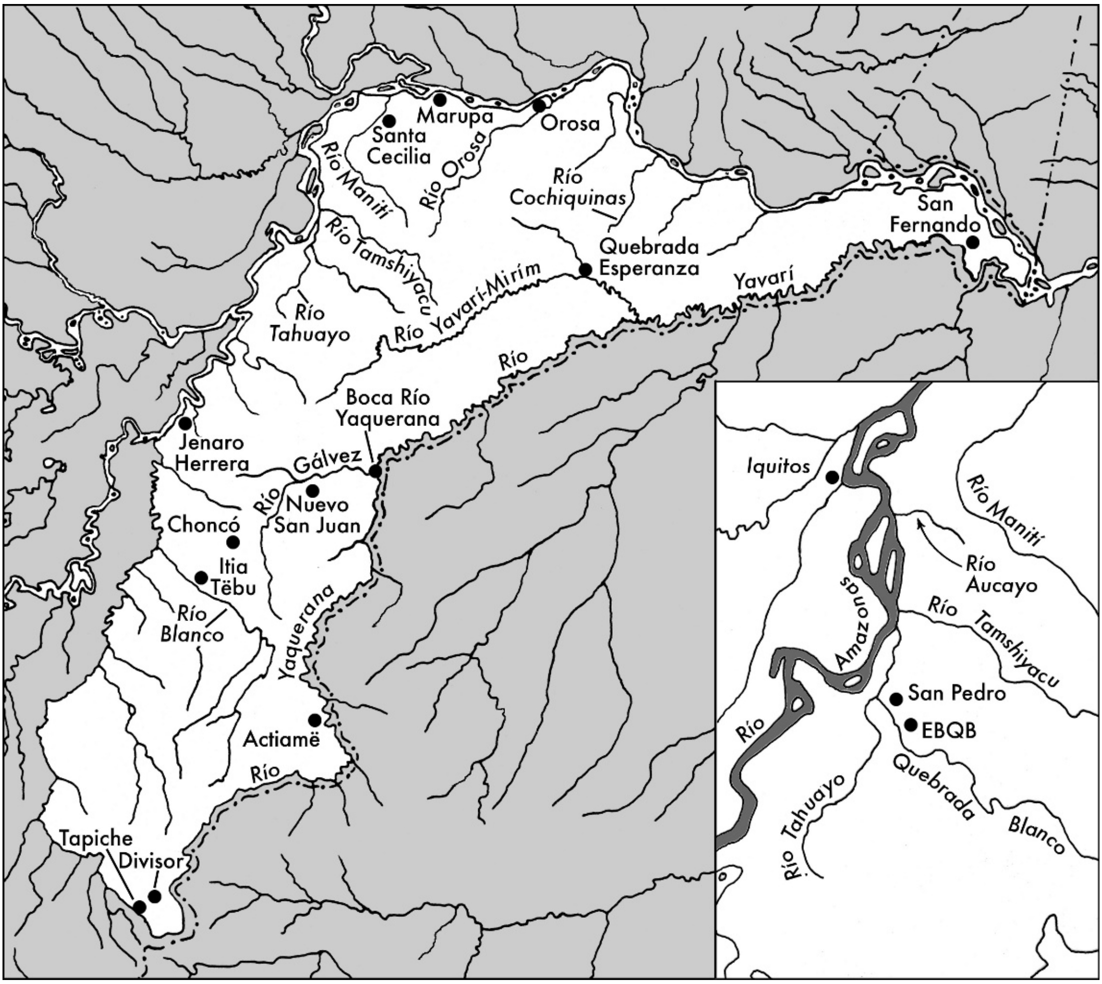

Fig. 2. Faunal inventory sites and collecting localities within the Yavarí-Ucayali interfluve (see appendix 2 for geographic coordinates and other information). Inset: Faunal inventory sites in or near the Tamshiyacu-Tahuayo watersheds (EBQB = Estación Biológica Quebrada Blanco).

tributary of the Tapiche) and in the adjacent headwater region of the Río Gálvez (a left-bank tributary of the Yavarí; Stallard, 2006). Rocks crop out in the remote headwaters of the Río Tapiche and the Río Yaquerana—which both arise in the Sierra del Divisor (Vriesendorp et al., 2006b)—but stones are unknown (except as exotic curiosities) elsewhere in the region, where streams have sandy or muddy bottoms.

The local climate is hot and wet, with an annual mean temperature close to 26° C and annual rainfall that increases from about 2500 mm in the south to about 3000 mm in the north (Marengo, 1983). At Jenaro Herrera, the average annual rainfall is almost 2900 mm, but as little as 1800 mm has been recorded at this site in some years and as much as 4000 mm in others (López-Parodi and Freitas, 1990). As in most other equatorial regions, seasonal temperature variation is trivial, but monthly rainfall exhibits significant variation. Typically, either March or April is the wettest month and either July or August the driest (e.g., at Jenaro Herrera and Angamos; Marengo, 1983). Local rivers rise and fall impressively in response to seasonal variation in rainfall. The Gálvez, for example, usually drops about 10 m from its highest water level in April to its lowest in August.

Whereas broad riverine beaches are exposed in the dry season, beaches are submerged and low-lying riparian forests are extensively flooded (for up to 1 km or more inland along the upper Yavarí) in the rainy season.

Except on seasonally exposed river beaches, and where trees have been cleared for agriculture near human settlements, the entire Yavarí-Ucayali interfluve is densely forested. Although the natural vegetation throughout the region can be broadly described as lowland rain forest, strikingly different forest types occur side by side at most sites that have been studied to date. Thus, López-Parodi and Freitas (1990) recognized nine types of forest in the vicinity of Jenaro Herrera, including two seral stages related to riverine succession, several distinct tree communities associated with seasonally or permanently flooded sites, and four kinds of forest growing on well-drained uplands. Other published surveys of local vegetation in the region, whether based on indigenous forest classification systems (e.g., Fleck and Harder, 2000) or rapid assessments by teams of botanical researchers (Pitman et al., 2003; Fine et al., 2006), have likewise stressed the importance of succession, flooding regimes, topography, and soils as local determinants of rainforest physiognomy and floristics. Diagrammatic vegetation profiles that illustrate the general character and site-to-site variability of forest vegetation in the region are in Bodmer (1990: fig. 2) and Fleck and Harder (2000: figs. 3, 4); color photographs of local vegetation are in Pitman et al. (2003) and Vriesendorp et al. (2006a).

In general, primary forests growing on well-drained clay and loam soils at upland sites are taller and more botanically diverse than seasonally flooded forests, swamp forests, forests growing on white sand, and early successional stages of floodplain forests. According to Pitman et al. (2003), the first 50 trees surveyed at an upland primary-forest site with relatively poor soil (about 20 km downriver from Colonia Angamos on the left bank of the Yavarí) represented 45 species, and upland sites with richer soils farther downriver appear to support even more speciose tree communities. Apparently, these tall, diverse, climax forests—which probably cover some 80%–90% of the local terrain—are floristically similar to those found elsewhere in northeastern Peru (e.g., near Iquitos; Vásquez-Martínez and Phillips, 2000). Numerically abundant and/or exceptionally speciose families of trees at one or more of the upland primary-forest sites visited by Pitman et al. (2003) and Fine et al. (2006) include (in alphabetical order) Annonaceae, Burseraceae, Euphorbiaceae, Lecythidaceae, Leguminosae, Moraceae, Myristicaceae, Palmae, Rubiaceae, Sapindaceae, and Sapotaceae. Striking floristic variation, however, was observed among upland sites differing in soil fertility, with the result that unique sets of families dominated the tree flora at each surveyed locality. Most well-drained sites (except those on white sand and on sandy hill crests) have a dense understory vegetation with abundant giant herbs (e.g., Heliconiaceae, Marantaceae), dwarf palms, shrubs, and seedling trees; a structurally complex subcanopy; a more or less closed canopy layer at 25–35 m; and scattered emergents that may be 40 m or more in height.

Forests growing on permanently waterlogged soils, although estimated to account for less than 10% of the regional landscape (Pitman et al., 2003), provide seasonally important habitats for local wildlife. Flooded to a depth of a meter or more in the rainy season, swamp forests have soil that is mucky underfoot even in the middle of the dry season. These habitats are much less botanically diverse than forests growing on adjacent upland sites; in one plot of swamp forest surveyed by Pitman et al. (2003), over half the trees belonged to just three families (Palmae, Clusiaceae, and Lepidobotryaceae). The most visually conspicuous elements of the swamp-forest flora are large palms, of which *Mauritia flexuosa* and *Euterpe precatoria*, are usually the most abundant (and faunally important) species. In general, swamp forests have a lower and more open canopy than upland forests and, near major rivers, they grade into a variety of seasonally flooded riparian formations.

A complex mosaic of successional floodplain habitats is maintained by rapid lateral channel migration along the Ucayali and the Amazon (Lamotte, 1990; Puhakka et al., 1992). Newly formed land (on point bars) is first colonized and stabilized by *Gynerium* *sagittatum* (Gramineae), which forms dense canebrakes up to 9 m high. These canebrakes are subsequently invaded by several species of trees, with distinct seral stages dominated in turn by *Cecropia membranacea* (Cecropiaceae) and *Ficus insipida* (Moraceae). Smaller, more slowly meandering rivers in the region (e.g., the Tapiche and the Yavarí) have a different successional sequence that usually begins with a narrow zone of shrubby vegetation (pioneered by *Alchornia castanaefolia* [Euphorbiaceae]) rather than canebrakes; successive seral stages include somewhat more diverse tree communities than occur behind the beach vegetation of larger rivers (Puhakka et al., 1993; Pitman et al., 2003). Mature floodplain forest ("riverine forest" sensu López-Parodi and Freitas, 1990) is very tall, floristically diverse, and contains many large and valuable timber species (e.g., *Cedrela odorata* and *Swietenia macrophylla* [Meliaceae]).

The presence of white-sand forests in the Yavarí-Ucayali interfluve was first inferred from satellite imagery (Räsänen et al., 1993) and later confirmed by a team of botanical researchers, who found that this unusual habitat is principally confined to flat hilltops in the Río Gálvez headwater region and along the adjacent upper Río Blanco (Vriesendorp et al., 2006a). White-sand forests have a unique flora that is depauperate in species by comparison with upland forests on adjacent hillsides with richer soils; they are composed of shorter, thinner trees that form a broken, uneven canopy; and they are supported by a thick rootmat that largely conceals the underlying mineral substrate. Although largely unstudied and doubtless exhibiting regional peculiarities, the white-sand forests of the Yavarí-Ucayali interfluve probably resemble those found elsewhere in Peru (e.g., near Iquitos; Ruokolainen and Tuomisto, 1993) and Brazil (Anderson, 1981) in most essential floristic and structural characteristics.

Human Communities

Whereas the Ucayali has been a major avenue for fluvial traffic throughout the historical record of eastern Peru, the Yavarí was much less frequently traveled until the rubber boom of the early 1900s. The scant recorded history of the Yavarí basin, punctuated at intervals by bloody encounters with its indigenous inhabitants, was reviewed by Bodmer and Puertas (2003), who noted that the nontribal population of this region has been in decline for many decades. Despite its proximity to Iquitos (a city large enough to boast an international airport), the Yavarí-Ucayali interfluve remains sparsely populated. Small communities of nontribal Amazonians (variously known as mestizos or ribereños) are scattered along the right banks of the Ucayali and the Amazon, and a few military outposts are sited at strategic points on the left bank of the Yavarí. Although several tribes (including the Kokama and the Yagua) once occupied the floodplains of the Ucayali and the Amazon, and others (including the Mayú/Morike, the Remo, and the Kapanawa) lived along the upper Río Tapiche, most of these groups are now either extinct or in an advanced state of culture and language loss. Today, the Matses and the Tikuna are the only culturally intact indigenous peoples that still inhabit the Yavarí-Ucayali interfluve. Whereas Tikuna territory is now restricted to a small wedge of land between the lower Yavarí and the Amazon, Matses communities are more extensively distributed in the forested interior, mostly along the Río Gálvez and the Quebrada Chobayacu.

The Matses were historically known as the Mayoruna (as they are still known in Brazil), but the latter term was also applied indiscriminately to other indigenous populations living in the Yavarí-Ucayali interfluve (Romanoff, 1984), some of which were clearly not Matses (Fleck, 2007). The Matses currently number about 2500 people living along the Río Yavarí and its tributaries in Peru and Brazil. Prior to 1969, the Peruvian Matses avoided contact by maintaining hostile relations with nontribal Peruvian and Brazilian communities, and by living in upland forests far from navigable rivers. Peaceful contact was initiated in 1969 by personnel of the Summer Institute of Linguistics (Vivar, 1975), and assimilation of the Peruvian Matses into the national culture is now proceeding rapidly. Because of their recent isolation, however, older individuals

(>35 years of age) still possess undiminished traditional knowledge. Many aspects of traditional Matses culture, including their subsistence technology, are described and illustrated by Romanoff et al. (2004).

Currently, most of the Matses continue to meet all their nutritional needs through traditional subsistence activities including hunting, fishing, trapping, swidden ("slash-and-burn") agriculture, and collection of wild fruits. Of particular relevance for this study, the Matses still obtain the majority of their dietary protein by hunting. Their most important game species are all large mammals, although caimans (*Caiman crocodilus*, *Paleosuchus* spp.), tortoises (*Geochelone* spp.), river turtles (*Podocnemis* spp.), birds (guans, curassows, trumpeters, tinamous, etc), and certain species of frogs are also eaten occasionally; unlike most other native Amazonians, the Matses do not eat insects or other invertebrates (Romanoff, 1976, 1983, 1984; Fleck, 1997; Fleck et al., 1999; Fleck and Harder, 2000).

The central importance of hunting expertise is reflected in many aspects of Matses culture, particularly their language, which is rich in vocabulary for accurately communicating relevant natural history information. For example, by combining vegetative and geomorphological descriptors, Matses hunters can distinguish >100 different rainforest habitat types, some of which appear to be differentially utilized by mammals (Fleck and Harder, 2000). The Matses also have a detailed zoological lexicon that includes names for every species of large (>1 kg) mammal known to occur in the Yavarí-Ucayali interfluve (Fleck, 1997). Although some details of Matses zoological nomenclature have been formally analyzed (Fleck et al., 1999, 2002; Fleck and Voss, 2006), other aspects of tribal knowledge about the local fauna remain undocumented.

Mammalogical Exploration

The first major collection of mammals from the Yavarí-Ucayali interfluve was made by Alfonso and Ramón Olalla, members of an Ecuadorean family of professional collectors employed by the American Museum of Natural History (AMNH), who camped at or near the mouth of the Río Orosa on the right (south) bank of the Amazon from 30 August to 11 December 1926 (Wiley, 2010). The Olallas' material from this locality, which is designated simply as "R. Amazonas, Orosa" on most of their skin tags, consists of 293 specimens taken on daily collecting expeditions among nearby islands and inland toward the Río Yavarí (unpublished report by A.M. Olalla, AMNH department of Ornithology archives). Unfortunately, no detailed itinerary or description of these forays is preserved, and few details are available concerning where or how individual specimens were obtained in the vicinity of Orosa.

Another early collection of mammals from the Yavarí-Ucayali interfluve was made by Celestino Kalinowski, a professional collector employed by the Field Museum of Natural History (FMNH), who worked along the lower Ucayali, the Amazon, and the Yavarí in 1956 and 1957. Kalinowski left no narrative account of his collecting activities, but a rough itinerary can be reconstructed from his field catalog of specimens (in the FMNH Division of Mammals archives). Kalinowski's first collecting station in the Yavarí-Ucayali interfluve was at Santa Cecilia, on the right (east) bank of the Río Manití, where he collected 106 mammals between 27 December 1956 and 21 January 1957. After an interval spent at various localities on the left (north) bank of the Amazon from February to April, and another period during which no mammals were collected in May and June, Kalinowski worked briefly at San Fernando on the left (north) bank of the lower Yavarí, where he collected 16 specimens from the 10th through the 15th of July. From here, Kalinowski moved upstream to the mouth of the Yaquerana (i.e., the confluence of the upper Yavarí and the Gálvez), where he collected from the 3rd through the 30th of August; 57 specimens are labeled as having been collected at this remote site ("Boca Río Yaquerana"), which was only a few kilometers upstream from the present-day military outpost of Angamos. After descending the Yavarí, Kalinowski next camped at Quebrada Esperanza on the lower Yavarí-Mirím, where he obtained 126 specimens in about three weeks (6–27 September). Seven specimens taken at San Vicente on the lower Yavarí on 2 October were the last that this indefatigable collector obtained in the Yavarí-Ucayali interfluve.

The establishment of a forestry research station near the town of Jenaro Herrera on the right bank of the Ucayali in the late 1960s provided a base of operations for faunal research that resulted in an early primate inventory (Aquino, 1978), descriptions of several new species of rodents and marsupials (Pacheco, 1991; Malygin et al., 1994; Solari, 2007), the first published list of bats from the Yavarí-Ucayali interfluve (Ascorra et al., 1993), and various ecological publications (e.g., Gorchov et al., 1993; Fleck and Harder, 1995). Substantial collections from this locality were made over several decades by mammalogists from the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM). Most of these collections—totaling 428 specimens of bats, marsupials, and rodents in the MUSM and AMNH—were made by Cesar Ascorra (from 30 November 1988 through 10 September 1991), Victor Pacheco (26 April–5 May 1990), Jessica Amanzo (6 March–6 April 1997, 8 June–24 July 2003), and Lynne Villalobos (9 June–24 July 2003). The holotype of *Amphinectomys savamis* and about 750 other specimens of small mammals collected by a Soviet research team that worked at Jenaro Herrera from 1985 to 1991 are preserved in the Zoological Museum of the M.V. Lomonosov University in Moscow (Pavlinov, 1994).

Another locus of faunal survey work in the region is the Quebrada Blanco, a right-bank tributary of the Río Tahuayo. Primatologists first worked here in 1975 (Castro and Soini, 1977), and the Estación Biológica Quebrada Blanco—established soon thereafter—has served as the base camp for numerous subsequent studies of the local primate fauna (e.g., Heymann, 1989, 1990; Garber, 1993; Heymann and Aquino, 1994; Aquino, 1998; Nickle and Heymann, 1996; Heymann et al., 2000; Nadjafzadeh and Heymann, 2008). Local ungulate populations have also been studied here (e.g., by Bodmer et al., 1988; Bodmer, 1990). Faunal studies based on the lower Quebrada Blanco often included observations made in the adjoining Reserva Comunal Tamshiyacu-Tahuayo, a protected area that extends from the headwaters of the Tamshiyacu and Tahuayo rivers across the hilly divide that separates the Amazon and Yavarí watersheds to the upper Yavarí-Mirím (Puertas and Bodmer, 1993; Hurtado-Gonzales and Bodmer, 2004).[2]

Faunal inventory work by Michael Valqui, formerly a graduate student based at the Florida Museum of Natural History (FLMNH), resulted in the first substantial collections of usable specimens from Tahuayo-Blanco watershed (Valqui, 1999, 2001). Valqui's study was centered at the village of San Pedro (about 4 km north of the Estación Biológica Quebrada Blanco), but he also collected specimens as far as 25 km upstream from San Pedro on the Quebrada Blanco (within the Reserva Comunal Tamshiyacu-Tahuayo), and at a settlement known as El Chino (about 5 km NW San Pedro) on the lower Río Tahuayo (see map inset; fig. 2). Valqui's collections from these localities, which were obtained between 14 May 1994 and 12 June 1998, include 609 specimens of marsupials and rodents at the FLMNH and MUSM.

Wildlife management research by Richard Bodmer and colleagues, originally based on the Quebrada Blanco in the late 1980s, was extended to the Río Yavarí-Mirím in the 1990s (Puertas and Bodmer, 1993; Hurtado-Gonzales and Bodmer, 2004). Mammalian sightings recorded on walked transect censuses along several trail systems on the upper and lower Yavarí-Mirím from from 1991 to 1998 were subsequently used to assess local diversity of the larger diurnal species by Valqui (2001) and Salovaara et al. (2003). Unfortunately, voucher specimens obtained in the course of wildlife-management research on the Yavarí-Mirím are currently unavailable for study.

Our own field research was based at Nuevo San Juan, a Matses village on the right bank of the Río Gálvez. Mammalian inventory fieldwork began here in 1995, when

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[2] The official name of this conservation unit is now the Área de Conservación Regional-Comunal Tamshiyacu-Tahuayo (E.W. Heymann, personal commun.), but we use the older name to conform with prevailing usage in the primatological literature.

Fleck collected specimens to voucher Matses folk taxonomy, and when he began trapping small mammals to assess mammalian community composition in different Matses-defined habitats; a total of 295 specimens were preserved for these purposes from 19 February 1995 through 12 July 1996. During a second episode of inventory work at Nuevo San Juan, from 19 May through 12 July 1998, Voss netted bats, trapped small marsupials and rodents, and preserved a few specimens of other taxa killed by Matses hunters; a total of 403 specimens were collected in this interval. During a third field season, from 28 August through 12 November 1999, Fleck employed several Matses hunters to search for bat roosts and hunt at night to supplement faunal sampling in previous years; 447 specimens were collected at this time. All of our collections from Nuevo San Juan, totaling 1145 specimens, are now preserved at the AMNH and the MUSM.

MATERIALS AND METHODS

Ethnobiological Methods

RECORDED MONOLOGS: From May to July of 1998, monologs about the natural history of local mammals were elicited from Matses men from four Peruvian Matses villages and recorded on digital minidisk. All monologs were recorded in the Matses language. To elicit these texts, informants were asked to talk about a single mammalian taxon (e.g., a species of monkey, or bats in general), which was mentioned only once by the interviewer (Fleck). Informants were asked to say as much as they liked about any topic relating to the taxon in question, and were not interrupted or asked to continue, regardless of the length of their monolog (see appendix 1 for a transcription and translation of one of these recorded monologs; the appendix also contains an explanation of the Matses orthography used in the accounts). Each informant's monologs were recorded with no other adults present in order to achieve independence of response. For each taxon, the interview was replicated a total of 7 or 8 times with different informants. These recordings were subsequently transcribed and translated by Fleck and literate Matses assistants, and checked for linguistic accuracy with several other Matses speakers. The texts were then checked with speakers other than the narrators to obtain second opinions on the validity of some of the less commonly asserted natural history details.

Sentences in the translated texts were sorted by topic (physical appearance and anatomy, habitat preference, social behavior, vocalizations, daily activities, and food), and then combined to obtain composite essays for each taxon. These essays, which are presented under the heading "Matses natural history" in the accounts that follow, are supplemented by editorial comments (in square brackets) only as necessary to interpret otherwise obscure passages or to identify botanical taxa corresponding to Matses plant names. To provide a more complete ethnographic picture, topics concerning Matses nomenclature, classification, hunting strategies, and cultural significance (summarized under the heading "Ethnobiology" in each species account) were elaborated using data from additional sources, including interview-style question-and-answer sessions and participant-observation, including more than 600 hours that Fleck spent hunting with the Matses.

PLANT IDENTIFICATIONS: Most of the plants mentioned by the Matses in their monologs were identified by various means. Palms were collected by Fleck in 1998 and 1999 from the area surrounding Nuevo San Juan with the help of Matses assistants, who named the palms while in the forest, prior to collection. Palm specimens were identified in the field using published identification guides (Henderson, 1994; Henderson et al., 1995), and voucher material was subsequently deposited at the herbarium at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima) and in the New York Botanical Garden (New York). Other plants, particularly dicotyledonous trees, were identified by Fleck and two Matses assistants at the arboretum of the Instituto de Investigaciones de la Amazonía Peruana. This arboretum is maintained at the Centro de Investigaciones Jenaro Herrera, a forestry research station located about 80 km northwest of Nuevo San Juan, where Swiss botanists have identified all trees >10 cm at breast height (Spichiger et al., 1989, 1990). Plants and trees in the proximity of Nuevo San Juan were also identified by Fleck using identification keys in Gentry (1993).

Botanical taxa corresponding to Matses plant names are provided in square brackets (under the heading "Matses Natural History" for each primate species account) using the following conventions: (1) The generic name alone is provided when the Matses plant name corresponds to all the species in a locally polytypic genus (e.g., bin [*Castilla* (Moraceae)]). (2) The generic name is followed by "sp." if the Matses plant name corresponds to just one unidentified local species in a genus (e.g., ichibin [*Matisia* sp. and *Eriotheca* sp. (Bombacaceae)]). (3) The generic name is followed by "spp." if the Matses plant name corresponds to two or more unidentified species, but not to all the local species of that genus (e.g., şhankuin [*Pourouma* spp. (Moraceae)]). Where alternative technical names for plant families are current in the literature (e.g., Palmae vs. Arecaceae, Clusiaceae vs. Guttiferae), the nomenclature used here follows Gentry (1993).

Primate Measurements

We measured total length (TL, from nose to fleshy tail tip), length of tail (LT, from basal flexure to fleshy tip), hind foot (HF, from heel to tip of longest claw), and Ear (from notch) on freshly killed specimens, and we computed head-and-body length (HBL) by subtracting LT from TL. For individual specimens discussed in the text, external measurements are provided in the format HBL × LT × HF × Ear (e.g., 528 × 589 × 137 × 34 mm for MUSM 11108, an adult male *Alouatta seniculus*). All external dimensions were recorded to the nearest millimeter (mm), and weights were recorded in grams (g) or kilograms (kg) using spring scales calibrated in those units.

The following craniodental measurements were taken with digital calipers and recorded to the nearest 0.01 mm (anatomical endpoints are illustrated in figure 3):

CIL (Condylo-incisive length): from the posterior articular surface of one occipital condyle to the anterior surface of the ipsilateral first incisor.[3]

OB (Orbital breadth): greatest transverse dimension across the bony orbits.

POC (Postorbital constriction): least transverse dimension immediately behind the orbits.

ZB (Zygomatic breadth): greatest transverse dimension across the zygomatic arches.

BB (Breadth of braincase): greatest transverse dimension of the calvarium, measured above the squamosal roots of the zygomatic arches.

PPL (Postpalatal length): from the midpoint of the inferior lip of the foramen magnum to the anteriormost margin of the mesopterygoid fossa (basion to palation; Thomas, 1905).

LMT (Length of maxillary tooth row): from the anterior enamelled base of the upper canine to the posterior margin of the ipsilateral upper third molar crown (in most species) or the ipsilateral second molar crown (in *Saguinus* and *Callithrix*, which lack M3).

BM1 (Breadth of M1): greatest transverse dimension of the first maxillary molar crown

M1–M1: Greatest transverse dimension across the right and left first upper molars

I2–I2: Greatest transverse dimension across the right and left second upper incisors.

Although we recorded craniodental measurements to the nearest 0.01 mm and used these values to compute sample statistics, craniodental measurements and their descriptive statistics are rounded to the nearest 0.1 mm in all the tables accompanying the species accounts below. Except as noted otherwise, all measurements and qualitative character data were recorded from specimens with completely erupted permanent dentitions, here regarded as adults in the absence of reliable indications of sexual maturity.

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[3] Although this measurement is equivalent to the "condylobasal length" of Hershkovitz (1977: 944), it is *not* equivalent to condylobasal length as traditionally defined (from the condyles to the anteriormost point of the premaxillae; Thomas, 1905).

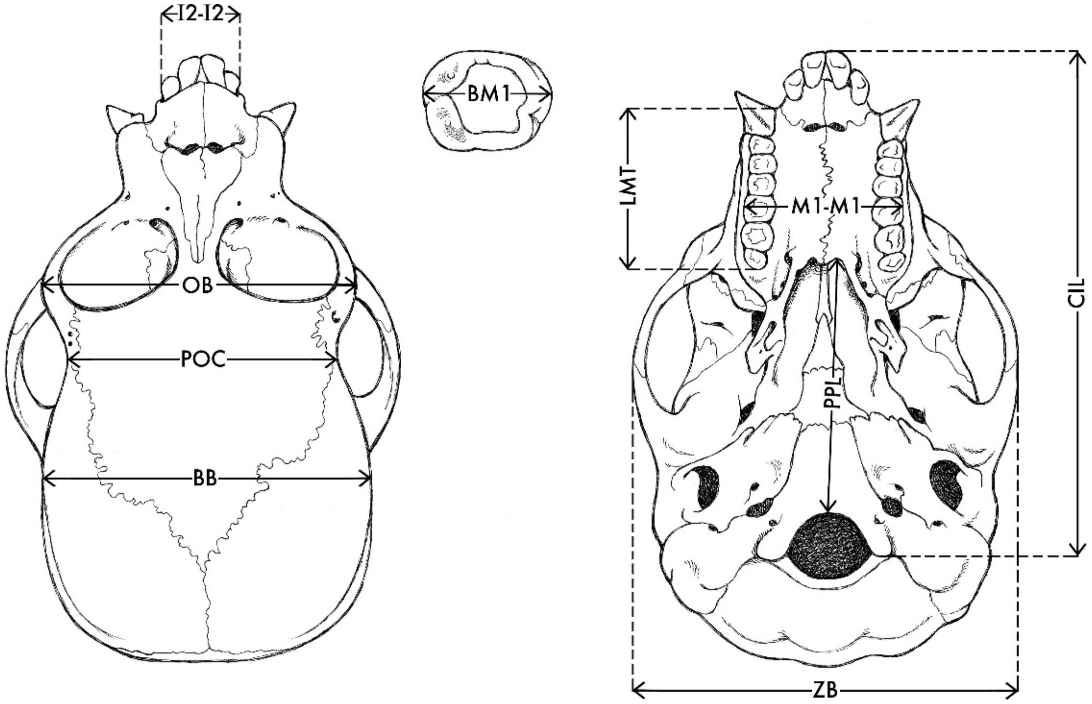

Fig. 3. Dorsal and ventral cranial views of *Pithecia monachus* showing the anatomical endpoints of measurements defined in the text.

SYSTEMATIC ACCOUNTS

Neotropical primates (platyrrhines) have been referred to two families (Callitrichidae and Cebidae; e.g., by Simpson, 1945), to three families (Callimiconidae, Callitrichidae, and Cebidae; Hershkovitz, 1977); or to four families (e.g., Aotidae, Atelidae, Cebidae, and Pitheciidae; Groves, 2005). None of these systems, however, is phylogenetically defensible because each contains one or more nonmonophyletic groups. The classification adopted here is consistent with recent phylogenetic analyses of DNA sequence data (Schneider, 2000; Opazo et al., 2006; Wildman et al., 2009) that provide compelling support for three major clades: Atelidae, Cebidae (including *Callimico*, other callitrichines, and *Aotus*), and Pitheciidae. Fourteen species belonging to nine genera in these families are definitely known to occur in the region covered by this report.

For each species, we list the specimens we examined from the Yavarí-Ucayali interfluve (under Voucher Material) and any published sightings (Unvouchered Observations) previously reported from this region. Few Neotropical primate genera have been comprehensively revised, and the nomenclature for many species that occur in the Yavarí-Ucayali interfluve is correspondingly problematic to some extent. Lacking the time and resources needed to resolve most relevant taxonomic issues, we had to settle for less than definitive solutions. Therefore, the Identification section of each species account provides a brief literature review and only enough additional information obtained from the material at hand to justify our use of technical names.

As explained above, we summarize information about cultural importance, hunting methods, folk beliefs, folk taxonomy, and other ethnological information gleaned from our fieldwork with the Matses under the Ethnobiology heading (which variously appears in the accounts for genera or species as explained below). By contrast with all other text sections (authored by Voss and/or Fleck), the essays entitled "Matses Natural History" are (as nearly as possible) in the words of the Matses themselves.

Atelidae Gray, 1825

Atelids include the largest species of New World primates, all of which are prehensile-tailed inhabitants of the primary forest canopy. Four genera are currently recognized, of which three (*Alouatta, Ateles, Lagothrix*), each represented by a single species, occur in the Yavarí-Ucayali interfluve.

Alouatta seniculus (Linnaeus, 1766)

VOUCHER MATERIAL (TOTAL = 3): Marupa (AMNH 98321, 98610), Nuevo San Juan (MUSM 11108).

UNVOUCHERED OBSERVATIONS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Orosa (Freese et al., 1982), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: Morphological revisions of howler monkeys have recognized as few as six valid species (Hill, 1962), but as many as 14 might be recognized on the basis of coat-color phenotypes (Groves, 2001; Gregorin, 2006). Cytogenetic and molecular research provides compelling support for some, but not all, of the species recognized in the recent taxonomic literature and underscores our still incomplete understanding of this geographically widespread genus. In the absence of any published synthesis of phenotypic and genetic data, the following remarks summarize the emerging taxonomic consensus, suggest where future research could usefully be focused, and explain our preferred binomen for the red howlers of the Yavarí-Ucayali interfluve.

Phylogenetic analyses of mitochondrial DNA sequence data (Cortés-Ortiz et al., 2003) support the recognition of just two trans-Andean howler species: *Alouatta palliata* (Gray, 1849), the mantled howler of Mesoamerica and northwestern South America, and *A. pigra* Lawrence, 1933, the black howler of Guatemala and southeastern Mexico.[4] The distinctness of these species, which was first clearly indicated by conspicuous cranial and pelage differences that are maintained in sympatry (Smith, 1970), is additionally supported by karyotypic data (Steinberg et al., 2008) and by patterns of allelic variation at eight microsatellite loci (Ellsworth and Hoelzer, 2006). By contrast, the nominal taxon *coibensis* Thomas, 1902 (from the Azuero Peninsula and Coiba Island, Panama), which was recognized as a valid species by Groves (2001, 2005), seems to be genetically indistinguishable from *A. palliata* (see Cortés-Ortiz et al., 2003).

The reciprocal monophyly of several morphologically distinctive cis-Andean species or species complexes is likewise supported by mitochondrial sequence data (Cortés-Ortiz et al., 2003), including: (1) the brownish howlers of the Atlantic Forest, for which the oldest available name is *Alouatta fusca* (E. Geoffroy, 1812; see Gregorin, 2006); (2) the sexually dichromatic howlers of eastern Bolivia, central Brazil, Paraguay, and northern Argentina, for which the oldest available name is *A. caraya* (Humboldt, 1812); (3) the red-handed howlers of southeastern Amazonia, for which the oldest available name is *A. belzebul* (Linnaeus, 1766); and (4) the reddish howlers of northern Colombia, Venezuela, the Guiana Region, and western Amazonia, for which the oldest available name is *A. seniculus*. The latter complex is the one represented in the Yavarí-Ucayali interfluve.

In addition to their reddish coloration, members of the *Alouatta seniculus* complex are uniquely distinguished from other simiiform primates by the presence of microchromosomes in all published karyotypic preparations (Consigliere et al., 1996; Sampaio et

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[4] Napier (1976) and Brandon-Jones (2006) argued that the long-accepted epithet *pigra* is a junior synonym of *villosa* Gray, 1845, based on a subadult female specimen from the "Brazils," the skin of which was subsequently lost. Lawrence (1933) and Groves (2001) reasonably treated Gray's name as a nomen dubium. The recent attempt to resurrect *villosa* based on a web of conjecture about what the skin might have looked like and where it might really have come from (Brandon-Jones, 2006) is nomenclatural pedantry at its destabilizing worst.

TABLE 1
Nominal Taxa of Red Howlers in the *Alouatta seniculus* Complex Recognized as Valid by Recent Authors[a]

Name	Type locality
amazonica Lönnberg, 1941[b]	"Codajáz" (= Codajás on left [north] bank of Amazon; Gregorin, 2006), Amazonas, Brazil
arctoidea Cabrera, 1940[c]	Northern Venezuela
insulanus Elliot, 1910[d]	"Island of Trinidad"
juara Elliot, 1910	"Rio Juara, Peruvian Amazon" (= Rio Juruá, Brazil; Gregorin, 2006)
macconnelli Elliot, 1910[e]	"Coast of Demerara" (= coastal Guyana)
puruensis Lönnberg, 1941[f]	Jaburu, Rio Purus, Amazonas, Brazil (fixed by lectotype selection; Gregorin, 2006)
sara Elliot, 1910	"Province of Sara" (= Provincia Gutiérrez; Paynter, 1992), Santa Cruz, Bolivia
seniculus Linnaeus, 1766	Cartagena, Bolívar, Colombia (fixed by lectotype selection; Husson, 1978)

[a] Rylands et al. (2000), Groves (2001, 2005), Gregorin (2006).

[b] A synonym of *juara* according to Groves (2001, 2005) and Gregorin (2006).

[c] Cabrera's *arctoidea* is a replacement name for *ursina* Humboldt, 1805 (preoccupied by *ursina* Kerr, 1792, a baboon) and, therefore, has the same type locality. According to Rylands and Brandon-Jones (1998), Humboldt's *ursina* was based on observations of red howlers along the Caribbean coast of Venezuela (from Aragua to Sucre), in the llanos of Apure, and along the lower Orinoco.

[d] A synonym of *macconnelli* according to Groves (2001, 2005), but on zoogeographic grounds it seems likely that the Trinidadian population is more closely related to howlers in northern Venezuela than to those in Guyana.

[e] Includes "*stramineus*" of authors (e.g., Lima and Seuánez, 1991; Bonvicino et al., 1995, 2001) according to Gregorin (2006).

[f] A synonym of *juara* according to Groves (2005).

al., 1996).[5] Eight nominal taxa of red howlers referable to the *seniculus* complex have been regarded as valid by recent authors (table 1). Although subtle differences in pelage color, sexual dichromatism, and hyoid morphology are said to exist among some of these forms (Gregorin, 2006), chromosomal comparisons provide the most compelling evidence for species recognition. Unfortunately, published karyotypes have only been reported for *arctoidea* (see Stanyon et al., 1995), *macconnelli* (including "*straminea*"; Lima et al., 1990; Lima and Seuánez, 1991; Vassart et al., 1996), *sara* (see Minezawa et al., 1985; Stanyon et al., 1995), and *seniculus* (see Yunis et al., 1976; Lima and Seuánez, 1991). Among other chromosomal differences described in this literature, a shared Y-autosome translocation in *arctoidea, macconnelli,* and *sara* has resulted in a $X_1X_2Y_1Y_2/X_1X_1X_2X_2$ sex-chromosome system, whereas *seniculus* has the standard XY/XX system. Chromosome painting (Consigliere et al., 1996; Oliveira et al., 2002), mtDNA sequence comparisons (Bonvicino et al., 2001; Cortés-Ortiz et al., 2003), and morphometric analyses (Bonvicino et al., 1995) provide additional evidence of genetic divergence among these four taxa.

The red howlers of the Yavarí-Ucayali interfluve are referable to *Alouatta juara* sensu Gregorin (2006), but the validity of this taxon seems questionable. Gregorin applied the name *juara* to western Amazonian (Brazilian and Peruvian) specimens collected south of the Amazon and west of the Purus, and he suggested that the name might also apply to unexamined Brazilian material collected north of the Amazon and west of the Negro. However, western Amazonian specimens geographically assignable to *juara* (sensu Gregorin, 2006) closely resemble typical *seniculus* in pelage coloration (Hill, 1962) and cranial morphology (Bonvicino et al., 1995). Likewise, the single available karyotype attributed to *juara*—obtained from an animal collected at Tefé

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[5] Gregorin (2006) suggested that the black howler monkey of the Tapajos-Madeira interfluve (*nigerrima* Lönnberg, 1941) might be part of this complex, but its divergent pelage and lack of microchromosomes (Armada et al., 1987) suggest otherwise. Apparently, the samples identified as *nigerrima* in published karyotypic and biochemical analyses (Armada et al., 1987; Bonvicino et al., 2001) were both taken from a captive individual of unknown provenance (C. Bonvicino, in litt. 18 May 2010). Therefore, the correct taxonomic allocation of this nominal taxon remains to be convincingly established by analyses of properly vouchered chromosomal preparations and sequence data.

TABLE 2
Craniodental Measurements (mm) of *Alouatta seniculus* from the Yavarí-Ucayali Interfluve

	AMNH 98610♂	MUSM 11108♂	AMNH 98321♀
CIL	123.7	121.2	84.7
OB	65.6	71.0	52.7
POC	39.5	42.8	38.0
ZB	—	85.7	64.9
BB	52.6	53.0	47.6
PPL	—	—	46.2
LMT	43.1	36.3	38.8
BM1	8.6	8.2	7.9
M1–M1	40.2	—	32.4
I2–I2	—	15.9	13.6

(on the south bank of the Amazon between the Juruá and the Purus)—was found to be “basically the same” (Lima and Seuánez, 1991: 154) as the karyotype of typical *seniculus* from Colombia. Morphological material that we examined from the Yavarí-Ucayali interfluve falls within the range of phenotypic variation (coat color and craniodental dimensions) present in large comparative series of typical *seniculus* from northern Colombia; in the absence of any compelling data to the contrary, we conclude that the populations in question are conspecific, and that *juara* is a synonym of *A. seniculus.*

Craniodental measurements of the few available specimens of howler monkeys from the Yavarí-Ucayali interfluve are provided in table 2. The only specimen accompanied by external dimensions is MUSM 11108, an adult male that measured 528 × 589 × 137 × 34 mm; unfortunately, no weight was obtained from this animal.

ETHNOBIOLOGY: The Matses have only one name for the howler monkey, achu, a word of uncertain etymology and one that is not synchronically segmentable. The pan-Panoan term for howler monkey is du/ru, a word with which the Matses are familiar, but which they do not consider a word in their language and therefore not a true synonym. Two or three varieties are recognized: achudapa “big howler monkey” (or achu piudapa “big red howler monkey”), tsusa (a small howler monkey), and achu çhëşhë “black howler monkey.” The first two varieties, achudapa and tsusa, are recognized by all Matses hunters, but the third, achu çhëşhë (which we have never seen) is not known by all. This darker variety is reported to be red, but its underparts and the insides of its arms and legs are said to be black. It is said to live only along the upper Gálvez. Only those Matses that recognize achu çhëşhë use the term achu piudapa to contrast the red and black varieties. The term tsusa, which is not analyzable, is used to refer to the small variety, which is said to live in larger troops and to be lazier. Some speakers say that achudapa and tsusa sometimes travel together. Achu çhëşhë is said to differ in habitat preference from the other two varieties because it is found in forest where the trees are all short (i.e., the white-sand habitats of the upper Gálvez).

Traditionally, only old people were permitted to eat howler monkeys. If a child or a young person eats howler monkey meat, the Matses believe they will become lazy. The small variety of howler monkey, tsusa, is worse in this respect. For this reason, Matses do not hunt howler monkeys as frequently as they do other monkeys. The lassitude induced by eating howler monkey meat can be cured with frog poison[6] and by following a special diet. In smaller villages, where game is still plentiful, howlers are not hunted at all, while in larger villages, howlers are killed more frequently, for older people to eat. Nowadays, despite disapproval from older and more traditional Matses, some younger people are ignoring this dietary taboo. Their justification is that non-Indians eat howler monkeys without any ill effect. Alternatively, some Matses say that only howlers of the tsusa variety must not be eaten. Howler monkey canines are sometimes used to make men’s tooth necklaces, and young howlers are sometimes raised as pets.

Matses kill howler monkeys by following the sound of their calls from far away. Once they stop howling, they are harder to locate, so a hunter chants “chimu tawin tsipun

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[6] Skin secretions of the frog *Phyllomedusa bicolor*, when applied to cutaneous capillary beds exposed by small burns, cause intense headaches and nausea, followed (after hours or days) by a sense of profound relief and renewed energy (Romanoff, 1984; Daly et al., 1992; Milton, 1994).

tsipun" (this is a phrase from a myth where people turned into howler monkeys by attaching a length of a vine called chimu as tails), as he walks toward the source of the howling, believing this will keep the monkeys from shutting up. When they see people, howlers that have not been exposed to hunting will come closer for a look, in which case they can be shot from the ground. Hunted animals will climb high up into a tree with vine tangles and hide in them. The hunter then climbs up to kill the monkeys with bow and arrow or shotgun. Less frequently, howlers are encountered at a mineral lick and killed there. They are easy to kill because they do not run off. Quite rarely, they are killed as they swim across a river. Matses do not imitate howler monkey calls or use dogs to hunt them.

MATSES NATURAL HISTORY: Howler monkeys are red, the color of a red brocket deer [*Mazama americana*], particularly on their backs. Red howler monkeys have large heads, large upper bodies, and small hindquarters. They have a large larynx in their throat, which makes their heads look elongated. They have a long tail that they use to grab onto branches. Their underparts are sparsely haired. Females are smaller than males. Males have long beards and a white scrotum.

Howler monkeys can be found in any primary forest habitat, but they do not come to abandoned swiddens. They are found mostly in floodplain forests and in swamp-palm [*Mauritia flexuosa*] swamps. They are also found in upland forest far from rivers, but not as frequently. They go to mineral licks to eat mud and drink muddy water, and they also descend to drink water from streams. Otherwise, they do not walk around on the ground. They sometimes forage very high up in trees. They can swim well, and troops cross rivers swimming all together, with the babies clinging onto the adults' backs.

Howler monkeys are found in small troops, always fewer than 10 individuals, counting the young. The troop is led by a large male that has a redder back than the other animals. This male has multiple females as mates. Males carry the young [there is some controversy among informants about this]. Eagles prey on smaller howler monkeys. The large male becomes aggressive when there is an eagle around. Jaguars can kill howler monkeys.

Howler monkeys wake up earlier than other monkeys. Howler monkeys howl saying "*yooo*" very early in the morning [from around 4 a.m.] until dawn [5–6 a.m.], stopping and then starting up again. The Matses can hear them from the village. They howl when it is going to be a nice day, so when Matses hear howler monkeys howl before daybreak, they know it will be a clear day. They also howl in the late afternoon [3–4 pm] and during full moons. During full moons they wake up to howl, but do not travel or feed. The big male howls first, and then the females and any other males join in. The males' howls are louder and deeper than females'. The troop congregates and may put their arms around each other as they howl. They scream a lot when they are hit with an arrow.

Right from where they slept, howler monkeys howl, defecating at the same place where they howl. At daybreak they start to move through the trees slowly, looking for food. They are lazy, and do not move around much, and when they do, they do so slowly. Because they stay in the same place for a long time, they defecate where they hang out and there are many flies and ants around where they are, and it stinks there. They go to sleep together at dusk in trees that have many vine tangles. They have two or three places to which they always return to sleep. These sleeping sites can be identified by the smell. They always come back to the same mineral licks, where they get all dirty eating mud. They do not go to mineral licks early in the day; they go in the afternoon. One monkey stays in the trees as a lookout, while the others make a hole in the bank of the mineral lick and eat inside the hole. They do not follow a fixed route, but have a fixed territory and always come back to the same sleeping trees and mineral licks.

Their favorite food is swamp-palm [*Mauritia flexuosa*] fruit. They also eat the fruit of other palms, including isan [*Oenocarpus bataua*]. They drink the liquid from some unripe palm fruits, like dapais [*Attalea phalerata*]. Howler monkeys are the only monkeys that eat tsadte [*Apeiba aspera* (Tiliaceae)] fruits. They also eat many types of dicot tree fruits, including këku [*Couma* *macrocarpa* (Apocynaceae)], diden këku [*Parahancornia peruviana* (Apocynaceae)], machishte [*Rhigospira quadrangularis* and ?*Mucoa duckei* (Apocynaceae)], mamuin [*Rheedia longifolia* (Guttiferae)], okodo mabis [an undetermined species of Guttiferae], moste [*Hymenaea* spp. (Leguminosae)], achu inkuente [*Inga* spp. (Leguminosae)], mannan tsipuis [*Inga* spp. and ?*Pithecellobium* (Leguminosae)], tankada [*Parkia igneiflora, P. multijuga, Pithecellobium auriculatum* (Leguminosae)], bin [*Castilla* (Moraceae)], dadain [*Clarisia racemosa* (Moraceae)], chiwish [*Ficus* spp., *Coussapoa* spp. (Moraceae)], piuşh bëchi [*Helicostylis tomentosa* and *H. elegans* (Moraceae)], şhankuin [*Pourouma* spp. (Moraceae)], bata [*Pseudolmedia* and *Maquira* spp. (Moraceae)], kose [*Manilkara bidentata* (Sapotaceae)], and taëpa [undetermined]. They also eat vine fruits, including poşhodi [*Passiflora nitida* (Passifloraceae)] and nënë pada [undetermined]. They also eat epiphyte fruits, including nënë pada [undetermined], and many types of young, soft leaves, including leaves of tote [*Eschweilera* spp. and *Lecythis* spp. (Lecythidaceae)] and iwise [?*Capirona* (Rubiaceae)] trees. They eat spiders, crickets [or katydids], beetle grubs, and other invertebrates for which they search in palm crowns, under tree bark, and in rotten wood. They gnaw on rotten wood, especially rotten swamp-palm trunks.

Ateles belzebuth (E. Geoffroy, 1806)

VOUCHER MATERIAL (TOTAL = 12): Nuevo San Juan (MUSM 11109, 11110), Orosa (AMNH 74027–74031), Boca Río Yaquerana (FMNH 88839–88843).

UNVOUCHERED OBSERVATIONS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Itia Tëbu (Amanzo, 2006), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Orosa (Freese et al., 1982), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006). (Note that previous reports of spider monkeys from the Yavarí-Ucayali interfluve identified the local species as either *Ateles chamek* or *A. paniscus* for reasons explained below.)

IDENTIFICATION: Kellogg and Goldman's (1944) revision of the spider monkeys recognized four polytypic species, of which two (*Ateles fusciceps, A. geoffroyi*) were trans-Andean endemics, one (*A. paniscus*) was restricted to Amazonia, and another (*A. belzebuth*) included both trans-Andean and Amazonian subspecies. Although Kellogg and Goldman's revision was largely based on pelage traits that some researchers (e.g., Hernández-Camacho and Cooper, 1976) have interpreted as infraspecific geographic variation, recent studies based on other kinds of data (reviewed by Collins, 2008) support the recognition of several valid species. The following paragraphs summarize the empirical basis for recognizing distinct species in Amazonia.

Amazonian spider monkeys consist of four allopatric nominal taxa, variously recognized as valid species or subspecies by modern authors: *paniscus* Linnaeus, 1758, which occurs north of the Amazon and east of the Rio Negro/Rio Branco; *belzebuth* E. Geoffroy, 1806, which occurs north of the Amazon and west of the Negro/Branco; *chamek* Humboldt, 1812, which occurs south of the Amazon and west of the Tapajos; and *marginatus* E. Geoffroy, 1809, which occurs south of the Amazon and east of the Tapajos. Kellogg and Goldman (1944) recognized *chamek* as a subspecies of *Ateles paniscus*, and *marginatus* as a subspecies of *A. belzebuth*, but subsequent analyses of allozymic, cytogenetic, morphometric, and sequence datasets provide compelling evidence that *paniscus* (sensu stricto) is a distinct species, and that *chamek* is more closely related to *belzebuth* and *marginatus*. Although skins of *belzebuth* (with buffy or whitish underparts) and *marginatus* (with whitish facial markings) are easily distinguished from those of *chamek* (which are almost completely black; see below), these three taxa are craniometrically similar (Froehlich et al., 1991), have the same diploid number of chromosomes (Medeiros et al., 1997; Nieves et al., 2005), and have been recovered as a clade in phylogenetic analyses of mitochondrial sequence data (Collins and Dubach, 2000; Collins, 2008). Because molecular analyses that have included representative samples of *belzebuth*, *chamek*, and *marginatus* suggest that these coat-

TABLE 3

External and Craniodental Measurements (mm) of *Ateles belzebuth* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
HBL	496 (494–497) 2	474 (431–532) 4
LT	776 (773–780) 2	820 (769–879) 4
HF	195 (195–195) 2	196 (189–203) 4
Ear	34 (32–35) 2	36 (32–39) 4
CIL	98.3 (97.7–98.9) 2	95.0 (92.8–99.3) 7
OB	63.2 (58.8–66.4) 4	61.4 (58.7–64.0) 8
POC	52.6 (50.1–54.6) 4	51.0 (49.0–53.3) 8
ZB	72.0 (71.2–72.7) 2	68.4 (66.4–71.0) 8
BB	62.5 (60.2–64.1) 4	60.5 (57.3–62.6) 8
PPL	49.6 (48.5–50.5) 4	48.6 (46.0–51.8) 6
LMT	32.1 (31.2–33.5) 3	30.8 (28.5–32.1) 7
BM1	5.9 (5.5–6.2) 4	5.9 (5.5–6.1) 7
M1–M1	33.1 (31.0–35.4) 4	31.4 (30.0–32.5) 8
I2–I2	16.8 (16.3–17.3) 2	18.3 (17.0–19.7) 5

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74027, 74028; FMNH 88842, 88843.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74029–74031; FMNH 88839–88841; MUSM 11109, 11110.

color phenotypes are not reciprocally monophyletic (Collins, 2008: fig. 3.3), and in the absence of any other morphological traits known to be correlated with coat-color differences in this complex, we see no justification for recognizing *chamek* and *marginatus* as distinct species (contra Groves, 2001, 2005).

Although some museum skins of spider monkeys from the Yavarí-Ucayali interfluve are completely black (consistent with most published descriptions of the *chamek* phenotype; e.g., Kellogg and Goldman, 1944; Emmons, 1997), patches of blond or buffy hairs are present along the inner thighs of other specimens (e.g., AMNH 74029, 74031), and the exposed skin of the nose and the central part of the face of large adults is often unpigmented (reddish in life, according to the Matses; see below). Cranial measurements of our material (table 3) fall within the range of variation in homologous dimensions of western Brazilian, northeastern Bolivian, and eastern Peruvian specimens previously reported by Kellogg and Goldman (1944 [as *Ateles paniscus chamek*]) and Lönnberg (1940a [as *A. ater peruviensis*]). Most specimens are unaccompanied by weight data, but an adult female from Nuevo San Juan (MUSM 11109) weighed 7400 g.

ETHNOBIOLOGY: The spider monkey is called çhëşhëid, a term that the Matses analyze as meaning "black one" (probably a valid etymology). The spider monkey is also called by the archaic synonyms mëshe (not analyzable, but apparently containing the prefix më- for "hand") and çhuna wisu (= "black çhuna"; çhuna is one of the archaic names of the woolly monkey). In the language used in the Matses' komok ceremony, spider and woolly monkeys are called şhëmën kudu (these are the only primates to have a name in the ceremonial language). All Matses hunters recognize two varieties of spider monkey, which are said to never occur in the same troop. One is called chëshëidtapa ("big spider monkey"), and the other variety is simply called tsidu, a word that is not analyzable and is only used to refer to this variety of spider monkey. The larger spider monkey subtype has a red nose and central part of its face, and is the "normal" or prototypical type of spider monkey. The tsidu spider monkey is much smaller, skinnier, has an all-black face, has less or no yellow hair on its inner thighs, has a higher-pitched call, lives in much smaller troops, is less common, and is found mostly in deep rainforest very far from rivers. Some tsidu spider monkeys are believed to be demons instead of real animals, and can cause hunters to miss them repeatedly, or, if killed, can make hunters get lost on the way back home. If a tsidu spider monkey makes a hunter get lost, he must dump the dead monkey, and only then will he find his way back home.

The principal economic importance of spider monkeys for the Matses is as food. Spider monkeys and woolly monkeys are the preferred primate game of the Matses. As with sloths and other large monkeys, the arm and leg bones of spider monkeys are broken (to tenderize the meat) before the carcass is bound with plaited palm leaves into a basketlike package, to which a tumpline made of a strip of bark is then attached for carrying. The normal way to cook large monkeys (≥ ca. 2 kg) is to singe the hair off, remove the viscera, cut off the appendages, and boil them in a big pot. Large monkeys are also smoked when much game is killed, or on long (multiple-day) hunting trips. The canines are sometimes used to make necklaces, although the larger teeth of other atelid species are preferred. Young spider monkeys make good pets, but captive-raised animals can become aggressive when they reach adulthood. The Matses believe that hunters cannot eat or touch the intestines of spider monkeys (and other primate game species), lest they lose their marksmanship.

One way that the Matses hunt monkeys (and ungulates) is by walking quickly along forest paths listening for calls and rustling branches; smelling the air; and looking for eaten food, spoor, and other signs of game. How the Matses hunt spider monkeys depends on how wary the local animals are, which in turn depends on how much previous experience a troop has had with hunters. As he walks, every so often a hunter will alternately imitate the calls of spider monkeys, woolly monkeys, and capuchin monkeys, hoping that one species or another will come or at least respond by calling back. If a spider monkey troop that is not wary hears the imitations, the monkeys will respond and come to the hunter. Troops that have had no experience with people will shake branches above the hunter, bark, defecate, urinate and throw branches down at him (which they also do when they see jaguars and anteaters). Or they may simply all come and stare at the person from above. Spider monkeys that are a bit wary will come, but once the large male that leads the troop sees the hunter, it screams and all the monkeys turn around and flee. Troops that are somewhat more wary will respond vocally to the hunter's call but without approaching him, in which case the hunter seeks the monkeys in the direction from which they responded. Troops that are a bit more wary will not respond to loud imitations, so the hunter must call softly and cannot detect wary monkeys that are far away. Very wary troops simply do not respond, and the wariest will hide or move quietly and quickly in the opposite direction when they hear the hunter's call. If no spider monkeys respond, the hunter may try a brown capuchin monkey call, which may make spider (or other) monkeys vocalize, thinking that capuchins have found fruits. The closer to the village a hunter is, the more wary the spider monkeys are likely to be, so as a hunter travels away from the village at first he only listens; then further out he makes low-volume spider monkey calls and/or capuchin monkey calls; and then further out calls spider monkeys at full volume. The hunter may simply imitate spider monkeys (and woolly monkeys) while walking to check if they might answer. Or he may be motivated to try the imitation upon finding dropped half-eaten fruits. Or if he comes across a sleeping tree early in the morning, he may call. When he is ready to turn back to the village, a hunter will make loud spider-, woolly-, and capuchin-monkey calls and listen for a while. In addition to listening and imitating calls, hunters also go to mineral licks (where there may be other game) to kill spider monkeys.

Ideally, the hunter sees the monkeys before they see him. If the troop comes toward the hunter after hearing his imitation (they can be heard approaching because they scream and make noise as they swing through the treetops), then the hunter hides and shoots them when they arrive. If they answer but do not come, the hunter must stalk them. If the hunter is able to catch them by surprise, he shoots the biggest one he can get a clear shot at, and chases a second one after the rest run off. When spider monkeys flee from a hunter, they split up and go in different directions (rather than fleeing all together, as uakari monkeys do). They move through the trees extremely quickly so that the hunter must run at full speed, and try get ahead of one and shoot it as it passes overhead, or he must keep up with one until it tires out. Because females that are carrying young go the slowest, they are the most easily killed. A hunter hunting alone generally kills only one or two spider monkeys from a troop.

The Matses traditionally hunted spider monkeys with bows and arrows, but now they hunt them almost exclusively with shotguns (in some villages bows and arrows are still used when there is no ammunition). Spider monkeys are hard for archers to kill because a shot monkey will pull out the arrow and keep running, dripping blood along the way. If the monkey dies without falling to the ground, the hunter must climb into the canopy to recover the carcass. If a spider monkey falls injured to the forest floor, it will try to bite any person or dog that approaches it.

MATSES NATURAL HISTORY: Spider monkeys have very long limbs and tails. They hold their tails stretched out, unlike woolly and capuchin monkeys, which coil up their tails as they travel. They use their tails to grab onto things, and when they travel swinging under the branches, they use their tail as an additional limb. They hang by their tails when they eat fruit, sometimes all spread out with limbs and tail grabbing onto separate branches. Their hands have only four fingers—that is why a fork is called "spider monkey's hand" [a recently coined term]. In contrast to their limbs, their heads are small. Their heads have little meat to eat on them, unlike woolly monkeys'. The spider monkey's head hair looks like it was combed forward from the back; this along with its red nose makes it look silly as it sits there scratching its small head. Adult males are larger than females and have more yellow hair on their inner thighs.

Spider monkeys are found in all primary forest habitats, but more often in upland forest than in floodplain forest. Spider monkeys mostly use the middle of the canopy, but often climb higher to forage, escape predators, and sleep. When they hear a tinamou fly, they climb up higher. They do not walk around or forage on the ground, unlike white-fronted capuchin monkeys, except when they go to mineral licks [see below].

Spider monkeys are more common than woolly monkeys. Troop size varies from one to very many [some narrators say up to 40], but 10 to 20 is more usual. A large male leads the troop. Females carry their young on their backs, unless the young are very small, in which case they carry them ventrally. Spider monkeys suckle their young in the same way that people do. Harpy eagles take the smaller animals, and jaguars and pumas may attack them at mineral licks. Spider monkeys defend themselves by grabbing and biting.

Spider monkeys have several different vocalizations. They scream very loudly to communicate over long distances saying "*eeeeEEee, eeeeEEee*"; they bark like a dog when they are mad saying "*aik, aik, aik*"; they communicate among themselves with soft vocalizations, saying "*oh, oh, oh*"; and they scream like people when they are shot. They make a lot of noise rustling branches as they move across the treetops.

When there is good weather, spider monkeys wake up early. When it is rainy, they get up later. They wake up calling loudly, calling their companions who are sleeping nearby, usually in the same tree. Once they are all together, they go in search of food. They travel through the trees screaming. They follow a daily route, traveling far in one day, but do not advance very fast [some say they complete their route in one day, others say it takes them 2–3 days, others say they simply use the same general area with no set route]. When in flight, they travel faster than any other monkey. Large males go the fastest, and females carrying young go slower. They travel swinging under the branches using their arms and tails, except when there are no small branches, in which case they run across the tops of large branches. They are most active in the morning, and they rest when the sun is high and hot. They rest lying on branches, while their young play. In the afternoon they are active again, but not as much as in the morning. When it rains, they sit in sheltered places such as under a tangle of vines or under large-leafed epiphytes.

They sleep in the same big tree every night [some speakers say it is only at one locality, others say there are two or three trees on their route where they sleep]. They sleep very high up, splitting into small groups that huddle together. They defecate and urinate where they sleep. Where they sleep, there are a lot of feces and defecated seeds on the ground. Especially common are the seeds of the isan palm [*Oenocarpus bataua*]. These seeds can be found sprouting under their sleeping trees. Sleeping sites stink very badly, and the Matses can smell them from far away. Spider monkeys come out and yell at night when there is a full moon.

Spider monkeys go to muddy mineral licks to eat mud and drink muddy water. They always go to the same mineral lick. Although the troop may split up to forage and eat fruits, they go to the mineral licks together as a group. At the mineral lick, some drink the muddy water while others stay up in the trees nearby watching for jaguars and people. Then they switch places. They make a hole in the walls of the mineral lick, like a cave, where they always collect mud. They drink from the mineral lick with their tails wrapped around trees. They descend and ascend via thin trees next to the mineral lick, and these trees are always covered with mud. After climbing back to the trees after drinking from the mineral lick, they sit there a while scratching their heads and eating their lice.

Spider monkeys eat mostly fruits. Large troops may split up to forage. When one spider monkey finds fruits, it starts eating, and then the others come to join it. The one that comes first finishes eating first and rests while waiting for the others to finish. Unlike other monkeys, they eat fruits without peeling them, swallowing even isan palm seeds and other large seeds [up to about the size of an acorn]. They eat palm fruits, especially isan palm fruits [which ripen during the early rainy season] and swamp-palm [*Mauritia flexuosa*] fruits, which ripen during the dry season]. They also drink the liquid or eat the soft endosperm of unripe niste palm [*Iriartea deltoidea*] fruits. They also eat a lot of dicot tree and vine fruits, especially këku [*Couma macrocarpa* (Apocynaceae)], şhankuin [*Pourouma* spp. (Moraceae)], dadain [*Clarisia racemosa* (Moraceae)], tonnad [species of Myristicaceae], moste [*Hymenaea* spp. (Leguminosae)] and chiwish [*Ficus* and *Coussapoa* spp. (Moraceae)], which are available during the rainy season. Other dicot tree fruits they eat include: wesnid debiate [*Anacardium giganteum* (Anacardiaceae)], machishte [*Rhigospira quadrangularis* and ?*Mucoa duckei* (Apocynaceae)], diden këku [*Parahancornia peruviana* (Apocynaceae)], ichibin [*Matisia* sp., *Eriotheca* sp. (Bombacaceae)], mamuin [*Rheedia longifolia* (Guttiferae], okodo mabis [an undetermined species of Guttiferae], mannan tsipuis [*Inga* spp. and ?*Pithecellobium* (Leguminosae)], tankada [*Parkia igneiflora, P. multijuga*, and *Pithecellobium auriculatum* (Leguminosae)], bin [*Castilla* (Moraceae)], şhanned [?*Brosimum* (Moraceae)], piuşh bëchi [*Helicostylis tomentosa* and *H. elegans* (Moraceae)], kuşhu tëbin [*Naucleopsis mello-barretoi* and *N. ternstroemiiflora* (Moraceae)], bata [*Pseudolmedia* and *Maquira* spp. (Moraceae)], mabis mabiskid [*Chrysophyllum prieurii* (Sapotaceae)], and kose [*Manilkara bidentata* (Sapotaceae)].

Lagothrix lagothricha (Humboldt, 1812)

VOUCHER MATERIAL (TOTAL = 11): Boca Río Yaquerana (FMNH 88827–88833), Nuevo San Juan (MUSM 11122–11124), Quebrada Esperanza (FMNH 88834).

UNVOUCHERED OBSERVATIONS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Itia Tëbu (Amanzo, 2006), Jenaro Herrera (Aquino, 1978), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Orosa (Freese et al., 1982), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006). (Note that some recent reports of woolly monkeys from the Yavarí-Ucayali interfluve identify the local species as *Lagothrix poeppigii*; see below.)

IDENTIFICATION: The genus *Lagothrix* was last revised by Fooden (1963), who recognized four subspecies of *L. lagothricha*, of which three occur in lowland Amazonia: *L. l. cana* (E. Geoffroy, 1812), *L. l. lagothricha* (Humboldt, 1812), and *L. l. poeppigii* Schinz, 1844. Fooden noted that these forms are distinguishable only by coat color, explicitly remarking the absence of morphometric and qualitative osteological differences among them. To date, not a shred of additional evidence has been provided to support the notion that *cana, lagothricha,* and *poeppigii* are valid species as recently proposed by Groves (2001, 2005). The species epithet of the Amazonian woolly monkey is often misspelled "*lagotricha,*" but the correct original spelling was validly fixed by Fooden (1963: 227) acting as first revisor in the sense of the International Code of Zoological Nomenclature (ICZN, 1999: Article 24).

The FMNH series from Boca Río Yaquerana and Quebrada Esperanza were examined by Fooden (1963), who identified the local form as *Lagothrix lagothricha poeppigii*. However, Matses hyponyms for woolly monkeys (see below) suggest that brownish (*poeppigii*-like) and grayish (*cana*-like) coat color

TABLE 4
External and Craniodental Measurements (mm) of *Lagothrix lagothricha* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
HBL	462 (376–515) 5	457 (450–470) 4
LT	622 (585–665) 5	658 (635–675) 4
HF	154 (148–160) 5	156 (150–159) 4
Ear	31 (30–32) 5	31 (30–32) 4
CIL	93.3 (91.0–95.8) 4	88.9 (84.9–93.7) 3
OB	64.2 (60.4–68.6) 6	59.5 (56.1–61.9) 5
POC	47.4 (45.3–49.3) 6	47.4 (45.6–48.3) 5
ZB	75.1 (72.4–79.0) 5	66.1 (63.1–69.3) 5
BB	57.9 (56.1–59.7) 6	58.3 (56.6–60.2) 5
PPL	50.7 (46.9–54.6) 5	45.6 (44.2–47.0) 2
LMT	32.8 (31.1–34.6) 6	32.2 (30.7–33.2) 4
BM1	6.4 (6.1–6.6) 6	6.5 (6.2–6.9) 5
M1–M1	32.8 (31.2–34.2) 6	31.7 (30.0–32.6) 5
I2–I2	15.9 (15.6–16.3) 4	17.3 (16.5–18.5) 4

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 88827, 88831–88834; MUSM 11124. External measurements of FMNH 88832 are obviously erroneous and were omitted from this tabulation.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 88828–88830; MUSM 11122, 11123. Anomalous external measurements of MUSM 11124 were omitted from this tabulation.

phenotypes may coexist in the Yavarí-Ucayali interfluve, as they do along the Rio Juruá (Peres, 1993a). External and craniodental measurements of adult vouchers that we examined are summarized in table 4. Most specimens are unaccompanied by weight data, but an adult female (MUSM 11123) from Nuevo San Juan weighed 5250 g, another (MUSM 11122) weighed 6600 g, and an adult male (MUSM 11124) from the same locality weighed 7500 g.

ETHNOBIOLOGY: The woolly monkey is usually called poshto (not analyzable in Matses, but in neighboring Panoan languages the cognate means "[pot] belly.") Additionally, there are four archaic synonymous terms for woolly monkeys: çhuna (the pan-Panoan term, not analyzable), abukkid "one that is high up," mëdante chued "one with big hands," and maksinkid "woolly one." Two to three subtypes (hyponyms) are usually recognized: poshto piu "red[-brown] woolly monkey," poshto tanun "gray woolly monkey" (or poshto uşhu "white/light-colored woolly monkey") and poshto çhëşhë "black/dark woolly monkey." The poshto piu variety has a red-brown back; the poshto tanun variety has grayish hair, and the poshto çhëşhë variety has contrastingly black venter and insides of limbs. Not all Matses consider poshto çhëşhë to be a distinct class, observing that either red-brown or gray woolly monkeys can have black undersides. Unlike other cases of primate overdifferentiation discussed here, most Matses do not claim that there are additional differences, such as morphological features or habitat preferences, consistently associated with these different color variants. They do, however, assert that different subtypes of woolly monkey do not occur together in the same troop. The Matses do not have a general term for "monkey," but woolly monkeys can be considered the prototypical monkey, and sometimes the word poshto is used generically to mean all game monkeys, or all large (noncallitrichine) monkeys in general.

All Matses eat woolly monkeys. It is a favorite food, and clearly the most appreciated primate game. Hunters cannot eat or touch the intestines of a woolly monkey (or any other monkey), lest they lose their marksmanship. As with any game species, the first time a hunter kills a woolly monkey, he cannot eat any of it, or he will lose his ability to kill woolly monkeys again. Young people (everyone under about 45 or 50) cannot eat the liver of woolly monkeys, lest their teeth fall out. Women must cook the intestines separately from the rest of the meat, and wash their hands thoroughly after touching the intestines in order to avoid contaminating the men's food. Woolly monkey canines are the preferred teeth for making men's tooth necklaces. Young woolly monkeys are often raised as pets.

Woolly monkeys were traditionally hunted with bow and arrow, but nowadays they are hunted mostly with shotguns. Before firearms, the mark of a top hunter was the ability to kill woolly monkeys, which are often high in the canopy and (because of their robust size) do not die unless hit in the right place. The most prestigious shot for a Matses hunter was to hit a woolly monkey in the eye with an arrow. For this reason, interviewees were all concerned with the fact that woolly monkeys are no longer killed with arrows. Furthermore, narrators expressed a common concern that woolly monkeys are now becoming scarce, especially in the vicinity of large permanent villages (traditionally, the Matses relocated their villages/ longhouses every three to seven years).

A single Matses hunter can kill up to four woolly monkeys when he encounters a troop. Hunters imitate woolly monkeys by inhaling while making a very loud "*choook*" call, with hands cupped around the mouth to amplify the sound. When they find partially eaten fruit on the ground, hunters call to see if any monkey responds. If the woolly monkeys have never been hunted, they respond and come. If they are a bit wary, they respond but do not come. And if they are very wary, they do not respond or come, thought they may respond to the imitated call of a brown capuchin monkey. According to the Matses, larger troops are more confident and therefore more likely to respond than smaller troops. Those troops that have not been hunted, especially larger troops, do not run off when they see hunters. Nonhunted animals may come to look at people, and may shake branches and defecate and urinate on them. Hunters prefer to kill large adult males, and will spend some time trying to get a clear shot at the largest male. After the first shot, the monkeys sometimes split up and run in different directions, and only later rejoin. After killing the first animal, the hunter will follow a second woolly monkey, preferably a male, until it gets tired and stops to rest in a place where the hunter can get a shot. If they stop in an inaccessible place, the hunter will shoo it by shaking vines until it moves on. If a wounded animal will not move to where a hunter can get off a second shot, he will climb the tree to finish it off. A hunter will also climb up to dislodge a dead animal that is stuck up in the tree. Sometimes a woolly monkey falls to the ground while fleeing, in which case it will run on the ground a bit and then climb back up. If they are shot in the eye with an arrow or in the chest with a shotgun they fall to the ground right away. If a second or third animal is killed quickly enough, the hunter may be able to hear another one moving through trees, and will leave the killed monkey and pursue another. (Impressively, hunters always remember where they killed each monkey and take little time to gather them up and pack them into a palm-leaf carrying pack.)

MATSES NATURAL HISTORY: Woolly monkeys have prehensile tails that they use for hanging onto branches. As they walk across the tops of branches, they hold their tails rolled up behind them. They are grayish or red-brown, and have black faces. They have many fleas in their genital area. Woolly monkeys are good-looking, especially the babies. The babies have sparsely haired underparts when they are first born.

Woolly monkeys are found in upland forest as well as floodplain forest. They prefer upland forest far from rivers, but go to riverside forest when the water level is high. They are most common in areas with good, productive soil. They can be found in hilltop forest and forest on hilly slopes. They use all levels of the canopy, including very high up. They do not walk around on the ground, but may drop to the ground to hide among buttressed roots when an eagle is spotted. They drink water up in the trees, from bromeliads growing in crotches of trees. They tear off the fruiting structure of the bromeliads to get at the water. They do not frequent mineral licks.

Some woolly monkey troops are large, up to 30 or 40 animals; other troops are small; and occasionally a solitary woolly monkey is found. Only females carry the young, the older ones on their backs and the younger ones ventrally. They suckle their young in the same way that people do.

To sleep, woolly monkeys spread out in small groups among the branches of different trees. At dawn they yell "*choook*" to each other from where they slept and then gather together. Unlike spider monkeys, they do not sleep in a fixed spot, but wherever they are when night falls. They also spread out into subgroups to find fruit, and if they find it, they call and gather to feed together. Large groups feed together, with the babies screaming and making a lot of racket. When they finish the fruits in the tree, they move on without resting, jumping across the branches, to look for more fruits. They travel far, without following a set route, jumping across the branches, noisily rustling the branches, calling to each other, with the young screaming. In the afternoon, when they are full and tired, they rest lying on the branches. The male that is the leader of the troops rests in the lower branches, keeping an eye out for hunters.

Woolly monkeys eat mostly dicot tree and vine fruits. They eat all kinds of dicot fruits, their favorites are këku [*Couma macrocarpa* (Apocynaceae)], ichibin [*Matisia* sp. and *Eriotheca* sp. (Bombacaceae)], şhankuin [*Pourouma* spp. (Moraceae)], and piuşh bëchi [*Helicostylis tomentosa* and *H. elegans* (Moraceae)]. Other dicot fruits they eat regularly include: şhupud [*Spondias mombin* (Anacardiaceae)], poshton tonte [?*Macoubea guianensis* (Apocynaceae)], machishte [*Rhigospira quadrangularis* and ?*Mucoa duckei* (Apocynaceae)], mamuin [*Rheedia longifolia* (Guttiferae)], moste [*Hymenaea* spp. (Leguminosae); this tree/fruit is also called poshton moste ''one that is crunched by woolly monkeys''], mannan tsipuis [*Inga* spp. and ?*Pithecellobium* (Leguminosae)], tankada [*Parkia igneiflora, P. multijuga,* and *Pithecellobium auriculatum* (Leguminosae)], chichombid [*Mouriri* spp. (Melastomataceae)], shannëd [?*Brosimum* (Moraceae)], bin [*Castilla* (Moraceae)], dadain [*Clarisia racemosa* (Moraceae)], chiwish [*Ficus* spp. and *Coussapoa* spp. (Moraceae)], kuşhu tëbin [*Naucleopsis mello-barretoi,* and *N. ternstroemiiflora* (Moraceae)], bata [*Pseudolmedia* and *Maquira* spp. (Moraceae)], poşhodi [*Passiflora nitida* (Passifloraceae)], mabis mabiskid [*Chrysophyllum prieurii* (Sapotaceae)], kose [*Manilkara bidentata* (Sapotaceae)], poshto kaçho neste [*Pouteria* (Sapotaceae); this name means ''woolly monkey back medicine''], taëpa [undetermined], and nënë pada [an undetermined epiphyte with lianalike stems]. They infrequently eat diden këku [*Parahancornia peruviana* (Apocynaceae)], and buku [*Cecropia* spp (Moraceae)]. They drink the fluid inside unripe niste palm [*Iriartea deltoidea*] fruits. Other palm fruits they eat include isan [*Oenocarpus bataua*], and swamp palm [*Mauritia flexuosa*]. They do not feed heavily on swamp-palm fruits, unlike uakari and howler monkeys. They also eat invertebrates including crickets and spiders. They look for insect larvae in rotten wood and under bark. They eat some leaf buds.

Family Cebidae Bonaparte, 1831

Cebids include night monkeys (Aotinae); capuchins and squirrel monkeys (Cebinae); and a distinctive clade of small, clawed species that includes Goeldi's monkey, marmosets, and tamarins (Callitrichinae). Eight cebid species in six genera are definitely known to occur in the Yavarí-Ucayali interfluve.

Subfamily Aotinae Elliot, 1913

Night (or owl) monkeys comprise eight currently recognized species in a single genus (*Aotus*) that ranges from Panama to northern Argentina (Groves, 2005). Seldom seen by day, and hard to see at night due to their weak eyeshine, night monkeys are more frequently detected by their distinctive vocalizations. Unfortunately, the taxonomy of night monkeys has never been comprehensively revised, and many questions of identification remain. In the absence of reliable criteria for field identification, night monkey identifications are usually justified by making assumptions about geographic range limits. Our attempt to identify collected specimens of night monkeys from the Yavarí-Ucayali interfluve, however, suggests that the current taxonomy is itself based on inadequately documented distributional assumptions.

Aotus nancymaae Hershkovitz, 1983

Voucher material (total = 11): Marupa (AMNH 98330, 98331), Nuevo San Juan (AMNH 268238; MUSM 11111–11113), Orosa (AMNH 73701, 73702, 74035), Quebrada Esperanza (FMNH 88868, 88869).

Unvouchered records: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Jenaro Herrera (Aquino, 1978), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Cochiquinas (Aquino and Encarnación, 1988), Río Orosa (Aquino and Encarnación, 1988), Río Tahuayo (Aquino and Encarnación, 1988), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006). (Note that some early reports of night monkeys from the Yavarí-Ucayali interfluve identified the local species as *Aotus trivirgatus*; see below.)

IDENTIFICATION: Night monkeys exhibit a limited range of phenotypic variation, mostly in pelage traits, and all of the named forms in this genus were once considered to belong to a single geographically variable species, *Aotus trivirgatus* (see Hershkovitz, 1949; Cabrera, 1958). However, subsequent karyotypic research by R.A. Brumback and N.S.F. Ma (reviewed by Hershkovitz, 1983) revealed unexpected geographic variation in diploid numbers (2*n*) and fundamental numbers (FN) that they interpreted as evidence for multiple species. The hypothesis that at least some night monkey karyomorphs represent valid taxa is supported by a variety of data, including correlated pelage traits, comparative serology, and clinical responses to experimental infection with malaria parasites (Hershkovitz, 1983); evidence of sympatry without apparent hybridization in the wild (Pieczarka et al., 1992); substantial mtDNA sequence divergence (Ashley and Vaughn, 1995; Plautz et al., 2009; Menezes et al., 2010); and reduced fertility in at least some hybrid pairings (Kumamoto and Houck, 2001). Together, these and other results (Ford, 1994; Defler and Bueno, 2007) effectively refute earlier notions that *Aotus* is monotypic, but many taxonomic issues remain unresolved.

The most frequently cited phenotypic character in the recent literature on *Aotus* concerns the coloration of the fur of the neck. The so-called "red-necked" and "gray-necked" phenotypes are defined by the presence or absence, respectively, of a lateral extension of the reddish ventral coloration along the neck below and behind the ear (Hershkovitz, 1983: fig. 1). Allegedly, the gray-necked forms of *Aotus* (for which the oldest available name is *trivirgatus* Humboldt, 1811) occur north of the Amazon, and red-necked forms (for which the oldest available name is *azarae* Humboldt, 1811) occur south of the Amazon, but Hershkovitz (1983) discussed some exceptions to this geographic pattern and others are indicated by specimens that we examined (see below). Although neck coloration is commonly used as the basis for recognizing species groups of *Aotus* (e.g., by Hershkovitz, 1983; Ford, 1994; Groves, 2001), recent sequencing studies do not support the reciprocal monophyly of gray-necked and red-necked night monkeys (Plautz et al., 2009; Menezes et al., 2010).

The original description of *Aotus nancymaae* was largely justified on the basis of karyotypic data, but no morphological voucher material of known geographic origin is apparently available for any chromosomal preparation attributed to this species, and existing vouchers of karyotyped laboratory animals do not consistently exhibit diagnostic pelage traits.[7] Instead, only indirect evidence is available to correlate chromosomes with phenotypes. According to Hershkovitz (1983), unvouchered night monkey karyotypes prepared by N.S.F. Ma from blood samples obtained at Peruvian localities on the south (right) bank of the Amazon (including the Yavarí-Ucayali interfluve) all have 54 chromosomes and 72 autosomal arms ($2n = 54$, $FN = 72$), whereas most karyotypes from the north (left) bank of the Peruvian Amazon have $2n = 46$ and $FN = 60$. Hershkovitz (1983) attributed divergent pelage traits to these karyotypes by examining skins from north-bank and south-bank Peruvian localities. He identified the north-bank $2n = 46$ karyotype as belonging to the gray-necked species *Aotus vociferans* (Spix, 1823), and he described a new species of red-necked night monkey, *A. nancymaae* (originally misspelled *nancymai*; see Groves, 2001) for the south-bank $2n = 54$ karyotype. However, an allegedly unique enclave of red-necked night monkeys with $2n = 54$ chromosomes (also referred to *A. nancymaae*) occurs along the lower Río Tigre, a north-bank tributary of the Amazon (Hershkovitz, 1983: fig. 9).

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[7] Of the two karyotypic vouchers of *Aotus nancymaae* mentioned by Hershkovitz, one (FMNH 123033 = Brumback lab #103) is unambiguously red necked, but the other (FMNH 123032 = Brumback lab #102) appears to be gray necked. Although Hershkovitz (1983: 228) said that these specimens were from "the series described by Brumback et al. (1971)," the FMNH mammal catalog states they originated from the Johns Hopkins Hospital Primate Colony, whereas Brumback et al.'s (1971) material came from other institutions. Instead, FMNH 123032 and 123033 are probably two of the three Johns Hopkins specimens karyotyped by Brumback (1973), who said they were collected in "the Leticia, Colombia-Iquitos, Peru area of the Amazon Basin south [sic] of the Andes mountains" (op. cit.: 285).

TABLE 5
Craniodental Measurements (mm) of *Aotus nancymaae* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
CIL	50.7 (50.3–51.0) 3	49.6 (49.4–49.8) 3
OB	43.6 (42.7–44.1) 3	42.9 (42.3–43.3) 3
POC	33.2 (32.6–34.0) 3	30.4 (28.3–31.6) 3
ZB	40.2 (38.1–41.8) 3	38.0 (37.4–39.1) 3
BB	34.7 (34.2–35.5) 3	32.8 (31.9–33.8) 3
PPL	26.0 (25.9–26.2) 2	25.0 (24.2–26.0) 3
LMT	18.1 (17.6–18.7) 3	17.8 (17.5–18.2) 3
BM1	4.0 (3.9–4.0) 3	4.2 (4.1–4.2) 3
M1–M1	20.6 (20.3–20.9) 3	20.0 (19.8–20.3) 3
I2–I2	11.2 (11.0–11.4) 3	11.6 (11.5–11.8) 2

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 73701, 98330; FMNH 88868.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 73702, 74035, 268238.

Although Aquino and Encarnación (1988) believed that *Aotus nancymaae* and *A. vociferans* are allopatrically distributed, recent reports of sympatry from several localities near Leticia (Pieczarka et al., 1992) and a few specimens of *nancymaae* from north-bank localities where only *vociferans* should occur (e.g., AMNH 74382, from Apayacu) suggest otherwise. Future fieldworkers should be alert to the possibility that both species could be present along either bank, where they might occupy adjacent but distinct habitats.

All of the night monkey specimens that we examined from the Ucayali-Yavarí interfluve match the pelage characters attributed to *Aotus nancymaae* by Hershkovitz (1983). In particular, the reddish ventral coloration extends up the side of the neck below and behind the ear (conforming to the red-necked phenotype of other south-bank Amazonian forms), the interscapular whorl (Hershkovitz, 1983: fig. 1) is absent, the flanks are predominantly grizzled-grayish, and the distal half of the tail is blackish above and below. A distinct middorsal blackish stripe is present on the proximal half of the tail in some specimens (e.g., AMNH 73701, 73702), but not in others (e.g., AMNH 74035, 268238). Craniodental measurements of these specimens (table 5) compare closely with homologous dimensions of topotypic material (Hershkovitz, 1983: table V). Most specimens from the Yavarí-Ucayali interfluve are unaccompanied by external measurements and weights, but an adult male (MUSM 11111) from Nuevo San Juan measured 307 × 343 × 89 × 32 mm and weighed 820 g; an adult female (AMNH 268238) from the same locality measured 308 × 390 × 96 × 32 mm and weighed 804 g.

Pending a critical revision of *Aotus*, we follow the currently accepted taxonomy (Groves, 2005) in referring our material to *A. nancymaae*, but it is not clear that this taxon is really diagnosable from *A. miconax* Thomas, 1927, a geographically adjacent species from the foothills of the eastern Andes. Hershkovitz (1983) admitted that *nancymaae* and *miconax* might be conspecific, and subsequent morphological analyses (Ford, 1994) have failed to discover any phenotypic trait that distinguishes them, but the karyotype of *miconax* is unknown. Although it would be reasonable to conclude on the basis of morphology that *miconax* is a senior synonym that should replace *nancymaae* as the oldest available name for the night monkeys of the Yavarí-Ucayali interfluve, we prefer to maintain existing usage and await karyotypic data from Andean foothill populations to support or refute this hypothesis.

Puertas and Bodmer (1993) suggested that *Aotus nigriceps* (another allegedly distinct red-necked species) might occur in the Reserva Comunal Tamshiyacu-Tahuayo—from which they also reported *A. nancymaae*—but noted that the species had only been recorded from vocalizations. In the absence of corroborating details, their identification is difficult to evaluate, but sympatry between congeneric species of night monkeys is not implausible (as noted above). Future primatological fieldworkers in the area should take care to record unusual vocalizations and (ideally) collect voucher specimens of locally co-occurring taxa.

REMARKS: One of our voucher specimens (AMNH 268238) was shot at 1500 h on the afternoon of 31 May 1996 as it followed a troop of *Saimiri sciureus* at a height of 15 m above the ground in secondary upland forest. Two other night monkeys were part of this mixed-species troop, an unusual association not reported by the Matses (see below) nor, apparently, one previously reported in the literature.

ETHNOBIOLOGY: The Matses call the night monkey dide, but another Matses name for the night monkey is diku. The term dide is the one usually overheard in everyday conversation, and diku is used mostly in myths. There is some controversy among the Matses as to whether diku is a synonym of dide or a less-commonly encountered subtype (different from dide).

The Matses eat night monkeys, but because the Matses traditionally did not hunt at night, and night monkeys are rarely encountered in the day, they were infrequently killed. Now that the Matses hunt at night with flashlights and shotguns (mainly for pacas, deer, tapirs, and caimans), they could kill night monkey more easily, but since night monkeys are small, the Matses are seldom willing to expend a shotgun shell to kill one. The Matses kill night monkeys opportunistically when the animals are detected at dawn entering tree holes, or when a monkey sticks its head out of its hole as a hunter passes by during the day. In the latter case, the hunter will shake vines and saplings to see if the animal exits the hole; if it does, the hunter will shoot from the ground. If the monkey stays inside its hole, the hunter may climb up a neighboring tree, make a bit of noise, and then shoot it when it sticks its head out again. If not, the hunter might climb the tree, plug the hole, and later return later with an axe to fell the tree or enlarge the hole to get the monkey(s) out.

The Matses believe that night monkeys "inform" people with their calls by revealing that large terrestrial game (especially white-lipped peccaries) or a jaguar is approaching or in the vicinity. The Matses consider night monkeys good and helpful because they provide this information.

MATSES NATURAL HISTORY: Night monkeys have big eyes, flat snouts, and striped foreheads. They have a gray body with a red chest, and a black tail-tip. They are the size of a squirrel monkey.

They live in small troops of about four individuals. They call saying "*ii ii ii ii*" [the vocalization attributed to night monkeys in traditional Matses ceremonial chants, not a phonetically accurate rendition of actual calls]. They are active at night and sleep in the day. They can see in the dark and forage for fruits in the dark. They sleep in holes in dicot trees and palm trees. They do not always sleep in the same hole. When they see that the day is dawning, they go inside their hole. Then at dusk they come out again.

They eat mostly dicot tree fruits, including diden këku [*Parahancornia peruviana* (Apocynaceae); this term means "night monkey's këku fruit"; këku is another fruit in the family Apocynaceae]. They surely eat other sweet dicot fruits that other monkeys eat, but it is hard to be certain which ones because they are seldom seen feeding.

Subfamily Callitrichinae

Callitrichines include the smallest New World primates, all of which have claws instead of nails. Western Amazonian callitrichines include Goeldi's monkey (*Callimico*), marmosets (*Callithrix*), and tamarins (*Saguinus*). Although the pygmy marmoset (*Callithrix pygmaeus*) was once placed in a separate genus (*Cebuella*), we follow Porter et al. (1997) in referring this taxon to the genus *Callithrix*. In our opinion, *Cebuella* and other clades of Amazonian marmosets (including *Mico* and *Callibella*) are more appropriately ranked as subgenera (as by Groves, 2001, 2005) than as full genera (contra Roosmalen and Roosmalen, 2003; Rylands et al., 2009).

Callimico goeldii (Thomas, 1904)

VOUCHER MATERIAL: None.

UNVOUCHERED RECORDS: Nuevo San Juan (D.W. Fleck, unpublished), Río Blanco (Izawa, 1979), Santa Cecilia (Hershkovitz, 1977), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: No specimen of *Callimico goeldii* is known from the Yavarí-Ucayali interfluve, but a skin and skull from Contayo (on the left bank of the upper Río Tapiche; AMNH 98281)[8] agrees in all qualitative external and craniodental charac-

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[8] We have not found Contayo on any recent map, but it appears at about 7°04′S, 74°14′W on the 1938 "Loreto" sheet of the American Geographic Society's 1:1,000,000 series. Like other vanished settlements that were once scattered along the upper Tapiche, Contayo may have been populated by itinerant rubber tappers at the time of Bassler's visit.

ters with published descriptions of the species (Thomas, 1904, 1913; Hershkovitz, 1977). The collector, Harvey Bassler (a petroleum geologist; Myers, 2000), recorded no external measurements, and the skull has been bisected longitudinally for anatomical study; as a result, transverse cranial measurements cannot be taken. However, other craniodental dimensions of this specimen, including condyloincisive length (CIL, 41.0 mm) and length of the maxillary toothrow (C1–M3, 15.4 mm) are within the published range of variation for *Callimico goeldii* (see Hershkovitz, 1977: appendix table 2).

REMARKS: No other western Amazonian callitrichine is completely black, so unvouchered reports by competent observers have high credibility. Our sighting at Nuevo San Juan (of a small troop moving through secondary vegetation close to the ground on the right bank of the Río Gálvez) was unambiguous, and several other sight records from the region seem trustworthy.

Izawa (1979: 5) reported that "*Callimico* occurs as a relatively high population from the head to the upper basin of the Río Blanco, a [right-bank] tributary of the Río Tapiche." Izawa also observed *Callimico* along the upper Río Tapiche, but did not specify on which bank(s) his observations were made. (Additional information from Izawa's primatological survey of the Tapiche-Blanco is apparently available in a Japanese-language publication that we have not seen [Izawa, 1978]). Recently, however, Jorge and Velazco (2006) reported *Callimico* at an inventory site on the right bank of the upper Tapiche.

Hershkovitz (1977: 928) attributed the Santa Cecilia sighting to the late Pekka Soini, whose correspondence (dated 28 June 1970) is still preserved in the FMNH Division of Mammals' archives. In fact, Soini did not explicitly mention Santa Cecilia, but stated that *Callimico goeldii* "seems to be definitely known … to some natives along the Maniti river." Santa Cecilia is a small community on the right (east) bank of the lower Manití (Robbins et al., 1991), a site where Soini might plausibly have interviewed local informants. Subsequent primate census work along the Río Manití, however, has not produced additional records of this elusive species (Tapia et al., 1990).

ETHNOBIOLOGY: A few Matses talk about a monkey called sipi çhëşhë "black tamarin," which is said to be different from tamarins, extremely rare, all black (including the area around its mouth), and to forage on the ground and very close to the ground. However, most Matses have never seen this species.

Callithrix pygmaea (Spix, 1823)

VOUCHER MATERIAL (TOTAL = 12): Boca Río Yaquerana (FMNH 88997–88999), Nuevo San Juan (AMNH 272828, MUSM 13301), Orosa (AMNH 73751, 74054–74056), Santa Cecilia (FMNH 87135–87137).

UNVOUCHERED REPORTS: Choncó (Amanzo, 2006), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Aucayo (Castro and Soini, 1977), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003).

IDENTIFICATION: The pygmy marmoset (formerly *Cebuella pygmaea*) was last reviewed in substantive detail by Hershkovitz (1977), who recognized only Spix's epithet as valid, treating *niveiventris* Lönnberg, 1940, as a strict synonym. However, other authors (e.g., Cruz Lima, 1945; Cabrera, 1958; Napier, 1976; Roosmalen and Roosmalen, 1997; Groves, 2001, 2005) have treated *C. p. pygmaea* and *C. p. niveiventris* as valid subspecies distinguishable by ventral fur color. Roosmalen and Roosmalen (1997) mapped these nominal taxa as allopatrically distributed north and south of the Amazon, respectively.

Spix's original material of *pygmaea* (the holotype, preserved in the Zoologischen Staatssamlung München; Kraft, 1983) was collected at Tabatinga, on the north (left) bank of the Amazon just upstream from the mouth of the Yavarí,[9] whereas Lönnberg's material of *niveiventris* (two syntypes in the Naturhistoriska Riksmuseet, Stockholm) was collected at Lago Ipixuna, about halfway between the Juruá and the Purus on the south (right) bank of the river. We have not

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[9] Lönnberg (1940b) and Groves (2001: 136) incorrectly located Tabatinga on the south bank of the Amazon (Rio Solimões).

TABLE 6
External and Craniodental Measurements (mm) of *Callithrix pygmaea* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
HBL	143 (141–147) 4	147 (143–150) 3
LT	186 (172–208) 4	187 (160–211) 3
HF	41 (39–43) 4	43 (41–44) 3
Ear	20 (19–22) 4	19 (18–20) 3
CIL	28.2 (27.5–28.9) 2	28.7 (27.4–30.3) 7
OB	21.2 (20.8–21.7) 3	20.6 (19.8–21.4) 5
POC	18.1 (17.7–18.8) 3	17.9 (17.8–18.1) 6
ZB	—	21.6 (20.6–22.8) 3
BB	20.9 (20.8–21.0) 3	20.6 (19.9–21.3) 6
PPL	13.9 (13.8–14.0) 2	14.5 (14.0–15.5) 7
LMT	8.4 (8.3–8.5) 2	8.7 (8.3–9.0) 7
BM1	2.3 (2.2–2.4) 3	2.3 (2.0–2.5) 7
M1–M1	10.9 (10.7–11.2) 3	10.9 (10.1–11.2) 7
I2–I2	4.9 (4.7–5.0) 3	5.1 (4.8–5.3) 7

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272828; FMNH 87135, 87136, 88897.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 73751, 74054–74056; FMNH 87137, 88898; MUSM 13301.

examined the type material of either taxon, but specimens from the Yavarí-Ucayali interfluve more closely resemble *niveiventris* by virtue of their mostly whitish underparts, by contrast with specimens from the adjacent north bank of the Amazon (e.g., AMNH 74360–74370), which have grizzled-brownish underparts (resembling those of typical *pygmaea* according to Hershkovitz, 1977). Ventral fur color does not, however, consistently distinguish specimens from opposite banks of the Amazon, and we agree with Hershkovitz (1977) that subspecific nomenclature does not usefully describe any currently recognized pattern of geographic variation among museum specimens of pygmy marmosets. Unfortunately, molecular data suggesting a high degree of genetic divergence within *C. pygmaea* were all obtained from captive individuals of unknown geographic origin (Tagliaro et al., 2000). External and craniodental measurements of specimens we examined from the Yavarí-Ucayali interfluve are provided in table 6. Most are unaccompanied by weights, but an old adult male from Nuevo San Juan (AMNH 272828) weighed 115 g, and a young adult female from the same locality (MUSM 13301) weighed 99 g.

ETHNOBIOLOGY: The Matses call the pygmy marmoset madun sipi, which means "demon's tamarin." The Matses have no synonymous names for pygmy marmosets, and no subtypes are recognized by them.

The Matses do not hunt or kill pygmy marmosets. They do not keep them as pets, since they believe they can cause illness. Recently, some people have caught them to sell to non-Indians as pets. All Matses know about pygmy marmosets, but many have not observed one closely.

MATSES NATURAL HISTORY: Pygmy marmosets are very cute. They are small and gray. They have a flat face and a mane that makes their head look big. They are the size of a dwarf squirrel [*Sciurillus pusillus*], but they are most similar to tamarins.

They climb on trees and vines in any forest type. They always return to the same large, smooth-barked trees where they feed. They spend most of their time hanging on the trunks of these large trees. They can be found high or low in the forest. They vocalize saying "*pss pss*" as if they were giggling. When they see people, they hide on the opposite side of the trunk. They only move about in the daytime.

Their food is the bark of large smooth-trunked dicot trees. [Other speakers simply say they gnaw on the trees without being specific about what they eat, but none mention explicitly that they consume sap.] They rarely or never eat fruits [one speaker said he has seen them eat some fruits, but others disagree].

Genus *Saguinus* Hoffmannsegg, 1807

Two species of *Saguinus* (tamarins) occur sympatrically throughout the Yavarí-Ucayali interfluve: the saddleback tamarin, *S. fuscicollis*, and the moustached tamarin, *S. mystax*. Although they are morphologically distinctive and are recognized as different species by the Matses, many aspects of their ethnobiology and natural history are similar, so it is convenient to summarize these topics in a joint account.

ETHNOBIOLOGY: Tamarins (and possibly Goeldi's monkey, see above) are called sipi (probably of onomatopoetic origin). Tamarins are also called by the synonym pishtadan (clearly of onomatopoetic origin, see below). Two to three types are recognized: sipi ëksed "white-lipped tamarin" (= moustached tamarin, *Saguinus mystax*), sipi kabëdi "spotted-back tamarin" (= saddleback tamarin, *Saguinus fuscicollis*), and sipi çhëşhë "black tamarin" (= Goeldi's monkey, *Callimico goeldii*, see above).

Traditionally, Matses hunters occasionally killed tamarins with arrows, sometimes just to test their marksmanship, but nowadays hunters will not expend a shotgun shell to kill one. Boys, however, sometimes kill them with arrows to roast and eat as a snack. They make good pets, so hunters will often try to catch young tamarins to give to their children. When they see a troop of tamarins, they wait until a mother sets her offspring on a branch to feed it, and then they spook the animals by yelling, and by shaking vines and saplings. The youngster will then often either fall or get left behind.

Matses natural history: Moustached tamarins have white teeth and white around their mouths. They are mostly black and have long black tails. Saddleback tamarins have spotted backs, black heads, and black tails. Moustached tamarins are larger than saddleback tamarins.

Moustached tamarins use higher levels of the forest than saddleback tamarins, but neither uses the highest levels of the canopy. Saddleback tamarins sometimes forage on the ground. They can both be found in all habitats, but moustached tamarins are more closely associated with primary forest, where there are many tall trees, whereas saddleback tamarins prefer thick, viney vegetation in secondary forest, in abandoned swiddens, and in old blowdowns. Saddleback tamarins are often seen at the edges of swiddens. [One narrator went further, claiming that moustached tamarins are *never* found in secondary forest, and that saddleback tamarins are *only* found in secondary forest.] Saddleback tamarins sometimes come to swiddens where they eat ripe plantains or papayas.

Tamarins live in medium-sized troops of about eight animals. When they see people, they say "*pishtadan pishtadan*." When they get separated from the rest of the troop, they say "*sii sii sii*" and others in the troop answer back. They make a lot of noise when they see people, jaguars, or peccaries. They only move about in the daytime. Both species of tamarin sleep in tree holes or on branches in thick vine tangles.

Tamarins eat ripe dicot tree fruit such as këku [*Couma macrocarpa* (Apocynaceae)], tinte [*Garcinia macrophylla* (Guttiferae)], mannan tsipuis [*Inga* spp. and ?*Pithecellobium* (Leguminosae)], şhannëd [?*Brosimum* (Moraceae)], chichombid [*Mouriri* spp. (Melastomataceae)], piuşh bëchi [*Helicostylis tomentosa* and *H. elegans* (Moraceae)], and bata [*Pseudolmedia* and *Maquira* spp. (Moraceae)]. When they eat şhankuin fruits [*Pourouma* spp. (Moraceae)] they do not swallow the seeds (unlike spider monkeys). They never eat unripe fruits, and they eat little or no palm fruits. They also eat crickets [or katydids; the Matses term is taxonomically ambiguous], caterpillars, other insects, and spiders, which they find on the undersides of leaves and elsewhere.

Saguinus fuscicollis (Spix, 1823)

Voucher material (total = 28): Marupa (AMNH 98292, 98294–98296), Nuevo San Juan (AMNH 268235, 268236, 272796; MUSM 11102), Orosa (AMNH 73742, 73746, 73748, 73749, 73984, 74038, 74040–74043, 74045, 74046, 74048, 74051, 74053), Quebrada Esperanza (FMNH 88874), San Fernando (FMNH 88873), Santa Cecilia (FMNH 86958, 86964, 86965).

Unvouchered reports: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Itia Tëu (Amanzo, 2006), Jenaro Herrera (Aquino, 1978), Orosa (Freese et al., 1982); Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Aucayo (Castro and Soini, 1977), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006).

Identification: The genus *Saguinus* was revised by Hershkovitz (1977), who referred specimens from Marupa, Orosa, Quebrada Esperanza, San Fernando, and Santa Cecilia

TABLE 7
Diagnostic Coat-color Differences Among Subspecies of *Saguinus fuscicollis* (sensu Hershkovitz, 1977) from the Yavarí-Ucayali and Adjacent Interfluvial Regions

	fuscicollis[a]	*illigeri*[b]	*lagonotus*[c]	*nigrifrons*[d]	*tripartitus*[e]
Forehead	grizzled-brownish	black	black	black	black
White frontal blaze	absent	absent	absent[f]	absent	present
Crown	grizzled-brownish	black	black	grizzled-brownish	black
Nape/mantle	grizzled-brownish	grizzled-brownish	red	grizzled-brownish	gold

[a] Juruá-Yavarí interfluve, but extending into the area between the upper Río Tapiche and the Río Blanco.
[b] Ucayali-Marañón interfluve.
[c] Marañón-Napo interfluve, excluding the area between the Río Napo and the Río Curaray.
[d] Yavarí-Ucayali interfluve.
[e] Between the Río Napo and the Río Curaray (part of the Marañón-Napo interfluve).
[f] Indistinct pale frontal markings are present in some AMNH specimens.

to the subspecies *S. fuscicollis nigrifrons* (I. Geoffroy, 1850). Our material from Nuevo San Juan is indistinguishable from the specimens examined by Hershkovitz and confirms his inference that a single coat-color phenotype (table 7) occurs throughout most of the Yavarí-Ucayali interfluve.[10] External and craniodental measurements from representative specimens are summarized in table 8. Most saddleback tamarin specimens from the Yavarí-Ucayali interfluve are unaccompanied by weight data, but an adult female (AMNH 268236) from Nuevo San Juan weighed 436 g, and an adult male (AMNH 272796) from the same locality weighed 420 g.

REMARKS: Currently recognized species limits within the *Saguinus nigricollis* group of Hershkovitz (1977) are difficult to justify on the basis of recent mtDNA sequence analyses and new information about geographic ranges. As revised by Hershkovitz, this group included two polytypic species—*S. nigricollis* and *S. fuscicollis*—which were thought to occur sympatrically in Ecuador and Peru. A third species of this group, *S. tripartitus*, was recognized by Thorington (1988) on the basis of distributional data suggesting that it occurs (or once occurred) sympatrically with *S. fuscicollis* (contra Hershkovitz, 1977), and Groves (2001, 2005) additionally recognized *S. graellsi* and *S. melanoleucus* (subspecies of *S. nigricollis* and *S. fuscicollis*, respectively, according to Hershkovitz, 1977) as valid species. However, recent primate surveys have failed to find any locality where two or more nominal taxa of the *S. nigricollis* group occur sympatrically (de la Torre, 1996, 2000; Heymann, 2000; Heymann et al., 2002; Rylands et al., 2011)[11], and there is at least one well-documented case of natural hybridization between distinct coat-color phenotypes currently ranked as species (Peres et al., 1996). Additionally, *S. fuscicollis* and *S. nigricollis* are not reciprocally monophyletic (whether or not *tripartitus*, *graellsi*, and/or *melanoleucus* are also recognized as full species), and pairwise genetic distances are generally lower within this complex than they are among most other currently recognized tamarin species (Cropp et al., 1999; Matauschek et al., 2011).

Pending a taxonomically comprehensive revision of the *Saguinus nigricollis* group that takes newly discovered facts about genetic sequence variation, geographic distributions, and hybridization into account, we follow Hershkovitz's (1977) nomenclature, but two plausible outcomes of future revisionary work could affect the nomenclature of populations in the Yavarí-Ucayali interfluve.

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[10] Subsequent primatological surveys suggest that the nominotypical race (*S. f. fuscicollis*) inhabits the area between the right bank of the upper Tapiche and the left bank of the Río Blanco (Hodun et al., 1981).

[11] A possible exception was recently reported by Montenegro and Escobedo (2004), who reported sightings of both *Saguinus fuscicollis* and *S. nigricollis* along the Río Yaguas (a right-bank tributary of the lower Putumayo). However, these authors provided no supporting details about the local form of *S. fuscicollis* (previously unreported from the Yaguas catchment), nor did they clearly state that these taxa occurred sympatrically (on the same bank of the Yaguas) at any surveyed site.

TABLE 8
External and Craniodental Measurements (mm) of *Saguinus fuscicollis* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
HBL	226 (220–236) 3	225 (215–234) 5
LT	328 (300–346) 3	337 (325–346) 5
HF	73 (72–73) 3	71 (69–74) 5
Ear	32 (30–33) 3	30 (28–32) 4
CIL	38.6 ± 1.0 (36.9–40.2) 12	38.8 ± 0.8 (37.6–40.5) 12
OB	26.5 ± 1.0 (24.6–28.8) 13	26.3 ± 1.1 (24.6–28.7) 13
POC	22.9 ± 1.0 (20.5–24.3) 13	23.2 ± 0.8 (21.9–25.3) 13
ZB	31.9 ± 1.2 (30.3–34.3) 10	31.8 ± 1.8 (29.0–34.9) 11
BB	26.3 ± 0.7 (25.3–28.0) 13	26.6 ± 1.0 (24.9–28.9) 12
PPL	18.6 ± 0.3 (18.2–19.0) 13	19.1 ± 0.5 (18.2–19.7) 11
LMT	11.5 ± 0.4 (10.5–12.0) 12	11.4 ± 0.5 (10.5–12.2) 13
BM1	3.0 ± 0.1 (2.7–3.1) 14	3.0 ± 0.1 (2.8–3.1) 12
M1–M1	16.1 ± 0.5 (15.5–17.1) 14	16.0 ± 0.6 (15.0–17.1) 13
I2–I2	7.6 ± 0.4 (7.0–8.1) 13	7.6 ± 0.3 (7.0–8.1) 12

[a] Summary statistics (mean, standard deviation [for $N \geq 10$], observed range in parentheses, and sample size) for measurements of AMNH 73742, 73746, 73748, 73749, 74038, 74040–74043, 98294, 98296, 272796; FMNH 86964, 88873.

[b] Summary statistics (mean, standard deviation [for $N \geq 10$], observed range in parentheses, and sample size) for measurements of AMNH 73984, 74045, 74046, 74048, 74051, 74053, 98292, 98295, 268235, 268236; FMNH 86958, 86965, 88874.

If all of the tamarins in this complex were judged to be conspecific, the appropriate binomen for populations throughout the region would be *S. nigricollis*. Alternatively, if all morphologically diagnosable haplotype clades were recognized as full species (Matauschek et al., 2011), then the voucher material we examined would be referrable to *S. nigrifrons* and the coat-color phenotype reported as occurring between the Río Tapiche and the Río Blanco (see above) would be called *S. fuscicollis*.

Six specimens of *Saguinus fuscicollis* (sensu Hershkovitz, 1977) are labeled as having been collected at Marupa (on the south bank of the Amazon) by Harvey Bassler; these include four examples of the *nigrifrons* phenotype and three examples of the *lagonotus* phenotype. The first four are listed above as vouchers, but the latter two (AMNH 98286, 98287) were alleged by Hershkovitz (1977) to have been collected on the opposite (north) bank of the Amazon. In the absence of any other material of *lagonotus* from south-bank localities, Hershkovitz's hypothesis that AMNH 98286 and 98287 were mislabeled seems plausible because other vertebrate specimens that passed through the hands of Harvey Bassler are likewise associated with problematic locality data (Wiley, 2010).

Saguinus mystax (Spix, 1823)

VOUCHER MATERIAL (TOTAL = 35): Marupa (AMNH 98288, 98289), Nuevo San Juan (AMNH 268237; MUSM 11105, 11106, 13303), Orosa (AMNH 73741, 73743–73745, 73747, 73750, 73985, 74039, 74044, 74047, 74049, 74050, 74052), Quebrada Esperanza (FMNH 88870–88872), Santa Cecilia (FMNH 86951–86957, 86959–86962, 87138–87140).

UNVOUCHERED OBSERVATIONS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Itia Tëbu (Amanzo, 2006), Jenaro Herrera (Aquino, 1978), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Aucayo (Castro and Soini, 1977), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: Hershkovitz (1977) examined the series from Marupa, Orosa, Quebrada Esperanza, and Santa Cecilia for his taxonomic revision of *Saguinus*, wherein this material was referred to *S. mystax mystax*. Our material from Nuevo San Juan is indistinguishable from that examined by Hershkovitz, conforming to his diagnosis of the nominotypical race by lacking both the

TABLE 9

External and Craniodental Measurements (mm) of *Saguinus mystax* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
HBL	257 ± 8 (248–272) 13	253 (245–265) 6
LT	390 ± 14 (372–423) 13	380 (365–392) 6
HF	76 ± 2 (72–79) 13	74 (72–77) 6
Ear	31 ± 2 (28–35) 13	28 (26–30) 6
CIL	42.6 ± 1.1 (40.7–44.2) 20	42.2 ± 1.1 (39.8–43.5) 10
OB	29.1 ± 0.8 (27.4–30.0) 18	28.9 ± 1.2 (26.8–30.9) 10
POC	24.1 ± 0.8 (22.7–25.7) 17	24.1 ± 0.6 (23.4–25.0) 10
ZB	34.7 ± 0.9 (32.1–36.0) 18	35.2 (32.5–36.6) 7
BB	28.8 ± 0.9 (27.0–30.6) 19	28.7 ± 1.0 (27.1–30.2) 11
PPL	20.5 ± 0.5 (19.9–21.8) 18	20.4 ± 0.6 (19.2–21.7) 10
LMT	12.9 ± 0.3 (12.2–13.4) 19	12.7 ± 0.6 (11.3–13.7) 11
BM1	3.3 ± 0.1 (3.1–3.6) 21	3.2 ± 0.2 (2.7–3.6) 11
M1–M1	17.1 ± 0.4 (16.4–17.8) 18	17.2 ± 0.7 (15.7–18.0) 10
I2–I2	8.6 ± 0.4 (8.0–9.8) 16	8.4 ± 0.5 (7.3–9.0) 10

[a] Summary statistics (mean plus or minus one standard deviation [for $N \geq 10$], observed range in parentheses, and sample size) for measurements of AMNH 98288, 73741, 73743–73745, 73747, 73750, 74039, 74044, 268237; FMNH 86951–86957, 86962, 87140, 88871, 88872; MUSM 13303.

[b] Summary statistics (mean plus or minus one standard deviation [for $N \geq 10$], observed range in parentheses, and sample size) for measurements of AMNH 98289, 73985, 74047, 74049, 74050, 74052; FMNH 86959–86961, 87138, 87139, 88870.

reddish coronal fur of *S. m. pileatus* (listed as a distinct species by Groves, 2001, 2005) and the whitish ventral tail base of *S. m. pluto*. Craniodental measurements from representative specimens are summarized in table 9. Most moustached tamarin specimens from the Yavarí-Ucayali interfluve are unaccompanied by weights, but an adult male (AMNH 268237) from Nuevo San Juan weighed 522 g, another (MUSM 13303) weighed 585 g, and an adult female from the same locality weighed 650 g.

Subfamily Cebinae Bonaparte, 1831

The subfamily Cebinae includes capuchins (*Cebus*), medium-sized monkeys with prehensile tails, and squirrel monkeys (*Saimiri*), which are much smaller and have nonprehensile tails. Two species of capuchins and one species of squirrel monkey are represented in the voucher material that we examined from the Yavarí-Ucayali interfluve.

Genus *Cebus* Erxleben, 1777

The white-fronted capuchin (*Cebus albifrons*) and the brown capuchin (*C. apella*) occur sympatrically throughout the region treated in this report. Their ethnobiology is conveniently summarized in a joint account.

ETHNOBIOLOGY: Capuchin monkeys are called bëchun by the Matses. They are also known by the archaic synonym koekid ‘‘one that says ‘*ko.*’ ’’ The monomorphemic term chidu is used in a Matses myth to refer to capuchin monkeys, and chidu is also the principal term for capuchin monkey in the closely related language of the Kulinas, whom the Matses raided and from whom they incorporated many captives. Most Matses speakers do not list chidu as part of the ‘‘official’’ game synonym set for capuchins (Fleck and Voss, 2006), but consider it a synonym reserved for telling myths. Other Matses insist that, because it is a legitimate and archaic name, it should not be excluded when listing game synonyms.

Two types of capuchin monkey are universally recognized by the Matses: bëchun çhëşhë ‘‘black/dark-colored capuchin’’ (the brown capuchin, *Cebus apella*) and bëchun uşhu ‘‘white/light-colored capuchin’’ (the white-fronted capuchin, *Cebus albifrons*). The term bëchun (unmodified by çhëşhë or uşhu) can refer generically to both local species of capuchin monkeys, or specifically to the brown capuchin. The brown capuchin is called by its full name, bëchun çhëşhë, only when there is a need to be specific. Some hunters recognize two varieties of brown capuchin: bëchun çhëşhëdapa "large dark capuchin monkey" and bëchun çhëşhëmpi "small dark capuchin." The large variety is said to travel in smaller troops, and be found more commonly in upland forest; the smaller variety is said to be the more common one and is found more frequently along rivers. Most hunters, however, do not recognize these subtypes of brown capuchin monkey.

Old people can eat capuchin monkeys, but young people believe they will become lazy and unenergetic if they eat them. As with the howler monkey (see above), this lassitude can be cured by application of frog poison to burns on the arms or chest. Some Matses say that young people will also age prematurely if they eat capuchin monkeys. Young capuchin monkeys are sometimes raised as pets, but most Matses prefer not to raise them because they are too mischievous, breaking chicken eggs, masturbating, and constantly getting into everything. The canines of brown capuchin monkeys are considered good for making tooth necklaces.

Both capuchin monkey species are hunted in the same way. Hunters usually do not make much of an effort to find capuchin monkeys because of the partial dietary taboo, especially now that mostly shotguns are used and hunters do not wish to expend valuable ammunition on food that only old people can eat. Matses hunters detect capuchin monkeys when they hear them knocking hard fruits against branches, or when they hear vocalizations or the noise of rustling branches as the monkeys travel through the canopy. When a Matses hunter imitates capuchin calls, the monkeys usually respond loudly but seldom actually come toward the hunter. When capuchins are being chased, they sometimes drop to the ground and run on the ground. When this happens, dogs will try to catch them, but capuchin monkeys are strong and easily kill dogs by biting them. Hunters must be ready to kill capuchin monkeys fighting with their hunting dogs, but capuchins also bite people if they are carelessly approached.

Cebus albifrons (Humboldt, 1812)

Voucher material (total = 7): Boca Río Yaquerana (FMNH 88854, 88855, 89173); Nuevo San Juan (MUSM 11119); Orosa (AMNH 73723, 74034); Santa Cecilia (FMNH 86932).

Unvouchered observations: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Jenaro Herrera (Aquino, 1978), Orosa (Freese et al., 1982), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003).

Identification: The last morphological revision of *Cebus* was by Hill (1960), who reviewed the tediously complex and unedifying nomenclatural history of this difficult genus. Most students of capuchin taxonomy (e.g., Elliot, 1913; Hershkovitz, 1949; Hill, 1960) have emphasized the distinction between "tufted" and "untufted" species based on the presence or absence of tufts or crests of coronal fur in adult males (additional characters diagnosing these groups were tabulated by Hershkovitz, 1949). As far as known, no local fauna anywhere in the Neotropics has more than one species of tufted capuchin or more than one untufted species, whereas tufted and untufted capuchins occur sympatrically throughout much of Amazonia. Thus, the distinction seems important, and Silva (2002) recently proposed that these groups be formally recognized as subgenera: *Cebus* Erxleben, 1777, for the untufted species; and *Sapajus* Kerr, 1792, for the tufted species. At least some genetic evidence suggests that these might, in fact, be reciprocally monophyletic taxa (Casado et al., 2010).

The untufted capuchin of western Amazonia, *Cebus albifrons*, has been divided into a number of subspecies by authors. Based on mapped geographic ranges in Hershkovitz (1949) and Hill (1960), the population inhabiting the Yavarí-Ucayali interfluve is assignable to *C. a. unicolor* (Spix, 1823), the type locality of which is Tefé (on the south bank of the Amazon between the Juruá and the Purus), Amazonas, Brazil. However, Defler and Hernández-Camacho (2002) argued that Spix's *unicolor* is phenotypically indistinguishable from the nominotypical race, the type locality of which (fixed by neotype selection) is "about 10 km north of Maypures … Vichada, Colombia" (op. cit.: 54). Our voucher material is somewhat darker and duller than the color illustration of the neotype of *C. a. albifrons* (in Defler and Hernández-Camacho, 2002), but we remain unconvinced of the need for trinomial nomenclature to distinguish minor pelage differences among Amazonian populations of this species. Measurements of specimens collected in the Yavarí-Ucayali interfluve (table 10) are slightly larger than most homologous dimensions of topotypical *C. a. albifrons* (in Defler and Hernández-Camacho, 2002), but sample sizes are too small for confident inference.

Matses natural history: White-fronted capuchin monkeys are light-colored, except for the tops of their heads, which are brown. Their backs and tails are darker than their faces, chests, and bellies. Like brown capuchin monkeys, white-fronted capuchin monkeys raise their eyebrows repeatedly when they see people. Males touch their penises when they see people.

White-fronted capuchin monkeys can be found in any habitat, but they are more common in upland forest than in riverside forest, whereas brown capuchin monkeys have the opposite preference. They sometimes come to the edge of swiddens. White-fronted capuchin monkeys spend more time foraging on the ground than any other type of monkey. They play on the ground in small clearings. They use mostly the lower canopy, but go high to feed when they find food up high.

Troops are medium-sized, numbering up to about 20 or 25 animals, though more frequently about 8 to10. They have many young in their troops, which scream a lot as they pass from tree to tree. Sometimes white-fronted capuchin monkeys travel with woolly monkeys, but never with squirrel monkeys. They are less commonly encountered than brown capuchin monkeys.

TABLE 10

External and Craniodental Measurements (mm) of *Cebus albifrons* from the Yavarí-Ucayali Interfluve

	FMNH 86932♂	FMNH 88854♂	AMNH 73723♀	FMNH 88855♀
HBL	400	440	—	371
LT	460	470	—	444
HF	130	143	—	139
Ear	35	37	—	36
CIL	74.7	82.1	69.1	70.6
OB	57.2	59.0	55.7	54.0
POC	40.2	42.7	40.6	42.7
ZB	63.8	71.7	62.3	60.4
BB	53.3	55.2	51.8	53.3
PPL	32.2	35.4	—	29.5
LMT	27.7	29.2	25.6	27.7
BM1	5.5	5.8	5.2	5.5
M1–M1	28.4	30.6	28.6	30.7
I2–I2	14.6	15.7	13.0	14.8

They call differently from brown capuchin monkeys, calling: "*kooo kooo kooo*," among other vocalizations. Like brown capuchin monkeys, they break off dead branches and palm fronds and pull off wasp nests and throw them down. They sleep together in a group up in a tree, unlike woolly monkeys, which spread out in different trees.

Their food is the same as that of brown capuchin monkeys [see below; however, unlike brown capuchins, they have not been observed to kill and eat titi monkeys]. They have the same ability to break open hard dicot fruits and palm nuts.

Cebus apella (Linnaeus, 1758)

Voucher material (total = 8): Boca Río Yaquerana (FMNH 88846), Nuevo San Juan (AMNH 268240, MUSM 11120), Orosa (AMNH 73989, 74032, 74033), Quebrada Esperanza (FMNH 88847, 88848).

Unvouchered observations: Actiamë (Amanzo, 2006), Chonćo (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Itia Tëbu (Amanzo, 2006), Orosa (Freese et al., 1982), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below

Angamos; Salovaara et al., 2003), Río Yavarí Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: The many nominal taxa of tufted capuchins—which collectively range from northern Colombia to northern Argentina—were all treated as synonyms or subspecies of the brown capuchin (*Cebus apella*) by Hershkovitz (1949) and Hill (1960), but some are now recognized as valid species by authors (e.g., Groves, 2001, 2005; Silva, 2002; Rylands et al., 2005). Unfortunately, the revisionary studies alleged to support the recognition of distinct species of tufted capuchin have never been published, the only published diagnoses (based on trivial sample sizes; Groves, 2001) are not useful for specimen identification, "undeniable evidence of some natural interbreeding" is admitted to exist (Groves, 2001: 152), and genetic distances among some "species" are unimpressive (e.g., 1.3% between cytochrome-*b* sequences of *C. apella* and *C. "cay"*; Casado et al., 2010). Therefore, a compelling case for recognizing multiple valid species among the nominal taxa traditionally regarded as synonyms or subspecies of *C. apella* has yet to be made. In particular, we are not convinced that any tufted species other than the brown capuchin inhabits Amazonian rainforests.

According to Hill (1960), the subspecies of *Cebus apella* in the Yavarí-Ucayali interfluve is *macrocephalus* Spix, 1823 (type locality "Lago Cactuá," presumably somewhere on the Brazilian Amazon), but geographically adjacent forms include *juruanus* Lönnberg, 1939 (type locality João Pessôa on the Rio Juruá, Brazil) and *peruanus* Thomas, 1901 (type locality Huaynapata, Cusco, Peru). In fact, representative skins from the Yavarí-Ucayali interfluve plausibly fit Grove's (2001) descriptions of each of these nominal taxa. Some (AMNH 268240), for example, have more or less distinct blackish middoral stripes (as described for *macrocephalus* and *juruanus*), whereas others (AMNH 73989) lack any trace of a black middorsal stripe (resembling *peruanus* in this and other respects). Cabrera (1958) treated both *juruanus* and *peruanus* as synonyms of *C. a. macrocephalus*, an arrangement that is consistent with our suspicion that all western Amazonian tufted capuchins are taxonomically indistinguishable.

TABLE 11
External and Craniodental Measurements (mm) of *Cebus apella* from the Yavarí-Ucayali Interfluve

	Males[a]	FMNH 88848♀
HBL	457 (436–476) 3	418
LT	448 (425–470) 3	422
HF	128 (123–131) 3	123
Ear	37 (35–38) 3	36
CIL	83.0 (76.0–87.0) 6	77.0
OB	56.3 (49.6–62.5) 6	55.0
POC	40.2 (38.4–41.4) 6	39.3
ZB	72.7 (61.9–80.6) 5	63.9
BB	53.6 (51.7–56.6) 6	51.1
PPL	37.6 (33.6–40.4) 6	32.7
LMT	31.0 (28.9–32.8) 6	—
BM1	6.5 (6.2–6.9) 6	6.4
M1–M1	31.2 (29.7–32.9) 6	31.4
I2–I2	16.5 (15.6–17.4) 6	16.4

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 73989, 74032, 74033, 268240; FMNH 88846, 88847.

Measurements of examined voucher material are summarized in table 11. Most specimens of *Cebus apella* from the Yavarí-Ucayali interfluve are unaccompanied by weights, but an adult male (AMNH 268240) from Nuevo San Juan weighed 5200 g and a lactating adult female from the same locality (MUSM 11120) weighed 2510 g.

ETHNOBIOLOGY: See the preceding account for capuchin ethnobiology.

MATSES NATURAL HISTORY: Brown capuchin monkeys have bald temples, especially the large males. Unlike woolly monkeys, they do not hang by their tails. They walk around on branches with their tails rolled up very tightly. Males are larger than females. Capuchin monkeys, including pets, raise their eyebrows repeatedly when they see people.

Brown capuchin monkeys are found in primary or secondary forest, in upland forest or in riverside forest. They are common along large streams. Sometimes they forage on the ground, but not as much as white capuchin monkeys do. They generally do not forage too high up.

Brown capuchin monkeys are in medium-sized troops, numbering up to about 15 animals. Sometimes a male is found alone. They very commonly travel and forage together with squirrel monkeys. Brown capuchin monkeys bully squirrel monkeys when they feed together with them. When capuchin and squirrel monkeys are together, they make a lot of noise. Like white-fronted capuchin monkeys, brown capuchin monkeys make a lot of noise banging hard dicot fruits and palm nuts to open them. They may spread out to forage, but when they find a lot of fruit they eat together.

Brown capuchin monkeys call out saying "*bëtsiton*" when they see people or jaguars. They also call out saying "*ko-o ko-o ko-o ko-o*."

Brown capuchin monkeys travel through the forest being mischievous: they pull down wasp and termite nests and toss them down to the ground. They also throw down palm fronds and dead branches as they go. In abandoned swiddens they throw down peach-palm [*Bactris gasipaes*] fruits without eating them. At night they sleep in any tree that has vine tangles.

Capuchin monkeys eat all kinds of dicot tree fruits, including, wësnid dëbiate [*Anacardium giganteum* (Anacardiaceae)], këku [*Couma macrocarpa* (Apocynaceae)], diden këku [*Parahancornia peruviana* (Apocynaceae)], machishte [*Rhigospira quadrangularis* and ?*Mucoa duckei* (Apocynaceae)], kapan çhëşhte [*Matisia bracteolosa* and *Quararibea ochrocalyx* (Bombacaceae)], mamuin [*Rheedia longifolia* (Guttiferae)], okodo mabis [undetermined, Guttiferae)], moste [*Hymenaea* spp. (Leguminosae)], mannan tsipuis [*Inga* spp. and ?*Pithecellobium* (Leguminosae)], tankada [*Parkia igneiflora, P. multijuga,* and *Pithecellobium auriculatum* (Leguminosae)], bin [*Castilla* (Moraceae)], buku [*Cecropia* spp. (Moraceae)], dadain [*Clarisia racemosa* (Moraceae)], piuşh bëchi [*Helicostylis tomentosa* and *H. elegans* (Moraceae)], kuşhu tëbin [*Naucleopsis mello-barretoi* and *N. ternstroemiiflora* (Moraceae)], şhankuin [*Pourouma* spp. (Moraceae)], bata [*Pseudolmedia* and *Maquira* spp. (Moraceae)], tonnad [all species of Myristicaceae], mabis mabiskid [*Chrysophyllum prieurii* (Sapotaceae)], kose [*Manilkara bidentata* (Sapotaceae)], dadan dëso [*Theobroma cacao* (Sterculiaceae)], tonkodo [*Theobroma* (Sterculiaceae)], kuëte mëdiad [undetermined], and taëpa [undetermined]. They also eat vine fruits. They eat swamp-palm [*Mauritia flexuosa*] fruits regularly and isan palm [*Oenocarpus bataua*] fruits occasionally. Because they can break open fruits by banging them on a branch, they eat some fruits that other monkeys cannot eat, including dadan dëso and other cacaolike fruits. They can break open unripe palm fruits and consume the liquid and/or soft endosperm inside. Some of the palm fruits they feed on include: niste [*Iriartea deltoidea*], budëd [*Attalea butyracea*], di pinchuk [*Astrocaryum chambira*], şhukkate pinchuk [*Astrocaryum murumuru*], and akte pinchuk [*Astrocaryum jauari*]. They bite open cabbage palm [*Euterpe precatoria*] seeds and eat the soft endosperm, but do not eat the ripe mesocarp of cabbage palm fruits. They pick and wastefully throw down many fruits that they do not eat. They pull off palm leaves to get at the heart. When there are no fruits to be found, they eat any little thing they can find. They eat beetle larvae they find in rotten wood that they break apart. They eat invertebrates including scorpions, millipedes, crickets [or katydids; the Matses term is taxonomically ambiguous], etc. They also eat baby birds. They occasionally kill and eat titi monkeys [*Callicebus cupreus*].

Saimiri sciureus (Linnaeus, 1758)

VOUCHER MATERIAL (TOTAL = 22): Boca Río Yaquerana (FMNH 88866), Marupa (AMNH 98269, 98270), Nuevo San Juan (AMNH 268245, 268246; MUSM 11155, 11156, 11158, 11159, 11161–11169), Quebrada Esperanza (FMNH 88867), San Fernando (FMNH 88865), Santa Cecilia (FMNH 86977).

UNVOUCHERED OBSERVATIONS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Itia Tëbu (Amanzo, 2006), Jenaro Herrera (Aquino, 1978), Río Orosa (Freese et al., 1982), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003).

IDENTIFICATION: Despite several decades of behavioral, chromosomal, morphological, and molecular research (reviewed by Hershkovitz, 1984; Thorington, 1985; Costello et al., 1993; Boinski and Cropp, 1999; Lavergne et al., 2010), the taxonomy of *Saimiri* (squirrel monkeys) remains profoundly unsatisfactory. The last formal taxonomic treatment of the genus (Hershkovitz, 1984) recognized a Central American species, *S. oerstedi* (Reinhardt, 1872) and three Amazonian species. The latter (in Hershkovitz's classification) consist of *S. boliviensis* (I. Geoffroy and de Blainville, 1834), *S. sciureus* (Linnaeus, 1758), and *S. ustus* (I. Geoffroy, 1843). A fourth Amazonian species, *S. vanzolinii* Ayres, 1985, was also recognized as valid by Groves (2001, 2005).

Saimiri boliviensis and *S. sciureus* have both been reported from the Yavarí-Ucayali interfluve. Based on his examination of museum specimens, Hershkovitz (1984) reported that *S. boliviensis* and *S. sciureus* occur sympatrically west of the Río Tapiche, whereas only *S. sciureus* occurs east of the Tapiche. Puertas and Bodmer (1993), however, reported unvouchered sightings of both species from the Reserva Comunal Tamshiyacu-Tahuayo (along the Quebrada Blanco and the Río Yavarí-Mirím), and Bennett et al. (2001) reported unvouchered sightings of *S. boliviensis* from both banks of the Tapiche. Given the discrepancy between Hershkovitz's specimen-based observations and the unvouchered observations of fieldworkers, the external characters by which *S. boliviensis* and *S. sciureus* can be distinguished are obviously relevant for assessing the reliability of sight identifications.

The only external characters by which Peruvian forms of *Saimiri boliviensis* and *S. sciureus* can be reliably distinguished are facial markings and caudal pelage: (1) As illustrated by Hershkovitz (1984: fig. 1), a broad arc of white fur extends onto the forehead above each eye in *S. sciureus*, separating the blackish superciliary vibrissae from the dark (greyish or blackish) fur of the crown; by contrast, the dark fur of the crown extends ventrally to the superciliary vibrissae in *S. boliviensis*, such that the vibrissae are harder to see. (2) The black tuft of long hairs at the end of the tail is thicker and more conspicuous in *S. sciureus* than in *S. boliviensis*. Unfortunately, neither of these characters is easily scored at a distance or in the absence of comparative material, and relevant illustrations in some field guides are inaccurate.[12] Because primatologists have seldom described the phenotypic criteria they used to identify squirrel monkeys in the field, most unvouchered observations of *Saimiri* from northeastern Peru cannot be reliably assigned to species.

All of the specimens of *Saimiri* that we examined from east of the Río Tapiche in the Yavarí-Ucayali interfluve are unambiguously referable to *S. sciureus* (sensu Hershkovitz, 1984). Among other diagnostic traits, all examined specimens have broad arcs of white fur above each eye (separating the blackish superciliary vibrissae from the grayish or blackish coronal fur), and the black tail tufts of these specimens are longer and thicker than those in comparative series of *S. boliviensis*. Males have grayish-agouti coronal fur and grayish sideburns, whereas the coronal fur and sideburns of females are conspicuously darker (sometimes blackish in part; e.g., AMNH 268246, FMNH 88867, MUSM 11166). Although the Matses report variation in arm pigmentation among local troops of squirrel monkeys (see below), all of the specimens we examined have grayish-agouti upper arms and yellowish forearms. Measurement and weight data are summarized in table 12.

As recognized by authors (e.g., Hershkovitz, 1984; Groves, 2001, 2005), *Saimiri sciureus* is polytypic, with several subspecies that are distinguishable by pelage pigmentation and karyotypes; specimens from the Yavarí-Ucayali interfluve are usually referred to *S. s. macrodon* (Elliot, 1907), the type locality of which is in eastern Ecuador. Although neither *S. sciureus* nor *S. s. macrodon* are consistently recovered as monophyletic groups in recent phylogenetic analyses of cytochrome-*b* sequence data (Lavergne et al., 2002, 2010), the taxonomic interpretation of these results is unclear. Absent a comprehen-

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[12] Illustrations of *boliviensis* and *sciureus* in Emmons (1990: pl. 11), for example, do not show any difference in the extent of white above the eye; instead, *boliviensis* is depicted with black coronal fur and *sciureus* with gray coronal fur. In fact, the coronal fur of both species is sexually dichromatic in northeastern Peru, females tending to have blackish crowns, whereas males have gray crowns (Hershkovitz, 1984).

TABLE 12
External and Craniodental Measurements (mm) and Weights (g) of *Saimiri sciureus* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
HBL	307 (301–319) 6	298 (288–305) 5
LT	434 (396–464) 6	440 (420–463) 4
HF	93 (90–95) 8	92 (88–97) 5
Ear	30 (27–32) 7	30 (27–33) 5
CIL	47.7 (43.6–51.2) 9	45.1 (41.4–47.5) 8
OB	35.7 (32.3–38.6) 9	34.7 (32.0–37.6) 8
POC	31.0 (29.0–32.6) 9	30.2 (29.5–30.8) 7
ZB	40.8 (37.6–44.0) 9	37.9 (35.2–40.1) 8
BB	36.6 (34.7–37.9) 9	36.1 (34.4–37.0) 8
PPL	23.5 (21.7–25.4) 9	21.6 (19.8–22.6) 8
LMT	17.8 (16.9–19.0) 8	16.3 (14.9–17.0) 7
BM1	4.2 (4.0–4.4) 9	4.0 (3.6–4.2) 8
M1–M1	20.0 (18.4–21.6) 8	18.9 (17.8–19.9) 8
I2–I2	9.7 (9.3–10.6) 6	9.6 (9.2–10.1) 7
Weight	1131 (842–1385) 7	939 (883–969) 3

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 268245, 98269; FMNH 88865; MUSM 11159, 11161, 11162, 11165, 11167, 11168.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 268246, 98270; FMNH 86977, 88866, 88867; MUSM 11158, 11163, 11166.

sive revision of *Saimiri* based on geographically dense sampling, multiple genes, and due attention to diagnostic morphological traits, we follow existing usage in referring our material to *S. sciureus* in its currently accepted sense.

ETHNOBIOLOGY: Squirrel monkeys are called tsanka. They are also called tsankekid "one that says *tsan*." The term tsanka appears to be a shorted form of tsankekid. Two subtypes are recognized: tsankadapa "big squirrel monkey" and tsankampi "little squirrel monkey." The larger variety is said to have whitish arms and to live in smaller troops (or alone), while the small variety is said to have bright yellow arms and to live in larger troops. The small variety is said to be more common in river-edge forest than the larger variety. The smaller variety is said to be the only one found to travel together with brown capuchin monkeys.

Very long ago, the Matses did not eat squirrel monkeys, lest they become thin (like a squirrel monkey). More recently, perhaps even before contact with missionaries, Matses began to eat squirrel monkeys, but as with titi monkeys, hunters usually do not make a special effort to find them because they are small. A Matses hunter may listen to their noisy rustling of branches, and then try to get a shot off before they see him. After the first shot, the hunter may chase the troop making them run through the trees until one pauses on a relatively low branch, when the hunter can shoot it with an arrow or shotgun. The Matses consider squirrel monkeys to be very abundant, easy to kill, and tasty, but nevertheless hunters do not often kill them.

The canines of large males are sometimes used to make men's tooth necklaces, but the teeth of larger monkeys are preferred. Squirrel monkeys are frequently kept as pets and are considered very good pets by some Matses. Attractive women are called "squirrel monkey" because squirrel monkeys, especially their babies, are considered cute.

MATSES NATURAL HISTORY: Squirrel monkeys are cute. They have white fur around the eyes. The area around their mouth is black, as if painted with genipap dye. They have a long tail with a black tail tip, like a night monkey does. They have a strong smell.

They are found in all types of habitats, but not too far from rivers [within a few kilometers]. They prefer riverside forest and also like swamp-palm [*Mauritia flexuosa*] swamps. They like riverside forest because there are a lot of legume pods and insects there. They like swamp-palm swamps, both for the swamp-palm fruits and because there are many insects there.

They live in very large troops, and stay together without splitting up. Sometimes they eat, travel, and even sleep with brown capuchin monkeys. They may forage together with woolly monkeys, but do not stay with them as long as they do with brown capuchin monkeys. The females carry the young on their back or underside.

They vocalize saying "*sii sii chan chan chan chan sii sii*." When they hear brown capuchin monkeys, they answer. The young also go "*sii sii sii*." They yell like that as they travel noisily through the trees.

Squirrel monkeys are active during the day. They wake up early and start vocalizing right away. They always travel spastically, as if they are always hungry. They descend to the ground to drink water. They are usually found low in the forest, but they climb very high up to eat fruits or to flee from humans or predators. They sleep mostly in the fronds of palm trees such as budëd palms [*Attalea butyracea*]. They even sleep on the thorny fronds of pinchuk palms [*Astrocaryum* spp.]. They all sleep together, not spread out. They bed down making a lot of noise at dusk, when it is almost dark. Sometimes they are awake during moonlit nights.

Squirrel monkeys eat dicot tree fruits, especially legume pods such as mannan tsipuis [*Inga* spp. and ?*Pithecellobium* (Leguminosae)] and achu inkuente [*Inga* spp. (Leguminosae)]. Other dicot fruits they eat include: wesnid dëbiate [*Anacardium giganteum* (Anacardiaceae)], këku [*Couma macrocarpa* (Apocynaceae)], mamuin [*Rheedia longifolia* (Guttiferae)], okodo mabis [undetermined sp. (Guttiferae)], moste [*Hymenaea* spp. (Leguminosae)], chichombid [*Mouriri* spp. (Melastomataceae)], şhannëd [?*Brosimum* (Moraceae)], bin [*Castilla* (Moraceae)], dadain [*Clarisia racemosa* (Moraceae)], piuşh bëchi [*Helicostylis tomentosa, H. elegans* (Moraceae)], kuşhu tëbin [*Naucleopsis mello-barretoi, N. ternstroemiiflora* (Moraceae)], bata [*Pseudolmedia* and *Maquira* spp. (Moraceae)], poşhodi [*Passiflora nitida* (Passifloraceae)], mabis mabiskid [*Chrysophyllum prieurii* (Sapotaceae)], and kose [*Manilkara bidentata* (Sapotaceae)]. They eat swamp-palm [*Mauritia flexuosa*] fruits in the dry season. They also eat a lot of spiders, crickets [or katydids; the Matses term is taxonomically ambiguous], and other insects.

Family Pitheciidae Mivart, 1865

The family Pitheciidae comprises four genera, of which three, each represented by a single species, occur in the Yavarí-Ucayali interfluve: *Cacajao* Lesson, 1840; *Callicebus* Thomas, 1903; and *Pithecia* Desmarest, 1804.

Cacajao calvus (I. Geoffroy, 1847)

Voucher material (total = 25): Nuevo San Juan (AMNH 272795; MUSM 11114, 11115, 13300), Orosa (AMNH 73716–73720), Quebrada Esperanza (FMNH 88810–88825).

Unvouchered observations: Jenaro Herrera (Aquino, 1978), Quebrada Blanco (Bartecki and Heymann, 1987), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006). For additional records, see Heymann and Aquino (2010).

Identification: The genus *Cacajao* was reviewed by Hershkovitz (1987b), who identified the specimens from Orosa and Quebrada Esperanza as *C. calvus ucayalii* Thomas, 1928. Our new material from Nuevo San Juan is morphologically indistinguishable from the Orosa and Quebrada Esperanza series. However, in none of the material that we examined (including specimens identified as *C. c. ucayalii* by Hershkovitz) is the dorsal surface of the tail blackish as he described it (op. cit.: 34); instead, the dorsal surface of the tail is densely covered with long reddish fur like that on the middle and lower back. External and craniodental measurement data from specimens collected in the Yavarí-Ucayali interfluve are summarized in table 13. Most specimens are unaccompanied by weights, but three adult females (AMNH 272794; MUSM 11114, 13300) from Nuevo San Juan weighed 2.9, 3.0, and 3.6 kg.

Ethnobiology: The Matses call the red uakari monkey senta, a term that is not etymologically analyzable. Some also call it bëşhuidkid piu, but most Matses do not consider this a true synonym. Unlike most other large monkeys, no subtypes of uakari monkey are recognized by any of the Matses.

There are no taboos against eating uakari monkeys (other than the general rule that a hunter should not eat or touch monkey intestines, or eat any of their first kill of a particular species). However, Matses who come from places where there are no uakari monkeys (e.g., along the Chobayacu), do not eat them saying "My father did not eat those," as their justification. Many Matses that live outside the range of uakari monkeys are not familiar with them, and it is likely that, as the Matses moved around in the past, they did not continuously live in areas inhabited by uakaris. This may explain the lack of linguistic attention and

TABLE 13

External and Craniodental Measurements (mm) of *Cacajao calvus* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
HBL	457 (426–465) 7	427 ± 14 (405–447) 11
LT	160 (145–180) 7	148 ± 8 (136–158) 11
HF	149 (144–152) 7	142 ± 5 (133–147) 11
Ear	30 (29–31) 7	30 ± 2 (28–33) 11
CIL	84.1 ± 2.1 (80.9–87.5) 10	78.3 ± 2.3 (74.4–82.0) 13
OB	52.5 (49.4–56.3) 8	48.3 ± 1.7 (46.0–51.0) 12
POC	43.3 (41.9–45.1) 8	41.6 ± 1.5 (39.6–44.2) 12
ZB	68.8 (64.1–71.9) 7	61.6 ± 2.4 (58.3–65.0) 12
BB	53.7 (51.7–55.4) 8	52.9 ± 2.0 (50.0–56.0) 12
PPL	40.3 ± 1.2 (38.4–42.5) 10	36.2 ± 1.9 (33.2–39.6) 13
LMT	28.5 ± 0.8 (27.5–29.8) 10	27.1 ± 0.5 (26.5–28.0) 13
BM1	5.0 ± 0.1 (4.9–5.2) 10	5.0 ± 0.2 (4.7–5.5) 13
M1–M1	27.7 (27.2–28.6) 8	26.3 ± 0.6 (25.5–27.7) 12
I2–I2	13.6 (12.8–14.4) 5	13.5 ± 0.4 (12.9–14.6) 12

[a] Summary statistics (mean plus or minus one standard deviation [for $N \geq 10$], observed range in parentheses, and sample size) for measurements of AMNH 73716–73718; FMNH 88813–88818, 88821.

[b] Summary statistics (mean plus or minus one standard deviation, observed range in parentheses, and sample size) for measurements of AMNH 73719, 73720, 272795; MUSM 13300; FMNH 88810–88812, 88819, 88820, 88822–88825.

the absence of uakari monkeys in Matses myths. The canines of large male uakari monkeys are used to make men's tooth necklaces.

The Matses do not imitate uakari monkey calls. Encountering uakari monkeys is relatively rare, so the Matses make no special effort to find them. Upon hearing their calls or rustling of branches, a Matses hunter will approach the troop and start shooting when he sees a large animal. When animals from a hunted troop see humans, they slowly move toward the upper canopy and/or move slowly away. When they hear a firearm report, they move away faster, but even then they do not seem to be too scared. Unlike spider monkeys, uakaris do not split up when they run away from hunters, but run in the same direction. Therefore, a good, solitary Matses hunter can easily kill several animals at a single encounter with a troop. They are packed for carrying and cooked in the same way as woolly and spider monkeys.

MATSES NATURAL HISTORY: Uakari monkeys are strikingly red, as if they had painted themselves with annatto dye. They have red body fur and bald, bright red heads and faces. Even the young are red. Their faces are swollen, as if they had been shot in the eye with an arrow. Their tails are markedly short, in contrast to all other monkeys. They can't grasp with their tails; instead, they eat fruits while hanging by their feet. In appearance they are most similar to saki monkeys, particularly with respect to their long pelage and bald foreheads. With respect to other characteristics, they are like woolly monkeys: their calls are similar to woolly monkeys', large males are strong like large male woolly monkeys, and their canines are like woolly monkeys' [and therefore desirable for making necklaces]. They have a strong smell, both in their fur and their meat, but they cannot be detected by hunters by smelling because they do not leave their odor.

Uakari monkeys do not occur in all of Matses territory. They are *not* found east of the Gálvez, on the Brazilian side of the lower Yavarí, or along the upper reaches of the Chobayacu [a left-bank tributary of the Yaquerana]. Uakari monkeys are found in primary upland and floodplain forest. They are frequently found in swamp-palm [*Mauritia flexuosa*] swamps and in flooded forest. After feeding for a while in floodplain forest, a uakari monkey troop may travel very far into upland forest. Sometimes one goes for many months without seeing any uakari monkeys, and then they appear again. They use mostly the middle canopy layer, lower than spider and howler monkeys, but they may climb higher when they see people, or when they find fruit there. They seldom descend to the ground. They call out saying "*kakaka kakaka kakaka*."

Uakari monkeys are found in huge troops [>100 individuals, according to some Matses who can count], with many females carrying young on their backs. They travel as a group, making much noise rustling the branches. In flooded forest they drop dead branches into the water. They like to stay together. They may split up to find fruit, and rejoin to eat together when a large amount of fruit is found. They sleep near each other in the branches of dicot trees. When they are not hunted, they ignore humans, or come down closer to the ground to look at them. Even troops that are hunted are not very scared of humans.

Uakari monkeys eat mostly dicot fruits. They eat many different kinds of sweet dicot fruits. These include wesnid dëbiate [*Anacardium giganteum* (Anacardiaceae)], këku [*Couma macrocarpa* (Apocynaceae)], diden këku [*Parahancornia peruviana* (Apocynaceae)], machishte [*Rhigospira quadrangularis* and ?*Mucoa duckei* (Apocynaceae)], ichibin [*Matisia* sp. and *Eriotheca* sp. (Bombacaceae)], mamuin [*Rheedia longifolia* (Guttiferae)], okodo mabis [undetermined sp. (Guttiferae)], moste [*Hymenaea* spp. (Leguminosae)], tankada [*Parkia igneiflora, P. multijuga,* and *Pithecellobium auriculatum* (Leguminosae)], şhannëd [?*Brosimum* (Moraceae)], bin [*Castilla* (Moraceae)], dadain [*Clarisia racemosa* (Moraceae)], piuşh bëchi [*Helicostylis tomentosa* and *H. elegans* (Moraceae)], kuşhu tëbin [*Naucleopsis mello-barretoi* and *N. ternstroemiiflora* (Moraceae)], şhankuin [*Pourouma* spp. (Moraceae)], bata [*Pseudolmedia* and *Maquira* spp. (Moraceae)], poşhodi [*Passiflora nitida* (Passifloraceae)], mabis mabiskid [*Chrysophyllum prieurii* (Sapotaceae)], kose [*Manilkara bidentata* (Sapotaceae)], and taëpa [undetermined]. They bite the fruits, and if they are unripe they throw them away. They come to the edges of rivers to eat legume pods: mannan tsipuis [*Inga* spp. and ?*Pithecellobium* (Leguminosae)] and achu inkuente [*Inga* spp. (Leguminosae)]. They also eat fruits of a few types of palms, most remarkably, the endosperm of unripe swamp-palm [*Mauritia flexuosa*] fruits. They also eat the mesocarp of swamp-palm and isan [*Oenocarpus bataua*] fruits. They also eat some insects and a few leaf buds. Their diet is similar to that of woolly monkeys.

Callicebus cupreus (Spix, 1823)

Voucher material (total = 16): Nuevo San Juan (AMNH 268239; MUSM 11116, 11117), Orosa (AMNH 73703–73708), Quebrada Esperanza (FMNH 88858–88860), San Fernando (FMNH 88856, 88857), Santa Cecilia (FMNH 86989, 86990).

Unvouchered observations: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Itia Tëbu (Amanzo, 2006), Jenaro Herrera (Aquino, 1978), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Orosa (Freese et al., 1982), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006). (Note that some reports of *Callicebus* from the Yavarí-Ucayali interfluve have identified the local species as *C. caligatus* or *C. moloch*; see below.)

Identification: The Amazonian forms of *Callicebus* (titi monkeys) were revised by Hershkovitz (1963), who recognized only two valid species, *C. moloch* and *C. torquatus*. However, Hershkovitz (1990) and Groves (2001) subsequently recognized 12 Amazonian species, and Roosmalen et al. (2002) recognized 22 Amazonian species that they assigned to four species groups.[13] Although most taxonomic diagnoses in this literature are based on coat-color differences, there is some evidence that the species groups recognized by Roosmalen et al. (2002) are morphometrically differentiated and have distinctive karyotypes (Kobayashi, 1995). Unfortunately, the karyotypes of many alleged species are unknown, and molecular evidence

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[13] Excluded from these tallies of Amazonian species are members of Roosmalen et al.'s (2002) Personatus Group (comprising several species from SE Brazil) and *Callicebus pallescens* (a member of the Donacophilus Group that lives in the Chaco and Pantanal). Additional Amazonian species have recently been described from western Bolivia (Wallace et al., 2006) and eastern Colombia (Defler et al., 2010).

supporting the recognition of distinct taxa within species groups is almost nonexistent.

Hershkovitz (1963) referred all of the *Callicebus* specimens he examined from the Yavarí-Ucayali interfluve to the subspecies *C. moloch cupreus*, but he later (Hershkovitz, 1990) identified some specimens of titi monkeys from the Yavarí-Ucayali interfluve as *C. cupreus* and others from the same region as *C. caligatus.* A small series of AMNH specimens from Orosa was listed among the material examined for both species in the latter publication, and an accompanying map (Hershkovitz, 1990: fig. 36) showed *C. cupreus* and *C. caligatus* as occurring sympatrically at Orosa. Later, Hershkovitz (personal commun., 1995) explained that this was an error caused by listing original and revised identifications of the same specimens in separate species accounts.

In fact, titi specimens from the Yavarí-Ucayali interfluve could be referred either to *Callicebus cupreus* or to *C. caligatus* as those species were diagnosed by Hershkovitz (1990). For example, the forehead is grayish or reddish agouti with only a narrow blackish brow-line (as described for *cupreus*) in most of our specimens (e.g., AMNH 73708, 268239), but in several others (e.g., AMNH 73705, 73706) the entire forehead and lower crown is blackish (as described for *caligatus*). Similarly, some of our specimens (e.g., AMNH 268239) have clear reddish hands, feet, and lower limbs (as in *cupreus*), whereas others (e.g., AMNH 73703, 73706) have dark reddish-brown or even blackish extremities (as in *caligatus*).

According to Roosmalen et al. (2002), only *Callicebus cupreus* inhabits the Yavarí-Ucayali interfluve, but some of our specimens more closely resemble their diagnosis of *C. caligatus*, particularly with respect to the presence of a blackish forehead and lower crown as described above. Additionally, the basal part of the tail is blackish in some of our specimens (e.g., AMNH 73703) and others (e.g., AMNH 268239) have extensively pale-tipped tails, both traits associated with *C. caligatus* rather than *C. cupreus* in their diagnoses. In effect, our material combines traits of both species as recognized by these authors, who do not list any material examined, and whose illustrations do not correspond closely with their text.[14]

We are not convinced that *Callicebus caligatus* or any of the other nominal taxa belonging to the Cupreus Group of Kobayashi (1995) and Roosmalen et al. (2002)—including *C. caquetensis*, *C. discolor*, *C. dubius*, *C. ornatus*, *C. stephennashi*, and probably *C. aureipalati*—are valid species distinct from *C. cupreus*. Although these forms collectively range across most of western Amazonia, they resemble one another in pelage markings (see Roosmalen et al., 2002: fig. 49; Defler et al., 2010: fig. 5; Wallace et al., 2006: figs. 4, 5), and at least some allegedly diagnostic differences seem to break down when large series of specimens (as opposed to just a few exemplars) are examined. Additionally, nonpelage differences among these taxa appear to be wanting: all analyzed forms are morphometrically similar (Kobayashi, 1995), have the same diploid number of chromosomes ($2n = 46$; Roosmalen et al., 2002; Defler et al., 2010), and seem to occupy the same ecological niche (inhabiting forest edges and disturbed vegetation; Roosmalen et al., 2002). Because no verifiable examples of sympatry are known among nominal species in this group, it is plausible that these taxa represent nothing more than geographic coat-color variants of the same biological species, a hypothesis that merits future evaluation with molecular sequence data and with targeted collecting in areas where different coat-color phenotypes might be expected to come in contact.

External and craniodental measurements of *Callicebus cupreus* specimens that we examined from the Yavarí-Ucayali interfluve are summarized in table 14. Most specimens are unaccompanied by weight data, but an adult male (MUSM 11116) from Nuevo San Juan weighed 1020 g, and an adult female (AMNH 268239) from the same locality weighed 1042 g.

ETHNOBIOLOGY: The Matses call the titi monkey wadë, which is not linguistically

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[14] For example, whereas the base of the tail, cheiridia, wrists, ankles, and tail base of *Callicebus caligatus* were described as "black" (Roosmalen et al., 2002: 12), the accompanying illustrations (op. cit.: 11, 49) show a monkey with reddish cheiridia, wrists, and ankles, and with a pale-brown tail base.

TABLE 14
Measurements (mm) of *Callicebus cupreus* from the Yavarí-Ucayali Interfluve

	Males[a]	AMNH 73708♀	AMNH 268239♀	FMNH 88860♀
HBL	337 (327–346) 5	—	—	315
LT	431 (390–456) 5	—	—	460
HF	92 (90–95) 5	—	93	90
Ear	29 (25–31) 5	—	32	30
CIL	53.4 (49.6–55.8) 9	53.2	52.8	—
OB	35.9 (34.4–37.3) 9	34.5	36.7	37.2
POC	30.1 (27.9–31.9) 9	30.5	31.9	31.9
ZB	40.1 (38.7–42.6) 8	39.1	41.0	41.0
BB	35.4 (33.7–36.7) 9	34.9	35.5	35.1
PPL	26.0 (24.4–28.1) 8	—	26.0	27.0
LMT	18.8 (18.2–19.9) 9	19.2	19.1	19.0
BM1	4.7 (4.4–5.2) 9	4.6	4.3	4.8
M1–M1	20.8 (19.6–22.3) 8	20.9	20.1	21.4
I2–I2	9.9 (9.4–10.2) 7	10.2	10.2	—

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 73703–73706; FMNH 86989, 86990, 88856, 88858, 88859.

analyzable. It has three other supposedly ancient synonyms, tsokon, sëdë, and masoko. The first synonym is onomatopoetic and unique to Matses. The other two are of uncertain etymology: both occur in neighboring Mayoruna languages, and therefore could easily be either borrowings or truly archaic words. Some Matses assert that masoko is not archaic, but a borrowing; there is no controversy about the other two names. Two subtypes are recognized, wadë piu "red titi monkey" and wadë çhëşhë "black (dark-colored) titi monkey." The first is the commonly seen variety, which is found close to rivers. The second variety is reported to live in upland forest far from rivers, where the red variety is absent. Not all Matses hunters are familiar with the darker variety or accept that two varies exist. Those that claim to have seen the darker variety do not know much about it. (Despite a considerable effort to find it, the darker variety was not collected during our mammal inventory at Nuevo San Juan; it probably represents another case of overdifferentiation of a single biological species.)

Matses eat titi monkeys, but because they are small, hunters usually do not make a special effort to find them. Traditionally, as larger game became scarce in a locality, more titi monkeys would be killed. Nowadays, most hunters will not expend a shotgun shell to kill one despite the shortage of game around the larger and more permanent villages. One way to kill titi monkeys is to simply shoot them from the ground. Another way is to climb up at tree where the titi monkeys are hiding. When the titi monkeys see the hunter up in the tree, they will usually drop and flee running on the ground, where waiting hunting dogs and/or a second hunter will chase them down and kill them. Matses do not imitate their call to hunt them.

As with all monkeys, titi monkey are dressed for the pot by singing off the fur and then gutting them. Unlike large monkeys, titi monkeys (and other small monkeys) may be roasted instead of boiled. Pregnant women or men with pregnant wives cannot eat titi monkeys, lest their children grow up to have bad teeth [titi monkeys have black teeth]. Young people will not eat the liver of a titi monkey, lest it make their teeth rot.

Matses natural history: Titi monkeys have red underparts, a black brow, black teeth, and a whitish tail. They are small, the size of a squirrel monkey.

Titi monkeys can be found in any forest type, but they strongly prefer habitats that have open canopies [i.e., where light shines through to the understory], such as abandoned swiddens, riverside forest, and secondary forest at blowdowns. When there are abundant ripe legume pods growing along rivers [November–January], titi monkeys are especially common there. They are not found very high up in the trees. They descend to the ground occasionally to drink water, eat insects or fruits, or to cross a swidden.

They live in small troops that number only up to about five or six animals. Sometimes one is found alone. The male always carries the babies. They carry the baby on their back or their belly, and give it to the female to suckle. They call out saying "*tsokon, tsokon, tsokon, on, on, on*" shortly before dawn [around 5 a.m.], later than howler monkeys, and then again later in the morning [around 8 a.m.], and sometimes at midday. The male sings first, and then the rest join in. They sing very loudly, and Matses always hear them from their homes.

Titi monkeys sleep hugging each other on a tree branch among thick vegetation, in vine tangles. Right from where they sleep they sing in the morning. They spread out to eat, but not too far from each other. After eating, they rest at midday. They do not travel far. They are curious, and animals that have not been hunted will stare from the forest edge at people passing by in boats.

Titi monkeys are the only monkeys that eat the ripe mesocarp of cabbage palm [*Euterpe precatoria*] fruits, and that is why they have black teeth [capuchins bite unripe cabbage palm fruits to eat the soft endosperm, but don't eat the ripe mesocarp]. They eat all types of dicot fruits, especially mannan tsipuis [*Inga* spp. and ?*Pithecellobium* (Leguminosae)] and achu inkuente [*Inga* spp. (Leguminosae)]. Other dicot fruits they eat include: wesnid dëbiate [*Anacardium giganteum.* (Anacardiaceae)], këku [*Couma macrocarpa* (Apocynaceae)], diden këku [*Parahancornia peruviana* (Apocynaceae)], machishte [*Rhigospira quadrangularis* and ?*Mucoa duckei* (Apocynaceae)], okodo mabis [undetermined sp. (Guttiferae)], mamuin [*Rheedia longifolia* (Guttiferae)], chichombid [*Mouriri* spp. (Melastomataceae)], şhannëd [?*Brosimum* (Moraceae)], piuşh bëchi [*Helicostylis tomentosa* and *H. elegans* (Moraceae)], bata [*Pseudolmedia* and ?*Maquira* spp. (Moraceae)], mabis mabiskid [*Chrysophyllum prieurii* (Sapotaceae)], kose [*Manilkara bidentata* (Sapotaceae)], and taëpa [undetermined].

Pithecia monachus E. Geoffroy, 1812

VOUCHER MATERIAL (TOTAL = 34): Nuevo San Juan (AMNH 26841–26844; MUSM 11126–11133, 11136, 11138, 11140–11151, 11153, 11154), Orosa (AMNH 73714, 74036, 74037), Quebrada Esperanza (FMNH 88862), San Fernando (FMNH 88861), Santa Cecilia (FMNH 87002).

UNVOUCHERED OBSERVATIONS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Itia Tëbu (Amanzo, 2006), Jenaro Herrera (Aquino, 1978), Reserva Comunal Tamshiyacu-Tahuayo (Puertas and Bodmer, 1993; Heymann and Aquino, 1994), Río Orosa (Freese et al., 1982), Río Tapiche (Bennett et al., 2001), Río Yavarí (left bank below Angamos; Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: Saki monkeys from the Yavarí-Ucayali interfluve were referred to *Pithecia hirsuta* by Hershkovitz (1979), but subsequent study of type material led Hershkovitz (1987c) to identify the same specimens as *P. monachus*. Although all of our material is referable to *P. monachus* as that taxon was briefly distinguished in Hershkovitz's (1987c) key, the taxonomic significance of phenotypic variation among western Amazonian populations of sakis remains to be convincingly established. Because our series from Nuevo San Juan ($N = 26$ adult specimens) is the largest sample available to document morphological variation within a local population of any *Pithecia* species, we provide a detailed description below.

The 11 adult male skins from the Río Gálvez exhibit limited variation in pelage characters. The dorsal body pelage and the pelage of the outer surfaces of the arms and legs is predominantly blackish, but the individual hairs have pale tips that produce a frosted mass effect; specimens with long, whitish hair tips (e.g., MUSM 11126) appear more heavily frosted than individuals with shorter, yellowish, or brownish terminal bands (MUSM 11142). The distinctive ruff or mane surrounding the head does not contrast in coloration with the rest of the body fur. The hands are distinctly paler than the arms, appearing whitish in most individuals, but the bases of the individual hairs on the hands are always dark. Most specimens also have whitish feet, but a few (e.g., MUSM 11128, 11129, 11145) have grizzled pedal fur that is not conspicuously paler than the fur of the thigh and shank.

Whereas the body pelage is long and lax, especially over the shoulders and nape (60–100 mm), the coronal pelage (from between the ears to the brow line) is abruptly shorter (<10 mm) and stiffer, forming a dense mat; the cheeks are densely and more or less uniformly covered by hairs that are similar in length and texture to those of the coronal pelage. This pelage of the crown and cheeks is also abruptly paler than the body fur, ranging in mass effect from whitish to yellowish or brownish gray; the individual facial hairs always have dark bases and/or

TABLE 15

External and Craniodental Measurements (mm) and Weights (g) of *Pithecia monachus* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
HBL	413 ± 21 (361–436) 14	390 ± 18 (362–419) 12
LT	476 ± 34 (429–521) 14	481 ± 30 (423–540) 12
HF	127 ± 6 (116–136) 14	124 ± 6 (110–132) 12
Ear	38 ± 2 (34–41) 14	37 ± 2 (32–39) 12
CIL	73.3 ± 2.2 (70.0–77.7) 13	68.4 ± 2.7 (62.3–71.7) 12
OB	44.3 ± 1.7 (41.7–47.2) 14	40.8 ± 1.4 (39.1–43.6) 12
POC	35.1 ± 1.7 (31.1–37.9) 14	35.2 ± 1.5 (32.4–37.7) 12
ZB	55.9 ± 2.2 (51.2–59.5) 14	50.7 ± 2.2 (47.2–53.7) 12
BB	43.5 ± 1.3 (41.3–45.6) 14	42.9 ± 1.6 (39.2–45.4) 12
PPL	35.1 ± 1.9 (31.8–39.2) 13	32.4 ± 1.9 (29.4–35.4) 11
LMT	24.9 ± 0.8 (23.7–26.0) 14	23.8 ± 0.8 (22.9–25.8) 12
BM1	4.8 ± 0.2 (4.5–5.2) 14	4.7 ± 0.2 (4.3–5.0) 12
M1–M1	24.1 ± 1.0 (22.2–25.5) 14	23.1 ± 1.0 (21.1–24.4) 12
I2–I2	12.5 ± 0.7 (11.7–13.7) 12	11.9 ± 0.6 (11.0–12.8) 11
Weight	2849 ± 306 (2150–3350) 14	2095 ± 335 (1640–2800) 12

[a] Summary statistics (mean plus or minus one standard deviation, observed range in parentheses, and sample size) for measurements and weights of AMNH 268241, 268244; MUSM 11126, 11128–11133, 11138, 11142, 11145, 11147, 11149,

[b] Summary statistics (mean plus or minus one standard deviation, observed range in parentheses, and sample size) for measurements and weights of AMNH 268243; MUSM 11127, 11136, 11140, 11141, 11146, 11148, 11150, 11151, 11153, 11154.

dark tips, however, so even the palest faces appear finely grizzled on close inspection. The muzzle is more sparsely haired than the cheeks and crown, and the exposed skin is blackish; a small patch of blackish skin is also exposed on the center of the forehead just above the brow line in most specimens. The throat is naked and glandular, but the chest has a prominent patch of long, pale-tipped fur; the abdominal pelage is sparse and uniformly black.

The female pelage is similar to the male condition, with a few exceptions. The most obvious difference is that the transition from the long, lax nuchal fur to the shorter fur of the head is not abrupt as it is in males; instead, the cranial hairs gradually decrease in length and increase in stiffness from occiput to forehead. The coronal pelage of females is also much more chromatically variable than that of males, with some females having conspicuously pale (whitish or beige) crowns and foreheads whereas others have much darker (brownish) cranial fur; the individuals with the palest (MUSM 11141) and the darkest (MUSM 11136) cranial fur in our series are both young adults as judged by tooth wear. Although the throat of females is mostly bare, the exposed gular skin is less obviously glandular than it is in males. The pectoral tuft of long, pale-tipped fur is also less well developed in females than it is in males.

Head-and-body length and several osteological measurements show strong sexual dimorphism in our sample (table 15). In general, the craniodental pattern is typical of that seen in most primates (Schultz, 1962) with dimorphism in the facial skull (rostrum, orbits, zygoma) and the canine teeth versus monomorphism in the braincase and postcanine dentition. Three qualitative cranial traits exhibit marked variation in our sample, which we analyzed for association with age ("young" adults versus "old" adults, as determined by toothwear and basicranial suture closure) and sex using Fisher's exact test. (1) The sagittal crest (coded as present or absent) is highly significantly associated with sex and with age ($p \ll 0.01$ for both tests), being present only in males and more frequently in old adults than in young adults. (2) The mesopterygoid fossa is quite variable in its anterior extent, terminating behind the toothrows in some individuals (e.g., AMNH 268244, MUSM 11145) and penetrating deeply between the molars in others (MUSM 11127, 11128), apparently independently of age and sex. (3) The pterygoid fossae are shallow and unenclosed by bone in most individuals but more deeply excavated in others (MUSM 11133, 11142, 11145), variation that also appears to be unassociated with age or sex.

In qualitative cranial characters, the Río Gálvez sakis all agree with Hershkovitz's (1987c: table IV) diagnosis of the *Pithecia monachus* group, an assemblage that includes *P. aequatorialis*, *P. albicans*, *P. irrorata*, and *P. monachus*. According to Hershkovitz, taxa within this group are distinguishable only by pelage traits. In the comparative material we examined, the distinguishing external characters of all the saki species recognized by Hershkovitz are readily apparent, at least in adult males; by his classification, our vouchers are unambiguously referable to *P. monachus*. By contrast, *P. irrorata* (which occurs south of the Amazon between the Juruá and the Tapajós; Hershkovitz, 1987c) has an almost-naked head, the exposed blackish skin of which is conspicuously set off by an encircling white-fringed ruff. Another geographically adjacent form, *P. aequatorialis* (which occurs north of the Amazon between the Tigre and the Napo; Bravo and Ríos, 2007; Aquino et al., 2009) has long reddish or red-based fur on the cheeks (resembling the mutton-chop whiskers of 19th-century gentlemen) and a conspicuously reddish chest. Pending a comprehensive analysis of character variation in the *monachus* group, these and other character differences seem sufficient to maintain the nominal taxa recognized by Hershkovitz as distinct, but whether or not these should be recognized as full species remains to be convincingly demonstrated.[15] In the event that a trinomial classification is judged to better represent the situation, our material from Nuevo San Juan would be referable to the nominotypical form *P. monachus monachus*.

ETHNOBIOLOGY: Saki monkeys are called bëşhuidkid, a term that is perhaps etymologically analyzable as meaning "white-faced one." Two subtypes are recognized by the Matses: mamu (with no meaning in Matses, but in closely related languages it means "pitch," a black adhesive made of beeswax and tree latex) and bëshudu (not analyzable, except possibly the prefix bë- "face/forehead"). The mamu variety is said to be larger, have a whiter face, whiter hands, and a bushier coat, while the bëshudu variety is said to be smaller, to have a black or darker face, less white on its hands and a thinner coat. Troops of mamu are said to be found more frequently in upland habitats far from large rivers, and bëshudu more frequently along rivers. A minority of Matses hunters do not recognize two varieties and consider mamu and bëshudu to be synonyms of bëşhuidkid. Fleck et al. (1999) discussed this ethnobiological issue in detail and summarized morphological and genetic evidence that the Matses overdifferentiate saki monkeys.

All Matses eat sakis. As with other monkeys, sakis are cooked by first singing the hair off and then boiling them; likewise, men cannot eat or touch the intestines. Children usually eat the head. The Matses believe that if they give a dog a saki monkey bone, the dog will die; therefore, they are always mindful of this when disposing of the bones.

The Matses hunt saki monkeys by listening for their grunts and calls or the noise they make rustling branches as they move through the trees, or by looking for their dropped half-eaten fruits. When a hunter with dogs encounters saki monkeys and the monkeys do not see him, he imitates their raptor-warning call, upon which all the monkeys drop to the ground. The hunter then looses his dogs, which chase the monkeys down as they run away. Hunters also run after monkeys on the ground and club them or slam them against a tree when they catch them. (Saki monkeys will bite and sometimes even kill dogs that are trying to catch them. They will also bite people, if they are not

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[15] A preliminary morphometric study (Marroig and Cheverud, 2004) suggested that at least some species of western Amazonian sakis are osteologically differentiated, but sample sizes were small (e.g., $N = 1$ for *Pithecia aequatorialis*). No taxonomic study of DNA sequence variation in the genus has been published to date. Bravo and Ríos (2007) reported what appeared to be mixed-species groups of sakis (including both *P. aequatorialis* and *P. monachus*) at three inventory sites and emphasized the need for new morphological and genetic research to assess the taxonomic status of these forms.

careful when grabbing them.) If saki monkeys are familiar with this trick, they will not drop to the ground when a hunter imitates their raptor-warning call.

Now that most Matses are using shotguns, hunters without dogs will often ignore saki monkeys early in the hunt because the amount of meat they have is hardly worth a shell. Likewise, if hunters have dogs but the saki monkeys will not drop to the ground, hunters will probably not shoot at them early in the hunt. If hunters encounter sakis on the way back from an unsuccessful hunt, however, they will often shoot.

Sakis in trees are shot from the ground with arrows or shotguns. When they see people, sakis will not drop to the ground but run away very fast over the tops of branches and jumping from tree to tree. Hunters may chase one down until it gets tired and then shoot it (the Matses do not usually shoot at moving targets). Sometimes a hunter will climb a tree to kill a tired-out saki monkey that he cannot shoot from the ground, but the monkey may evade the hunter by dropping to the ground and running off.

Matses natural history: Saki monkeys have a lot of hair. Their bodies are actually small, but they look big because of all the hair. Their coats look like their hair has started to go gray, like an old person's hair. Their faces and hands are white. The tail is furry and looks big, but it does not have much meat on it and cannot be used to grab onto things. Their head hair is also long, but not on the forehead. They are strong and run very fast through the trees without falling down. They run fast on the ground as well. They run fast even with their young on their backs. Saki monkeys can drop to the ground without hurting themselves.

Saki monkeys are found in all types of habitats, in upland forest and floodplain forest, in primary forest and in blowdowns. They travel high or low in the trees.

They are found in small troops, fewer than 10 animals, or sometimes alone. The troop usually stays together to travel, feed, and sleep, though occasionally they split up to search for food. Saki monkeys wake up just before dawn. When they wake up in the morning they go "*she she she aa aa aa.*" When they see a jaguar, they say "*waa waa waa.*" Sometimes they feed in the same tree with woolly or uakari monkeys. The whole troop sleeps in the same tree, wherever they are when night falls [i.e., they have no permanent sleeping sites].

Saki monkeys eat mostly dicot fruits, including wesnid dëbiate [*Anacardium giganteum* (Anacardiaceae)], këku [*Couma macrocarpa* (Apocynaceae)], diden këku [*Parahancornia peruviana* (Apocynaceae)], machishte [*Rhigospira quadrangularis* and ?*Mucoa duckei* (Apocynaceae)], mamuin [*Rheedia longifolia* (Guttiferae)], okodo mabis [undetermined sp. (Guttiferae)], moste [*Hymenaea* spp. (Leguminosae)], mannan tsipuis [*Inga* spp. and ?*Pithecellobium* (Leguminosae)], tankada [*Parkia igneiflora, P. multijuga,* and *Pithecellobium auriculatum* (Leguminosae)], şhupuduşh [*Brosimum parinarioides* (Moraceae)], şhupud [*Brosimum* and *Poulsenia* (Moraceae)], şhannëd [?*Brosimum* (Moraceae)], bin [*Castilla* (Moraceae)], dadain [*Clarisia racemosa* (Moraceae)], piuşh bëchi [*Helicostylis tomentosa* and *H. elegans* (Moraceae)], kuşhu tëbin [*Naucleopsis mello-barretoi* and *N. ternstroemiiflora* (Moraceae)], şhankuin [*Pourouma* spp. (Moraceae)], bata [*Pseudolmedia* and *Maquira* spp. (Moraceae)], poşhodi [*Passiflora nitida* (Passifloraceae)], mabis mabiskid [*Chrysophyllum prieurii* (Sapotaceae)], and kose [*Manilkara bidentata* (Sapotaceae)]. They eat some of the dicot fruits before they are ripe. They throw down a lot of fruits as they eat. They eat palm fruits, especially swamp-palm [*Mauritia flexuosa*] fruit and some isan [*Oenocarpus bataua*] fruit. They also eat some leaves and insects.

DISCUSSION

Primates comprise less than 10% of the mammalian species known to inhabit the Yavarí-Ucayali interfluve, so it is premature to draw any general conclusions about the local fauna, or about the Matses' knowledge of its natural history, from such a small sample. Additionally, most primates are relatively large, eurytopic, highly mobile, visually oriented, social, diurnal, frugivorous, and arboreal. The extent to which this unique ensemble of ecobehavioral traits may have influenced primate biogeography, our ability (as taxonomists) to detect phenotypic differ-

TABLE 16

Diurnal Transect Effort at Selected Localities in the Yavarí-Ucayali Interfluve

Locality[a]	Focal taxon	km[b]	Reference
Divisor	Large mammals[c]	65	Jorge and Velazco (2006)
Quebrada Blanco (seven trail systems, bank not specified)	Primates	120	Puertas and Bodmer (1993)
Río Orosa (various sites along main river)	Primates	22	Freese et al. (1982)
Río Tahuayo (seven sites along right-bank tributaries)	Primates	177	Heymann and Aquino (1994)
Río Tapiche (two sites on right bank)	Primates	105	Bennett et al. (2001)
Río Yavarí (three sites on left bank below Angamos)	Large mammals[c]	507	Salovaara et al. (2003)
Río Yavarí-Mirím (four trail systems; bank not specified)	Primates	170	Puertas and Bodmer (1993)
Río Yavarí-Mirím (two study areas)	Large mammals[c]	1827	Salovaara et al. (2003)
Tapiche	Large mammals[c]	111	Jorge and Velazco (2006)

[a] See figure 2 and appendix 2.

[b] Total distance of walked transects as reported by authors, including repeats.

[c] Edentates, primates, ungulates, carnivores, and rodents > 1 kg.

ences among primate taxa, or the Matses' ability (as hunters) to learn primate habits is unknown, but it seems unlikely that valid inferences about the entire mammalian fauna can be based on information summarized above. Therefore, we restrict the following discussion to primatological topics and defer broader generalizations to subsequent reports.

Primate Diversity in the Yavarí-Ucayali Interfluve

Available information about primate diversity in the Yavarí-Ucayali interfluve is based on 225 examined specimens collected at eight different localities and published sight records from another 16 localities. Although we are unable to analyze these aggregate data (obtained over many years using different methods) to statistically assess inventory completeness, the 600+ hours that Fleck spent hunting with the Matses at Nuevo San Juan and impressive faunal-sampling effort at several other localities (table 16) suggest that few (if any) additional primate species remain to be discovered in the region. Nevertheless, unconfirmed reports of other taxa (e.g., *Saimiri boliviensis* and *Aotus nigriceps* in the Reserva Comunal Tamshiyaco-Tahuayo; Puertas and Bodmer, 1993) merit the attention of future researchers, who should collect specimens to voucher any new records.

The 14 primate species definitely known to occur in the Yavarí-Ucayali interfluve are sympatric at Nuevo San Juan and may eventually be found together elsewhere, but short-term inventories have found fewer species at most sites. One species (*Callimico goeldii*) is rare, and another (*Cacajao calvus*) is migratory and patchily distributed, so many local primate communities probably consist of only 12 ecologically interacting species, and some sites with unusual habitats may have even fewer. The white-sand forests of the upper Gálvez/Río Blanco, for example, seem likely to have relatively depauperate primate faunas; only eight species were recorded at the single surveyed site in this habitat (Amanzo, 2006).

The primate fauna that occurs between the Yavarí and the Ucayali resembles those of adjacent interfluvial regions in some respects but differs in others (table 17). All of these western Amazonian faunas share a core assemblage of six widespread species that include *Alouatta seniculus*, *Lagothrix lagothricha*, *Callithrix pygmaea*, *Cebus albifrons*, *Cebus apella*, and *Pithecia monachus*. A seventh widespread species, *Ateles belzebuth*, is (inexplicably) absent only in the Napo-Putumayo interfluve. Other shared taxa include *Aotus* and *Saimiri*, which are represented in each region by geographically replacing species. Each region also has at

TABLE 17
Primate Faunal Composition in Five Interfluvial Regions[a]

	Juruá-Yavarí[b]	Yavarí-Ucayali[c]	Ucayali-Marañón[d]	Marañón-Napo[e]	Napo-Putumayo[f]
Alouatta seniculus	X	X	X	X	X
Ateles belzebuth	X	X	X	X	
Lagothrix lagothricha	X	X	X	X	X
Aotus nancymaae		X	X	(X)	(X)
Aotus nigriceps	X				
Aotus vociferans				X	X
Callimico goeldii		(X)	(X)	(X)	
Callithrix pygmaea	X	X	X	X	X
Saguinus fuscicollis[g]	X	X	X	X	(X)
Saguinus nigricollis				(X)	X
Saguinus mystax	X	X	X		
Cebus albifrons	X	X	X	X	X
Cebus apella	X	X	X	X	X
Saimiri boliviensis		(X)[h]	X		
Saimiri sciureus	X	X		X	X
Cacajao calvus	(X)	X	(X)		
Callicebus cupreus	X	X			
Callicebus discolor			X	X	(X)
Callicebus lucifer				X	X
Callicebus regulus	X				
Pithecia aequatorialis				(X)	
Pithecia monachus	X	X	X	X	X
TOTAL SPECIES	14	15	14	16	13

[a] In the absence of any existing convention for naming Amazonian interfluvial regions, we do so counterclockwise from the southeast (see figure 1). Taxonomy in cited publications has been changed to conform with usage recommended in this report. Abbreviations: X = widely distributed in region; (X) = apparently rare or with restricted distribution in region.

[b] Peres (1988, 1993a).

[c] This report.

[d] Hershkovitz (1977, 1983, 1990), Soini (1986), Bowler et al. (2009).

[e] Hershkovitz (1977), Freese et al. (1982 [Nanay]), Aquino and Encarnación (1988), Heymann et al. (2002)

[f] Freese et al. (1982 [Ampiyacu]), Hershkovitz (1983), Brooks and Pando-Vasquez (1997), Montenegro and Escobedo (2004), AMNH collections from Apayacu.

[g] Sensu Hershkovitz (1977): including *tripartitus*.

[h] West of the Río Tapiche.

least one member of the *Saguinus nigricollis* group (sensu Hershkovitz, 1977; including *S. fuscicollis*) and one member of the *Callicebus cupreus* group (sensu Roosmalen et al., 2002; including *C. discolor*). By contrast, other primate taxa have more restricted distributions: *Saguinus mystax* (which belongs to a different species group than *S. fuscicollis* and *S. nigricollis*) and *Cacajao calvus* are only found south of the Marañón/Amazon, members of the *Callicebus torquatus* group (sensu Roosmalen et al., 2002: including *C. lucifer* and *C. regulus*) do not occur between the Yavarí and the Marañón, and *Pithecia aequatorialis* only occurs between the Marañón and the Napo. *Callimico goeldii* has a poorly documented distribution; in northeastern Peru it is only known to occur in the Yavarí-Ucayali, Ucayali-Marañón, and Marañón-Napo interfluves.

As a consequence of these distributional phenomena, the primate fauna of the Yavarí-Ucayali interfluve is unique, conspicuously differing from faunas on the north bank of the Marañón/Amazon by having uakaris and two sympatric species of tamarins, and from adjacent south-bank faunas east of the Yavarí by lacking collared titis (species of the *Callithrix torquatus* complex). The primate fauna of the Yavarí-Ucayali interfluve is most similar to

TABLE 18
Matses Utilization of Local Monkey Species

	Food	Pets	Ornaments[a]
Aotus nancymaae	sometimes	no	no
Alouatta seniculus	sometimes[b]	sometimes	sometimes
Ateles belzebuth	yes	yes	yes
Lagothrix lagothricha	yes	yes	yes
Cebus albifrons	sometimes[b]	sometimes	no
Cebus apella	sometimes[b]	sometimes	yes
Saimiri sciureus	sometimes	yes	sometimes
Callimico goeldii	no	no	no
Callithrix pygmaeus	no	no	no
Saguinus fuscicollis	sometimes[c]	yes	no
Saguinus mystax	sometimes[c]	yes	no
Cacajao calvus	yes	no	yes
Callicebus cupreus	sometimes	no	no
Pithecia monachus	yes	no	no

[a] Tooth necklaces worn by men.

[b] Traditionally eaten only by old people.

[c] Too small for adult consumption; mostly killed and eaten by children.

adjacent south-bank faunas east of the Ucayali/Tapiche, which differ only by having replacing species of *Saimiri* and *Callicebus*.

Matses Interactions with Local Primate Species

Primates represent a substantial fraction of total mammalian biomass in undisturbed Neotropical rain forests (Janson and Emmons, 1990; Peres, 1999), so it is not surprising that they are routinely eaten by indigenous Amazonians (Vickers, 1984; Redford and Robinson, 1987; Milton, 1991; Jerozolimski and Peres, 2003; Cormier, 2007). However, like many other native Amazonians, the Matses are selective about the monkey species they consume, strongly preferring some and avoiding others (table 18). Additionally, some Matses dietary preferences reflect common trends in primate consumption by native Amazonians, who usually prize large species (especially those that get fat from eating fruit in the rainy season), but who often avoid eating *Alouatta* when other atelids are locally available (Cormier, 2007). Although it is tempting to seek utilitarian explanations for the Matses' traditional proscriptions about what species and organs may not be eaten, and by whom, cross-site comparisons of Amazonian dietary taboos suggest that these may be nothing more than superstitions or culinary prejudices subsidized by the local abundance of game (Jerozolimski and Peres, 2003). In other words, the Matses (like the Matsigenka; Shepard, 2002) can afford to be picky eaters because there is plenty of meat to go around.

Whereas hunting for food is obviously the primary motivation for Matses men—from whom all of our interviews were obtained—to learn as much as possible about the habits of preferred game species, some species are occasionally hunted to obtain ornaments or pets. Boyhood memories of stalking tamarins (the secondary growth surrounding Matses villages is routinely patrolled by gangs of juvenile archers) and nonpredatory encounters with primates throughout a lifetime spent in close proximity to the forest (titis call from the edges of clearings at dawn, howlers roar at the full moon every month, and other species are often seen foraging in riverside vegetation by canoe travelers) doubtless also contribute to the available fund of adult knowledge. Information gained at second hand may also be important. The habits of game animals are popular topics of male conversation in Matses society, and the sights and sounds of the day's hunt are often told over the evening meal. By such informal but culturally vital mechanisms, individual experiences are shared among the local community of hunters, with the result, perhaps, that even rarely observed behaviors of game species become widely known. Therefore, our interviewees surely drew from deep wells of individual and collective memory in telling us what they knew about monkeys.

Matses Knowledge of Primate Natural History

Matses knowledge about primates varies considerably in recorded details, and this variation is clearly correlated with cultural importance and physical size. The composite essay for *Ateles belzebuth*, a preferred game species and the largest monkey in Matses territory, for example, can be parsed into 86 observations about its ecology and/or behavior (see below), whereas the composite essay for *Callithrix pygmaea*, a tiny nongame species, contains only nine observations about these topics. The ecobehavioral information content of composite essays about other taxa reflects the same trend: many more observations were provided about the habits of such large and/or culturally salient monkeys as *Lagothrix lagothricha* and *Alouatta seniculus* than about small species of little cultural significance (e.g., *Aotus nancymaae*, *Saguinus* spp.). Clearly, the Matses are more strongly motivated to observe some species than others.

Nevertheless, the range of recorded information, even for some of the smaller monkeys, is impressive. The Matses routinely provided species-specific information about habitat and microhabitat use, group size and composition, other aspects of social behavior, vocalizations, and diet. The latter category is especially rich in recorded details, often including long lists of commonly consumed items. Of particular interest are observations of phenomena rarely observed by field biologists, such as predation and predator-avoidance behavior. Assessing the reliability of all this information is obviously important for a variety of potential applications, so we undertook a detailed analysis of one exemplar taxon.

SPIDER MONKEY NATURAL HISTORY: We analyzed recorded monologs about spider monkeys by enumerating units of ecobehavioral information that could be checked for consistency against the scientific literature (after Townsend, 1995). Because there have been relatively few field studies of the local species, *Ateles belzebuth*, we regarded Matses observations as corroborated by the scientific literature if similar observations had been published by field biologists for any spider monkey species. Also, because some field studies provide incomplete taxonomic identifications of ingested fruits, we assessed dietary information about food plants at the generic level.

Of the 86 ecobehavioral information units tallied from Matses monologs about *Ateles belzebuth*, two concerned unidentified plant taxa in its diet: şhanned (possibly corresponding to one or more species of *Brosimum* [Moraceae]) and okodo mabis (an undetermined species of Guttiferae). As no confident assessment of these dietary items is possible in the absence of positive botanical matches, they were excluded from consideration. Of the remaining 84 ecobehavioral information units, 63 (75%) were corroborated by published information from scientific field studies (table 19). These corroborated observations include traits that are common to all spider monkey species, such as tail-assisted brachiation (item 3) and frugivory (item 59), as well as behaviors that could be species or site specific. Examples of species-specific traits might be the complex of behaviors associated with visiting mineral licks (items 48–56), which are apparently unknown in other well-studied congeners; another might be the habit of eating unpeeled fruits (item 61), a behavior that is apparently not shared with *A. paniscus* (see Roosmalen, 1985). An example of a site-specific behavior might be use of the middle level of the canopy (item 7): as suggested by Mittermeier (1978), use of different canopy levels could represent behavioral plasticity in response to differences in forest structure among study sites rather than evolved species-specific traits.

Of the remaining 21 uncorroborated ecobehavioral observations that the Matses reported for *Ateles belzebuth*, we judged 20 to be plausible because they (1) are reasonable extrapolations from published scientific observations, (2) could be expected to depend on local conditions, (3) are behaviors that

TABLE 19

Ecobehavioral Information Recovered from Matses Monologs about Spider Monkeys (*Ateles belzebuth*)

Matses observation	Assessment
1. Hold tails stretched out (not coiled) when traveling	Corroborated (Carpenter, 1935; Cant, 1986; Youlatos, 2002)
2. Use tails to grab onto things	Corroborated (Carpenter, 1935; Cant, 1986; Youlatos, 2002)
3. Travel swinging under branches, using arms and tail	Corroborated (Carpenter, 1935; Cant, 1986; Youlatos, 2002)
4. Hang by their tails when they eat fruit, all spread out	Corroborated (Mittermeier, 1978; Cant, 1986; Youlatos, 2002)
5. Found in all primary forest habitats	Corroborated (Terborgh, 1983; Wallace, 2006)
6. Prefer upland forest to floodplain forest	Corroborated (Stevenson et al., 2000)
7. Use mostly the middle of the canopy	Corroborated (Mittermeier, 1978)
8. Climb higher to forage	Plausible (fruiting trees often canopy emergents)
9. Climb higher to escape predators	Plausible
10. Climb higher to sleep	Corroborated (Roosmalen, 1985; Chapman, 1989)
11. Climb higher when they hear a tinamou fly	Plausible (see text)
12. Do not walk on ground except at mineral licks	Corroborated (Campbell et al., 2005)
13. More common than woolly monkeys	Plausible (see text)
14. Troop size varies from one to many	Corroborated (Carpenter, 1935; Klein and Klein, 1977; Symington, 1988b)
15. Large male leads the troop	?
16. Females carry young on back	Corroborated (Carpenter, 1935; Roosmalen, 1985; Symington, 1988a)
17. Very small young carried ventrally	Corroborated (Carpenter, 1935; Roosmalen, 1985; Symington, 1988a)
18. Suckle young like people do	Plausible (subjective)
19. Smaller ones taken by harpy eagles	Plausible (see text)
20. Attacked by large cats at mineral licks	Corroborated (Matsuda and Izawa, 2008)
21. Defend themselves by grabbing and biting	Plausible (see Carpenter, 1935: 180)
22. Have several different vocalizations	Corroborated (Carpenter, 1935; Roosmalen, 1985)
23. Communicate over long distances by screaming	Corroborated (Roosmalen, 1985)
24. Bark like dogs when angry	Corroborated (Carpenter, 1935; Roosmalen, 1985)
25. Communicate among themselves softly	Corroborated (Eisenberg and Kuehn, 1966)
26. Scream like people when shot	Plausible
27. Rustle branches noisily as they move across treetops	Plausible
28. Wake up early in good weather	Plausible
29. Wake up later when rainy	Corroborated (Klein and Klein, 1977; Wallace, 2001)
30. Wake up calling loudly to their companions	Plausible
31. Search for food when united	Plausible
32. Travel through the trees screaming	Plausible
33. Follow a regular (daily) route	Corroborated (Carpenter, 1935; Di Fiore and Suarez, 2007)
34. Travel faster in flight than other monkeys	Plausible
35. Large males go fastest	Plausible (see text)
36. Females carrying young go slowest	Plausible (see text)
37. Run along tops of large branches	Corroborated (Cant, 1986; Youlatos, 2002)
38. Most active in the morning	Corroborated (Carpenter, 1935; Roosmalen and Klein, 1988; Wallace, 2001)
39. Rest when the sun is high and hot	Corroborated (Carpenter, 1935; Klein and Klein, 1977; Wallace, 2001)
40. Rest lying on branches while young play	Corroborated (Carpenter, 1935; Roosmalen, 1985; Wallace, 2001)
41. Active again in late afternoon	Corroborated (Carpenter, 1935; Klein and Klein, 1977; Roosmalen, 1985)
42. Sit under sheltering vegetation when it rains	Corroborated (Wallace, 2001)

TABLE 19
(Continued)

Matses observation	Assessment
43. Sleep in same big tree(s) every night	Corroborated (Carpenter, 1935; Roosmalen, 1985; Chapman, 1989; Wallace, 2001)
44. Sleep very high up, huddled in small groups	Plausible (see Roosmalen, 1985:)
45. Defecate and urinate where they sleep	Corroborated (Roosmalen, 1985; Link and Di Fiore, 2006)
46. Many feces and seeds under sleeping trees	Corroborated (Chapman, 1989; Russo and Augspurger, 2004)
47. Come out and yell at night when moon is full	Corroborated (Emmons, 1997)
48. Visit mineral licks	Corroborated (Izawa, 1975, 1993; Izawa et al., 1979; Montenegro, 2004)
49. Eat mud at mineral licks	Corroborated (Matsuda and Izawa, 2008)
50. Drink muddy water at mineral licks	Corroborated (Izawa, 1975, 1993; Izawa et al., 1979)
51. Whole group visits mineral lick together	Corroborated (Izawa et al., 1979)
52. Lookouts posted to watch for predators at mineral lick	Corroborated (Izawa et al., 1979)
53. Lookouts later switch places with drinkers	Corroborated (Izawa et al., 1979)
54. Make holes in walls of mineral lick to collect mud	Corroborated (Suarez [in Di Fiore, 2002])
55. Drink from mineral lick with tails wrapped around trees	Plausible
56. Descend and ascend on thin trees	Corroborated (Izawa, 1975: fig. 3)
57. Tree used for this purpose become muddy	Plausible
58. Rest up in trees after visiting mineral lick	Corroborated (Matsuda and Izawa, 2008)
59. Eat mostly fruit	Corroborated (see literature reviewed by Di Fiore et al. [2008])
60. Large troops may split up to forage	Corroborated (Klein and Klein, 1977; Roosmalen, 1985; Symington, 1988a)
61. Eat fruits without peeling them	Corroborated (Dew, 2005, 2008; Di Fiore et al., 2008)
62. Swallow even large seeds	Corroborated (Klein and Klein, 1977; Roosmalen, 1985; Dew, 2005, 2008)
63. Eat *Oenocarpus* (Palmae) fruits	Corroborated (Klein and Klein, 1977; Russo et al., 2005; Suarez, 2006)
64. Eat *Mauritia* (Palmae) fruits	Corroborated (Nunes, 1998; Aquino and Bodmer, 2004)
65. Eat unripe *Iriartea* (Palmae) seeds	Corroborated (Dew, 2005)
66. Eat *Couma* (Apocynaceae) fruits	Corroborated (Castellanos and Chanin, 1996)
67. Eat *Pourouma* (Moraceae) fruits	Corroborated (Roosmalen, 1985; Dew, 2005; Suarez, 2006)
68. Eat *Clarisia* (Moraceae) fruits	Corroborated (Roosmalen, 1985; Castellanos and Chanin, 1996; Wallace, 2005)
69. Eat Myristicaceae fruits	Corroborated (Carpenter, 1935; Klein and Klein, 1977; Roosmalen, 1985)
70. Eat *Hymenaea* (Leguminosae) fruits	Corroborated (Iwanaga and Ferrari, 2001; Suarez, 2006)
71. Eat *Ficus* and/or *Coussapoa* (Moraceae) fruits	Corroborated (Carpenter, 1935; Klein and Klein, 1977; Roosmalen, 1985; Felton et al. (2008)
72. Eat *Anacardium* (Anacardiaceae) fruits	Corroborated (Carpenter, 1935; Roosmalen, 1985; Castellanos and Chanin, 1996)
73. Eat *Rhigospira* (Apocynaceae) fruits	Plausible
74. Eat *Parahancornia* (Apocynaceae) fruits	Corroborated (Roosmalen, 1985; Simmen and Sabatier, 1996)
75. Eat *Matisia* and/or *Eriotheca* (Bombacaceae) fruits	Corroborated (Dew, 2005; Suarez, 2006; Wallace, 2005)
76. Eat *Rheedia* (Guttiferae) fruits	Corroborated (Carpenter, 1935; Klein and Klein, 1977; Roosmalen, 1985)
77. Eat *Inga* (Leguminosae) fruits	Corroborated (Carpenter, 1935; Klein and Klein, 1977; Roosmalen, 1985; Wallace, 2005)
78. Eat *Parkia* and/or *Pithecellobium* (Leguminosae) fruits	Corroborated (Roosmalen, 1985)
79. Eat *Castilla* (Moraceae) fruits	Corroborated (Stevenson et al., 2000)
80. Eat *Helicostylis* (Moraceae) fruit	Corroborated (Carpenter, 1935; Roosmalen, 1985; Castellanos and Chanin, 1996; Wallace (2005)
81. Eat *Naucleopsis* (Moraceae) fruit	Corroborated (Dew, 2005; Russo et al., 2005; Suarez, 2006)

TABLE 19
(Continued)

Matses observation	Assessment
82. Eat *Pseudolmedia* and/or *Maquira* (Moraceae) fruit	Corroborated (Klein and Klein, 1977; Suarez, 2006; Wallace, 2005)
83. Eat *Chrysophyllum* (Sapotaceae) fruit	Corroborated (Carpenter, 1935; Klein and Klein, 1977; Roosmalen, 1985)
84. Eat *Manilkara* (Sapotaceae) fruit	Corroborated (Simmen and Sabatier, 1996; Suarez, 2006)

only monkey hunters might think to mention, and/or (4) represent subjective judgments of similarity. An example of a plausible observation in the first category is that small spider monkeys are taken by harpy eagles (item 19). Although harpy eagle (*Harpia harpyja*) predation on spider monkeys has not been reported in the scientific literature, harpy eagles are known to take howler monkeys (Peres, 1990; Sherman, 1991) and there is a report of a crested eagle (*Morphnus guianensis*) taking a young spider monkey (Julliot, 1994). Another plausible observation of the first kind is that spider monkeys climb higher when they hear a tinamou fly (item 11). Although this also seems not to have been reported in the literature, Roosmalen (1985) notes that Guianan spider monkeys (*A. paniscus*) become upset by the flight of alarmed terrestrial animals (including tinamous), and climbing higher would be a prudent response to the arrival of an unseen predator.

An example of a plausible observation in the second category is that spider monkeys are more common than woolly monkeys. Although we have not encountered any published study in which this has been reported (indeed, most reports suggest that *Lagothrix* is more common than *Ateles* where both taxa are present; e.g., Izawa, 1975), it is reasonable to assume that some aspect of the local flora or phenology might favor *Ateles* in the Yavarí-Ucayali interfluve. Examples of plausible observations in the third category include items 35 and 36, neither of which is addressed in the scientific literature, but which are consistent with inferences from spider monkey kills by other native Amazonian hunters (Shepard, 2002; da Silva et al., 2005). A plausible observation of the fourth kind is the remark that spider monkeys suckle their young like people do (item 18), a simile that does not appear in the scientific literature, and one that we are unable to evaluate in the absence of any explicit, published description of nursing in *Ateles*.

In effect, only one Matses observation about *Ateles belzebuth* seems potentially problematic: that a large male leads the troop (item 15). This behavior does not appear to have been reported in any published field study of spider monkeys. Indeed, at least one study suggests that a dominant female leads most foraging parties (Roosmalen, 1985). Perhaps the Matses, who do not carry binoculars, are confused about the sex of leading animals, or they may assume that behavioral dominance in agonistic encounters between adult males and females implies a leadership role for males. A third possibility, of course, is that the Matses are correct, and that the local population of *A. belzebuth* differs in this respect from populations at other spider monkey research sites.

COMMUNITY PATTERNS: Although we have not undertaken similarly detailed analyses of Matses natural history accounts for other monkeys, we tabulated interspecific comparisons of diet, habitat use, and other behaviors to illustrate various aspects of primate community structure that can be reconstructed from recorded monologs. These are interesting topics in themselves, and they provide another context for ethnobiological fact-checking. Because there have been no long-term synecological primate studies in the Yavarí-Ucayali interfluve, Matses observations are a potentially useful source of information about patterns of resource use by the local primate community.

Matses information about feeding behavior (table 20) is broadly consistent with the results of many field studies that have identified frugivory as the dominant trophic characteristic of Neotropical primate faunas

TABLE 20

Diets of Local Primate Species Based on Matses Natural History Monologs[a]

	Fruit	Seeds	Leaves	Wood	"Bark"	Animals	Mud
Aotus nancymaae	X						
Alouatta seniculus	X	X	X	X		X[b]	X
Ateles belzebuth	XX	X[c]					X
Lagothrix lagothricha	XX	X[c]	(X)			X[b]	
Cebus albifrons	X	X	X[d]			X[e]	
Cebus apella	X	X	X[d]			X[e]	
Saimiri sciureus	X					X[b]	
Callithrix pygmaea					X		
Saguinus fuscicollis	X					X[b]	
Saguinus mystax	X					X[b]	
Cacajao calvus	XX	X[f]	(X)			X[b]	
Callicebus cupreus	X					X[b]	
Pithecia monachus	XX		(X)			X[b]	

[a] Key: XX, identified as primary component of diet; X, present in diet; (X), identified as minor component of diet.

[b] Invertebrates only.

[c] Only liquid endosperm of unripe *Iriartea deltoidea* (Palmae) fruits mentioned.

[d] Only palm hearts mentioned.

[e] Vertebrates and invertebrates.

[f] Only endosperm of unripe *Mauritia flexuosa* (Palmae) fruits mentioned.

(Izawa, 1975; Mittermeier and Roosmalen, 1981; Soini, 1986; Terborgh, 1983; Rylands, 1987; Peres, 1993b). Additionally, the Matses accurately describe many taxon-specific dietary features (described or referenced by the same authors), such as leaf consumption by *Alouatta*, geophagy by *Alouatta* and *Ateles*, vertebrate predation by both species of *Cebus*, "bark" (gum) consumption by *Callithrix*, and consumption of unripe fruits by *Pithecia*. However, Matses informants failed to mention several aspects of primate diets documented by scientific field studies. The Matses admit that they know little about the foods eaten by night monkeys, but other notable omissions from recorded monologs include arthropod consumption by *Callithrix pygmaea* (see Soini, 1988) and vertebrate predation by both local species of *Saguinus* (see Heymann et al., 2000). The general pattern apparent in these data is that Matses dietary observations are less complete for the smaller primates than they are for larger monkeys, but there are a few omissions even for the largest species.[16]

Information gleaned from Matses monologs about community use of specific food plants (table 21) indicates that some fruits are eaten promiscuously, affording nourishment to many species of monkeys, whereas other fruits are eaten by just a few species. Fruits in the first category include some that are popular items in primate diets elsewhere in western Amazonia (Terborgh, 1983; Stevenson et al., 2000), notably including several genera of Moraceae. However, other locally important food-plant taxa are rarely mentioned in the primate literature. The family Apocynaceae, for example, is seldom represented among lists of important primate fruits at other Amazonian localities, and the swamp palm (*Mauritia flexuosa*) has only been identified as an important food resource for primates at one other site in northeastern Peru (Aquino and Bodmer, 2004). Some higher-taxonomic absences are also noteworthy. Among others, the families Annonaceae and Sapindaceae, both commonly eaten by primates in southeastern Peru (Terborgh, 1983) are not represented among the fruits positively identified as local monkey fodder by the Matses. Because there are noteworthy floristic, climatic, and edaphic differences between Matses hunting grounds in the Yavarí-Ucayali interfluve and

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[16] Leaf consumption, for example, is a minor but consistently reported component of spider monkey diets (Klein and Klein, 1977; Roosmalen, 1985; Simmen and Sabatier, 1996; Russo et al., 2005; Felton et al., 2008).

TABLE 21

Fruits Eaten by Local Primate Species Based on Matses Monologs

	Primate consumers
Palms	
Palmae (Arecaceae)	
Astrocaryum chambira	*Cebus*
Astrocaryum jauari	*Cebus*
Astrocaryum murumuru	*Cebus*
Attalea butyracea	*Cebus*
Attalea phalerata	*Alouatta*
Euterpe precatoria	*Cebus*, *Callicebus*
Iriartea deltoidea	*Ateles, Lagothrix*, *Cebus*
Mauritia flexuosa	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Cacajao*, *Pithecia*
Oenocarpus bataua	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Cacajao*, *Pithecia*
Dicots	
Anacardiaceae	
Anacardium giganteum	*Ateles*, *Cebus*, *Saimiri*, *Cacajao*, *Callicebus*, *Pithecia*
Spondias mombin	*Lagothrix*
Apocynaceae	
Couma macrocarpa	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Saguinus*, *Cacajao*, *Callicebus*, *Pithecia*
Parahancornia peruviana	*Aotus*, *Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Cacajao*, *Callicebus*, *Pithecia*
machishte[a]	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Cacajao*, *Callicebus*, *Pithecia*
poshton tonte[b]	*Lagothrix*
Bombacaceae	
ichibin[c]	*Ateles*, *Lagothrix*, *Cacajao*
kapan çhëşhte[d]	*Cebus*
Guttiferae (Clusiaceae)	
Garcinia macrophylla	*Saguinus*
Rheedia longifolia	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Cacajao*, *Callicebus*, *Pithecia*
okodo mabis[e]	*Alouatta*, *Ateles*, *Cebus*, *Saimiri*, *Cacajao*, *Callicebus*, *Pithecia*
Leguminosae (incl. Caesalpineaceae & Mimosaceae)	
Hymenaea spp.	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Cacajao*, *Pithecia*
Inga spp.	*Saimiri*, *Cacajao*, *Callicebus*
mannan tsipuis[f]	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Cacajao*, *Callicebus*, *Pithecia*
tankada[g]	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Cacajao*, *Pithecia*
Melastomataceae	
Mouriri spp.	*Lagothrix*, *Saimiri*, *Saguinus*, *Callicebus*
Moraceae (incl. Cecropiaceae)	
Brosimum parinarioides	*Pithecia*
Castilla	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Cacajao*, *Pithecia*
Cecropia spp.	*Lagothrix*, *Cebus*
Clarisia racemosa	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Cacajao*, *Pithecia*
Helicostylis (2 spp.)	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Saguinus*, *Cacajao*, *Callicebus*, *Pithecia*
Naucleopsis (2 spp.)	*Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Cacajao*, *Pithecia*
Pourouma spp.	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saguinus*, *Cacajao*, *Pithecia*

TABLE 21
(Continued)

	Primate consumers
bata[h]	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Saguinus*, *Cacajao*, *Callicebus*, *Pithecia*
chiwish[i]	*Alouatta*, *Ateles*, *Lagothrix*
ṣhannëd[j]	*Ateles*, *Lagothrix*, *Saimiri*, *Saguinus*, *Cacajao*, *Callicebus*, *Pithecia*
ṣhupud[k]	*Pithecia*
Myristicaceae (undetermined)	*Ateles*, *Cebus*
Passifloraceae	
Passiflora nitida	*Alouatta*, *Lagothrix*, *Saimiri*, *Cacajao*, *Pithecia*
Sapotaceae	
Chrysophyllum prieurii	*Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Cacajao*, *Callicebus*, *Pithecia*
Manilkara bidentata	*Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Saimiri*, *Cacajao*, *Callicebus*, *Pithecia*
Pouteria	*Lagothrix*
Sterculiaceae	
Theobroma cacao	*Cebus*
Theobroma (other)	*Cebus*
Tiliaceae	
Apeiba aspera	*Alouatta*
Undetermined	
kuëte mëdiad (tree)	*Cebus*
nënë pada (epiphyte)	*Alouatta*, *Lagothrix*
taëpa (tree)	*Alouatta*, *Lagothrix*, *Cebus*, *Cacajao*, *Callicebus*

[a] *Rhigospira quadrangularis* and ?*Mucoa duckei*.
[b] ?*Macoubea guianensis*.
[c] *Matisia* sp., *Eriotheca* sp.
[d] *Matisia bracteolosa* and *Quararibea ochrocalyx*.
[e] Undetermined.
[f] *Inga* spp., ?*Pithecellobium*.
[g] *Parkia igneiflora*, *P. multijuga*, and *Pithecellobium auriculatum*.
[h] *Pseudolmedia* and *Maquira* spp.
[i] *Ficus* spp. and *Coussapoa* spp.
[j] ?*Brosimum*.
[k] *Brosimum* and *Poulsenia*.

many other Amazonian study sites, environmental factors may be responsible for some local peculiarities of primate fruit consumption.[17] Additionally, almost all of the plant taxa mentioned in Matses monologs are trees, and important primate food plants that have other growth forms (e.g., Sapindaceae, many of which are vines) might be underrepresented because they are seldom named by the Matses.

Other interactions between the local primate fauna and particular plant taxa raise some interesting questions. Matses informants definitely assert that only howler monkeys eat the fruit of *Apeiba aspera* (Tiliaceae), but elsewhere in Amazonia the fruit of *A. aspera* is one of the preferred foods of capuchins and is strongly avoided by howlers (Stevenson et al., 2000). Similarly, the Matses assert that only titi monkeys eat the fruit of the palm *Euterpe precatoria* (capuchins are said to eat just the unripe

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[17] The Yavarí-Ucayali interfluve receives almost 1000 mm more rainfall annually than Terborgh's (1983) study site at Cocha Cashu, for example, and it has a much less pronounced dry season. Additionally, most of Matses territory consists of well-drained upland forests, whereas Cocha Cashu is in the seasonally inundated floodplain of a white-water river.

TABLE 22
Habitat Utilization by Local Primate Species Based on Matses Monologs[a]

	Primary forest		
	Upland	Floodplain[b]	Secondary forest[c]
Alouatta seniculus	X	XX	
Ateles belzebuth	XX	X	
Lagothrix lagothricha	XX	X	
Cebus albifrons	XX	X	X
Cebus apella	X	XX	X
Saimiri sciureus	X	XX	X
Callithrix pygmaea	X	X	X
Saguinus fuscicollis	(X)	(X)	XX
Saguinus mystax	X	X	(X)
Cacajao calvus	X	X	
Callicebus cupreus	(X)	X	XX
Pithecia monachus	X	X	X

[a] Key: XX, preferred habitat; X, habitat utilized; (X), habitat used less often than others in which species occurs.
[b] Including palm swamps.
[c] Abandoned swiddens, blowdowns, etc.

seeds), but the fruit of *E. precatoria* is eaten by spider monkeys at many other localities (Roosmalen, 1985; Castellanos and Chanin, 1996; Iwanaga and Ferrari, 2001; Wallace, 2006). Whether such anomalies are attributable to intersite differences in environmental factors alleged to influence primate food preferences (Russo et al., 2005) or to observer error is unknown.

Community patterns of habitat and substrate use reconstructed from Matses monologs (tables 22, 23) are generally consistent with the scientific literature. All of the atelids, for example, are accurately portrayed as using only the canopy of primary forest; howlers and squirrel monkeys are said to strongly prefer floodplain forest; *Cebus apella* and *C. albifrons* are said to prefer floodplain and upland forest respectively; titis are said to strongly prefer forest edges and secondary growth; the locally sympatric tamarins are said to differ in their preference for primary forest versus secondary growth; etc (Castro and Soini, 1977; Rylands, 1987; Peres, 1993c, 1997; Haugaasen and Peres, 2005; Parry et al., 2007). Significantly, the Matses say that uakaris use both floodplain and upland forests, in agreement with recent field studies conducted within the Yavarí-Ucayali interfluve but in contrast with reports from other regions, where these monkeys are said to be flooded-forest specialists (Aquino, 1998; Heymann and Aquino, 2010).

Matses observations about interspecific interactions (table 24) are not extensive, but they include some that are familiar from the scientific literature, such as the common association between *Cebus apella* and *Saimiri sciureus* (see Podolski, 1990). Interestingly, the Matses observation that *C. albifrons* does not associate with *Saimiri* conflicts with the results of field studies in southern Peru (where *Saimiri* seems to associate with both *C. apella* and *C. albifrons*; Terborgh, 1983), but it is easier to reconcile with field studies from adjacent regions in northern Peru (where *Saimiri* associates much more frequently with *C. apella* than with *C. albifrons*; Soini, 1986). Most of the other interspecific interactions reported by the Matses are unremarkable, but to our knowledge there has been only one previous report that *Cebus apella* kills and eats titi monkeys (Sampaio and Ferrari, 2005). The lack of Matses observations about interactions involving *Ateles* and *Alouatta* is consistent with published generalizations that these genera rarely associate with other primates (Neville et al., 1988; Roosmalen and Klein, 1988). However, unreported interactions between *Saguinus fuscicollis* and *S. mystax* (which often form mixed troops; Heymann, 1990; Peres, 1993b;

TABLE 23
Substrate Use by Local Primate Species Based on Matses Monologs[a]

	Canopy	Subcanopy/Undergrowth	Ground
Alouatta seniculus	XX		X[b]
Ateles belzebuth	XX		X[b]
Lagothrix lagothricha	XX		X[c]
Cebus albifrons	X	XX	X[d]
Cebus apella	?	XX	X
Saimiri sciureus		XX	X[e]
Callithrix pygmaea	X	X	
Saguinus fuscicollis	?	X	X
Saguinus mystax	X	X	
Cacajao calvus	X[f]		(X)
Callicebus cupreus		X	X
Pithecia monachus	X	X	X[c]

[a] Key: XX, said (or implied) to be preferred substrate; X, substrate said (or implied) to be utilized; (X), substrate said to be used infrequently.

[b] Only to eat mud or drink muddy water at mineral licks.

[c] Only to escape from eagles.

[d] Said to spend more time foraging on the ground than other monkeys.

[e] Only to drink.

[f] Said to use middle canopy, lower than *Ateles* and *Alouatta*.

Heymann and Buchanan-Smith, 2000) may reflect cultural inattention to the habits of small monkeys.

In summary, most Matses observations about primate behavior and natural history seem to be accurate (to the extent that they overlap with the results of published field studies) or to be plausible extensions of previously reported facts. Although the Matses are clearly biased observers, providing much more extensive and detailed information about large game species than about small species of little or no cultural importance, the format-free context of our recorded monologs may have been responsible for the omission of some relevant information even about culturally important taxa. A great deal more information about primate natural history could presumably have been obtained from question-and-answer interviews, but there is an obvious risk of eliciting misleading responses to leading questions when interviewees are eager to please.

Primatologists may be encouraged by these results to explore the ethnobiological knowledge of other native Amazonians, which might be a cost-effective alternative to lengthy fieldwork for some research objectives. However, there are significant linguistic barriers to effective cross-cultural communication. Some degree of bilingual fluency is obviously essential on the part of the interviewer or the interviewee, but it is also important to understand relevant aspects of ethnobiological classification and nomenclature. Among the Matses, these include a surprisingly large number of zoologically redundant names (synonyms and hyponyms) as explained below.

Matses Folk Classification and Nomenclature of Primates

Most primates are known to the Matses by multiple names that can be assigned to several categories based on usage and cultural context (table 25). The following analysis extends our previous work on Matses folk classification and nomenclature (Fleck et al., 1999, 2002; Fleck and Voss, 2006) by focusing on primate nomenclature, by providing new information about majority and minority name usage, and by treating the problem of overdifferentiation in greater detail.

PRINCIPAL TERM: The name for each species that we designate the "principal term" is (1) the term most frequently overheard; (2)

TABLE 24
Interspecific Interactions among Local Primates Based on Matses Monologs[a]

Lagothrix lagothricha: [sometimes forages with squirrel monkeys; feeds in the same tree with sakis.]
Cebus albifrons: sometimes travels with woolly monkeys, never with squirrel monkeys.
Cebus apella: bullies squirrel monkeys when they feed together [sometimes also travels and sleeps with squirrel monkeys]; sometimes kills and eats titi monkeys.
Saimiri sciureus: sometimes eats, travels, and sleeps with brown capuchins; may forage with woolly monkeys.
Cacajao calvus: [sometimes feeds in the same tree with sakis.]
Callicebus cupreus: [is sometimes killed and eaten by brown capuchins.]
Pithecia monachus: sometimes feeds in the same tree with woolly monkeys or uakaris.

[a] Species with no stated interactions with other primates are not listed. Observations in square brackets are derived from monologues about other species.

the one that everyone knows, including children; (3) the first term offered when eliciting names using field guides or specimens; and (4) the term that speakers themselves say is the principal name when more than one name applies to a species. There is no informant disagreement about principal terms for primates. Intervillage lexical variation for principal names of other mammals is restricted to poorly known and culturally unimportant taxa, such as short-eared dogs (*Atelocynus microtis*, which are extremely rare), and opossums (which are seldom observed and of no cultural significance). Apparently, the pygmy marmoset (*Callithrix pygmaea*) is not quite obscure enough to be among the taxa for which there is disagreement about principal names.

“Archaic” synonyms: Many game species have, in addition to the principle name, several synonyms that every good Matses hunter is expected to know (Fleck and Voss, 2006). Fathers and grandfathers teach their sons and grandsons these synonym sets, and visiting older men routinely quiz young men on these terms. Although these synonyms are said to be tsusiobon onkete “old men’s speech,” there are etymological reasons to doubt that all are genuinely archaic terms. Polymorphemic (linguistically segmentable) synonyms that are obviously descriptive (e.g., abukkid “one that is high up” for woolly monkeys) or onomatopoetic (such as pishtadan for tamarins), for example, seem likely to be of recent origin. By contrast, monomorphemic (unsegmentable) terms with cognates in other Panoan languages (e.g., çhuna, another synonym for wooly monkeys) might have been inherited from some ancestral protolanguage, or they might be modern borrowings from a sister tongue.

There is a clear pattern in Matses folkbiological nomenclature that culturally important species (e.g., *Lagothrix lagothricha*) tend to have more synonyms than culturally insignificant species (e.g., *Callithrix pygmaea*), but this correlation is less apparent among species of intermediate cultural salience. For example, one would expect the uakari monkey (*Cacajao calvus*) to have at least one or two synonyms given that the smaller and less important titi monkey (*Callicebus cupreus*) has three. Historical factors might explain anomalies like this if synonymy reflects long-term rather than current cultural importance. (It is clear from Matses testimonials and from known historical accounts that the Matses have not been in continuous contact with uakari monkeys in the past.) The saki monkey (*Pithecia monachus*) might also be expected to have synonyms, but we note that a minority of Matses informants who do not recognize varieties of saki monkeys consider the terms mamu and bëshudu to be synonyms of bëşhuidkid. We will return to this distinction between synonyms and hyponyms (named subtypes or varieties) in our discussion of overdifferentiation below.

Ceremonial terms: This category applies to words from a secret language that was formerly chanted or spoken only in the komok or “singing souls” ceremony (Romanoff 1984; Romanoff et al., 2004), when invented, archaic, or borrowed words were substituted for common usage in Matses. The pattern noted above, of giving special linguistic attention to culturally important animals, can also be seen in the komok ceremonial language. Of the 56 documented substitute terms in the komok language, 19 are animal names, of which 14 apply to game species and two to other culturally significant animals (jaguar/dog and bushmaster).

Only the two most culturally important primates, the woolly monkey and the spider monkey, have a komok ceremonial term, and the same substitute name (şhëmën kudu) is used for both species. This follows a general trend in the komok lexicon: ceremonial terms are often less specific (and never more specific) than non-ceremonial terms. Two other examples of this type of underdifferentiation occur among the ceremonial terms for mammals. The term mëndu is used for both the jaguar and the domestic dog (a pattern also found in everyday usage in other Panoan languages, but not with a cognate term), and the term ana pachi is used for both the paca and the agouti, which in everyday usage have completely different Matses names.

OVERDIFFERENTIATED VARIETY: This category refers to one of three logical possibilities that can result from comparisons of "folk species" and biological species: (1) one-to-one correspondence; (2) underdifferentiation; and (3) overdifferentiation. One-to-one correspondence is the result when a single folk species (e.g., senta) corresponds to exactly one biological species (*Cacajao calvus*; table 25); underdifferentiation results when a single folk species (e.g., cuesban) corresponds to more than one biological species (at least 57 species of bats; Fleck et al., 2002); and overdifferentiation refers to cases where a single biological species (e.g., *Pithecia monachus*) is denoted by two or more non-synonymous folk species names (bëshudu and mamu; Fleck et al., 1999).

With the exception of the komok ceremonial term that applies to both spider monkeys and woolly monkeys, as discussed above, there are no cases of underdifferentiation in the Matses primatological lexicon, and there are only five unambiguous examples of one-to-one correspondence (*Cacajao calvus*, *Cebus albifrons*, *Saguinus fuscicollis*, *S. mystax*, and *Callithrix pygmaea* each have unique names; table 25). By contrast, overdifferentiation is relatively common. Although overdifferentiation results in multiple names that apply to the same biological species, these names are hyponyms rather than synonyms because they apply to different real or alleged varieties.

As with the synonym sets described above, good hunters are expected to know hyponyms for different game animals and how to identify the corresponding overdifferentiated varieties, whereas this knowledge is absent or incomplete for children, women, and "worthless men." Also, as noted by Fleck and Voss (2006), there is a tendency for overdifferentiated species to be the same culturally important ones that receive multiple synonyms. Part of the explanation for this may be that hunters have frequent opportunities to inspect the physical details of killed game animals, and this personal experience allows them to detect subtle phenotypic differences among individuals or age cohorts that might be interpreted as analogous to the discontinuities that exist between closely related species. In fact, Matses hyponyms for saki monkeys (bëshudu and mamu) appear to be based on age-correlated variation in size and pelage traits rather than genetic differences (Fleck et al., 1999). Information summarized in the preceding species accounts suggest that Matses hyponyms for other primates may also reflect ontogenetic or individual variation in size and pelage, but we cannot rule out two alternative explanations for some names: (1) the possibility, however remote, that additional primate taxa remain to be discovered in the Yavarí-Ucayali interfluve; or (2) that the Matses retain information in their lexicon about species previously encountered by the tribe before they settled in their current territory.

By contrast with game synonym sets, there seems to be no conscious attempt by the Matses to standardize overdifferentiation (e.g., by ritually quizzing young men and boys; Fleck and Voss, 2006), perhaps because overdifferentiation is the result of observing biological variability and is therefore subject to individual interpretation. In effect, hyponyms denote purported discontinuities between named varieties that some hunters may eventually find to be false. Accordingly, some hyponyms are topics of speaker disagreement

TABLE 25
Matses Names for Primates Ordered by Cultural Importance[a]

	Status of name	
Matses term	majority view	minority view
Lagothrix lagothricha (1°G)		
poshto	principal term	same
çhuna	"archaic" synonym	same
abukkid	"archaic" synonym	same
mëdantechued	"archaic" synonym	same
maksinkid	"archaic" synonym	same
şhëmën kudu	ceremonial term	same
poshto piu	overdifferentiated variety	same
poshto tanun	overdifferentiated variety	same
poshto çhëşhë	overdifferentiated variety	not recognized
Ateles belzebuth (1°G)		
çhëşhëid	principal term	same
çhuna wisu	"archaic" synonym	same
mëshe	"archaic" synonym	same
şhëmën kudu	ceremonial term	same
çhëşhëidtapa	overdifferentiated variety	same
tsidun	overdifferentiated variety	same
Pithecia monachus (2°G)		
bëşhuidkid	principal term	same
bëshudu	overdifferentiated variety	"archaic" synonym
mamu	overdifferentiated variety	"archaic" synonym
Cacajao calvus (2°G)		
senta	principal term	same
bëşhuidkid piu	not recognized	"archaic" synonym
Callicebus cupreus (3°G)		
wadë	principal term	same
tsokon	"archaic" synonym	same
sëdë	"archaic" synonym	same
masoko	"archaic" synonym	not recognized
wadë piu	overdifferentiated variety	not recognized
wadë çhëşhë	overdifferentiated variety	not recognized
Saimiri sciureus (3°G)		
tsanka	principal term	same
tsankekid	"archaic" synonym	same
tsankadapa	overdifferentiated variety	same
tsankampi	overdifferentiated variety	same
Aotus nancymaae (3°G)		
dide	principal term	same
diku	"archaic" synonym	overdifferentiated variety
Alouatta seniculus (PT)		
achu	principal term	same
achudapa/achu piudapa	overdifferentiated variety	same
tsusa	overdifferentiated variety	same
achu çhëşhë	overdifferentiated variety	not recognized
Cebus spp.		
bëchun	principal term	same
koekid	"archaic" synonym	same

TABLE 25
(Continued)

	Status of name	
Matses term	majority view	minority view
chidu	myth term	"archaic" synonym
Cebus apella (PT)		
bëchun (çhëşhë)	principal term	same
bëchun çhëşhëdapa	not recognized	overdifferentiated variety
bëchun çhëşhëmpi	not recognized	overdifferentiated variety
Cebus albifrons (PT)		
bëchun uşhu	principal term	same
Saguinus spp.		
sipi	principal term	same
pishtadan	"archaic" synonym	same
Saguinus mystax (4°G)		
sipi ëksed	principal term	same
Saguinus fuscicollis (4°G)		
sipi kabëdi	principal term	same
Callithrix pygmaea (NE)		
madun sipi	principal term	same

[a] Abbreviations: 1°G = primary game (preferred, large); 2°G = secondary game (medium-sized); 3°G = tertiary game (small); 4°G = quaternary game (too small to merit adult attention); PT = partial dietary taboo; NE = not eaten. Ordering was determined by multiple interviews with Matses men and women as to which species are traditionally preferred based on size, taboo, tendency to have fat, and taste.

(with corresponding majority and minority views; table 25).

Several additional aspects of Matses ethnobiological overdiffertiation are noteworthy. One is that speaker disagreement about hyponyms for primates (and other taxa) usually involves species of intermediate cultural importance. Part of the reason for this is that small and/or culturally insignificant species are not overdifferentiated by anyone, perhaps because they are infrequently observed (e.g., *Cebuella pygmaea*) and seldom talked about. Large, culturally important species, on the other hand, are often seen and frequently discussed, so that hyponyms become widely known and accepted among hunters.

Another interesting aspect of Matses overdifferentiation is that there is often one superordinate term and two hyponyms. The three exceptions among the primate examples are woolly and howler monkeys, each of which has three hyponyms, and the night monkey (*Aotus*), which has no superordinate term. As if motivated by such anomalies, we find interspeaker disagreement about the classification of these species. Nomenclature for folk "genera" with two local species—bëchun (*Cebus*) and sipi (*Saguinus*)—follow this same pattern, suggesting that these biologically legitimate classifications may have been the model for the apparently superfluous practice of overdifferentiating game species. With respect to this labeling pattern, we note that sometimes the hyponyms are descriptive modifications of the superordinate term (e.g., achu çhëşhë "black howler monkey"), while in other cases one or two hyponyms will be monomorphemic.

In three of the five cases where there is disagreement about the status of an "archaic" synonym, the disagreement hinges upon whether the term is really a synonym or a hyponym; examples include the two saki monkey (*Pithecia*) names bëshudu and mamu. By contrast, the disputed "archaic" synonyms masoko (for the titi monkey, *Callicebus cupreus*) and chidu (for capuchin monkeys, *Cebus* spp.) are simply not recognized as legitimate by a subset of hunters who claim they are a borrowing and a term used only in myths, respectively. Closer inspection reveals that all cases of disagreement about whether a hyponym exists at all as a legitimate term involve descriptive polymorphemic terms, whereas disagreements about whether a term is a hyponym or a synonym involve monomorphemic terms. The Matses are conscious of this linguistic distinction. When they argue about animal nomenclature, the nature of the term in question will be focused on. If a speaker is trying to discredit an overdifferentiated variety that is designated by a descriptive hyponym, he may say the term is simply an ad hoc expression that can be used to describe individuals in a variable but continuous species (the high phenotypic variability of domestic dogs is often mentioned as an example). Alternatively, when the hyponym in question is monomorphemic, the person discrediting the overdifferentiated category is unlikely to suggest discarding the term. Rather, he will typically suggest it is actually a synonym (as with saki monkeys) or less frequently, a borrowing (as with titi monkeys).

ACKNOWLEDGMENTS

We are grateful to all of our Matses friends—especially Joaquín Rojas René, Fernando Shoque Uaquí Bëso, and Antonio Jiménez Tajur—who hosted our many visits to Nuevo San Juan and helped us in innumerable other ways. In Lima, Victor Pacheco and Sergio Solari (both at MUSM) provided crucial assistance in obtaining collecting and export permits from 1995 to 1999. Field research funding was provided to Fleck by a Latin American Studies Program Tinker Foundation Foreign Field Research Grant, a National Science Foundation Minority Graduate Fellowship, an Ohio State University (OSU) Dean's Fellowship, an OSU Osbourn Graduate Fellowship, and a Rice University Provost's Fellowship. Additional support was provided to Voss by grants from the National Geographic Society and the AMNH Center for Conservation and Biodiversity.

Back at the museum Patricia Brunauer and Ingrid Lennon helped us track down dozens of important bibliographic items (every bit as elusive as shy primates), and Patricia J. Wynne drew figures 1–3. Paúl Velazco kindly measured several vouchers specimens in Lima, and Larry Heaney hosted a weeklong visit to the Field Museum where Voss was able to examine Kalinowski's important material from Boca Río Yaquerana, Quebrada Esperanza, and Santa Cecilia. Haven Wiley shared the results of his then unpublished research on the Olallas' collecting activities in Loreto and helped us locate accurate geographic coordinates for Marupa. Lastly, we thank Louise Emmons, Eckhard Heymann, Anthony Rylands, Paúl Velazco, and Peter Whiteley for reading our manuscript and making helpful suggestions to improve it.

REFERENCES

Amanzo, J. 2006. Medium and large mammals, appendix 6. *In* C. Vriesendorp, N. Pitman, and J.I. Rojas M., et al. (editors). Perú: Matsés (Rapid Biological Inventories 16): 205–213, 320–327. Chicago: Field Museum.

Anderson, A.B. 1981. White-sand vegetation of Brazilian Amazonia. Biotropica 13: 199–210.

Aquino, R. 1978. La fauna primatológica en áreas de Jenaro Herrera. Proyecto de Asentamiento Rural Integral en Jenaro Herrera, Boletín Técnico 1: 1–14 + six unnumbered pages of tabular data.

Aquino, R. 1988. Preliminary survey on the population densities of *Cacajao calvus ucayalii.* Primate Conservation 9: 24–26.

Aquino, R. 1998. Some observations on the ecology of *Cacajao calvus ucayalii* in the Peruvian Amazon. Primate Conservation 18: 21–24.

Aquino, R., and R.E. Bodmer. 2004. Plantas útiles en la alimentación de primates en la cuenca del río Samiria, Amazonía peruana. Neotropical Primates 12: 1–6.

Aquino, R., and F. Encarnación. 1988. Population densities and geographic distribution of night monkeys (*Aotus nancymai* and *Aotus vociferans*) (Cebidae: Primates) in northeastern Peru. American Journal of Primatology 14: 375–381.

Aquino, R., F.M. Cornejo, E.P. Lozano, and E.W. Heymann. 2009. Geographic distribution and demography of *Pithecia aequatorialis* (Pitheciidae) in Peruvian Amazonia. American Journal of Primatology 71: 964–968.

Armada, J.L.A., C.M.L. Barroso, M.M.C. Lima, J.A.P.C. Muniz, and H.N. Seuánez. 1987.

Chromosome studies in *Alouatta belzebul*. American Journal of Primatology 13: 283–296.

Ascorra, C.F., D.L. Gorchov, and F. Cornejo. 1993. The bats from Jenaro Herrera, Peru. Mammalia 57: 533–552.

Ashley, M.V., and J.L. Vaughn. 1995. Owl monkeys (*Aotus*) are highly divergent in mitochondrial cytochrome *c* oxidase (COII) sequences. International Journal of Primatology 16: 793–806.

Bartecki, U., and E.W. Heymann. 1987. Sightings of red uakaries, *Cacajao calvus rubicundus*, at the Rio Blanco, Peruvian Amazonia. Primate Conservation 8: 34–36.

Bennett, C.L., S. Leonard, and S. Carter. 2001. Abundance, diversity, and patterns of distribution of primates on the Tapiche River in Amazonian Peru. American Journal of Primatology 54: 119–126.

Bodmer, R.E. 1990. Responses of ungulates to seasonal inundations in the Amazon floodplain. Journal of Tropical Ecology 6: 191–201.

Bodmer, R.E., and P. Puertas. 2003. A brief history of the Yavarí valley. *In* N. Pitman, C. Vriesendorp, and D. Moskovits (editors). Perú: Yavarí (Rapid Biological Inventories 11): 172–176. Chicago: Field Museum.

Bodmer, R.E., T.G. Fang, and L.M. Ibáñez. 1988. Ungulate management and conservation in the Peruvian Amazon. Biological Conservation 45: 303–310.

Boinski, S., and S.J. Cropp. 1999. Disparate data sets resolve squirrel monkey (*Saimiri*) taxonomy: implications for behavioral ecology and biomedical usage. International Journal of Primatology 20: 237–256.

Bonvicino, C.R., M.E.B. Fernandes, and H.N. Seuánez. 1995. Morphological analysis of *Alouatta seniculus* species group (Primates, Cebidae): a comparison with biochemical and karyological data. Human Evolution 10: 169–176.

Bonvicino, C.R., B. Lemos, and H.N. Seuánez. 2001. Molecular phylogenetics of howler monkeys (*Alouatta*, Platyrrhini), a comparison with karyotypic data. Chromosoma 110: 241–246.

Bowler, M., J.N. Murrieta, M. Recharte, P. Puertas, and R. Bodmer. 2009. Peruvian red uakari monkeys (*Cacajao calvus ucayalii*) in the Pacaya-Samiria national reserve—a range extension across a major river barrier. Neotropical Primates 16: 34–37.

Brandon-Jones, D. 2006. Apparent confirmation that *Alouatta villosa* (Gray, 1845) is a senior synonym of *A. pigra* Lawrence, 1933 as the species-group name for the black howler monkey of Belize, Guatemala, and Mexico. Primate Conservation 21: 41–43.

Bravo, A., and J.A. Ríos. 2007. Mammals. *In* C. Vriesendorp et al. (editors). Perú: Nanay-Mazán-Arabela (Rapid Biological Inventories 18): 140–145, 226–232. Chicago: Field Museum.

Brooks, D.M., and L. Pando-Vasquez. 1997. Crossing the great barrier: *Callicebus discolor* north of the Napo River. Neotropical Primates 5: 11.

Brumback, R.A. 1973. Two distinctive types of owl monkeys (*Aotus*). Journal of Medical Primatology 2: 284–289.

Brumback, R.A., R.D. Staton, S.A. Benjamin, and C.M. Lang. 1971. The chromosomes of *Aotus trivirgatus* Humboldt, 1812. Folia Primatologica 15: 264–273.

Cabrera, A. 1958 ("1957"). Catálogo de los mamíferos de América del Sur [part 1]. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Ciencias Zoológicas) 4 (1): i–iv, 1–307.

Campbell, C.J., et al. 2005. Terrestrial behavior of *Ateles*. International Journal of Primatology 26: 1039–1051.

Cant, J.G.H. 1986. Locomotion and feeding postures of spider and howling monkeys: field study and evolutionary interpretation. Folia Primatologica 46: 1–14.

Carpenter, C.R. 1935. Behavior of red spider monkeys in Panama. Journal of Mammalogy 16: 171–180.

Casado, F., et al. 2010. Mitochondrial divergence between 2 populations of the hooded capuchin, *Cebus* (*Sapajus*) *cay* (Platyrrhini, Primates). Journal of Heredity 101: 261–269.

Castellanos, H.G., and P. Chanin. 1996. Seasonal differences in food choice and patch preference of long-haired spider monkeys (*Ateles belzebuth*). *In* M.A. Norconk, A.L. Rosenberger, and P.A. Garber (editors). Adaptive radiations of Neotropical primates: 451–466. New York: Plenum.

Castro, R., and P. Soini. 1977. Field studies on *Saguinus mystax* and other callitrichids in Amazonian Peru. *In* D.G. Kleiman (editors). The biology and conservation of the Callitrichidae: 73–78. Washington, DC: Smithsonian Institution Press.

Chapman, C.A. 1989. Spider monkey sleeping sites: use and availability. American Journal of Primatology 18: 53–60.

Chapman, C.A. 1990. Association patterns of spider monkeys: the influence of ecology and sex on social organization. 26: 409–414.

Collins, A.C. 2008. The taxonomic status of spider monkeys in the twenty-first century. *In* C.J. Campbell (editors). Spider monkeys: behavior, ecology, and evolution of the genus *Ateles*: 50–78. Cambridge: Cambridge University Press.

Collins, A.C., and J.M. Dubach. 2000. Phylogenetic relationships of spider monkeys (*Ateles*) based on mitochondrial DNA variation. International Journal of Primatology 21: 381–420.

Consigliere, S., R. Stanyon, U. Koehler, G. Agoramoorthy, and J. Wienberg. 1996. Chromosome painting defines genomic rearrangements between red howler monkey subspecies. Chromosome Research 4: 264–270.

Cormier, L. 2007. A preliminary review of Neotropical primates in the subsistence and symbolism of indigenous lowland South American peoples. Ecology and Environmental Anthropology 2: 14–32.

Cortés-Ortiz, L., et al. 2003. Molecular systematics and biogeography of the Neotropical monkey genus *Alouatta*. Molecular Phylogenetics and Evolution 26: 64–81.

Costello, R.K., C. Dickinson, A.L. Rosenberger, S. Boinski, and F.S. Szalay. 1993. Squirrel monkey (genus *Saimiri*) taxonomy, a multidisciplinary study of the biology of species. *In* W.H. Kimbel and L.B. Martin (editors). Species, species concepts, and primate evolution: 177–210. New York: Plenum.

Cropp, S.J., A. Larson, and J.M. Cheverud. 1999. Historical biogeography of tamarins, genus *Saguinus*: the molecular phylogenetic evidence. American Journal of Physical Anthropology 108: 65–89.

Cruz Lima, E. da. 1945. Mammals of Amazonia, vol. 1. General introduction and Primates. Rio de Janeiro: Belém do Pará: Museu Paraense Emílio Goeldi.

Daly, J.W., et al. 1992. Frog secretions and hunting magic in the upper Amazon: identification of a peptide that interacts with an adenosine receptor. Proceedings of the National Academy of Sciences of the United States of America 89: 10960–10963.

da Silva, M.N.F., G.H. Shepard, Jr., and D.W. Yu. 2005. Conservation implications of primate hunting practices among the Matsigenka of Manu National Park. Neotropical Primates 13 (2): 31–36.

Defler, T.R., and M.L. Bueno. 2007. *Aotus* diversity and the species problem. Primate Conservation 22: 55–70.

Defler, T.R., and J.I. Hernández-Camacho. 2002. The true identity and characteristics of *Simia albifrons* Humboldt, 1812: description of neotype. Neotropical Primates 10: 49–64.

Defler, T.R., M.L. Bueno, and J. García. 2010. *Callicebus caquetensis*: a new and critically endangered titi monkey from southern Caquetá, Colombia. Primate Conservation 25: 1–9.

de la Torre, S. 1996. Notes on the distributions of the Ecuadorean callitrichids. Neotropical Primates 4: 88.

de la Torre, S. 2000. Primates de la Amazonía del Ecuador (Serie Fauna del Ecuador 1). Quito: SIMBIOE.

Dew, J.L. 2005. Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagothricha poeppigii* and *Ateles belzebuth belzebuth*. International Journal of Primatology 26: 1107–1135.

Dew, J.L. 2008. Spider monkeys as seed dispersers. *In* C.J. Campbell (editors). Spider monkeys: behavior, ecology, and evolution of the genus *Ateles*: 155–182. Cambridge: Cambridge University Press.

Di Fiore, A. 2002. Predator sensitive foraging in ateline primates. *In* L.E. Miller (editors). Eat or be eaten: predator sensitive foraging among primates: 242–267. Cambridge: Cambridge University Press.

Di Fiore, A., and S.A. Suarez. 2007. Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. Animal Cognition 10: 317–329.

Di Fiore, A., A. Link, and J.L. Dew. 2008. Diets of wild spider monkeys. *In* C.J. Campbell (editors). Spider monkeys: behavior, ecology, and evolution of the genus *Ateles*: 81–137. Cambridge: Cambridge University Press.

DMA. 1989. Gazetteer of Peru. 2nd ed. Washington, DC: Defense Mapping Agency.

DMA. 1990. Francisco de Orellana, Peru, 2364 J631. 1st ed. [1:100,000 topographic sheet]. Washington, DC: Defense Mapping Agency (Interamerican Geodetic Survey).

DMA. 1995. Remoyacu, Peru, 2260 J631. 1st ed. [1:100,000 topographic sheet]. Washington, DC: Defense Mapping Agency (Interamerican Geodetic Survey).

Dubost, G. 1988. Ecology and social life of the red acouchy, *Myoprocta exilis*; comparison with the orange-rumped agouti, *Dasyprocta leporina*. Journal of Zoology (London) 214: 107–123.

Eisenberg, J.F., and R.E. Kuehn. 1966. The behavior of *Ateles geoffroyi* and related species. Smithsonian Miscellaneous Collections 151 (8): i–iv, 1–63, 6 pls.

Elliot, D.G. 1913 ("1912"). A review of the primates. Vol. 2. New York: American Museum of Natural History.

Ellsworth, J.A., and G.A. Hoelzer. 2006. Genetic evidence on the historical biogeography of Central American howler monkeys. *In* S.M. Lehman and J.G. Fleagle (editors). Primate biogeography: 81–103. New York: Springer.

Emmons, L.H. 1988. A field study of ocelots (*Felis pardalis*) in Peru. Revue d'Ecologie (La Terre et la Vie) 43: 133–157.

Emmons, L.H. 1990. Neotropical rainforest mammals: a field guide. Chicago: University of Chicago Press.

Emmons, L.H. 1997. Neotropical rainforest mammals: a field guide. 2nd ed. Chicago: University of Chicago Press.

Erikson, P. 1994. Los Mayoruna. *In* Santos-Granero, F. and F. Barclay (editors). Guía etnográfica de la Alta Amazonía, vol. 2: 1–127. Quito: Facultad Latinoamericana de Ciencias Sociales.

Erikson, P. 2000. The social significance of pet-keeping among Amazonian Indians. *In* A.L. Podberscek, E.S. Paul, and J.A. Serpell (editors). Companion animals and us; exploring the relationships between people and pets: 7–26. Cambridge: Cambridge University Press.

Faura-Gaig, G.S. 1964. Los ríos de la Amazonía peruana. Callao: Colegio Militar Leoncino Prado.

Felton, A.M., A. Felton, J.T. Wood, and D.B. Lindenmayer. 2008. Diet and feeding ecology of *Ateles chamek* in a Bolivian semihumid forest: the importance of *Ficus* as a staple food resource. International Journal of Primatology 29: 379–403.

Fine, P., N. Dávila, R. Foster, I. Mesones, and C. Vriesendorp. 2006. Flora and vegetation. *In* C. Vriesendorp, N. Pitman, and J.I. Rojas M., et al. (editors). Perú: Matsés (Rapid Biological Inventories 16): 174–183. Chicago: Field Museum.

Fleck, D.W. 1997. Mammalian diversity in rainforest habitats recognized by the Matses Indians in the Peruvian Amazon. M.S. thesis, Ohio State University, Columbus.

Fleck, D.W. 2007. ¿Quiénes eran los mayoruna de Tessmann? Amazonía Peruana 30: 305–331.

Fleck, D.W., and J.D. Harder. 1995. Ecology of marsupials in two Amazonian rain forests in northeastern Peru. Journal of Mammalogy 76: 809–818.

Fleck, D.W., and J.D. Harder. 2000. Matses Indian rainforest habitat classification and mammalian diversity in Amazonian Peru. Journal of Ethnobiology 20: 1–36.

Fleck, D.W., and R.S. Voss. 2006. On the origin and cultural significance of unusually large synonym sets in some Panoan languages of western Amazonia. Anthropological Linguistics 48: 335–368.

Fleck, D.W., R.S. Voss, and J.L. Patton. 1999. Biological basis of saki (*Pithecia*) species recognized by Matses Indians of Amazonian Peru. International Journal of Primatology 20: 1005–1028.

Fleck, D.W., R.S. Voss, and N.B. Simmons. 2002. Underdifferentiation and sublexemic categories: an example from Matses bat classification. Journal of Ethnobiology 22: 63–104.

Flynn, J.J., and A.R. Wyss. 1998. Recent advances in South American mammalian paleontology. TREE 13: 449–454.

Fooden, J. 1963. A revision of the woolly monkeys (genus *Lagothrix*). Journal of Mammalogy 44: 213–247.

Ford, S.M. 1994. Taxonomy and distribution of the owl monkey. *In* J.F. Baer, R.E. Weller, and I. Kakoma (editors). *Aotus*: the owl monkey: 1–57. San Diego, CA: Academic Press.

Freese, C.H., P.G. Heltne, N. Castro R, and G. Whitesides. 1982. Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. International Journal of Primatology 3: 53–90.

Froehlich, J.W., J. Supriatna, and P.H. Froehlich. 1991. Morphometric analyses of *Ateles*: systematic and biogeographic implications. American Journal of Primatology 25: 1–22.

Garber, P.A. 1993. Seasonal patterns of diet and ranging in two species of tamarin monkeys: stability versus variability. International Journal of Primatology 14: 145–166.

Gentry, A.H. 1993. A field guide to the families and genera of woody plants of northwest South America (Colombia, Ecuador, Peru) with supplementary notes on herbaceous taxa. Washington, DC: Conservation International.

Goodnight, C.J., and M.L. Goodnight. 1943. Phalangida from South America. American Museum Novitates 1234: 1–19.

Gorchov, D.L., F. Cornejo, C. Ascorra, and M. Jaramillo. 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. *In* T.H. Fleming and A. Estrada (editors). Frugivory and seed dispersal: 339–349. Dordrecht: Kluwer Academic Publishers.

Gregorin, R. 2006. Taxonomia e variação geográfica das espécies do gênero *Alouatta* Lacépède (Primates, Atelidae) no Brasil. Revista Brasileira de Zoologia 23: 64–144.

Groves, C. 2001. Primate taxonomy. Washington, DC: Smithsonian Institution Press.

Groves, C. 2005. Order Primates. *In* D.E. Wilson and D.M. Reeder (editors). Mammal species of the world, 3rd ed., vol. 1: 111–184. Baltimare, MD: Johns Hopkins University Press.

Haugaasen, T., and C.A. Peres. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. American Journal of Primatology 67: 243–258.

Henderson, A. 1994. The palms of the Amazon. New York: Oxford University Press.

Henderson, A., G. Galeano, and R. Beranal. 1995. Field guide to the palms of the Americas. Princeton, NJ: Princeton University Press.

Hernández-Camacho, J., and R.W. Cooper. 1976. The nonhuman primates of Colombia. *In* R.W. Thorington and P.G. Heltne (editors). Neotropical primates, field studies and conservation: 35–69. Washington, DC: National Academy of Sciences.

Hershkovitz, P. 1949. Mammals of northern Colombia, preliminary report no. 4: monkeys (Primates), with taxonomic revisions of some forms. Proceedings of the United States National Museum 98: 323–427.

Hershkovitz, P. 1963. A systematic and zoogeographic account of the monkeys of the genus *Callicebus* (Cebidae) of the Amazonas and Orinoco river basins. Mammalia 27: 1–79, pls. I–XI.

Hershkovitz, P. 1977. Living New World monkeys (Platyrrhini), with an introduction to Primates. Vol. 1. Chicago: University of Chicago Press.

Hershkovitz, P. 1979. The species of sakis, genus *Pithecia* (Cebidae, Primates), with notes on sexual dichromatism. Folia Primatologica 31: 1–22.

Hershkovitz, P. 1983. Two new species of night monkeys, genus *Aotus* (Cebidae, Platyrrhini): a preliminary report on *Aotus* taxonomy. American Journal of Primatology 4: 209–243.

Hershkovitz, P. 1984. Taxonomy of squirrel monkeys genus *Saimiri* (Cebidae, Platyrrhini): a preliminary report with description of a hitherto unnamed form. American Journal of Primatology 7: 155–210.

Hershkovitz, P. 1987a. A history of the Recent mammalogy of the Neotropical region from 1492 to 1850. Fieldiana Zoology (new ser.) 39: 11–98.

Hershkovitz, P. 1987b. Uakaries, New World monkeys of the genus *Cacajao* (Cebidae Platyrrhini): a preliminary taxonomic review with the description of a new subspecies. American Journal of Primatology 12: 1–53.

Hershkovitz, P. 1987c. The taxonomy of South American sakis, genus *Pithecia* (Cebidae, Platyrrhini): a preliminary report and critical review with the description of a new species and a new subspecies. American Journal of Primatology 12: 387–468.

Hershkovitz, P. 1990. Titis, New World monkeys of the genus *Callicebus* (Cebidae, Platyrrhini): a preliminary taxonomic review. Fieldiana Zoology (new ser.) 55: 1–109.

Heymann, E.W. 1989. Observaciones preliminares del mono huapo rojo, *Cacajao calvus ucayalii* (Primates: Platyrrhini) en el Río Blanco, Amazonía Peruana. Medio Ambiente 10: 113–117.

Heymann, E.W. 1990. Interspecific relations in a mixed-species troop of moustached tamarins, *Saguinus mystax*, and saddle-back tamarins, *Saguinus fuscicollis* (Platyrrhini: Callitrichidae), at the Río Blanco, Peruvian Amazonia. American Journal of Primatology 21: 115–127.

Heymann, E.W. 2000. Field observations of the golden-mantled tamarin, *Saguinus tripartitus*, on the Río Curaray, Peruvian Amazonia. Folia Primatologica 71: 392–398.

Heymann, E.W., and R. Aquino. 1994. Exploraciones primatológicas en las quebradas Blanco, Blanquillo, y Tangarana (Río Tahuayo, Amazonía Peruana). Folia Amazónica 6: 125–138.

Heymann, E.W., and R. Aquino. 2010. Peruvian red uakaries (*Cacajao calvus ucayalii*) are not flooded forest specialists. International Journal of Primatology 31: 751–758.

Heymann, E.W., and H. Buchanan-Smith. 2000. The behavioural ecology of mixed-species troops of callitrichine primates. Biological Reviews 75: 169–190.

Heymann, E.W., C. Knogge, and E.R. Tirado H. 2000. Vertebrate predation by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*. American Journal of Primatology 51: 153–158.

Heymann, E.W., F. Encarnación C, and J.E. Canaquin Y. 2002. Primates of the Río Curaray, northern Peruvian Amazon. International Journal of Primatology 23: 191–201.

Hill, W.C.O. 1960. Primates, comparative anatomy and taxonomy. IV. Cebidae, part A. Edinburgh: Edinburgh University Press.

Hill, W.C.O. 1962. Primates, comparative anatomy and taxonomy. V. Cebidae, part B. Edinburgh: Edinburgh University Press.

Hodun, A., C.T. Snowdon, and P. Soini. 1981. Subspecific variation in the long calls of the tamarin *Saguinus fuscicollis*. Zeitschrift für Tierpsychologie 57: 97–110.

Hoorn, C. 1993. Geología del nororiente de la Amazonia peruana: la formación Pebas. *In* R. Kalliola, M. Puhakka, and W. Danjoy (editors). Amazonía peruana: vegetación húmeda tropical en el llano subandino: 69–85. Jyväskylä: Proyecto Amazonia, Universidad de Turku.

Hurtado-Gonzales, J.L., and R.E. Bodmer. 2004. Assessing the sustainability of brocket deer hunting in the Tamshiyacu-Tahuayo Communal Reserve, northeastern Peru. Biological Conservation 116: 1–7.

Husson, A.M. 1978. The mammals of Suriname. Zoölogische Monographieën van het Rijksmuseum van Natuurlijke Historie 2: i–xxxiv, 1–569, 151 pls.

ICZN. 1999. International code of zoological nomenclature. 4th ed. London: International Trust for Zoological Nomenclature.

Iwanaga, S., and S.F. Ferrari. 2001. Party size and diet of syntopic atelids (*Ateles chamek* and

Lagothrix cana) in southwestern Brazilian Amazonia. Folia Primatologica 72: 217–227.

Iwanaga, S., and S.F. Ferrari. 2002. Geographic distribution and abundance of woolly (*Lagothrix cana*) and spider (*Ateles chamek*) monkeys in southwestern Brazilian Amazonia. American Journal of Primatology 56: 57–64.

Izawa, K. 1975. Foods and feeding behavior of monkeys in the upper Amazon Basin. Primates 16: 295–316.

Izawa, K. 1976. Group sizes and composition of monkeys in the upper Amazon Basin. Primates 17: 367–399.

Izawa, K. 1978. A preliminary survey of uacari and Goeldi's monkey in Río Tapiche, Peru. Monkey 22: 6–13 [in Japanese; not seen].

Izawa, K. 1979. Studies on the peculiar distribution pattern of *Callimico*. Kyoto University Overseas Research Reports of New World Monkeys (1979): 1–19.

Izawa, K. 1993. Soil-eating by *Alouatta* and *Ateles*. International Journal of Primatology 14: 229–242.

Izawa, K., K. Kimura, and A. Samper N. 1979. Grouping of the wild spider monkey. Primates 20: 503–512.

Janson, C.H., and L.H. Emmons. 1990. Ecological structure of the nonflying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. *In* A.H. Gentry (editors). Four Neotropical rainforests: 314–338. New Haven: Yale University Press.

Jerozolimski, A., and C.A. Peres. 2003. Bringing home the biggest bacon: a cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. Biological Conservation 111: 415–425.

Jorge, M.L.S.P., and P.M. Velazco. 2006. Mammals. *In* C. Vriesendorp et al. (editors). Perú: Sierra del Divisor (Rapid Biological Inventories 17): 196–204. Chicago: Field Museum.

Julliot, C. 1994. Predation of a young spider monkey (*Ateles paniscus*) by a crested eagle (*Morphnus guianensis*). Folia Primatologica 63: 75–77.

Kalliola, R., M. Puhakka, and W. Danjoy (editors). 1993. Amazonía peruana: vegetación húmeda tropical en el llano subandino. Jyväskylä: Proyecto Amazonia, Universidad de Turku.

Kellogg, R., and E.A. Goldman. 1944. Review of the spider monkeys. Proceedings of the United States National Museum 96 (3186): 1–45.

Klein, L.L., and D.B. Klein. 1977. Feeding behavior of the Colombian spider monkey. *In* T.H. Clutton-Brock (editors). Primate ecology: studies of feeding and ranking behavior in lemurs, monkeys, and apes: 153–181. London: Academic Press.

Kobayashi, S. 1995. A phylogenetic study of titi monkeys, genus *Callicebus*, based on cranial measurements: I. Phyletic groups of *Callicebus*. Primates 36: 101–120.

Kraft, R. 1983. Die von J.B. von Spix beschreibenen neotropischen Primaten und Chiropteren. Verzeichnis der in der Zoologischen Staatssammlung München aufbewahrten Typusexemplare. Spixiana suppl. 9: 429–441.

Kumamoto, A.T., and M.L. Houck. 2001. Cytogenetic identification of a hybrid owl monkey, *Aotus nancymaae* × *Aotus lemurinus griseimembra*. Journal of Zoo and Wildlife Medicine 32: 130–133.

Lamotte, S. 1990. Fluvial dynamics and succession in the lower Ucayali River basin, Peruvian Amazonia. Forest Ecology and Management 33/34: 141–156.

Lavergne, A., S. Lacote, F. Catzeflis, O. Mercereau-Puijalon, and H. Contamin. 2002. Taxonomie et relations phylogénétique des singes-écureuils (genre *Saimiri*) en Amérique du Sud: l'apport du gène mitochondrial cytochome *b*. Primatologie 5: 249–274.

Lavergne, A., et al. 2010. Phylogeny and phylogeography of squirrel monkeys (genus *Saimiri*) based on cytochrome *b* genetic analysis. American Journal of Primatology 72: 242–253.

Lawrence, B. 1933. Howler monkeys of the *palliata* group. Bulletin of the Museum of Comparative Zoology 75: 315–354.

Lessa, E.P., and R.A. Fariña. 1996. Reassessment of extinction patterns among the Late Pleistocene mammals of South America. Paleontology 39: 651–662.

Lessa, E.P., B. Van Valkenburgh, and R.A. Fariña. 1997. Testing hypotheses of differential mammalian extinctions subsequent to the Great American Biotic Interchange. Palaeogeography, Palaeoclimatology, Palaeoecology 135: 157–162.

Lima, M.M.C., and H.N. Seuánez. 1991. Chromosome studies in the red howler monkey, *Alouatta seniculus stramineus* (Platyrrhini, Primates): description of an $X_1X_2Y_1Y_2/X_1X_1X_2X_2$ sex-chromosome system and karyological comparisons with other subspecies. Cytogenetic and Genome Research 57: 151–156.

Lima, M.M.C., et al. 1990. Chromosome and protein variation in red howler monkeys. Revista Brasileira de Genética 13: 789–802.

Link, A., and A. Di Fiore. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. Journal of Tropical Ecology 22: 235–246.

Lönnberg, E. 1940a. Notes on some members of the genera *Lagothrix* and *Ateles*. Arkiv för Zoologi 32A (25): 1–14.

Lönnberg, E. 1940b. Notes on marmosets. Arkiv för Zoologi 32A (10): 1–22.

López-Parodi, J., and D. Freitas. 1990. Geographical aspects of forested wetlands in the Lower Ucayali, Peruvian Amazonia. Forest Ecology and Management 33/34: 157–168.

Malygin, V.M., V.M. Aniskin, S.I. Isaev, and A.N. Milishnikov. 1994. *Amphinectomys savamis* gen. et sp. n., a new genus and a new species of water rat (Cricetidae, Rodentia) from Peruvian Amazon. Zoologicheskii Zhurnal 73: 195–208 [in Russian].

Marengo, J.A. 1983. Estudio agroclimático en la zona de Jenaro Herrera (Requena/Loreto) y climático en la selva baja norte del Perú. Unpublished thesis, Universidad Nacional Agraria La Molina, Lima, Peru.

Marroig, G., and J.M. Cheverud. 2004. Cranial evolution in sakis (*Pithecia*, Platyrrhini) I: Interspecific differentiation and allometric patterns. American Journal of Physical Anthropology 125: 266–278.

Marshall, L.G., and T. Semper. 1993. Evolution of the Neotropical Cenozoic land mammal fauna in its chronologic, stratigraphic, and tectonic context. *In* P. Goldblatt (editors). Biological relationships between Africa and South America: 329–392. New Haven: Yale University Press.

Matauschek, C., C. Roos, and E.W. Heymann. 2011. Mitochondrial phylogeny of tamarins (*Saguinus* Hoffmannsegg 1807) with taxonomic and biogeographic implications for the *S. nigricollis* species group. American Journal of Physical Anthropology 144: 564–574.

Matsuda, I., and K. Izawa. 2008. Predation of wild spider monkeys at La Macarena, Colombia. Primates 49: 65–68.

Medeiros, M.A., et al. 1997. Radiation and speciation of spider monkeys, genus *Ateles*, from the cytogenetic viewpoint. American Journal of Primatology 42: 167–178.

Menezes, A.N., C.R. Bonvincino, and H.N. Seuánez. 2010. Identification, classification and evolution of owl monkeys (*Aotus*, Illiger 1811). BMC Evolutionary Biology 10: 248 (15 pp.).

Milton, K. 1991. Comparative aspects of diet in Amazonian forest-dwellers. Philosophical Transactions of the Royal Society of London B Biological Sciences 334: 253–263.

Milton, K. 1994. No pain, no game. Natural History 103: 44–50.

Minezawa, M., M. Harada, O.C. Jordan, and C.J.V. Borda. 1985. Cytogenetics of Bolivian endemic red howler monkeys (*Alouatta seniculus sara*): accessory chromosomes and Y-autosome translocation related numerical variations. Kyoto University Overseas Research Report of New World Monkeys 5: 7–16.

Mittermeier, R.A. 1978. Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus*. Folia Primatologica 30: 161–193.

Mittermeier, R.A., and M.G.M. van Roosmalen. 1981. Preliminary observations on habitat utilization and diet in eight Surinam monkeys. Folia Primatologica 36: 1–39.

Montenegro, O.L. 2004. Natural licks as keystone resources for wildlife and people in Amazonia. Ph.D. dissertation, Department of Wildlife Ecology and Conservation, University of Florida, Gainesville.

Montenegro, O., and M. Escobedo. 2004. Mammals. *In* N. Pitman., et al. 2004. Perú: Ampiyacu, Apayacu, medio Putumayo (Rapid Biological Inventories 12): 165–171, 254–261. Chicago: Field Museum.

Myers, C.W. 2000. A history of herpetology at the American Museum of Natural History. Bulletin of the American Museum of Natural History 252: 1–232.

Nadjafzadeh, M.N., and E.W. Heymann. 2008. Prey foraging of red titi monkeys, *Callicebus cupreus*, in comparison to sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*. American Journal of Physical Anthropology 135: 56–63.

Napier, P.H. 1976. Catalogue of primates in the British Museum (Natural History). Part 1: families Callitrichidae and Cebidae. London: British Museum (Natural History).

Neville, M.K., K.E. Glander, F. Braza, and A.B. Rylands. 1988. The howling monkeys, genus *Alouatta*. *In* R.A. Mittermeier, A.B. Rylands, A.F. Coimbra-Filho, and G.A.B. da Fonseca (editors). Ecology and behavior of Neotropical primates, vol. 2: 349–453. Washington, DC: World Wildlife Fund.

Nickle, D.A., and E.W. Heymann. 1996. Predation on Orthoptera and other orders of insects by tamarin monkeys, *Saguinus mystax mystax* and *Saguinus fuscicollis nigrifrons* (Primates: Callitrichidae), in north-eastern Peru. Journal of Zoology (London) 239: 799–819.

Nieves, M., M.S. Asunce, M.I. Rahn, and M.D. Mudry. 2005. Phylogenetic relationships among some *Ateles* species: the use of chromosomic and molecular characters. Primates 46: 155–164.

Nunes, A. 1998. Diet and feeding ecology of *Ateles belzebuth belzebuth* at Maracá Ecological Station, Roraima, Brazil. Folia Primatologica 1998: 61–76.

Oliveira, E.H.C. de., et al. 2002. The phylogeny of howler monkeys (*Alouatta*, Platyrrhini): reconstruction by multicolor cross-species chromosome painting. Chromosome Research 10: 669–683.

Opazo, J.C., D.E. Wildman, T. Prychitko, R.M. Johnson, and M. Goodman. 2006. Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). Molecular Phylogenetics and Evolution 40: 274–280.

Pacheco, V. 1991. A new species of *Scolomys* (Muridae: Sigmodontinae) from Peru. Publicaciones del Museo de Historia Natural Universidad Nacional Mayor de San Marcos (Serie A, Zoología) 37: 1–3.

Parry, L., J. Barlow, and C.A. Peres. 2007. Large-vertebrate assemblages of primary and secondary forests in the Brazilian Amazon. Journal of Tropical Ecology 23: 653–662.

Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America. *In* A. Keast, F.C. Erk, and B. Glass (editors). Evolution, mammals, and southern continents: 247–309. Albany: State University of New York Press.

Pavlinov, I.J. 1994. Mammals of Peruvian Amazonia in collection of Zoological Museum of Moscow M.V. Lomonosov University. *In* V.E. Sokolov (editors). Mammals of Peruvian Amazonia: 296–299. Moscow: Nauka. [in Russian].

Paynter, R.A., Jr. 1992. Ornithological gazetteer of Bolivia, 2nd. ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Peres, C.A. 1988. Primate community structure in western Brazilian Amazonia. Primate Conservation 9: 83–87.

Peres, C.A. 1990. A harpy eagle successfully captures an adult male red howler monkey. Wilson Bulletin 102: 560–561.

Peres, C.A. 1993a. Notes on the primates of the Juruá River, western Brazilian Amazonia. Folia Primatologica 61: 97–103.

Peres, C.A. 1993b. Structure and spatial organization of an Amazonian terra firme forest primate community. Journal of Tropical Ecology 9: 259–276.

Peres, C.A. 1993c. Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins in an Amazonian *terra firme* forest. Journal of Zoology (London) 230: 567–592.

Peres, C.A. 1997. Primate community structure at twenty western Amazonian flooded and unflooded forests. Journal of Tropical Ecology 13: 381–405.

Peres, C.A. 1999. The structure of nonvolant mammal communities in different Amazonian forest types. *In* J.F. Eisenberg and K.H. Redford (editors). Mammals of the Neotropics, vol. 3: 564–581. Chicago: University of Chicago Press.

Peres, C.A., J.L. Patton, and M.N.F. da Silva. 1996. Riverine barriers and gene flow in Amazonian saddle-back tamarins. Folia Primatologica 67: 113–124.

Pieczarka, J.C., R.M.de S. Barros, C.Y. Nagamachi, R. Rodrigues, and A. Espinel. 1992. *Aotus vociferans* × *Aotus nancymai*: sympatry without chromosomal hybridation [sic]. Primates 33: 239–245.

Pieczarka, J.C., R.M.de S. Barros, F.M. de Faria, Jr, and C.Y. Nagamachi. 1993. *Aotus* from the southwestern Amazonian region is geographically and chromosomally intermediate between *A. azarae boliviensis* and *A. infulatus*. Primates 34: 197–204.

Pitman, N., C. Vriesendorp, and D. Moskovits (editors). 2003. Perú: Yavarí (Rapid Biological Inventories 11). Chicago: Field Museum.

Plautz, H.L., E.C. Gonçalves, S.F. Ferrari, M.P.C. Schneider, and A. Silva. 2009. Evolutionary inferences on the diversity of the genus *Aotus* (Platyrrhini, Cebidae) from mitochondrial cytochrome oxidase *c* subunit II gene sequences. Molecular Phylogenetics and Evolution 51: 382–387.

Podolski, R.D. 1990. Effects of mixed-species association on resource use by *Saimiri sciureus* and *Cebus apella*. American Journal of Primatology 21: 147–158.

Porter, C.A., et al. 1997. Sequences of the primate ε-globin gene: implications for systematics of the marmosets and other New World primates. Gene 205: 59–71.

Puertas, P., and R.E. Bodmer. 1993. Conservation of a high diversity primate assemblage. Biodiversity and Conservation 2: 586–593.

Puhakka, M., R. Kalliola, M. Rajasilta, and J. Salo. 1992. River types, site evolution, and successional vegetation patterns in Peruvian Amazonia. Journal of Biogeography 19: 651–665.

Puhakka, M., R. Kalliola, J. Salo, and M. Rajasilta. 1993. La sucesión forestal que sigue a la migración de ríos en la selva baja Peruana. *In* R. Kalliola, M. Puhakka, and W. Danjoy (editors). Amazonía peruana: vegetación húmeda tropical en el llano subandino: 167–201. Jyväskylä: Proyecto Amazonia, Universidad de Turku.

Räsänen, M., R. Kalliola, and M. Puhakka. 1993. Mapa geoecológico de la selva baja peruana: explicaciones. *In* R. Kalliola, M. Puhakka, and W. Danjoy (editors). Amazonía peruana: vegetación húmeda tropical en el llano subandino: 207–216. Jyväskylä: Proyecto Amazonia, Universidad de Turku, Finland.

Redford, K.H., and J.G. Robinson. 1987. The game of choice: patterns of Indian and colonist hunting in the Neotropics. American Anthropologist 89: 650–667.

Robbins, M.B., A.P. Capparella, R.S. Ridgely, and S.W. Cardiff. 1991. Avifauna of the Río Manití and Quebrada Vainilla, Peru. Proceedings of the Academy of Natural Sciences of Philadelphia 143: 145–159.

Romanoff, S. 1976. El uso de la tierra por los Matses. Amazonía Peruana 1: 97–130.

Romanoff, S. 1983. Women as hunters among the Matses of the Peruvian Amazon. Human Ecology 11: 339–343.

Romanoff, S. 1984. Matses adaptations in the Peruvian Amazon. Ph.D. dissertation, Columbia University, New York.

Romanoff, S., D.M. Jiménez Huanan, F.S. Uaquí Bëso, and D.W. Fleck. 2004. Matsesën nampid chuibanaid: la vida tradicional de los Matsés. Lima: Centro Amazónico de Antropología y Aplicación Práctica.

Roosmalen, M.G.M. van. 1985. Habitat preferences, diet, feeding strategy, and social organization of the black spider monkey (*Anteles paniscus paniscus* Linnaeus 1758) in Surinam. Acta Amazonica 15 (3/4, suppl.): 1–238.

Roosmalen, M.G.M. van., and L.L. Klein. 1988. The spider monkeys, genus *Ateles*. *In* R.A. Mittermeier, A.B. Rylands, A.F. Coimbra-Filho, and G.A.B. da Fonseca (editors). Ecology and behavior of Neotropical primates, vol. 2: 455–537. Washington, DC: World Wildlife Fund.

Roosmalen, M.G.M. van., and T. van Roosmalen. 1997. An eastern extension of the geographical range of the pygmy marmoset, *Cebuella pygmaea*. Neotropical Primates 5: 3–6.

Roosmalen, M.G.M. van., and T. van Roosmalen. 2003. The description of a new marmoset genus, *Callibella* (Callitrichinae, Primates), including its molecular phylogenetic status. Neotropical Primates 11: 1–10.

Roosmalen, M.G.M. van., T. van Roosmalen, and R. Mittermeier. 2002. A taxonomic review of the titi monkeys, genus *Callicebus* Thomas, 1903, with the description of two new species, *Callicebus bernhardi* and *Callicebus stephennashi*, from Brazilian Amazonia. Neotropical Primates 10 (suppl.): 1–52.

Ruokolainen, K., and H. Tuomisto. 1993. La vegetación de terrenos no inundables (tierra firme) en la selva baja de la amazonia peruana. *In* R. Kalliola, M. Puhakka, and W. Danjoy (editors). Amazonía peruana: vegetación húmeda tropical en el llano subandino: 139–153. Jyväskylä: Proyecto Amazonia, Universidad de Turku.

Russo, S.E., and C.K. Augspurger. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecology Letters 7: 1058–1067.

Russo, S.E., C.J. Campbell, J.L. Dew, P.R. Stevenson, and S.A. Suarez. 2005. A multiforest comparison of dietary preferences and seed dispersal by *Ateles* spp. International Journal of Primatology 26: 1017–1037.

Rylands, A.B. 1987. Primate communities in Amazonian forests: their habitats and food resources. Experientia 43: 265–279.

Rylands, A.B., and D. Brandon-Jones. 1998. Scientific nomenclature of the red howlers from the northeastern Amazon in Brazil, Venezuela, and the Guianas. International Journal of Primatology 19: 879–905.

Rylands, A.B., et al. 2000. An assessment of the diversity of New World primates. Neotropical Primates 8: 61–93.

Rylands, A.B., M.C.M. Kierulff, and R.A. Mittermeier. 2005. Notes on the taxonomy and distribution of the tufted capuchin monkeys (*Cebus,* Cebidae) of South America. Lundiana 6 (suppl.): 97–110.

Rylands, A.B., A.F. Coimbra-Filho, and R.A. Mittermeier. 2009. The systematics and distributions of the marmosets (*Callithrix*, *Callibella*, *Cebuella*, and *Mico*) and callimico (*Callimico*) (Callitrichidae, Primates). *In* S.M. Ford, L.M. Porter, and L.C. Davis (editors). The smallest anthropoids, the marmoset/callimico radiation: 25–61. New York: Springer.

Rylands, A.B., et al. 2011. The range of the golden-mantled tamarin, *Saguinus tripartitus* (Milne Edwards, 1878): distributions and sympatry of four tamarins in Colombia, Ecuador, and northern Peru. Primates 52: 25–39.

Salovaara, K., R. Bodmer, M. Recharte, and C. Reyes F. 2003. Diversity and abundance of mammals. *In* N. Pitman et al. (editors). Perú: Yavarí (Rapid Biological Inventories 11): 156–164. Chicago: Field Museum.

Sampaio, D.T., and S.F. Ferrari. 2005. Predation of an infant titi monkey (*Callicebus moloch*) by a tufted capuchin (*Cebus apella*). Folia Primatologica 76: 113–115.

Sampaio, M.I.da C., M.P.C. Schneider, and H. Schneider. 1996. Contribution of genetic distance studies to the taxonomy of *Ateles*, particularly *Ateles paniscus paniscus* and *Ateles paniscus chamek*. International Journal of Primatology 14: 895–903.

Schneider, H. 2000. The current status of the New World monkey phylogeny. Anais da Academia Brasileira de Ciências 72: 165–172.

Schultz, A.H. 1962. Metric age changes and sex differences in primate skulls. Zeitschrift für Morphologie und Anthropologie 52: 239–255.

Shepard, G.H., Jr. 2002. Primates in Matsigenka subsistence and world view. *In* A. Fuentes and L.D. Wolfe (editors). Primates face to face: the conservation implication of human-nonhuman primate interconnections: 101–136. Cambridge: Cambridge University Press.

Sherman, P.T. 1991. Harpy eagle predation on a red howler monkey. Folia Primatologica 56: 53–56.

Silva, J.de S., Jr. 2002. Taxonomy of capuchin monkeys, *Cebus* Erxleben, 1777. Neotropical Primates 10: 29.

Simmen, B., and D. Sabatier. 1996. Diets of some French Guianan primates: food composition and food choices. International Journal of Primatology 17: 661–693.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85: i–xvi, 1–350.

Simpson, G.G. 1969. South American mammals. *In* E.J. Fittkau et al. (editors). Biogeography and ecology of South America: 879–909. The Hague: W. Junk.

Simpson, G.G. 1980. Splendid isolation, the curious history of South American mammals. New Haven, CT: Yale University Press.

Smith, J.D. 1970. The systematic status of the black howler monkey, *Alouatta pigra* Lawrence. Journal of Mammalogy 51: 358–369.

Soini, P. 1986. A synecological study of a primate community in the Pacaya-Samiria National Reserve, Peru. Primate Conservation 7: 63–71.

Soini, P. 1988. The pygmy marmoset, genus *Cebuella*. *In* R.A. Mittermeier, A.F. Coimbra-Filho, and G.A.B. da Fonseca (editors). Ecology and behavior of Neotropical primates, vol. 2: 79–129.

Sokolov, V.E., and V.M. Malygin. 1994. Essay of the theriofauna of Peruvian Amazonia. *In* V.E. Sokolov (editors). Mammals of Peruvian Amazonia: 5–20. Moscow: Nauka. [in Russian]

Solari, S. 2007. New species of *Monodelphis* (Didelphimorphia: Didelphidae) from Peru, with notes on *M. adusta* (Thomas, 1897). Journal of Mammalogy 88: 319–329.

Spichiger, R., J. Méroz, P.A. Loizeau, and L. Stutz de Ortega. 1989–1990. Contribución a la flora de la Amazonía peruana: los árboles del arboretum Jenaro Herrera. Boissiera 43: 1–359, 44: 1–565.

Stallard, R.F. 2006. Landscape processes: geology, hydrology, and soils. *In* C. Vriesendorp et al. (editors). Perú: Matsés (Rapid Biological Inventories 16): 168–174. Chicago: Field Museum.

Stanyon, R., et al. 1995. Cytogenetic analysis shows extensive genomic rearrangements between red howler (*Alouatta seniculus* Linnaeus) subspecies. American Journal of Primatology 35: 171–183.

Steinberg, E.R., et al. 2008. The karyotype of *Alouatta pigra* (Primates: Platyrrhini): mitotic and meiotic analyses. Cytogenetic and Genome Research 122: 103–109.

Stephens, L., and M.A. Traylor, Jr. 1983. Ornithological gazetteer of Peru. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Stevenson, P.R., M.J. Quiñones, and J.A. Ahumada. 2000. Influence of fruit availability on ecological overlap among four Neotropical primates at Tinigua National Park, Colombia. Biotropica 32: 533–544.

Suarez, S.A. 2006. Diet and travel costs for spider monkeys in a nonseasonal, hyperdiverse environment. International Journal of Primatology 27: 411–436.

Symington, M.M. 1988a. Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. American Journal of Primatology 15: 45–67.

Symington, M.M. 1988b. Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). Behavior 105: 117–134.

Tagliaro, C.H., M.P.C. Schneider, H. Schneider, I. Sampaio, and M. Stanhope. 2000. Molecular studies of *Callithrix pygmaea* (Primates, Platyrrhini) based on transferrin intronic and NDI regions: implications for taxonomy and conservation. Genetics and Molecular Biology 23: 729–737.

Tapia, J., F. Encarnación, R. Aquino, L. Moya, and P. Soini. 1990. Censos poblacionales y sacas periódicas de primates en la Amazonía peruana. *In* N.E. Castro-Rodríguez (editors). La primatología en el Perú. Investigaciones primatológicas (1973–1985): 325–341. Lima: Proyecto Peruano de Primatología "Manuel Moro Sommo."

Terborgh, J. 1983. Five New World primates, a study in comparative ecology. Princeton: Princeton University Press.

Thomas, O. 1904. New *Callithrix*, *Midas*, *Felis*, *Rhipidomys*, and *Proechimys* from Brazil and Ecuador. Annals and Magazine of Natural History (ser. 7) 14: 188–196.

Thomas, O. 1905. Suggestions for the nomenclature of the cranial length measurements and of the cheek-teeth of mammals. Proceedings of the Biological Society of Washington 18: 191–196.

Thomas, O. 1913. On some rare Amazonian mammals from the collection of the Para Museum. Annals and Magazine of Natural History (ser. 8) 11: 130–136.

Thorington, R.W. 1985. The taxonomy and distribution of squirrel monkeys (*Saimiri*). *In* L.A. Rosenblum and C.L. Coe (editors). Handbook of squirrel monkey research: 1–33. New York: Plenum.

Thorington, R.W. 1988. Taxonomic status of *Saguinus tripartitus* (Milne-Edwards, 1878). American Journal of Primatology 15: 367–371.

Townsend, W.R. 1995. Cultural teachings as an ecological data base: Murui (Witoto) knowledge about primates. Latinamericanist 31: 1–7.

Valqui, M. 1999. Inventario de mamíferos de San Pedro del río Blanco, Loreto, Perú. Colaboración entre la población local y profesionales. *In* T.G. Fang, O.L. Montenegro, and R.E. Bodmer. 1999. Manejo y conservación de fauna silvestre en América Latina: 343–349. La Paz, Bolivia: Instituto de Ecología, Universidad Mayor de San Andrés.

Valqui, M. 2001. Mammal diversity and ecology of terrestrial small rodents in western Amazonia [Ph.D. dissertation, Department of Wildlife Ecology and Conservation, University of Florida, Gainesville]. Ann Arbor: UMI Dissertation Services.

Vásquez-Martínez, R., and O.L. Phillips. 2000. Allpahuayo: floristics, structure, and dynamics of a high-diversity forest in Amazonian Peru. Annals of the Missouri Botanical Garden 87: 499–527.

Vassart, M., et al. 1996. Chromosomes of *Alouatta seniculus* (Platyrrhini, Primates) from French Guiana. Journal of Heredity 87: 331–334.

Vickers, W.T. 1984. The faunal components of lowland South American hunting kills. Interciencia 9: 366–376.

Vivar, J.E. 1975. Los mayoruna: en la frontera Perú-Brasil. América Indígena 35: 329–347.

Voss, R.S., and L.H. Emmons. 1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. Bulletin of the American Museum of Natural History 230: 1–115.

Vrba, E.S. 1993. Mammalian evolution in the African Neogene and a new look at the Great American Interchange. *In* P. Goldblatt (editors). Biological relationships between Africa and South America: 393–432. New Haven, CT: Yale University Press.

Vriesendorp, C., et al. (editors). 2006a. Perú: Matsés (Rapid Biological Inventories 16). Chicago: Field Museum.

Vriesendorp, C, et al. (editors). 2006b. Perú: Sierra del Divisor (Rapid Biological Inventories 17). Chicago: Field Museum.

Wallace, R.B. 2001. Diurnal activity budgets of black spider monkeys, *Atles chamek*, in a southern Amazonian tropical forest. Neotropical Primates 9: 101–107.

Wallace, R.B. 2005. Seasonal variations in diet and foraging behavior of *Ateles chamek* in a southern Amazonian tropical forest. International Journal of Primatology 26: 1053–1075.

Wallace, R.B. 2006. Seasonal variations in black-faced black spider monkey (*Ateles chamek*) habitat use and ranging behavior in a southern Amazonian tropical forest. American Journal of Primatology 68: 313–332.

Wallace, R.B. 2008. The influence of feeding patch size and relative fruit density on the foraging behavior of the black spider monkey *Ateles chamek*. Biotropica 40: 501–506.

Wallace, R.B., H. Gómez, A. Felton, and A.M. Felton. 2006. On a new species of titi monkey, genus *Callicebus* Thomas (Primates, Pitheciidae), from western Bolivia with preliminary notes on distribution and abundance. Primate Conservation 20: 29–39.

Webb, S.D., and A. Rancey. 1996. Late Cenezoic evolution of the Neotropical mammal fauna. *In* J.B.C. Jackson, A.F. Budd, and A.G. Coates (editors). Evolution and environment in tropical America: 335–358. Chicago: University of Chicago Press.

Wesselingh, F.P., et al. 2002. Lake Pebas: a palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia. Cainozoic Research 1: 35–81.

Wildman, D.E., N.M. Jameson, J.C. Opazo, and S.V. Yi. 2009. A fully resolved genus level phylogeny of Neotropical primates. Molecular Phylogenetics and Evolution 53: 694–702.

Wiley, R.H. 2010. Alfonso Olalla and his family: the ornithological exploration of Amazonian Peru. Bulletin of the American Museum of Natural History 343: 1–68.

Youlatos, D. 2002. Positional behavior of black spider monkeys (*Ateles paniscus*) in French Guiana. International Journal of Primatology 23: 1071–1093.

Yunis, E.J., O.M.T. de Caballero, C. Ramírez, and E. Ramírez Z. 1976. Chromosomal variations in the primate *Alouatta seniculus seniculus*. Folia Primatologica 25: 215–224.

APPENDIX 1

Sample Natural History Monolog about Woolly Monkeys

The text below is a transcription and translation of a natural history monolog about woolly monkeys recorded from a 35-year-old Matses hunter on 27 June 1998 at Nuevo San Juan; the recording is two minutes and 58 seconds long. The translated text from this interview was combined with seven other texts (similarly derived from recorded interviews with other Matses men; see Materials and Methods) to produce the composite essay on woolly monkeys found on pp. 25–26. The text is presented here with a four-line analysis: the first (text) line is a phonemic transcription in the Matses language; in the second (morpheme-break) line, words have been segmented into morphemes; the third (morpheme gloss) line contains glosses for each morpheme; and the fourth (free translation) line is an English rendering of the entire sentence.

The orthography used in the first and second lines is phonemic: *a*, *e*, *ë* (a high central unrounded vowel), *i*, *o*, *u*, *p*, *t*, *k* (glottal stop syllable-finally), *b*, *d* (flap intervocalically), *m*, *n* (velar nasal before *k*), *s*, *sh* (ʃ), *şh* (ş = apico-alveolar retroflex fricative), *ts*, *ch* (tʃ), *çh* (tş = apico-alveolar retroflex affricate), *w*, *j*. Only basic forms, rather than conditioned allomorphs, are used in the morpheme-break line of the examples.

Morpheme gloss abbreviations: 1 = First Person, 3 = Third Person, Act.Nzr = Action Nominalizer, Advzr = Adverbializer, Agt.Nzr = Agent Nominalizer, Aug = Augmentative, Caus = Causative, Conjec = Conjecture, Deintens = De-intensifier, Diff.Arg = Different Set of Arguments, Dim = Diminutive, Dist.Past = Distant Past, Emph = Emphasis, Erg = Ergative, Ev.Init = Event Initiation, Gen = Genitive, Hab = Habitual, Incep = Inceptive, Incho = Inchoative, Indic = Indicative, Inst = Instrument, Inst.Nzr = Instrument Nominalizer, Intent = Intention, Intr = Intransitive agreement, Loc = Locative, Manr = Manner, Neg.A.Nzr = Negative Agent Nominalizer, Npast = Non-Past, Pat.Nzr = Patient Nominalizer, Redup = Reduplication, Rflx = Reflexive, S/A>A = subject of subordinate clause coreferential with the subject of transitive matrix clause, S/A>S = subject of subordinate clause coreferential with the subject of intransitive matrix clause, Separ = Separate, Tr = Transitive agreement.

(01) poshto chuinu
poshto chui-nu
woolly.monkey tell-Intent:1
"I'm going to tell about the woolly monkey."

(02) poshto nadkid nek
poshto nad-kid ne-e-k
woolly.monkey do.thus-Agt.Nzr be-Npast-Indic
"The woolly monkey is one that does like this."

(03) poshto kuëte bakuë chekid nek
poshto kuëte bakuë che-kid ne-e-k
woolly.monkey dicot.tree fruit eat.unchewed-Agt.Nzr be-Npast-Indic
"The woolly monkey is a tree fruit eater."

(04) poshton inkuente ikek kuëte kuidi widënuate
poshto-n inkuente ik-e-k kuëte kuidi widënua-te
woolly.monkey-Gen tail be-Npast-Indic dicot.tree branch hold-Inst.Nzr
"The woolly monkey has a tail, one for holding onto branches."

(05) adekbidi poshton ubuşhëno matish dadpenkio ikkid
adekbidi poshto-n ubuşhë-no matish dadpen-kio ik-kid
likewise:Intr woolly.monkey-Gen testicles-Loc flea many-Aug be-Hab
"Also, there are many fleas on woolly monkeys' testicles."

(06) poshto këku chekid nek kuëte
poshto këku che-kid ne-e-k kuëte
woolly.monkey tree.species eat.unchewed-Agt.Nzr be-Npast-Indic dicot.tree
bakuë abitedi
bakuë abitedi
fruit all
"Woolly monkeys are ones that eat këku fruits, all types of dicot tree fruits."

(07) adekbidi poshto uşhek mais maisek
adekbidi poshto uşh-e-k mais Redup-ek
likewise:Intr woolly.monkey sleep-Npast-Indic spread.out Iter-while:S/A>S
uşhkid poshto nek
uşh-kid poshto ne-e-k

sleep-Agt.Nzr woolly.monkey be-Npast-Indic
"Also, woolly monkeys sleep…they are ones that sleep all spread out (in different trees)."
(08) poshto utsi tanun tanumpambo iknubik
poshto utsi tanun Redup-pambo ik-nuk-bi-k
woolly.monkey other gray Deintens-Aug be-while:Diff.Arg-Emph-Separ
utsi piu piumbo poshto tsadkid
utsi piu redup-mbo poshto tsad-kid
other red Deintens-Aug woolly.monkey sit-Hab
"While some woolly monkeys are grayish, others woolly monkeys are [lit. "sit"] reddish."
(09) dadpenkio ikkid poshto nek
dadpen-kio ik-kid poshto ne-e-k
many-Aug be-Agt.Nzr woolly.monkey be-Npast-Indic
"Woolly monkeys are ones that are very many [i.e., they live in large troops]."
(10) padnuen tëmaktsëkkidëmpi tëmambo iktsëkid poshto
padnuen tëma-tsëk-kid-mpi tëma-mbo ik-tsëk-kid poshto
by.contrast few-Dim-Agt.Nzr-Dim few-Aug be-Dim-Hab woolly.monkey
daëdpatsëk
daëdpatsëk
few
"By contrast, other small troops….other [troops of] woolly monkeys are few."
(11) maisaşh uşhtoaşh badiadnuk
mais-aşh uşh-to-aşh badiad-nuk
spread.out-after:S/A>S sleep-Incho-after:S/A>S dawn-while:Diff.Arg
tsidadkid poshto sidkek
tsid-ad-kid poshto sidke-ek
gather-Rflx-Hab woolly.monkey vocalize-while:S/A>S
"After spreading out and after going to sleep, the woolly monkeys vocalize as they gather together as the day dawns."
(12) çhook kek poshto tsidadkid
imitation ke-ek poshto tsid-ad-kid
woolly.monkey.call say-while:S/A>S woolly.monkey gather-Rflx-Hab
"The woolly monkeys yell, "chooc" as they gather into a group."
(13) adashik poshto adek tsidadşhun poshton
adashik poshto adek tsid-ad-şhun poshto-n
then woolly.monkey thus:Intr gather-Rflx-after:S/A>A woolly.monkey-Erg
kapishto chedo chekid kuëte bakuë chedo
kapishto chedo che-kid kuëte bakuë chedo
cricket too/etc eat.unchewed-Hab dicot.tree fruit too/etc
"After that, after gathering together like that, the woolly monkeys eat crickets and similar animals, and dicot tree fruits, too."
(14) adashik poshto mannanënkio nadekiaşh makuëşh
adashik poshto mannan-n-kio nadeke-aşh makuëşh
then woolly.monkey hill-Loc-Aug bound.through.trees-after:S/A>S hill
potsen nadekid
potse-n nade-kid
halfway-Loc bound.through.tree-Hab
"After that, woolly monkeys bound through the trees on hill tops and on hill inclines."
(15) adashik aktiaçhon ikkid poshto nek
adashik aktiaçho-n ik-kid poshto ne-e-k
then floodplain.forest-Loc be-Agt.Nzr woolly.monkey be-Npast-Indic
"Also, woolly monkeys are ones that are found in floodplain forest."
(16) akte kuëman ikkid poshto nek
akte kuëma-n ik-kid poshto ne-e-k
river edge-Loc be-Agt.Nzr woolly.monkey be-Npast-Indic
"Woolly monkeys are ones that are found along rivers."
(17) inkuente chokid poshto nek
inkuente cho-kid poshto ne-e-k
tail have-Agt.Nzr woolly.monkey be-Npast-Indic
"The woolly monkey is one that has a tail."
(18) adekbidi bëçhëşh bëçhëşhkio poshto ikek
adekbidi bë-çhëşhë Redup-kio poshto ik-e-k

likewise:Intr face-black partly-Aug woolly.monkey be-Npast-Indic
"Also, woolly monkeys' faces are partly black."

(19) bëdapatsëk isadkid poshto nek
bëda-patsëk is-ad-kid poshto ne-e-k
good-Dim see-Rflx-Agt.Nzr woolly.monkey be-Npast-Indic
"Woolly monkeys are good-looking ones."

(20) poshton aton bakuë dekid
poshto-n aton bakuë de-kid
woolly.monkey-Erg 3Gen seedling carry.on.back-Hab
"Woolly monkeys carry their young on their backs."

(21) chishmekid poshton matsesën
chish-me-kid poshto-n matses-n
suck-Caus-Hab woolly.monkey-Erg Matses-Erg
chishmiakbimbuen
chish-me-ak-bi-mbo-en
suck-Caus-Act.Nzr-like-Aug-Manr:Tr
"Woolly monkeys suckle their young like Matses do."

(22) nidaidën kapuesa poshto nek
nidaid-n kapu-esa poshto ne-e-k
ground-Loc locomote-Neg.A.Nzr woolly.monkey be-Npast-Indic
"Woolly monkeys are ones that do not walk on the ground."

(23) abukuidi ikkid
abuk-wid-bi ik-kid
high-only-Emph be-Hab
"They stay high up (in the trees)."

(24) inkuenten widënuaşh poshto pudun pudunkid kuëte
inkuente-n widënua-aşh poshto pudun Redup-kid kuëte
tail-Inst hold-after:S/A>S woolly.monkey jump Iter-Hab dicot.tree
utsin yad yadek
utsi-n yad Redup-e-k
other-Erg pass Iter-Npast-Indic
"Woolly monkeys hold on with their tail, and then jump to another tree, constantly passing to other trees."

(25) nëbi poshto matsesën pied poshto nek
nëbi poshto matses-n pe-aid poshto ne-e-k
now woolly.monkey Matses-Erg eat-Pat.Nzr woolly.monkey be-Npast-Indic
"Now, woolly monkeys…woolly monkeys are ones that are eaten by Matses."

(26) matsesën pian seşhun pekid poshto
matses-n pia-n se-şhun pe-kid poshto
Matses-Erg arrow-Inst pierce-after:S/A>A eat-Hab woolly.monkey
"Matses kill them with arrows and then eat the woolly monkeys."

(27) nëbien chompianën kuessun pepek
nëbien chompian-n kues-şhun pe-pa-e-k
nowadays shotgun-Inst kill-after:S/A>A eat-Comment-Npast-Indic
poshto
poshto
woolly.monkey
"Nowadays, they kill them with shotguns and eat up the woolly monkeys."

(28) pian ënden seşhun penëdaşh matsesën
pia-n ënden se-şhun pe-nëdaşh matses-n
arrow-Inst before pierce-after:S/A>A eat-Dist.Past.Conjec Matses-Erg
"Before, in the past, Matses used to kill them with arrows and then eat them."

(29) nëbi chompianën kuessun pek
nëbi chompian-n kues-şhun pe-e-k
now shotgun-Inst kill-after:S/A>A eat-Npast-Indic
"Now they kill them with shotguns and eat them."

(30) nëbi poshto daëdpatsëkkio yanaşh
nëbi poshto daëd-patsëk-kio ik-an-aşh
now woolly.monkey two-Dim-Aug be-Incep-Conjec
"Now, there has probably started to be very few woolly monkeys."

(31) ëndenkio pebennëdaşh matsesën poshto
ënden-kio pe-ben-nëdaşh matses-n poshto
before-Aug eat-go.do.continue-Dist.Past.Conjec Matses-Erg woolly.monkey
"A long time ago, Matses ate the woolly monkeys as they went (i.e., as they changed residence every few years)."

(32) aden piaid poshto nek
ad-en pe-aid poshto ne-e-k
do.thus-Advzr:Tr eat-Pat.Nzr woolly.monkey be-Npast-Indic
"Woolly monkeys are ones that are eaten like that."

(33) abitedişhun matsesën piaid poshto nek
abitedi-şhun matses-n pe-aid poshto ne-e-k
all-Ev.Init:Tr Matses-Erg eat-Pat.Nzr woolly.monkey be-Npast-Indic
"Woolly monkeys are ones that are eaten by all Matses."

APPENDIX 2

Gazetteer

Below we list the principal localities from which primates have been collected or observed in the Ucayali-Yavarí interfluvial region as well as other faunal inventory sites or geographical features mentioned in our text. Boldface identifies locality names as they appear in the text (alternative names or spellings are cited parenthetically). Except as noted otherwise, all localities are mapped in figures 1 and 2.

Actiamë (6°19′S, 73°09′W; Vriesendorp et al., 2006a): inventory site in floodplain of Río Yaquerana surveyed for primates and other large mammals from 2–7 November 2004 (Amanzo, 2006).

Angamos (also known as "Colonia Angamos" [not mapped]; 5°11′S, 72°53′W; DMA, 1989): military outpost on left bank of the Río Yavarí just downstream from confluence of the Gálvez and the Yaquerana.

Boca Río Yaquerana (ca. 5°12′S, 72°53′W): collecting locality of C. Kalinowski at confluence of Yaquerana with Río Gálvez, 3–30 August 1957. The combined waters of the Yaquerana and the Gálvez form the Río Yavarí (Faura-Gaig, 1964), but the Yaquerana is sometimes also known as the Alto Yavarí (Faura-Gaig, 1964), not the "Alto Yaquerana" (contra Stephens and Traylor, 1983).

Choncó (5°33′S, 73°36′W; Vriesendorp et al., 2006a): inventory site in hilly terrain between Río Tapiche and Río Gálvez surveyed for primates and other large mammals by J. Amanzo from 25–28 October 2004 (Amanzo, 2006).

Divisor (7°12′S, 73°53′W; Vriesendorp et al., 2006b): inventory site near Tapiche (q.v.) east of upper Río Tapiche in Sierra del Divisor (250–600 m), surveyed for primates and other mammals by M.L.S.P. Jorge and P.M. Velazco from 19 to 23 August 2005 (Jorge and Velazco, 2006).

Itia Tëbu (5°51′S, 73°46′ W; Vriesendorp et al., 2006a): inventory site in white sand forest on right bank of Río Blanco (q.v.), surveyed for primates and other large mammals by J. Amanzo from 29 October to 2 November 2004 (Amanzo, 2006).

Jenaro Herrera (sometimes misspelled "Genaro Herrera" or "Henaro Errera"; 4°55′S, 73°40′W): botanical field station ca. 2.5 km inland from right bank of Río Ucayali surveyed for primates by Aquino (1978), for bats by Ascorra et al. (1993), and for small nonvolant mammals by several research teams (e.g., Sokolov and Malygin, 1994; Fleck and Harder, 1995).

Marupa (or "Morupa"; ca. 3°28′S, 72°38′W; DMA, 1990): collecting locality on right (south) bank of Amazon just downstream from mouth of Río Napo (H. Bassler, 1–9 May and 3 September 1926). Hershkovitz (1977: 656, 928) placed this locality on the Río Marañón and claimed that the Olallas collected here, but he is incorrect on both counts. Marupa lies well below the confluence of the Marañón and the Ucayali, so it is unambiguously on the Amazon (Río Amazonas; for Peruvian fluvial nomenclature, see Faura-Gaig, 1964). None of the Marupa skins we examined bear Olalla labels, nor are they prepared like Olalla-labelled skins from other localities. The Olallas' extensive correspondence with AMNH ornithologists and mammalogists (analyzed by Wiley, 2010) provides no evidence that they ever worked at this locality, and the dates associated with Marupa specimens are impossible to reconcile with the Olallas' known itineraries.

Nuevo San Juan (5°15′S, 73°10′W; DMA, 1995): inventory site on right bank of Río Gálvez, intensively sampled for mammals from 1995 to 1999 by D.W. Fleck and from 19 May to 12 July 1998 by R.S. Voss.

Orosa (ca. 3°32′S, 72°11′W; Wiley, 2010): collecting locality on the right (south) bank of the Amazon, where Alfonso and Ramón Olalla worked from 30 August to 11 December 1926 (probably near the modern village of San José de Orosa with above coordinates; Wiley, 2010).

Hershkovitz (1977: 928) incorrectly associated this locality with the Río Marañón (see entry for Marupa, above).

Quebrada Blanco (also known as "Río Blanco"; mouth at ca. 4°19′S, 73°14′W; Valqui, 2001: fig. 2-2): right-bank tributary of Río Tahuayo and site of much primatological research (e.g., by Heymann, 1990; Heymann and Aquino, 1994), some of which extended into the nearby Reserva Comunal Tamshiyacu-Tahuayo (q.v.). Valqui's inventory site at San Pedro (q.v.) was on the lower Quebrada Blanco. Not to be confused with the Río Blanco (q.v.), a tributary of the Río Tapiche.

Quebrada Esperanza (ca. 4°20′S, 71°55′S; Stephens and Traylor, 1983): collecting locality of C. Kalinowski on left bank of Río Yavarí-Mirím (q.v.), 6–27 September 1957. Faura-Gaig (1964) gave the coordinates of Quebrada Esperanza at its confluence with the Yavarí-Mirím as 4°18′S, 71°56′W.

Reserva Comunal Tamshiyacu-Tahuayo (recently renamed the "Área de Conservación Regional-Comunal Tamshiyacu-Tahuayo"): a protected area of predominantly well-drained upland forest extending from the headwaters of the Río Tamshiyacu and the Río Tahuayo (both right-bank tributaries of the Amazon) to the upper Yavarí-Mirím (a left-bank tributary of the Yavarí), comprising about 322,500 ha (Puertas and Bodmer, 1993: fig. 1). This area has been the focus of many primatological research projects, including the cited study by P. Puertas and R.E. Bodmer and others by E.W. Heymann and colleagues (e.g., Heymann and Aquino, 1994).

Río Aucayo (mouth at 3°50′S, 73°05′W): minor right-bank tributary of the Amazon where R. Castro and P. Soini carried out early field studies of callitrichine behavioral ecology (Castro and Soini, 1977).

Río Blanco (mouth at 5°34′S, 73°52′W; DMA, 1989): right-bank tributary of the Río Tapiche, surveyed for primates by Izawa (1979); not to be confused with the Quebrada Blanco (q.v.), a tributary of the Río Tahuayo.

Río Cochiquinas (mouth at 3°38′S, 71°33′W; DMA, 1989): right-bank tributary of the Amazon where Aquino and Encarnación (1988) observed night monkeys.

Río Gálvez (mouth at 5°12′S, 72°53′W; DMA, 1989): one of two principal headwater tributaries of the Río Yavarí (see Boca Río Yaquerana, above). Our inventory site at Nuevo San Juan (q.v.) is on the right bank of the middle Gálvez.

Río Orosa (mouth at 3°31′S, 72°06′W; DMA, 1989): right-bank tributary of the Amazon and site of primate surveys by C.H. Freese and colleagues, who conducted transect censuses along nearly the entire navigable length of the river in 1974 (Freese et al., 1982).

Río Tapiche (mouth at 5°03′S, 73°51′W): major right-bank tributary of the lower Ucayali. Bennett et al. (2001) reported the results of primate surveys conducted in a 20 km^2 area of seasonally flooded forest spanning both banks of the Tapiche near 5°39′S, 74°00′W.

Río Yavarí (mouth at 4°21′S, 70°02′W; DMA, 1989): major right-bank tributary of the Amazon, formerly an important source of wild rubber but now almost uninhabited (Bodmer and Puertas, 2003). Three sites along the left bank of the Yavarí between Angamos (q.v.) and the mouth of the Yavarí-Mirím (q.v.) were surveyed for primates and other large mammals by Salovaara et al. (2003): Quebrada Curacinha (5°03′S, 72°44′W), Quebrada Buenavista (4°50′S, 72°23′W), and Quebrada Limera (4°31′S, 71°54′W).

Río Yavarí-Mirím (also known as the "Yavarí-Mirí", "Yavari-Mirín", or "Yavarí Chico"; mouth at 4°31′S, 71°44′W): principal left-bank tributary of the Río Yavarí. The results of extensive transect census studies conducted at various sites along the upper and middle river were reported by Puertas and Bodmer (1993) and Salovaara et al. (2003).

San Fernando (4°09′S, 70°14′W; DMA, 1989): collecting locality of C. Kalinowski on left bank of the lower Río Yavarí, 10–15 July 1957.

San Pedro (4°20′S, 73°12′W; Valqui, 2001): ribereño village on lower Quebrada Blanco (q.v.) adjacent to Reserva Comunal Tamshiyacu-Tahuayo (q.v.). San Pedro was the site of a faunal inventory study by Valqui (1999, 2001), whose results were based on fieldwork conducted from 1993 to 1999. Local habitats include flooded and unflooded primary forest and secondary growth.

Santa Cecilia (3°33′S, 72°53′W; Robbins et al., 1991): collecting locality of C. Kalinowski on right (east) bank of Río (or Quebrada) Manití, 27 December 1956–21 January 1957. According to Robbins et al. (1991), who collected birds around Santa Cecilia in 1983, the predominant natural habitat is well-drained forest on level terrain. The Manití is a minor right-bank tributary of the Amazon below Iquitos.

San Vicente (coordinates unknown): collection locality of C. Kalinowski on Río Yavarí, 2 October 1957 (FMNH). Although this locality is not marked on any map we have seen and is not mentioned by Faura-Gaig (1964), it is presumably on the left bank of the Yavarí below the mouth of the Yavarí-Mirím (at 4°31′S, 71°44′W), where Kalinowski collected until 27 September (at Quebrada Esperanza, q.v.); by 7 October, Kalinowski was collecting on the Amazon.

Tapiche (7°12′S, 73°56′W; Vriesendorp et al., 2006b): inventory site on right (east) bank of upper Río Tapiche, surveyed for primates and other mammals by M.L.S.P. Jorge and P.M. Velazco from 12 to 17 August 2005 (Jorge and Velazco, 2006).