7

Mammals

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Costa Rica is one of the most biotically diverse countries on earth, with 4% of known terrestrial plant and animal species in only 0.04% of the world's land surface. The country's mammal fauna is equally diverse, with more than 207 species (4.8% of the world's 4629 species) in an area of 51,022 km². The majority of the world's mammal species and Monteverde's fauna are small (< 0.5 kg), nocturnal, and secretive. We know considerably less about most neotropical mammals and other vertebrates than we do about birds, which are more easily observed and communicate with sounds audible to humans. Although certain species of mammals have been studied in Costa Rica (Janzen 1983a, Timm 1994, Vaughan and Rodríguez 1994), and Monteverde is one of the best-known regions of the country biologically, there has been little work on the ecology, distribution, abundance, altitudinal zonation, systematic relationships, and biogeography of most mammals. Deforestation and other human disturbances have had a significant impact on the native mammals of the region; knowledge of Monteverde's mammals is vital to understand how habitat changes affect tropical montane mammals.

In this chapter, we provide an overview of the mammal fauna of the Monteverde area. We discuss the biology and abundance of some of the area's species, document how these are changing, and explore conservation issues. Most of the research on mammals at Monteverde has centered on bats or rodents, the two most diverse groups. Much of our knowledge of other species consists of isolated observations. We augment published reports with unpublished observations made by ourselves and colleagues. We also examined most of the Monteverde mammal specimens in museum collections to verify species identifications and to understand better their systematics, ecology, and distribution. We integrate this information into a list of the mammals that occur in the region, document their occurrence in each life zone, and estimate their overall abundance (see Appendix 10).

7.1. Methods

Although six major life zones are included in the Monteverde region (Holdridge 1967; see Table 3.1 and

Fig. 1.5), the mammal communities are more appropriately divided into four elevational/vegetational areas: (1) the Monteverde community and San Luis valley (1150–1500 m), premontane moist forest and premontane wet forest (just below the cloud forest) on the Pacific slope (distributional Zones 1 and 2); (2) cloud forest (1500–1800 m), lower montane wet forest and lower montane rain forest (Zones 3 and 4); (3) the Peñas Blancas valley (800–1400 m on the Atlantic slope), premontane rain forest and premontane rain forest/tropical wet forest transition belt (Zone 5 and part of Zone 6); and (4) Poco Sol (800 m), tropical wet forest (Zone 6 only).

In the text, we refer to the first area as the "community," the second as the "preserve," and the third and fourth as the "Peñas Blancas valley" (including Poco Sol). Life zones appear to extend to lower elevations in the upper San Luis valley, so that a site at 1150 m where many mammal observations have been made actually appears to be in premontane wet forest rather than premontane moist forest as predicted by elevational criteria. We use "region" for all four areas combined. We refer to mammals by their common names; scientific names are in Appendix 10.

To assess mammal community structure and population density, a trapping regime for sampling small terrestrial mammals and a netting regime for sampling bats are needed. Research collections that house significant holdings of mammals from the Monteverde region include the Chicago Field Museum, Los Angeles County Museum, University of Kansas Natural History Museum, the University of Michigan Museum of Zoology, the U.S. National Museum of Natural History, and the Universidad de Costa Rica. The majority of specimens from the 1960s and 1970s in collections with the locality "Monteverde" or "Monte Verde" are from the lower and mid-Monteverde community (1200–1450 m). The province is sometimes listed as Guanacaste, but all of these older specimens actually came from Puntarenas Province.

Another Costa Rican locality named Monteverde is in the Atlantic lowlands of Limón Province (10°06'N, 83°26'W). Early specimens of shrews reportedly from Monteverde in Limón Province gave a misleading impression of how widespread these shrews were (Woodman and Timm 1993).

7.2. Distribution, Species Richness, and Diversity

Monteverde's mammals include elements from both North and South America and endemic species. Central America hosts more than 275 species of mammals in 10 orders and 31 families; 18% of the species are

endemic. Costa Rica's mammals include more than 207 species in the same 10 orders and 31 families, with 9 species (4%) being endemic to the country. Monteverde's fauna of 121 species includes the same 10 orders and 25 families, with 2 species endemic to the region (2%; see Appendix 10). Both endemic species, a shrew and a harvest mouse, are of North American origin. The mammal fauna of the Monteverde region includes 6 species of marsupials, 3 shrews, at least 58 bats, 3 primates, 7 xenarthrans (edentates), 2 rabbits, 1 pocket gopher, 3 squirrels, 1 spiny pocket mouse, at least 15 long-tailed rats and mice (family Muridae), 1 porcupine, 1 paca, 1 agouti, 2 canids, 5 mustelids, 4 procyonids, 6 cats, 2 peccaries, 2 deer, and 1 tapir (Appendix 10). More species will undoubtedly be found, especially bats. The list includes several additions and corrections to the previous lists of the fauna of the region (Wilson 1983, Hayes et al. 1989), and new distributional information.

Two species that have been locally extirpated, the Giant Anteater and the White-lipped Peccary, were apparently hunted out in the 1940s. Two other species, the Mountain Lion and the Jaguar, are rare. Although Mountain Lions are rare in the region, they may be as abundant now as they have ever been (Fig. 7.1). Mountain Lions are primarily a species of more open areas, especially where White-tailed Deer

Figure 7.1. Mountain Lion (*Felis concolor*). Photograph by Richard K. LaVal.

(Fig. 7.2) are common. Jaguars, however, are exceedingly rare throughout the region but are present in the Peñas Blancas valley.

The majority of small mammals at lower elevations (below 1300 m on the Pacific slope and below 1000 m on the Caribbean slope) are widespread species, typical of neotropical lowland forests. The species of higher elevations (above 1500 m) are also typical of high elevations in other highlands of Costa Rica. In general, lowland species tend to be broadly distributed, whereas high-elevation species often have limited distributions, and many are endemic. Most Costa Rican endemic mammals are species of middle to high elevations. The mammal faunas of Costa Rica's three main mountain ranges (Tilarán, Central, and Talamanca cordilleras) are similar, although all three have some species that are endemic.

7.3. Research on Mammals in Monteverde

Scientific study on the mammals of the region first began in the mid-1960s, conducted by researchers associated with the field courses sponsored by the Organization for Tropical Studies (OTS). The first published accounts of mammals from Monteverde were in 1968. From the 1970s to the mid-1990s, publications and theses on four categories of subjects appeared on mammals in Monteverde: systematics and distribution, community structure and reproductive ecology, mammal-plant interactions, and mammal-insect interactions.

7.3.1. Systematics and Distributions

Studies on systematics, distributions, and natural history are the building blocks for conservation. For example, the discovery and description of the Golden Toad helped call attention to and conserve the biologically unique Monteverde Cloud Forest Preserve (MCFP; see Savage, "Discovery of the Golden Toad," p. 171). Papers on systematic relationships among species and geographic distributions are especially important for poorly known regions such as the Monteverde region because they identify the species present in an area, delineate species' distributions, and clarify relationships between closely related species.

Participants in the courses sponsored by the Council on International Educational Exchange and the Education Abroad Program (University of California) have carried out research projects focusing on mammals. These include 22 projects on bats (15 of which dealt with feeding behavior), 9 on rodents, 1 on Two-toed Sloths, and 1 on White-faced Capuchin monkeys. Researchers and residents have made observations which, although anecdotal, add to our knowledge of the mammals of Monteverde (see Timm and LaVal, "Observations on Monteverde's Mammals," p. 235).

Starrett and Casebeer (1968) reported on a single Fringe-lipped Bat caught along the Río Guacimal, which was only the second known specimen of this bat from the country; it is now known as a widely distributed species. Later that year, Hooper (1968) reported a sight record of the Water Mouse, a poorly known animal. Since then, 47 reports have been published on Monteverde's mammals as of 1998.

The order of mammals that has received the most study in Monteverde is Chiroptera (bats), which is unusual, as bats are generally among the least known mammal groups. Early surveys reported 24 species of bats (LaVal and Fitch 1977). LaVal (1973) reported specimens of the bat *Myotis nigricans* from the region in his systematic revision of the genus *Myotis* in Central and South America. Distribution records and in-

Figure 7.2. White-tailed Deer (*Odocoileus virginianus*). Photograph by Barbara L. Clauson.

formation on reproduction for seven other rare species of bats were added: *Hylonycteris underwoodi* (Fig. 7.3) and *Anoura cultrata* (nectar feeders); *Enchisthenes hartii*, *Platyrrhinus vittatus*, and *Sturnira mordax* (frugivores); and *Myotis oxyotus* and *Myotis riparius* (aerial insectivores; LaVal 1977). A checklist of mammals from several OTS sites, including Monteverde, provided the first comprehensive appraisal of mammal distributions in the area. This checklist included 71 species for the Monteverde region, and listed another 11 species as "expected to occur" in the region (Wilson 1983). Dinerstein (1983) reported that he encountered 35 species of bats in Monteverde. The first Costa Rican records of the Doubtful Oak Bat and Tacarcuna Bat were from Monteverde (Dinerstein 1985). Alston's Brown Mouse was studied by E. Hooper and colleagues (Hill and Hooper 1971, Hooper 1972, 1975, Carleton et al. 1975, Hooper and Carleton 1976). This mouse is almost wholly diurnal, with the greatest activity taking place in the morning (0700–1100 hr). It feeds predominantly on insects. Vocalizations contain both sonic and ultrasonic components. Adult mice have a repertoire of squeaks of various intensities and a long (10 sec), sustained call that has been termed a song. The songs carry well in

Figure 7.3. Underwood's Long-tongued Bat (*Hylonycteris underwoodi*). Photograph by Barbara L. Clauson.

the field and some are audible to the human ear. The Brown Mouse is one of four species of singing mice in Monteverde (see Langtimm, "Singing Mice," p. 236).

Small-eared shrews are extremely abundant but seldom seen in the Monteverde area (Woodman 1992, Woodman and Timm 1993). Blackish Small-eared Shrews occur in a wide array of habitats from 870 to 1800 m. Two other species of small-eared shrews occur at higher elevations in the Monteverde region, and one is being described as a new species by N. Woodman and R. Timm.

In a revision of the pygmy rice mice of the genus *Oligoryzomys*, Carleton and Musser (1995) reported that two species (*O. fulvescens* and *O. vegetus*) occur at Monteverde, which is one of the few localities where the two species are sympatric. The only reported species in this genus in Costa Rica was *O. fulvescens*. However, *O. vegetus* (Fig. 7.4), which was previously known only from Panama, has now been captured in the Monteverde community, in the MCFP, and on adjacent Cerro Amigos. In the Monteverde area, *O. vegetus* ranges in elevation from 1400 to 1760 m. *Oligoryzomys fulvescens* occurs only at lower elevations in the community (1400 m), and in the Guanacaste and Caribbean lowlands.

Other studies that include specimens from Monteverde are concerned with the taxonomy of shrews (Choate 1970) and opossums (Gardner 1973), phylogenetic relationships of rodents (Carleton 1980, Steppan 1995), taxonomy of deer mice (Huckaby 1980), biogeography of rodents (McPherson 1985, 1986), distribution of pocket gophers (Hafner and Hafner 1987), systematics of water mice (Voss 1988), ecology and distribution of bats and rodents (Timm et al. 1989), systematics of spiny pocket mice (Rogers 1989, 1990), and distributions of rodents and bats (Reid and Langtimm 1993).

Reid (1997) provided an extremely useful, beautifully illustrated guide to the mammals of Central America. Much of this work was based on her studies of living and preserved specimens of mammals from Monteverde. Emmons (1997) also provides a well-illustrated field guide to the neotropical mammals; her emphasis, however, is on species found below 1500 m. Another guide (Timm and LaVal 1998), an illustrated key to the Costa Rican bats, is designed for use in the field and has up-to-date diagnostic characters and taxonomy designed for students, wildlife managers, and the lay public.

7.3.2. Community Structure and Reproductive Ecology

Most mammals reproduce seasonally. The ultimate cause is generally seasonal variation in food availability mediated by ambient temperature or rainfall.

Figure 7.4. Pygmy Rice Mouse (*Oligoryzomys vegetus*). Photograph by Barbara L. Clauson and Robert M. Timm.

A study of tropical bat faunas compared the structure, movements, and reproductive patterns of the diverse bat communities in Monteverde, La Selva (tropical wet forest), and La Pacífica (tropical dry forest; LaVal and Fitch 1977). The highest species diversity of bats was at La Selva. Much of this diversity is from insectivorous bats, both foliage-gleaners and aerial feeders. The three locations were similar in species diversity of nectar- and pollen-feeding bats, and in frugivorous species, which were common at all three sites. Although most tropical bats breed seasonally, bats in the tropical dry forest, with its clearly defined wet and dry seasons, have the briefest and most distinctly delimited reproductive periods. An extended reproductive season was typical for bats in the lowland tropical wet forest. Bats of the premontane forests of the Monteverde region were intermediate (LaVal and Fitch 1977).

Tropical bats are important in dispersing the seeds of a wide array of tropical shrubs, trees, epiphytes, and vines. Reproductive activity of fruit bats in Monteverde coincides with seasonal peaks in fruit abundance (Dinerstein 1983, 1986). Many of the bat-dispersed plants have two seasonal fruiting peaks per year. The first corresponds to the dry season/wet season transition, the second to late wet season. Fruit-eating bats must consume considerable amounts of fruit; for example, *Artibeus toltecus* eats twice its weight in fruit per night without weight gain (Fig. 7.5). Fruits eaten by Monteverde bats are high in water content (> 80% fresh weight), soluble carbohydrates, and proteins and are higher in nitrogen than many tropical and temperate fruits eaten by birds but are low in lipids. Forty species of plants are consumed by the seven most common species of fruit bats. The diet of fruit-feeding bats is almost exclusively fruits;

Variation in photoperiod (daylength) is often the proximate cue used to trigger or suppress reproduction. Studies on mammal community structure and reproductive ecology in Monteverde, and most other studies of neotropical mammals, are restricted to bats and rodents.

Figure 7.5. Leaf tent of the Lowland Fruit-eating Bat (*Artibeus toltecus*) in the Monteverde Cloud Forest Preserve.

they consume very few insects. This contrasts with nectar-feeding bats, which often consume insects, presumably taken in flowers.

An 18-month study of the population dynamics of individually marked Naked-footed Mice (Fig. 7.6) showed that they ate both arthropods and fruits, and that arthropod consumption was highest in the early wet season, especially in breeding females (Anderson 1982; see Anderson, "Reproduction and Dynamics of Deer Mice, p. 238"). Naked-footed Mice readily consumed all animal material presented to them. Reproduction was seasonal, with a peak in the wet season (May–July), when 100% of the females bred. Adult females may have two (rarely three) litters per year, and they seldom breed in the season of their birth. The average litter size for 14 captive-born litters was 2.8 young (see Anderson, "Reproduction and Dynamics of Deer Mice," p. 238). Survivorship can be remarkably high in these high-elevation mice; 75% of the Naked-footed Mice that were individually marked in 1986 were captured in the same area the next year (R. Timm, unpubl. data). Naked-footed Mice reproduce primarily during the rainy season in Monteverde. During the dry season, females ovulate routinely and often mate; however, implantation usually does not occur and no pregnancies proceed beyond mid-gestation (Heideman and Bronson 1992, 1993, Bronson and Heideman 1993). In the laboratory, Naked-footed Mice did not respond to variations in photoperiod, but patterns similar to wild mice could be obtained with mild food restriction. Naked-footed Mice have an opportunistic breeding strategy, which forces them to reproduce seasonally (Heideman and Bronson 1993).

Many Monteverde mammals use both the canopy and the forest floor (see Langtimm, "Arboreal Mammals," p. 239). A variety of high-elevation rodents are behaviorally and morphologically adapted for climbing (Langtimm 1992). Monteverde's arboreal mammal community is more complex than those of both the Caribbean and Guanacaste lowlands.

7.3.3. Mammal-Plant Interactions

Research on mammal-plant interactions has addressed the pollination of a high-elevation flower (*Blakea chlorantha*) by rodents (Lumer 1980, 1983, Lumer and Schoer 1986; see Lumer, "Reproductive Biology of *Blakea* and *Topobea*," p. 273). The pollination system in *B. chlorantha*, a hemiephytic shrub of the cloud forest, is of interest because its odd-shaped flower (it is bell-shaped rather than open as in other species of *Blakea*) opens at night, points downward, and produces a sucrose-rich nectar. Lumer observed two species of rodents covered with pollen and feeding on the flowers of *Blakea* at night. Her initial conclusion was that the rodents were the obligate pollinators of *Blakea*. However, insects (e.g., beetles, hawk moths), hummingbirds, and tanagers have also been observed feeding on the nectar and pollen of *Blakea*, which suggests that the pollination system might be opportunistic or generalized (see Langtimm and Unnasch, "Mice, Birds, and Pollination," p. 241). The photograph Lumer published of a mouse (1980, p. 515) identified as *Oryzomys devius* (=*albigularis*; Tome's Rice Rat) feeding at a flower is more likely the Chiriquí Harvest Mouse, a common species in the habitat where the photograph was taken. Further observations would resolve this question.

The phenomenon of tent-making by bats was previously only known from lowland species. The smaller, high-elevation *Artibeus* of Monteverde also cut leaves to create diurnal roosts (Timm 1987, Timm and Clauson 1990). In the preserve, the fruit-eating bat *Artibeus toltecus* cuts the basal and side veins and interconnected tissues of broad leaves such as philodendrons, causing the sides and tip of the leaf to droop down (Fig. 7.5). The roosting bats hang from the midribs of the leaves and are protected by their tents from predators and the elements (Timm 1987).

Figure 7.6. Naked-footed Mouse (*Peromyscus nudipes*). Photograph by Barbara L. Clauson.

7.3.4. Mammal-Insect and Mammal-Bird Interactions

An insect-vertebrate interaction, that of rove beetles of the tribe Amblyopinini (Coleoptera: Staphylinidae) and their mammal hosts, was discovered in Monteverde (see Sec. 4.3). Amblyopinine beetles have a unique obligate association with mammals. Most of the 40,000 described species of staphylinids are free-living predators (Ashe and Timm 1987a,b), but all known species of amblyopinines are found attached to the fur of mammalian hosts or in the hosts' nests. Until recently, amblyopinines were believed to be obligate, blood-feeding ectoparasites (Fig. 7.7). Central American *Amblyopinus* have a mutualistic relationship with their hosts, not a parasitic one. In Monteverde, Naked-footed Mice (Fig. 7.6) and Chiriquí Harvest Mice (Fig. 7.8) are the primary hosts for *Amblyopinus tiptoni;* Tome's Rice Rat is the primary host for *A. emarginatus* (Figs. 7.9, 7.10). Rather than feeding on blood as was previously supposed, amblyopinine beetles at Monteverde feed on blood-sucking arthropods (fleas, mites, and ticks) and thus have a mutualistic relationship with their rodent hosts. These large, active beetles are host specific; their densities increase with increasing elevations, as do those of fleas. The beetles attach themselves firmly to their rodent hosts by grasping a small cluster of hairs with their mandibles at night while the host is actively moving around (Fig. 7.10). During the day, while the host occupies a nest, the beetles hunt for parasitic arthropods in the nest or on the host's body (Ashe and Timm 1987a,b, 1995, Timm and Ashe 1988).

In Monteverde, flocks of Brown Jays were observed successfully defending nests from Variegated Squirrels, White-faced Capuchins, and domestic cats (Lawton and Lawton 1980). The location of jay nests— high and in isolated trees—and the aggressive defense provided by these large, cooperatively nesting birds may account for low levels of nest predation (see Williams and Lawton, "Brown Jays"). Five jay nests located in trees whose crowns touched other trees were destroyed by nocturnal predators (Lawton and Lawton 1980).

Margays and Long-tailed Weasels have been observed preying on nesting Resplendent Quetzals (*Pharomachrus mocinno*). Quetzals have been observed vigorously defending their nests against squirrels (Wheelwright 1983). Mexican Mouse Opossums are common nest predators of House Wrens (*Troglodytes aedon*) in Monteverde (Young 1996). Artificial wren nest boxes placed along fence rows and along woodlot edges sustained high predation by mouse opossums; those placed on isolated trees or posts had lower predation. Predation on wren nests by all predators was unrelated to brood size. A White-nosed Coati was also observed to prey on wren nests (B. Young, pers. obs.).

7.4. Migration

Many species of birds migrate latitudinally, and as many as half of Costa Rican bird species are likely to be altitudinal migrants (Stiles 1988; see Chap. 6, Birds). Altitudinal migration has also been docu-

Figure 7.7. Steve Ashe (left) and Robert Timm (right) carrying out research on the mouse-beetle relationship in Monteverde. Photograph by Barbara L. Clauson.
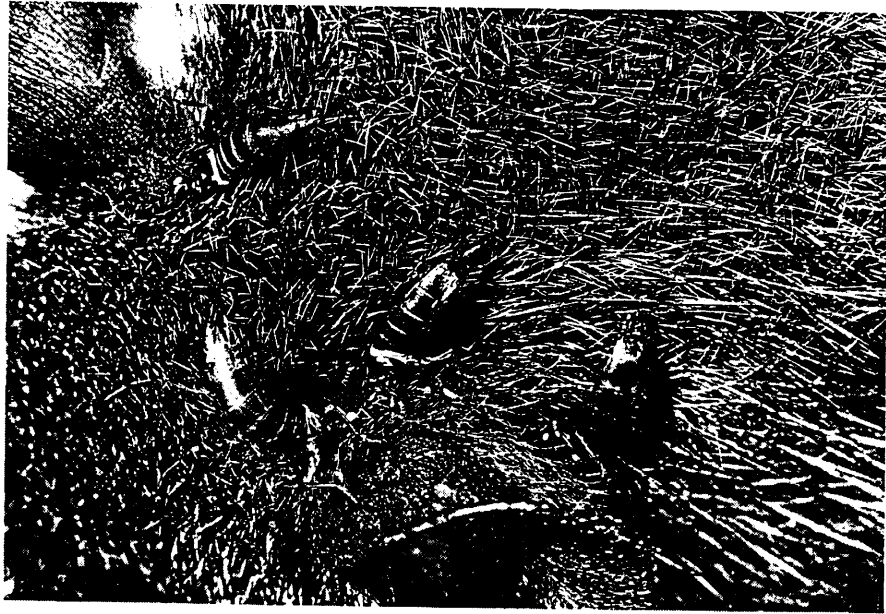
Figure 7.8. (top left) Chiriquí Harvest Mouse (Reithrodontomys creper). Photograph by Barbara L. Clauson and Robert M. Timm. Figure 7.9. (top right) Tome's Rice Rat (Oryzomys albigularis) with mutualistic rove beetles. Photograph by Barbara L. Clauson. Figure 7.10. (above) Amblyopinine beetle behind ear of Tome's Rice Rat (Oryzomys albigularis). Photograph by Barbara L. Clauson.

mented in butterflies (see Sec. 4.4). Only recently has seasonal altitudinal migration been considered significant in tropical mammals. Seasonal migration is well documented for mammals in the north temperate zone but not in the tropics. Long-term studies on bats demonstrate that some species show strong seasonal variation in abundance in Monteverde (LaVal 1977), which we interpret as migrations into and out of the area. Of the 58 species of bats known from the region (based on more than 7500 captures over 15 years), 10 are captured in sufficient numbers that seasonal abundances can be examined, and of these, five species (*Artibeus lituratus, A. toltecus, Carollia brevicauda, Sturnira lilium*—all frugivores—and *Hylonycteris underwoodi* (a nectivore; Fig. 7.3) show a strong seasonal pattern in abundance. Two of the five species (*A. lituratus* and *S. lilium*) are absent from Monteverde for most of the year and common from September through November. *Artibeus lituratus* (Fig. 7.11) and *S. lilium* are primarily lowland species; it is likely they migrate up the Tilarán highlands during part of the year to take advantage of seasonally available fruits. A third species (*H. underwoodi*) is common only from May through October. The remain-

ing two species are present year-round but with strong seasonal peaks in abundance.

The simplest explanation for species with strongly seasonal captures is that they migrate altitudinally to track food resources. Increased capture rates of these species corresponds with the seasonal increases in abundance of preferred foods in Monteverde. Because both adult males and females are captured in high numbers, we do not believe that these data represent seasonal demographic patterns (e.g., a flush of young entering the population) or behavioral changes (e.g., lactating females restricting their movements).

Alternative explanations to seasonal migration exist. It could be that these five species are present in Monteverde year-round in equal numbers but are flying or foraging in spaces where no netting activity was carried out. This explanation could apply to *Artibeus lituratus*, a fig specialist that feeds in the canopy but is frequently captured in ground-level nets. *Hylonycteris underwoodi*, a nectarivore, might be feeding only on flowers in the canopy during part of the year. However, *Sturnira lilium, Carollia brevicauda*, and *Artibeus toltecus* feed on the fruits of early successional shrubs and are easily netted, so it is unlikely that they were present but not captured. These species of bats could have moved from the area where netting was carried out without moving any significant elevational distance. However, knowledge of phenological sequences of flowering and fruit ripening (W. Haber, pers. comm.; see Chap. 3, Plants) leads to the prediction that bats moving in search of food would necessarily fly up- or downhill; a short downhill flight from Monteverde can result in an elevational change of 500–1000 m, often in less than 1 km. Future research should include mark-recapture studies, radiotelemetry to follow individuals, and studies of flowering and fruiting of bat-pollinated and bat-dispersed fruits along elevational gradients. We also suspect that Baird's Tapirs and White-lipped Peccaries are seasonal altitudinal migrants, but few data on these species exist (see Lawton, "Baird's Tapir," pp. 242–243).

7.5. Changes in Altitudinal Limits of Life Zones as Suggested by Bats

Many climatologists believe that global warming is taking effect. Widespread deforestation and El Niño events may also affect Costa Rica's climate. In general, short-term impacts on Monteverde's climate are making it drier and less predictable. During an El Niño year, Monteverde experiences dry periods in the rainy season, which could especially affect species that are at or near their climatic or vegetational tolerance lim-

Figure 7.11. Big Fruit-eating Bat (*Artibeus lituratus*). Photograph by Barbara L. Clauson.

its (see Chap. 5, Amphibians and Reptiles). Weather records from Monteverde for the last decade suggest that we are in a period of reduced rainfall and slightly warmer temperatures (although in 1995, 1996, and 1998, rainfall was higher than normal). Changes in mammal altitudinal limits, distributions, and abundance at Monteverde may be correlated with climate changes.

Bats were intensively sampled in Monteverde in 1973 and 1981 (Dinerstein 1983, 1986, R. LaVal, unpubl. data). Subsequently, LaVal has mist-netted bats in Monteverde on 10–20 nights each year. Several lowland species of bats (*Micronycteris hirsuta*, *M. sylvestris*, *Mimon cozumelae*, and *Phyllostomus discolor*, which are gleaners, and *Vampyrodes caraccioli*, a frugivore) were captured in Monteverde for the first time during the last 4 years. *Sturnira lilium*, also a lowland species, was very rare in 1973 (2 captures), more common in 1981 (38 captures), and seasonally abundant in 1995. *Desmodus rotundus*, the Common Vampire Bat (Fig. 7.12), was not encountered in 1973. In 1981, nine were captured, a rate that has continued. Large numbers of cattle were introduced to this dairy farming region in the 1950s, but vampire bats did not arrive for at least 25 years, even though cattle, pigs, dogs, and chickens had existed in nearby areas even in the 1940s. The trend of lowland species moving up into Monteverde has also been observed in birds, reptiles, and amphibians (see Chaps. 5 and 6). These patterns support the climatic change hypothesis for these and other lowland tropical species (see Timm and LaVal, "Observations," p. 235). Long-term weather and population data for a variety of species are needed to assess the climatic factors that affect mammals in Monteverde.

7.6. Historical Use and Change in Abundance of Mammals

The San Luis area (ca. 1100 m) was first settled in 1915 (see Timm, "Prehistoric Cultures and Inhabitants," p. 408); the Monteverde–Cerro Plano area was first settled in 1929. During the 1930s, settlers moved into the San Luis and Santa Elena areas (ca. 1250 m) on the Pacific slope and into San Carlos on the Caribbean slope. Families moved into the Monteverde community area during the 1930s and 1940s (see Chap. 11, Agriculture). The original settlers cleared considerable forest for lumber, pastures, and homesites, creating fragmented patches of forest that exist today as a complex mosaic of primary and secondary habitats, including open pastures. By the late 1940s, appreciable deforestation had taken place at lower and mid-elevations.

Early settlers relied heavily on local wildlife (especially mammals and larger birds) as a source of protein for themselves and their dogs. Overhunting played a role in the decline or extirpation of several species. Guans and chachalacas were so heavily hunted in the 1950s and early 1960s that they became rare in Monteverde, although their populations have increased with protection. Common food items of early Monteverde residents were Black-handed Spider Monkeys, Pacas, Brocket Deer, and Baird's Tapirs. At lower elevations, White-tailed Deer and White-lipped Peccaries were also hunted for meat. Agoutis were generally fed to dogs. Locally obtained animals were many families' primary source of meat. However, many hunters shot everything they saw, and if an animal was not a preferred meat species, they simply left it. At least two species, the Giant Anteater and

Figure 7.12. Common Vampire Bat (*Desmodus rotundus*). Photograph by Barbara L. Clauson.

White-lipped Peccary, were extirpated from the region within a few decades of settlement.

To assess the historical changes in mammal distributions and abundances of the region, we interviewed long-term residents about wildlife species.

Common Vampire Bat Vampire bats have been present in San Luis since at least the 1930s. However, they were absent from Monteverde before the late 1970s. By 1980, they had arrived but were uncommon in the Monteverde community.

Black-handed Spider Monkey The earliest colonists of the region regularly used spider monkeys for meat, for medicinal purposes, and as pets. Spider monkeys, Mantled Howler Monkeys, and White-faced Capuchins were abundant in the San Luis Valley in the 1940s and were hunted for food (M. Leitón, pers. comm.). Spider monkeys were preferred for meat and were still common in what is now the lower Monteverde community, including Bajo del Tigre, in the 1940s (I. Arguedas and M. Vargas, pers. comm.). Spider monkeys were observed by J. and D. Campbell just below the preserve in the 1950s, and they were seen in the lower parts of the Monteverde community in the early 1950s. One troop still exists in El Valle; the Peñas Blancas population is also recovering. R. Lawton saw 20 spider monkeys near the television towers in 1993. R. LaVal saw two individuals above the dairy plant in 1995.

Mantled Howler Monkey Howler monkeys have always been common above 1400 m in the community, but apparently there were few below that elevation in the 1950s.

White-faced Capuchin M. Rockwell remembers the White-faced Capuchin as the only primate found in the Monteverde community, Cerro Plano, and Santa Elena in the 1950s. The yellow fever epidemic that swept through human and primate populations of Costa Rica and much of southern Central America in the early 1950s decimated primate populations in Monteverde (Fishkind and Sussman 1987, Timm et al. 1989, Stoner 1993).

Giant Anteater Giant Anteaters were present in the San Luis region in the 1940s (M. Leitón, pers. comm.). There have been no sightings of Giant Anteaters in the region for several decades; the species is assumed to be extirpated from the region.

Forest Rabbit Rabbits, once common in the area, are now rare.

Cherrie's Pocket Gopher Pocket gophers were common in the community at least into the late 1970s but have since disappeared. Gardeners at higher elevations of the community suffered considerable loss of garden produce to pocket gophers in the 1960s and 1970s.

Variegated Squirrel This large, colorful, and easily identified squirrel was uncommon in the Monte-

verde area when the Quakers first arrived; they are now locally abundant. Variegated Squirrels are common in edge and disturbed habitats, but they are rarely observed in primary forest.

Coyote Within the past 25 years, Coyotes have expanded their range through Costa Rica and are found in Panama. They are abundant throughout Costa Rica's Pacific lowlands, the high elevations of the Talamanca Mountains, and the Chiriquí Highlands of Panama. The original Costa Rican distribution of the Coyote prior to the Spanish colonial period was northernmost Guanacaste (Vaughan 1983, Monge-Nájera and Morera Brenes 1987). Coyotes are associated with human disturbance; it is unlikely that they occurred in pristine tropical montane forests. Coyotes first appeared in San Luis during the early 1970s. They became common in Monteverde in the 1980s, when there was a pack within 200 m of R. LaVal's house, and they could be heard regularly in the lower parts of the Monteverde community. Coyotes are currently uncommon throughout the region.

Gray Fox Foxes have always been common in the area.

Striped Hog-nosed Skunk Skunks fluctuate in abundance but are much less abundant than they were before the 1980s.

Tayra J. and D. Campbell informed us that tayras were seen in groups in their forest before 1960, whereas now only individuals are observed.

Grison Grisons had never been observed in the community until 1996.

Southern River Otter Otters have always been present but never abundant in the rivers.

White-nosed Coati (Fig. 7.13) Coatis were more abundant in the past, with many large groups. R. LaVal

Figure 7.13. White-nosed Coati (*Nasua narica*). Photograph by Robert M. Timm.

saw a large group in 1995 above the dairy plant and another in 1997 near the Estación Biológica.

Ocelot Ocelots were very common in the 1950s and 1960s, and the population appears stable. In the early years of settlement of the region, ocelots were known to attack chickens.

Jaguar Jaguars were relatively common throughout the region through the late 1950s. They preyed on livestock and were shot whenever possible. Jaguars were common in the San Luis region in the 1940s, but most were shot; the last two killed were in the early 1960s. M. Leitón believes a small population exists in the upper reaches of the San Luis valley, which includes parts of the Children's Rain Forest and the preserve.

Collared Peccary In the 1930s and 1940s, Collared Peccaries were common in the San Luis valley and in Bajo del Tigre. They were uncommon to rare in the community when the Quakers first arrived in the region, and were found only as low as the wetter forests below the preserve. However, since the 1970s, peccaries have become more common and are gradually expanding down the mountain.

White-lipped Peccary White-lipped Peccaries have never been seen in the Monteverde community, according to the older residents interviewed. However, they were common in San Luis in the 1930s and 1940s (M. Leitón, pers. comm.).

White-tailed Deer Deer were not originally present in the Monteverde community. They were common in San Luis until they were hunted out in the 1940s. Since 1990, deer have expanded their range and are now seen throughout the community.

Baird's Tapir Historically, Baird's Tapir was widely distributed throughout all forested habitats in Costa Rica. Tapirs are the largest native terrestrial mammals in the country (150–300 kg), and their meat was highly prized. Populations of tapirs have been greatly reduced throughout the country due to overhunting and habitat destruction. Tapirs were largely eliminated from the higher elevations in the Monteverde area, but they have become relatively common with nearly complete protection from hunting. The distinctive tracks of tapirs can be seen along many of the trails in the preserve (see Lawton, "Baird's Tapir," p. 242).

Tapirs were present in forests above Santa Elena in the 1950s. The population was centered around El Valle, but hunting on the area's margins gradually reduced their numbers (W. Guindon, pers. comm.). Tapirs existed in the San Luis Valley in the 1930s and 1940s, but they disappeared due to overhunting (M. Leitón, pers. comm.). Tapirs were less common in the Monteverde community in the 1940s but were abundant in what is now the preserve. J. and D. Camp-bell observed tapir tracks below the preserve in the 1950s but have seen none there since then.

With protection, tapir abundance has increased; they are common in the preserve. Areas lacking tapirs for many years are gradually being reoccupied, based on increased sightings of tracks of females with young. Adult tapirs range widely, as do females with older calves. However, females tend to stay in specific areas for parturition and when accompanied by young calves. These are remote from human habitations and activities and are densely vegetated. In the 1960s, 20–30 tapirs were killed per year in the region (W. Guindon, pers. comm.).

Throughout their ranges, all species of tapirs are considered endangered (Terwilliger 1978). The tapir population in Monteverde is small (30–50 individuals; C. Guindon, unpubl. data). The present protected area could support an estimated 115 tapirs. However, a population size of about 185 individuals would be needed to have a high likelihood population viability over even the short term. With 185 individuals, the effective population size would be only 50 because many individuals do not breed in a population of large, widely dispersed herbivores, and selective killing of females with young by hunters may result in a skewed sex ratio (C. Guindon, pers. comm.). For long-term survival, an effective population size of 200 would be needed, requiring a protected area vastly larger than the existing one. Three factors threaten the continued survival of tapirs in the region: (1) the population is isolated, probably permanently, (2) both the present and potential population sizes are low enough to create concern about inbreeding and loss of heterozygosity, and (3) approximately one tapir each year is killed illegally by hunters.

7.7. Conservation of Monteverde Mammals

Families in most rural areas in Costa Rica and the neotropics have traditionally relied heavily on wildlife as a source of protein. In Monteverde, Baird's Tapirs, Pacas, Agoutis, and White-lipped and Collared Peccaries were highly prized meats. Tapirs, White-lipped Peccaries, White-tailed Deer, Pacas, and Black-harded Spider Monkeys are now generally uncommon in Costa Rica, even where adequate habitat remains, except in some national parks. White-lipped Peccaries have been extirpated from much of the country. In the Monteverde region, populations of large mammals were decimated outside of protected areas. Populations of many small and medium-sized mammals have decreased due to widespread habitat fragmen-

tation and hunting. A few generalists (opossums, coyotes, foxes, coatis, raccoons, and some rodents) have adjusted to human disturbances and have even increased in abundance. However, specialists (Giant and Silky Anteaters and bats such as the large predaceous phyllostomatines) have been unable to adapt to human disturbance and habitat fragmentation and are now extremely rare. Elimination of keystone mammal species may have far-reaching impacts on the forest ecosystem. The elimination of White-lipped Peccaries, for example, may alter the structure of Monteverde's forests because peccaries are both major seed dispersers and seed predators.

In terms of mammals, Monteverde is the best-known high-elevation site in Central America, with at least 121 documented species. Mammalogists have worked in the region since the 1960s. As of 1998 nearly 50 publications have been based on Monteverde's mammals, and museum collections hold numerous specimens from the area, but the ecology of its mammals remains poorly documented. Rapid destruction of natural habitats requires expanded conservation efforts to document and conserve the biota.

Deforestation in Costa Rica and elsewhere in Central America began with the earliest human inhabitants (see Timm, "Prehistoric Cultures and Inhabitants," p. 408). Human populations have increased rapidly in the past several decades, resulting in extensive deforestation throughout Central America. Between 70% and 80% of Costa Rica's forests have been cut since the 1960s, among the highest rates in Central America. During the 1980s, the rate of deforestation in Costa Rica averaged 60,000 ha per year; during the early 1990s, forests were disappearing at a mean rate of 20,000 ha per year (Environment Min-

istry, unpubl. data). Costa Rica's current human population growth rate of 2.4% will result in a doubling of its population in less than 30 years. Existing wildlands must be effectively protected, new protected areas be established, and resources be managed for both human use and mammal diversity.

OBSERVATIONS ON MONTEVERDE'S MAMMALS
Robert M. Timm & Richard K. LaVal

ests of Mexican Mouse Opossums have been observed on several occasions in Monteverde.

N. Nadkarni observed a mouse opossum nest high (20 m) in the canopy, hanging from a liana. The nest was a large ball of moss approximately 0.5 m in diameter. P. Heideman observed a mouse opossum nest approximately 3 m off the ground in a dead *Cecropia* leaf. In both cases, single mouse opossums were in the nest. R. and M. LaVal have observed nests in bunches of ripening bananas. A pair of mouse opossums they kept in captivity for a year

would kill and eat large insects and eat a variety of fruits. The captive pair built a nest from plant leaves and stems and slept curled up together within the nest.

Blackish Small-eared Shrews and other shrew species are commonly found dead along trails in habitats where they are common in Monteverde. Mammalian predators such as Gray Foxes, Coyotes, and the smaller cats (including house cats) commonly attack shrews. However, once the shrew is tasted, it is discarded. Most of the specimens of shrews from Monte-

verde in museum collections were found dead, presumably discarded by predators.

Alfaro's Pygmy Squirrels were observed by R. LaVal, R. Timm, and W. Alverson feeding on the sap of the tree *Quararibea costaricensis* in the preserve. These diminutive squirrels are often seen hanging by all four feet on the trunks of trees, chewing at the bark. The squirrels neatly peel the bark off in large patches with their incisors. The squirrels then feed on the sap exuded by the tree. These feeding patches can be extensive (0.5 × 0.5 m), representing an impressive amount of work for a squirrel whose head and body length is only 125–150 mm. Removal of the bark and cambium likely damages the trees.

White-faced Capuchins have been observed feeding at bromeliads on several occasions. N. Nadkarni described them actively ripping bromeliads apart and apparently consuming insects from the cups at their centers. R. LaVal has observed these monkeys chewing on the base of each bromeliad leaf prior to discarding it. The chewing marks can be seen on the dropped leaves.

Hispid Cotton Rats were first taken by collectors at Monteverde in the 1980s. The distribution and abundance of cotton rats in the region merit further study. In the midwestern United States, cotton rat populations fluctuate (often dramatically) from year to year, with local climatic conditions having a great influence on population sizes. A similar phenomenon may occur in the Monteverde region.

Olingos frequently feed during daylight hours at the hummingbird feeders at the preserve headquarters. They climb down the wire holding the feeders and consume the rich sugar water. Bats also feed on sugar water at these feeders at night.

SINGING MICE
Catherine A. Langtimm

ommunication by long-distance vocalizations is common among birds, insects, frogs, and large mammals but relatively rare among mice and rats. In Monteverde, four species of mice make calls that can be heard by humans. Although the functions of these vocalizations are obscure, the calls and songs are loud and appear to communicate information to other individuals that are relatively distant from the mouse making the call.

Alton's Brown Mouse
(*Scotinomys teguina*)

Alston's Brown Mouse (Fig. 7.14). is a small mouse (9–16 g) that trills like a cicada and chirps like a bird. It forages on the ground, eating primarily insects. In contrast to most mice, it is active in the early morning and late afternoon (Hooper and Carleton 1976, Langtimm 1992) instead of at night. Its trill was first described by Hooper and Carleton (1976), who labeled it a "song," which they characterized as similar in duration and complexity to the songs of birds and insects. The mice readily sing in captivity and are especially vocal at dusk. When a mouse sings, it rises on its haunches into a bipedal stance, holds its forefeet before it, throws back its head with the snout pointed upward, and opens its mouth. The sound emanates from the back of the throat; the exact mechanism of sound production is unknown.

The song consists of a series of short loud bursts in rapid succession. At the beginning, the pulses are rapid. As the song progresses, loudness increases and both the pulse and interpulse intervals lengthen into clearly enunciated individual beats. Decreasing cadence and increasing loudness of the pulses give a characteristic signature to the song which distinguishes it from the vocalizations of other species. The songs of individuals in Monteverde were 5.8–8.6 sec long with 72–96 pulses per song (C. Langtimm, unpubl. data). The average duration of a song and the average number of pulses per song vary among populations of *S. teguina* at other sites in Central America (Hooper and Carleton 1976). Sonograms reveal that each pulse consists of a broad range of frequencies starting above 30 kHz to as low as 14 kHz (Hooper and Carleton 1976, C. Langtimm, unpubl. data). The majority of the sound is in the ultrasonic range and only when the pulse sweeps below about 15–20 kHz is it audible to the human ear.

Males sing more frequently than females in captivity, suggesting that the song may function in maintaining territories (Hooper and Carleton 1976). A similar pattern resulted in trials in which a male was held in captivity with a female (Metz 1990, C. Langtimm, unpubl. data). When a pair was separated, singing increased for both sexes, but the female usually sang more frequently, suggesting that mate contact may also be an important function.
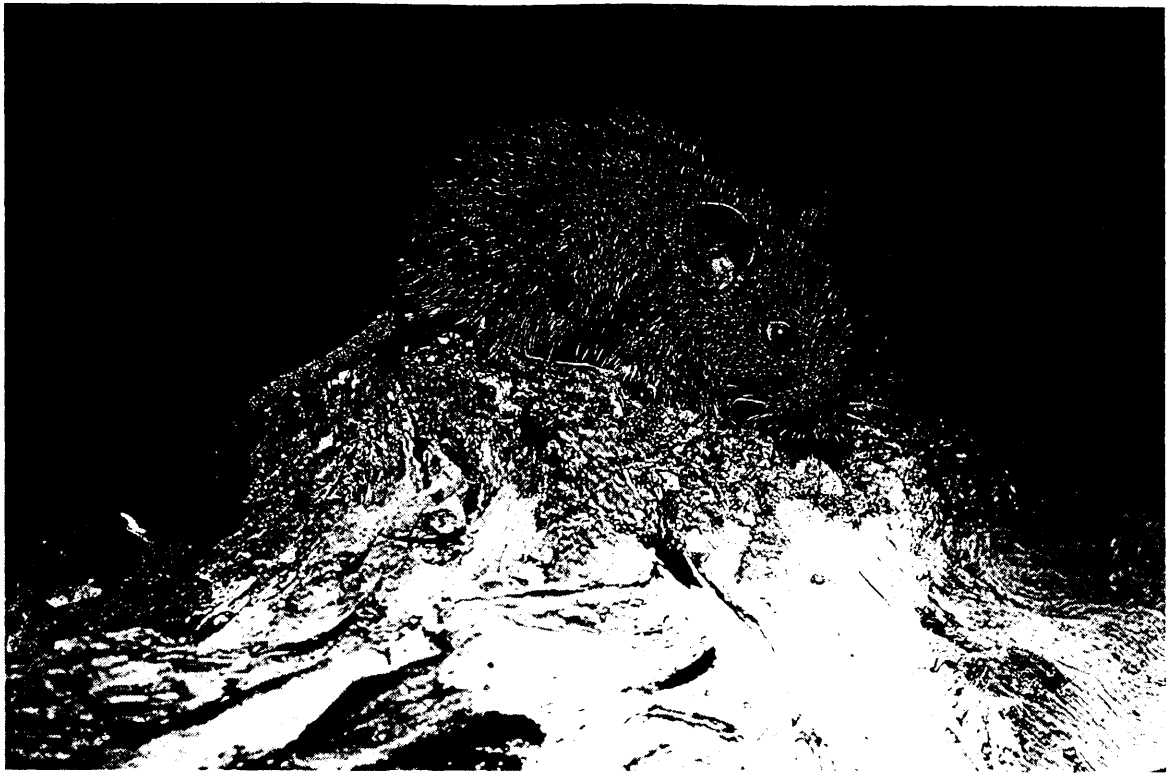
Figure 7.14. Alston's Brown Mouse (*Scotinomys teguina*). Photograph by Richard K. LaVal.

Slender Harvest Mouse
(*Reithrodontomys gracilis*)

The Slender Harvest Mouse is small (8–14 g) and produces a two-note high-pitched whistle. The call is commonly heard in the forest and pastures at dusk and after dark (Uyehara 1990, C. Langtimm, unpubl. data). The species is extremely arboreal, spending a large portion of its time climbing in plants of pastures and the forest understory and in the crowns of canopy trees (Langtimm 1992). They do not call readily in captivity. Sonograms of calls I recorded from the understory and in the canopy (22 m above the forest floor) show that the dominant frequency of a note ranges between 9 and 10.5 kHz. The second note immediately follows the first and is slightly lower in frequency. Single note calls are also commonly heard. The duration of the entire two-note call ranges from only 0.85 to 0.99 sec (C. Langtimm, unpubl. data). The function of the call is unknown.

Reithrodontomys sp.

This undescribed mouse species makes one-, two-, and three-note calls. It is larger than the Slender Harvest Mouse (ca. 18 g) but similarly appears to be par-

tially arboreal, based on the capture of two individuals in traps located 2–3 m above the forest floor onto branches (C. Langtimm and F. Reid, unpubl. data). The call is similar to that of the Slender Harvest Mouse but differs in that the dominant frequency is 1 kHz lower and three-note calls are common; no more than two successive notes have been heard for the Slender Harvest Mouse (C. Langtimm and F. Reid, unpubl. data). The call is similar to that described for *R. fulvescens* in Louisiana by Svihla (1930): "a tiny, clear high-pitched bugling sound." The occurrence of long-distance vocalizations in two other species of *Reithrodontomys* in Monteverde and the similarity in the structure of their calls suggest that long-distance auditory communication may be common in the genus.

Sumichrast's Vesper Rat
(*Nyctomys sumichrasti*)

Sumichrast's Vesper Rat is the largest of the vocalizing mice in Monteverde (38–67 g). The species is arboreal (Genoways and Jones 1972, Langtimm 1992). It eats primarily fruits and seeds and is active at night. Calls consisted of single chirps repeated at variable time intervals. The peak frequency of a chirp (near 3.5

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kHz) is lower than that of the calls of the other vocalizing species.

Vocalizations of the Vesper Rat during close social interactions in captivity were first noted by Birkenholz and Wirtz (1965). Long-distance vocalizations are an important aspect of their behavior (C. Langtimm, unpubl. data). After sunset on two occasions 1 month apart, I heard loud chirps in the rafters at opposite ends of the house, where I saw two adult Vesper Rats. As they climbed toward each other, they called repeatedly and loudly. On contact, the vocalizations continued but were softer in volume. One individual mounted the other and attempted copulation. Similar vocalizations and behavior (without attempted copulations) have been observed in the wild in Panama (F. Greenwell, pers. comm.), suggesting that Vesper Rats living in the maze of branches and tree trunks of their habitat use vocalizations to locate and navigate toward prospective mates.

REPRODUCTION AND DYNAMICS OF DEER MICE
Stephen D. Anderson

he Naked-footed or Deer Mouse of Monteverde (*Peromyscus nudipes*, family Muridae; see Fig. 7.6) is of ecological interest because it is the most abundant rodent locally and because other species in this well-studied genus are widespread and abundant throughout North America, inviting comparative studies. I carried out mark-recapture and captive studies of *Peromyscus* in Monteverde for 18 months (1978–1980), to describe reproduction and dynamics in this population (Anderson 1982). The study involved three trapping grids at different elevations (1540 m, 1420 m, and 1400 m) and around 13,500 trap-nights.

Population density varied with season and site. It ranged from 8 to 22 individuals per hectare and was lowest in May–July, the beginning of the breeding season. Breeding was correlated with rainfall (and presumably food abundance). The percentage of adult females visibly pregnant or lactating fell to zero during the dry season (January–March), rose to 100% during the early wet season (May–July), fell in August, and had a secondary peak in September–October. Consistent with the breeding pattern, the percentage of immatures in the population was 30–40% in September–December, zero in February–May, and increased in July–August. Survival of field-born juveniles to capturable age was estimated at 55–75%.

"Neutral-arena" encounter experiments and observations in a large outdoor enclosure indicated that overt aggression is low in *P. nudipes*, particularly in adult-juvenile confrontations. Home range size was estimated at 0.2 ha, based on recapture data, and varied little with gender, site, year, or season. Negative dispersion (nonoverlapping home ranges) was observed within "old" (i.e., established adult resident) males and within old females. In contrast, dispersion for old males with respect to old females was positive or random, and that for new animals (with respect to old males, old females, or other new animals) was generally random. These results suggest a system of density regulation based on mutual recognition and avoidance between same-sex adults rather than aggressive adult-juvenile interactions as reported for some temperate mice species.

The average litter size (from 14 captive born litters) was 2.8 ± 0.7 individuals. The average neonate weight was 3.6 ± 0.4 g. Young mice attained 50% of adult weight by 35 days and 90% by 80 days of age. They had pinnae up at 5.6 days and dorsal fur at 10.4 days. Lower incisors erupted at 11.2 days, upper incisors erupted at 13.9 days, ears opened at 16.5 days, and eyes opened at 21 days. Weaning at around 25 days. Later developmental events took longer in field-caught animals than in captives, underscoring the danger of relying solely on data from captive litters. For field animals, molting began at 55 days and ended at 90 days, mature testis size in males was observed at 170 days, vaginal perforation in females at 90 days, and first conception at 175 days or longer. There was high variability in these events. Many juveniles, on first capture in the field, weighed 17–22 g, corresponding to an age of 25–36 days. Adult *P. nudipes* weighed 44–46 g. They ate a variety of plant and animal foods, particularly beetles, orthopterans, and moths. Arthropod consumption (estimated from fecal analysis) was highest in the early wet season and higher for breeding females than for males or immatures.

Most animals in this population probably have life spans between one and two years. Recapture data indicate that individual female *P. nudipes* breed two or three times per season, generally do not breed in the season of their birth, and produce a total of two

to six litters in their lifetime, which is far below their reproductive potential (Heideman and Bronson 1993).

In comparison to the widespread and well-studied temperate species *P. maniculatus* and *P. leucopus*, *P. nudipes* in Monteverde exhibits larger body size, slower growth rate, delayed sexual maturity, and lower reproductive effort, four characters that are strongly correlated with each other. *Peromyscus nudipes* also exhibit smaller litter size and less variability in home range size than do temperate species. For these traits, temperate and tropical *Peromyscus* fit the predictions of classic "*r* versus *K* selection" theory.

On the other hand, compared to *P. maniculatus* and *P. leucopus*, Monteverde deer mice exhibit lower breeding frequency, less aggression, and more random dispersion of "new" individuals. These observations are contrary to the predictions of r/K theory, which assumes that increased competition leads to increased aggression and territoriality. Finally, according to r/K theory, one would expect *P. nudipes* to exhibit higher density, reduced density fluctuation, aseasonal breeding, "type 1" or "type 2" survivorship curve, increased lifespan, reduced habitat vacancy, reduced year-to-year and site-to-site variability in density, higher ratio of neonate weight to adult weight, and greater age at weaning. However, the tropical and temperate species cannot be distinguished in terms of these characters. This may be explained by recognizing that environments (e.g., food availability, precipitation, temperature) in Monteverde are seasonal and/or unpredictable, much like those in temperate habitats.

ARBOREAL MAMMALS
Catherine A. Langtimm

ith a pair of binoculars, visitors to the Monteverde Cloud Forest Preserve can scan the treetops and observe differences in the flora and fauna between the forest floor and canopy. The change in species composition in epiphytes and birds among the vertical strata of the forest is dramatic. No less striking is the diversity of climbing mammals that inhabit the forest. Some arboreal species, such as monkeys, spend the majority of their time foraging in the trees, while other semi-arboreal species such as coatis spend time foraging on the ground and in the trees.

Larger mammals are the more conspicuous and better known of the climbing species. Mantled Howler Monkeys, White-faced Capuchins, Black-handed Spider Monkeys, Prehensile-tailed Porcupines, Tayras, coatis, Two-toed Sloths, and several species of squirrels (e.g., *Sciurus granatensis*) are often seen by daytime visitors to the forest. If one ventures out at night, eyeshine from kinkajous (Fig. 7.15), olingos, raccoons, coatis, and a diversity of marsupials from Mexican Mouse Opossum (*Marmosa mexicana*) to the Woolly Opossum is often reflected back from the light of a head lamp. The majority of these larger species belong to genera that are primarily tropical in distribution. The same or similar species occur at lowland tropical research stations such as La Selva and Barro Colorado Island.

A diverse community also exists of small mammals (primarily mice and rats) that forage in plants of the

Figure 7.15. Kinkajou (*Potos flavus*) foraging at night. Photograph by Richard K. LaVal.

understory and canopy. Because of their small size (10–250 g), nocturnal habits, and climbing nature, they are rarely seen. Live-trapping at different altitudinal elevations has revealed eight climbing species (Table 7.1). Most of these species belong to genera of the neotomine-peromyscines (family Muridae, subfamily Sigmodontinae), which are primarily temperate and North American in distribution (Carleton 1980). The species that range into Central America are characteristically found in cool high-elevation tropical forests.

How high individuals range within the trees in Monteverde is known for only a few species. The Vesper Rat and the Slender Harvest Mouse apparently forage throughout the vertical strata of leeward cloud forest. I have caught both species in live traps placed at varying heights, including 22 m above the ground in the crowns of canopy trees (Langtimm 1992). The Naked-footed Mouse, on the other hand, is semiarboreal and forages only at lower heights. It was never captured more than 3 m off the ground (Langtimm 1992). The remainder of the species in Table 7.1 have only been captured 2–4 m above the forest floor. Trapping in the higher strata of the forest, particularly in the canopy, has been limited, and more work is needed to define their vertical distribution. Studies thus far have identified two species of harvest mouse new to the area. One species is new to science (R. Timm, pers. comm.); the second (*R. gracilis*) was previously known only from low-elevation, dry, deciduous forests (Reid and Langtimm 1993). Trapping studies have found climbing mice to be diverse and abundant in Monteverde, but their importance in the ecosystem is poorly understood. Undoubtedly, they are important prey to vertebrate predators such as owls, snakes, and large mammals such as White-faced Capuchins or Tayras.

Table 7.1. Climbing mice and rats inhabiting the Monteverde cloud forest.

Species	Common name
Nyctomys sumichrasti	Vesper Rat
Tylomys watsoni	Watson's Climbing Rat
Ototylomys phyllotis	Big-eared Climbing Rat
Peromyscus nudipes	Naked-footed Mouse
Reithrodontomys creper	Chiriquí Harvest Mouse
Reithrodontomys gracilis	Slender Harvest Mouse
Reithrodontomys sp.	Harvest Mouse (undescribed species)
Oligoryzomys vegetus	Pygmy Rice Mouse

Mice are also important consumers of invertebrates, plants, and fungi. The inclusion of plant parts in their diets has implications for the reproductive success of plants. In January 1984, I observed a Vesper Rat foraging for 20 min in the crown of a fruiting understory shrub, *Psychotria gracilis* (Rubiaceae). Despite a strong northeast trade wind, it hung from its hind feet to reach fruit and then used its tail as a counterweight to maintain its balance on a branch as it sat on its haunches and manipulated fruit with its forefeet. It ate only the fruit pulp, discarding the seeds and the skin. The mouse may have assisted in dispersing seeds to a site away from the parent plant.

Arboreal mice may also act as seed predators, destroying the plant embryo and reducing seedling establishment. One individual of *Reithrodontomys gracilis* in captivity readily consumed mistletoe seeds collected from the feces of birds (Sargent 1995). If the Slender Harvest Mouse routinely feeds in the wild on mistletoe seeds after they have been dispersed, the species could significantly reduce the number of seeds that germinate. Arboreal seed predators such as rodents could be responsible for the 60% loss of dispersed mistletoe seeds documented in a study of *Phoradendron robustissium* in Monteverde (Sargent 1995; see Sargent "Mistletoes," pp. 81–82).

Mice also feed on plant nectar and could be plant pollinators. Lumer (1980) documented flower visitation by mice in a hemiepiphyte, *Blakea chlorantha*, which grows at higher elevations in the preserve. The plant produces nectar only at night; Lumer suggested that the principal pollinators are climbing mice. Although mice were commonly trapped in plants, fluorescent dye experiments indicated pollen transfer occurred only during the day when birds visit the flowers (see Langtimm and Unnasch, "Mice, Birds, and Pollination," p. 241). More research in needed on this pollination system.

Climbing mice may also act as dispersal agents for the spores of mycorrhizal fungi (Johnson 1996). Many tropical plants require a symbiotic association with fungi to increase the mineral uptake of their roots (Janos 1983). Rodents in temperate regions eat sporocarps and pass viable spores in their feces (Maser et al. 1978), and spore dispersal by rodents has been documented in one lowland tropical forest (Janos et al. 1995). This may also be the case in cloud forest and is supported by the results of one Organization for Tropical Studies field project conducted in Monteverde, which found mycorrhizal spores in the feces of four species of mice including the arboreal Slender Harvest Mouse (Bakarr 1990).

MICE, BIRDS, AND POLLINATION OF *BLAKEA CHLORANTHA*
Catherine A. Langtimm & Robert Unnasch

n Monteverde, Lumer (1980) documented flower visitation by rodents for the first time in any neotropical plant species. Based on the unusual floral shape and phenology of *Blakea chlorantha*, observations and photographs of rodent visitors, and pollen found in rodent stomachs, she proposed that the plant had evolved specific adaptations for pollination by climbing nocturnal rodents and that rodents were the principal pollinators for this species (see Lumer, "Reproductive Biology of *Blakea* and *Topobea*," pp. 273–276).

Pollination by nonflying mammals is relatively rare in the western hemisphere. Although flower visitation by primates (Janson et al. 1981), marsupials (Janson et al. 1981, Steiner 1981), and procyonids (Janson et al. 1981) has been documented in the neotropics, no study has demonstrated successful pollination. Data on pollen transfer and subsequent seed maturation as a result of exclusive visits by a potential pollinator are needed to document pollination unequivocally. To that end, we extended the research begun by Lumer by examining pollen transfer by nocturnal mice and by birds, another group of visitors we observed at flowers during the day.

To document pollen loads on flower visitors, we captured rodents and birds at the flowers and lightly rubbed cellophane tape across the throat and face of each animal to collect pollen. The pollen was placed on a microscope slide and examined under a compound microscope for the distinctive pollen of *Blakea*. To trap rodents, we tied Sherman live traps (1–2.5 m high) onto the branches of two adjacent *B. chlorantha* that were flowering. To eliminate the possibility that the mice were grooming away the pollen while confined in a trap, we spent one night checking the traps every hour and taking pollen samples. To capture birds, we set up mist nets adjacent to the blooming plants.

We tested for pollen transfer using a fluorescent dye technique. We applied a paste of fluorescent powder and water onto the pollen-producing anthers of open *Blakea* flowers. The paste dries to a fragile crust that is easily broken by flower visitors but not by wind. The powder readily adheres to the visitor and transfers to other flowers if the visitor contacts the sticky stigma. The dye is easily detected on flowers under a dissecting microscope illuminated with ultraviolet light. We looked for nocturnal pollen transfer on eight nights, applying the dye to 12 flowers each night and collecting untreated open flowers at dawn

the following day. To test for diurnal pollen transfer, we did similar trials on four days but applied the dye at dawn and collected flowers at dusk.

During nine nights of trapping within the crowns of *B. chlorantha*, we caught four species of rodents: Watson's Climbing Rat ($n = 1$), Naked-footed Mouse ($n = 1$), Pygmy Rice Mouse ($n = 2$), and Chiriquí Harvest Mouse ($n = 1$). Voucher specimens were deposited in the mammal collection of the U.S. National Museum of Natural History. The five individuals were trapped a total of 15 times in the crowns. No *Blakea* pollen was detected on the samples from any of these individuals, nor was fluorescent powder detected on any flower during the nocturnal dye experiment. However, 13% of the flowers collected during the diurnal dye experiment had powder adhering to the stigmas and the corolla of the flowers, indicating that pollen had been transferred from one flower to another during daylight hours.

During six hours of diurnal observations, we had 12 sightings of four species of birds feeding at *Blakea* flowers. The birds were apparently feeding on nectar remaining from the previous evening. There were two species of tanagers, Sooty-capped Bush-Tanager and Common Bush-Tanager; and two species of hummingbirds, Purple-throated Mountaingem and Violet Sabrewing. We observed one male mountain-gem defending a large *Blakea* in bloom. On two occasions, we captured three of these species in mist nets and found large amounts of *Blakea* pollen on the cellophane tape samples collected from their throats.

The results of our experiments did not confirm pollen transfer by climbing mice, but rather documented that birds visit the flowers of *B. chlorantha* and can transfer pollen between adjacent plants. The definitive experiments to document if these floral visitors succeed in transferring pollen that results in seed maturation are still lacking. The research thus far has focused on plants accessible to biologists from the ground. Many plants, however, inhabit the crowns of mid- to upper canopy trees. Langtimm (1992) documented vertical stratification of the rodent assemblage in the lower elevations of Monteverde, but the assemblage at the elevations where *B. chlorantha* is found is completely different. Information is lacking on the ecology, behavior, and vertical distribution of mice within the high-elevation forest. These interactions will be a rich field of future investigation for botanists and zoologists in Monteverde.

BAIRD'S TAPIR
Robert O. Lawton

he ancestral tapiroids were widespread in the vast broad-leaved forests that covered North America and Eurasia in the early Tertiary. By the mid-Eocene, around 55 million years ago, lineages leading to rhinos and tapirs had diverged, and by the Oligocene, tapirs were well established as a diverse group of forest browsers (Simpson 1945). More recent history has not treated tapirs as well. By the end of the Pliocene, the shrinkage of the mesic broad-leaved forests of the northern hemisphere had restricted tapirs to eastern North America and southeastern Asia. With the opening of the Central American land bridge 3 million years ago, tapirs colonized South America (Marshall et al. 1982), but in the megafaunal extinctions associated with human invasion of the New World about 12,000 years ago, tapirs were eliminated in eastern North America (Martin 1973). They persist in the tropical forests of Central and South America (Martin 1973), although all three neotropical species are threatened by hunting (Janzen 1983b, Bodmer 1988).

Tapirs are large (150–300 kg as adults), shy and secretive where hunted, but accepting of nonthreatening observers in protected areas (Terwilliger 1978). They browse on a broad but selective variety of plants in the forest understory and will stand on their hind legs and grope with their flexible proposces to reach favored forage (Terwilliger 1978, Janzen 1982). Little is known of population densities and patterns of land use. Tapirs live in small loose herds in which individuals forage and sleep alone but meet commonly at creeks, pools, and favored feeding areas. The lowland forest on Barro Colorado Island supported 0.5 individuals per kilometer (Terwilliger 1978).

Baird's Tapir (*Tapirus bairdii*, "danta" locally) undoubtedly roamed both slopes of the Cordillera de Tilarán in the recent past. In the 1930s, men from Guacimal hunted tapirs in what are now the communities of Cerro Plano and Monteverde (F. Arguedas, pers. comm.). Hunting and habitat destruction have now restricted tapirs to the least accessible parts of the Cordillera, the cloud forests of the crest, and the rugged Caribbean slopes. In 1987 and 1988, Wolf Guindon and I established a tapir-monitoring circuit around a high bowl on the crest of the Cordillera in an area of about 3 km². The bowl is bounded to the west by Cerros Amigo and Roble, to the north by Cerro Frio, and to the east by the drop into the Peñas Blancas

valley; it is an area of conspicuous tapir presence. Judging from track and trail patterns, it appeared that four to seven tapirs, including a mother and half-grown juvenile, were using the area. Foraging seemed concentrated in areas of lesser relief and away from the worst tangles of the swampy area in the center of the bowl.

What little we know of tapir foraging in the Cordillera de Tilarán comes from interpretation of the signs of browsing along tapir trails. In the presence of fresh tapir tracks and the absence of deer or peccary tracks, we assume that recent browsing was done by tapirs. From this type of evidence, tapirs feed on a broad variety of understory plants, including common herbaceous shrubs of the Acanthaceae (species of *Hansteinia*, *Justicia*, *Razisea*, and *Poikilacanthus*), woody and herbaceous Rubiaceae, palms, bamboos, and tree saplings. This concurs with other reports (Janzen 1982) but gives little perspective on how vegetation structure and composition influence tapirs' food choice and habitat use, or how tapirs influence vegetation.

In the study area, well-worn tapir trails descended from high ridges, crossed creeks, and surrounded a set of pools on Quebrada Danta, apparently used for bathing and defecation. With the first major winter storm in December, tapirs left the area, apparently descending a well-worn trail into the Peñas Blancas valley, and did not return until the end of the dry season. Reconnaisance throughout the Cordillera by Guindon suggests that tapir activity in the mountain range is concentrated in a limited number (10 or so) of favored sites. Such sites lie mostly above 1500 m along the crest of the Cordillera in areas of lesser relief such as the Brillante saddle and below 1200 m on the flanks of major valleys. The precipitous and landslide-scarred slopes in between are crossed by well-worn tapir trails following narrow ridgecrests but do not seem to be used often in foraging.

Conservation of the Cordillera's tapirs must be a priority. As a major forest browser, they may influence forest regeneration and composition (Janzen 1983b). As prey, they may influence the abundance and activity of the few jaguar remaining in the area. Better estimates of population size and a better picture of the patterns of land use are needed. Estimates of the Cordillera's current carrying capacity is about 100 tapirs (C. Guindon, unpubl. data). A herd of at least 200 would be required to avoid potentially

deleterious consequences of inbreeding over the next few centuries. On a more optimistic note, tapirs are raising young in the Cordillera and are returning to areas that had been deserted due to earlier hunting.

Given that a small group on Barro Colorado Island has survived for over 60 years, tapirs may persist in Monteverde despite their current limited population size.

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PREHISTORIC CULTURES AND INHABITANTS
Robert M. Timm

ecent archaeological, linguistic, and genetic information document that the modern Amerindian groups of Costa Rica are descendants of pre-Columbian groups that occupied the area for thousands of years, rather than transition cultures between the major groups of northern Central America and Mexico or of South America. Indigenous peoples inhabited the Monteverde region for millennia as documented by pottery shards found in the vicinity of Santa Elena, but we know little of their population density and impact on the local environment.

The first human inhabitants of Costa Rica were bands of hunters and gatherers who arrived in the area roughly between 12,000 and 8000 B.C. Archaeological evidence of workshops and artifacts have been recorded in the Turrialba valley, in Guanacaste, and from Lake Arenal. One of the earliest artifacts known, a Clovis-style point made from local quartz (chalcedony), is from Lake Arenal, dated at 10,000 B.C. The cultures inhabiting the mountains from Volcán Orosi to Monteverde were similar and distinct from those to the west in Guanacaste and to the east in the Atlantic lowlands. The region has been termed the Cordilleran cultural subarea (Sheets et al. 1991, Sheets 1994).

The combination of deposits of volcanic ash associated with the eruptions of Volcán Arenal (Melson 1984, 1994), radiocarbon dates from charcoal, and stratigraphic relationships from pottery and stone implements has allowed investigators to document much about the lives of people living in the vicinity of Lake Arenal during the past 6000 years (Sheets et al. 1991, Sheets and McKee 1994). Around the second or third millennium B.C., early agriculture was practiced, the staple crops being tubers, fruit trees, berries, and palms. Expanding agriculture changed the indigenous societies, which led to the establishment of permanent settlements, the development of ceramics, and social changes. During the Archaic Period (3300–2000 B.C.),

subsistence shifted from primarily hunting and gathering to agriculture. Villages were established, although population densities were low. The Early and Late Tronadora phases (2000–500 B.C.) are characterized by well-built houses and extensive use of ceramics and by many small villages scattered throughout the region.

The period from 500 B.C. to A.D. 300 in Costa Rica marked a transition from small tribal societies to chiefdom societies associated with the cultivation of seeds, primarily maize. A mixed system of horticulture involving tubers, berries, and fruit trees and seed agriculture (primarily corn, beans, and squash) was present throughout much of the country. Main villages contained constructions such as stone foundations, house mounds, paved causeways, ovens, storage wells, and statuary. Many of the carved jade objects and ceremonial metates now exhibited in museums are funerary offerings during this period.

The major occupancy of the Arenal area occurred during the Early and Late Arenal phases (500 B.C.–A.D. 600). There is evidence of large-scale land clearing during this time, which was related to an increase in the human populations living along the lake and an expansion beyond the lakeshores (Piperno 1994). Some of the early volcanic eruptions of Arenal could have weathered by this time to form relatively fertile soils. The general pattern throughout Costa Rica is a rapid population increase until about A.D. 500. Deforestation increased rapidly after 500 B.C., as a result of increased cultivation. The population density in the Arenal region and throughout the mountains reached its peak during these phases (Sheets 1994).

During the period from A.D. 300–800, the organization of societies in Costa Rica evolved from simple chiefdoms to complex chiefdoms with structures such as foundations, paved causeways, mounds, and burial sites. From A.D. 800 until the arrival of the Spaniards in the sixteenth century, large villages with intricate

infrastructure were formed. Some of the elements of Costa Rican societies at the time of the Conquest included multiple, simple, and complex cemeteries; elaborate structures in main villages (house mounds, aqueducts, public squares, paved causeways, and supporting walls); a diversity of domestic property; regional exchange of goods; the introduction of goldwork; and the rivalry of chiefdoms.

At Lake Arenal during the Silencio Phase (A.D. 600–1300), the Río Piedra valley was heavily populated. Settlements were large but widely separated. Population may have shifted to the west away from the lake in response to increased volcanic activity from adjacent Volcán Arenal (Mueller 1994). The Silencio and Tilarán phases were periods of general population decline and abandonment of long-used sites. Population declines during these phases were not directly correlated with volcanism and are thought to be a regional phenomenon (Mueller 1994). Based on analysis of the carbon isotopes $^{13}C/^{12}C$ from human bone recovered from burial sites, less than 12% of the diet was maize, which is a far lower percentage than was consumed by most historical populations in Mesoamerica (Friedman and Gleason 1984, Bradley 1994).

The arrival of the Spaniards in A.D. 1502 began a painful transition period for the indigenous societies of Costa Rica, with marked population declines of the indigenous peoples, the decimation of cultures, and the extinction of some tribal groups. The cultures that the Spanish found in Costa Rica fiercely resisted them for two generations. Costa Rica was the last of the Central American countries to be conquered by the Spanish. The most recent estimate of the peak pre-Columbian population of indigenous peoples is about 400,000 people (Denevan 1992). The population was reduced to 80,000 by 1563 (MacLoed 1973, J. W. Hoopes, pers. comm.).

The combination of wild-gathered and garden-cultivated plants along with protein provided by wild game was probably the characteristic diet of most indigenous people in Costa Rica (Hoopes and Chenault 1994, Sheets and McKee 1994). People seemed to prefer living in the drier life zones present on Arenal, the tropical moist forest/premontane transition, and humid premontane forest. Highland areas above 1500 m in the Cordillera de Tilarán generally were not inhabited.

Throughout much of the period of occupancy, the cultures of the Arenal region appear to have been self-sufficient and relatively independent of outside groups, compared to other Mesoamerican villages. Maize was cultivated by 2000 B.C., but did not become the mainstay of the diet. The cultures living around the lake instead based their subsistence on the exploitation of the rich and diverse indigenous flora and fauna. Population densities fluctuated considerably but in general were relatively low compared with densities farther north in Mesoamerica or in the Andes of South America. However, the peoples of the Arenal region had an impact on their environment and were responsible for considerable deforestation (Sheets et al. 1991).

Appendix 10

Mammals of Monteverde

Robert M. Timm
Richard K. LaVal

Scientific Name	Common Name[a]	Abundance[b]	Distribution[c]
Marsupialia	*Marsupials*		
Didelphidae	American opossums		
Caluromys derbianus	Woolly Opossum	Uncommon	1, 2, 3
	Zorro colorado		
Chironectes minimus	Water Opossum	Uncertain	1
	Zorro de agua		
Didelphis marsupialis	Common Opossum	Abundant	1, 2, 3, 4, 5, 6
	Zorro pelón or Zarigüeya		
Marmosa mexicana	Mexican Mouse Opossum	Common	2, 3, 5, 6
	Zorro ici or Zorricí		
Micoureus alstoni	Alston's Opossum	Uncommon	2, 3, 6
	Zorro ici or Zorricí		
Philander opossum	Gray Four-eyed Opossum	Uncommon	1, 2, 3, 5
	Zorricilla or Zorillo		
Insectivora	*Shrews*		
Soricidae	Shrews		
Cryptotis nigrescens	Blackish Small-eared Shrew	Common	2, 3, 4, 6
	Musaraña, Antitorinco, or Topo		
Cryptotis sp.[d]	Small-eared Shrew	Rare	4
	Musaraña		
Cryptotis sp.	Small-eared Shrew	Rare	3
	Musaraña		
Chiroptera[e]	*Bats*		
Emballonuridae[f]	Sac-winged bats		
Mormoopidae	Mustached bats		
Pteronotus gymnonotus	Big Naked-backed Bat	Rare	1, 2, 3, 4
Pteronotus parnellii	Parnell's Mustached Bat	Uncommon	1, 2, 3, 4, 6

Scientific Name	Common Names[a]	Abundance[b]	Distribution[c]
Phyllostomidae	Leaf-nosed bats		
Phyllostominae	Gleaning bats		
Lonchorhina aurita	Sword-nosed Bat	Uncommon	5, 6
Micronycteris hirsuta	Hairy Big-eared Bat	Rare	2
Micronycteris microtis[g]	Little Big-eared Bat	Uncommon	1, 2, 3, 4, 6
Micronycteris schmidtorum	Schmidt's Big-eared Bat	Uncertain	6
Micronycteris sylvestris	Tri-colored Big-eared Bat	Rare	2
Mimon bennettii/cozumelae	Big-eared Bat	Rare	2
Phylloderma stenops	Peters' Spear-nosed Bat	Rare	6
Phyllostomus discolor	Pale Spear-nosed Bat	Common	1, 2
Phyllostomus hastatus	Greater Spear-nosed Bat	Rare	6
Tonatia sp.	Round-eared Bat	Uncertain	6
Trachops cirrhosus	Fringe-lipped or Frog-eating Bat	Uncommon	1, 2, 3, 4, 6
Vampyrum spectrum	False Vampire Bat	Rare	2, 3, 4, 6
Glossophaginae	Nectar-feeding bats		
Anoura cultrata	Handley's Tailless Bat	Uncommon	2, 3, 4, 6
Anoura geoffroyi	Geoffroy's Tailless Bat	Common	1, 2, 3, 4, 5
Choeroniscus godmani	Godman's Long-nosed Bat	Uncommon	1, 2, 3, 4
Glossophaga commissarisi	Commissaris' Long-tongued Bat	Common	1, 2, 3, 4
Glossophaga soricina	Pallas' Long-tongued Bat	Common	1, 2, 3, 6
Hylonycteris underwoodi	Underwood's Long-tongued Bat	Common	2, 3, 4, 5
Lonchophyllinae	Nectar-feeding bats		
Lonchophylla robusta	Panama Long-tongued Bat	Rare	2, 3, 6
Carolliinae	Short-tailed bats		
Carollia brevicauda	Silky Short-tailed Bat	Common	1, 2, 3, 4, 5, 6
Carollia castanea	Allen's Short-tailed Bat	Uncommon	1,2,6
Carollia perspicillata	Short-tailed Fruit Bat	Rare	1, 2, 6
Stenoderminae	Fruit-eating bats		
Artibeus aztecus	Highland Fruit-eating Bat	Rare	2, 6
Artibeus jamaicensis	Jamaican Fruit Bat	Common	1, 2, 3, 4, 6
Artibeus intermedius	Davis' Fruit Bat	Uncommon	2
Artibeus lituratus	Big Fruit Bat	Uncommon	1, 2, 3, 4
Artibeus phaeotis	Pygmy Fruit-eating Bat	Uncommon	6
Artibeus toltecus	Lowland Fruit-eating Bat	Abundant	1, 2, 3, 4, 5, 6
Centurio senex	Wrinkle-faced Bat	Rare	1, 2, 3
Chiroderma sp.	Shaggy-haired Bat	Rare	6
Ectophylla alba	Caribbean White Bat	Rare	6
Enchisthenes hartii	Little Fruit-eating Bat	Uncommon	1, 2, 3, 4
Sturnira lilium	Yellow-shouldered Bat	Uncommon	1, 2
Sturnira ludovici	Anthony's Bat	Abundant	1, 2, 3, 4, 5, 6
Sturnira mordax	Talamancan Bat	Common	2, 3, 4, 5, 6
Vampyrodes caraccioli	Great Stripe-faced Bat	Rare	2
Vampyressa pusilla	Little Yellow-eared Bat	Rare	2, 3
Platyrrhinus vittatus	Greater Broad-nosed Bat	Common	1, 2, 3, 4, 5
Desmodontinae	Vampire bats		
Desmodus rotundus	Common Vampire Bat Vampiro	Uncommon	1, 2, 3, 5, 6
Diphylla ecaudata	Hairy-legged Vampire Bat Vampiro	Rare	2
Natalidae	Funnel-eared bats		
Natalus stramineus	Mexican Funnel-eared Bat	Uncertain	1
Thyropteridae	Disk-winged bats		
Thyroptera tricolor	Spix's Disk-winged Bat	Uncommon	2, 3, 4, 6
Vespertilionidae	Vespertilionid bats		
Antrozous dubiaquercus	Doubtful Oak Bat	Rare	2, 3
Eptesicus brasiliensis (= andinus)	Brazilian Brown Bat	Uncommon	2, 3, 4
Eptesicus fuscus	Big Brown Bat	Uncommon	2, 3, 4
Lasiurus blossevillii (= borealis)	Southern Red Bat	Rare	2, 4
Lasiurus castaneus	Tacarcuna Bat	Rare	4
Lasiurus ega	Southern Yellow Bat	Rare	2, 4
Myotis elegans	Elegant Myotis	Uncommon	6
Myotis keaysi	Hairy-legged Myotis	Abundant	2, 3, 4, 5
Myotis nigricans	Black Myotis	Common	1, 2, 3, 4
Myotis oxyotus	Montane Myotis	Rare	1, 2

Scientific Name	Common Names[a]	Abundance[b]	Distribution[c]
Myotis riparius	Riparian Myotis	Rare	1, 2
Molossidae	Free-tailed bats		
Eumops auripendulus	Shaw's Mastiff Bat	Uncertain	6
Molossus sinaloae	Sinaloan Mastiff Bat	Uncertain	1, 2
Tadarida brasiliensis	Brazilian Free-tailed Bat	Uncertain	2
Primates	*Primates*		
Cebidae	New-World monkeys		
Alouatta palliata	Mantled Howler Monkey	Common	1, 2, 3, 4, 5, 6
	Mono congo		
Ateles geoffroyi	Black-handed Spider Monkey	Rare	3, 4, 5, 6
	Mono colorado		
Cebus capucinus	White-faced Capuchin	Common	1, 2, 3, 4, 5
	Mono carablanca		
Xenarthra	*Edentates*		
Bradypodidae	Three-toed sloths		
Bradypus variegatus	Brown-throated Three-toed Sloth	Rare	1
	Perezoso de tres dedos		
Choloepidae	Two-toed sloths		
Choloepus hoffmanni	Hoffmann's Two-toed Sloth	Common	1, 2, 3, 4, 5, 6
	Perezoso de dos dedos		
Dasypodidae	Armadillos		
Cabassous centralis	Northern Naked-tailed Armadillo	Rare	2, 3, 4
	Cusuco zopilote		
Dasypus novemcinctus	Nine-banded Armadillo	Abundant	1, 2, 3, 4, 5, 6
	Cusuco		
Myrmecophagidae	Anteaters		
Cyclopes didactylus	Silky Anteater	Uncertain	2, 6
	Serafín de platanar or Tapacara		
Myrmecophaga tridactyla	Giant Anteater		
	Oso caballo or Hormiguero	Extirpated	
Tamandua mexicana	Northern Tamandua	Uncommon	1, 2, 3, 5, 6
	Oso hormiguero		
Lagomorpha	*Rabbits*		
Leporidae	Rabbits and hares		
Sylvilagus brasiliensis	Forest Rabbit	Rare	2, 3
	Conejo		
Sylvilagus floridanus	Cottontail Rabbit	Uncommon	1
	Conejo		
Rodentia	*Rodents*		
Geomyidae	Pocket gophers		
Orthogeomys cherriei	Cherrie's Pocket Gopher	Uncommon	1, 2, 3, 6
	Taltusa or Tartusa		
Sciuridae	Squirrels		
Microsciurus alfari	Alfaro's Pygmy Squirrel	Common	2, 3, 4, 5, 6
	Ardillita		
Sciurus granatensis[h]	Neotropical Red Squirrel	Common	1, 2, 3, 4, 5, 6
	Ardilla or Chisa negra		
Sciurus variegatoides	Variegated Squirrel	Abundant	1, 2, 3
	Ardilla or Chisa rosilla		
Heteromyidae	Pocket mice		
Heteromys desmarestianus	Desmarest's Spiny Pocket Mouse	Common	1, 2, 3, 4, 5, 6
	Rata		
Muridae	Long-tailed rats and mice		
Nyctomys sumichrasti	Sumichrast's Vesper Rat	Uncommon	1, 2
	Ratón		

Scientific Name	Common Names[a]	Abundance[b]	Distribution[c]
Oligoryzomys fulvescens	Pygmy Rice Mouse Ratón	Rare	2, 3
Oligoryzomys vegetus	Pygmy Rice Mouse Ratón	Rare	2, 4
Oryzomys albigularis	Tome's Rice Rat Ratón	Uncommon	3, 4
Oryzomys alfaroi	Alfaro's Rice Rat Ratón	Uncommon	2, 3
Oryzomys bolivaris (= *bombycinus*)	Long-whiskered Rice Rat Ratón	Rare	6
Ototylomys phyllotis	Big-eared Climbing Rat Ratón	Uncertain	1, 2
Peromyscus nudipes	Naked-footed Mouse Ratón	Abundant	1, 2, 3, 4, 5
Reithrodontomys creper	Chiriquí Harvest Mouse Ratón	Uncommon	4
Reithrodontomys gracilis	Slender Harvest Mouse Ratón	Common	1, 2, 3, 6
Reithrodontomys sp.[i]	Harvest Mouse Ratón	Rare	4
Rheomys raptor	Goldman's Water Mouse Ratón	Rare	2, 3, 4, 6
Scotinomys teguina	Alston's Brown Mouse Ratón	Uncommon	2, 3, 4, 6
Sigmodon hispidus	Hispid Cotton Rat Ratón	Rare	1, 2
Tylomys watsoni	Watson's Climbing Rat Rata azul	Common	2, 3, 4, 5, 6
Erethizontidae	Porcupines		
Coendou mexicanus	Prehensile-tailed Porcupine Puercoespín	Common	1, 2, 3, 4, 5, 6
Agoutidae	Pacas		
Agouti paca	Paca Tepezcuintle	Uncommon	1, 2, 3, 4, 5, 6
Dasyproctidae	Agoutis		
Dasyprocta punctata	Agouti Guatusa	Common	1, 2, 3, 4, 5, 6
Carnivora	*Carnivores*		
Canidae	Coyotes, foxes, and dogs		
Canis latrans	Coyote Coyote	Uncommon	1, 2
Urocyon cinereoargenteus	Gray Fox Tigrillo or Zorragris	Common	1, 2, 3, 5
Mustelidae	Skunks, weasels, and otters		
Conepatus semistriatus	Striped Hog-nosed Skunk Zorro hediondo	Common	1, 2, 3, 4, 6
Eira barbara	Tayra Tejón or Tolomuco	Common	1, 2, 3, 4, 5
Galictis vittata	Grison Grisón or Tejón	Rare	2, 3, 5, 6
Lutra longicaudis	Southern River Otter Perro de agua or Nutria	Rare	1, 2, 3, 4, 5, 6
Mustela frenata	Long-tailed Weasel Comadreja	Uncommon	1, 2, 3, 4, 5, 6
Procyonidae	Raccoons		
Bassaricyon gabbii	Olingo Martilla	Common	1, 2, 3, 5, 6
Nasua narica	White-nosed Coati Pizote	Abundant	1, 2, 3, 4, 5, 6
Potos flavus	Kinkajou Martilla or Mico de noche	Common	1, 2, 3, 4, 5, 6
Procyon lotor	Raccoon Mapachín	Common	1, 2, 3, 4, 5, 6

Scientific Name	Common Names[a]	Abundance[b]	Distribution[c]
Felidae[i]	Cats		
Felis concolor	Puma	Uncommon	1, 2, 3, 4, 5, 6
	Puma or León de montaña		
Felis pardalis	Ocelot	Uncommon	1, 2, 3, 4, 5, 6
	Manigordo or Ocelote		
Felis tigrina	Little Spotted Cat	Uncertain	1, 3, 4, 6
	Tigrillo or Gato tigre		
Felis wiedii	Margay	Uncommon	2, 3, 4, 5, 6
	Caucél		
Felis yaguarondi	Jaguarundi	Uncommon	1, 2, 3, 4, 5, 6
	Tcholomuco		
Panthera onca	Jaguar	Rare	3, 4, 5, 6
	Tigre		
Artiodactyla	*Deer and peccaries*		
Dicotylidae	Peccaries		
Tayassu pecari	White-lipped Peccary		
	Chancho de monte or Cariblanco	Extirpated	
Pecari tajacu	Collared Peccary	Common	3, 4, 5, 6
	Saíno or Zahino		
Cervidae	Deer		
Mazama americana	Brocket Deer	Uncommon	1, 3, 4, 5, 6
	Cabro or Corzo		
Odocoileus virginianus	White-tailed Deer	Uncommon	1, 2
	Venado cola blanca		
Perissodactyla	*Tapirs and horses*		
Tapiridae	Tapirs		
Tapirus bairdii	Baird's Tapir	Uncommon	3, 4, 5, 6
	Danta		
Species introduced into the area by humans[k]			
Mus musculus	House Mouse	Abundant	Commensal
	Ratón		
Rattus rattus	Black or Roof Rat	Abundant	Commensal
	Ratón		

[a]The common name(s) for each species is in English and Spanish. Spanish names are used within the Monteverde area. Because non-mammalogists cannot easily distinguish bats, there are few local common names in Spanish, other than "murciélago" or "vampiro."

[b] Abundance categories: Abundant = often observed and/or captured in appropriate habitats; Common = frequently observed in appropriate habitats; Uncommon = only occasionally observed in appropriate habitats; Rare = very few records for Monteverde; Extirpated = previously known from the area but no longer in the region due to overhunting and habitat destruction; Uncertain = of unknown abundance.

[c]Distribution numbers indicate Holdridge (1967) life zones (see Fig. 1.5).

[d]An undescribed species (Woodman 1992, Woodman and Timm 1993).

[e]Undoubtedly other species of molossids occur in the area, but have yet to be detected.

[f]This family is widespread in the tropical lowlands, and we suspect that several species will be found at the lower elevations in the area.

[g]The species referred to as *Micronycteris megalotis* in the literature was a composite of two valid species: *Micronycteris microtis*, which occurs from Mexico through Central America to northern South America, and *M. megalotis*, which occurs throughout much of the northern half of South America. All previous literature references to *M. megalotis* in Costa Rica should be attributed to *M. microtis*.

[h]Previous lists report the medium-sized squirrel from Monteverde as being *Sciurus deppei*. *S. granatensis* and *S. deppei* are similar in appearance and difficult to distinguish in the field. Both species are medium-sized brown squirrels, although *S. granatensis* is larger (total length for *S. deppei*, 343–387 mm; for *S. granatensis*, 382–440 mm). The distinguishing field characters are presence of a small white throat patch in *S. deppei*; the throat of *S. granatensis* is orange. The tail of *S. deppei* is narrower and darker than that of *S. granatensis*, and the tail hairs throughout the length of the tail in *S. deppei* are tipped with white, whereas the tail of *S. granatensis* is bushier and tipped with tan, orange, or reddish hairs.

[i]A new species being described by R. Timm.

[j]A variety of generic names for species of cats are in use, reflecting different opinions as to their systematic relationships. Wozencraft (1993) used *Puma concolor* for the Puma, *Leopardus pardalis* for the Ocelot, *Leopardus tigrinus* for the Little Spotted Cat, *Leopardus wiedii* for the Margay, and *Herpailurus yaguarondi* (frequently spelled *yagouaroundi*) for the Jaguarundi.

[k]These introduced Old-World rodents will cross forested tracts but are found in abundance only around human habitations and rarely occur in natural areas.

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