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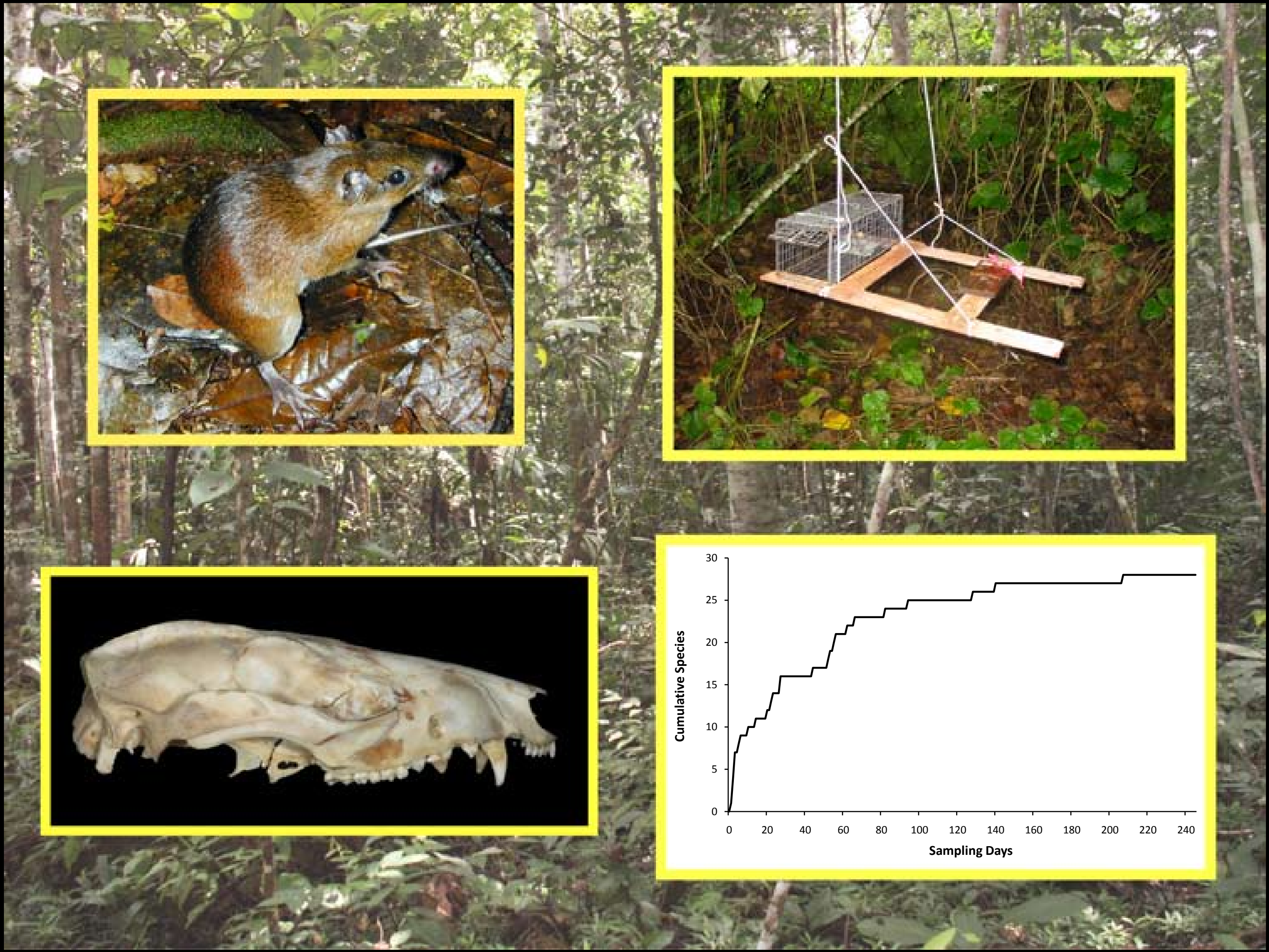
THE NON-VOLANT MAMMALS OF THE RESERVA NACIONAL ALLPAHUAYO-MISHANA, LORETO, PERU



CHRISTINE L. HICE AND PAÚL M. VELAZCO

Front cover: Four important components of small mammal inventories include species diversity (*Proechimys quadruplicatus*, top left), capture methods (arboreal trap station, top right), specimen identification (*Didelphis marsupialis*, bottom left), and data analysis (bottom right). Cover design by Paúl M. Velazco.

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THE NON-VOLANT MAMMALS OF THE RESERVA NACIONAL ALLPAHUAYO-MISHANA, LORETO, PERU

CHRISTINE L. HICE AND PAÚL M. VELAZCO

ABSTRACT

South American mammals have received increasing attention in recent years, in part due to their high species diversity, functional complexity at the level of communities, and endangerment as a result of anthropogenic activities. Human impacts include deforestation and habitat alteration, the two major threats to biodiversity in the Neotropics. Indeed, many habitats are being lost before basic inventories of plant and animal communities can be compiled. In addition, basic natural history information is lacking for many, if not most, Neotropical species, especially in the Amazon Basin. Such basic information is essential for natural resource management and conservation to be successful. To obtain such information at one site, the small mammal community at the Reserva Nacional Allpahuayo-Mishana (RNAM) in northeastern Peru was monitored for 18 months. Data were collected to describe and quantify small mammal communities in pristine habitats and to document the impacts of disturbance on these communities. These data represent one of the most comprehensive data sets on non-volant mammals ever collected from one site in Amazonia. A total of 37 small mammal species, 13 marsupials and 24 rodents, were documented at the site, which represents one of the most species-rich communities reported from the Neotropics. Estimates of local species richness indicate that the small mammal community was sampled approximately 90% completely, but that only 64% of species that potentially occur in the region were documented.

Key words: marsupials, Peru, rainforest, rodents, South America, species accounts

INTRODUCTION

Tropical regions boast the highest level of biodiversity on Earth and are estimated to contain two-thirds of all species (May 1988). Tropical rainforests harbor as much as half of the biodiversity on the planet (Myers 1988; Wilson 1988a). Of these regions, the Amazon Basin is undoubtably the most biodiverse (Chesser and Hackett 1992; Cody 1996), despite recent arguments to the contrary (Mares 1992a, 1992b). This diversity exhibits an east-to-west gradient, with the highest level of diversity in the western sub-region along the base of the Andes, where over 200 species of mammals could occur sympatrically (Emmons 1984; Voss and Emmons 1996; Emmons and Feer 1997).

Regrettably, the pace of deforestation in the Neotropics is accelerating, and with it, the loss of habitats and their resident plants, arthropods, and vertebrates (Wilson 1988b). Most deforestation is anthropogenic in origin and varies widely in its extent (Jordan 1986). Obviously, forests are cleared to extract timber, both for export and to support the demands of burgeoning local populations for shelter and firewood. Forests also are cleared for agricultural purposes, including large-scale ranching operations and small-scale subsistence farming by local people. These are the largest causes of deforestation in the Peruvian Amazon (Reading et al. 1995). Although the impact of large-scale logging and ranching practices in lowland Neotropical forests has been highly publicized, the largest threat to the integrity of Amazonian rainforest habitats is expanding human populations with their need for firewood and their use of unsustainable slash-and-burn agricultural practices (Myers 1980, 1984; Ehrlich 1988; Raven 1988; Lieth and Werger 1989; Reading et al. 1995).

The systematics and distribution of mammals in the Amazon Basin are relatively poorly known, especially for diminutive taxa. However, important studies of Neotropical mammals have been made at several areas (usually reserves) where concentrated efforts have been made to exhaustively survey the local mammalian fauna. A non-inclusive list of these areas includes La Selva, Costa Rica (Wilson 1983; Timm et al. 1989; Wilson 1990; Timm 1994); Barro Colorado Island, Panama (Enders 1930, 1935; Glanz 1982, 1990); Kartabo, Guyana (Anthony 1921; Beebe 1925); Arataye, French Guiana (Guillotin 1982; Julien-Laferrière 1991); Paracou, French Guiana (Simmons and Voss 1998; Voss et al. 2001); Cunucunuma, Venezuela (Handley 1976); Manaus, Brazil (Emmons 1984; Malcolm 1990); Xingu, Brazil (Voss and Emmons 1996: Appendix 8); Rio Juruá, Brazil (Patton et al. 2000); Balta, Peru (Voss and Emmons 1996: Appendix 9); Cocha Cashu, Peru (Terborgh et al. 1984; Janson and Emmons 1990; Pacheco et al. 1993; Ascorra et al. 1996; Pacheco and Vivar 1996); and Cuzco Amazónico, Peru (Woodman et al. 1991). A summary of the mammals from 10 of these areas can be found in Voss and Emmons (1996). Four of these reserves (two in Central America) have been studied for over 20 years, whereas the remainder have been sampled for 10 years or less. However, these areas comprise only a minuscule portion of the Neotropics. Complete inventories for most areas in the Amazon Basin are nonexistent. This makes comparisons of mammalian faunas across Amazonia difficult, hampering our understanding of mammal community structure and how this structure changes across the geography of the region (Emmons 1984; Lacher and Mares 1986; Eisenberg 1990; Voss and Emmons 1996).

Compiling complete mammal inventories at specific sites in Amazonia has been complicated by the lack of understanding and consensus about the systematics of Neotropical mammals. Only in the last decade have many groups of small mammals been sufficiently studied to facilitate positive identification of individuals. Nonetheless, identification of individuals requires careful examination by experienced systematists. It is more important than ever that voucher specimens be prepared so systematists can reclassify specimens as the taxonomy is clarified. Only in this manner can species lists be updated and made comparable for use in biogeographic analyses.

The purpose of this research was to compile, as completely as possible, an inventory of the small non-volant mammals inhabiting the Reserva Nacional Allpahuayo-Mishana (RNAM) and to contribute to the fundamental natural history of small mammals in lowland Neotropical forests. RNAM was chosen as the study site because it was easily accessible from Iquitos and represents the most pristine forest in the Iquitos area. Easy access was particularly important because tissues had to be transported daily to Iquitos to be preserved for concurrent viral-isolation studies (e.g., Aguilar et al. 2004). Moreover, no inventory of mammals north of the Amazon River was available for this part of the Amazon Basin and the distribution of many species in this region was unknown.

This monograph has been organized in the following manner. First, the study site and the habitats that occur there are described. The sampling methods are described in detail, as are the measurements taken for each taxa and the statistical analyses used to differentiate similar taxa. Species accounts of all species encountered or expected (based on geographic range data) at the site are then presented. These discuss the ecology of the species at RNAM and the systematics and distribution of the species at a larger scale. Next, general trapping results and adequacy of effort for documenting the mammals that occur at RNAM are presented and discussed in the context of other inventories of Neotropical mammals. Finally, the mammalian fauna at RNAM is compared to that of other sites within the Neotropics and regional patterns of mammalian diversity are discussed.

MATERIALS AND METHODS

Description of Study Site.—Research was conducted at the Reserva Nacional Allpahuayo-Mishana (RNAM; 3°58' S; 73°25' W), a 57,667 ha national reserve operated by the Instituto de Investigaciones de la Amazonía Peruana (IIAP), located 28 km southwest of Iquitos on the Iquitos-Nauta highway, Province of Maynas, Department of Loreto, northeastern Peru (Fig. 1). The Fuerte Militar Otorongo (FMO; 3°57' S; 73°22' W), located approximately 10 km northeast of Allpahuayo on a dirt road east of the Iquitos-Nauta highway, was added as a second site after the initial year of research (Fig. 1). The climate in the area is tropical, with a mean annual temperature of 26°C; the highest average monthly temperature (31°C) occurs in November and the lowest (22°C) in July (Salati 1985). Daily temperatures fluctuate approximately 10°C between daytime highs and nighttime lows. Average rainfall is 2,945 mm per year, with a slightly drier season from June to September (Johnson 1976). The elevation of the sites ranges from 110 to 180 m.

The sites are located in the Humid Tropical Forest Botanical Province of the Holdridge System (Tosi 1960), and comprise one major habitat type, low-terrace broadleaf tropical rainforest (López-Parodi and Freitas 1990), a type of non-flooded forest or terra firme. Three types of upland primary forest occur within Allpahuayo: *monte alto*, *franco arcilloso*, and *varillal* (Álvarez 1997). Each corresponds to soil characteristics. *Monte alto* occurs on clay soil, *franco arcilloso* is on mixed sandy/clay soils, and *varillal* is on sandy soil. Vegetation differences between habitats are subtle, but there are distinctions among them.

Varillal (Fig. 2), or white sand forest, encompasses the smallest spatial extent of the three habitats and

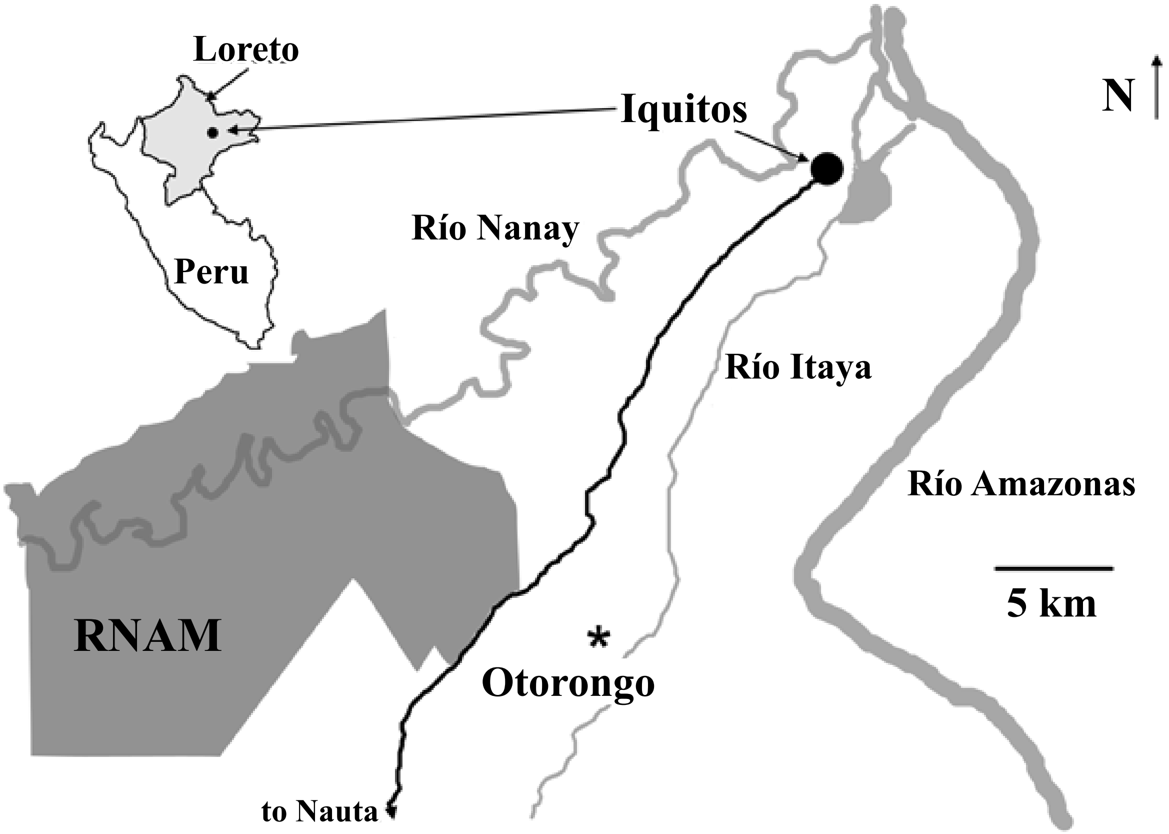


Figure 1. Location of study sites. Black line is a paved road from Iquitos to Nauta. Gray lines are rivers.

Figure 2. *Varillal* habitat. Notice the absence of palms and large trees, and the presence of bromeliads and multi-trunked trees. Photo by Christine L. Hice.

has the most distinctive vegetation. It occurs in small patches (2–10 ha) within the forest generally located on plateaus of small hills (Álvarez 1997). There are nine types of *varillal* (Álvarez 1997), but this research focused on the most distinct type: high, dry *varillal*. This *varillal* is characterized by pure white sand soils with excellent drainage. The flora is unique and contains many endemic species found nowhere else in Peru (Álvarez 1997; Álvarez et al. 1999; Álvarez and Soini 2003). In general, there are very few palms or lianas present and an abundance of bromeliads often carpets the forest floor. The trees tend to be small in stature (maximum height is 20 m) with straight narrow trunks and several tree species that occur there are characterized by multiple trunks. Many tree species are highly sought after for building material because they require little preparation after harvesting and some have termite resistant properties. In areas accessible to trucks, the nearly pure white sand is extracted and used in construction. Along the Iquitos-Nauta highway large holes that represent destroyed *varillal* habitats are a common sight.

Monte alto (Fig. 3) is, in several ways, the opposite habitat type from *varillal*. *Monte alto* has the largest spatial extent of the three primary habitat types and represents the typical rainforest of the area. It occurs in low-lying areas on nearly pure clay soils with poor drainage. This habitat is characterized by a closed canopy of approximately 30 m with large emergent trees reaching 40 m in height. Palms dominate the understory levels of this habitat, many of which are economically important for their fruits and fronds, the latter of which are used as building materials. The large trees present in this habitat support an abundance of lianas and epiphytes. Lianas contribute to the complex vertical structure of the habitat, and epiphytes create a diverse arboreal ecosystem in the canopy. Unfortunately, these same large trees are in high demand by lumber companies, and it is not uncommon to find remnants of the largest trees, surrounded by sawdust and rough-hewn boards, several hours' walk into the forest.

Franco arcilloso (Fig. 4) often occurs in the transition areas between *monte alto* and *varillal* as the

Figure 3. *Monte alto* habitat. This large tree surrounded by small palms is typical of the habitat. Photo by Christine L. Hice.

Figure 4. *Franco arcilloso* habitat. Notice the tree fall gap in the background. Photo by Christine L. Hice.

soil type grades from clay to sand, but there also are expanses of *franco arcilloso* within the more extensive *monte alto*. *Franco arcilloso* has characteristics intermediate between the other two habitats, and these characteristics vary with soil composition and elevation. The habitat is characterized by a high frequency of tree-falls, which creates a heterogeneous mosaic of different aged habitats. Palms are common in some areas and occur in lower abundance in others. The trees do not reach the size of the large trees found in *monte alto*, but are larger than those trees present in *varillal*. The understory plant density tends to be higher in this habitat because of increased light intensity due to frequent tree falls. This also is the most likely habitat to be cleared for agriculture because it is the most fertile of the three soil types. The fields of local people (ribereños) can be located up to two hours' walk from the nearest house and are preferentially located in this habitat. Each family maintains 3–5 fields (average size is 0.5 ha) of varying ages.

A qualifying statement about what comprises "primary" forest in the Iquitos area is in order. In our experience, no truly pristine primary forest exists within a large radius of Iquitos. These study sites fall within this radius. Primary forest in this area is generally in some state of recovery from anthropogenic use, such as the removal of large trees to build houses, make canoes, and sell timber. Moreover, several species of palms are intensively harvested for construction materials, and many types of fruit also are harvested on a regular basis. Therefore, the primary forest referred to throughout this paper may be better described as 50 to 100-year-old secondary growth that receives a great deal of human use. It will most likely never fully recover to a pristine state, but it is as close to "primary" forest as there is in the area.

A variety of more recently disturbed areas also exist within Allpahuayo, and all of Otorongo is composed of highly disturbed habitats. These are generally small areas (1–4 ha) of converted *franco arcilloso* habitat, ranging in age from 3 to 20 years. The age of the habitat is the time since it became fallow and allowed to regenerate. Elements of the local disturbance regime include understory clearing, selective harvesting of large trees, planting of fruit trees, and complete clearing for agricultural purposes, usually *yuca* or sugar cane operations (Fig. 5).

Figure 5. Field of *yuca*, plantain, and pineapple. This combination is typical for a cultivated field in this area. Photo by Christine L. Hice.

Sampling Methods.—The small mammal community was assessed with several different methods, including grids, pitfall traplines, arboreal transects, and line transects. Traps deployed included standard folding Sherman live traps (22.9 x 7.6 x 8.9 cm), four sizes of Tomahawk live traps (40 x 14 x 14 cm, 48 x 17 x 17 cm, 51 x 19 x 19 cm, and 66 x 23 x 23 cm), and Victor snap-type rat traps. The latter was the preferred type of snap trap because the smaller Victor mouse traps and Museum Special back-break traps are too small to effectively capture many Neotropical rodents (R. Timm, pers. comm.). A wide array of methods is necessary to sufficiently sample small mammals in Neotropical rainforest because of the large variety of mammals found there (Voss and Emmons 1996; Patton et al. 2000). These mammals vary greatly in body size (5 g to 1.5 kg), diet (frugivorous to carnivorous), and habit (semifossorial to arboreal). Such diversity can best be sampled with an equally diverse variety of trap types and placement.

In total, 18 grids, 13 pitfall traplines, 4 arboreal transects, and 12 line transects were established to assess small mammal communities (Fig. 6). Spatial sampling design attempted to maximize distance between grids and transects within the logistical limits of carrying 300 traps to any given grid, collecting captured mammals each morning, preparing specimens all day, and returning to the grid in the afternoon to bait and re-set the traps. After considerations of placing a minimum of two grids in each forested habitat type, transporting traps was a major factor in grid layout. The specific design of the trap layout for each grid is discussed in detail below. Unless otherwise stated, traps were checked, captured animals and remaining bait were removed, and traps sprung at dawn. They were subsequently baited and armed in the afternoon.

Several types of bait were used, including green and ripe plantains, *yuca* (manioc), canned cat food, canned tuna, dry salted fish, peanut butter mixed with pork fat and oatmeal, and cotton balls saturated with peanut butter and pork fat. The last of these was the most effective and lasted throughout the night in the traps, so was used most extensively. It is referred to as peanut butter bait in the text.

The temporal sampling schedule attempted to maximize time between grid assessments while allowing each habitat type to be sampled during both the rainy and dry seasons (Appendix I). A minimum of six months was allowed between consecutive trapping cycles on grids (with the exception of the grids in Otorongo). This was to assure that not all animals were removed from an area and to allow time for recovery of mammal populations. No information is available about the impact trapping has on small mammal populations in Neotropical rainforests. In North America, grids are often sampled every three months, but because of the lower population density of Neotropical species, more time was allowed for populations to recover. Nonetheless, a sharply lower capture rate was observed in the second assessment of the grids. Three novel grids were established and assessed following this trapping cycle (September 1998). The same lower capture rate was observed upon assessing the new grids, indicating some other factor was influencing capture rate. In a few cases, a trapping cycle was cut short due to illness or misunderstandings with local authorities.

A total of 18 grids was established (Fig. 6; Appendix I). The four initial grids were smaller than subsequent grids. These grids consisted of a 7 x 7 trap array with 15 m spacing between stations (1.1 ha total area). Each station contained four traps of the same type arranged symmetrically around a central flag with their entrances facing outward. There were four sizes of Tomahawk traps (one of each at each station) on grid 1C, Victor traps on grid 2C, and Sherman traps on grid 3C. Grid 4B, which was assessed for seven nights, had to be abandoned because of theft of traps. Traps were assessed for 20 consecutive nights on the other three grids to determine the length of time necessary to adequately assess the small mammal community in each primary forest type.

The remaining 14 grids consisted of a 10 x 10 array (Jones et al. 1996) with 15 m spacing between stations (2.25 ha total area). At Allpahuayo each station contained one Victor, one Sherman, and one Tomahawk trap. At Otorongo (grids O-1 and O-2) each station contained either one Sherman or one Tomahawk trap. These two grids were added in August 1998 for a febrile illness study being conducted by the U.S. Army. Trapping sessions were only five weeks apart because of time constraints imposed by the Army. Traps were mostly baited with peanut butter, but sometimes with

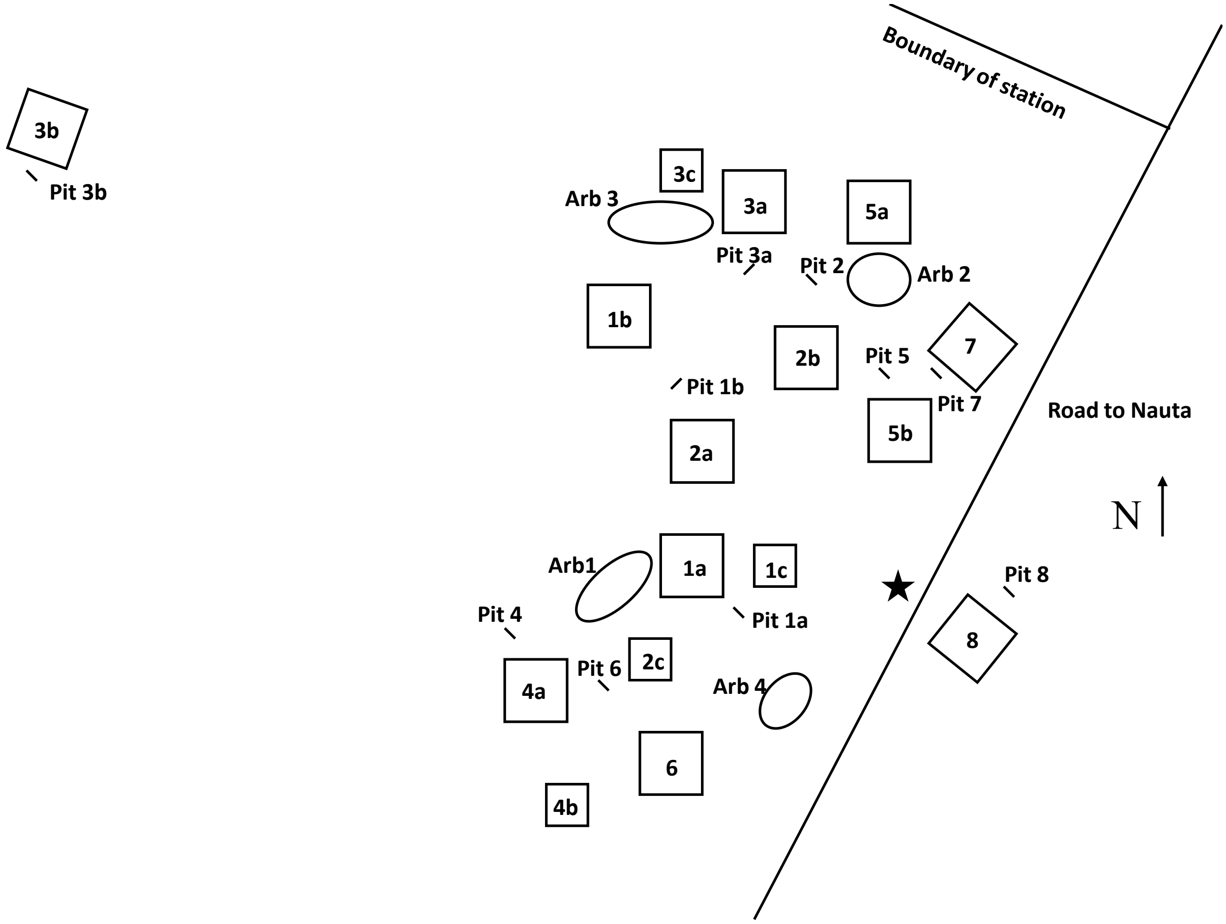


Figure 6. Location of grids, pitfall traplines, and arboreal transects at the Reserva Nacional Allpahuayo-Mishana. Line transects are not on the map because many of them were distant from the grids. The large squares (i.e., 3a, 5a) are 150 m x 150 m. Star = main entrance to the station.

dried salted fish or *yuca*. Grids were assessed for 10 consecutive nights. Replicate grids were constructed in habitats that were of sufficient spatial extent to encompass more than one grid. This was generally possible in forested sites, but not possible in most of the disturbed sites.

Thirteen pitfall traplines were constructed (Fig. 6; Appendix I). Ten of the lines were associated with an adjacent grid in the same habitat (four grids, 3B, 5A, O-1, and O-2, did not have an associated pitfall trapline). The remaining three lines were placed several hours walk from the road and assessed once. Pitfall traplines consisted of eleven 20 L buckets buried flush to the ground and placed 5 m apart under a continuous 50 m drift fence made of plastic (Jones et al. 1996; Voss and Emmons 1996; Fig. 7). Holes were drilled in the bottom of each bucket to allow accumulated rainwater to drain. Traps were assessed for 10 consecutive nights approximately concurrently with the corresponding grid in the same habitat and checked each morning at dawn. No bait was used and no liquid was intentionally introduced into the buckets (Sikes et al. 2011).

Four arboreal transects were constructed (Fig. 6; Appendix II). These were located near a grid in each of the three primary forest habitats and in the oldest secondary growth. No arboreal transects were constructed in younger secondary growth due to the absence of trees sufficiently large to climb. Transects consisted of 25 stations modeled after Malcolm (1991; Fig. 8), although traps were placed side-by-side and

Figure 7. Pitfall trapline in *monte alto* habitat. Pitfall traplines could not be straight to avoid large roots and trees. Photo by Christine L. Hice.

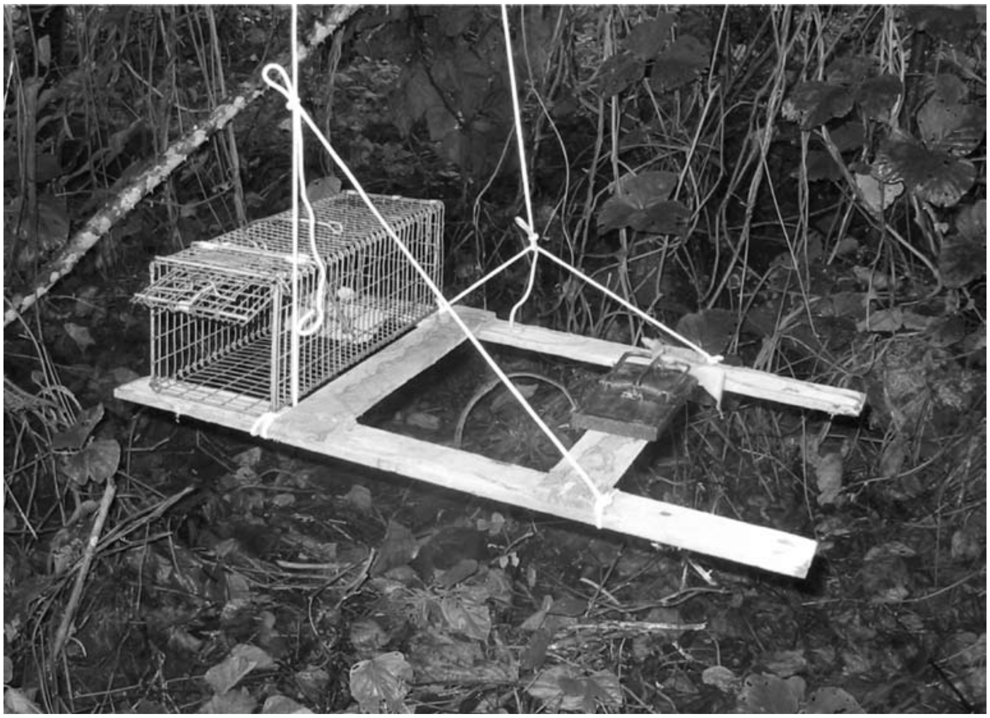


Figure 8. Arboreal station with a Tomahawk and Victor trap on the platform. Photo by Christine L. Hice.

not stacked. An additional five stations were placed on fallen logs and lianas and did not require the construction of a permanent station. Distance between arboreal stations varied from 5 to 20 m because only particular sizes or forms of trees could be climbed. Diameter at breast height (dbh) ranged from 26 to 146 cm, and heights of the stations ranged from 2.4 to 15.6 m (Appendix II). Traps on fallen logs and lianas were located below 2 m. Each station had a total of four traps, two arboreal and two terrestrial, with a Victor trap in the tree and on the ground and Sherman and Tomahawk traps alternating in the arboreal or terrestrial position. During the first trapping cycle, only 10 stations were completed and these were assessed for 15 consecutive nights to determine the species/time curve for arboreal species. During subsequent trapping cycles, all 30 stations were assessed for 10 consecutive nights. Arboreal traps were baited with dry salted fish because this bait type endured longer in the traps. Due to time contraints, arboreal traps were left open all day and bait replaced every 3–5 days. No animal was ever captured in an arboreal trap during daylight hours. Terrestrial traps were baited with peanut butter.

Twelve line transects were placed opportunistically in small areas of disturbed habitat as well as in forested habitats much further from the road than were the grids (Appendix I). Transects varied widely in length and number of traps per station, ranging from 16 to 120 stations placed 10 m apart, with one trap or a variety of traps at each station. Occasionally, a few traps would be placed up to 10 m high in a tree. Transects were assessed for 4–10 consecutive nights. Those transects located a long distance from the road were checked and rebaited in the morning and not revisited in the afternoon. Dried salted fish was used as bait on those transects to ensure that some bait persisted that night. On transects nearer the station, peanut butter bait was used.

A few additional mammals were captured by local hunters, including some bats and larger mammals. These animals were not used in any analyses, but they are included in the species accounts of mammals present at the station (excluding the bats). A complete list of species and analysis of the bat community at RNAM was published by Hice et al. (2004).

A voucher specimen was prepared from each mammal captured. Vouchers consisted of a standard museum skin and skull, a skin with skull and partial skeleton, a complete skeleton, or fluid specimens (preserved in 10% formalin and maintained in 70% ethanol) with the skull removed and cleaned. In addition, orbital blood samples and tissues (including any combination of liver, spleen, muscle, lung, brain, stomach, reproductive organs, and embryos) were collected aseptically and stored at -70° C for concurrent viral investigations. Specimens are deposited at the Museum of Texas Tech University, Lubbock, Texas (TTU), the Los Angeles County Museum of Natural History, Los Angeles, California (LACM), and the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM). Tissue and blood samples are deposited at TTU and University of Texas Medical Branch, Galveston, Texas (UTMB).

Habitat Assessment.—An overall habitat and vegetative description of each grid, pitfall trapline, and arboreal transect was completed by Juan Ruiz, botanist at the Universidad Nacional de la Amazonía Peruana. For this, the names of the dominant 3–6 species of canopy tree, understory tree, palm, shrub, liana, and herbaceous plant were recorded (Appendix III). For arboreal stations, heights of each station were recorded to the nearest decimeter, dbh of each tree containing a station was recorded, and the tree was identified to species (Appendix II).

Specimen Measurements and Age Classes.—External measurements of individuals were taken prior to specimen preparation and recorded as follows:

TOL - Total length, from tip of nose to tip of terminal tail vertebra.

TAL - Tail length, from dorsal flexure at tail base to last tail vertebra.

HF - Hind foot length, from proximal border of calcaneus to tip of longest claw.

E - Ear length, from notch to tip of pinna.

Cranial measurements were taken with digital calipers linked to a computer. This allowed measurements to be recorded directly into a spreadsheet to the nearest 0.01 mm. A different set of measurements was taken for marsupials, cricetid rodents, and echimyid rodents, as summarized below.

Marsupials: A series of 15 measurements, developed from Patton et al. (2000) and Gardner (1973), was recorded for each individual, including:

GLS - Greatest length of skull, greatest midline length obtainable from anterior margin of premaxillary bones to posterior-most extension of skull.

CBL - Condylobasal length, midline distance from anterior margin of foramen magnum to anterior surface of premaxillary bones.

PL - Palatal length, midline distance from anterior surface of premaxillary bones to posterior margin of palate.

BOL - Basioccipital length, distance from anterior margin of foramen magnum to basioccipital-basisphenoid suture.

ZB - Zygomatic breadth, greatest breadth across zygomatic arches.

MB - Mastoid breadth, breadth across mastoid bones.

IOC - Interorbital constriction, least distance across skull between orbits.

RL - Rostral length, length from anterior margin of orbit to midline tip of nasal bones.

NL - Nasal length, midline distance from anterior tip to posterior margin of nasal bones.

RW - Rostral width, width across rostrum at level of the canines.

CM4 - Length of maxillary toothrow, distance from anterior surface of canine to posterior surface of M4.

LMTR - Length of molar toothrow, distance from anterior margin of M1 to posterior margin of M4, taken on labial margin.

PW - Palatal width, width of palate taken across lateral margins of M3.

OCB - Occipital condyle breadth, breadth across outer margins of occipital condyles.

CD - Cranial depth, vertical distance between top of cranium and a horizontal line drawn from posterior margin of palate to anterior margin of foramen magnum.

Marsupial age classes generally follow the scheme of tooth eruption and wear defined for *Didelphis* by Gardner (1973), as modified by Tyndale-Biscoe and Mackenzie (1976) for didelphids and Tribe (1990) for marmosines. However, adult data are summarized only for those individuals with fully erupted fourth upper molars (M4; age classes 5, 6, and 7), and do not include sexually mature individuals in age class 4 as in Gardner (1973).

Cricetid rodents: A series of 17 measurements, developed from Patton et al. (2000) and Musser et al. (1998), was recorded for each individual, including:

GLS - Greatest length of skull, greatest midline length obtainable from anterior margin of nasal bones to posterior-most extension of skull.

ZB - Zygomatic breadth, greatest breadth across zygomatic arches.

IOC - Interorbital constriction, least distance across skull between orbits.

MB - Mastoid breadth, breadth across mastoid bones.

LR - Rostral length, length from anterior margin of the orbit to midline tip of nasal bones.

LN - Nasal length, midline distance from anterior tip to posterior margin of nasal bones.

BR - Rostral breadth, breadth of rostrum across nasolacrymal capsule.

BZP - Breadth of zygomatic plate, taken at midheight from anterior to posterior margins of plate.

LD - Length of diastema, from posterior face of incisors to anterior edge of M1.

CBL - Condylobasal length, midline distance from anterior margin of foramen magnum to posterior surface of incisors.

PPL - Postpalatal length, midline distance from anterior margin of foramen magnum to posterior margin of palate.

LBP - Length of bony palate, distance from posterior margin of incisive foramen to posterior margin of palate.

BBP - Breadth of bony palate, breadth across lateral margins of M1.

LIF - Length of incisive foramen, greatest length of incisive foramen.

BIF - Breadth of incisive foramen, greatest breadth across the lateral margins of incisive foramina.

LMTR - Length of molar toothrow, crown length of maxillary toothrow.

DB - Braincase depth, vertical distance between top of cranium and ventral surface of bullae.

Specimens were assigned to age categories based on molar eruption and toothwear patterns similar to the method of Myers and Carleton (1981) for *Oligoryzomys*, with the exception of *Scolomys* for which, due to its unique toothwear pattern, we follow Gómez-Laverde et al. (2004). Only adult individuals in age classes 3, 4, and 5 (4–7 for *Scolomys*) were used in data summaries and analyses.

Echimyid rodents: A series of 19 measurements, developed from Patton et al. (2000), was recorded for all individuals, including:

GLS - Greatest length of skull, greatest midline length obtainable from anterior margin of nasal bones to posterior-most extension of skull.

ZB - Zygomatic breadth, greatest breadth across zygomatic arches.

IOC - Interorbital constriction, least distance across skull between orbits.

MB - Mastoid breadth, breadth across mastoid bones.

LR - Rostral length, length from anterior margin of the orbit to midline tip of nasal bones.

LN - Nasal length, midline distance from anterior tip to posterior margin of nasal bones

BR - Rostral breadth, breadth of rostrum taken at the premaxillary-maxillary suture.

LD - Length of diastema, from posterior face of incisor to anterior edge of M1.

CBL - Condylobasal length, midline distance from anterior margin of foramen magnum to posterior surface of incisors.

PPL - Postpalatal length, midline distance from anterior margin of foramen magnum to posterior margin of palate.

LBP1 - Length of bony palate 1, midline distance of palate from posterior margin of incisive foramina to posterior margin of palate.

LBP2 - Length of bony palate 2, distance from anterior margin of PM4 to posterior margin of palate.

LMF - Length of mesopterygoid fossa, maximum midline length from anterior margin to posterior extensions of hamular processes.

BBP - Breadth of bony palate, maximum breadth of palate across juncture of M3 and M4.

LIF - Length of incisive foramen, greatest length of incisive foramen.

BIF - Breadth of incisive foramen, maximal breadth across the lateral margins of incisive foramina.

WMF - Width of mesopterygoid fossa, maximum width taken at the suture between palatine and pterygoid bones.

LMTR - Length of molar toothrow, crown length of maxillary toothrow.

DB - Braincase depth, vertical distance between top of cranium and ventral surface of bullae.

Specimens were assigned to age categories based on molar eruption and toothwear patterns established by Patton and Rogers (1983). Only adult individuals in age classes 8–10 were used in data summaries and analyses.

Statistical Analyses.—Two programs were used to perform all statistical analyses. Summaries of morphometric variables were conducted with SPSS (Version 3.0). When non-geographic variation was examined (i.e., sex and age effects) the multivariate analysis of variance (2-way MANOVA; random effects model) and concordant univariate analysis of variance (2-way ANOVA; random effects model) also were conducted with SPSS. If only one effect or the other (sex or age) could be examined because of small sample size, a one-way MANOVA and concordant ANOVAs were conducted. In all cases, if the MANOVA was not significant, subsequent ANOVA results are not presented (Willig et al. 1986). However, if the MANOVA was significant, ANOVA results were examined to determine which variables contributed most to the morphometric differences, although this may or may not be meaningful (Willig et al. 1986). Multivariate analyses were conducted with log10 transformed cranial variables. A sequential Bonferroni adjustment was applied to ANOVA p-values to hold experiment-wise significance levels to 5% (Rice 1989). A p-value of 0.05 or less was considered significant.

Although MANOVA was the principal analysis used to differentiate morphologically similar species within genera, discriminant function analysis (DFA) was utilized when further differentiation was necessary. This analysis was conducted with MatLab (version 5.3). DFA is a multivariate statistical method that constructs a set of linear combinations of variables to maximize discrimination among a priori groups (Tatsuoka 1971).

Individuals of the genus *Proechimys* were problematic to identify to species. Adults were classified with the function "CLASSIFY" in MatLab which uses minimum Mahalanobis distances to place unknown individuals into previously identified groups (in this case, adults that had been positively identified by mitochondrial DNA [mtDNA] cytochrome-*b* sequence analysis conducted by James Patton of the University of California, Berkeley). To minimize misclassifications, 1,000 iterations were run. Nonetheless, three individuals were placed with equal frequency into two species (either *P. cuvieri* or *P. quadruplicatus*). The species identity of these individuals was confirmed with mtDNA cytochrome-*b* sequence analysis.

Juvenile *Proechimys* were especially problematic and required a special suite of statistical analyses also performed in MatLab. To classify these individuals, a size-free principal component analysis (PCA) was conducted on positively identified adults and all juveniles. The first two PCA loadings for each variable were plotted as vectors and the most divergent variable (in this case LMTR because all cheek teeth had not yet erupted in juveniles) was eliminated. The size-free PCA was run again with the restricted data (no LMTR) and the loadings plotted as vectors. This vector plot was examined and all vectors were of nearly the same magnitude and direction, so no additional variables were eliminated. Euclidean distances of the first three size-free PCA scores for each juvenile were calculated from the centroids of the PCA scores for the adults of each of the three species of *Proechimys*. Species identity was assigned by using the shortest Euclidean distance to one of the three centroids. In the few (6) cases where Euclidean distances were nearly equal to two species, the individuals were manually classified. Subsequent mtDNA cytochrome-*b* sequence analysis confirmed species identifications of questionable individuals.

The Jaccard similarity index is a commonly used faunal index that is easy to calculate and requires only presence/absence data. This was used to determine the similarity of the non-volant fauna at RNAM to other sites in the Neotropics that have been relatively completely sampled. It is calculated by:

$$C_J = j / (a + b - j)$$

where j is the number of species found at both sites and a is number of species at site A and b is the number of species at site B (Magurran 1988). The index ranges from 0 to 1, a 1 indicates that the species present at both sites are identical. To create a dendrogram based on Jaccard's index, the index was transformed into a distance measure by using $1 - C_J$. Presence/absence data for 12 Neotropical sites was obtained from Voss et al. (2001: Appendix 2). Distance matrices calculated from Jaccard's indices were clustered with an unweighted pair-group method using arithmetic averages (UPGMA). Correlation between faunal similarity and geographic proximity was analyzed with a Mantel test (Smouse et al. 1986) conducted in MatLab.

Local species richness was estimated by extrapolation using several nonparametric methods based on sampling intensity and empirical species abundance distribution (see Colwell and Coddington 1994). Extrapolation methods can be divided into those based on individuals or those based on time. The first type includes CHAO1 (Chao 1984), which is calculated using the number of rare species in a sample, called singletons and doubletons (i.e., those species represented by either one or two individuals). This estimate of species richness (S_1*) based on CHAO1 is given by:

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

where S_{obs} is the observed number of species, a is the number of singletons, and b is the number of doubletons. The variance about S_1* is calculated with the formula:

$$\mathrm{var}\ (S_1{}^*) = b\ [\{(a/b)/4\}^4 + (a/b)^3 + \{(a/b)/2\}^2].$$

The other 3 methods are based on time and use unicates and duplicates (i.e., those species captured on only one or two sampling dates). The estimate of species richness (S_2*) based on CHAO2 (Chao 1984) is the simplest to calculate:

$$S_2{}^* = S_{obs} + (L2/2M)$$

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

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

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

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

All estimates were calculated for the fauna at RNAM, but only CHAO1 was calculated for other sites because total count data were available for them, but data about when the individuals were captured were not available.

SPECIES ACCOUNTS

These accounts summarize the taxonomy, distribution, habitat preference, and natural history of the non-volant mammals collected during trapping efforts at the Reserva Nacional Allpahuayo-Mishana (RNAM) and the Fuerte Militar Otorongo (FMO). Also included are larger mammals secured by other means. Finally, species whose range and habitat preferences suggest they could be present at RNAM are included. Each account is standardized for marsupials and rodents, with separate sections for the description, comparisons with similar species, distribution and habitat preferences, reproduction, and other comments. However, if the species was not collected, the account is necessarily less detailed and is presented in one section. This also is true for larger species for which only one or a few specimens were collected. For the orders Carnivora, Perissodactyla, and Artiodactyla, accounts are summarized at the familial level. Primates and bats are excluded from species accounts because permits to obtain the former were not issued and the latter were not sampled by the methods employed.

Taxonomic order generally follows that of Voss and Jansa (2009) for marsupials, Musser and Carleton (2005) and Weksler et al. (2006) for cricetid rodents, and Woods and Kilpatrick (2005) for hystricognath rodents. Any difference in nomenclature is documented in the accounts.

Details of morphometric features to distinguish similar species are discussed where appropriate. Photographs of crania are provided when these facilitate comparisons among species. Morphometric analysis of cranial measurements was conducted for those groups for which sufficient sample size was available. These analyses quantify differences among closely related species and assess variation due to age and sex within a given species. Measurements given in the text are in mm unless otherwise stated.

ORDER DIDELPHIMORPHIA Gill 1872

Family Didelphidae Gray 1821

The taxonomy of this family has changed dramatically due to the recent work of Voss and Jansa (2009). Based on strongly supported molecular and morphological analyses, they recognize four subfamilies in Didelphidae: Caluromyinae (for *Caluromys* and *Caluromysiops*); Glironiinae (*Glironia*); Hyladelphinae (*Hyladelphys*); and Didelphinae. Addititonally, they recognize four tribes in Didelphinae: Didelphini (for *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*); Marmosini (*Marmosa*, *Monodelphis*, and *Tlacuatzin*); Metachirini (*Metachirus*); and Thylamyini (*Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, *Marmosops*, and *Thylamys*). Another taxonomic change suggested by Voss and Jansa (2009) is the placement of the genus *Micoureus* as a subgenus of *Marmosa*.

Twelve species of marsupials were collected at RNAM. This represents one of the most species-rich marsupial faunas reported in the Neotropics and is comparable with other sites in the Amazon Basin. Solari et al. (2002) reported 17 species for the Lower Urubamba Region in Peru, which has the highest species richness in the Amazon basin. Voss and Emmons (1996) reported 12 species of marsupials from the combined sites of Cocha Cashu and Pakitza in southeastern Peru, stating "Because Pakitza is at approximately the same elevation as Cocha Cashu and there are no known zoogeographic barriers between them, we combine inventory data from the two sites below" (p. 107). Eight species have been documented at Cocha Cashu (Pacheco et al. 1993) and nine at Pakitza (Pacheco et al. 1993; Pacheco and Vivar 1996). Woodman et al. (1991) report nine species (plus one probable species) from Cuzco Amazónico, also in southeastern Peru. Eleven species complete with voucher specimens have been reported from Balta, Río Curanja, located slightly north of the previous two Peruvian sites in central-eastern Peru (Voss and Emmons 1996). Ten species (one is reported from tracks only) have been reported from Panguana Biological Station in central Peru (Hutterer et al. 1995). At Jenaro Herrera, the site located closest to RNAM (approx. 500 km west), eight species of marsupials were reported (Fleck and Harder 1995). A total of 10 species were reported by Patton et al. (1982) from the upper Marañon river basin at the foothills of the Andes in northwestern Peru, with a maximum of nine species taken at any one site. Outside of Peru, Patton et al. (2000) report 13 species of marsupials along the length of the Rio Juruá in western Brazil, with a maximum of 11 species at any given site. Near Manaus, Brazil, nine species were reported from the Minimum Critical Size of Ecosystems Reserves (Malcolm 1990). Voss et al. (2001) reported 12 species from Paracou, French Guiana, and 11 species from the Arataye catchment, also in French Guiana. Other sites within the Amazon Basin that have been assessed sufficiently to allow comparisons of species richness are located in areas known to have a lower species richness than that in the central and western Amazon Basin, such as Guyana, eastern Brazil (Río Xingu), and Venezuela (Voss and Emmons 1996; Voss et al. 2001).

Even with such an impressive list of marsupials, several species that probably occur at RNAM have yet to be documented with voucher specimens. *Chironectes minimus* has been sighted at the reserve

(C. Rivera, pers. comm.). *Caluromysiops irrupta* may occur there, as well as two additional species of *Marmosa* (*M. lepida* and *M. rubra*) and *Marmosops* (*M. impavidus* and *M. neblina*). *Didelphis albiventris* has been captured nearby. Finally, additional species of both *Monodelphis* and *Gracilinanus* may occur at RNAM. In light of this, there could be 17–22 species of marsupials present at RNAM.

Subfamily Caluromyinae Reig, Kirsch, and Marshall 1987

Caluromys Allen 1900

***Caluromys lanatus* (Olfers 1818)**

(Fig. 9)

Description.—A handsome, medium-sized, arboreal opossum, *Caluromys lanatus* has long, dense, woolly fur that is reddish brown dorsally. Juvenile dorsal pelage is much longer and grayer than that of the adult. The head and face are grayish with a prominent dark stripe down the center extending from between the ears to the nose. The fur on the posterior portion of the venter is yellowish-orange, with gray-based yellow-tipped fur on the chest and neck. The tail is thickly furred for half its length above and one-fifth its length below. The non-furred portion of the tail is yellowish mottled with brown spots.

One adult male and one juvenile female (age class 3) were collected. Selected measurements of the adult (TTU 99025) are TOL 720, TAL 402, HF 48, E 35, GLS 60.61, PL 32.43, BOL 8.93, ZB 35.57, IOC 10.89, RL 20.46, NL 25.95, RW 12.94, CM4 21.53, LMTR 10.06, PW 17.55, CD 17.37.

Distribution and Habitat.—This species occurs throughout northern and central Colombia, northwestern and southern Venezuela, eastern Ecuador, eastern Peru, eastern Bolivia, eastern and southern Paraguay, northern Argentina (Misiones), and western and southern Brazil (Gardner 2008a). Its preferred habitat is mature rainforest, where it may act as a pollinator for some plant species (Gribel 1988). The young female was captured in January 1998, in a Tomahawk trap placed in a tree (*Parkia nitida*, dbh = 70 cm) at a height

Figure 9. Dorsal and ventral views of the skull of *Caluromys lanatus* (TTU 99025). Scale bar = 10 mm. Photo by T. Kennedy.

of 7.3 m in *franco arcilloso* habitat. The adult male was collected by a hunter in October 1998.

Reproduction.—Testes size of the male was 10 x 8 mm.

Comments.—Malcolm (1990, p. 349) reports *C. philander* as the "second most abundant nonflying mammal in the forest" at the Minimum Critical Size of Ecosystems Reserves near Manaus, Brazil. In 2,040 arboreal station nights, he captured 56 individuals (Malcolm 1990). Malcolm's (1991) arboreal station design was used during this research, but only one *C. lanatus* was captured in 3,000 station nights at RNAM. *C. lanatus* is larger than *C. philander* (310–410 g versus 140–270 g; Emmons and Feer 1997), so there are likely fewer individuals of *C. lanatus* present in a given area compared to *C. philander*. Their larger size also may inhibit *C. lanatus* from readily entering Tomahawk traps. Nonetheless, Patton et al. (2000) report 17 individuals of *C. lanatus* in 9,278 station nights on the Juruá River, Brazil. This suggest that *C. lanatus* occurs at lower densities or is less trappable in northeastern Peru than in western Brazil, and attains far lower densities than does *C. philander* near Manaus, Brazil.

Specimens Examined.—(n = 2): 1♀ TTU 101044; 1♂ TTU 99025.

Caluromysiops Sanborn 1951
***Caluromysiops irrupta* Sanborn 1951**

Description.—*Caluromysiops irrupta*, another medium-sized, arboreal opossum, is similar in overall size and proportions to *Caluromys lanatus*, but can easily be distinguished from the latter by its grayish brown (as opposed to reddish brown) color and prominent black patches across the shoulders that extend back along the spine as narrow stripes and forward along the inner foreleg.

Comments.—No individuals of this species were collected during this study even though arboreal traps were placed in its preferred habitat, mature rainforest. *C. irrupta* is rare in collections, known from fewer than 30 specimens (Emmons and Feer 1997). Specimens with confirmed origins have been recorded from four localities in southeastern Peru (Sanborn 1951; Izor and Pine 1987; Solari et al. 2002) and one in western Brazil (Vivo and Gómes 1989). One specimen recorded from Leticia, Colombia, is of unknown origin because many mammals are sent there from elsewhere for export (Simonetta 1979; Izor and Pine 1987; Vivo and Gómes 1989). Given the paucity of specimens and the habitat preferences of this species, it could occur at RNAM.

Subfamily Didelphinae Gray 1821
Tribe Didelphini Gray 1821
Chironectes Illiger 1811
***Chironectes minimus* (Zimmerman 1780)**

Description.—A very distinctive marsupial, its black and white marbled coat is unmistakable, as are prints left by its completely webbed hind feet. Both sexes have a watertight pouch, which the female uses to protect her young and the male uses to protect his scrotum while swimming.

Comments.—*Chironectes minimus* has been sighted at RNAM, but no specimens were obtained. Hunters in Mishana report it from small streams that drain into the black water Río Nanay, and C. Rivera (pers. comm.) observed one in a small stream at RNAM in 1999. *Chironectes* occurs near streams, where it has access to fish, crustaceans, insects, and frogs, its preferred prey items (Mondolfi and Padilla 1957; Marshall 1978). It apparently occurs throughout Amazonia and into Central America (McCarthy 1982), although it may be absent from some white-water river systems (Emmons and Feer 1997). It undoubtably occurs at RNAM.

Didelphis Linnaeus 1758
***Didelphis albiventris* Lund 1840**

Description.—Similar to *Didelphis marsupialis*, it is distinguished by having a white head with sharp black bars from the ear through the eyes to the nose, white ears with a black base, and a white throat (Emmons and Feer 1997).

Comments.—*Didelphis albiventris* has been reported approximately 15 km east of RNAM in sympatry with *D. marsupialis* (Díaz and Willig 2004). Both were captured in an agricultural field planted primarily with *yuca.* Although this species was not captured at RNAM, it likely occurs there given the nearness of this record and the lack of geographic barriers between the site and RNAM.

Didelphis marsupialis Linnaeus 1758
(Fig. 10)

Description.—This is the largest marsupial that occurs at RNAM and is distinct from other members of the marsupial community. It has coarse black or gray guard hairs over dense white underfur. It cannot be confused with any other marsupial at RNAM (*D. albiventris* have white ears among other distinguishing characteristics). Only black phase individuals were captured at RNAM, which is in accord with the observation by Emmons and Feer (1997) that rainforest populations are usually black. The tail, usually longer than head and body length (HBL), is naked and black for the proximal half and white for the distal half. This species also has a distinctive odor, revealing its presence even when it is not seen.

Six individuals were collected, all of which were age class 4 or younger. Because of the small number of individuals collected and because all of them were sub-adults or younger, variation due to age or gender

Figure 10. Dorsal, ventral, and lateral views of the skull of *Didelphis marsupialis* (TTU 101144). Scale bar = 10 mm. Photo by T. Kennedy.

could not be assessed, although both of these factors contribute to mensural variation in the species (Gardner 1973).

Distribution and Habitat.—*Didelphis marsupialis* is wide-ranging, occurring from Mexico throughout Central America and all of the Amazon Basin. It occurs in sympatry with *D. albiventris* (Catzeflis et al. 1997; Lavergne et al. 1997; Díaz and Willig 2004) and *D. aurita* (Cerqueira 1985) in parts of its range in South America, where these species can be difficult to distinguish. At RNAM, all but one individual was captured in areas heavily used by humans and one was taken in mature *monte alto* forest; all individuals were captured at ground level.

Reproduction.—Young individuals (age class 2) were taken in November, January, April, and July. No adult females were captured. Average testes size of the two sub-adult males captured was 16 x 11.5 mm.

Comments.—This species is probably more common at RNAM than indicated by capture rate. Traps containing other mammals were often moved and animals in the traps were damaged, killed, or removed (if in a snap trap). Additionally, bait was often removed from Tomahawk traps and the trap tripped, but no animal captured. Footprints indicate *Didelphis* to be responsible for many of these events. In this manner, *Didelphis* made its presence known in primary forest sites as well as disturbed areas. Tomahawk traps large enough to accommodate adult *Didelphis* were deployed, but very few *Didelphis* were captured, suggesting this species was hesitant to enter traps or that the bait was undesirable.

Didelphis marsupialis is one of the better studied marsupials in the Neotropics, with several systematic studies that involve both morphometrics (Allen 1902; Gardner 1973; Varejão and Valle 1982; Cerqueira 1985) and genetics (Kirsch et al. 1993; Lavergne et al. 1997). Moreover, information about its ecology is readily available (Fleming 1973; Tyndale-Biscoe and Mackenzie 1976; Cajal 1981; Sunquist et al. 1987; Atramentowicz 1988; Sunquist and Eisenberg 1993; Catzeflis et al. 1997) in contrast to most other species of Neotropical marsupials.

Specimens Examined.—(n = 6): 1♀ TTU 101000; 5♂♂ TTU 98898, 98951, 98996, 101053, 101144.

Philander Brisson 1762

Four-eyed opossums are medium-large members of the marsupial community. They have gray to black dorsal pelage and creamy white to gray ventral fur that sometimes has an orange tinge. Their common name derives from the presence of two well-defined white or cream colored spots above their eyes, mirroring the cotton in the orbits of museum skins. The tail is about the same length as the head and body and is densely furred at the base. The remainder of the tail is naked and black for its proximal two-thirds and white at the end.

Three species are currently recognized in Amazonia (Patton and da Silva 2008). *Philander opossum* ranges most widely and is found throughout the region. *P. mcilhennyi* is restricted to the Amazon Basin south of the Río Amazonas, whereas *P. andersoni* occurs north of the river. *P. frenatus* is found only in the Atlantic forests of Brazil, Paraguay, and Argentina (Patton and da Silva 2008). Sympatry of *P. opossum* and *P. mcilhennyi* has been documented at several localities (Gardner and Patton 1972; Fleck and Harder 1995; Hutterer et al. 1995; Patton et al. 2000). Based on the specimens collected during this study, Hice (2001) reported the first record of sympatry between *P. opossum* and *P. andersoni*.

***Philander andersoni* (Osgood 1913)**

(Figs. 11–12)

Description.—This species is easily distinguished from *Philander opossum* by the appearance of a distinctive dark medial band of fur 2–3 cm wide along the back. Sides are a uniform gray and the venter of individuals captured at RNAM is creamy gray, occasionally with an orangish wash. Additionally, the white fur under the chin extends well up behind the mouth to just in front of the pinnae. The eye spot is separated from this extension by a narrow (2–3 mm) band of black. The tail is furred for the proximal 18% of its length and the terminal portion is naked and black with the distal one-third to one-half white.

Figure 11. Dorsal and ventral views of the skulls of *Philander andersoni* (TTU 101157, left) and *P. opposum* (TTU 101253, right). Scale bar = 10 mm. Photo by T. Kennedy.

Figure 12. Lateral views of the skulls of *Philander andersoni* (TTU 101157, top) and *P. opposum* (TTU 101253, bottom). Scale bar = 10 mm. Photo by T. Kennedy.

Two adult females and eight adult males were collected. Selected measurements of adults are given in Table 1. Sexual dimorphism was analyzed and found to be non-significant (ANOVA results were not significant for any variable). Nonetheless, Patton et al. (2000) also observed no sexual size dimorphism for other species of *Philander*.

Comparisons.—Both species of *Philander* could superficially be confused with *Metachirus* (see account for *M. nudicaudatus*). *P. andersoni* differs substantially from *P. opossum* in pelage coloration. *P. opossum* lacks the black dorsal band present in *P. andersoni*. Moreover, the white fur under the chin terminates below the pinnae in *P. opossum* (Hutterer et al. 1995). Additionally, the proportion of the tail that is white is much larger in *P. andersoni* than *P. opossum*, with the white portion limited to the distal 5 cm in *P. opossum*, at least in specimens from RNAM. The palate of *P. andersoni* is longer and narrower than that of *P. opossum* (Fig. 12). Additionally, the posterior margin of the nasal bone extends nearly to the supraorbital processes in *P. andersoni*, but stops short of them in *P. opossum* (Fig. 11). This is less evident in quantitative analyses, with *P. andersoni* significantly larger than *P. opossum* in only one of 15 cranial measurements (MANOVA, $p = 0.006$; Table 1).

Distribution and Habitat.—*Philander andersoni* was only captured in *monte alto* and *franco arcilloso* forested habitats and not taken in *varillal* or disturbed habitats. One was captured on a fallen log at a height of 1.7 m; the remainders were captured on the ground. All but one (a young individual captured in a Victor trap) were captured in Tomahawk traps, three with peanut butter bait and seven with dry salted fish.

Reproduction.—Only two females were captured, one each in April and October; both carried pouch young. The one taken in October had two young (40

Table 1. Selected external and cranial measurements (mm) of Philander andersoni *and* P. opossum. *Sexes are pooled because sexual dimorphism was not significant. Significance levels are based on one-way ANOVA (na = not included in MANOVA; ns =* $p > 0.05$*; ** $p < 0.05$ *with sequential Bonferroni adjustment).*

Variable	*Philander andersoni*				*Philander opossum*		
	Mean ± SE	Range	n	*p*	Mean ± SE	Range	n
TOL	593.5 ± 17.2	563 – 676	6	na	536.9 ± 6.4	494 – 599	16
TAL	290.5 ± 8.8	270 – 330	6	na	255.8 ± 2.6	241 – 279	16
HF	38.5 ± 1.5	32 – 43	6	na	40.7 ± 0.5	37 – 44	16
E	36.3 ± 0.8	34 – 40	6	na	32.5 ± 0.4	30 – 36	16
GLS	72.19 ± 1.93	65.50 – 80.03	6	ns	68.86 ± 0.71	64.62 – 75.24	17
CBL	67.90 ± 1.72	63.07 – 75.33	6	ns	65.26 ± 0.61	61.57 – 70.60	17
PL	42.65 ± 1.20	39.47 – 48.07	6	ns	42.44 ± 0.45	39.63 – 46.26	17
BOL	8.53 ± 0.17	8.01 – 9.22	6	0.014	8.02 ± 0.10	7.02 – 8.67	17
ZB	37.36 ± 1.50	33.15 – 42.41	5	0.019	34.42 ± 0.41	31.99 – 37.61	17
MB	22.11 ± 0.62	20.64 – 24.89	6	ns	21.60 ± 0.25	20.07 – 23.63	16
IOC	8.60 ± 0.15	8.21 – 9.06	6	ns	8.79 ± 0.07	8.33 – 9.27	17
RL	27.69 ± 0.76	25.86 – 30.87	6	ns	26.55 ± 0.34	23.90 – 28.96	17
NL	35.53 ± 1.12	32.50 – 40.43	6	0.005	32.27 ± 0.45	29.21 – 35.51	17
RW	11.56 ± 0.47	10.21 – 13.55	6	0.015	10.46 ± 0.17	9.45 – 12.02	17
CM4	30.30 ± 0.43	28.53 – 31.53	6	ns	29.49 ± 0.28	27.43 – 31.61	17
LMTR	14.23 ± 0.20	13.54 – 14.92	6	0.003*	13.18 ± 0.15	12.23 – 14.71	17
PW	19.56 ± 0.38	18.11 – 20.58	6	0.005	18.54 ± 0.19	17.41 – 20.53	17
OCB	13.04 ± 0.33	12.03 – 14.44	6	0.044	12.61 ± 0.12	11.54 – 13.64	17
CD	20.18 ± 0.63	18.08 – 22.38	6	0.049	19.14 ± 0.21	17.78 – 21.36	17

mm crown-rump length); the other had four fully furred young (166–176 mm total length; 97–101 HBL; weight 22–24 g). This implies year-round breeding for the species, although sample size is quite small. Average testes size in adult males was 15.8 x 11 mm (n = 6).

Specimens Examined.—(n = 14): 2♀♀ TTU 98891, 99036; 8♂♂ LACM 96120, TTU 98740, 98869, 99041, 101054, 101149, 101157, 101246; young in pouch: 2♀♀ TTU 99038, 101244; 2♂♂ TTU 99039, 101245.

Philander opossum **(Linnaeus 1758)**
(Figs. 11–12)

Description.—Individuals collected at RNAM have short fur and are uniformly gray in dorsal pelage color with a white to cream venter that often has an orangish wash. The base of the tail is covered with short fur for less than 15% of its length. Most of the tail is black with the terminal 5 cm or less lighter or white.

A total of 14 females and 18 males were collected. Of these, seven adult females and nine adult males had intact crania, allowing preliminary assessment of sexual dimorphism. As with *P. andersoni*, this was nearly non-existent (MANOVA *p* = 0.219). Selected measurements are given in Table 1.

Comparisons.—See account for *Philander andersoni*.

Distribution and Habitat.—Philander opossum was the only species of *Philander* captured in secondary growth, where all individuals were captured. It occurred in newly created *yuca* fields, recently abandoned fields, and thick tangles of secondary vegetation. All individuals, with the exception of one young individual caught in a Victor trap, were captured in Tomahawk traps set on the ground. However, this species was seen climbing on fallen trees up to 3 m off the ground. Emmons and Feer (1997) stated that their nests may be 8–10 m above the forest floor. Most individuals (21) were captured with dry salted fish as bait; the remainder (11) were taken with peanut butter. Capture patterns suggest the two species of *Philander* present at RNAM subdivide the landscape by level of disturbance, with *P. opossum* in more anthropogenically disturbed areas and *P. andersoni* restricted to forested areas.

Reproduction.—All 10 adult females captured were either pregnant (1) or carrying pouch young. These were obtained in the months of July, August, and November. Two females captured on 27 August had fully furred young in pouch (weights ranged from 17–24 g). Weight at weaning is 50–75 g (Hershkovitz 1997). Given that the period from birth to weaning is 68–75 days (Charles-Dominique 1983), this suggests breeding peaks early in the dry season (June or July) with weaning early in the rainy season (October). However, three individuals taken in November were either pregnant (one with two 9 mm embryos in utero) or pouch-gravid, suggesting year-round breeding for this species in northeastern Peru, but no adult females were captured at other times of the year, making conclusions about the seasonality of reproduction in this species tentative. Elsewhere in Peru (Jenaro Herrera) it has been suggested that reproductive activity of *P. opossum* increased during the rainy season, although sample sizes were also small (Fleck and Harder 1995). Average litter size was 3.8 (n = 10; range 2–5) and pouched young ranged from 13–128 mm crown-rump length (n = 29). The nearly mature young taken from the two females captured in August ranged from 158–199 mm TOL and 93–109 mm HBL (n = 7). Average testes size of adult males was 17.2 x 11.4 mm (n = 11).

Comments.—Fleck and Harder (1995) report *Philander opossum* and *P. andersoni* from Jenaro Herrera on the south bank of the Río Ucayali (a tributary of the Río Amazonas). No voucher specimens were prepared, but photos taken of *P. andersoni* were subsequently re-identified as *P. mcilhennyi* (Patton and da Silva 1997), which is the species expected to occur in sympatry with *P. opossum* south of the Río Amazonas. Voss and Emmons (1996) suggested that there may only be one species of *Philander* north of the Río Amazonas in Peru. The series of *Philander* collected during this study definitively establishes the occurrence of two species in this region (Hice 2001).

Specimens Examined.—(n = 39): 14♀♀ LACM 96121, TTU 98945, 98949, 98953, 98583, 100984, 101136, 101141, 101142, 101181, 101186, 101190, 101253, 101258; 18♂♂ LACM 96122, TTU 98574, 98755, 98842, 98579, 98588, 98589, 98591, 98592, 98993, 98595, 98596, 100975, 101178, 101191, 101192, 101196, 101256; young in pouch: 1♀ TTU 98586; 6♂♂ TTU 98584, 98585, 101184, 101185, 101187, 101188.

Tribe Marmosini Hershkovitz 1992

Marmosa Gray 1821

Members of this genus are small-bodied, semi-arboreal, widely distributed marsupials that are sometimes common members of the marsupial community in lowland rainforests. Up to five species could occur at RNAM, but only one member of the subgenus *Marmosa* (*M. waterhousei*) and 2 of the subgenus *Micoureus* (*M. demerarae* and *M. regina*) were captured there. *M. lepida* was supposedly seen at the reserve (J. Alvarez, pers. comm.), but the individual may have been misidentified as it ran along a branch at night. *M. rubra* also could occur at RNAM.

Marmosa (Marmosa) waterhousei (Tomes 1860)
(Fig. 13)

Description.—This species has brown dorsal fur and yellowish fur on the venter. The eye rings are large and prominent and extend forward to the nose. The fur surrounding the eye rings is paler than the remainder of the face. The tops of all four feet are whitish. The tail is longer than HBL, naked, and tan in color. The scales on the tail are large and diamond shaped.

Nine individuals (3 ♀♀, 6 ♂♂) were captured. Selected external and cranial measurements are given in Table 2. Sample size was too small to evaluate sexual dimorphism.

Comparisons.—*Marmosa waterhousei* is easily distinguished from woolly mouse opossums (subgenus *Micoureus*) which have dense, woolly fur and are larger. It could be confused with other species of the genus *Marmosa*. *M. rubra*, although of similar size, has much redder fur and an orangish venter. *M. lepida* has more chestnut-colored fur and is much smaller. *M. waterhousei* also may easily be confused with members of the genus *Marmosops*. Externally, *M. waterhousei* tends to be more chestnut dorsally and the pale ventral midline is bordered by a broad band of gray-based hairs. The ventral hairs of *Marmosops* lack the gray base and instead are cream-colored to the base. The dorsal hair on the front feet is white in *M. waterhousei* and brown or tan in *Marmosops*. The tail scales are larger and arranged in bands in *Marmosa*, whereas they are smaller and arranged in spirals in *Marmosops*. A triad of scale hairs is associated with each tail scale in both genera, but they are thick and longer than each individual scale in *Marmosops*, with the central hair of each triad black or dark brown. In *Marmosa*, the scale hairs are inconspicuous and shorter than the scales. Cranially, the genera are readily distinguished by prominent supraorbital ledges in *Marmosa* and by the presence of anterior buttresses on the alisphenoid portion of the bullae in *Marmosops* (Fig. 13).

Distribution and Habitat.—This species is broadly distributed throughout the Amazon Basin (Creighton and Gardner 2008a). It was taken in all three types of forested habitats and in older secondary growth where medium-sized trees were present. One was taken at a height of 6.1 m in a Victor trap (tree species = *Tetrastylidium peruvianum*, dbh = 37 cm). The remainder were captured on the ground, two in Tomahawk traps and six in Victor traps.

Reproduction.—Both adult females, taken in October and November, were lactating. Males were captured in June, July, October, and November. Average testes size was 8.6 x 5.4 mm (n = 5).

Specimens Examined.—(n = 9): 3♀♀ TTU 98654, 98716, 101098; 6♂♂ LACM 96112, TTU 98717, 98934, 100922, 101153, 101219.

Marmosa (Micoureus) demerarae Thomas 1905
(Fig. 13)

Description.—This medium-sized opossum has dense woolly fur which is longer than that of other species of the subgenus *Micoureus*, averaging about 1 cm on the rump. Dorsal fur is gray-brown and ventral fur is yellowish with a distinct gray base. Prominent dark eye rings that extend slightly toward the nose are present. The tail is heavily furred around the base for 3–4 cm. The remainder of the tail is naked and solid brown in color.

Only two females and three males were collected. Selected measurements of the three adults (1 ♀, 2 ♂♂) are as follows: TOL 545, TAL 258.0, HF 26.0 (25–27), E 26.5 (26–27), GLS 44.64 (43.94–45.61), CBL 40.99 (39.73–42.25), PL 24.15 (23.22–25.19), BOL 5.65 (5.47–5.76), ZB 24.75 (24.59–24.91), MB 16.31 (15.99–16.66), IOC 8.08 (7.98–8.24), RL 16.01 (15.69–16.24), NL 19.87 (19.22–20.25), RW 7.75 (7.53–8.02), CM4 17.63 (17.31–18.06), LMTR 8.84 (8.67–9.04), PW 13.29 (13.17–13.41), OCB 8.88 (8.66–9.23), CD 12.47 (11.90–12.85). Sample size was too small to permit analysis of sexual dimorphism, although Patton et al. (2000) found significant sexual dimorphism in all four external and eight of 15 cranial measurements.

Comparisons.—*Marmosa demerarae* is similar to the other woolly opossum in the area, *M. regina*. Externally, they are generally the same size, but differ in the amount of gray on the venter and the extent to

Table 2. Selected external and cranial measurements (mm) of Marmosa waterhousei.

Variable	Mean ± SE	Range	n
TOL	347.7 ± 6.0	328 – 367	6
TAL	206.7 ± 2.9	196 – 212	6
HF	20.7 ± 1.2	17 – 24	6
E	24.2 ± 0.6	23 – 27	6
GLS	36.71 ± 0.66	34.77 – 38.85	5
CBL	33.65 ± 0.52	31.79 – 35.00	6
PL	20.11 ± 0.37	19.00 – 21.63	7
BOL	4.62 ± 0.13	4.14 – 5.04	6
ZB	20.19 ± 0.27	19.37 – 21.30	7
MB	13.37 ± 0.18	12.76 – 13.94	6
IOC	6.37 ± 0.20	5.61 – 7.08	7
RL	13.38 ± 0.25	12.34 – 14.04	7
NL	15.93 ± 0.36	14.82 – 17.39	7
RW	6.28 ± 0.16	5.69 – 6.74	7
CM4	13.94 ± 0.15	13.36 – 14.42	7
LMTR	6.95 ± 0.07	6.66 – 7.20	7
PW	10.25 ± 0.11	9.95 – 10.74	7
OCB	7.32 ± 0.16	6.79 – 7.79	5
CD	10.71 ± 0.13	10.19 – 10.98	6

which the base of the tail is furred. *M. demerarae* has more gray-based fur on the venter, sometimes nearly meeting medially, leaving little to no buff colored fur separating the lateral gray stripes, whereas the gray is usually widely separated by a strip of pure buff colored fur in *M. regina*. The base of the tail is furred for more than 2.5 cm in *M. demerarae*, but less than 2.0 cm in *M. regina*. The dorsal fur, especially on the rump, also is longer in *M. demerarae*, with lengths greater than 1 cm in *M. demerarae* and about half that length in *M. regina*.

The skulls of the two species are quite distinctive (Fig. 13). This is particularly true of interorbital breadth and palatal breadth, which are much narrower in *M. demerarae*. Because of the small number of adult individuals captured of each species (3 *M. demerarae* and 2 *M. regina*), no meaningful statistical comparisons could be undertaken.

Distribution and Habitat.—This species occurs throughout the Amazon Basin in both mature and secondary forest. At RNAM, individuals were captured in *varillal* habitat and in older secondary growth where it grades into less disturbed forest. Two individuals were taken in arboreal traps, one at a height of 6.8 m in a *Tovomita brasiliensis* (dbh = 36 cm), the other at 7.0 m in a *Metteniusa tessmanniana* (dbh = 39 cm). Two others were captured on the ground, and the remaining one was collected by a hunter.

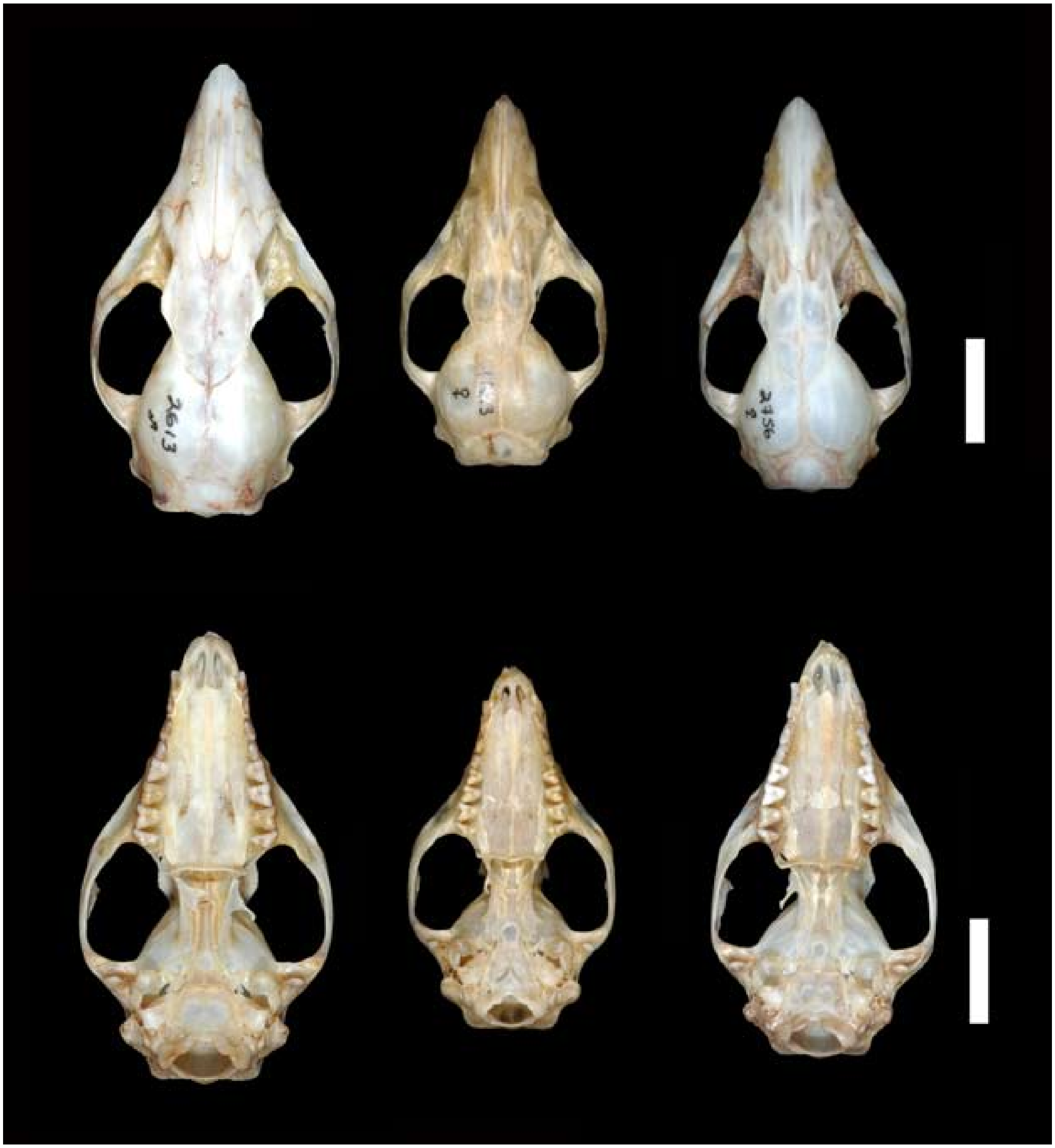


Figure 13. Dorsal and ventral views of the skulls of *Marmosa demerarae* (TTU 98988, left), *M. waterhousei* (TTU 98716, center), and *M. regina* (TTU 99000, right). Scale bar = 10 mm. Photo by T. Kennedy.

Reproduction.—One lactating female was captured in October and one young female (age class 2) was captured in April. One adult male collected in August had testes that measured 11 x 7 mm. The other two male specimens, collected in January, consisted of only skulls.

Comments.—Patton et al. (2000) collected 55 individuals each of *Marmosa demerarae* and *M. regina* (110 individuals total) along the Rio Juruá. Additionally, Woodman et al. (1995) collected 45 individuals of *M. regina* in southeastern Peru. In both studies, most individuals were captured in arboreal traps. Although arboreal trap effort was about one-third of Patton's trap effort (3,000 versus 9,278 station nights), and more than Woodman's effort (2,400 station nights), only five individuals of *M. demerarae* and two of *M. regina* were captured at RNAM, suggesting members of this subgenus may be less common at RNAM than at other locations within Amazonia.

Specimens Examined.—(n = 5): 2♀♀ TTU 101094, 101236; 3♂♂ TTU 98845, 98846, 98988.

Marmosa (Micoureus) regina **Thomas 1898**

(Fig. 13)

Description.— Similar in appearance to *M. demerarae*, this gray-brown opossum has a buff-colored venter in which the ventral fur retains a buffy tip, but becomes gray-based laterally. The fur is dense but shorter (5 mm on the rump) than that of *M. demerarae*, and the furred part of the tail is much shorter (< 2 cm).

Only two individuals were captured, both females, with selected measurements as follows: TOL 397.0 (380–414), TAL 228.5 (220–237), HF 23.5 (23–24), E 23, GLS40.66 (40.42–40.90), CBL 37.61 (37.47–37.75), PL 22.49 (22.28–22.70) BOL 4.98, ZB 22.62 (22.05–23.18), MB 14.70 (14.45–14.95), IOC 7.09 (6.99–7.19), RL 14.88 (14.84–14.91), NL 18.09 (18.00–18.17), RW 6.94 (6.84–7.03), CM4, 16.21 (16.04–16.38), LMTR 7.94 (7.84–8.04), PW 11.81 (11.70–11.92), OCB 8.28, CD 11.13 (10.87–11.38).

Comparisons.—See account for *Marmosa demerarae*.

Distribution and Habitat.—Both individuals were collected on the ground in Victor traps baited with dry salted fish, in *monte alto* forest several hours walk from the road deep into the forest.

Reproduction.—Neither female, both collected in September, showed signs of reproductive activity.

Comments.—See account for *Marmosa demerarae*.

Specimens Examined.—(n = 2): 2♀♀ TTU 99000, 101208.

Monodelphis Burnett 1830

Short-tailed opossums are terrestrial, chiefly insectivorous, opossums that forage in the leaf litter on the forest floor, filling the niche of shrews which are absent from the Amazon Basin. Several species of *Monodelphis* occur there. *M. adusta* (the only species captured at RNAM) has been reported from southern Panama, and the eastern slopes of the Andes from Colombia and western Venezuela, south into northern Peru (Solari 2007). Given the current information about the distributions of the other members of this genus within Amazonia, it is possible that two other species (*M. brevicaudata* and *M. peruviana*) occur at RNAM.

Monodelphis adusta **(Thomas 1897)**

(Fig. 14)

Description.—This is a small, shrew-like opossum with a short tail. Upperparts are a uniform dark brown and the fur is very short. Underparts are lighter brown and often have a cream streak originating on the upper chest and extending down the mid-line of the venter. The feet lack the opposable pollex present in other Didelphimorphia. The tail is much shorter than HBL. Ears are very short and naked. The skull is flattened dorsal-ventrally and the braincase is squarish.

Four males and two females were captured. Both females were sub-adults (age class 3), so measurements are only given for males (Table 3).

Comparisons.—This species cannot be confused with any other opossums captured in the area. Its short tail and shrew-like appearance are unmistakable. The other species of *Monodelphis* that could occur at RNAM are much larger with reddish rufous fur dorsally and have a completely or partially furred tail. The tail of *M. adusta* is sparsely furred.

Distribution and Habitat.—This species was captured in all three primary forest types at RNAM. It was not captured in secondary growth, as has been reported for this and other species of this genus. Five of the six individuals were captured in pitfall traps; the other was taken in a Sherman trap baited with peanut butter.

Figure 14. Dorsal and ventral views of the skull of *Monodelphis adusta* (TTU 101075). Scale bar = 10 mm. Photo by T. Kennedy.

Reproduction.—The females were captured in March, but were sub-adults and showed no signs of reproductive activity. Average testes size was 6.5 x 4.25 mm for the four males taken in May, August, November, and December.

Comments.—All species of *Monodelphis* in the Amazon Basin tend to be rare in collections. However, this may be due to the types of traps used to assess the small mammal community. If pitfall traps are not used to sample small mammals, these species could easily be missed. This is further supported by five additional captures of *M. adusta* in pitfall traps at RNAM subsequent to this research. Although members of this genus appear to be rare, this is probably partially due to sampling bias (Hice and Schmidly 2002).

Specimens Examined.—(n = 6): 2♀♀ TTU 98864, 101075; 4♂♂ TTU 98686, 98923, 101019, 101164.

Tribe Metachirini Hershkovitz 1992

Metachirus Burmeister 1854

***Metachirus nudicaudatus* (Geoffroy St-Hilaire 1803)**

(Fig. 15)

Description.—This species superficially resembles *Philander* because of the presence of two cream-colored spots above its eyes. However, it is distinguished by its longer, more gracile legs, longer and narrower feet, a completely naked tail that exceeds HBL, and overall more brown than gray pelage color. Moreover, females lack a pouch. The skull lacks postorbital processes and supraorbital ridges, and the interorbital region is rounded. Captive individuals often make a distinct sound produced by chattering their teeth.

Twelve females and nine males were captured. Selected measurements are presented in Table 4.

Table 3. Selected external and cranial measurements (mm) of Monodelphis adusta.

Variable	Mean ± SE	Range	n
TOL	161.3 ± 2.3	157 – 165	3
TAL	54.0 ± 1.5	52 – 57	3
HF	15.3 ± 0.3	15 – 16	3
E	11.7 ± 0.3	11 – 12	3
GLS	26.69 ± 0.22	26.34 – 27.09	3
CBL	25.44 ± 0.27	24.92 – 25.80	3
PL	14.26 ± 0.18	13.91 – 14.50	3
BOL	3.72 ± 0.04	3.64 – 3.78	3
ZB	14.54 ± 0.01	14.53 – 14.55	2
MB	11.65 ± 0.09	11.46 – 11.77	3
IOC	5.46 ± 0.03	5.41 – 5.49	3
RL	10.41 ± 0.26	10.15 – 10.92	3
NL	12.71 ± 0.18	12.37 – 13.00	3
RW	4.41 ± 0.07	4.28 – 4.50	3
CM4	11.10 ± 0.17	10.82 – 11.42	3
LMTR	6.07 ± 0.03	6.03 – 6.13	3
PW	8.18 ± 0.11	8.00 – 8.37	3
OCB	6.68 ± 0.11	6.54 – 6.90	3
CD	7.30 ± 0.11	7.16 – 7.51	3

Sexual dimorphism appears to be non-existent (1 variable, cranial depth, was significantly different at $p = 0.002$), which is consistent with the findings of Patton et al. (2000).

Distribution and Habitat.—*Metachirus nudicaudatus* occurs throughout Central America and Amazonia and is currently considered one species (Gardner and Dagosto, 2008). However, molecular analysis suggests it could represent a complex of species (Patton et al. 2000). At RNAM, this species was captured in all three types of forested habitat, particularly *varillal*, and in dense secondary growth. One individual was captured in a Tomahawk trap on a fallen log at a height of 1.6 m. All others were captured on the ground, six in Victor and 15 in Tomahawk traps.

Reproduction.—Ten of 11 adult females captured were carrying young (3) or lactating (7). Pouch-gravid individuals were taken in March, September, and November. Litter size ranged from 7–8, and the crown-rump length of embryos was 7–24 mm. Lactating females without young attached were taken in March, July, August, October, and November. These months span both rainy and dry seasons, indicating year-round reproductive activity and apparent use of a nest or creche. Average testes size of adult males was 14.2 x 10.2 mm (n = 5).

Specimens Examined.—(n = 22): 12♀♀ LACM 96123, TTU 98619, 98667, 98726, 98888, 98908, 99012, 100842, 101091, 101143, 101180, 101207; 9♂♂ LACM 96124, TTU 98587, 98633, 98882, 98948,

Figure 15. Dorsal and ventral views of the skull of *Metachirus nudicaudatus* (TTU 100926). Scale bar = 10 mm. Photo by T. Kennedy.

98957, 100921, 100926, 101090; 1 ? (gender unknown) TTU 101095.

Tribe Thylamyini Hershkovitz 1992
Gracilinanus Gardner and Creighton 1989

This genus was proposed by Gardner and Creighton (1989) to include species of the *Marmosa microtarsus* group of Tate (1933). Members of this genus are tiny opossums (weight 10–30 g) whose distribution and natural history are possibly the least known of all Neotropical marsupials because of the paucity of specimens. The contents of this genus have changed substantially during the last decade, and two new genera have been described to include species formerly placed in this genus: *Hyladelphys* Voss, Lunde, and Simmons 2001 to include *kalinowskii*, and *Cryptonanus* Voss, Lunde, and Jansa 2005 to include *agricolai*, *chacoensis*, *guahybae*, *ignitus*, and *unduaviensis*. Voss, Lunde, and Jansa (2005) provided an extensive review of the genus. Although no specimens of this genus were collected during this fieldwork, it is probable that at least one species of *Gracilinanus* occurs at RNAM (Creighton and Gradner 2008b; Voss et al. 2009).

Marmosops Matschie 1916

These small to very small opossums are the commonest component of the marsupial community at RNAM. They are reddish brown to dark brown in coloration, with a creamy white to white venter. Hind feet are white above, but forefeet tend to be brownish, especially in live specimens. Dark eye rings are present but tend to be less distinct than those of *Marmosa*.

As many as four species of *Marmosops* occur sympatrically at localities in the Amazon Basin (Patton et al. 2000), two of which (*M. noctivagus* and *M. bishopi*) were collected at RNAM. These represent the large-bodied and small-bodied mouse opossums, respectively. It is not unreasonable to expect that two medium-bodied species, probably *M. impavidus* and *M. neblina*, will eventually be recorded there as well (Gardner and Creighton 2008).

Table 4. Selected external and cranial measurements (mm) of Metachirus nudicaudatus.

Variable	Mean ± SE	Range	n
TOL	556.8 ± 7.8	523 – 626	13
TAL	299.8 ± 5.3	275 – 338	13
HF	40.1 ± 0.4	38 – 43	13
E	33.0 ± 1.1	23 – 36	12
GLS	57.06 ± 0.55	52.47 – 60.08	13
CBL	53.30 ± 0.58	48.76 – 55.64	13
PL	32.02 ± 0.34	29.33 – 33.33	13
BOL	7.22 ± 0.09	6.86 – 7.81	13
ZB	27.81 ± 0.40	25.91 – 30.78	13
MB	17.09 ± 0.15	16.29 – 18.28	13
IOC	8.90 ± 0.09	8.07 – 9.36	13
RL	22.68 ± 0.31	20.48 – 24.30	12
NL	27.18 ± 0.44	23.50 – 28.89	12
RW	9.35 ± 0.17	8.35 – 10.77	13
CM4	23.80 ± 0.19	22.39 – 25.24	13
LMTR	11.49 ± 0.08	10.98 – 12.03	13
PW	16.26 ± 0.24	14.83 – 17.89	13
OCB	11.45 ± 0.13	10.66 – 12.15	13
CD	15.15 ± 0.12	14.48 – 15.96	13

***Marmosops bishopi* (Pine 1981)**
(Fig. 16)

Description.—The smallest of the slender mouse opossums in this area, its upperparts are smoky brown that grades to gray-based white-tipped fur ventrally, with a band of pure white medially on the venter. Eye rings are present but may be indistinct in some individuals. Legs and feet are very thin and delicate. Adults weigh less than 20 g. Selected measurements are given in Table 5.

Twelve individuals (4 ♀♀, 7 ♂♂, 1 unknown) were collected at RNAM. Although sample size is small, this represents the largest series of this species taken at any single locality. No cranial variables differed significantly between females and males, suggesting little to no sexual dimorphism within this species. However, this result is not definitive because of small sample size.

Comparisons.—This species is readily distinguished from adults of other species of small marsupials in the area by its diminutive size. However, in hand, it could be confused with juveniles of all other species of *Marmosops* and *Marmosa*. The cranium is distinctive because all molars and premolars are erupted even though the skull is the size of that of juveniles of other species. Moreover, the canine has a small extra cusp on its posterior margin which is absent in other species.

Figure 16. Dorsal and ventral views of the skulls of *Marmosops bishopi* (TTU 99032, left) and *M. noctivagus* (TTU 98590, right). Scale bar = 10 mm. Photo by T. Kennedy.

Table 5. Selected external and cranial measurements (mm) of Marmosops bishopi.

Variable	Mean ± SE	Range	n
TOL	245.0 ± 6.5	222 – 259	5
TAL	136.4 ± 5.1	123 – 150	5
HF	16.8 ± 0.3	16 – 18	6
E	20.2 ± 0.5	19 – 22	6
GLS	28.70 ± 0.28	27.75 – 29.80	7
CBL	26.06 ± 0.39	24.55 – 27.80	7
PL	15.10 ± 0.22	14.21 – 16.05	7
BOL	3.75 ± 0.06	3.55 – 3.97	7
ZB	14.82 ± 0.17	14.38 – 15.49	6
MB	10.35 ± 0.09	10.08 – 10.82	7
IOC	5.45 ± 0.05	5.33 – 5.70	7
RL	11.24 ± 0.07	10.93 – 11.48	7
NL	12.50 ± 0.11	12.15 – 12.92	7
RW	4.67 ± 0.07	4.26 – 4.85	7
CM4	11.45 ± 0.09	11.16 – 11.75	7
LMTR	5.85 ± 0.04	5.74 – 6.04	7
PW	8.07 ± 0.10	7.63 – 8.40	7
OCB	6.67 ± 0.07	6.35 – 6.85	6
CD	8.21 ± 0.10	7.74 – 8.46	7

Marmosops bishopi is significantly smaller than *M. noctivagus* in every cranial measure (ANOVA $p < 0.001$, MANOVA $p < 0.001$). Patton et al. (2000) used the linear relationship of cranial variables to a univariate measure of overall size (condyloincisive length - CIL) to distinguish species of *Marmosops*. They found LMTR versus CIL separated the four species present on the Rio Juruá into three non-overlapping groups. It did not distinguish the two medium-sized species, which formed one large group. This method (using GLS instead of CIL) adequately differentiates the two species captured at RNAM (Fig. 17).

Distribution and Habitat.—Current distribution of this species includes western Amazonia south of the Amazon river in Brazil, Bolivia, and Peru (Gardner and Creighton 2008). This species was only captured in primary forested habitats and was taken most frequently in *franco arcilloso* habitat. All individuals were captured on the ground, most frequently in Victor traps (8) with peanut butter as bait. Three males were taken in the same pitfall trap on the same day and one individual was captured in a Sherman trap. It appears to be widespread but rare, even in extensively surveyed areas.

Reproduction.—One lactating female was captured in November. The other three females, taken in March, July, and October, showed no signs of lactation. Males were captured in July, October, November, and December. Average testes size was 6.7 x 4.3 mm (n = 7).

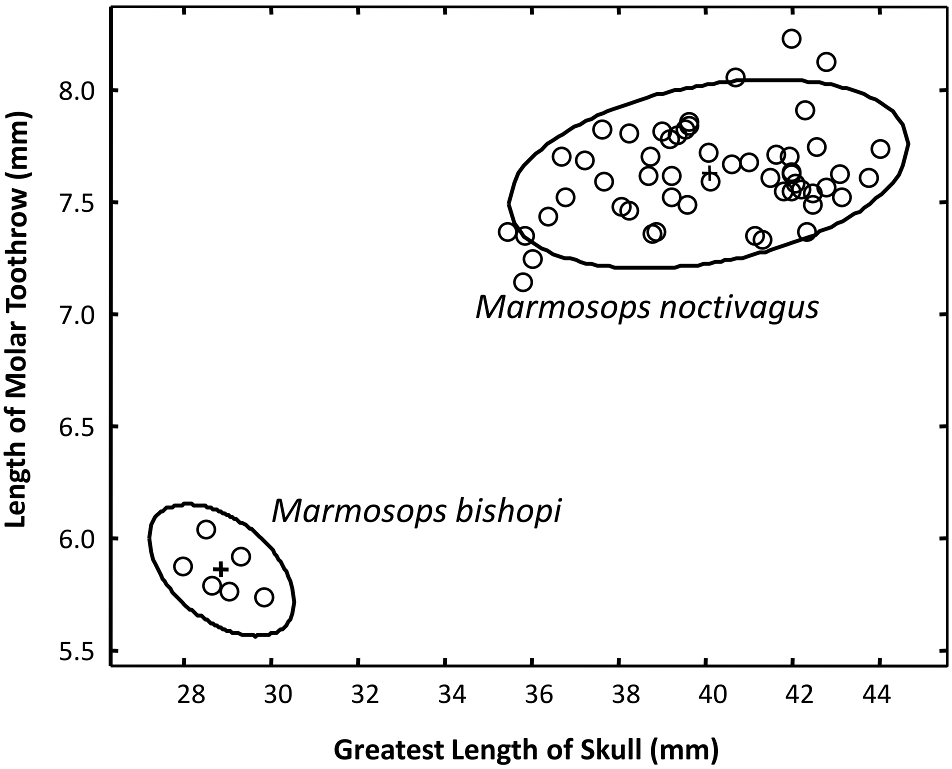


Figure 17. Bivariate plots of length of molar toothrow against greatest length of skull for *Marmosops bishopi* and *M. noctivagus*.

Specimens Examined.—(n = 12): 4♀♀ TTU 98857, 98964, 101238, 101257; 7♂♂ LACM 96113, TTU 98702, 99031, 99032, 100941, 101155, 101239; 1? (gender unknown) TTU 98653.

Marmosops noctivagus (Tschudi 1845)
(Fig. 16)

Description.—The larger of the slender mouse opossums in the area, the dorsal color of this species is more orange-brown than that of *Marmosops bishopi*. The venter is creamy white and is sometimes bordered by a narrow band of gray-based hairs laterally, especially in the abdominal region. The relatively distinct black eye rings extend toward the nose. The dorsal side of the forefeet is light brown with white toes and the hind feet are whitish. The skull is large with well-developed supra-orbital beading in older individuals (Fig. 16).

Effects of age and gender were analyzed and the overall MANOVA was significant for effects of gender ($p = 0.005$), but there were no effects of age ($p = 0.119$), or an interaction between gender and age categories ($p = 0.953$). One-way ANOVAs for effects of gender indicate males are larger than females, with significant differences in 11 of 15 cranial measures (Table 6).

Comparisons.—See accounts for *Marmosops bishopi* and *Marmosa waterhousei*.

Distribution and Habitat.—*Marmosops noctivagus* is known from the western Amazon basin of eastern Ecuador, Peru, Bolivia, and from Brazil south of the Río Amazonas (Gardner and Creighton 2008). This species was common north of the Río Amazonas and was registered in all habitat types and on nearly every grid. Three individuals were captured on fallen logs at heights of 0.3–1.9 m. The remaining 98 individuals were captured on the ground. Most (80%) were captured in Victor traps.

Table 6. Selected external and cranial measurements (mm) of Marmosops noctivagus. *Significance levels for effects of sexual dimorphism are based on one-way ANOVA (na = not included in MANOVA; ns =* $p > 0.05$*; ** $p < 0.05$ *with sequential Bonferroni adjustment).*

Variable	Females				Males		
	Mean ± SE	Range	n	*p*	Mean ± SE	Range	n
TOL	331.9 ± 5.4	298 – 410	20	na	366.8 ± 3.2	332 – 406	34
TAL	179.6 ± 2.2	165 – 203	20	na	201.3 ± 1.9	178 – 233	34
HF	18.2 ± 0.4	15 – 22	22	na	19.6 ± 0.3	17 – 22	34
E	21.7 ± 0.8	11 – 24	16	na	24.2 ± 0.4	21 – 33	31
GLS	37.86 ± 0.30	35.40 – 40.04	22	0.000*	41.59 ± 0.24	38.66 – 44.01	32
CBL	34.54 ± 0.31	31.75 – 36.66	22	0.000*	38.37 ± 0.22	35.54 – 40.50	33
PL	20.91 ± 0.19	19.22 – 22.38	22	0.000*	23.01 ± 0.12	21.72 – 24.37	34
BOL	4.61 ± 0.06	4.05 – 5.09	22	0.000*	5 .22 ± 0.04	4.62 – 5.78	33
ZB	19.15 ± 0.14	18.19 – 20.36	22	0.000*	20.90 ± 0.14	19.08 – 22.37	34
MB	13.04 ± 0.09	12.40 – 13.99	22	0.000*	13.90 ± 0.06	13.10 – 14.57	33
IOC	6.34 ± 0.05	5.65 – 6.79	22	ns	6.35 ± 0.06	5.44 – 7.16	34
RL	14.74 ± 0.15	13.50 – 15.74	22	0.000*	16.43 ± 0.12	14.92 – 18.17	33
NL	17.37 ± 0.19	16.03 – 18.93	22	0.000*	19.45 ± 0.16	17.56 – 21.91	33
RW	6.16 ± 0.06	5.67 – 6.65	22	0.000*	6.80 ± 0.05	6.11 – 7.43	34
CM4	15.51 ± 0.12	14.35 – 16.18	22	0.000*	16.61 ± 0.06	15.87 – 17.38	34
LMTR	7.56 ± 0.04	7.15 – 7.83	22	ns	7.68 ± 0.03	7.34 – 8.24	34
PW	10.77 ± 0.08	10.13 – 11.41	22	ns	11.25 ± 0.07	10.54 – 12.12	34
OCB	8.08 ± 0.04	7.78 – 8.40	22	0.016	8.43 ± 0.05	7.62 – 8.93	30
CD	10.57 ± 0.06	10.11 – 11.32	22	0.000*	11.17 ± 0.05	10.64 – 11.58	33

Reproduction.—Of 35 adult females captured, one contained embryos, three had pouch young, and 12 were lactating but had no young attached. Pouch-gravid females were captured in April (1) and August (2). The individual with embryos was captured in August. Average number of embryos was 7.75 (n = 4; range 6–9). Crown-rump length ranged from 7–9 mm (3 mm for in utero embryos). Lactating females were captured in March, May, July, August, October, November, and December, indicating year-round reproductive activity. Average testes size was 9.8 x 6.4 mm (n = 43).

Comments.—Many of the individuals collected in this series are much larger than those reported from other localities. The largest individual captured at RNAM had a TOL of 406 mm and an HBL of 205 mm. Patton et al. (2000) report the largest individual collected along the Rio Juruá to be 348 mm TOL. Emmons and Feer (1997) report the upper range for HBL of this species to be 160 mm. This indicates the *M. noctivagus* at RNAM are larger than those previously reported, with the largest captured individual 16% larger in TOL than the largest reported by Patton et al. (2000), and 28% larger in HBL than the largest individual examined by Emmons and Feer (1997). The largest individuals were invariably the oldest males. Nonetheless, this could suggest a different subspecies north of the Río Amazonas. Species identity was confirmed by mtDNA cytochrome-*b* sequence analysis performed by James Patton. Individuals across the entire size range of those collected at RNAM were analyzed and found to have less than 0.05% sequence divergence, confirming they all belong to the same species.

Specimens Examined.—(n = 101): 45♀♀ LACM 96114, 96116, 96119, TTU 98601, 98648, 98684, 98733, 98736, 98796, 98801, 98822, 98850, 98875, 98895, 98922, 98926, 98959, 98973, 98974, 98976, 99010, 99016, 99024, 99044, 100898, 100937, 101001, 101013, 101059, 101069, 101088, 101093, 101100, 101134, 101147, 101150, 101151, 101163, 101168, 101193, 101216, 101218, 101227, 101232, 101251; 54♂♂ LACM 96115, 96117, 96118, TTU 98590, 98634, 98680, 98704, 98715, 98742, 98794, 98814, 98841, 98851, 98861, 98876, 98889, 98905, 98909, 98914, 98930, 98935, 98938, 98954, 98956, 98958, 98978, 98985, 99002, 99013, 99017, 100832, 100855, 100875, 100914, 100924, 100951, 101012, 101017, 101023, 101045, 101060, 101073, 101081, 101097, 101111, 101115, 101139, 101165, 101167, 101169, 101176, 101205, 101218, 101243; 2? (gender unknown) TTU 99035, 101237.

Subfamily Glironiinae Voss and Jansa 2009
Glironia Thomas 1912
***Glironia venusta* Thomas 1912**

Description.—Glironia is pale or cinnamon brown in color with distinctive broad black stripes through the eyes from the crown to the nose. The tail is fully furred to the tip, which, with the facial markings, distinguishes this species from other arboreal marsupials.

Comments.—No individuals of this species were collected at RNAM. However, during fieldwork conducted subsequent to this research, an adult male was captured in secondary growth on the eastern border of RNAM (Díaz and Willig 2004). A Peruvian biologist claims to have captured one at a remote location within RNAM prior to this capture (C. Reyes, pers. comm.). However, no voucher specimen was available for examination.

Subfamily Hyladelphinae Voss and Jansa 2009
Hyladelphys Voss, Lunde, and Simmons 2001

This monotypic genus was erected and described by Voss et al. (2001) from within the genus *Gracilinanus*. Several cranial characters distinguish this genus from *Gracilinanus*, but the most prominent character is the presence of two pairs of mammae in *Hyladelphys* as opposed to four pairs and a single median mammae in *Gracilinanus*.

***Hyladelphys kalinowskii* (Hershkovitz 1992)**

Description.—A very tiny, delicate opossum. Dorsal fur is reddish brown with a pure white venter. Eye rings are well-defined and extend to the whiskers. The area between the eye rings on top of the nose is pale orange. Ears are very long and reach the base of the whiskers when folded forward. Tail is slightly longer than HBL and is covered with very fine, long hairs visible with a hand lens.

One young (age class 3) female was collected. The animal weighed 4 g and measured: TOL 132, TAL 76, HF 10, E 10.

Comparisons.—This species could be confused with young *Marmosa lepida* or *Marmosops bishopi*, also very small-bodied opossums. Both species have shorter ears and relatively longer tails than does *Hyladelphys kalinowskii*. Moreover, the hairs associated with the tail scales are shorter and stouter than those of *H. kalinowskii*.

Distribution and Habitat.—Hyladelphys kalinowskii is known from northern French Guiana, southern Guyana, Amazonian Brazil, and eastern Peru (Gardner 2008b). Our individual was captured in May in a Victor rat trap baited with dry salted fish. The trap was located on the ground in *monte alto* forest about a 3 hour walk north from the road, near the eastern border of RNAM.

Specimens Examined.—(n = 1): 1♀ TTU 98925.

ORDER CINGULATA Illiger 1811

Five species of armadillos are present throughout most of Amazonia, with four present in the western portion of this region. However, some taxa are elusive (i.e. *Cabassous*) and others are rare (i.e. *Priodontes*), so inventories are difficult to complete. All four expected species have been recorded from Kartabo, Guyana; Paracou, French Guiana; and Balta, Peru (Voss and Emmons 1996; Voss et al. 2001). Four species of armadillos also are expected to occur at RNAM (Voss and Emmons 1996). However, only two species have been documented with voucher specimens. Although this research does not specifically address armadillos, they are included here for completeness.

Family Dasypodidae Gray 1821

Two species of armadillos were collected at RNAM, *Dasypus novemcinctus* and *Cabassous unicinctus*. The female *Dasypus* was collected in December, weighed 1.1 kg, and measured TOL 562, TAL 286, HF 75, E 40. This species is relatively common and heavily hunted for meat. The *Cabassous* (sex unknown) is represented by a skull only and no measurements are available, as it was collected from an individual being roasted over a local farmer's fire. It was captured in a funnel-shaped dead-fall trap in slightly disturbed *monte alto* habitat. This species is secretive and infrequently encountered. Two other species of armadillos (*D. kappleri* and *Priodontes maximus*) could possibly occur at RNAM, but neither was collected during this study. *D. kappleri* is similar in appearance to *D. novemcinctus*, but is larger and has projecting scales on the knees. They are difficult to identify confidently at a distance, so field sightings are suspect. *Priodontes maximus* occurred historically throughout RNAM as evinced by old burrows, but hunters have virtually extirpated it. It may occur in the farthest reaches of the reserve, where fresh burrows can still be found occasionally.

Specimens Examined.—(n = 2): *Dasypus novemcinctus* 1♀ MUSM 16502; *Cabassous unicinctus* 1? (gender unknown) MUSM 33409.

ORDER PILOSA Flower 1883

SUBORDER FOLIVORA Delsuc, Catzeflis, Stanhope, and Douzery 2001

Four species of sloths are present throughout most of Amazonia, with three present in the western portion of this region. Two of the expected species have been recorded from Kartabo, Guyana; Paracou, French Guiana; and Balta, Peru (Voss and Emmons 1996; Voss et al. 2001). Three species of sloths are expected to occur at RNAM (Voss and Emmons 1996). However, only two species have been documented with voucher specimens. Although this research does not specifically address sloths, they are included here for completeness.

Family Bradypodidae Gray 1821

Bradypus Linnaeus 1758

***Bradypus variegatus* Schinz 1825**

Brown-throated sloths are distinctive mammals highly adapted for their arboreal lifestyle. They are usually found hanging upside-down high in the forest canopy and are virtually unable to walk on the ground. These sloths have three long, curved claws on each foot. Fur is long, shaggy, and dark brown, often with a greenish tinge, with patches of dirty white, especially on the lower back and hind legs. Eyes are surrounded by a black stripe that extends back toward the ears. Males have a large dorsal patch of short orange fur with a brown stripe through the center.

One male and one female were collected at RNAM by local hunters. They are common and widespread throughout Amazonia, occurring in both primary and secondary habitats at high densities.

Specimens Examined.—(n = 2): 1♀ MUSM 33610; 1♂ MUSM 33611.

Family Megalonychidae Gervais 1855

Choloepus Illiger 1811

***Choloepus didactylus* (Linnaeus 1758)**

Linnaeus's two-toed sloths have three long, curved claws on their hind feet and two on the forefeet. They are tan in color with long, coarse fur. The anterior most pair of teeth is long and sharp. They are quite aggressive and do not hesitate to use their long claws and teeth to defend themselves. One adult female with offspring and one juvenile female were collected at RNAM by local hunters. Juveniles were taken in December and January. They are more common in primary forest than in secondary growth and occur throughout the Amazon Basin.

Specimens Examined.—(n = 3): 3♀♀ TTU 101039, 101061, 101062.

Choloepus hoffmanni Peters 1858

Hoffmann's two-toed sloths are difficult to distinguish from *Choloepus didactylus* in the field. The most obvious external character is a pale brown throat that contrasts with the chest, which is impossible to see on an animal in a tree. None were captured at RNAM, and the geographic limits of *Choloepus* species are not well known in western Amazonia. Several authors (Wetzel and Ávila-Pires 1980; Wetzel 1982; Voss and Emmons 1996; Gardner and Naples 2008) suggest northeastern Peru as a location of possible sympatry between the two species of *Choloepus*. *Choloepus hoffmanni* may occur at RNAM, but it is probably rare.

SUBORDER VERMILINGUA Illiger 1811

Families Cyclopedidae Pocock 1924 and Myrmecophagidae Gray 1825

Three anteaters could potentially occur at RNAM, including *Mymecophaga tridactyla*, *Tamandua tetradactyla*, and *Cyclopes didactylus*. The range of all three species spans the entire Amazon Basin (Gardner 2008c). The giant anteater occurred historically at RNAM, as evinced by a skin of one hanging on a lodge wall in Mishana (25 km southwest of Iquitos on the Río Nanay). Unfortunately, they have probably been extirpated from the area by hunting pressure. This species is not common in rainforest and is found at higher densities in grassland habitats throughout its range.

Tamaduas are generally uncommon over their range. One female was collected and another observed at RNAM. Both had the partially vested fur coloration pattern. The one collected was taken in April and measured TOL 1200, TAL 630, HF 92, E 44.

No pygmy anteaters were collected at RNAM, but they have been sighted in the area (W. Lamar, pers. comm.). The smallest anteater in the area, it has smokey golden fur that is soft and silky. It is widespread, especially in thick tangles of secondary growth, but difficult to observe.

Specimens Examined.—(n = 1): *Tamandua tetradactyla* – 1♀ MUSM 16504.

ORDER CARNIVORA Bowdich 1821

Up to 16 species of carnivores could occur at RNAM (Voss and Emmons 1996). Carnivores are generally elusive and hard to see in the forest, so most inventories are incomplete. The highest carnivore richness recorded from one site in Amazonia is 15 (Balta, Peru: Voss and Emmons 1996). Four species were recorded from RNAM with voucher specimens. Three other species have been sighted. Again, although this research does not specifically address carnivores, they are included here for completeness.

Family Canidae Fischer 1817

The two species of canids whose distributions include northeastern Peru, *Speothos venaticus* and *Atelocynus microtis*, are extremely rare in their ranges. They are highly secretive and rarely sighted, even by experienced hunters. Two sightings of *Speothos* have been reported from or near RNAM (P. Soini and W. Sanchez, pers. comms.), but no sightings of *Atelocynus* are known.

Family Felidae Fischer 1817

No cats were collected at RNAM. The largest cats, *Puma concolor* and *Panthera onca*, probably occurred there historically, but have most likely been extirpated by hunting or loss of prey. Occasional reports of prints and sightings of *Panthera onca* still occur, and a skin of one was found hanging in a lodge in Mishana (25 km southwest of Iquitos on the Río Nanay). The smaller spotted cats, including *Leopardus pardalis*, *L. tigrinus*, and *L. wiedii*, undoubtably still occur there. Both ocelot and margay skins have been seen in nearby villages. *Puma yaguarondi* has been sighted in the area (W. Sanchez, pers. comm.). All felids present at RNAM are extremely rare and intensively hunted for their skins.

Family Mustelidae Fischer 1817

Three mustelids were collected at RNAM, including *Galictis vittata* (MUSM 16460 ♂), *Lontra longicaudus* (MUSM 16461 ♂), and *Eira barbara* (MUSM16459 - unknown). The latter, the tayra, is common at RNAM, and can be seen rambling along fallen logs during the day. The grison (*Galictis*) is rare everywhere in its range. Neotropical river otters (*Lontra longicaudus*) are uncommon at RNAM. However, in addition to the one collected, another was seen crossing the Iquitos-Nauta highway at km 23.5 near the reserve in mid-afternoon in April 2002. Two other mustelids may also occur at RNAM. *Pteronura brasiliensis*, the giant otter, may have occurred historically in the larger rivers that border the area. The Amazon weasel, *Mustela africana*, is probably present at RNAM, but is secretive and difficult to capture.

Family Procyonidae Gray 1825

Only one procyonid was collected during this study, *Potos flavus*. Kinkajous are fairly common at RNAM. The one collected (MUSM 16462 – sex unknown) was taken in January and is represented by a skull. Another common procyonid at RNAM is *Nasua nasua*. Although none were collected, it was often kept as a pet in nearby villages. Less common is the olingo, *Bassaricyon gabbii*, although it undoubtably occurs there. Finally, *Procyon cancrivorus* has been reported from RNAM, although it must be quite rare in the area, as most locals queried did not recognize its picture.

ORDER PERISSODACTYLA Owen 1848

Family Tapiridae Gray 1821

The only tapir in the area, *Tapirus terrestris*, occurred historically at RNAM, but has probably been extirpated by hunting. A few individuals may still remain in the farthest reaches of the reserve, as stories are occasionally heard of a hunter taking one. They are prized for their meat, as demonstrated by their local name, *sachavaca*, which literally translates as "jungle cow."

ORDER ARTIODACTYLA Owen 1848

Family Tayassuidae Palmer 1897

Both peccaries, *Pecari tajacu* and *Tayassu pecari*, are still present at RNAM. A skull of a *P. tajacu* was collected (MUSM 30845 ♂) by a local family in April 2002, and hunters are familiar with both species. White-lipped peccaries (*T. pecari*) are less common than collared peccaries (*P. tajacu*; Emmons and Feer 1997) and the populations of both have been heavily impacted by hunting in the area.

Family Cervidae Goldfuss 1820

Both species of Amazonian brocket deer (*Mazama americana* and *M. nemorivaga*) are probably present at RNAM. Two male red brockets (*M. americana*) were collected by local hunters, one each in June and July. Red brocket deer are more common than brown brocket deer throughout Amazonia (Emmons and Feer 1997).

Specimens Examined.—(n = 2): 2♂♂ MUSM 16457, 16458.

ORDER RODENTIA Bowdich 1821

A total of 24 rodent species were documented at RNAM, including two squirrels, 12 cricetids, seven echimyids, one erethizontid, one agouti, and one paca. This is one of the most diverse rodent faunas reported from Amazonia. The most species-rich location among other sites is Manu, Peru, where 27 species have been documented (Voss and Emmons 1996). As with marsupials, this includes the combined sites of Cocha Cashu (23 species; Pacheco et al. 1993) and Pakitza (21 species, five of which are not represented by vouchers; Pacheco et al. 1993; Pacheco and Vivar 1996). Elsewhere in Peru, Woodman et al. (1991) reported

22 species from Cuzco Amazoníco. In Balta, 24 species of rodents were documented (Voss and Emmons 1996). At Panguana Biological Station, which had an extremely long list for marsupials, only 16 species of rodents were recorded (Hutterer et al. 1995). Patton et al. (1982) reported a total of 25 species of native rodents for the upper Marañon river basin with a maximum of 19 species from a single location. Species richness in the Amazon Basin outside of Peru is comparable at several sites. A total of 39 species of rodents were collected along the Rio Juruá, Brazil, with a maximum of 22 (range 16–22) from an individual sampling locality (Patton et al. 2000). Near Manaus, Brazil, 17 species were reported from the Minimum Critical Size of Ecosystems Reserves (Malcolm 1990). At the Smithsonian collecting site on the Rio Xingú in extreme eastern Brazil, 23 species were recorded (Voss and Emmons 1996; Voss et al. 2001). Voss et al. (2001) reported 22 species from Paracou and 24 species from the Arataye catchment, both in French Guiana. Additional sites with reasonably well inventoried rodent communities report less than 20 species.

Although our list is impressive, it is far from complete. There are undoubtably more species to be recorded for all major groups of rodents. This could include up to 2–3 additional squirrels, five more cricetids, 1–2 additional porcupines and caviids, and four echimyids. This would bring the total species richness of rodents at RNAM to somewhere between 24 and 40 species.

Family Sciuridae Fischer 1817

Squirrels are a somewhat common component of the arboreal rodent community in the Amazon Basin, with 3–5 species occurring sympatrically in western Amazonia (Emmons and Feer 1997). According to Thorington and Hoffman (2005), there are three genera of squirrels within Amazonia, *Sciurus*, *Microsciurus*, and *Sciurillus*. The genus *Sciurus* can be divided into large red squirrels, encompassing the *S. igniventris-spadiceus* group (subgenus *Urosciurus*; Thorington and Hoffman 2005), and medium-sized grayish or yellowish squirrels, such as *S. aestuans* (subgenus *Guerlinguetus*; Thorington and Hoffman 2005). The other two genera, *Microsciurus* and *Sciurillus*, the dwarf and pygmy squirrels respectively, are small squirrels with shorter, less bushy tails.

No recent review of South American squirrels is available, although Patton (1984) examined geographic variation in *S. igniventris* and *S. spadiceus* in Ecuador and Peru. Lawrence (1988) also compared these two species on a larger geographic scale. The current classification was proposed by Allen (1915), although new molecular techniques could offer fresh perspectives on the systematics of this group.

No special effort was made to collect squirrels during this study, and they did not enter traps. Only three specimens of two species were collected by locals, one *Microsciurus flaviventer* and two *Sciurus igniventris*.

Microsciurus Allen 1895
Microsciurus flaviventer **(Gray 1867)**

This small brown squirrel was infrequently seen in the forest, mostly because it is difficult to spot. One animal was observed about 6 m away in the typical head-down position about 3 m high on a large tree trunk. This individual was observed for about 5 minutes before it scurried off into the forest. It was indiscernible from the forest after it had moved 1-2 m from where it was originally spotted. One lactating adult female was collected in November in *varillal* habitat. Its measurements are: TOL 293, TAL 126, HF 40, E 15, GLS 40.08, ZB 23.96, IOC 13.99, LR 15.59, LN 10.55, BR 10.11, LD 10.40, CBL 30.24, PPL 14.08, LBP 11.87, BBP 9.09, LMTR 6.04.

Specimens Examined.—(n = 1): 1♀ TTU 99040.

Sciurillus Thomas 1914
Sciurillus pusillus **(Geoffroy Saint-Hilaire 1803)**

No pygmy squirrels were collected. The distribution of this species is poorly known, and it tends to be distributed patchily within forested areas. It likely occurs at RNAM, although it certainly would be difficult to observe in the forest.

Sciurus Linnaeus 1758
***Sciurus igniventris* Wagner 1842**

This species is a large rufous squirrel with a long bushy tail. The tops of the feet are a uniform rusty orange, unlike those of *Sciurus spadiceus* which has a mixture of orange and black hairs. *S. spadiceus* is expected in the area, with perhaps another *Sciurus* present as well. Taxa in this genus seem to be the most common squirrels in the forest, as they are the most frequently seen, but this may simply be because of their large size and bright coloration. Two adult male *Sciurus igniventris* were collected, one each in March and April. Both had abdominal testes. Selected measurements are: TOL 522 (520–524), TAL 273.5 (272–275), HF 61 (60–62), E 32 (31–33), GLS 58.67 (58.54–58.80), ZB 33.43 (32.82–34.04), IOC 18.70 (17.90–19.49), LR 23.22 (23.08–23.35), LN 17.90 (17.80–17.99), BR13.27 (13.06–13.48), LD 14.03 (13.86–14.20), CBL 44.41 (44.08–44.73), PPL 18.05 (17.56–18.54), LBP 18.63 (18.50–18.75), BBP 14.40 (13.71–15.09), LMTR 10.36 (10.29–10.42).

The ecology of squirrels in the genus *Sciurus* is poorly known in Amazonia. No studies have been conducted on *S. igniventris*, but two studies that focus on food and foraging of *S. granatensis* in Panama (Heaney and Thorington 1978; Glanz et al. 1982) suggest that this species consumes large fruits and seeds available seasonally. One study in Brazil on *S. aestuans* suggests palm nuts are an important food source and that squirrels are a major seed predator as well as disperser of palm nuts (Galetti et al. 1992).

Specimens Examined.—(n = 2): 2♂♂ TTU 98890, 101104.

Family Cricetidae Fischer 1817
Subfamily Sigmodontinae Wagner 1843

Rodents of this family inhabit a diverse array of habitats, from cultivated fields to dense tangles of secondary growth to primary forest. Some species occur across all of these habitat types while others are quite specific in their habitat preference. There are terrestrial, semi-arboreal, and strictly arboreal species. Their size in Amazonia ranges from tiny (13 g) to fairly large (400 g or more). The Sigmodontinae is comprised of several tribes, only two of which are reported from RNAM. The Oryzomyini consists of seven genera at RNAM. The ubiquitous *Hylaeamys* was the most frequently captured cricetid and is a habitat generalist. *Oligoryzomys* and *Holochilus* were residents of cultivated areas. *Nectomys* was restricted to forested areas near streams. Two genera, *Scolomys* and *Neacomys*, have spinous fur. The former was restricted to forest, whereas the latter was captured in all habitats. Finally, *Oecomys*, the most speciose genus, occupied all habitats, including the canopy, although several members of this genus were restricted to the forest. The remaining genus, *Rhipidomys*, of the tribe Thomasomyini, was extremely rare and collected only in forest canopies. Two other tribes are known from Western Amazonian sites: *Oxymycterus incae* (Akodontini) and *Neusticomys peruviensis* (Ichthyomyini). The former is limited to the southern portion of the basin and is almost certainly absent from RNAM, while the latter is very difficult to capture and may well occur in forest streams at RNAM.

A total of 12 species of cricetids were documented at RNAM. This richness is typical of the cricetid rodent community at other Amazonian sites. The richest cricetid fauna, 13 species, is reported by Patton et al. (2000) along the Rio Juruá in Brazil. Two sites were home to 12 species, including another site on the Rio Juruá, Brazil (Patton et al. 2000) and the Arataye Basin in French Guiana (Voss and Emmons 1996; Voss et al. 2001). An additional 4–5 species of cricetids could possibly occur at RNAM, including another *Nectomys*, two additional *Oecomys*, one *Euryoryzomys*, and perhaps another *Rhipidomys*.

Many of the species within these genera are difficult to distinguish, especially in hand, and sometimes even with cleaned skulls and teeth. The genera *Oryzomys* (Weksler 2006; Weksler et al. 2006) and *Scolomys* (Patton and da Silva 1995; Gómez-Laverde et al. 2004) have recently been revised, the former recast in 10 new genera, and most others are in need of revision. Differences among species are highlighted and morphological variation is summarized. Habitat preferences are presented and differences between species within each genus are discussed.

Tribe Oryzomyini Vorontsov 1959

Holochilus Brandt 1835

***Holochilus sciureus* Wagner 1842**

Description.—Marsh rats are medium-sized rodents with dense, soft fur that is dull brown dorsally. Underparts are grayish with an orange to buff wash. The individual captured at RNAM had a strong orange wash both dorsally and ventrally. The tail is sparsely haired and shorter than HBL. Ears are short and round and furred inside and out to the tips. Hind feet have a narrow heel and broad plantar surface, appearing wedge-shaped. The feet are slightly webbed.

One adult was captured. The skull was damaged, so no cranial measurements are available. External measurements were: TOL 323, TAL 138, HF 36, E 19.

Comparisons.—*Holochilus* can only be confused with members of the genus *Nectomys*. Both have soft, dense fur and webbing between the toes of the hind feet. However, the tail of *Nectomys* is slightly longer than HBL and is hairier. The tail hairs are usually densest mid-dorsally and sometimes form somewhat of a "keel." Moreover, the sole of the hind foot of *Nectomys* is covered with roundish scales whereas no scales are present on the hind feet of *Holochilus*. Finally, *Holochilus* has an orange wash on the sides and venter that is generally weak or absent in *Nectomys*.

Distribution and Habitat.—*Holochilus sciureus* is broadly distributed throughout the Amazon Basin. It is not found in forested areas, but frequents grasslands, marshes, and agricultural areas within the Amazon Basin (Twigg 1962; Veiga-Borgeaud et al. 1987; Martino and Aguilera M. 1989), where they can reach high densities and cause damage to crops (Hershkovitz 1955). At RNAM they were collected only in cultivated areas or recently abandoned fields invaded by grasses.

Reproduction.—The adult female was taken in November and was pregnant. The six embryos measured 15 mm crown-rump length.

Specimens Examined.—(n = 1): 1♀ TTU 98745.

Hylaeamys Weksler, Percequillo, and Voss 2006

This genus occurs principally in humid forested areas east of the Andes. Seven species are currently recognized. Members of this genus are "average-sized" rats (100–150 g) that are habitat generalists, occurring in disturbed and forested areas alike. They are the most frequently captured cricetid in Amazonia, exceeded in trappability only by *Proechimys*. Dorsal pelage varies from reddish-brown to darkish-brown and is usually short. The venter is grayish-white to gray. Young individuals are uniformly gray. The dorsal portion of the feet is white. The tail is naked, scales are clearly visible to the naked eye, and it is about equal in length to HBL. Ears are medium-sized and naked.

The taxonomy of Neotropical members of this genus was recently revised by Weksler (2006) and Weksler et al. (2006). Two species, *H. perenensis* and *H. yunganus*, were documented at RNAM.

***Hylaeamys perenensis* (Allen 1901)**

(Fig. 18)

Description.—Dorsal fur is darkish to reddish-brown with a great deal of variation in color, even between individuals taken on the same grid. The venter appears gray, although hairs are tipped with white. A total of 168 individuals were captured, selected measurements for which are given in Table 7. There was no evidence of sexual dimorphism (MANOVA $p = 0.066$), but age variation was highly significant (MANOVA $p < 0.001$; Table 8). This pattern is typical of other species of *Hylaeamys* (Patton et al. 2000), suggesting that similar-aged individuals from broad geographic regions need to be compared to prevent the confounding effects of age.

Comparisons.—*Hylaeamys perenensis* can be confused with *H. megacephalus* and *H. yunganus*; each specimen requires careful examination to identify it. It can be distinguished from *H. megacephalus* on the basis of size (*H. perenensis* is larger), distribution (it occurs in western Amazon west of the mouth of the Rio Juruá), karyotype (2n = 52 in *H. perenensis* and 2n = 54 in *H. megacephalus*), and mtDNA cytochrome–*b* sequence data (Patton et al. 2000).

Figure 18. Dorsal and ventral views of the skulls of *Hylaeamys perenensis* (TTU 98692, left) and *H. yunganus* (TTU 101027, right). Scale bar = 10 mm. Photo by T. Kennedy.

Hylaeamys perenensis can be confidently distinguished from *H. yunganus* by cranial characteristics. The most useful of these is the absence of a medial fossettid on the second lower molars of *H. perenensis* that is present in *H. yunganus*. Additional characters, useful in older individuals in which the cusps have been obliterated, include an increased development of palatal excrescences in *H. perenensis* and the shape of the incisive foraminal septum. It is important that such comparisons be carefully matched by age as the differences can be quite subtle.

Hylaeamys perenensis is significantly larger than *H. yunganus* in all external measurements and in 12 of 17 cranial measures (overall MANOVA $p < 0.001$; Table 8). Even with this apparently large difference in size, PCA fails to separate the species (Fig. 19). PC1, which is generally defined as the "size" axis, explains 65.1% of the variation between the two species, but there is a considerable amount of overlap in size. This emphasizes the need to carefully examine each specimen using the aforementioned characters to determine species identity and not depend solely on classification based on statistical analysis.

Distribution and Habitat.—According to Patton et al. (2000), this species is restricted to the western Amazon Basin. At RNAM, it was captured in all habitat types, but was more common in forested habitats. Most individuals were captured in traps placed on the ground, but a few were captured in traps placed on fallen logs up to 1 m in height.

Reproduction.—A total of 48 adult females were collected. Pregnant (20) and lactating (7) individuals were captured year-round. Rates of reproductive activity (pregnant plus lactating individuals) varied monthly from 0% – 100%, with an overall rate of 56.2%. The largest peaks occurred in December and January with additional peaks in March and August, although sample size is small (n = 2–4) in each of the latter two months (Fig. 20). Average litter size was 3.4 (n = 20; range = 2–6) and crown-rump length of embryos ranged from 1–28 mm.

Reproductively active males also were captured year-round. Of 93 adult males, 67 had scrotal testes (two juveniles of age class 2 also had scrotal testes). However, as with females, the proportion of reproductively active males varied from month to month (Fig. 20), with a high from September to December and another peak in June. Average testes size was 9.2 x 4.9 mm (n = 92).

Comments.—Musser et al. (1998) concluded that there was insufficient morphological evidence to separate *Hylaeamys perenensis* from *H. megacephalus*. Instead, they stated there was an "eastern" and "western" Amazonian form of *H. megacephalus* that were characterized by a cline in size. However, evidence subsequently amassed by Patton et al. (2000) and Weksler (2006) supports the recognition of *H. perenensis* as a species distinct from *H. megacephalus*. They differ not only in size, but also in haplotype and mtDNA cytochrome–*b* sequence.

Specimens Examined.—(n = 168): 59♀♀ LACM 96025, 96026, 96027, 96029, TTU 98602, 98603, 98608, 98610, 98614, 98617, 98635, 98643, 98693, 98694, 98706, 98727, 98735, 98763, 98826, 98830, 98844, 98863, 98932, 98939, 98968, 98980, 98986, 99021, 100824, 100828, 100829, 100843, 100850, 100854, 100872, 100881, 100889, 100908, 100909, 100910, 100913, 100915, 100918, 100931, 100939, 100945, 100956, 101035, 101040, 101050, 101052, 101076, 101119, 101121, 101129, 101135, 101175, 101209, 101220; 108♂♂ LACM 96024, 96028, 96030, 96031, TTU 98600, 98607, 98616, 98625, 98627, 98631, 98632, 98638, 98641, 98644, 98647, 98650, 98655, 98656, 98659, 98660, 98662, 98664, 98666, 98668, 98669, 98670, 98674, 98675, 98690, 98692, 98697, 98699, 98700, 98703, 98707, 98712, 98719, 98720, 98722, 98724, 98732, 98746, 98748, 98798, 98805, 98806, 98815, 98835, 98840, 98847, 98870, 98883, 98904, 98915, 98928, 98929, 98946, 98962, 98998, 99011, 99022, 99026, 99028, 100830, 100831, 100833, 100837, 100844, 100848, 100853, 100857, 100860, 100861, 100862, 100866, 100870, 100874, 100876, 100882, 100886, 100887, 100888, 100900, 100903, 100904, 100905, 100917, 100929, 100930, 100932, 100940, 100955, 100963, 100970, 100981, 100981, 101009, 101014, 101025, 101032, 101057, 101077, 101096, 101099, 101126, 101152 101174, 101202, 101234; 1? (gender unknown) TTU 100878.

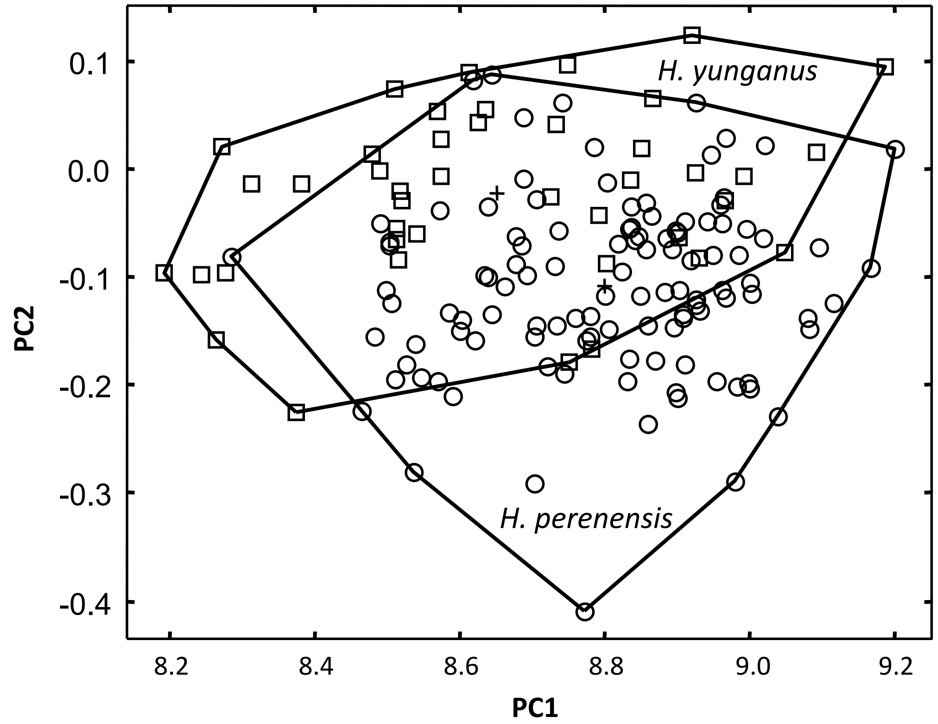


Figure 19. Bivariate plots of first and second principal components of two species of *Hylaeamys* illustrating the overlap in size (PC1) between the two species. Circles = *Hylaeamys perenensis*. Squares = *H. yunganus*. Plus sign = centroids of both species.

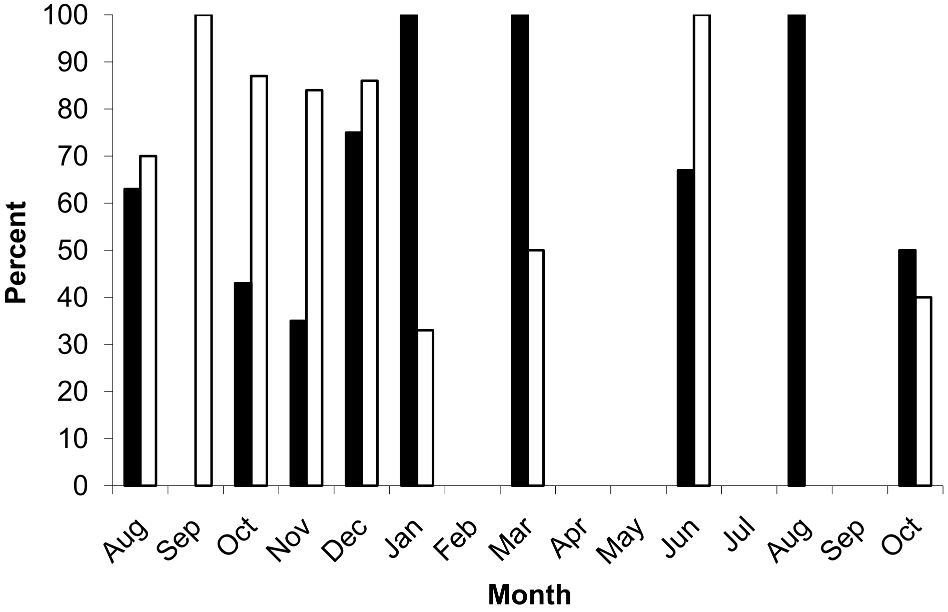


Figure 20. Reproductive activity of *Hylaeamys perenensis* on a monthly basis. Black bars = females. White bars = males.

Hylaeamys yunganus (Thomas 1902)
(Fig. 18)

Description.—A dark brownish rat that sometimes has a dark reddish-brown sheen. The venter is often much grayer than that of *Hylaeamys perenensis*, giving it an overall darker appearance. It also is smaller in all external and most cranial measurements (Table 7). Nearly equal numbers of females (29; 24 adults) and males (35; 28 adults) were collected. This species exhibited no sexual dimorphism (MANOVA $p = 0.131$), but did exhibit significant age effects (MANOVA $p = 0.022$, Table 8), as in *H. perenensis*. However, unlike the analysis of *H. perenensis*, there was an interaction effect between sex and age (MANOVA $p = 0.014$, no one-way ANOVA was significant).

Comparisons.—See account for *Hylaeamys perenensis*.

Distribution and Habitat.—This species is broadly distributed throughout the Amazon Basin. It was taken in all habitat types, but was rare in the most recently disturbed habitats. Among forested habitats, it was captured most frequently in *varillal* and less frequently in *monte alto*.

Reproduction.—Reproductively active females were captured year-round with six pregnant individuals captured in January, March, June, October, and November. Lactating females (8) were captured in May, August, November, and December. Sample size was too small in most months (n = 1) to examine reproductive activity on a monthly basis. Males with scrotal testes were taken in March, August, October, November, and December. Average testes size was 9.4 x 4.7 mm (n = 27). These data suggest that reproduction occurs throughout the dry and rainy seasons.

Specimens Examined.—(n = 64): 29♀♀ LACM 96034, 96035, TTU 98622, 98673, 98701, 98705, 98713, 98721, 98730, 98849, 98852, 98862, 98919, 98969, 98982, 100859, 100879, 100901, 100912, 100916, 100925, 100989, 101008, 101082, 101083, 101105, 101131, 101160; 35♂♂ LACM 96033, 96036, TTU 98606, 98640, 98663, 98665, 98676, 98681, 98683, 98685, 98688, 98709, 98751, 98775, 98782, 98866, 98878, 98879, 98961, 100836, 100864, 100885, 100893, 100894, 100896, 100920, 100928, 100936, 100947, 100950, 100954, 101027, 101072, 101212, 101247.

Neacomys Thomas 1900

Members of the genus *Neacomys* are small chestnut-colored mice with spiny fur. This genus has never been revised, and four of the seven species currently recognized within Amazonia have been recently described (Patton et al. 2000; Voss et al. 2001). A large-bodied species, *N. spinosus*, occurs throughout the Amazon Basin. This large species occurs sympatrically with several small-bodied species that replace each other geographically. The taxonomy of the small-bodied species is poorly understood. The diagnostic morphological characters of many of these species have never been published, making comparisons with other, potentially new species difficult. The name currently applied to small *Neacomys* in western Amazonia is *N. tenuipes*. However, it is highly probable that specimens collected during this research project may represent an undescribed species (J. Patton, pers. com.).

Neacomys spinosus (Thomas 1882)
(Fig. 21)

Description.—*Neacomys spinosus*, the largest species of this genus, has the typical coloration of spiny mice, with reddish-brown dorsal pelage streaked with black and a pure white venter. The fur is spiny, but the spines are not especially stout. The tail is obviously scaley and is about equal in length to HBL. This species weighs roughly twice that of the smaller species of *Neacomys* present at RNAM.

A total of 45 individuals were captured, including 22 females and 23 males. Selected measurements of adults with intact crania are given in Table 9. Sexual dimorphism was assessed by MANOVA and not found to be significant ($p = 0.661$), a common finding among cricetid rodents.

Comparisons.—Only one other genus (*Scolomys*) of small spiny mice occurs in Amazonia. *Neacomys* is readily distinguished from this genus by its pure white venter and chestnut dorsal color, compared to the gray

Table 7. Selected external and cranial measurements (mm) of Hylaeamys perenensis *and* H. yunganus. *Sexes are combined because sexual dimorphism was not significant. Significance levels are based on one-way ANOVA (ns =* p *> 0.05; ** p *< 0.05 with sequential Bonferroni adjustment).*

Variable	*Hylaeamys perenensis*				*H. yunganus*		
	Mean ± SE	Range	n	*p*	Mean ± SE	Range	n
TOL	261.3 ± 1.6	222 – 299	107	0.000*	240.7 ± 4.1	185 – 297	40
TAL	119.2 ± 0.9	94 – 139	107	0.000*	106.0 ± 2.3	84 – 143	40
HF	30.1 ± 0.1	26 – 34	109	0.000*	28.3 ± 0.3	22 – 32	41
E	19.9 ± 0.1	16 – 23	108	0.000*	18.8 ± 0.3	16 – 22	41
GLS	33.73 ± 0.15	29.15 – 37.78	113	0.000*	32.29 ± 0.33	29.03 – 36.87	42
ZB	16.68 ± 0.07	14.48 – 18.21	111	0.000*	16.14 ± 0.14	13.90 – 17.84	42
IOC	5.48 ± 0.02	4.91 – 6.01	113	0.000*	5.26 ± 0.05	4.68 – 5.90	42
MB	12.39 ± 0.05	11.37 – 13.52	113	0.022	12.18 ± 0.10	10.47 – 13.61	42
LR	12.90 ± 0.07	11.07 – 14.79	113	0.000*	12.05 ± 0.17	10.25 – 14.44	42
LN	12.52 ± 0.08	10.43 – 14.46	113	0.000*	11.73 ± 0.15	10.08 – 13.98	42
BR	5.82 ± 0.03	5.08 – 6.70	113	0.002*	5.61 ± 0.07	4.78 – 6.82	42
BZP	3.71 ± 0.03	2.85 – 4.32	113	ns	3.62 ± 0.05	2.69 – 4.28	42
LD	9.03 ± 0.05	7.82 – 10.66	113	0.000*	8.63 ± 0.12	7.31 – 10.00	42
CBL	26.18 ± 0.13	22.40 – 29.87	113	0.000*	25.13 ± 0.27	22.22 – 28.54	42
PPL	11.32 ± 0.07	9.26 – 13.44	113	0.000*	10.77 ± 0.13	9.08 – 12.38	42
LBP	7.76 ± 0.04	6.84 – 8.95	113	0.000*	7.28 ± 0.09	6.17 – 8.38	42
BBP	6.34 ± 0.02	5.71 – 6.83	113	ns	6.39 ± 0.04	5.66 – 7.14	42
LIF	4.49 ± 0.03	3.53 – 5.47	113	0.013	4.65 ± 0.06	3.68 – 5.73	42
BIF	2.35 ± 0.01	2.00 – 2.74	113	ns	2.40 ± 0.02	2.13 – 2.80	42
LMTR	5.10 ± 0.02	4.73 – 5.53	113	0.001*	4.99 ± 0.03	4.52 – 5.35	42
DB	11.44 ± 0.05	10.41 – 12.81	112	0.000*	11.08 ± 0.09	10.08 – 12.39	42

ventral and dorsal fur of *Scolomys*. Additionally, the tail of *Scolomys* is much shorter than HBL, whereas that of *Neacomys* is about equal to HBL. *N. spinosus* can be distinguished from other species of *Neacomys* by its larger size. In fact, *N. spinosus* is larger than the small-bodied *Neacomys* captured at RNAM in every external and cranial character (MANOVA and ANOVA *p* < 0.001). This is most evident in the length of its molar toothrow, which was always greater that 2.9 mm in *N. spinosus* and smaller than 2.9 mm in the smaller species at RNAM (Fig. 22). This simple univariate comparison was sufficient to properly classify the two species 100% of the time at RNAM.

Distribution and Habitat.—This species occurs throughout the western Amazon Basin, with specimens from southeastern Colombia and eastern Ecuador and Peru, north to northern Bolivia and east to the Rio Juruá in Brazil. Individuals of this species were rarely taken in forested habitats (5 of 45), but were

Table 8. Effects of age on mensural characters of Hylaeamys perenensis *and* H. yunganus*. Significance levels are based on one-way ANOVA (ns =* $p > 0.05$*; ** $p < 0.05$ *with sequential Bonferroni adjustment).*

Variable	*Hylaeamys perenensis*	*Hylaeamys yunganus*
TOL	<0.001*	0.003*
TAL	0.002*	0.003*
HF	ns	ns
E	<0.001*	0.015
GLS	<0.001*	<0.001*
ZB	<0.001*	<0.001*
IOC	ns	ns
MB	<0.001*	<0.001*
LR	<0.001*	0.002*
LN	<0.001*	0.008
BR	<0.001*	0.002*
BZP	<0.001*	<0.001*
LD	<0.001*	<0.001*
CBL	<0.001*	<0.001*
PPL	<0.001*	<0.001*
LBP	<0.001*	0.023
BBP	<0.001*	<0.001*
LIF	0.034	<0.001*
BIF	ns	0.001*
LMTR	ns	ns
DB	<0.001*	0.001*

frequently captured in secondary growth and cultivated areas. It seems to partition the available habitats with *Neacomys* sp. nov., which was captured primarily in forested areas.

Reproduction.—Of the 22 females captured, four were juveniles (age class 2 or lower) and 18 were adults. One of the four juveniles was pregnant (captured in November with two 1 mm embryos). Five adults, taken in November and December, were lactating. Nine of the remaining adult females were pregnant. These were captured in June, November, and December. Average litter size was 3.1 (n = 10; range 2–4). Crown-rump length ranged from 1–23 mm. The only female captured in June was pregnant with near-term fetuses (crown-rump length = 23 mm). In total, 14 of 18 adult females captured showed signs of reproductive activity.

Five of the males captured were juveniles, but one captured in November had scrotal testes that measured 5 x 3 mm. Adults with scrotal testes (12 of 18)

Figure 21. Dorsal and ventral views of the skulls of *Neacomys spinosus* (TTU 100979, left) and *N.* sp. nov. (TTU 98802, right). Scale bar = 10 mm. Photo by T. Kennedy.

Table 9. Selected external and cranial measurements (mm) of Neacomys spinosus.

Variable	Mean ± SE	Range	n
TOL	188.1 ± 1.9	167 – 209	28
TAL	88.1 ± 1.1	78 – 105	28
HF	21.6 ± 0.2	19 – 24	32
E	14.2 ± 0.2	12 – 16	28
GLS	24.13 ± 0.12	22.71 – 25.60	33
ZB	12.35 ± 0.08	11.42 – 13.44	33
IOC	4.56 ± 0.03	4.22 – 4.87	33
MB	10.32 ± 0.05	9.78 – 10.83	33
LR	8.34 ± 0.05	7.60 – 9.08	33
LN	9.09 ± 0.06	8.30 – 9.83	33
BR	4.38 ± 0.03	4.00 – 4.77	33
BZP	2.14 ± 0.02	1.89 – 2.45	33
LD	6.28 ± 0.06	5.57 – 7.13	33
CBL	17.77 ± 0.13	16.31 – 19.13	33
PPL	7.94 ± 0.07	7.07 – 8.87	33
LBP	4.29 ± 0.03	3.92 – 4.73	33
BBP	4.71 ± 0.04	4.35 – 5.14	33
LIF	3.58 ± 0.04	3.11 – 4.18	33
BIF	1.72 ± 0.02	1.47 – 2.05	33
LMTR	3.20 ± 0.02	2.97 – 3.52	33
DB	9.03 ± 0.04	8.64 – 9.52	33

were taken in June, August, September, November, and December. Average testes size of adults was 9.3 x 4.7 mm (n = 18).

The nearly year-round occurrence of reproductively active males and the pregnant female captured in June (the beginning of the dry season), plus the remaining pregnant females taken in November and December suggest year-round breeding for the species, perhaps with a peak at the beginning of the rainy season (November). The mating system of this species is not known, but the following evidence may suggest a monogamous mating system. In five cases, male-female pairs of animals were captured either at the same (2 pairs) or adjacent (3) trap station either on the same day (2) or consecutive days (3). The males of all pairs had descended testes and one female was lactating and one was pregnant. Although catching the animals together does not necessarily mean that they were traveling together, the probability that this would occur five times is small. It also occurred three times in *Neacomys* sp. nov. (see species account). Moreover, opposite sex pairs of other genera were not captured together. Same sex pairs (male-male) only occurred once in *Oligoryzomys microtis* and *Oecomys bicolor*, and did not occur at all in other cricetid species. Ge-

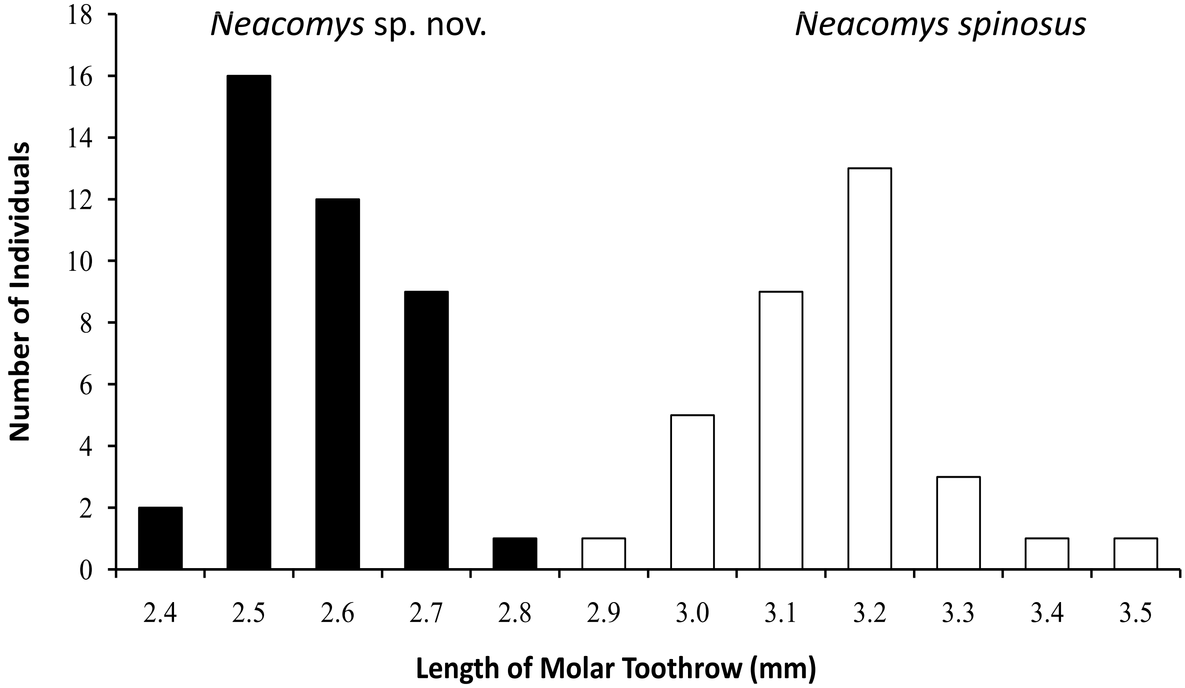


Figure 22. Histogram of length of molar toothrow for *Neacomys spinosus* and *Neacomys* sp. nov.

netic analyses to determine paternity of the embryos could provide further insight about the reproductive behavior in this genus.

Comments.—Patton et al. (2000) found this species to be strongly monophyletic (average divergence of 2.00%) leaving little question that, indeed, only one species of large-bodied *Neacomys* is present in Amazonas. However, there is a large degree of variation in pelage color across its range, suggesting possible subspecific variation.

Specimens Examined.—(n = 45): 22♀♀ LACM 96047, TTU 98749, 98768, 98776, 98778, 98780, 98786, 98788, 98811, 98817, 98940, 100826, 100869, 100974, 100996, 100997, 100998, 101002, 101006, 101021, 101030, 101034; 23♂♂ LACM 96046, TTU 98698, 98764, 98767, 98774, 98781, 98784, 98785, 98789, 98808, 98812, 98827, 98992, 100960, 100979, 100986, 100991, 100995, 101007, 101018, 101020, 101124, 101171.

Neacomys sp. nov.
(Fig. 21)

Description.—A very small spiny mouse, with coloration similar to *N. spinosus* but slightly more streaked with black, giving it an overall darker appearance, also was captured at RNAM. The venter is usually pure white, but in some individuals a weak buff wash is present. Average weight of adults is 13.8 g compared to 27.6 g for *N. spinosus*. It has the primitive carotid arterial system common to most members of the genus, confirming that it is not *N. musseri*, which has the derived arterial system. A total of 63 individuals were captured. No sexual dimorphism was detected for any mensural characters (MANOVA $p = 0.338$), which are presented in Table 10.

Comparisons.—See account for *Neacomys spinosus*.

Table 10. Selected external and cranial measurements (mm) of Neacomys *sp. nov.*

Variable	Mean ± SE	Range	n
TOL	152.5 ± 1.5	140 – 177	31
TAL	73.2 ± 0.9	64 – 85	31
HF	18.9 ± 0.2	17 – 21	37
E	13.1 ± 0.2	11 – 18	32
GLS	20.65 ± 0.09	19.55 – 21.99	40
ZB	10.61 ± 0.07	9.68 – 11.54	38
IOC	4.25 ± 0.02	3.96 – 4.58	40
MB	9.35 ± 0.04	8.82 – 10.17	40
LR	7.07 ± 0.05	6.50 – 7.71	40
LN	7.84 ± 0.07	6.98 – 9.03	40
BR	3.79 ± 0.07	3.43 – 4.10	40
BZP	1.76 ± 0.02	1.59 – 2.06	40
LD	5.13 ± 0.04	4.57 – 5.57	40
CBL	14.87 ± 0.08	13.92 – 16.10	40
PPL	6.87 ± 0.05	6.23 – 7.63	40
LBP	3.65 ± 0.03	3.08 – 4.04	40
BBP	3.93 ± 0.02	3.53 – 4.18	40
LIF	2.61 ± 0.03	2.15 – 3.04	40
BIF	1.42 ± 0.02	1.21 – 1.65	40
LMTR	2.62 ± 0.02	2.43 – 2.82	40
DB	7.88 ± 0.03	7.58 – 8.28	40

Distribution and Habitat.—This species represents one of seven clades of small-bodied *Neacomys* in the Amazon Basin as discerned by haplotypes (Patton et al. 2000). The clade these specimens probably belong to occurs in northwestern Peru and eastern Ecuador (clade 3 of Patton et al. 2000, pp. 94–96). This species was taken in all forest types at RNAM with nearly equal frequency. It was captured infrequently in older secondary growth adjacent to forest and was not found in more recently disturbed areas.

Reproduction.—A total of 15 adult females was captured. Ten were reproductively active, four lactating (captured in May, November, and December) and six pregnant (captured in March, May, November, and December). Average litter size was 2.3 (n = 6; range 1–3) and crown-rump length ranged from 3–26 mm.

Males demonstrated descended testes in July, August, October, November, and December. Over the entire study period, 28 of 35 individuals captured had descended testes. Percentage of individuals with scrotal testes varied from 60% in December, 83% in October, and 100% in November. Either one or no individuals were captured in other months. Average testes size of adults was 6.1 x 3.0 mm (n = 30).

These data indicate that breeding occurs year-round in this species. As with *N. spinosus*, three male-female pairs of animals were captured at the same (2) or adjacent (1) trap stations on the same day. Again, all males had descended testes and two females were pregnant. This could suggest a monogamous mating system for members of this genus.

Comments.—Although small-bodied *Neacomys* captured in western Amazonia have been assigned to the species *tenuipes* in the literature (Lawrence 1941; Woodman et al. 1995), recent mtDNA cytochrome-*b* analysis suggests this species is a complex of morphologically similar species. No name is available for the clade these specimens represent (see Patton et al. 2000, for a discussion of the taxonomy). Unfortunately, diagnostic morphological characters are not available in the literature for many of the small-bodied *Neacomys*, making a detailed morphological comparison of this new species with other species beyond the scope of this study.

Specimens Examined.—(n = 61): 18♀♀ LACM 96050, 96051, TTU 98645, 98652, 98678, 98725, 98777, 98816, 98920, 100847, 100935, 100942, 100944, 101024, 101026, 101028, 101085, 101249; 41♂♂ LACM 96048, 96049, TTU 98649, 98661, 98710, 98711, 98718, 98728, 98731, 98737, 98739, 98741, 98744, 98802, 98804, 98813, 98818, 98819, 98823, 98824, 98825, 98916, 98971, 99033, 100863, 100871, 100877, 100919, 100934, 100949, 100952, 100953, 100958, 100973, 100999, 101010, 101016, 101029, 101114, 101148, 101242; 2? (gender unknown) TTU 100966, 101033.

Nectomys Peters 1861

***Nectomys apicalis* Peters 1861**

(Fig. 23)

Description.—This is a large dark brown rat with soft, dense fur that is grizzled with yellow and black dorsally. The sides are somewhat paler and grade to a gray venter with no distinct line of demarcation. A weak orange wash is sometimes present on the venter. The tail is robust and slightly longer than HBL. It is furred at the base and lightly haired over its length, although it appears to be naked from a distance. Like *Holochilus*, the hind foot is wedge-shaped and the toes are partially webbed. Unlike *Holochilus*, the sole is covered with roundish scales. Only four individuals were captured, three adults (all male) and one juvenile (female). Selected measurements of the three adults are: TOL 466.7 (456–478), TAL 266.7 (215–240), HF 51.7 (50–53), E 22, GLS 48.28 (47.55–49.12), ZB 25.63 (25.24–25.92), IOC 7.55 (7.11–7.97), MB 16.64 (16.18–17.30), LR 17.65 (17.24–17.94), LN 19.71 (19.33–20.28), BR 10.12 (9.84–10.28), BZP 5.14 (5.07–5.27), LD 13.30 (13.07–13.57), CBL 37.91 (36.54–38.71), PPL 16.09 (14.85–16.91), LBP 10.67 (10.47–11.02), BBP 9.82 (9.34–10.16), LIF 7.69 (7.46–8.13), BIF 3.17 (2.96–3.55), LMTR 7.42 (7.23–7.64), DB 13.61 (13.39–13.89).

Comparisons.—See account for *Holochilus sciureus*.

Distribution and Habitat.—*Nectomys apicalis* is limited to the western Amazon Basin, where it may occur sympatrically with another chromosomal morph of *Nectomys* (Patton et al. 2000). The *N. apicalis* chromosomal morph (2n = 38–42) has been documented in eastern Ecuador, northeastern and southern Peru, and the Rio Juruá, Brazil. The other chromosomal morph (2n = 52–54), whose earliest available name is *N. mattensis* (Patton et al. 2000), occurs throughout Amazonia.

Nectomys usually is captured in inundated areas of forest or near streams and rarely occurs in dry areas (Handley 1976; Ernest and Mares 1986). Ernest and Mares (1986) suggest this may be due to a strong physiological dependence on water availability. *N. apicalis* was captured only in mature forest near streams at RNAM.

Reproduction.—The one female, taken in November, was quite young (age class 1) and showed no signs of reproductive activity. All three males had scrotal testes (average size 19.0 x 10.7 mm) and were captured in September and October.

Comments.—The diploid number of the specimens captured at RNAM is unknown. However, the average interparietal ratio (Hershkovitz 1944) of these specimens is 0.514 (range 0.423–0.562, n = 3). Based

Figure 23. Dorsal and ventral views of the skull of *Nectomys apicalis* (TTU 100883). Scale bar = 10 mm. Photo by T. Kennedy.

on this measure, species collected at RNAM belong to *N. apicalis* as defined at the subspecies level by Hershkovitz (1944) and modified by Patton et al. (2000). One other species, *N. mattensis*, might occur at RNAM.

S*pecimens Examined.*—(n = 4): 1♀ TTU 100933; 3♂♂ TTU 98642, 98994, 100883.

Oecomys Thomas 1906

Arboreal rice rats are small- to medium-sized semi-arboreal rodents that occur in habitats ranging from primary forest to highly disturbed areas, including houses. This is a diverse group that occurs throughout Amazonia. At least two and as many as five species may occur sympatrically at some sites. The most recent taxonomic revision was conducted when the genus was still considered a subgenus of *Oryzomys* (Hershkovitz 1960). The current taxonomy of this genus has been inadequately resolved. Musser and Carleton (2005) recognized 15 species, twelve of which occur in the Amazon Basin.

The genus can be distinguished by its short, broad hind feet with pink soles and proportionally longer toes. The feet are generally white dorsally with brown patch over the metacarpals and metatarsals. The tail is longer than HBL, covered with short hairs, and usually terminates in a short pencil of hairs. Dorsal fur is orangish to reddish brown with a white to slightly buffy venter sometimes bordered by gray laterally. The eyes appear quite large and the whiskers are dense and form a fan above the nose.

Three species were captured at RNAM, *Oecomys bicolor*, *O. paricola*, and *O. roberti*. *O. bicolor* was quite common, but *O. paricola* is only represented by two specimens and *O. roberti* by only one. Patton et al. (2000) reported four species from one location on the Rio Juruá in Brazil, and five species were reported from Kartabo, Guyana (Voss and Emmons 1996).

***Oecomys bicolor* (Tomes 1860)**

(Fig. 24)

Description.—This was the smallest species of *Oecomys* encountered at RNAM. It is tawny, reddish-brown dorsally with a pure white venter. A narrow band of gray-based fur may occur at the transitional boundary between the dorsal and ventral pelage. The tail is uniformly colored, long, and covered with short hairs and ends in a short but distinct pencil. The skull is small with a short toothrow.

Thirty-eight (21 female, 16 male, 1 unknown) individuals were captured. No sexual dimorphism or effects of age were apparent in mensural characters (MANOVA sex, p = 0.343; age, p = 0.336). This contrasts with the findings of Patton et al. (2000), who reported no sexual dimorphism but significant differences due to age. However, our sample size is about half that analyzed by Patton and colleagues. The power to differentiate would be diminished by smaller sample sizes, given identical age-distributions in the samples, However, Patton et al. (2000) do not report an overall MANOVA result, only Pearson product moment correlation coefficients for each p value. In the population at RNAM, significant differences for age were detected in 12 of 17 characters (six each at $p < 0.05$ and $p < 0.01$), but the overall MANOVA was not significant. As demonstrated by Willig et al. (1986) there is little correspondence between ANOVA and MANOVA results, and univariate analyses can lead to erroneous conclusions. These data, if examined only by univariate methods (as in Patton et al. 2000), would indicate significant effects of age. However, the multivariate analysis (the more appropriate method) indicates no significance. See Table 11 for selected measurements.

Comparisons.—This genus is easily distinguished from other sigmodontines in the area. The genera *Neacomys* and *Scolomys* have spiny fur. *Holochilus* and *Nectomys* are larger and have partial webbing between the toes of their hind feet. *Oligoryzomys* has longer, narrower feet, gray based fur on most of the venter, and a nearly naked tail. *Hylaeamys* also has these characters and a shorter tail. In contrast, the fur of *Oecomys* is soft and dense, the feet are relatively short and broad, the fur on the venter is pure white, and it has a furred tail that is longer than HBL. The only genus it could be confused with is *Rhipidomys*. However, *Rhipidomys* has longer (reaching the shoulder when pushed back), coarser whiskers, a dark patch covering most of the surface of the hind foot, and a longer tail pencil.

Oecomys bicolor can be differentiated from other species of *Oecomys* by its shorter dorsal fur, especially over the rump, its small size, and its pure white venter with little to no gray-based fur on the lateral edges of the abdomen. Because of the few number of individuals of other species available, no statistical analyses of cranial differences could be attempted.

Distribution and Habitat.—This species occurs throughout Amazonia and is a habitat generalist. It was captured on virtually every grid established at RNAM and in every habitat type, although it was less common in severely disturbed areas such as cultivated fields. It was also taken in houses in small villages in the jungle. It was often seen in the roof and kitchen of the senior author's house in Mishana, a village on the northern border of RNAM. It was taken in all trap types, but most were captured in Victor traps. Seven (of 38) individuals were captured in canopy traps. Trap heights ranged from 4–8.1 m and tree dbh from 35–136 cm. Tree species included *Dendropanax umbellatus*, *Tetrastylidium peruvianum*, *Iranthera tessmannii*, *Theobroma obovatum*, and *Helicostylis tometosa*.

Reproduction.—Most females captured showed signs of reproductive activity. Seven were lactating and seven were pregnant (total adult females = 17). These individuals were captured throughout the year, in January, April, May, July, August, September, November, and December. Average litter size was 2.1 (n = 7, range 2–3) and crown-rump length ranged from 1–25 mm. Males with descended testes were captured in January, May, and August. Only five of 14 individuals captured had scrotal testes. Two of these were juveniles of age class 2 (total individuals of age class 2 was six). Aver-

Figure 24. Dorsal and ventral views of the skulls of *Oecomys bicolor* (TTU 98829, left), *O. paricola* (TTU 98907, center), and *O. roberti* (TTU 98797, right). Scale bar = 10 mm. Photo by T. Kennedy.

age testes size of adults (age class 3 and higher) was 5 x 2.4 mm (n = 5). This suggests year-round breeding, and although most males may not be in active reproductive condition, it appears that many females are pregnant or lactating at any given time.

Specimens Examined.—(n = 38): 21♀♀ LACM 96042, TTU 98766, 98772, 98821, 98829, 98894, 98897, 98942, 98944, 100834, 100841, 100948, 100978, 101003, 101036, 101058, 101107, 101113, 101177, 101201, 101250; 16♂♂ LACM 96043, TTU 98613, 98621, 98734, 98809, 98828, 98834, 98884, 98917, 99030, 100983, 101015, 101031, 101089, 101117, 101137; 1? (gender unknown) TTU 101022.

Table 11. Selected external and cranial measurements (mm) of Oecomys bicolor.

Variable	Mean ± SE	Range	n
TOL	213.8 ± 3.6	177 – 236	15
TAL	105.9 ± 2.0	85 – 120	15
HF	20.1 ± 0.2	19 – 22	18
E	13.7 ± 0.3	12 – 16	16
GLS	26.66 ± 0.27	23.53 – 28.63	22
ZB	14.04 ± 0.14	12.72 – 15.10	22
IOC	4.73 ± 0.06	4.31 – 5.30	22
MB	10.96 ± 0.08	10.01 – 11.43	22
LR	8.77 ± 0.13	7.12 – 9.67	22
LN	8.89 ± 0.16	7.26 – 10.42	22
BR	4.67 ± 0.06	4.26 – 5.17	22
BZP	2.11 ± 0.05	1.56 – 2.39	22
LD	6.88 ± 0.10	5.82 – 7.63	22
CBL	20.27 ± 0.23	17.56 – 21.84	22
PPL	9.29 ± 0.13	7.85 – 10.27	22
LBP	4.65 ± 0.06	4.12 – 5.06	22
BBP	5.07 ± 0.05	4.53 – 5.46	22
LIF	4.44 ± 0.05	3.97 – 4.82	22
BIF	2.08 ± 0.04	1.73 – 2.41	22
LMTR	3.88 ± 0.03	3.62 – 4.11	22
DB	10.24 ± 0.05	9.67 – 10.69	22

***Oecomys paricola* (Thomas 1904)**

(Fig. 24)

Description.—This is the smallest of the large-bodied species of *Oecomys* collected at RNAM. With longer dorsal fur than *O. bicolor*, this reddish brown mouse has a white venter with a yellow to orange wash. The dorsal fur averages 9 mm in length, and when brushed against the grain, it falls back in place smoothly, unlike *O. bicolor* whose fur falls back in clumps. Only two individuals, one adult and one juvenile male, were collected. Selected measurements of the adult are: TOL 251, TAL 132, HF 22, E 14, GLS 29.59, ZB 15.25, IOC 5.53, MB 11.45, LR 10.25, LN 10.49, BR 5.57, BZP 2.67, LD 8.07, CBL 23.14, PPL 10.31, LBP 5.65, BBP 5.40, LIF 4.97, BIF 2.28, LMTR 4.25, DB 10.97.

Comparisons.—See account for *Oecomys bicolor*.

Distribution and Habitat.—Both individuals were captured in *franco arcilloso* habitat, one on the ground in a Victor trap baited with peanut butter, and one on a fallen log in a Tomahawk trap baited with dried fish at a height of 0.3 m.

Reproduction.—The adult male was captured in April and had abdominal testes that measured 5 x 3 mm.

Specimens Examined.—(n = 2): 2♂♂ TTU 98907, 101252.

Oecomys roberti (Thomas 1904)

(Fig. 24)

Description.—Adult coloration is similar to that of other large-bodied *Oecomys*. The tail appears naked to the naked eye, but is densely covered with fine hairs when examined under magnification, and has an insubstantial tail pencil. One sub-adult (age class 2 in molt) was collected. No cranial measurements are available.

Comparisons.—See account for *Oecomys bicolor*.

Distribution and Habitat.—The one individual was captured in a pitfall trap in *franco arcilloso* habitat.

Specimen Examined.—(n = 1): 1♂ TTU 98797.

Oligoryzomys Bangs 1900

Oligoryzomys microtis (Allen 1916)

(Fig. 25)

Description.—This is a small yellowish-brown mouse with a gray venter. The venter has an orangish wash on individuals captured at RNAM. The fur is quite short. The tail is thin, equal in length to HBL, and naked with prominent scales. Neither sexual dimorphism nor variation due to age were significant (MANOVA sex, $p = 0.327$; age, $p = 0.142$). These results are not in agreement with the findings of Patton et al. (2000), who found significant age differences in 16 of 20 cranial characters. However, this sample size (19) is far smaller than theirs (157), so these results could be an artifact of small sample. See Table 12 for selected measurements.

Comparisons.—Pygmy rice rats are readily distinguishable from all other rodent species present at RNAM by their small size, grayish or brownish venter, yellowish (as opposed to reddish) brown fur, and long naked tail.

Distribution and Habitat.—The genus is widespread, occurring from Mexico to Tierra del Fuego, but *Oligoryzomys microtis* is only reported from Brazil, Paraguay, Peru, and Bolivia. This species was taken only in highly disturbed areas such as cultivated fields and pastures. Some extremely light (2–6 g), very young individuals were captured in pitfall traps in the same habitat.

Reproduction.—*Oligoryzomys* begin reproducing at a young age (age class 2), before they complete their molt to adult pelage. Of nine captured females age class 2 and older, two were lactating and two were pregnant. Average litter size was four with crown-rump lengths of 6 and 12 mm. Of 15 adult males (age class 3 and higher) 10 had scrotal testes. Average testes size was 7.7 x 4.1 mm (n = 14). As this species was only captured in November, no statement about seasonal cycles of reproduction can be made.

Comments.—Patton et al. (2000) found practically all adult female *Oligoryzomys* they captured were either pregnant or lactating and all males were reproductively active. Most of their captures were in dense grassy areas along the banks of the Rio Juruá. This habitat is seasonally flooded and varies substantially in its spatial extent throughout the year.

Such high levels of reproductive activity were not encountered in the population at RNAM. However, *Oligoryzomys* were collected in cultivated fields, a habitat that changes in spatial extent, but irregularly and not to the degree as seasonally flooded habitats. Although this species demonstrates an r-selected life history, the difference in reproductive rates between the population at RNAM and that sampled by Patton et al. (2000) could be a local adaptation.

Specimens Examined.—(n = 31): 12♀♀ LACM 96044, TTU 98752, 98761, 98762, 98770, 98792, 100965, 100971, 100980,100985 100994; 20♂♂ LACM 96045, TTU 98750, 98759, 98760, 98765,

Figure 25. Dorsal and ventral views of the skull of *Oligoryzomys microtis* (TTU 100967). Scale bar = 10 mm. Photo by T. Kennedy.

98771, 98779, 98783, 98787, 98790, 98791, 100957, 100964, 100967, 100968, 100977, 100982, 100987, 100988, 100992.

Scolomys Anthony 1924

***Scolomys melanops* Anthony 1924**

(Fig. 26)

Description.—This is a small mouse with spiny fur that is dark reddish brown to blackish gray. Older, especially male, individuals tend to have the reddish-brown color. The venter is a uniform gray. The feet and ears are short and the tail is shorter than HBL. The skull also is distinctive, with a short, blunt rostrum and proodont to orthodont upper incisors (Fig. 26). One of the most striking characters is that the molars have weakly developed cusps that obliterate quickly with wear, making it difficult to age adults by toothwear pattern. A total of 24 individuals (5 females, 19 males) were captured, the most ever collected at a single site. Although sample size of females is small, sexual dimorphism was examined and found to be insignificant. No overall MANOVA results were obtained because of the small number of females, but no one-way ANOVA was significant for any mensural character. Selected measurements are given in Table 13.

Comparisons.—*Scolomys* can only be confused with members of the genus *Neacomys*. For comparisons, see account of *N. spinosus*.

Distribution and Habitat.—The distribution of this species is still incompletely known, mostly because of the small number of specimens that have been collected. Another fairly large series of this species

Table 12. Selected external and cranial measurements (mm) of Oligoryzomys microtis.

Variable	Mean ± SE	Range	n
TOL	188.2 ± 2.2	173 – 209	19
TAL	94.7 ± 1.2	84 – 104	19
HF	21.0 ± 0.3	18 – 22	19
E	12.8 ± 0.1	12 – 13	13
GLS	23.59 ± 0.21	21.90 – 25.22	19
ZB	11.98 ± 0.12	11.01 – 12.94	19
IOC	3.73 ± 0.04	3.47 – 3.98	19
MB	10.08 ± 0.06	9.68 – 10.64	19
LR	8.14 ± 0.11	7.41 – 8.93	19
LN	8.82 ± 0.12	7.75 – 9.92	19
BR	4.05 ± 0.04	3.72 – 4.38	19
BZP	2.10 ± 0.04	1.82 – 2.51	19
LD	5.83 ± 0.09	5.04 – 6.40	19
CBL	17.49 ± 0.19	16.05 – 19.07	19
PPL	8.13 ± 0.09	7.46 – 9.03	19
LBP	4.25 ± 0.06	3.82 – 4.78	19
BBP	4.20 ± 0.03	4.02 – 4.48	19
LIF	3.74 ± 0.04	3.26 – 4.02	19
BIF	1.66 ± 0.02	1.46 – 1.93	19
LMTR	3.12 ± 0.03	2.89 – 3.35	19
DB	8.95 ± 0.06	8.43 – 9.46	19

was collected along the Rio Juruá in Brazil (Patton et al. 2000). A few other specimens are known from eastern Ecuador, extreme northern Peru, and the Río Tigre in northern Peru. This suggests it is restricted to the northwestern portion of the Amazon Basin. It was captured only in undisturbed forest at RNAM, although two individuals were taken at the forest edge. It was captured about equally in all three forest types. Two were captured on a fallen log at a height of 0.6 m. Eleven of the 24 individuals were captured in pitfall traps. Because this trap type is infrequently deployed when assessing mammal communities in the Neotropics, *Scolomys* may be more common than the current number of specimens would suggest (Hice 2001; Hice and Schmidly 2002).

Reproduction.—Two of the four adult females were pregnant. These were captured in March and April. Litter size was two or three and crown-rump length was 10 and 12 mm, respectively. Reproductively active males were captured in March, October, and November. Of 16 adults, eight had scrotal testes. Average testes size was 5.7 x 3.1 mm (n = 11).

Figure 26. Dorsal and ventral views of the skull of *Scolomys melanops* (TTU 85490). Scale bar = 10 mm. Photo by T. Kennedy.

Comments.—This genus, originally described from six specimens from eastern Ecuador in 1924 (Anthony 1924), is still poorly known. Two species have been described since the first (*Scolomys melanops*). These include *S. ucayalensis* (Pacheco 1991) and *S. juruaense* (Patton and da Silva 1995). However, the latter of these is now regarded as a synonym of *S. ucayalensis* (Gómez-Laverde et al. 2004). The currently known distribution of *S. ucayalensis* extends from northern Colombia to just south of the Río Amazonas, so the two species could occur sympatrically at RNAM. However, no record of sympatry between species of *Scolomys* has yet been reported.

Specimens Examined.—(n = 24): 5♀♀ TTU 85486, 85489, 85493, 85501, 85503; 19♂♂ LACM 96052, TTU 85487, 85488, 85490, 85491, 85492, 85494, 85495, 85496, 85497, 85498, 85499, 85500, 85502, 85504, 99029, 99034, 101240, 101241.

Tribe Thomasomyini Steadman and Ray 1982

Rhipidomys Tschudi 1845

***Rhipidomys leucodactylus* (Tschudi 1845)**

Description.—A large, stout arboreal rat, *Rhipidomys leucodactylus* is well-adapted for climbing. It has large, broad hind feet with relatively long, curved claws, and an extremely long tail. Only one individual was captured and the tail was 154% of HBL. The tail is covered with long, fine hairs that terminate in a penciled tuft 29 mm long. The ears are small, rounded, and naked. It has orangish-brown dorsal pelage and a white venter with gray-based fur. External measurements are: TOL 338, TAL 176, HF 31, E 19.

Comparisons.—See accounts for *Oecomys bicolor* and *Hylaeamys perenensis*.

Distribution and Habitat.—This species (as currently defined) appears to be broadly distributed

Tab*le 13. Selected external and cranial measurements (mm) of* Scolomys melanops.

Variable	Mean ± SE	Range	n
TOL	160.0 ± 6.5	141 – 174	5
TAL	62.6 ± 5.9	43 – 78	5
HF	18.8 ± 0.4	17 – 20	10
E	14.9 ± 0.2	14 – 16	10
GLS	21.80 ± 0.24	20.65 – 23.22	13
ZB	12.65 ± 0.16	11.59 – 13.47	13
IOC	5.14 ± 0.07	4.75 – 5.70	13
MB	10.85 ± 0.11	10.32 – 11.82	13
LR	7.07 ± 0.11	6.48 – 7.87	13
LN	7.63 ± 0.13	6.92 – 8.35	13
BR	4.77 ± 0.07	4.39 – 5.17	13
BZP	1.70 ± 0.06	1.23 – 1.98	13
LD	6.14 ± 0.09	5.67 – 6.58	13
CBL	17.23 ± 0.20	16.21 – 18.36	13
PPL	8.10 ± 0.10	7.56 – 8.70	13
LBP	3.81 ± 0.08	3.36 – 4.52	13
BBP	4.64 ± 0.06	4.37 – 5.03	13
LIF	3.86 ± 0.06	3.57 – 4.37	13
BIF	2.55 ± 0.05	2.26 – 2.85	13
LMTR	2.48 ± 0.03	2.24 – 2.62	13
DB	8.86 ± 0.11	8.38 – 9.67	13

throughout Amazonia, but is extremely rare or difficult to capture through most of its range, although high numbers were collected north of Manaus, Brazil (Malcolm 1990). The lone individual was captured in the transition zone between flooded and upland forest in a Tomahawk trap on a canopy platform at a height of 10.4 m (tree species = *Licaria macrophylla*; dbh = 17.3 cm). It probably is restricted to forested habitats because of its arboreal lifestyle.

Reproduction.—The specimen was obtained in November and no signs of reproductive activity were apparent.

Comments.—The taxonomy of *Rhipidomys* is poorly resolved, mostly because of a scarcity of specimens. Tribe's (1996) revision has greatly expanded our knowledge, but much remains unclear. His revision recognized only a single species from lowland Amazonia, but subsequently new species have been described in this genus (Patton et al. 2000; Rocha et al. 2011; Tribe 2005; de Andrade Costa et al. 2011). Clearly, more specimens are needed to better resolve the systematics of this rare genus.

Specimen Examined.—(n = 1): 1♀ MUSM 34068.

Family Erethizontidae Bonaparte 1845

Porcupines are rare in collections and the group is in need of taxonomic revision (Voss and da Silva 2001). The distribution of most species is incompletely known and little to no natural history information is available. Two individuals of the most common and widespread species, *Coendou prehensilis*, were collected at RNAM, both in disturbed habitat in the early evening (Fig. 27). One, a young male, was captured in March, weighed 3 kg, measured: TOL 1000, TAL 500, HF 89, E 27, and had tiny abdominal testes. The other, an adult female, was captured in May, weighed 4 kg, measured: TOL 1080, TAL 570, HF 98, E 14, and was pregnant with one young measuring 50 mm crown-rump. Other species of porcupines probably occur at RNAM, but because of large gaps in the knowledge of the distribution of most porcupines, it is difficult to hypothesize what species they might be. One possibility is the new species of short-spined porcupine, *Sphiggurus ichillus*, recently described by Voss and da Silva (2001). This species occurs from eastern Ecuador to Iquitos, so it could occur at RNAM. To substantiate this possibility, one individual of this species was captured, photographed, and released by W. Lamar (July 2002) on the Río Momón near Iquitos, a mere 20 km from RNAM. Local hunters recognize a short-spined species of porcupine (probably *C. prehensilis*) and a smaller, long-spined species, which they consider rare.

Specimens Examined.—(n = 2): 1♀ MUSM 34604; 1♂ MUSM 34605.

Family Caviidae Fischer 1817

Capybaras (*Hydrochoerus hydrochaeris*) are uncommon at RNAM, mostly because their preferred habitat, extensive vegetated areasnear rivers, is lacking. Moreover, capybara are easy targets for hunters and represent a large source of protein. No specimens were collected, but footprints of capybara were occasionally seen on sandbars along the Río Nanay, the northern border of RNAM.

Family Dasyproctidae Bonaparte 1838

The agoutis (*Dasyprocta*) and acouchies (*Myoprocta*) belong to this family. These two taxa can be distinguished by their size and tail length. Agoutis are larger (3–5 kg) and have a shorter tail (20–40 mm) than acouchies (1 kg, >50 mm). One species, *D. fuliginosa*, was collected during this study by local hunters. This species is common in the area, with three females and four males collected. It is an important source of meat for local people. *M. pratti*, the green acouchy, has been sighted in the area (P. Soini, pers. comm.) and is known by local hunters as the "punchana," but none were collected.

Specimens Examined.—(n = 6): 3♀♀ TTU 98856, 114376, 114377; 4♂♂ MUSM 16501, 34081, 34082, 34083.

Family Cuniculidae Miller and Gidley 1918

Pacas (*Cuniculus paca*) are still fairly common at RNAM. One damaged skull was obtained from a hunter on 24 March 1998. This species is extensively hunted for meat and has been extirpated near populated areas. Pacas prefer dense, swampy habitats, and sometimes escape hunters where other sources of meat are more easily obtained.

Specimens Examined.—(n = 1): 1? TTU 98885.

Family Echimyidae Gray 1825

The family Echimyidae includes tree rats and terrestrial spiny rats. Relationships among echimyids are generally poorly resolved and the three traditionally recognized subfamilies (Dactylomyinae, Echimyinae, and Eumysopinae) are not supported by molecular analyses (Lara et al. 1996; Leite and Patton 2002; Galewski et al. 2005). Nonetheless, this scheme will be followed in lieu of any available alternative. Arboreal echimyids are difficult to observe or capture, so little is known about their natural history or distributional boundaries. Their taxonomy also is unclear, with several new genera and species recently described (e.g. Emmons 1988, 1993; Vi et al. 1996; Patton et al. 2000; Emmons 2005; Iack-Ximenes et al. 2005a, b; Patterson and Velazco 2006) and undoubtably more changes to come in the near future. Contrary to this, terrestrial spiny rats (genus *Proechimys*) are some of the most abundant species of the terrestrial mammal community

Figure 27. Live *Coendou prehensilis* (MUSM 34605) collected in the village of Mishana on the northern border of RNAM. Photo by Christine L. Hice.

in Amazonia and are easily captured. The species limits for this group eluded taxonomists for many decades. This was due to the large amount of intraspecific variation present throughout the genus which led Oldfield Thomas (1928, p. 262) to declare: "The bewildering instability of characters makes it at present impossible to sort them according to locality into separate species, subspecies, or local races." Their taxonomy is now fairly well known, mostly because of the efforts of James Patton and his coworkers (Patton and Gardner 1972; Patton and Rogers 1983; Gardner and Emmons 1984; da Silva 1985, 1998; Patton 1987; Patton and Reig 1989). However, individuals are challenging to identify to species and defining geographic boundaries for species has proven extremely difficult.

Four genera (*Proechimys*, *Mesomys*, *Makalata*, and *Isothrix*) and seven species (four *Proechimys* and one each of the other three genera) were documented at RNAM. This represents slightly more that half of the species and genera that could occur at RNAM. This richness is typical of echimyid species richness reported at other localities within Amazonia. The highest richness of eight species is reported at two locations along the Rio Juruá in Brazil (Patton et al. 2000) and was achieved only with use of shotguns. Additional species expected to occur at RNAM include another *Proechimys*, two additional *Makalata*, and one each of *Dactylomys*, *Echimys*, and *Toromys*. *Dactylomys* sp. (most likely *D. dactylinus*) was frequently heard calling at night in flooded forest within the reserve, and one individual was sighted at a height of about 7 m on a large tree branch. It moved slowly along the branch into a hole in the main trunk. Unfortunately, none were collected. Only those species documented with voucher specimens will be discussed in the accounts that follow.

Subfamily Echimyinae Gray 1825
Isothrix Wagner 1845
***Isothrix bistriata* Wagner 1845**

Description.—Along with the monotypic genera, *Callistomys* and *Santamartamys*, members of the genus *Isothrix* are unique among the family Echimyidae in that they have soft fur, no spines, and the tail is densely furred to the tip. This particular species is a grizzled yellowish-brown color with black hairs intermixed. The face has well-defined supraorbital black stripes that extend along the forehead and border a creamy white median area. The bushy tail is reddish-golden colored for the basal two-thirds and black for the distal third. They superficially resemble squirrels which sometimes confuses natives, who group them with squirrels (Patton et al. 1982).

Isothrix was generally not taken in traps; most specimens were collected by local hunters in flooded forest. A single individual was captured in a Tomahawk trap on a vine in flooded forest. They are not difficult to see in this habitat, where they often sit with their heads protruding from their tree hole. Six females and three males were collected. External measurements of the four adults are: TOL 520.8 (515–525), TAL 254.2 (250–260), HF 45.2 (44–46), E 17 (16–19).

Comparisons.—This species cannot be confused with any other species of rodent in the area. Large squirrels are red and have a bushier tail that is usually held upright.

Distribution and Habitat.—This species is restricted to the western Amazon Basin. It was captured only in flooded forest habitats along the Río Nanay which forms the northern border of RNAM.

Reproduction.—Of the six females collected, one taken in January was lactating and one each taken in January and May were pregnant. Each contained a single fetus with a crown-rump length of 40 and 23 mm, respectively. Although sample size is small, this suggests reproduction may occur year-round. The two adult males had abdominal testes with an average size of 17.5 x 9.5 mm.

Comments.—The genus *Isothrix* was revised by Patton and Emmons (1985), Emmons (2005), and Patterson and Velazco (2008). Currently six species are recognized (Patterson and Velazco 2008).

Specimens Examined.—(n = 8): 5♀♀ MUSM 34088, 34089, 34085, 34087, 114378; 3♂♂ MUSM 34084, 34086, 114379.

Makalata Husson 1978
***Makalata macrura* (Wagner 1842)**

Description.—A medium-large rodent, red–nosed tree rats are dark reddish-brown dorsally with a gray-brown venter. The nose is bright reddish-orange. The pelage is a combination of bristly fur with flat, flexible spines. The tail is short (less than HBL), naked, and lacks a terminal tuft of hairs.

Red-nosed tree rats were infrequently sighted or trapped, suggesting they may be uncommon or rare at RNAM. It has been suggested that they are locally common at some sites (Emmons and Feer 1997). They have a long colon suggestive of a folivorous diet, so perhaps baits such as peanut butter were not attractive.

Five individuals (all female) were collected, three in Tomahawk traps placed on vines in flooded forest and two others were shot. External measurements of two adults are: TOL 472 (471–473), TAL 216.5 (216–217), HF 43 (40–46), E 17 (16–18).

Comparisons.—Members of the genus *Makalata* could be confused with species of the genus *Mesomys*. The pelage of *Mesomys* is spinier and dull gray-brown, it lacks the bright red nose, the tail is longer than HBL, is sparsely haired, has a tuft of fur at the tip. *Makalata* was only taken in trees, has grayish-orange ventral hair, and the tail is densely furred at the base.

Distribution and Habitat.—Red-nosed tree rats occur throughout the Amazon Basin. *Makalata macrura* is the most widespread species, present in central and western Amazonia. As with *Isothrix*, individuals were only captured in flooded forest habitat at RNAM, although one young individual was seen in upland forest.

Reproduction.—One individual taken in May was lactating and one taken in June gave birth while in the trap to two males (total length of 175 and 193 mm). Too few individuals were captured to draw any conclusions about when reproduction occurs in this species, although Patton et al. (2000) captured one pregnant female in September.

Comments.—Patton et al. (2000) indicate that several species, including *M. macrura*, demonstrate well-differentiated geographic units that are supported by divergent mtDNA cytochrome–*b* sequences.

Specimens Examined.—(n = 3): 3♀♀ MUSM 34090, 34091, TTU 114375.

Subfamily Eumysopinae Rusconi 1935

Mesomys Wagner 1845

Mesomys hispidus **(Desmarest 1817)**

(Fig. 28)

Description.—This is a relatively small arboreal echimyid with heavily spinose dorsal pelage. The sparsely furred tail is longer than HBL and ends in a distinct pencil of hair. The feet are broad and short with well-developed plantar pads and sharply decurved claws, indicative of its arboreal lifestyle. Four females and six males were captured. Selected external and cranial measurements of adults are presented in Table 14. Sexual dimorphism was slight to non-existent, with seven of 19 cranial variables significant by one-way ANOVA (MB, LN, CBL, LBP1 $p < 0.05$; GLS, LR, LD $p < 0.01$). MANOVA could not be conducted because of the small sample size.

Comparisons.—See account for *Makalata macrura*.

Distribution and Habitat.—*Mesomys hispidus* is common throughout the Amazon Basin, from the western base of the Andes to the mouth of the Río Amazonas. This was the most frequently captured arboreal echimyid, usually taken in mature forest habitats (excluding *varillal*); two individuals also were captured in the oldest disturbed habitat. Their absence from disturbed habitats is most likely due to the absence of suitable trees in these habitats. Of 10 individuals captured, six were taken in arboreal traps. Trap heights ranged from 4–8.5 m and tree dbh from 58–84 cm. Tree species included *Dendropanax umbellatus*, *Parkia nitida*, *Tovomita spruceana*, *Puteria guianensis*, *Sterculia frondosa*, and *Helicostylis tometosa*.

Reproduction.—One lactating female was captured in April and one pregnant individual with two embryos (crown-rump length = 65 mm) was captured in December. Average testes size of adult males was 13.5 x 7.0 mm (n = 4) and one individual captured in April had descended testes. Although sample size was too small to reach any conclusions about reproductive patterns for this species, Patton et al. (2000) captured pregnant females and males with enlarged testes year-round.

Comments.—A new species of *Mesomys* (*M. occultus*) was described from Brazil (Patton et al. 2000). It is only known from two locations in western Brazil south of the Rio Solimões (Amazonas). This species is extremely similar to *M. hispidus* morphologically, and was not recognized as a distinct species until genetic data were examined. It might occur at RNAM.

Specimens Examined.—(n = 10): 4♀♀ LACM 96053, TTU 98910, 98981, 100867; 6♂♂ TTU 98609, 98906, 98975, 101056, 101101, 101120.

Proechimys Allen 1899

Terrestrial spiny rats were the most abundant small mammals in all habitat types at RNAM. This is often the case throughout the range of the genus, from Honduras in Central America to Paraguay in South America. They are fairly large rats (250–600 g), which, coupled with their abundance, makes them an important component of the mammalian biomass in Neotropical ecosystems (Fleming 1971; Eisenberg and Thorington 1973; Eisenberg 1980; Valqui 1995). In contrast to other Amazonian echimyids, members of this genus are wholly terrestrial. This is evident in their stocky body form, long narrow hind feet with slender toes and small plantar tubercles, a tail shorter than HBL, and large erect ears. The dorsal pelage is reddish brown with a mixture of soft hair (setiform) and stiffened spines (artisiform) of varying strength (Moojen 1948). The venter is generally white, although some species demonstrate varying degrees of reddish or grayish coloration on the throat, thorax, and inner thighs. Juveniles are uniformly gray dorsally with very weak artisiform hairs. The venter is colored as in adults. The tail is often missing in individuals, and breaks very easily for the first 3–5 caudal vertebrae. The frequent absence of a tail, overall chunky appearance, and tasty flesh has earned them the vernacular name of *sachacuy*, which literally translates as "jungle guinea pig."

Although recent contributions to the systematics of *Proechimys* have improved our understanding of the genus substantially, much remains unresolved, especially at geographic scales (Patton et al. 2000). The morphological variation within local populations and across the large geographic ranges of species makes

Figure 28. Dorsal and ventral views of the skull of *Mesomys hispidus* (TTU 100867). Scale bar = 10 mm. Photo by T. Kennedy.

delimiting species difficult. Even haplotypes, which have proven useful in differentiating other sympatric taxa, are quite variable. Compounding this problem, individuals continue to grow throughout life (Patton and Rogers 1983), so care must be taken to compare same-aged individuals so results are not confounded by age-related variation.

Despite these problems, large steps toward clarifying the systematics of this genus have been made (Patton and Gardner 1972; Patton and Rogers 1983; Gardner and Emmons 1984; da Silva 1985, 1998; Patton 1987; Patton and Reig 1989). All species of *Proechimys* have been allocated to nine species-groups, five of which occur in Amazonia (Patton 1987). Local communities can have 3–5 species, which, using qualitative craniodental and bacular characteristics (Patton et al. 2000), can be confidently identified to species with practice. However, as more regional faunas are examined in detail, additional species may be discovered and currently well-characterized species may prove to be composites of species that warrant taxonomic recognition.

Our knowledge of the ecology of *Proechimys* exceeds that of any other lowland Neotropical rodent genus (Alho 1980; Emmons 1982; Gliwicz 1984; Adler and Seamon 1991; Forget 1991; Alberico and González-M. 1993; Adler 1994, 1995, 1996, 1998, 2000; Henry 1994; Adler and Beatty 1997; Adler et al. 1997; Adler and Lambert 1997; Adler and Kestell 1998; Adler et al. 1998; Tomblin and Adler 1998). Unfortunately, most of this knowledge comes from Panama, where only one species of (*P. semispinosus*) occurs. Moreover, studies in Panama have focused on insular populations, which most likely differ ecologically from mainland populations.

Table 14. Selected external and cranial measurements (mm) of Mesomys hispidus.

Variable	Mean ± SE	Range	n
TOL	362.3 ± 3.8	355 – 368	3
TAL	167.7 ± 5.9	159 – 179	3
HF	30.4 ± 0.4	29 – 33	8
E	12.6 ± 0.3	11– 14	8
GLS	43.97 ± 0.58	41.54 – 46.21	8
ZB	23.31 ± 0.27	21.99 – 24.22	8
IOC	11.17 ± 0.24	9.97 – 12.17	8
MB	19.34 ± 0.20	18.38 – 19.89	8
LR	14.35 ± 0.27	13.39 – 15.42	8
LN	12.69 ± 0.37	11.36 – 14.15	8
BR	7.28 ± 0.16	6.84 – 8.20	8
LD	9.73 ± 0.26	8.54 – 10.60	8
CBL	32.86 ± 0.50	30.84 – 34.94	8
PPL	18.66 ± 0.30	17.46 – 20.03	8
LBP1	7.38 ± 0.15	6.70 – 7.99	8
LBP2	5.02 ± 0.08	4.62 – 5.27	8
LMF	7.05 ± 0.15	6.51 – 7.72	8
BBP	7.60 ± 0.12	7.16 – 8.17	8
LIF	3.73 ± 0.08	3.41 – 4.17	8
BIF	1.83 ± 0.28	1.16 – 3.72	8
WMF	3.61 ± 0.12	3.02 – 3.98	8
LMTR	7.18 ± 0.09	6.93 – 7.73	8
DB	14.21 ± 0.10	13.79 – 14.56	8

Proechimys brevicauda **(Gunther 1877)**
(Fig. 29)

Description.—A medium-sized species of spiny rat, *Proechimys brevicauda* tends to have an overall darker coloration than other species of *Proechimys* at RNAM. The dorsal pelage is reddish-brown streaked with black. The artisiform hairs are narrow and somewhat stiff. The venter has a distinctive rufous wash across much of the throat and lateral abdominal region, sometimes covering most of the whitish venter. Despite its name, *P. brevicauda* does not have a substantially shorter tail than other species at RNAM. The tail is about 64% of HBL as opposed to 67–84% for other species. The tail is more unicolored than in other species, although it is sometimes darker brown above and lighter brown below. The top of the hind feet is usually dark brown to black and sometimes there is a white band around the ankle. The baculum is elongate with a broad shaft and expanded base, distinguishing it from other species. The penis also is quite large and massive.

Several qualitative cranial features are helpful in species identification. The most useful include the shape of the incisive foramen and mesopterygoid fossa. In *P. brevicauda* the incisive foramen is lyrate in shape with strongly constricted posterolateral margins. These form grooves that extend onto the anterior palate. The mesopterygoid fossa extends into the posterior palate to the posterior margin of M3 (Fig. 29).

A total of 66 individuals were captured. After eliminating non-adults (age class 7 and lower) and damaged skulls, 34 individuals remained. Selected measurements are given in Table 15. These were analyzed for variation due to sex and age. The interaction of sex and age (MANOVA $p = 0.825$) and the effect of sex ($p = 0.294$) were not significant. However, age was significant ($p = 0.008$) with significant one-way ANOVAs for 15 of 19 cranial characters (Table 16) with older individuals significantly larger. Large morphometric variation due to age is typical for the genus and sexual dimorphism is generally not apparent, so the population at RNAM follows a pattern typical for the genus.

Young individuals are extremely difficult to distinguish to species because of their lack of pelage differentiation, incompletely developed baculum, and because cranial measurements cannot be directly compared to adult measurements, especially measurements involving tooth and palatal development. A special suite of statistical tests (described in the Materials and Methods section) was used to classify these individuals to species.

Comparisons.—It is unlikely that *Proechimys* would be confused with other genera. Other spiny rats, such as *Mesomys* and *Makalata*, have more spinose fur, a tail longer than or equal to HBL, and short broad feet with well-developed plantar tubercles. All other rats of this size have soft fur. However, distinguishing among species of *Proechimys* is difficult. Nonetheless, a few characters distinguish the species at RNAM, but are unlikely to differentiate other species, or even these species at other sites. The most useful character is the size and shape of the baculum. The baculum of *P. brevicauda* is much larger than that of any other species at RNAM. It is quite wide and nearly twice as long as wide. This is encased in an equally broad and elongate phallus. This is in contrast to the baculum of *P. cuvieri*, which is as wide as it is long and has well developed apical extensions. The baculum of *P. quadruplicatus* is much less massive than either of these, being fairly long and narrow, especially when compared to *P. cuvieri*. *Proechimys simonsi* has an almost delicate baculum that is longer and narrower than that of *P. quadruplicatus*. See Patton et al. (2000) for illustrations of the bacula.

Of course, the baculum provides no use for identifying females. Other characters that can be used in the field include the rufous wash on the throat and abdominal region that is present in most (but not all) individuals of *P. brevicauda* and absent in all other species, which have pure white venters. The color of the dorsal surface of the hind feet varies among species (and to a lesser extent within species). In *P. brevicauda*, the hind feet are often (not always) black or dark brown with a paler color sometimes extending from the inner surface of the hind limbs across the tarsal joint. Occasionally this pale color extends onto the foot. The hind feet of *P. cuvieri* are seldom black, but range from medium brown to creamy white. Those of *P. quadruplicatus* are usually distinctly bicolored, with the outer half black and the inner half white. This distinct line extends from the ankle to the toes. *P. simonsi* has white feet that are extremely long and narrow.

Cranially, *P. brevicauda* can be distinguished from both *P. quadruplicatus* and *P. simonsi* by the extent of the mesopterygoid fossa into the posterior palate, with the fossa extending well into M3 and M2, respectively, for the latter two species (Fig. 29). It never extends past the posterior margin of M3 in *P. brevicauda*. However, this character alone is not sufficient to distinguish it from *P. cuvieri*, whose mesopterygoid fossa also extends to the posterior margin of M3 or slightly into the posterior half of this tooth. For this pair, the shape of the incisive foramen is more useful. Whereas the incisive foramen of both species is lyrate in shape, the posterolateral margins are weakly flanged and only form a weak groove on the anterior portion of the palate in *P. cuvieri*. In *P. brevicauda* these flanges

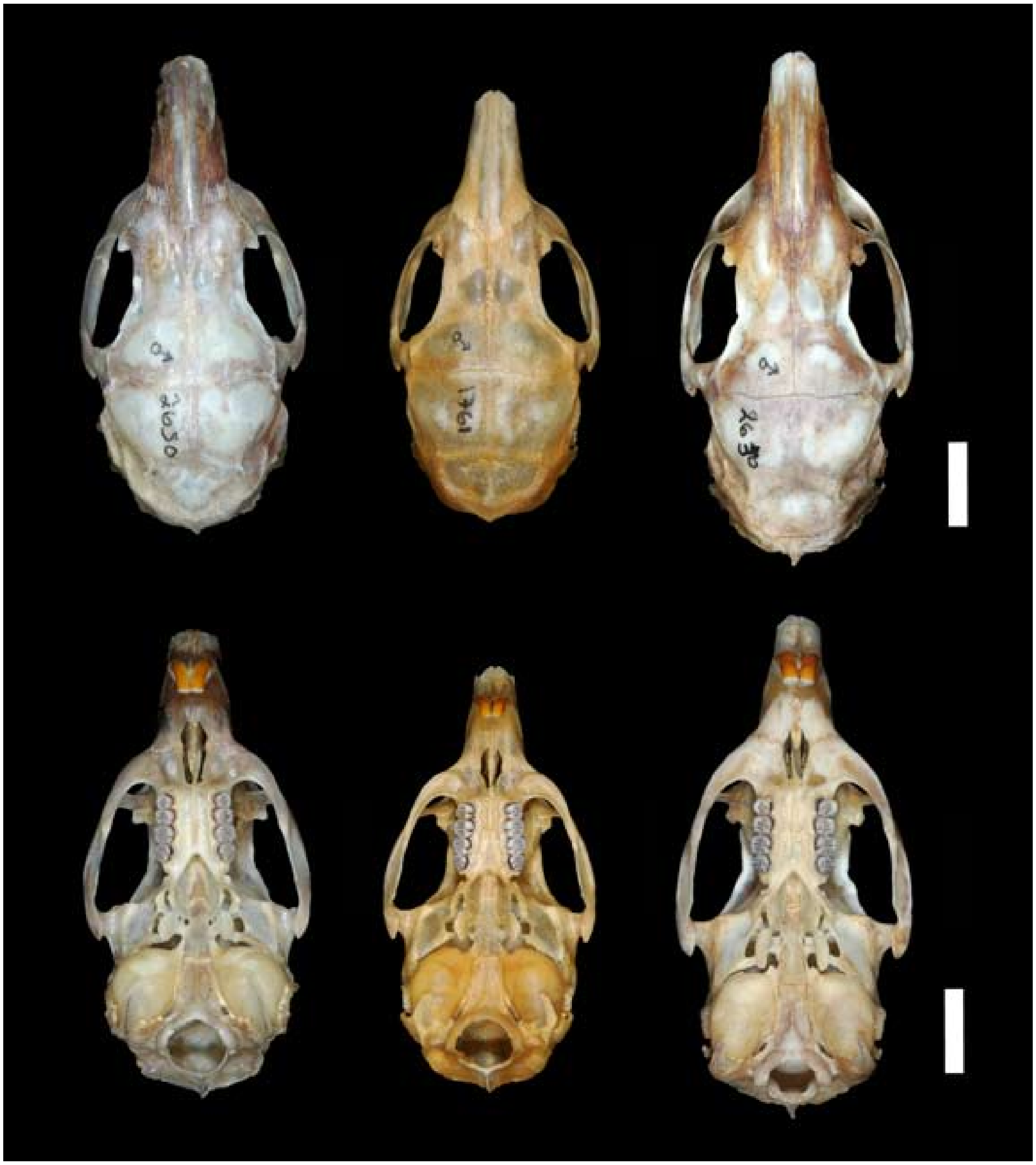


Figure 29. Dorsal and ventral views of the skulls of *Proechimys brevicauda* (TTU 101194, left), *P. cuvieri* (TTU 98687, center), and *P. quadruplicatus* (TTU 98581, right). Scale bar = 10 mm. Photo by T. Kennedy.

are well-developed and form deep grooves on the palate (Fig. 29). Moreover, the maxillary portion of the incisive foramen is obviously keeled in *P. brevicauda,* but the keel is slight to absent in *P. cuvieri* (Fig. 29).

Several other characters are useful in species identification, although the forgoing ones have been the most useful in discriminating among the species of *Proechimys* at RNAM. For a complete summary of other characters see Patton et al. (2000). Regardless of the number of available characters, identification to species takes practice, patience, and methodical, careful examination of each specimen to insure positive identification.

Table 15. Selected external and cranial measurements (mm) of Proechimys brevicauda.

Variable	Mean ± SE	Range	n
TOL	371.0 ± 8.0	315 – 498	23
TAL	134.8 ± 2.9	109 – 159	23
HF	45.4 ± 0.5	40 – 52	33
E	20.8 ± 0.3	19 – 23	31
GLS	54.81 ± 0.58	49.67 – 63.38	34
ZB	26.01 ± 0.23	23.95 – 29.10	34
IOC	11.50 ± 0.13	10.18 – 13.25	34
MB	20.05 ± 0.18	18.55 – 22.26	33
LR	21.36 ± 0.31	18.23 – 25.64	34
LN	19.66 ± 0.30	16.55 – 24.09	34
BR	8.56 ± 0.09	7.67 – 9.69	34
LD	11.47 ± 0.05	10.04 – 13.28	34
CBL	38.56 ± 0.41	34.34 – 43.95	34
PPL	19.70 ± 0.22	17.45 – 22.88	34
LBP1	9.43 ± 0.14	8.13 – 11.85	34
LBP2	7.53 ± 0.08	6.43 – 8.85	34
LMF	7.53 ± 0.12	6.28 – 9.27	34
BBP	9.61 ± 0.12	8.16 – 11.35	34
LIF	5.86 ± 0.11	4.46 – 7.49	34
BIF	2.79 ± 0.05	2.29 – 3.46	34
WMF	5.34 ± 0.07	4.53 – 6.40	34
LMTR	8.92 ± 0.06	8.17 – 9.60	34
DB	14.99 ± 0.09	13.80 – 16.23	33

Statistical tests also were useful in differentiating the species. A MANOVA conducted on external and cranial measurements of three species (*Proechimys simonsi* was not included because no intact adult crania were obtained) was highly significant ($p < 0.001$), and only one character (ear length) was not significantly different by one-way ANOVA. All remaining characters were significant at the $p < 0.001$ level, with the exception of HF, LBP1, BIF ($p < 0.01$) and LBP2 ($p < 0.05$). Discriminant function analysis (DFA) separated the three species into totally non-overlapping groups (Fig. 30) which are consistent with bacular characteristics and results of mtDNA cytochrome–*b* sequence analysis.

Distribution and Habitat.—Proechimys brevicauda is limited in distribution to the western Amazon Basin, where two distinct clades (12% sequence divergence) are apparent (Patton et al. 2000). One of these is in southern Peru on the Río Madre de Dios (Manu).

The other includes specimens from the headwaters of the Rio Juruá in Brazil and from northern Peru.

This was the most common species of *Proechimys* in disturbed habitats, especially in young secondary growth. They were infrequently taken in forested habitats, with only 18 of the 66 total captures of this species recorded from forested habitats.

Reproduction.—A total of 24 adult females were captured, 13 of which were pregnant and two lactating. The lactating individuals were captured in August and November; pregnant individuals were taken in January, August, September, October, November, and December. The overall percentage of reproductively active females was 62.5%. A slight peak in the proportion of pregnant individuals was detected from November to January, but too few individuals were captured in other months to determine seasonal variation in reproductive activity. Regardless, reproduction occurs year-round. Average litter size was 2.1 (n = 13; range 1–4) and crown-rump length ranged from 1–41 mm.

Unlike members of the family Cricetidae, the testes of *Proechimys* do not generally descend into the scrotum when adult males are in breeding condition. The only way to determine whether or not a male is reproductively active is by examining the epididymis. This data were not noted for specimens collected during this research, so no estimate of reproductive activity of males can be presented for any of the species of *Proechimys*. Average testes size of adult males was 28.1 x 15.4 mm (n = 19).

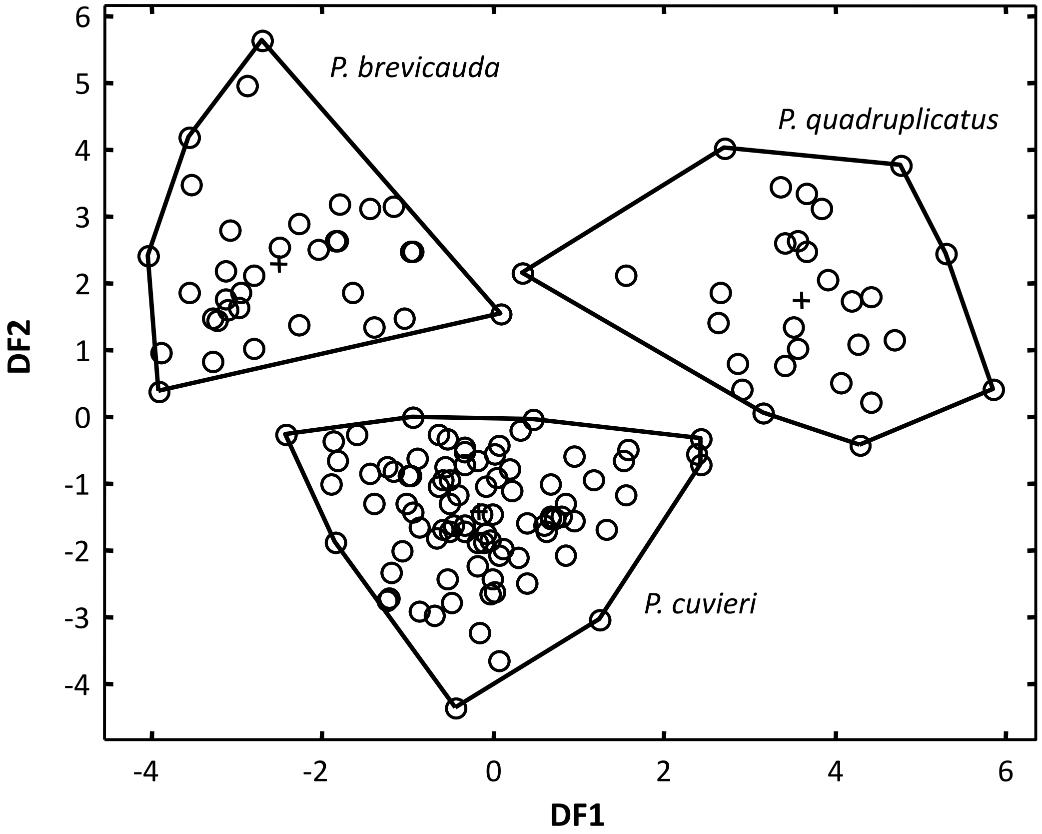


Figure 30. Bivariate plots of the first and second discriminant axes comparing morphometric variation among the 3 species of *Proechimys* captured at RNAM.

Specimens Examined.—(n = 66): 31♀♀ LACM 96128, TTU 98615, 98624, 98657, 98747, 98753, 98754, 98793, 98795, 98810, 98921, 98943, 98987, 98575, 98577, 98580, 98593, 99037, 98597, 98598, 100846, 100961, 100972, 100990, 100993, 101047, 101055, 101159, 101195, 101213, 101226; 34♂♂ LACM 96125, 96126, 96127, 96129, TTU 98605, 98618, 98773, 98800, 98838, 98913, 98924, 98952, 98960, 98963, 98582, 99015, 98599, 100827, 100845, 100873, 100959, 101005, 101042, 101046, 101051, 101112, 101116, 101127, 101154, 101158, 101166, 101183, 101194, 101248; 1? (gender unknown) TTU 99042.

Proechimys cuvieri **Petter 1978**
(Fig. 29)

Description.—Another medium-sized *Proechimys*, this species is similar in external morphology to *P. brevicauda*. The artisiform hairs are somewhat longer and wider than those of any other species of *Proechimys* at RNAM and the overall coloration of this species tends to be lighter and redder. The venter is pure white, but can appear dingy white on museum skins, especially in the lateral abdominal region. The tops of the hind feet are often light brown to cream, but can be quite dark or nearly white. The baculum is distinctive and is broad and short with well-developed apical wings. The skull is large with well-developed supraorbital ridges, as is true of all members of this genus at RNAM. The mesopterygoid fossa usually extends into the posterior half of M3. The incisive foramen is lyrate with posterolateral margins that are weakly flanged and usually do not extend onto the anterior palate as grooves, or if they do, are only weakly apparent (Fig. 29).

Eighty-six females and 83 males were captured, making this the most abundant *Proechimys* at RNAM. See Table 17 for selected measurements. Variation due to sex and age was examined in adults and found to be weakly significant for sex ($p = 0.011$; Table 16), but not for age ($p = 0.181$) or interaction effects ($p = 0.625$). Males were larger in 12 of 19 cranial variables, although only two of these variables are significantly larger if a sequential Bonferroni adjustment is used (Table 16). This is not the pattern that would be expected for members of this genus. Generally, no sexual dimorphism is detected and effects of age are highly significant. Patton et al. (2000) reported no sexual dimorphism in his sample (n = 46) of this species from the Rio Juruá. Currently, we have no explanation for the sexual dimorphism in the population at RNAM. However, the effect of sex is quite weak and could be an artifact of the large sample size, as small differences in morphology can be detected with large samples.

Comparisons.—See account for *Proechimys brevicauda*.

Distribution and Habitat.—*Proechimys cuvieri* is widespread across the Amazon Basin. Haplotypes indicate that *P. cuvieri* might be a composite of three or more species, but until further sampling is conducted and large-scale analysis of the species undertaken, they remain under one name (Patton et al. 2000). The haplotypes are not readily distinguished morphologically.

At RNAM, this species was infrequently taken in older disturbed habitats and never in currently cultivated fields. It was frequently taken in forested habitats, where it was captured with nearly equal frequency in all three forest's types.

Reproduction.—A total of 55 adult females were captured, 39 of which (70.9%) were either pregnant (29) or lactating (10). The proportion of reproductively active females ranged from 44% to 100% (Fig. 31). An insufficient number (1–4 individuals) of females was captured during the months during which all females were either pregnant or lactating to establish a true reproductive rate. It is unlikely that 100% of the population was reproductively active during those months, although a high proportion probably was. Given this, no peak of activity is readily discernible from the data. However, it is apparent that this species breeds year-round. Average liter size was 2.1 (n = 29; range 1–4) and crown-rump length ranged from 4–53 mm. Average testes size was 27.8 x 15.1 mm (n = 56).

Specimens Examined.—(n = 171): 86♀♀ LACM 96140, 96141, 96143, 96144, 96145, TTU 98576, 98578, 98612, 98629, 98637, 98639, 98658, 98671, 98677, 98691, 98723, 98743, 98807, 98831, 98833, 98853, 98855, 98860, 98872, 98874, 98881, 98886, 98899, 98900, 98901, 98912, 98931, 98933, 98936,

Table 16. Effects of age or gender on cranial characters of Proechimys brevicauda *and* P. cuvieri. *Significance levels are based on one-way ANOVA (ns = p > 0.05; * p < 0.05 with sequential Bonferroni adjustment).*

Variable	*Proechimys brevicauda*	*P. cuvieri*
	age	gender
GLS	<0.001*	0.021
ZB	<0.001*	0.049
IOC	0.001*	<0.001*
MB	<0.001*	0.013
LR	<0.001*	0.033
LN	<0.001*	ns
BR	<0.001*	0.024
LD	<0.001*	0.006
CBL	<0.001*	0.014
PPL	0.002*	0.011
LBP1	ns	0.048
LBP2	ns	ns
LMF	0.002*	ns
BBP	<0.001*	ns
LIF	0.024	ns
BIF	ns	ns
WMF	0.040	<0.001*
LMTR	ns	ns
DB	0.013	0.021

98941, 98947, 98967, 98977, 98983, 98995, 98999, 99003, 99007, 99014, 99018, 99019, 99020, 100839, 100851, 100856, 100858, 100865, 100880, 100891, 100892, 100897, 100902, 100907, 100938, 100946, 100969, 101037, 101063, 101064, 101068, 101074, 101078, 101079, 101080, 101084, 101102, 101106, 101109, 101122, 101125, 101132, 101133, 101138, 101173, 101179, 101182 ,101199, 101210, 101211, 101225, 101231; 83♂♂ LACM 96137, 96138, 96139, 96142, TTU 98594, 98611, 98620, 98626, 98630, 98636, 98651, 98672, 98679, 98682, 98687, 98689, 98696, 98708, 98714, 98729, 98799, 98832, 98836, 98854, 98858, 98859, 98865, 98867, 98873, 98877, 98887, 98902, 98911, 98918, 98927, 98937, 98965, 98966, 98984, 99001, 99004, 99005, 99009, 99027, 99043, 100825, 100835, 100840, 100849, 100852, 100884, 100890, 100895, 100906, 100911, 100923, 100927, 101038, 101041, 101043, 101048, 101065, 101067, 101071, 101086, 101087, 101103, 101108, 101110, 101128, 101145, 101146, 101170, 101172, 101204, 101206, 101214, 101217, 101223, 101224, 101229, 101230, 101235; 2? (gender unknown) TTU 98628, 100899.

Table 17. Selected external and cranial measurements (mm) of Proechimys cuvieri.

Variable	Mean ± SE	Range	n
TOL	361.7 ± 3.5	302 – 436	69
TAL	136.6 ± 1.5	102 – 166	69
HF	45.4 ± 0.3	32 – 52	89
E	22.0 ± 0.2	15 – 25	87
GLS	52.94 ± 0.30	47.04 – 59.76	88
ZB	25.16 ± 0.12	22.73 – 27.39	89
IOC	11.75 ± 0.06	10.41 – 13.13	89
MB	19.46 ± 0.09	17.95 – 22.09	89
LR	20.53 ± 0.14	17.72 – 23.90	89
LN	19.37 ± 0.15	16.47 – 22.88	89
BR	7.88 ± 0.05	6.74 – 8.88	89
LD	10.92 ± 0.07	9.67 – 12.47	89
CBL	36.96 ± 0.23	32.66 – 42.12	88
PPL	18.54 ± 0.12	16.41 – 21.90	88
LBP1	10.04 ± 0.08	8.40 – 11.91	89
LBP2	7.65 ± 0.06	6.12 – 9.25	89
LMF	7.00 ± 0.05	5.67 – 8.15	86
BBP	9.07 ± 0.06	7.92 – 10.39	89
LIF	4.87 ± 0.04	3.97 – 5.77	89
BIF	2.57 ± 0.03	1.98 – 3.25	89
WMF	4.70 ± 0.04	3.88 – 5.76	89
LMTR	8.33 ± 0.03	7.59 – 9.05	89
DB	14.89 ± 0.05	13.65 – 15.73	88

Proechimys quadruplicatus **Hershkovitz 1948**

(Fig. 29)

Description.—This handsome, stocky *Proechimys* is the largest species of this genus that occurs at RNAM. The artisiform hairs are not particularly stiff to the touch and the fur on the venter is quite soft and velvety. These two characters give this animal a much softer feeling than other species. The pure white venter sharply contrasts with the rich chestnut colored sides. The dark mid-dorsal stripe present in all species is wider and darker in *P. quadruplicatus* than other species. The dorsal side of the hind feet is usually (not always) bicolored, with a dark brown outer band and a white to cream inner band that extends from the ankles to the tips of the toes. The baculum is narrow and long, but not as long as that of *P. simonsi*. Both the baculum and the penis are far less massive than those of *P. brevicauda* and *P. cuvieri*. The skull is large with a long and narrow rostrum. The incisive foramen is lyrate and the

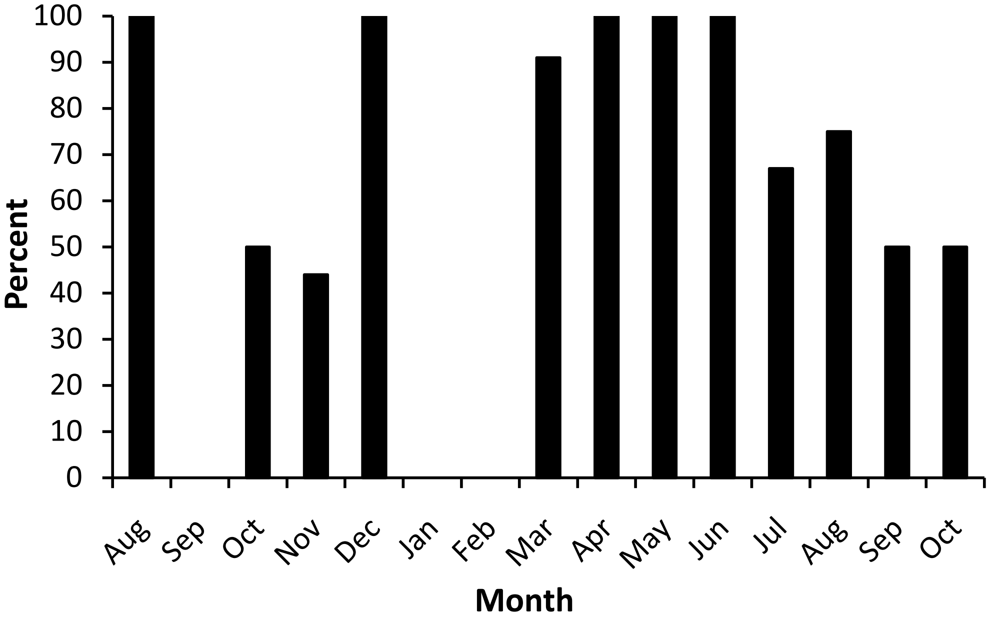


Figure 31. Monthly pregnancy rates of adult *Proechimys cuvieri*.

posterolateral ridges are well-developed and extend onto the anterior palate as grooves, as seen in *P. brevicauda*, but to a lesser extent. The mesopterygoid fossa extends deeply into the posterior margin of the palate, sometimes to the posterior margin of M2 (Fig. 29).

No variation in cranial measurements was attributable to age (MANOVA $p = 0.621$) or sex (MANOVA $p = 0.816$), nor was there any interaction effect. This pattern is not typical for the genus, but this could be attributed to small sample size (n = 28). See Table 18 for selected measurements.

Comparisons.—See account for *Proechimys brevicauda*.

Distribution and Habitat.–Proechimys quadruplicatus is found north of the Río Amazonas from the eastern foothills of the Andes as far east as Manaus, Brazil. Whereas Patton et al. (2000) report *P. steerei* (which replaces *P. quadruplicatus* south of the Río Amazonas) only from flooded forest habitats along the Rio Juruá in Brazil, *P. quadruplicatus* was frequently captured in upland habitats. Flooded forest habitat was not assessed during this study, but has been during subsequent fieldwork. It was the most frequently captured *Proechimys* in flooded forest, but certainly was not absent from terra firme, as Patton et al. (2000) report for *P. steerei*. This species also was taken in disturbed habitats and seems to have the least specific habitat requirements of any of the species of *Proechimys* at RNAM.

Reproduction.—Eleven of 18 (61.1%) adult females were either pregnant (8) or lactating (3). Lactating individuals were taken in March, July, and September. Pregnant females were captured in January, March, April, July, August, and September, indicating year-round breeding for this species. Average liter size was 2.5 (n = 8; range 1–4) and crown-rump length ranged from 9–43 mm. Average testes size was 23.3 x 12.6 mm (n = 21).

Specimens Examined.—(n = 59): 33♀♀ LACM 96135, TTU 98604, 98623, 98695, 98738, 98769, 98820, 98837, 98848, 98871, 98880, 98893, 98950, 98955, 98972, 98979, 98990, 98991, 98997, 100838, 100868, 100943, 100962, 100976, 101004, 101070, 101092, 101156, 101161, 101162, 101197, 101215, 101233; 25♂♂ LACM 96133, 96134, 19136, TTU 98581, 98756, 98757, 98758, 98803, 98839, 98892, 98896, 98970, 98989, 99006, 99008, 99023, 101011, 101049, 101123, 101130, 101140, 101198, 101200, 101221, 101222; 1? (gender unknown) TTU 101203.

Table 18. Selected external and cranial measurements (mm) of Proechimys quadruplicatus.

Variable	Mean ± SE	Range	n
TOL	400.4 ± 9.0	337 – 557	22
TAL	147.3 ± 2.8	121 – 180	22
HF	50.7 ± 1.2	21 – 56	28
E	21.8 ± 0.2	20 – 24	28
GLS	56.89 ± 0.73	48.96 – 67.03	28
ZB	27.66 ± 0.24	25.65 – 30.30	26
IOC	13.15 ± 0.18	11.11 – 15.77	28
MB	21.13 ± 0.25	18.13 – 23.96	28
LR	22.25 ± 0.35	18.58 – 27.61	28
LN	21.27 ± 0.38	17.32 – 27.65	28
BR	8.65 ± 0.12	7.34 – 10.35	28
LD	11.98 ± 0.21	10.02 – 14.37	28
CBL	40.15 ± 0.53	35.17 – 47.01	28
PPL	21.15 ± 0.26	18.91 – 24.20	28
LBP1	10.32 ± 0.18	8.75 – 12.35	28
LBP2	7.24 ± 0.13	5.84 – 8.72	28
LMF	7.89 ± 0.11	6.65 – 9.06	27
BBP	10.01 ± 0.11	8.82 – 10.94	28
LIF	4.90 ± 0.14	3.20 – 6.22	28
BIF	2.56 ± 0.06	1.88 – 3.24	28
WMF	4.82 ± 0.09	3.96 – 6.01	28
LMTR	8.99 ± 0.08	7.85 – 9.96	28
DB	15.86 ± 0.13	14.05 – 17.06	28

Proechimys simonsi Thomas 1900

Description.—Another large species of spiny rat, *Proechimys simonsi*, is the most distinctive *Proechimys* present at RNAM. It has an elongate body, long face and ears, long hind feet, and a long tail [average 84% of HBL reported by Patton et al. (2000); the one adult captured at RNAM had a tail 92% of HBL]. The dorsal coloration is somewhat paler than other *Proechimys* and the venter is pure white. The tail is distinctly bicolored. The artisiform spines are not particularly stiff but somewhat stiffer that those of *P. quadruplicatus*. The dorsum of the hind feet is usually white. The baculum is extremely long and narrow. The skull also is long and narrow, with a mesopterygoid fossa that extends into the palate to the level of M2. The incisive foramen is ovate rather than lyrate in shape. Overall, this is a long, lanky *Proechimys*.

Only two individuals (1 sub-adult female, 1 adult male) were captured. The sub-adult (age class 5) was captured in June and the adult in October. The skull of the adult was badly damaged in a Victor trap, so cranial measurements are unavailable. External measurements of the adult were TOL 405, TAL 194, HF 49, E 25 and it weighed 245 g.

Comparisons.—See account for *Proechimys brevicauda*.

Distribution and Habitat.—Proechimys simonsi is limited to the western Amazon Basin. It was quite rare at RNAM, and both individuals were captured in undisturbed habitat, specifically *varillal* and *franco arcilloso*.

Reproduction.—No sign of reproductive activity was apparent. Testes of the adult male measured 10 x 11 mm.

Specimens Examined.—(n = 2): 1♀ TTU 101118; 1♂ TTU 98646.

Results

Trapping Effort and Sampling Success.—Fieldwork was conducted for 16 months, from August 1997 to November 1998. Trapping occurred nearly continuously during this time, although trap effort varied from month to month (Table 19). In total, 100,677 trap nights were compiled on standardized grids and during *ad hoc* sampling in all major upland habitat types in the area. Total effort for each grid and transect is presented in detail in Appendix IV. This effort yielded a total of 1,030 specimens, 961 of which were captured in traps. The remaining 69 specimens were captured by other methods or brought to us by local people. Those captured in traps represent 12 marsupial and 16 rodent species (Table 20). Most of the 69 specimens brought by local people were bats (40 individuals of 13 species). The remainder were marsupials (2 species), xenarthrans (5), carnivores (4), artiodactyls (2), or rodents (3).

Capture Rate.—The overall capture rate for the entire 16-month field season was 0.96%. However, capture rate varied among trap types (Fig. 32a), temporally (Fig. 32b-f), seasonally, and across habitat types. Overall, pitfall traps had the highest capture rate, followed by Victor, Tomahawk, and Sherman traps (Fig. 32a). Capture rate for all trap types varied monthly from 0.48–2.11% (Fig. 32b). If capture rate is examined temporally for each trap type, it is apparent that it varied more or less concordantly through time for all conventional trap types (Fig. 32c-e). Pitfall traps followed a different pattern (Hice and Schmidly 2002; Fig. 32f).

Arboreal capture rate was exceedingly low, at 0.40%. This lowered the overall capture rate, but not substantially. Terrestrial capture rate was 1.00%. If arboreal effort is removed and terrestrial effort is examined separately on a monthly basis, little change is apparent (Fig. 33a). Arboreal capture rate was too low to be examined on a monthly basis.

Given that pitfall capture rate varied discordantly from other, more conventional, trap types and was generally much higher (Hice and Schmidly 2002), terrestrial capture rates were examined excluding pitfall trap nights and captures (Fig. 33b). The capture rate decreased slightly from the overall terrestrial rate, from 1.00–0.97%. As with removing arboreal data, little effect was apparent, but the peaks were somewhat lower (Fig. 33b).

If the year is divided into wet (January-June) and dry (July-December) seasons, capture rate steadily declined from dry (1997: 1.45%), to rainy (1998: 0.96%), to dry season (1998: 0.59%). One other study that examines effect of season on capture rate in the Amazon Basin reports a higher capture rate during the rainy season (Woodman et al. 1995). However, a strong El Niño Southern Oscillation (ENSO) occurred in 1998, which most likely affected trap success that year. So, the contrary results of that study may reflect ENSO effects.

Table 19. Number of trap nights of each trap type per month for duration of study.

Month	Victor	Sherman	Tomahawk	Pitfall	Total Terrestrial	Victor Arboreal	Sherman Arboreal	Tomahawk Arboreal	Total Arboreal	TOTAL
August 1997	1747	467	663	22	2899				0	2899
September		196		44	240				0	240
October	3920	3724	3920		11564				0	11564
November	4000	4000	4000	440	12440				0	12440
December	2106	2061	2061	220	6448	90	45	45	180	6628
January 1998	1044	789	789		2622	510	255	255	1020	3642
February					0				0	0
March	2820	2760	2760	330	8670	120	60	60	240	8910
April	1680	840	840		3360	1080	540	540	2160	5520
May	1000			220	1220			200	200	1420
June	1100	1100	1100	121	3421				0	3421
July	3300	3150	3150	330	9930	300	150	150	600	10530
August	1800	2250	2250	99	6399	900	450	450	1800	8199
September	2400	2100	2200	110	6810			60	60	6870
October	4900	4300	4300	319	13819			120	120	13939
November	1980	1000	1000	275	4255			200	200	4455
TOTAL	33797	28737	29033	2530	94097	3000	1500	2080	6580	100677

Table 20. Summary of non-volant mammals captured at RNAM by type of trap.

Species	Victor	Sherman	Tomahawk	Pitfall	Arboreal	Total
Caluromys lanatus					1	1
Didelphis marsupialis	1		5			6
Hyladelphys kalinowskii	1					1
Marmosa demerarae			2		2	4
Marmosa regina	2					2
Marmosa waterhousei	6		2		1	9
Marmosops bishopi	8	1		3		12
Marmosops noctivagus	80	4	12	4	1	101
Metachirus nudicaudatus	6		15			21
Monodelphis adusta		1		5		6
Philander andersoni	1		6		3	9
Philander opossum	1		38			39
Holochilus sciureus	1					1
Hylaeamys perenensis	102	36	29	1		168
Hylaeamys yunganus	34	16	9	5		64
Neacomys spinosus	24	15	3	2		44
Neacomys sp. nov.	26	22		15		63
Nectomys apicalis	1		3			4
Oecomys bicolor	19	6	1	5	7	38
Oecomys paricola	1		1			2
Oecomys roberti				1		1
Oligoryzomys microtis	16	8	1	7		32
Scolomys melanops	9	2	1	11		23
Mesomys hispidus	1	1	2		6	10
Proechimys brevicauda	32	1	33			66
Proechimys cuvieri	72	21	79			172
Proechimys quadruplicatus	26	6	27			59
Proechimys simonsi		1		1		2
Total	471	141	270	59	21	961

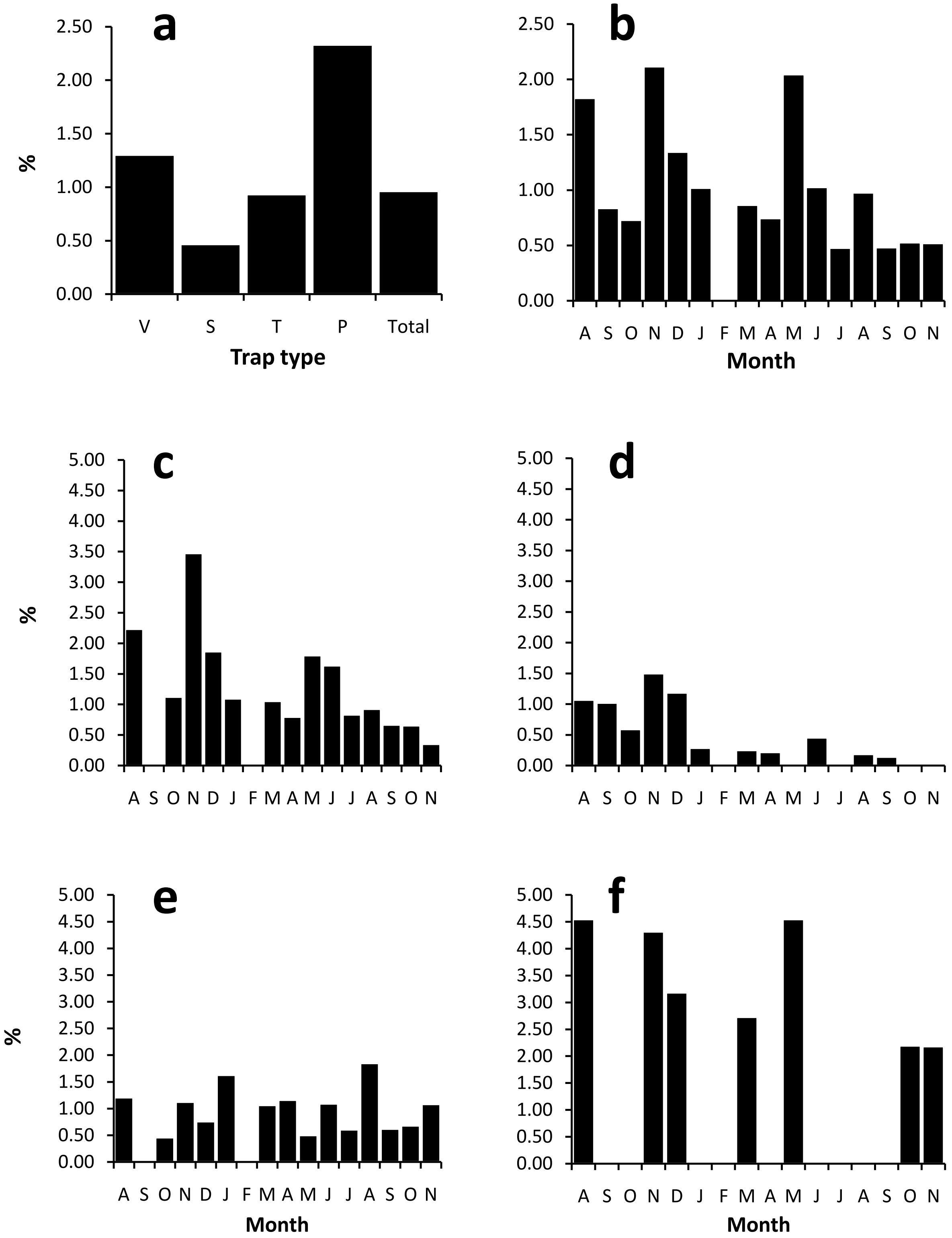


Figure 32. Capture rates (captures per 100 trap nights) during study period for a) each trap type and overall capture rate, and by month for b) all trap types, c) Victor traps, d) Sherman traps, e) Tomahawk traps, and f) pitfall traps. Time scale is August 1997 to November 1998. V = Victor, S = Sherman, T = Tomahawk, P = Pitfall.

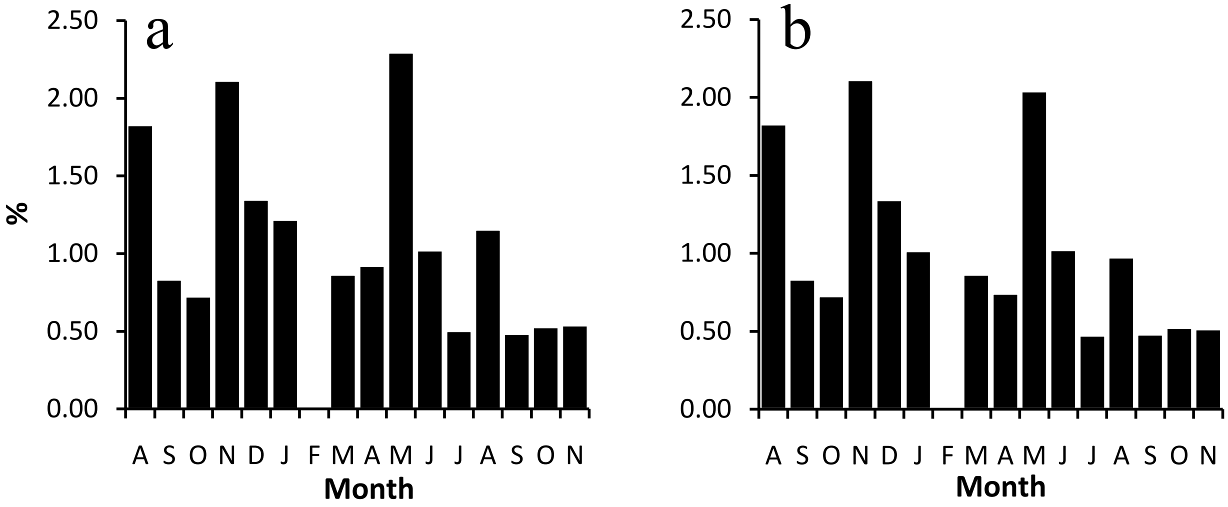


Figure 33. Capture rate during study period by month for terrestrial traps, a) does not include arboreal traps, and b) does not include pitfall traps. Time scale is August 1997 to November 1998.

Capture rate also varied across habitat types, with higher capture rates in disturbed habitats (1.13%) compared to forested habitats (0.91%). This may be because a higher density of mammals was supported by crops in disturbed areas. Capture rate declined with increasing age of previously disturbed habitats, with the highest rates in 3-year-old (1.47%), followed by 7-year-old (1.01%), and 15-year-old (0.96%). Within forested habitats, the highest capture rate was recorded from *franco arcilloso* (1.07%), followed by *varillal* (0.98%), and *monte alto* (0.84%).

The 12 standardized (10 x 10) grids were assessed a total of 20 times. If only these grids are examined, number of individuals captured tended to decline over the 10-night sampling periods (Fig. 34), which is expected given that all animals were removed upon capture. However, the decline was not smooth or steep, and only slightly more than half (62%) of all individuals were captured through day 5. An average of 2.74 animals were captured per grid per night. Maximum capture success occurred at any time from day 1 to day 10. In four cases, maximum capture success was equal on two days during a 10-day trapping period. In these cases, the second day was either day 3, 6, 8, or 10. If these are removed, maximum capture success occurred as late as day 8. Maximum capture success occurred 10 times on day 1, thrice on day 2, once on day 5, five times on day 6, and once on day 8. The maximum number of captures recorded on one grid in one night was 18, while the minimum was 0.

Analysis of Sampling Methods.—None of the sampling methods captured all of the species that were recorded at RNAM. Some techniques worked better for some taxa than did others. A summary of results based on sampling method follows. The methods are broken down in the manner of Voss et al. (2001) to facilitate comparisons with their site in Paracou. Tomahawk traps are treated separately here because they were not included in the discussion of conventional trapping in Voss et al. (2001).

All Methods: Unlike the methods used by Voss et al. (2001), almost all of the species of marsupials and rodents recorded at RNAM were captured in traps; hunting, census, and interview techniques were not used during this study. Therefore, although sampling effort (i.e., number of trap nights) was different each day, if the number of days in the field and cumulative captures are used as sampling units, they are not confounded by sightings or interview results. Species accumulated rapidly, particularly during the first 27 days and 105 captures, by which time 16 species had been recorded (Fig. 35). This is a rate of 0.6 species per day for the first month. After that time, species accumulation rate fell to about 0.1 until field day 100 and dropped to 0.02 new species per day for the remainder of the study. Nonetheless, no convincing asymptote is apparent in either graph, suggesting additional sampling would yield additional species. This has been verified during subsequent fieldwork.

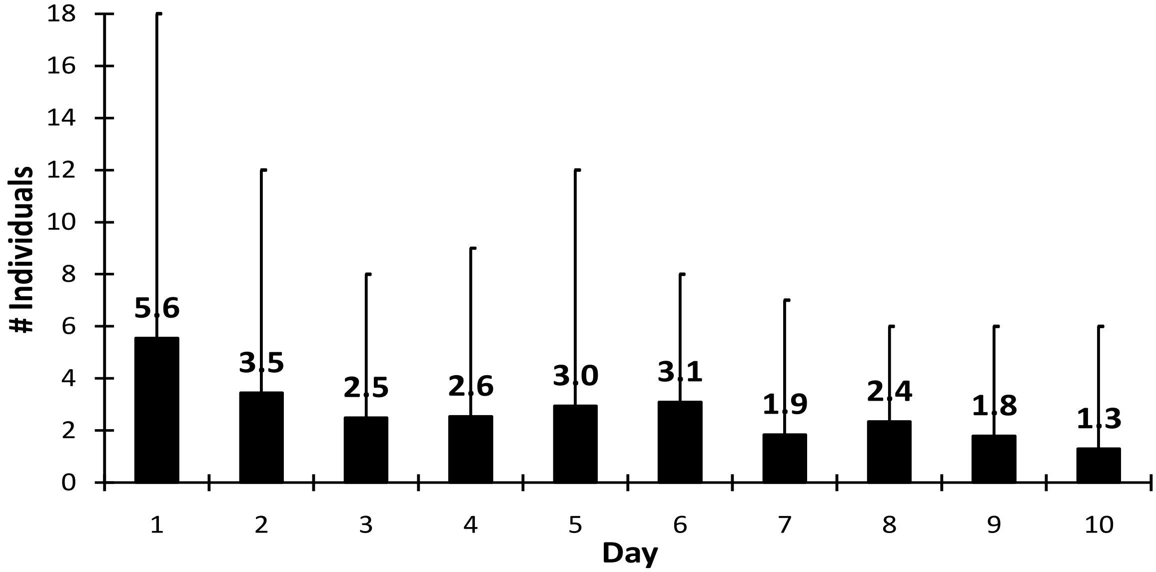


Figure 34. Number of individuals captured on all standardized grids per consecutive day of trapping. Number over histogram bar indicates average number of individuals captured on that day. Overlay range bar indicates the total range of number of individuals captured on each day. Note that all ranges include zero.

Conventional Trapping: Most conventional trapping with Victor and Sherman traps at or near ground level was conducted on grids established at the beginning of the study and used throughout the study period (August 1997 to November 1998). Additional conventional trapping was conducted simultaneously with arboreal trapping and separately on temporary transects (see Methods section). In 62,534 trap nights, 611 individuals representing 25 species of marsupials and rodents were captured with this method. These include the only examples of *Hyladelphys kalinowskii*, *Marmosa regina*, and *Holochilus sciureus* captured at RNAM (Table 20).

As is typical, species accumulated rapidly at first, with the first 15 species recorded in the first 92 captures (Fig. 36b). This is approximately one new species for every six individuals captured. This coincides with about 6,700 trap nights, or a new species every 450 trap nights. During the subsequent 519 captures, 10 additional species were recorded, or about one for every 50 individuals captured. Therefore, in the subsequent 55,800 trap nights, one new species was added every 5,600 trap nights.

Capture rate was lower during the first 10,000 trap nights than during the subsequent 10,000 (Fig. 36a). This can be attributed to seasonality, as the first 10,000 trap nights occurred during the dry season and the next 10,000 early in the rainy season. Subsequent trapping was not as successful in the remainder of the rainy season nor in the dry or rainy season of the following year. For example, during the initial dry season, capture rate was 1.1% (112 captures/10,254 trap nights). During the subsequent early rainy season, the capture rate was 2.2% (258/11,800). This fell to 0.6% (241/40,480) for all trapping conducted after December 1997. This cannot be attributed to a change in habitat type or deployment of traps.

No sign of an asymptote is apparent in a graph of species accumulation verus captures (Fig. 36). In fact, the last three new species captured were extremely rare, represented by one or two individuals. Therefore, even though it appears that species were sampled to completeness based on number of trap nights accumulated (Fig. 36a, dashed line), this most likely represents an artifact of declining trap success rather than complete sampling of the pool of local species.

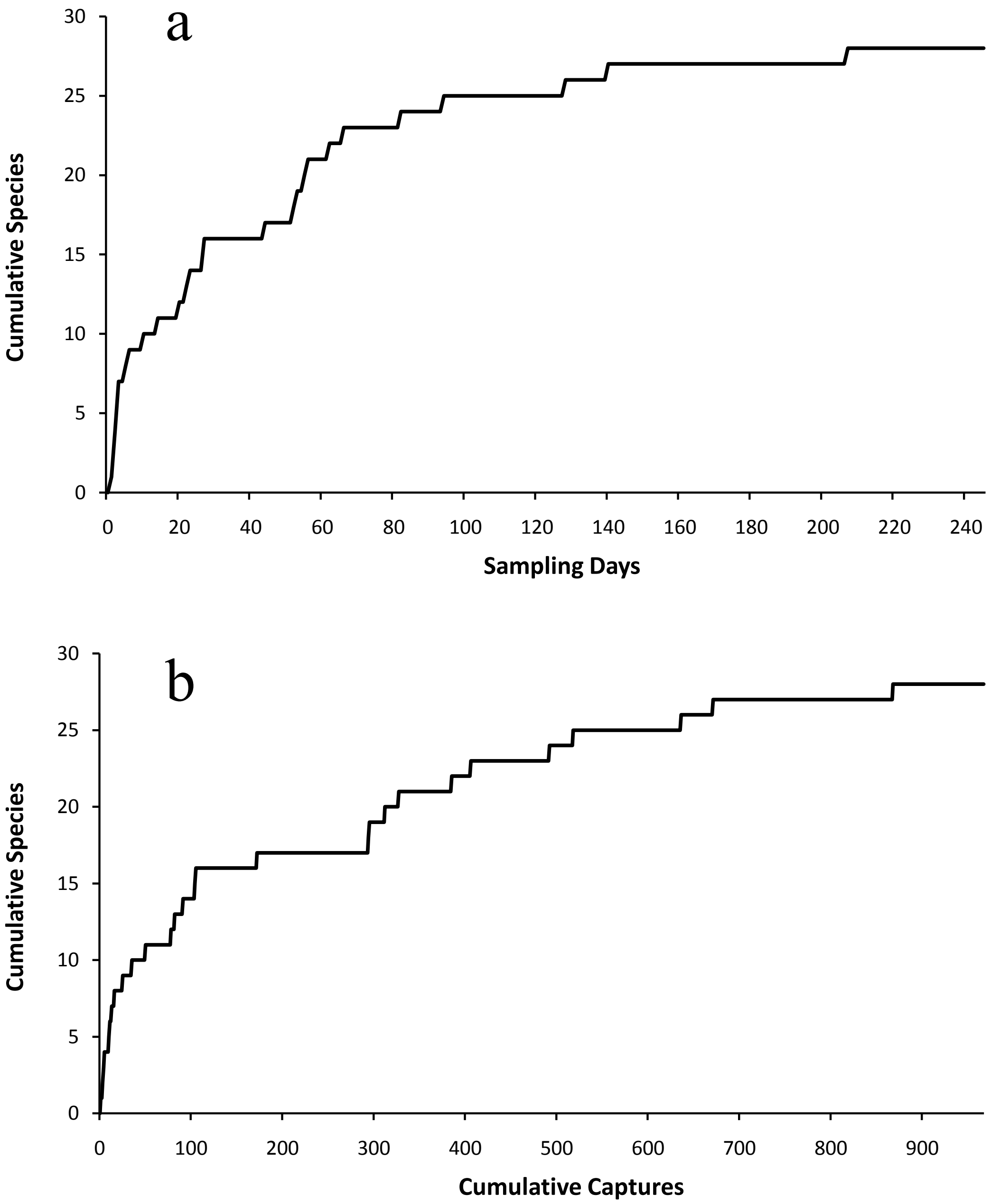


Figure 35. Number of species recorded at RNAM through time based on a) sampling effort in days and b) total number of individuals captured. Includes conventional (Victor, Sherman, and Tomahawk traps) terrestrial trapping, pitfall trapping, and arboreal trapping. A total of 961 individuals representing 28 species of marsupials and rodents were captured from August 1997 to November 1998.

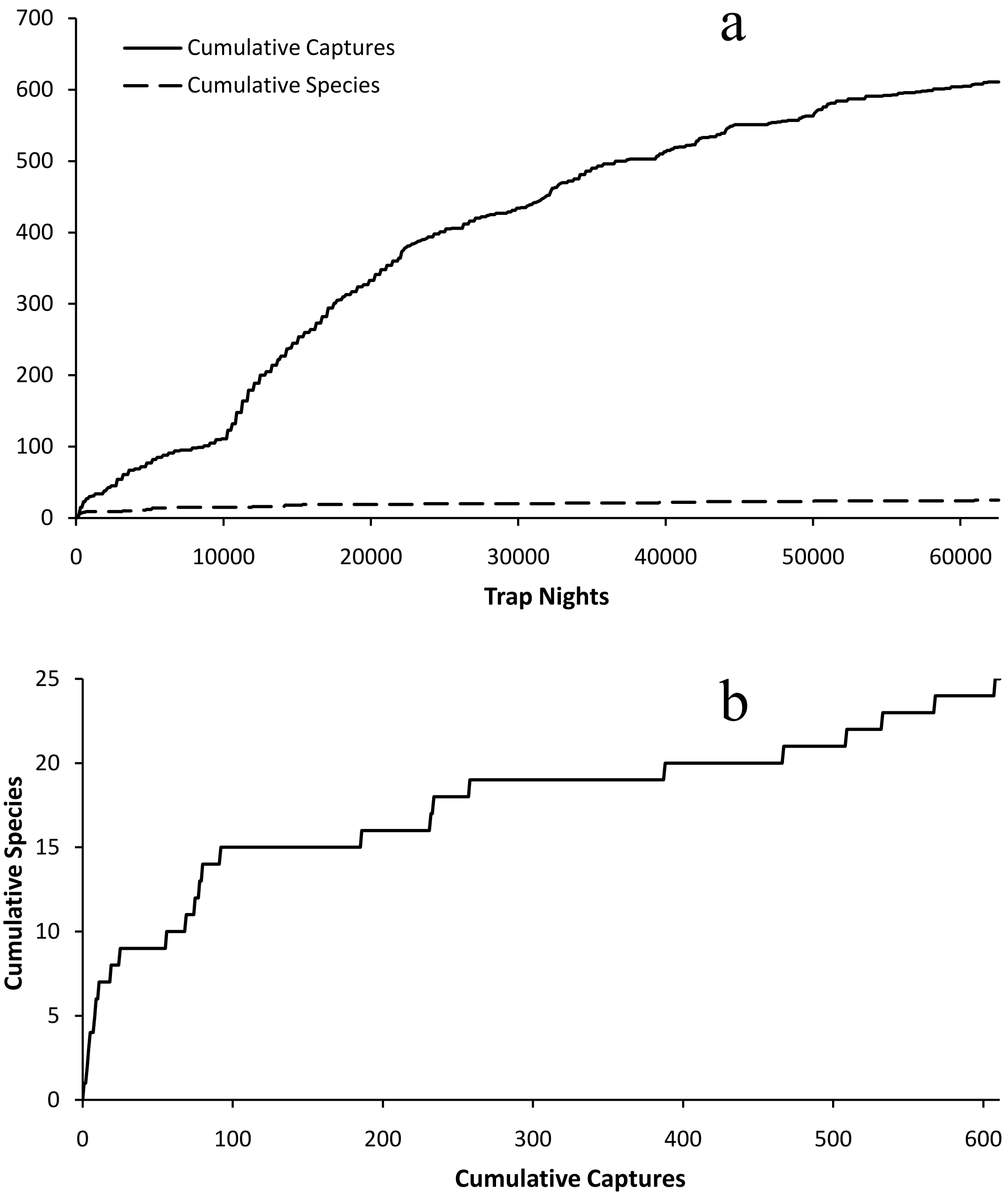


Figure 36. Results of terrestrial trapping using Victor and Sherman traps at RNAM based on a) cumulative number of trapnights and b) cumulative species. In 62,534 trap nights, 611 captures of 25 species were recorded.

Conventional Trapping with Large Traps: Tomahawk traps were deployed simultaneously and at the same traps stations as Victor and Sherman traps on grids, on arboreal transects, and on temporary transects. In 29,033 trap nights, 270 individuals representing 20 species were captured (Table 20). No unique species were taken in Tomahawk traps, although larger taxa were preferentially captured by them. Again, species accumulated quickly, with 17 of the 20 species encountered in the first 76 captures, or one new species for every 4.5 captures (Fig. 37b). This coincides with about 9,000 trap nights, or one new species every 530 trap nights (Fig. 37a). Subsequently, species accumulation slowed dramatically, with only three new species in 194 captures, or one new species for every 65 captures. These three species were captured in approximately 20,000 trap nights, or 1 new species per 6,600 trap nights. This is similar to the rate observed for Victor and Sherman trapping.

As with the Victor and Sherman trapping, capture rate was lower during the first 5,000 trap nights because traps were first deployed during the dry season. Captures accumulated more rapidly during the subsequent rainy season. The rapid increase in cumulative captures at around 20,000 trap nights is attributed to moving to a different location with a high density of *Philander opossum* and *Proechimys* spp., both of which are relatively large and preferentially captured in the larger Tomahawk traps.

The graph of cumulative species versus cumulative captures indicates a clear asymptote for species accumulation (Fig. 37b) as does species accumulation plotted against trap nights (Fig. 37a, dashed line). Trapping in the same area subsequent to this research yielded only one novel species in a Tomahawk trap in an additional ~30,000 trap nights and 270 captures, suggesting the asymptotes are real and all the species present in the area that could be captured in Tomahawk traps with the baits used are represented in this sample.

Pitfall Trapping: Pitfall traps were assessed simultaneously with conventional traps on grids and temporary transects. A total of 59 captures in 2,530 trap nights was recorded. These represent 11 species, one of which (*Oecomys roberti*) was taken only with this trapping method (Table 20). Species accumulated extremely rapidly, with seven species recorded in the first 12 captures (Fig. 38b). That is one new species every 1.7 captures. This coincides with approximately 300 trap nights, or one new species every 43 trap nights (Fig. 38a). Species accumulation tapered off after this time, with only four additional new species in 47 captures and 2,200 trap nights. This translates to one new species for every 12 individuals captured or every 550 trap nights. This accumulation rate is much higher than that found for conventional trap types at any point in the trapping schedule.

Accumulated captures plotted by trap nights, is fairly steady until about 1,100 trap nights, after which time no individuals were captured for about 1,000 trap nights (Fig. 38a). This period of stasis was from May to October 1998, the dry season in the Iquitos area. This effect is not apparent in the dry season of 1997 because pitfall traps were not deployed en masse until November 1997, after the rainy season had begun. Species accumulation does not demonstrate a convincing asymptote based on trap effort or cumulative captures, indicating additional pitfall trapping would likely have produced additional species.

Arboreal Trapping: Arboreal transects were assessed for 10 or 20 consecutive nights throughout the study period. Trap nights are used here instead of station nights used by Voss et al. (2001), Patton et al. (2000), and Malcolm (1991) because not all of the arboreal stations in the study always contained the same number or kinds of traps (see Methods section). Only 21 individual marsupials and rodents representing six species were captured in 6,580 trap nights (Table 20), and only *Caluromys lanatus* was uniquely captured by this trapping method. Species accumulation was very rapid, with five species recorded in the first nine captures or 1,600 trap nights (Fig. 39a-b). This yields a species accumulation rate of one new species per approximately two captures or per 320 trap nights. Subsequently, this rate dropped to one new species every 12 captures or 5,000 trap nights.

No asymptote in species richness is apparent based on either sampling effort or cumulative captures (Fig. 39a-b). In fact, during arboreal sampling conducted after the completion of this study, at least

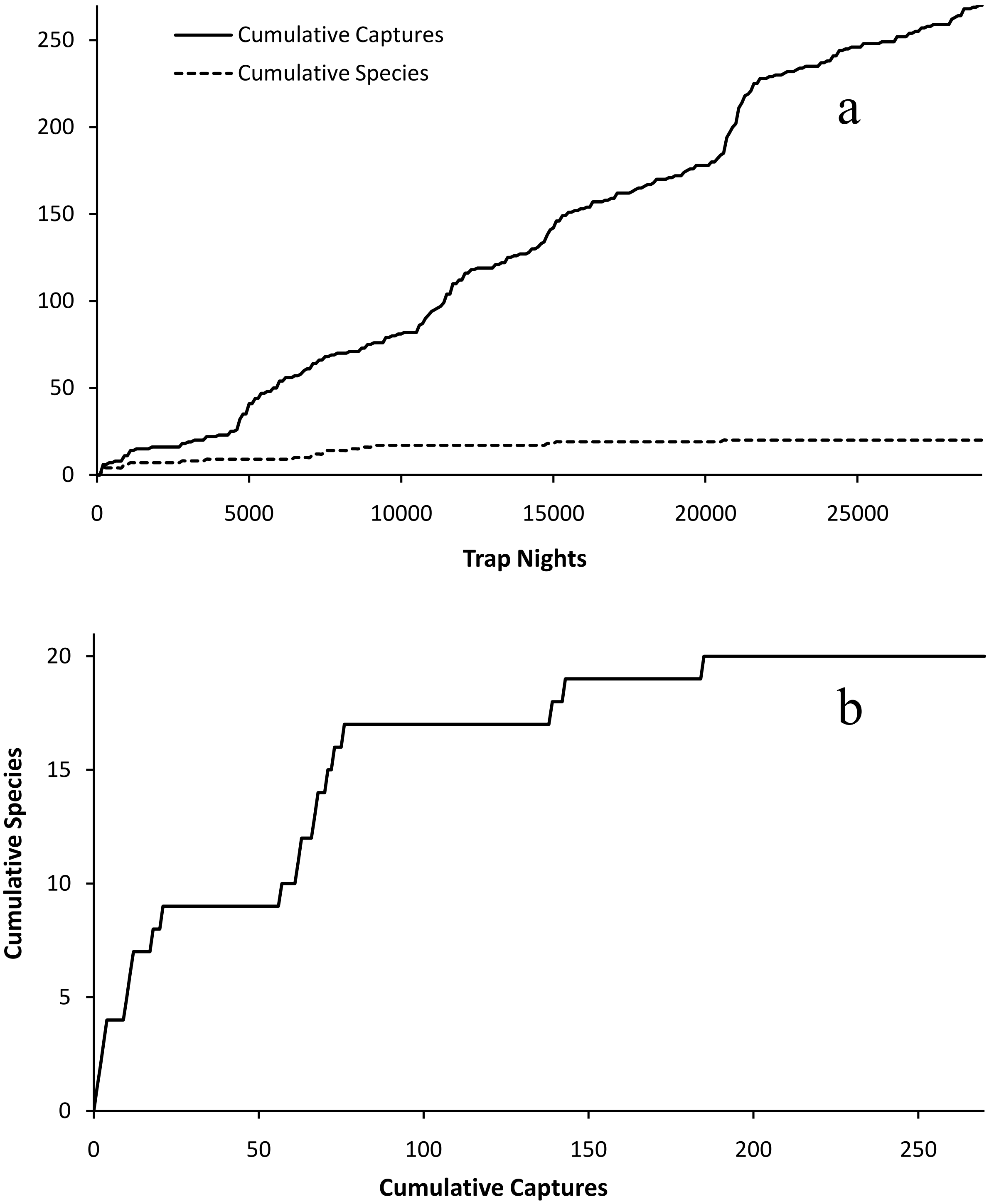


Figure 37. Results of terrestrial trapping using Tomahawk traps at RNAM based on a) cumulative number of trapnights and b) cumulative species. In 29,033 trap nights, 270 captures of 20 species were recorded.

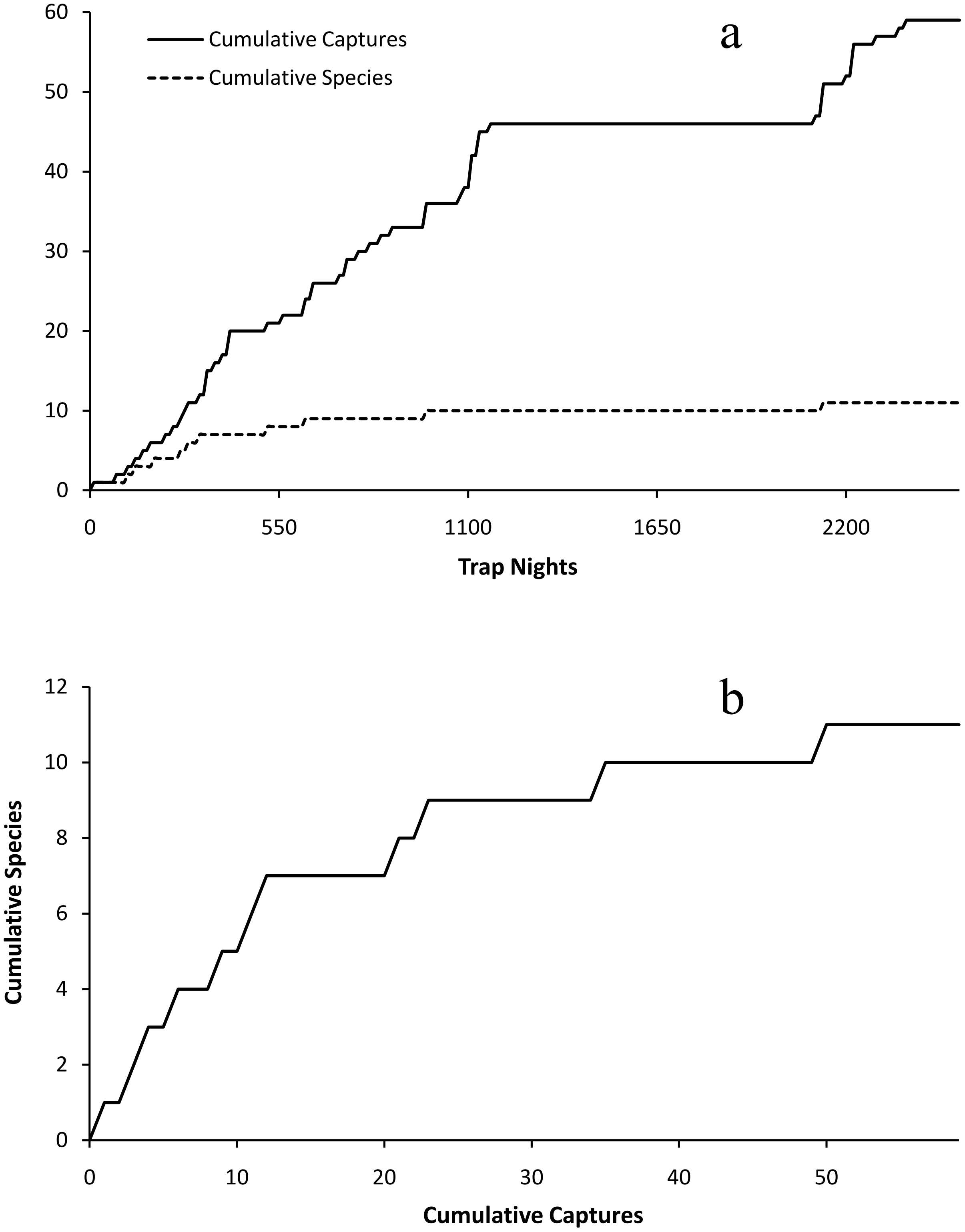
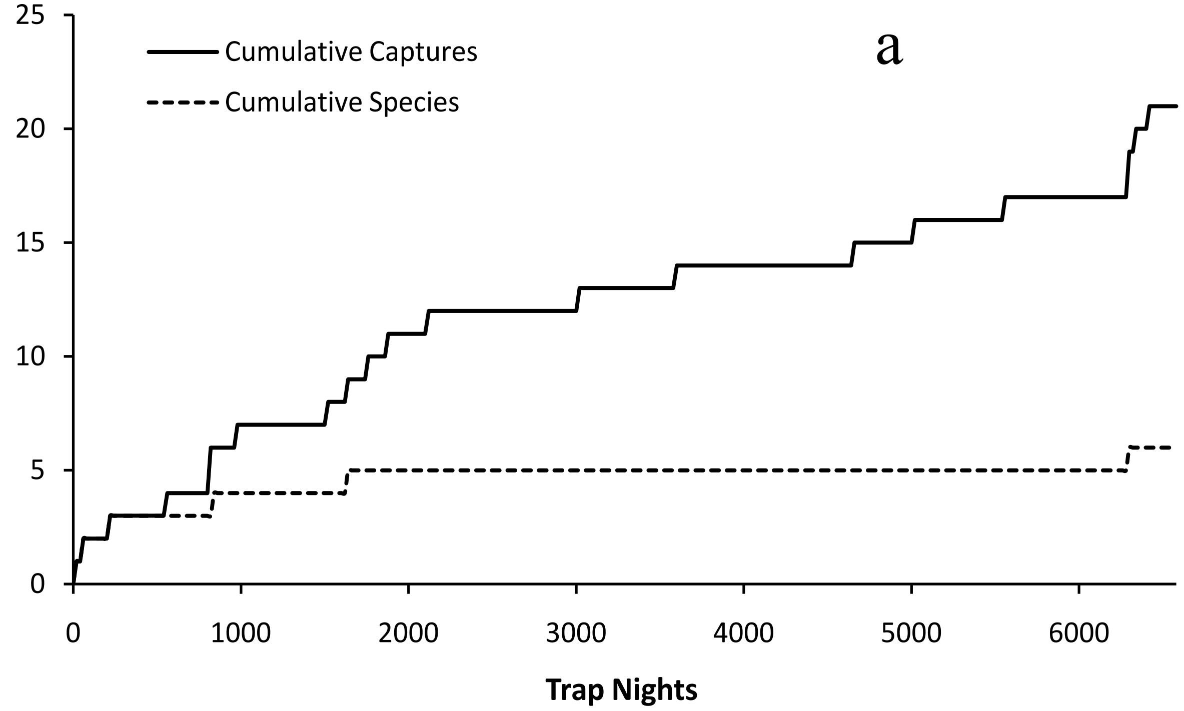


Figure 38. Results of terrestrial trapping using pitfall traps at RNAM based on a) cumulative number of trapnights and b) cumulative species. In 2,530 trap nights, 59 captures of 11 species were recorded.



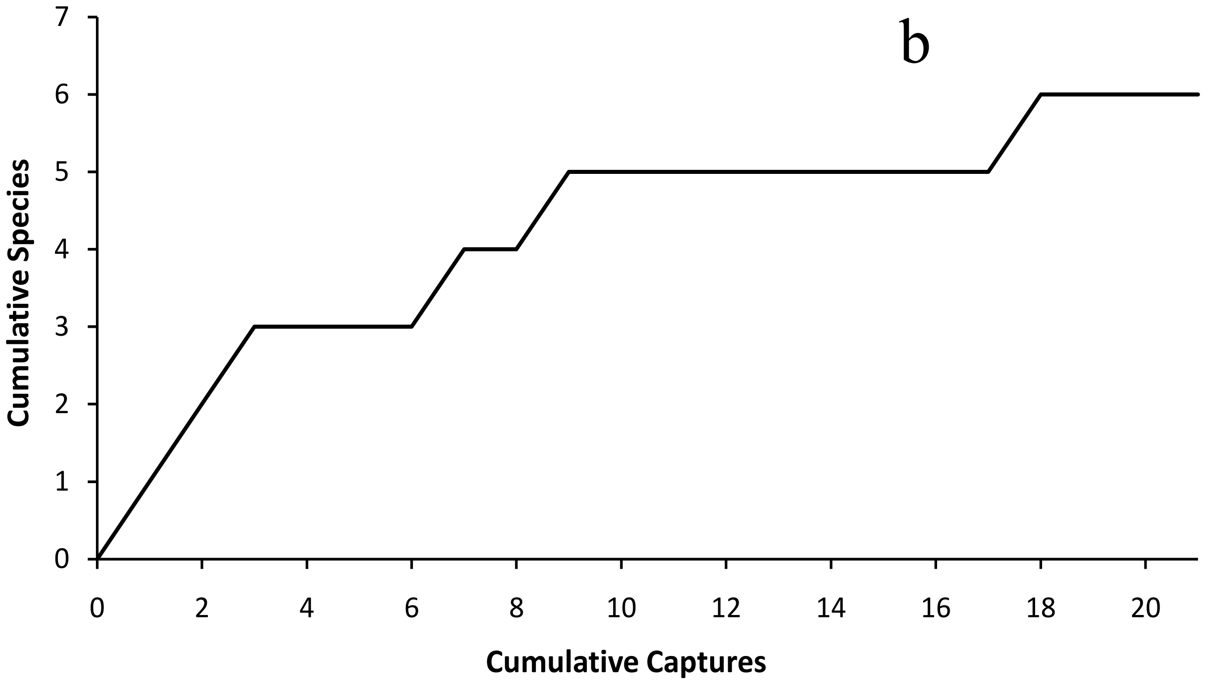


Figure 39. Results of arboreal trapping using Victor, Sherman, and Tomahawk traps at RNAM based on a) cumulative number of trapnights and b) cumulative species. In 6,580 trap nights, 21 captures of 5 species were recorded.

five additional species were captured in arboreal traps, indicating that indeed, the initial inventory of arboreal species was incomplete.

Adequacy of Sampling Period.—Before trapping was conducted on standardized grids, a preliminary study was conducted to determine the appropriate length of trapping period to sufficiently sample the small mammal community on each grid to allow meaningful comparisons of communities among habitat types at RNAM. It has been suggested that traps be set for a minimum of seven consecutive nights in lowland Neotropical forest to sufficiently sample both common and rare species and to estimate community structure (Woodman et al. 1995). This rule-of-thumb was followed by Patton et al. (2000), who used eight and 11 consecutive nights for terrestrial and arboreal traps, respectively. Nonetheless, the number of consecutive nights necessary to adequately assess small mammal communities in lowland Neotropical forest is unknown and may differ among sites (Voss and Emmons 1996; Voss et al. 2001). Traps were set for 20 consecutive nights during the preliminary study to assure that the optimal number of nights would fall within this time period.

All species captured on all grids during the preliminary study were captured in the first 11 nights (Fig. 40a). If each grid is examined individually, new species were encountered until night 15 on one grid and until night 11 on the other two grids (Fig. 40b-d). When this analysis was conducted immediately after the trapping cycle, most individuals had not yet been identified to species, so accumulation was examined at the generic level. Summarizing across grids, all genera were captured by night seven. If each grid is examined individually, all genera were captured by night 1, 7, or 15. If the one outlier on night 15 is removed, all other genera for that grid were captured by night two. Because most genera comprise more than one species at RNAM, traps were assessed for 10 consecutive nights in case some species were captured after night seven that were not initially distinguished.

Several problems are associated with simple species accumulation curves (Colwell and Coddington 1994; Voss and Emmons 1996; Simmons and Voss 1998; Voss et al. 2001). In addition to plotting cumulative species as a function of time, the data also were analyzed by graphing the cumulative number of species versus cumulative number of captures (Fig. 41a-d). During the preliminary study, when grids were assessed for 20 consecutive nights, an asymptote was reached between 18 and 36 captures, which are near night 11 and 15, respectively (Fig. 41b-d). If the grids are examined simultaneously, the asymptote is reached after 68 captures, which also coincides with 11 nights (Fig. 41a). For those grids assessed for 10 consecutive nights, a convincing asymptote was reached only five out of 20 times, with new species frequently added with the last four captures (Appendix V). However, 78% of all species were captured by night five, and 90% were captured by night seven. This indicates that, if the goal is to sample as close as possible to 100% of species present on a grid, a sampling period of 15 nights is recommended. If time constraints do not allow such a long sampling period, seven nights may be sufficient for relative comparisons of the small mammal community among grids.

Estimates of Local Species Richness.—Several methods were used to determine if all of the small mammal species present at RNAM were encountered. A graph of cumulative species versus sampling days provides a general indication of trends. Very little indication of an asymptote is apparent even after 28 species were collected (Fig. 35a). Because sampling days are not commensurate units of sampling effort, a graph of cumulative species versus cumulative captures can be a more effective way to examine this trend (Fig. 35b). This graph revealed a similar trend to that for sampling days, with even less indication of an asymptote. Furthermore, three additional species were recorded at this site during sampling conducted subsequent to this research.

A more accurate way to estimate local species richness is with one of several non-parametric methods that use extrapolation based on sampling data (Table 21). Of the species that could be expected to occur at RNAM based on regional species pools, 61% were actually recorded. However, using methods that estimate local species richness, we estimate that 85–90% of the local species were recorded. If the upper 95% confidence interval about the CHAO1 estimate of local species richness is used for a conservative estimate, the

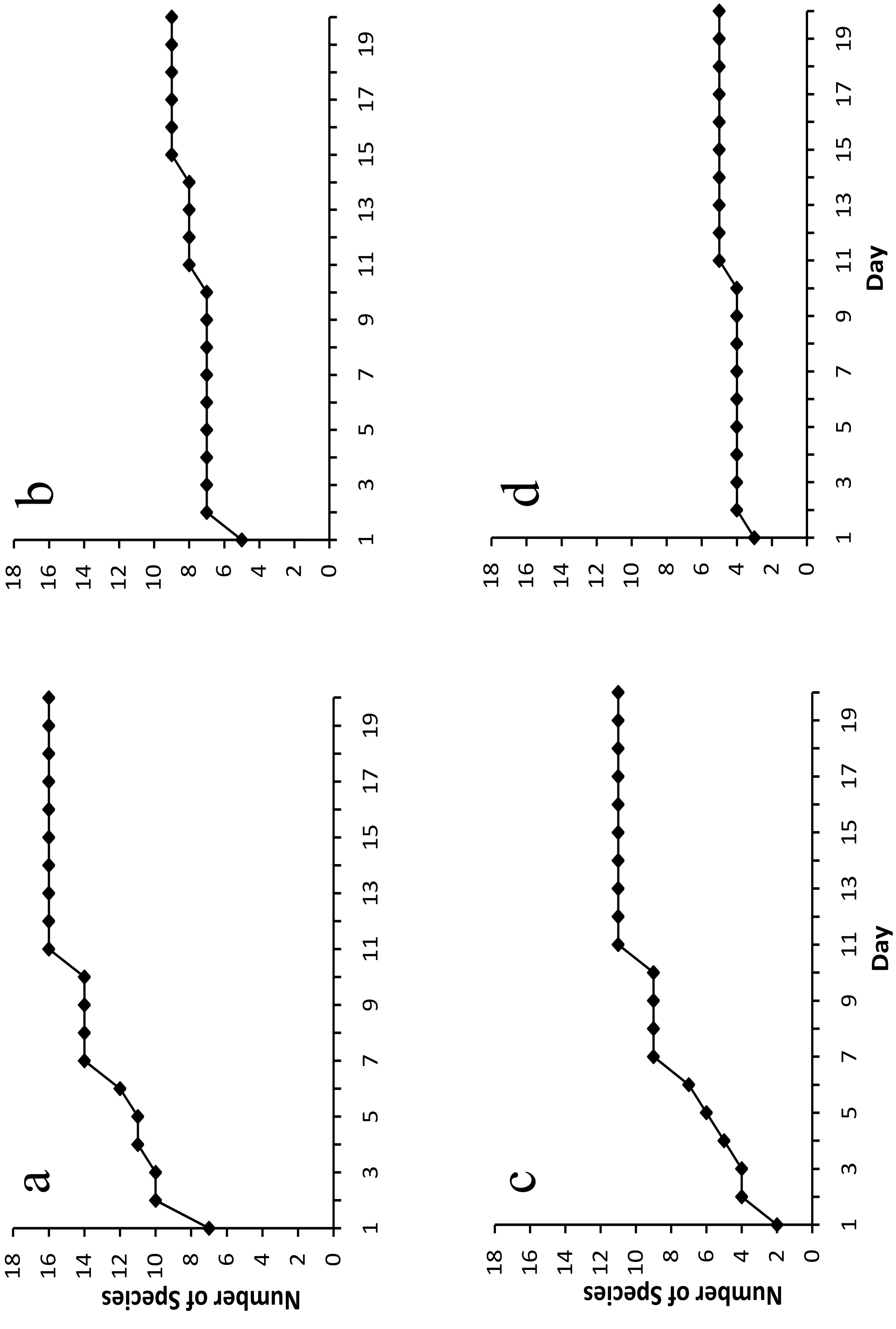


Figure 40. Empirical species accumulation curves through time for grids monitored for 20 days, a) all grids, b) grid 1C, c) grid 2C, and d) grid 3C.

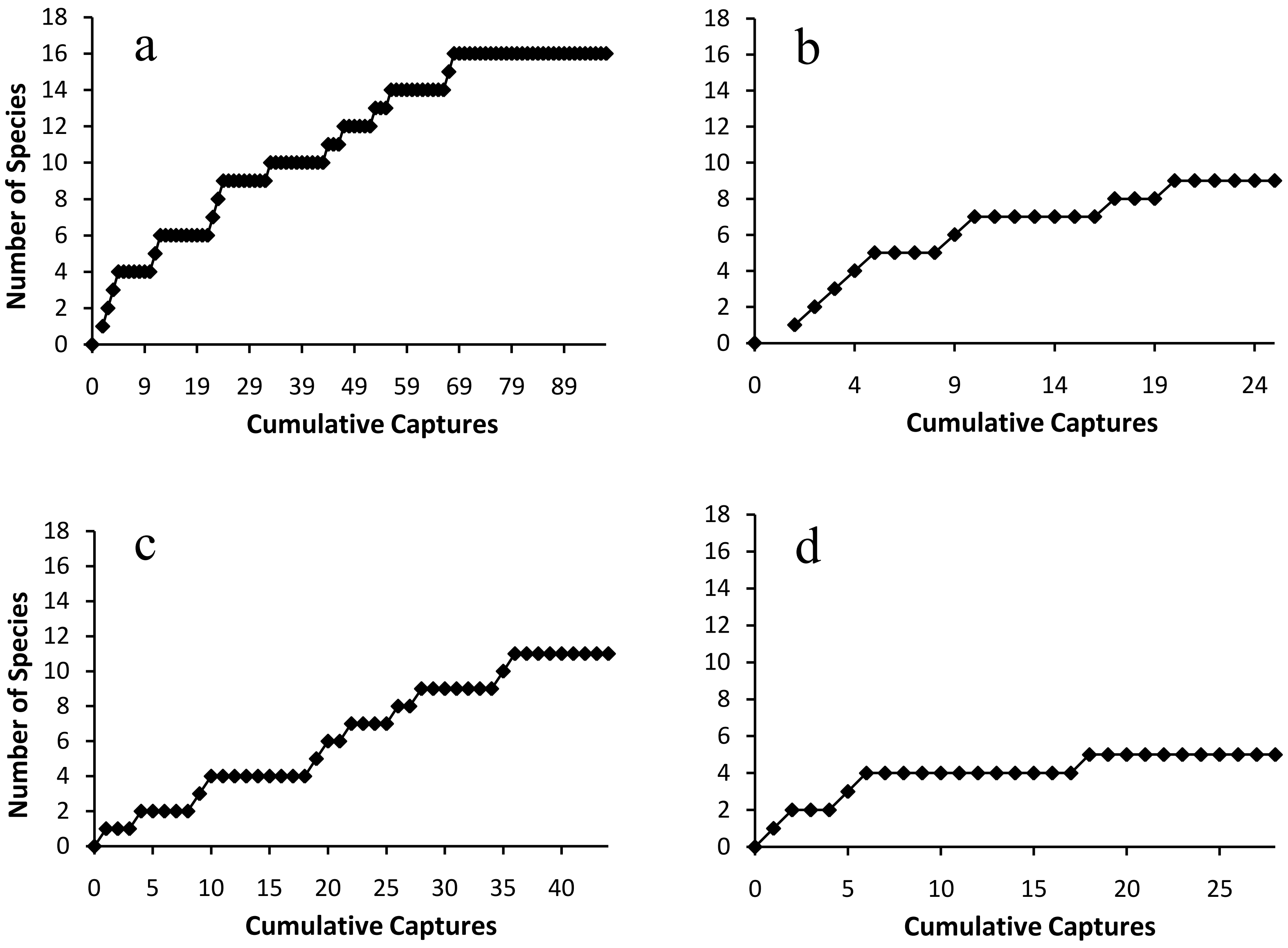


Figure 41. Species accumulation curves using cumulative captures for grids monitored for 20 days, a) all grids, b) grid 1C, c) grid 2C, and d) grid 3C. Note that all x-axes have different scales.

fauna was sampled 72% completely. This suggests that local species richness is less than regional species richness and that the fauna was sampled reasonably well.

The completeness of faunal samples differed by trapping method, but not by habitat type (Table 21). Arboreal traps were the least effective, capturing only 62–71% of the small mammal species present in the canopy, and perhaps as little as 31% if the upper 95% confidence interval about the CHAO1 estimate is used as a conservative estimate. Pitfall traps were slightly less effective than arboreal traps, at 69–85%. Conventional terrestrial trapping was very successful, capturing 90–96% of the species that occur on the ground. Disturbed and undisturbed habitats were sampled approximately equally well, at 81–92% for disturbed and 89–96% in undisturbed habitats. This suggests that the small fauna present in all habitats was sampled equally by the methods used.

Regional Comparisons.—Twelve other Neotropical sites that have been sampled relatively completely for which published faunal lists exist (Voss et al. 2001). Pair-wise similarities among the 13 sites were quantified with Jaccard's similarity index (Table 22). These results were then clustered with a UPGMA (Fig. 42). Sites grouped as expected into major geographic regions, including Central America, the western Amazon Basin, and the Guianan subregion of the Amazon Basin. RNAM was most similar to Cuzco Amazónico, followed by Balta and Manu. It was least similar to La Selva. A Mantel test indicated a strong correlation between faunal similarity and geographic proximity (r = 0.8117, Z = 2.22 x 105, $p < 0.001$).

Table 21. Estimates of local species richness for the overall community, disturbed and undisturbed habitats, and trap type. S_{obs} = observed species richness, a = number of species represented by singletons (single captures) or unicates (captures on a single occasion; these were identical for all except pitfall traps, which had 2 and 3, respectively), b = number of doubletons (2 individuals) or duplicates (2 occasions), S_{exp} = expected species richness based on eco-geographic range data (regional species richness), CI_{max} = upper 95% confidence interval about CHAO1. Percent completeness was calculated by S_{obs} / estimate of interest (i.e., CHAO1) x 100.

	S_{obs}	a	b	S_{exp}	CHAO1	CI_{max}	CHAO2	JACK1	JACK2
Species richness	28	4	3	46	31	39	31	32	33
Percent complete				61	90	72	90	88	85
Disturbed	22	5	5	na	24	30	24	27	27
Percent complete					92	73	92	81	81
Undisturbed	24	3	4	na	25	27	25	27	25
Percent complete					96	89	96	89	96
Pitfall	11	2/3	1	na	13	22	16	14	16
Percent complete					85	50	71	79	69
Arboreal	5	2	1	na	7	16	7	7	8
Percent complete					71	31	71	71	62
Terrestrial	26	3	4	na	27	29	27	29	28
Percent complete					96	90	96	90	93

Table 22. Percent faunal similarity (lower left triangle) based on Jaccard's index among 13 Neotropical rainforest non-volant mammal faunas. Inter–site distances in km appear in the upper right triangle.

Site	LSe	BCI	Ima	Kar	Par	Ara	Cun	Mus	Xin	Balt	Man	CAm	EBA
La Selva (LSe)		388	2452	2820	3379	3435	2131	3057	3788	2652	2829	2995	1991
Barro Colorado (BCI)	30		1989	2335	3004	3037	1656	2596	3315	2320	2508	2655	1627
Imataca (Ima)	11	19		250	1023	1076	649	1220	1613	2281	2454	2428	1886
Kartabo (Kar)	6	14	58		672	744	840	948	1316	2288	2448	2372	2024
Paracou (Par)	12	15	54	55		136	1458	1217	994	2714	2838	2732	2501
Arataye (Ara)	11	17	64	60	71		1456	1162	859	2636	2754	2640	2476
Cunucunuma (Cun)	8	12	32	35	33	39		993	1701	1643	1847	1849	1198
Manaus (Mus)	6	13	56	52	53	63	38		850	1465	1584	1448	1491
Xingu (Xin)	6	15	39	45	43	47	29	48		2220	2284	2119	2336
Balta (Balt)	11	18	25	21	30	31	24	26	24		200	346	727
Manu (Man)	8	13	23	16	22	23	18	24	25	73		223	912
Cuzco Amazónico (CAm)	9	16	24	19	26	27	22	25	26	65	59		1076
Allpahuayo (EBA)	8	14	24	23	29	30	26	28	32	40	40	51	

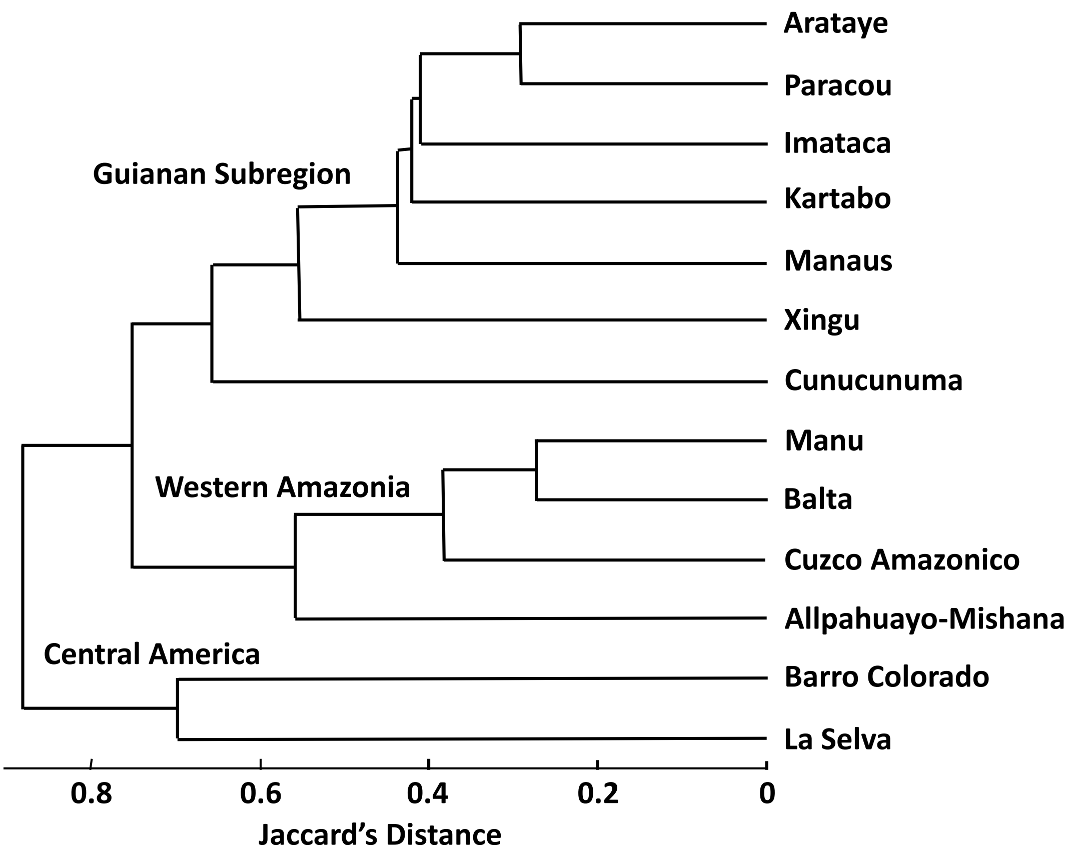


Figure 42. Analysis of faunal similarity of the non-volant fauna of 13 Neotropical sites based on Jaccard's similarity index and clustered with UPGMA. The bottom scale indicates the clustering level based on Jaccard's distance (1 - *J*).

DISCUSSION

*Techniques.—**Capture Rate***: Overall capture rate at RNAM (0.96%) was lower than rates reported at other Amazonian sites, which ranged from 1.9% at Paracou (0.6 - 3.6% by annual sampling period, Voss et al. 2001), 5.3% in Cuzco Amazónico (Woodman et al. 1996), to 5.9% along the Rio Juruá (2.4–12.2% by site, Patton et al. 2000). Although monthly capture rate at RNAM varied and sometimes exceeded 2%, there does not appear to be a distinct seasonal pattern in capture rate (see Fig. 32b). Arboreal capture rate also was lower at RNAM (0.40%) than at other sites, with 1.5% along the Rio Juruá (0.4–4.6% by site, Patton et al. 2000), 0.8% in Paracou (Voss et al. 2001), and 4.3% in Manaus (Malcolm 1990). The exact reason for lower capture rates at RNAM is unknown. It is possible that the density of mammals is simply lower than it is at other sites, or that the mammals are particularly trap shy, both of which could be attributed to the proximity of the study site to Iquitos, and thus, to the impact of people – and human trapping and hunting – on the mammals at the site. The other sites are more remote than RNAM and there is less pressure on the small mammal population as a food source. One other possible explanation is that a particularly strong El Niño event occurred in 1998 and this impacted small mammal densities. Although there are no published data to support this hypothesis, a herpetologist working in the area during this time reported extremely low amphibian and reptile densities as well, and this same investigator has noted lower densities of herptiles during other El Niño events over the past 15 years (W. Lamar, pers. comm.). Moreover, Voss et al. (2001) also reported depressed capture rates in 1992 compared to 1991, coinciding with an El Niño event in 1992. Regardless, capture rates in lowland rainforest are typically considerably lower than those experienced in temperate regions (e.g., the thesis work of the first author on Galveston Island, Texas, yielded 40–90% capture rates, Hice and Schmidly 1999) and contribute to the difficulty in understanding the ecology of tropical non-volant mammals.

Sampling Methods: The four different sampling methods used at RNAM (conventional, large traps, pitfall, and arboreal) sampled different subsets of the mammal community. All but one (large traps) yielded unique species that were not captured using other methods. This is mostly in agreement with the findings of Voss et al. (2001), although they did not record any unique species in arboreal traps. As would be expected, species accumulation rates based on effort and cumulative captures slowed through time, similar to what is observed at other sites. Convincing asymptotes were rarely reached for any of the methods, however, indicating that additional effort with any of the methods would likely yield additional species. The results from RNAM and Paracou reinforce the observation that a variety of traps and placements (and baits) should be used to sample as completely as possible the small mammals in lowland Neotropical rainforest.

***Sampling Period*:** Traps should be set for many consecutive nights – on the order of 10 to 15 – to capture all species present on a grid or transect. However, 90% of species were taken by night 7, but only if all grids are pooled (Fig. 40). This is in accord with the findings of Woodman et al. (1995), who captured new species until night 12 (of a 12-day trapping period), but encountered 90% of all species by night 7 if grids were pooled. Patton et al. (2000) sampled terrestrial mammals for eight consecutive nights along the Rio Juruá, and at some locations captured new species on night 8. Of course, these studies only consider species that were captured. Some additional species may have been present but so rare or trap shy that they were not recorded. If all species that were captured at a local site over the duration of the study are considered, even 20 nights seems to be inadequate for sampling all species. For example, 11 additional species of small mammals were captured on other grids and transects that were not taken on the grids used to assess adequacy of sampling period. Along the Rio Juruá, Patton et al. (2000) documented a total of 28 species, but only 22 species were captured in the first eight nights of standardized trapping (including arboreal traps) at any location, suggesting more species may have been captured if traps had been assessed for a longer period of time. Nonetheless, time and resources are limited, so depending on the goal of the research (i.e., complete mammal inventory or equal sampling for faunal comparisons across sites) 7–10 nights would be an adequate sampling period in most cases.

Estimates of Local Species Richness: Local species richness can be estimated by several methods, the simplest of which is to plot the cumulative number of species encountered versus some unit of sampling effort (e.g., see Fig. 35). However, many difficulties are encountered when using this method, including changes in sampling effort, use of *ad hoc* collecting versus standardized effort, uneven spatial and temporal distribution of species and individuals, and other factors inherent in sampling methodology and the fauna itself. These problems have been reviewed at length (Voss and Emmons 1996; Simmons and Voss 1998; Voss et al. 2001) and alternative methods of estimating local species richness are available (Colwell and Coddington 1994).

Estimates of local species richness using these non-parametric methods are often compared to regional species richness (based on ecogeographic distribution data) to determine how completely the local fauna has been sampled. However, it is well documented that local species richness is often lower than regional species richness and that the discrepancy due to beta diversity (spatial variation due to often subtle habitat differences) is greatest at lower latitudes (Stevens and Willig 2002). Results of mammalian inventories should be viewed in light of this relationship.

One other study in the Neotropics has used several methods to exhaustively estimate completeness of sampling and local species richness (Paracou, French Guiana: Voss et al. 2001). The overall goal of the study at Paracou was to inventory the entire mammalian fauna at the study site as completely as possible by using a wide variety of techniques (Voss et al. 2001). Thus larger mammals, such as primates, carnivores, edentates, and ungulates, were included in their estimates of local species richness. This was not the case at RNAM, where such estimates were limited to small rodents and marsupials. Nonetheless, some comparisons between Paracou and RNAM can be made.

The fauna at RNAM was sampled almost as completely as that at Paracou. If only trapping data comparable to that conducted at RNAM (e.g., conventional, pitfall, and arboreal trapping) are used from Paracou, 21 species of small rodents and marsupials were captured there. Using CHAO1 to estimate local species richness, 23 species would be expected, indicating that the local community was sampled 91% completely (Table 23). If observed species richness of rodents and marsupials is compared to regional species richness at Paracou, 64% of the regional species were documented in the local community. Both estimates are similar to those for RNAM, with 90% and 61%, respectively (see Table 21).

Voss et al. (2001) applied the same technique to estimate sampling completeness by sampling method. They found conventional ground-level trapping sampled the fauna most completely at 95%, arboreal trapping the next most completely at 85%, and pitfall the least at 57% (Table 23). Sampling completeness by sampling method at RNAM was 93% for terrestrial traps, 62% for arboreal, and 69% for pitfalls (see Table 21). These estimates make intuitive sense based on subjective criteria and field experience, with the exception of arboreal sampling at Paracou, which was rather high.

The exercise of analyzing data for sampling completeness is educational and facilitates the understanding of the incomplete nature of data collected in the field. Because field data are never 100% complete, they are less than ideal, but are the only data available for testing ecological hypotheses.

***Regional Comparisons*:** Jaccard's similarity index values previously have been clustered using UPGMA to compare the non-volant fauna across sites in the Neotropics in several publications (Voss and Emmons 1996; Voss et al. 2001). Data from RNAM were added to the existing matrix in Voss et al. (2001: Appendix II) and the new matrix was reanalyzed to see where RNAM would appear in the dendrogram. As expected, it clusters with other sites in the western Amazon Basin (see Fig. 42). Increasing faunal similarity was correlated with geographic proximity (Voss et al. 2001), and the addition of RNAM did not change this relationship. The spatial distribution of sites for which small mammal data were available was fairly broad and covered the four major Neotropical regions, from Central America to the southeastern Amazon. However, data from only one site (Xingú) in the southeastern subregion of the Amazon Basin were available. Moreover, this inventory was not particularly complete. An inventory from an additional site in this subregion would clarify the relationships of mammalian faunas in this subregion to faunas in other subregions.

Concluding Remarks.—Although this study spanned 16 months, it did not obtain sufficient data to address many ecological questions. Long-term studies, on the order of five or more years, are needed to understand changes in species abundance, community structure, and populations through time. Species distributions are patchy, especially in the Neotropics, and the dynamics of these distributions in space and time are almost entirely unknown. There is a seasonal component to these fluctuations, but there also is a multi-annual component that manifests itself in changes in dominant species in a local community over several years. It will require long-term studies to document these patterns at local and regional scales. Once a pattern is identified, the underlying causal mechanism for the observed pattern can be elucidated. This will involve community assembly rules, recovery of flora and fauna after natural and anthropogenic disturbance, and the interplay between local and regional species richness, ecological filters, competition, and niche partitioning. This will require not only thorough censuses of the fauna in various habitats and regions throughout the Neotropics, but manipulative experiments.

Currently, most work on mammals in tropical America is descriptive. The natural history information gathered by such studies provides a framework for ecological questions. Unfortunately, the natural history of most Neotropical mammals is still poorly known. Nonetheless, it is time to move beyond simply censusing the mammalian fauna at a site. Other techniques, such as mark-recapture and radio tracking, need to be applied to fill in large gaps in the knowledge of species

Table 23. CHAO1 estimates of local species richness at Paracou, French Guiana. S_{obs} = observed species richness, a = number of singletons, b = number of doubletons, S_{exp} = expected species richness based on ecogeographic range data (regional species richness), CI_{max} = upper 95% confidence interval about CHAO1. Percent completeness was calculated by S_{obs} / estimate of interest (i.e. CHAO1 or S_{exp}) x 100. The number of singletons and doubletons were obtained from Table 48 in Voss et al. (2001), including only marsupials, and cricetid and echimyid rodents captured in terrestrial, pitfall, or arboreal traps.

Sampling Method	S_{obs}	CHAO1	%	S_{exp}	%
All	21	23	91	33	64
Pitfall	12	21	57	na	na
Arboreal	6	7	86	na	na
Terrestrial	18	19	95	na	na

natural history. Advances in mammal ecology need not wait until everything is known about the natural history of the resident species. Examples of studies that could provide information of both types include removal experiments to examine competition among small mammals. To better understand how floral and faunal communities recover after a disturbance event, communities must be subjected to different kinds of disturbance and closely monitored as they recover. A combination of methodologies is needed if the rainforest ecosystem is to be preserved intact. However, such studies are often prohibitively expensive and funding is often not available over the long-term, if at all.

Fortunately, the recent surge of interest in emerging diseases has afforded opportunities to fund longer-term field studies. Resources never before (or only rarely) available to field biologists are becoming available through this avenue in collaborative projects. Moreover, virologists and epidemiologists are beginning to understand the importance of including a mammalogist or ecologist in studies of emerging diseases, so the reservoir species can be correctly identified and their ecology elucidated. This information is essential to develop predictive models about zoonoses and how to eliminate or diminish epidemics in human populations. The current interest in emerging diseases is unlikely to ebb in the near future, with the recent concern about global pandemics and bioterrorism. Mammalogists and ecologists should take full advantage of such funding opportunities to provide the necessary resources for long-term ecological studies world-wide.

This study represents one such collaborative project. Although results presented here represent a classical study of mammalian natural history, the data were collected under the auspices of the National Institutes of Health in search of emerging tropical diseases. Data about mammals obtained during this study included their systematics and identification, the techniques used to collect them, and information about their diversity and community structure. Correctly identifying individuals to species is important not only in studying their autecology, but also in understanding community structure and how it changes across space. It is particularly important when attempting to understand the ecology of a virus with a sylvatic reservoir and a cycle that occasionally causes outbreaks of human disease. The techniques used to collect mammals are important, because different techniques sample different subsets of the mammal community. Data gathered using unsuitable or insufficient techniques yield less accurate estimates of species compostiton and diversity, and consequently such data cannot be used to compare community structure among sites (Voss et al. 2001).

Although this was a classical natural history study, specimens were collected in such a manner as to facilitate systematic studies. Specimens collected included not only a standard museum skin and skull/skeleton, but also tissue samples that are essential for clarifying systematic relationships. The fields of ecology and systematics are complementary. Unfortunately, they have become divorced, with systematists unfamiliar with the ecology of the species they are attempting to differentiate, and ecologists ignorant of the phylogenetic relationships of the species they are studying. Both fields need to advance in concert to realize substantial gains in the understanding of Neotropical mammals.

Whereas systematics was not the focus of this research, it played an important role from several perspectives. Primarily, positive identification to species of many Neotropical taxa is problematic and often requires expert assistance. Specific problems concerning the identification of species were discussed at length in the species accounts and will not be discussed here.

Obviously, if specimens collected during a natural history study are misidentified, conclusions drawn about their natural history will be inaccurate. This also is true of ecological studies, particularly if comparisons of small mammal community structure are the basis for conservation recommendations. To alleviate this problem, specimens collected during this research were identified by experts of particular taxonomic groups (i.e., G. Musser for oryzomyines, J. Patton for echimyids, and R. Voss for marsupials). Unfortunately, such experts in mammalian systematics in general, and Neotropical mammals in particular, are dwindling in number.

One exciting aspect of working with small Neotropical mammals is that many species have yet to be described. Of course, new species cannot be recognized without a thorough understanding of the systematics of those species that have already been described. During this study, one undescribed species of *Neacomys* was obtained. Not only are there new species yet to be discovered in the Neotropics, but the distributional ranges of most species of small mammals are not well delineated. More collecting sites are needed to establish more accurate range boundaries. This study recorded important range extensions for three species (*Philander opossum*, *Monodelphis adusta*, and *Hyladelphys kalinowskii*; Hice 2001).

Information about the biogeography of Neotropical mammals has recently been melded with systematics in the relatively new field of phylogeography. In this manner, the evolutionary history of a species can be better understood. If all the species in a region are examined from this perspective, broad-scale patterns of the ecological diversification of a region can be discerned. Methods that integrate several divergent fields, such as systematics, ecology, and biogeography, will be the most likely to give rise to holistic conservation strategies.

Finally, emerging zoonotic diseases have come to the forefront of public concern. To attempt to control outbreaks of these diseases, the systematics and ecology of the reservoir, which are often wild mammals, must be understood. The importance of systematics is twofold: first, the reservoir must be properly identified, and second, closely related species that also could harbor the disease should be recognized and studied. Once this is accomplished, the transmission cycle of the disease must be determined. This requires information about the natural history of the implicated species, and about the ecology of the ecosystem where it occurs. Once again, systematics and ecology must be used in concert to answer complicated natural history questions.

Concern about current rates of species extinction is at an all-time high (Wilson 1988a). The implications of this loss of biodiversity for ecosystem function at local, regional, and global scales are only now coming into focus. Conservation biology attempts to preserve ecosystems and their constituent species in the face of inexorable anthropogenic destruction. Of particular concern are tropical rainforests, which comprise 7% of the earth's terrestrial area, but may harbor as much as 50% of its species (Myers 1988; Wilson 1988b). However, it is difficult to preserve what is not understood, or in many cases, even known. Basic natural history research, from local inventories to autecological and community studies, are needed to supply the information necessary to make sound conservation decisions based on research, not caprice or misguided perceptions (Patterson 1991).

Such research also is needed to understand larger-scale patterns in diversity. Fortunately, there are now data from several sites throughout the Neotropics, which can be used to address questions about species assembly rules, local versus regional diversity, and biogeographical patterns in community structure. Although data from no site are 100% complete, they are sufficient to use in preliminary analyses. Results of such analyses will yield insights into many basic ecological questions, as well as direct future research. The time is ripe to begin analyzing the data that are now available, with all of their limitations, instead of focusing on the inadequacies and calling for more research. Natural history and ecological data are never perfect, and never will be for Neotropical sites, where mammals are rare and trap shy, and financial constraints and logistical problems make long-term intensive studies difficult. Despite these difficulties, a synthesis of available information is imperative to conserving the very habitat which we are trying to understand.

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APPENDIX I

Sampling schedule of grids, pitfall traplines, arboreal transects, and line transects used to assess mammal communities at Allpahuayo and Otorongo.

Grid/Transect	Habitat	Dates assessed
Grid 1A	*monte alto*	11–21 Dec 1997
		20–30 July 1998
Grid 1B	*monte alto*	13–23 Sep 1998
Grid 1C	*monte alto*	14–17 Aug 1997
		09–29 Oct 1997
Grid 2A	*franco arcilloso*	14–24 Mar 1998
		16–26 Oct 1998
Grid 2B	*franco arcilloso*	02–12 Nov 1997
		30 Jul–09 Aug 1998
		12–15 Oct 1998
Grid 2C	*franco arcilloso*	30 Sep–20 Oct 1997
		06–11 Nov 1998
Grid 3A	*varillal*	31 Oct–10 Nov 1997
		24 Jun–04 Jul 1998
Grid 3B	*varillal*	24 Mar–03 Apr 1998
		17–27 Oct 1998
Grid 3C	*varillal*	15–17 Aug 1997
		29 Sep–19 Oct 1997
Grid 4A	*varillal* that grades to *monte alto*	05–15 Oct 1998
Grid 4B	*varillal* that grades to *monte alto*	09–16 Aug 1997
Grid 5A	older selectively cut forest (*varillal*), similar to Grid 3A, but more open	13–23 Mar 1998
		02–12 Oct 1998
Grid 5B	younger selectively cut forest, similar to Grid 6, but older trees	02–12 Sep 1998
Grid 6	15 year old secondary growth	10–20 Dec 1997
		25 Jun–05 Jul 1998
Grid 7	6-7 year old secondary growth	11–21 Nov 1997
		06–16 Jul 1998
Grid 8	2-3 year old field	14–24 Nov 1997

APPENDIX I (CONT.)

Grid/Transect	Habitat	Dates assessed
Grid O-1	6 and 15 year old secondary growth	22 Aug–01 Sep 1998
		07–17 Nov 1998
Grid O-2	3 and 10 year old secondary growth	22 Aug–01 Sep 1998
		07–17 Nov 1998
Pit 1A	*monte alto*	11–21 Dec 1997
		14–24 Mar 1998
		20–30 Jul 1998
Pit 1B	*monte alto*	06–11 Nov 1998
Pit 2A	*franco arcilloso*	02–12 Nov 1997
		13–23 Mar 1998
Pit 2B	*franco arsilloso*	30 Jul–09 Aug 1998
		25 Oct–04 Nov 1998
Pit 3	*varillal*	31 Oct–10 Nov 1997
		13–23 Mar 1998
		24 Jun–04 Jul 1998
		19–29 Oct 1998
Pit 4	*varillal* that grades to monte alto	05–15 Oct 1998
Pit 5	younger selectively cut forest, similar to Grid 6, but older trees	02–12 Sep 1998
		31 Oct–10 Nov 1998
Pit 6	15 year old secondary growth	25–27 Aug 1997
		17–21 Sep 1997
		10–20 Dec 1997
		25 Jun–05 Jul 1998
Pit 7	6-7 year old secondary growth	12–22 Nov 1997
		06–16 Jul 1998
Pit 8	2-3 year old field	13–23 Nov 1997
Pit Temp 4	*monte alto*	05–15 May 1998
Pit Temp 5	*monte alto*	19–29 May 1998
Pit Temp 8	*monte alto*	30 Oct–09 Nov 1998

APPENDIX I (CONT.)

Grid/Transect	Habitat	Dates assessed
Arb 1	*monte alto*	13–28 Jan 1998
		30 Mar–09 Apr 1998
		20–30 Jul 1998
Arb 2	*franco arsilloso*	26 Dec 1997–10 Jan 1998
		08–18 Apr 1998
		09–19 Aug 1998
Arb 3	*varillal*	27 Dec 1997–11 Jan 1998
		11–21 Apr 1998
		11–21 Aug 1998
Arb 4	15 year old secondary growth	08–23 Jan 1998
		28 Mar–07 Apr 1998
		31 Jul–10 Aug 1998
Line A-1	15 year old secondary growth	05–09 Aug 1997
Line A-2	15 year old secondary growth	24–27 Aug 1997
Line A-3	15 year old secondary growth	12–16 Apr 1998
Line 1	6 year old secondary growth	30 Dec 1997–09 Jan 1998
Line 2	grassy area - age unknown	03–13 Jan 1998
Line 3	currently disturbed field	15–25 Jan 1998
Line 4	*monte alto*	05–15 May 1998
Line 5	*monte alto*	18–28 May 1998
Line 6	orchard	07–17 Sep 1998
Line 7	*monte alto*	24 Sep–04 Oct 1998
Line 8	*monte alto*	29 Oct–05 Nov 1998
Line 9	*monte alto*	29 Oct–05 Nov 1998

APPENDIX II

Arboreal station heights, diameter at breast height (DBH), and species identity of each tree on the 4 arboreal transects.

ARB 1	Tree species	Station height (m)	DBH (cm)
1	*Tetrastylidium peruvianum*	7.3	64
2	*Protium divarigatum*	5.0	75
3	*Tetrastylidium peruvianum*	7.4	35
4	*Micropholis egensis*	3.1	66
5	*Pseudolmedia laevigata*	6.2	84
6	*Virola elongata*	5.7	95
7	*Iryanthera tessmannii*	5.4	41
8	*Ruizterania trichanthera*	5.1	70
9	*Tetrastylidium peruvianum*	11.3	65
10	*Pouteria guianensis*	5.4	70
11	*Leonia glycycarpa*	7.2	46
12	*Tetrastylidium peruvianum*	6.5	36
13	*Leonia crassa*		5.1
14	*Tetrastylidium peruvianum*	6.1	37
15	*Eschweilera parvifolia*	12.3	95
16	*Sloanea grandiflora*	5.7	29
17	*Protium* sp.	7.6	61
18	*Virola elongata*	5.1	49
19	*Nealchornea yapurensis*	5.1	55
20	*Tetrastylidium peruvianum*	7.3	50
21	*Iryanthera tessmannii*	5.0	31
22	*Leonia glycycarpa*	5.2	46
23	*Buchenavia grandis*	5.5	64
24	*Sterculia frondosa*	5.5	64
25	*Iryanthera tessmannii*	5.3	35
26	fallen	1.4	na
27	fallen	1.7	na
28	fallen	1.0	na
29	fallen	0.6	na
30	fallen	1.8	na

Appendix II (cont.)

ARB 2	Tree species	Station height (m)	DBH (cm)
1	*Macrolobium microcalyx*	6.4	64
2	*Ruptilocarpum caracolito*	5.5	140
3	*Virola peruviana*	7.2	60
4	*Micranda spruceana*	6.4	60
5	*Pterocarpus rohrii*	7.8	41
6	*Dendropanax umbellatus*	8.1	136
7	*Dendropanax umbellatus*	8.5	58
8	*Parkia nitida*	7.3	70
9	*Parkia nitida*	8.5	70
10	*Albizia niopoides*	8.8	64
11	*Chrysophyllum bombycinum*	7.5	46
12	*Tovomita spruceana*	5.5	70
13	*Brosimum alicastrum*	11.3	64
14	*Dendropanax umbellatus*	5.7	67
15	*Swartzia racemosa*	11.3	79
16	*Protium trifoliolatum*	6.3	35
17	*Dialium guianense*	4.0	85
18	*Roucheria punctata*	5.5	30
19	*Tetrameranthus pachycarpus*	6.1	60
20	*Tovomita umbellata*	6.4	50
21	*Miconia tomentosa*	5.5	55
22	*Tachigali paniculata*	5.8	43
23	*Picramnia bullata*	7.1	82
24	*Chrysophyllum guanensis*	5.3	56
25	*Diclinanona calycina*	5.3	50
26	fallen	1.0	na
27	fallen	1.7	na
28	fallen	1.9	na
29	fallen	1.1	na
30	fallen	0.3	na

APPENDIX II (CONT.)

ARB 3	Tree species	Station height (m)	DBH (cm)
1	*Dendropanax umbellatus*	5.8	60
2	*Chrysophyllum bombycinum*	5.8	40
3	*Dendropanax umbellatus*	6.3	40
4	*Theobroma obovatum*	5.8	47
5	*Maytenus macrocarpa*	5.0	45
6	*Ternstroemia klugiana*	8.1	47
7	*Guatteria elata*	5.1	37
8	*Tovomita brasiliensis*	6.8	36
9	*Swartzia polyphylla*	7.0	46
10	*Chrysophyllum manaosense*	5.8	66
11	*Diclinanona calycina*	6.0	35
12	*Licania heteromorpha*	4.8	60
13	*Ternstroemia klugiana*	7.9	50
14	*Calyptranthes* sp.	6.9	40
15	*Calyptranthes* sp.	7.1	51
16	*Calyptranthes* sp.	6.8	40
17	*Licania reticulata*	5.8	32
18	*Metteniusa tessmanniana*	7.0	39
19	*Ocotea* sp.	5.8	55
20	*Ladenbergia ulei*	5.6	70
21	*Pouteria torta*	15.6	146
22	*Calyptranthes* sp.	8.2	56
23	*Couepia williamsii*	7.7	68
24	*Chrysophyllum manaosense*	7.2	44
25	*Tovomita spruceana*	7.5	71
26	fallen	1.0	na
27	fallen	1.8	na
28	fallen	1.1	na
29	fallen	1.2	na
30	fallen	1.0	na

APPENDIX II (CONT.)

Arb 4	Tree species	Station height (m)	DBH (cm)
1	*Nealchornea yapurensis*	5.3	76
2	*Perebea guianensis*	4.8	140
3	*Simarouba amara*	5.4	123
4	*Maytenus macrocarpa*	5.0	68
5	*Leonia glycycarpa*	5.7	68
6	*Tetrastylidium peruvianum*	4.8	62
7	*Ocotea aciphylla*	6.6	71
8	*Inga* sp.	5.9	47
9	*Helicostylis tometosa*	4.0	84
10	*Tetrastylidium peruvianum*	6.3	65
11	*Sloanea grandiflora*	5.1	43
12	*Tetrastylidium peruvianum*	5.5	44
13	*Tetrastylidium peruvianum*	5.6	65
14	*Tetrastylidium peruvianum*	6.6	78
15	*Tachigali formicarum*	4.4	41
16	*Tetrastylidium peruvianum*	5.6	61
17	*Eschweilera coriacea*	13.0	57
18	*Tetrastylidium peruvianum*	4.7	58
19	*Nealchornea yapurensis*	12.2	75
20	*Inga* sp.	3.6	71
21	*Virola elongata*	5.0	116
22	*Tetrastylidium peruvianum*	4.5	26
23	*Tetrastylidium peruvianum*	4.4	75
24	*Sorocea hirtella*	5.4	45
25	*Vismia macrophylla*	2.4	66
26	fallen	1.7	na
27	fallen	1.0	na
28	fallen	1.6	na
29	fallen	1.0	na
30	fallen	1.6	na

APPENDIX III

List of the most common plant species present on each grid, pitfall trapline, and arboreal transect.

Grids 1A, 1B, 1C, Pit 1A, Pit 1B, Arb 1

Habitat: *Monte Alto*

Tall trees:
Parkia nitida
Couepia bracteosa
Hyeronima oblonga
Apeiba membranasea
Bunchosia hookeriana

Smaller trees:
Inga puriens
Trichilia maynasiana
Rinorea macrocarpa
Guarea grandifolia

Shrubs:
Maietia guianensis
Piper itayanum
Cybianthus nanayensis

Palms:
Iriartea deltoidea
Socratea exorrhiza
Oenocarpus bataua
Astrocaryum chambira
Astrocaryum macrocalyx

Lianas:
Rourea camptoneura
Bauhinia brachicalyx
Dalbergia monetaria

Herbaceous:
Tabernaemontana macrocalyx
Anthurium atropurpurium
Aechmea moorei
Heliconia juruana

APPENDIX III (CONT.)

Grid 2A, 2B, 2C, Pit 2A, Pit 2B, Arb 2

Habitat: *Franco Arcilloso*

Tall trees:
Brosimum utile
Brosimum alicastrum
Caryocar glabrum
Guatteria elata
Eschweilera coriacea

Smaller trees:
Protium spruceanum
Tetrastylidium peruvianum
Rinorea lindeniana

Shrubs:
Lepidocarium tenue

Palms:
Geonoma tessmannii

Lianas:
Schlegelia cauliflora
Gurania rhizantha
Dioclea virgata

Herbaceous:
Piper bellidifolium
Geophila macropoda
Clavija longifolia

Grid 3A, Pit 3

Habitat: Wetter *varillal*

Tall trees:
Pouteria guianensis
Inga ruiziana
Virola elongata

Smaller trees:
Macrolobium macrocalyx
Licania heteromorpha
Pterocarpus rohrii

APPENDIX III (CONT.)

Shrubs:
Ryania speciosa
Potalia amara

Palms:
Bactris hirta
Oenocarpus mapora

Lianas:
Adenocalymna impressum
Anemopaegma floridum
Martinella obovata
Memora cladotricha
Paragonia pyramidata

Herbaceous:
Piper serpens
Calathea altissima
Faramea capillepis
Anthurium atropurpureum

Grid 3B

Habitat: Drier *varillal* (no tall trees)

Dominant trees:
Dicymbe uaiparuensis
Haploclathra paniculata
Parkia multijuga
Ternstroemia klugiana
Tabebuia incana
Dendropanax umbellatus
Tovomita brasiliensis
Psychotria racemosa
Picramnia magnifolia

Shrubs:
Drymonia coccinea
Monstera sp.
Cybianthus minotiflorus

Palms:
Bactris sp.

APPENDIX III (CONT.)

Lianas:
Doliocarpus dentatus
Curarea tecunarum
Dilkea sp.
Securidaca longifolia

Herbaceous:
Hamelia patens
Piper reticulatum

Bromeliads:
Anthurium clavijerum
Aechmea moori
Pitcairnia sp.

Grid 3C

Habitat: Drier *varillal*

Tall trees:
Aspidosperma spruceanum
Pouteria torta
Micrandra elata

Smaller trees:
Oxandra euneura
Tachigali melinonii
Mabea nitida

Shrubs:
Garcinia sp.
Psychotria sp.
Neea macrophylla

Palms:
Bactris sp.

Lianas:
Odontadenia macrantha
Dilkea sp.

Herbaceous:
Piper sp.
Anthurium sp.

APPENDIX III (CONT.)

Arb 3

Habitat: Transitional *varillal*

Tall trees:
Hymenolobium nitidum
Ocotea sp.
Tachigali formicarum

Smaller trees:
Iryanthera polynura
Chrysophyllum manaosense
Oenocarpus bataua

Shrubs:
Commelina diffusa
Guzmania sp.
Urera baccifera

Palms:
Lepidocaryum tenue
Astrocaryum chambira

Lianas:
Dioscorea iquitoensis
Doliocarpus dentatus
Smilax gilva

Herbaceous:
Rauwolfia macranthra
Brunfelsia grandiflora
Dulacia inopiflora

Grid 4A, 4B, Pit 4

Habitat: *Monte alto* grading to *varillal*

Tall trees:
Aspidosperma schultesii
Tetrameranthus pachycarpus
Tapirira guianensis

Smaller trees:
Lissocarpa stenocarpa
Dendrobangia multinervia
Oxandra euneura

APPENDIX III (CONT.)

Shrubs:
Piper loretoanum
Psychotria brachybotrya
Aegiphila cuneata

Palms:
Astrocaryum macrocalyx
Socratea exorrhiza
Geonoma interrupta

Lianas:
Strychnos asperula
Bauhinia guianensis
Philodendron solimoesense
Passiflora auriculata

Herbaceous plants:
none

Grid 5A, 5B, Pit 5

Habitat: selectively cut forest. Grid 5A is most similar to Grid 3A as it was originally wet *varillal*. Grid 5B and Pit 5 are most similar to Grid 6 as more trees were selectively cut.

Tall trees:
Parkia nitida
Ladenbergia magnifolia
Inga oersteniana
Buchenavia macrophylla
Parkia igneiflora
Hymenaea oblongifolia

Smaller trees:
Micropholis egensis
Chrysophyllum sanguinolentum
Matayba macrocarpa
Ficus insipida
Vochysia braceliniae
Sapium marmierii

Shrubs:
Psychotria racemosa
Tovomita spruceana
Miconia symplectocaulos
Vernonia patens
Palicourea nigricans

APPENDIX III (CONT.)

Palms:
Iriartella stenocarpa
Scheelea cephalotes
Oenocarpus mapora
Euterpe precatoria

Lianas:
Marcgravia longifolia
Norantea guianensis
Paullinia alata
Manettia divaricata
Acacia paraensis

Herbaceous:
Piper sp.
Citronella melliodora
Vernonia patens
Isertia hypoleuca
Solanum kioniotrichum

Grid 6, Pit 6, Arb 4

Habitat: secondary growth of 15 years

Tall trees:
Cecropia ficifolia
Cecropia sciadophylla
Apeiba membranacea
Iryanthera macrophylla
Virola multinervia
Eschweilera tessmannii

Smaller trees:
Inga thibaudiana
Cecropia membranacea
Miconia pilgeriana
Nealchornea yapurensis
Mollia gracilis

Shrubs:
Casearia pitumba
Croton palanostigma
Trymatococcus amazonicus
Heliconia hirsuta
Maieta guianensis

APPENDIX III (CONT.)

Palms:
Astrocaryum macrocalyx
Socratea exorrhiza
Iriartella setigera

Lianas:
Tynanthus panurensis
Uncaria tomentosa
Desmoncus longifolius
Davilla nitida
Uncaria guianensis
Mascagnia sinemariensis

Herbaceous plants:
Asplenium cuneatum
Clidemia pilosa
Lindernia crustacea
Centropogon cornutus
Tournefortia bicolor
Leandra nanayensis

Grid 7, Pit 7

Habitat: secondary growth of 6–7 years

Common plants:
Saccharum officinarum
Vismia angusta
Trema micrantha
Cecropia ficifolia
Myrcia sylvatica
Acacia sp.
Costus scaber
Piper sp.
Lantana camara

Grid 8, Pit 8

Habitat: secondary growth of 4 years

Common plants:
Pueraria phaseoloides–vine
Ochroma pyramidale–small tree

APPENDIX III (CONT.)

Grid O-1

Habitat: secondary growth of 6 and 15 years
- Cut everything down in NE corner after first trapping period

Cut trees:
Cavanillesia umbellata
Apuleia leiocarpa
Pseudolmedia laevigata

Smaller trees:
Cercropia sciadophylla
Pourouma guianensis
Tetrathylacium macrophyllum

Lianas:
Acacia sp.

Herbaceous plants:
Heliconia stricta
Costus arabicus
Psychotria macrophylla

Grid O-2

Habitat: secondary growth of 3 and 10 years

Trees:
Inga pruriens
Miconia poeppigii
Isertia hypoglauca
Ochroma pyramidale

Shrubs:
Casearia pitumba
Leonia glycicarpa
Siparuna guianensis

Vines:
Pueraria phaseoloides
Acacia sp.

Herbaceous plants:
Selaginella lechleri

APPENDIX IV

Trap effort and trap type for each grid, pitfall trapline, arboreal transect and line transect at Allpahuayo and Otorongo.

Grid/Line Number	Trap type	Trap nights
Grid 1A	Victor	2000
	Sherman	2000
	Tomahawk	2000
		Total = 6000
Grid 1B	Victor	1000
	Sherman	1000
	Tomahawk	1000
		Total = 3000
Grid 1C	Tomahawk	4508
Grid 2A	Victor	2000
	Sherman	2000
	Tomahawk	2000
		Total = 6000
Grid 2B	Victor	2300
	Sherman	2300
	Tomahawk	2300
		Total = 6900
Grid 2C	Victor	4900
Grid 3A	Victor	2000
	Sherman	2000
	Tomahawk	2000
		Total = 6000
Grid 3B	Victor	2000
	Sherman	2000
	Tomahawk	2000
		Total = 6000
Grid 3C	Sherman	4312
Grid 4A	Victor	1000
	Sherman	1000
	Tomahawk	1000
		Total = 3000

APPENDIX IV (CONT.)

Grid/Line Number	Trap type	Trap nights
Grid 4B	Victor	1372
Grid 5A	Victor	2000
	Sherman	2000
	Tomahawk	2000
		Total = 6000
Grid 5B	Victor	1000
	Sherman	1000
	Tomahawk	1000
		Total = 3000
Grid 6	Victor	2000
	Sherman	2000
	Tomahawk	2000
		Total = 6000
Grid 7	Victor	2000
	Sherman	2000
	Tomahawk	2000
		Total = 6000
Grid 8	Victor	1000
	Sherman	1000
	Tomahawk	1000
		Total = 3000
Grid O–1	Sherman	1000
	Tomahawk	1000
		Total = 2000
Grid O–2	Sherman	1000
	Tomahawk	1000
		Total = 2000
Pit 1A	Pit	330
Pit 1B	Pit	55
Pit 2A	Pit	220
Pit 2B	Pit	220

APPENDIX IV (CONT.)

Grid/Line Number	Trap type	Trap nights
Pit 3	Pit	462
Pit 4	Pit	110
Pit 5	Pit	220
Pit 6	Pit	286
Pit 7	Pit	220
Pit 8	Pit	110
Pit Temp 4	Pit	110
Pit Temp 5	Pit	110
Pit Temp 8	Pit	77
Arb 1	Victor	750
	Sherman	375
	Tomahawk	375
	Victor–arboreal	750
	Sherman–arboreal	375
	Tomahawk–arboreal	375
		Total = 3000
Arb 2	Victor	750
	Sherman	375
	Tomahawk	375
	Victor–arboreal	750
	Sherman–arboreal	375
	Tomahawk–arboreal	375
		Total = 3000
Arb 3	Victor	750
	Sherman	375
	Tomahawk	375
	Victor–arboreal	750
	Sherman–arboreal	375
	Tomahawk–arboreal	375
		Total = 3000

APPENDIX IV (CONT.)

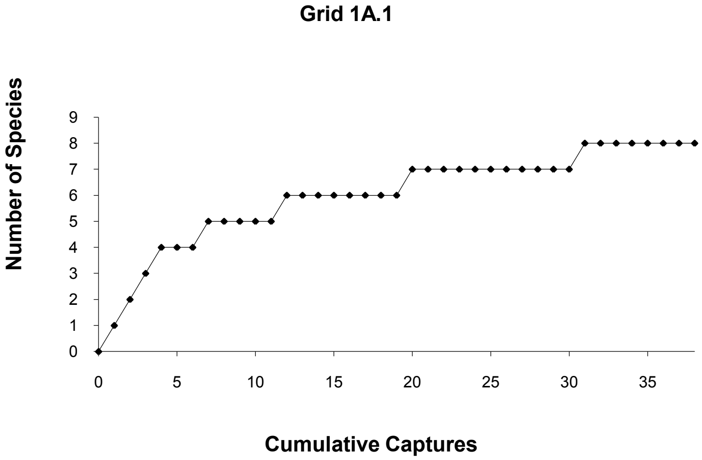
Grid/Line Number	Trap type	Trap nights
Arb 4	Victor	750
	Sherman	375
	Tomahawk	375
	Victor–arboreal	750
	Sherman–arboreal	375
	Tomahawk–arboreal	375
		Total = 3000
Line A–1	Victor	300
Line A–2	Victor	75
	Sherman	75
	Tomahawk	75
		Total = 225
Line A–3	Victor	300
Line 1	Victor	160
	Sherman	160
	Tomahawk	160
		Total = 480
Line 2	Victor	160
	Sherman	160
	Tomahawk	160
		Total = 480
Line 3	Victor	230
	Sherman	230
	Tomahawk	230
		Total = 690
Line 4	Victor	500
	Tomahawk–arboreal	100
		Total = 600
Line 5	Victor	500
	Tomahawk–arboreal	100
		Total = 600
Line 6	Victor	100
	Tomahawk	100
		Total = 200

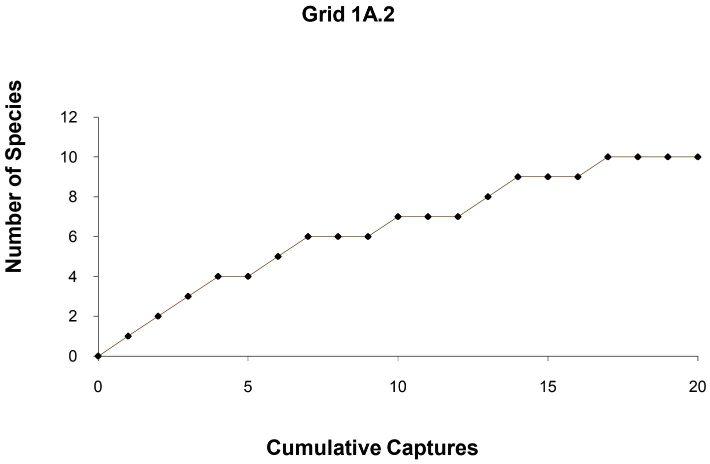
APPENDIX IV (CONT.)

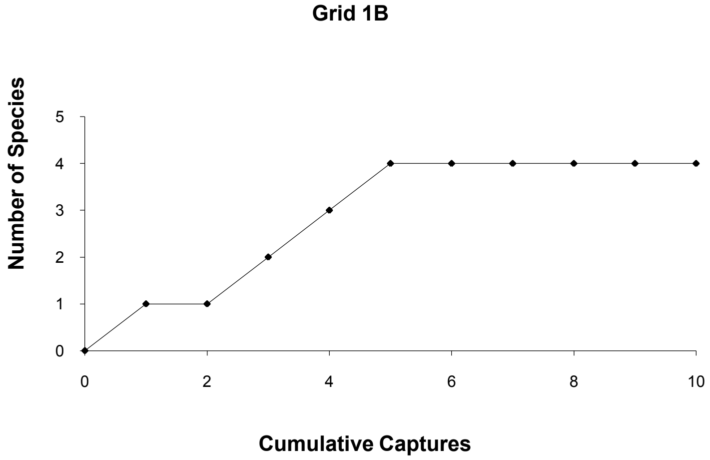
Grid/Line Number	Trap type	Trap nights
Line 7	Victor	500
	Tomahawk–arboreal	100
		Total = 600
Line 8	Victor	700
	Tomahawk–arboreal	140
		Total = 840
Line 9	Victor	700
	Tomahawk–arboreal	140
		Total = 840
	GRAND TOTAL	= 100,677

APPENDIX V

Species accumulation curves using cumulative captures for grids assessed for 10 days each time the grid was assessed. Each graph is labeled with the grid number and trapping period. For example, Grid 1A.2 represents the second time grid 1A was assessed. Note variable scales of axes.

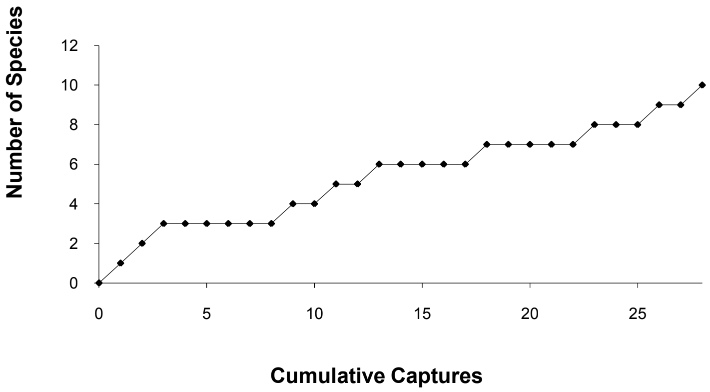




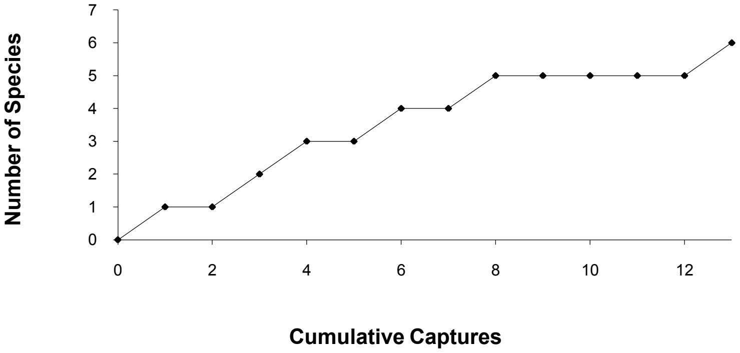


APPENDIX V (CONT.)

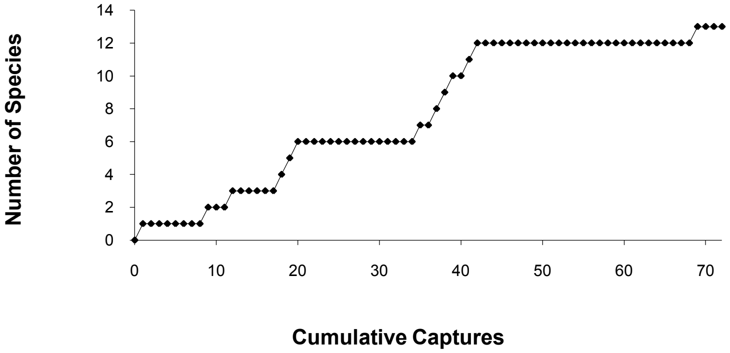
Grid 2A.1



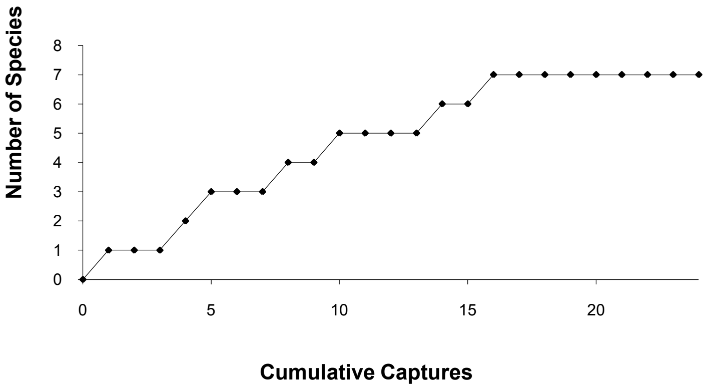
Grid 2A.2



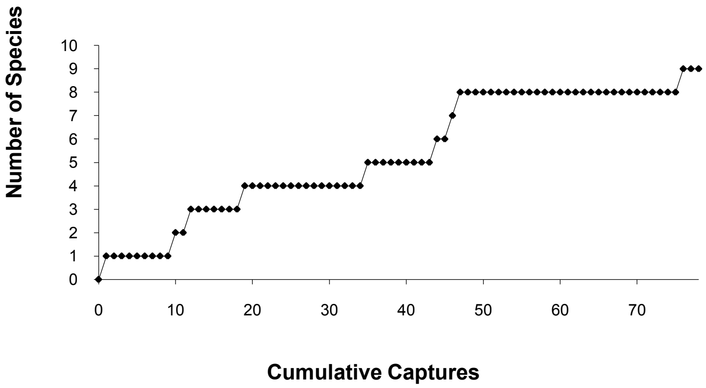
Grid 2B.1



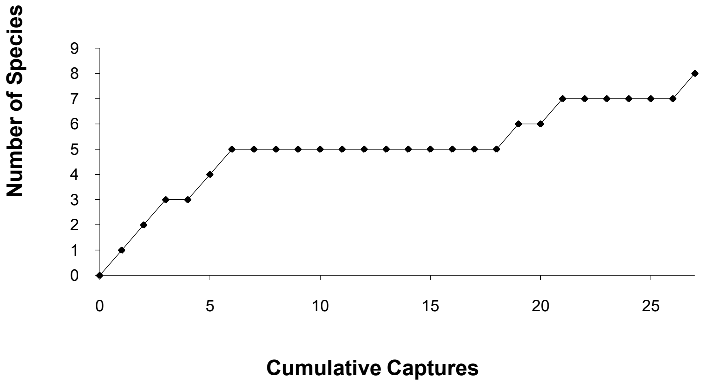
APPENDIX V (CONT.)



Grid 2B.2



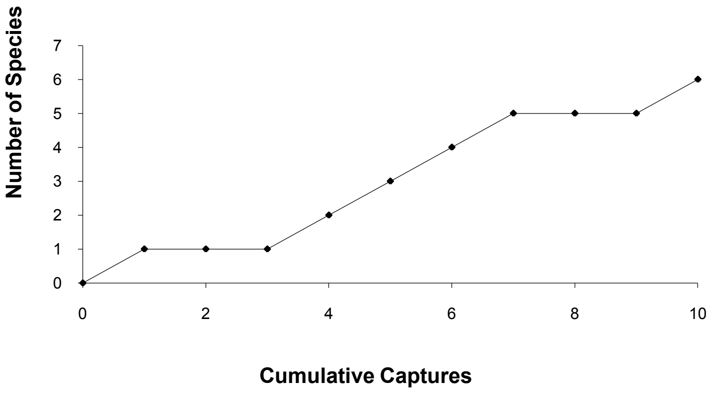
Grid 3A.1



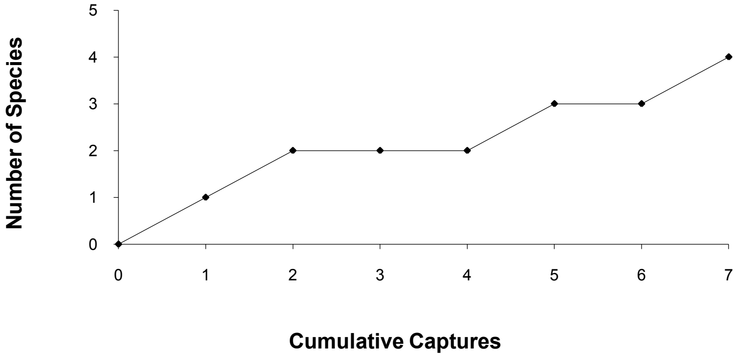
Grid 3A.2

APPENDIX V (CONT.)

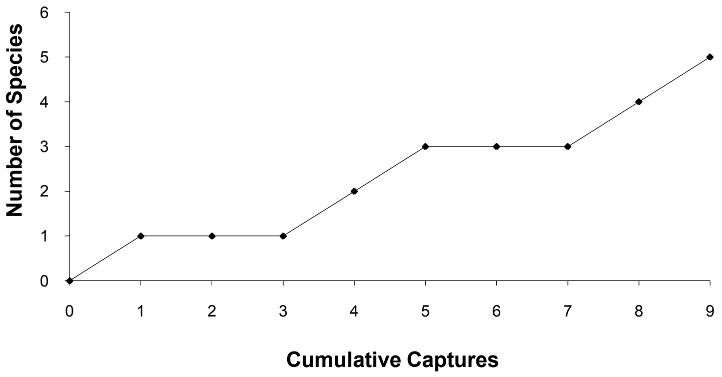
Grid 3B.1



Grid 3B.2

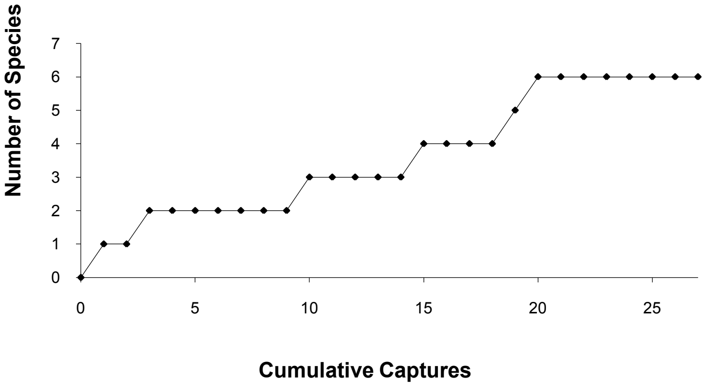


Grid 4A

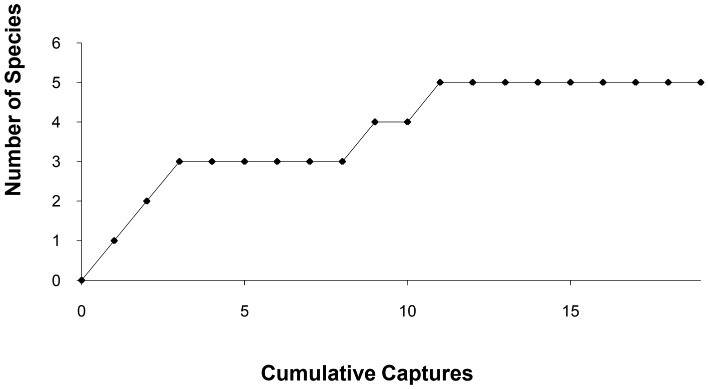


APPENDIX V (CONT.)

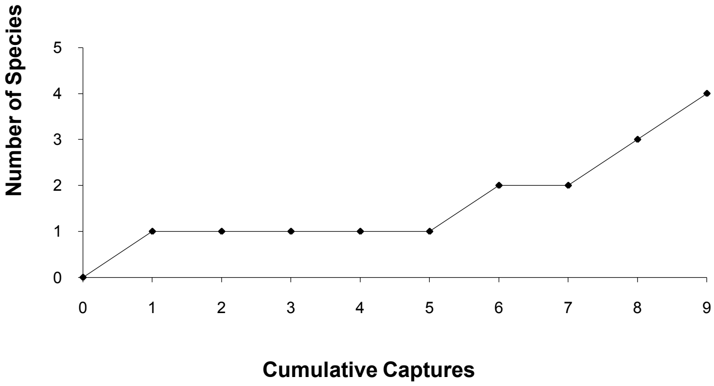
Grid 5A.1



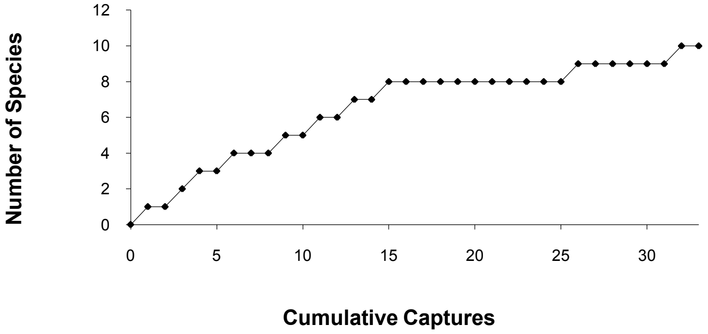
Grid 5A.2



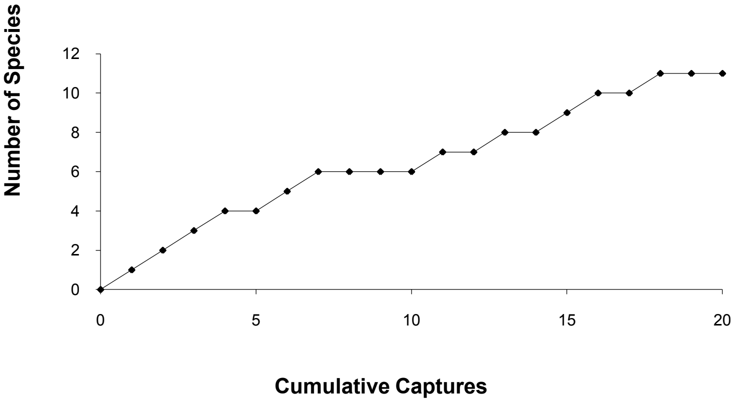
Grid 5B



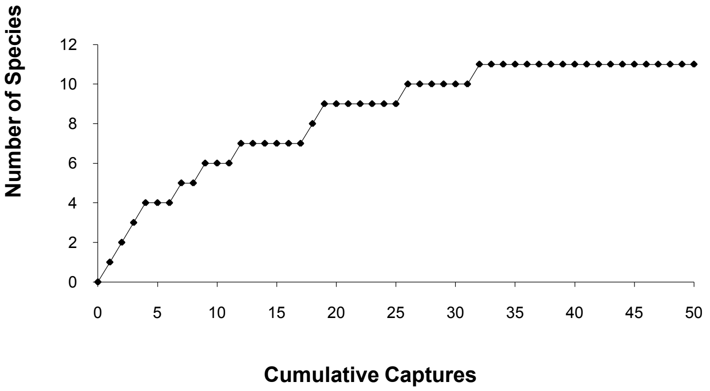
APPENDIX V (CONT.)



Grid 6.1



Grid 6.2



Grid 7.1

APPENDIX V (CONT.)