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# COSTA RICAN NATURAL HISTORY

EDITED BY

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## 9 MAMMALS

## INTRODUCTION

D. H. Janzen and D. E. Wilson

The contemporary mammalian fauna of Costa Rica (Goodwin 1946) is not exceptional either in the species it contains or in its ecological diversity when compared with the fauna of the rest of Central America or even tropical lowland Mexico. Almost all Costa Rican mammals have ranges encompassing Central America, and many extend into South and North America. Although this essay is focused on Costa Rica, it has wider application.

The wild mammals that have been studied most intensively in Costa Rica include the frugivorous bat *Carollia perspicillata* (Heithaus and Fleming 1978), vampire bat, *Desmodus rotundus* (Turner 1975), disk-winged bat, *Thyroptera tricolor* (Findley and Wilson 1974; Wilson and Findley 1977), howler monkey, *Alouatta palliata* (Glander 1975), and pocket mice, *Liomys salvini* and *Heteromys desmarestianus* (Fleming 1974, 1977a,b; Fleming and Brown 1975; Vandermeer 1979; Janzen 1982b,c; Bonoff and Janzen 1980; Hallwachs and Janzen 1983). As a group, bats have received the most attention (Brown 1968; Gardner, Laval, and Wilson 1970; Gardner and Wilson 1971; LaVal 1970, 1977; Fleming, Hooper, and Wilson 1972; Fleming, Heithaus, and Sawyer 1977;

Mares and Wilson 1971; Howell and Burch 1974; Heithaus, Opler, and Baker 1974; Heithaus, Fleming, and Opler 1975; Bradbury and Vehrencamp 1976a,b, 1977a,b; LaVal and Fitch 1977; Vehrencamp, Stiles, and Bradbury 1977), and large mammals the least (Janzen 1981a,b, 1982a). Free-ranging cows and horses are grossly understudied in view of their ease of observation, contemporary ecological importance, and similarity to the large Pleistocene herbivores that once influenced Costa Rican vegetation (Janzen and Martin 1982).

Except in the national parks, all large and many small Costa Rican wild mammal populations are subjected to extreme hunting pressure or habitat destruction. Only now are large-mammal densities in the national parks beginning to recover following intensive hunting and competition from livestock for the past one hundred to two hundred years. A reliable informant told Franklin Chaves, the director of Santa Rosa National Park, that in 1947-49 he shot thirty-six tapirs in the bottomlands of the area when it was not yet a park; a Nicaraguan hunter with dogs is rumored to have shot sixteen jaguars and mountain lions in the same area in one year during the mid-1960s.

Fortunately, a rapidly spreading enlightenment of the Costa Rican populace is alleviating the hunting pressure and is resulting in the preservation of substantial pieces



Front view of skull of adult paca (*Cuniculus paca*). This 10 kg nocturnal forest-floor rodent lives in burrows and hollow logs in the daytime. If disturbed, it growls like a dog; the enlarged rugose cheekbones serve as resonating chambers, magnifying the sound. Santa Rosa National Park, Costa Rica (photo, D. H. Janzen).

of habitat as well. Costa Rica has set aside no fewer than twenty-four national parks and reserves, totaling 2,093 km<sup>2</sup> (4.1% of the country) in the past nineteen years (Bonilla 1979). However, in the unprotected portions of Costa Rica there are several subtle aspects of local mammal extinction and population reduction that are poorly understood. In most habitats, many species still exist as widely scattered individuals, transients from more protected areas, or individuals that have adjusted to new diets. However, their interactions with indigenous food sources and types, with other mammals, and with conspecifics have been heterogeneously interrupted, extinguished, or distorted to a largely unknowable degree. Rapidly changing selective pressures have resulted in ecological and behavioral repertoires containing indecipherable mixtures of historical constraints and environmental demands. Great care is needed, for example, in interpreting the adaptive nature of the behavior of bats such as *Artibeus*, *Glossophaga*, and *Carollia* in relation to the flower-fruit-insect cycles in the brushy cow pastures and woodlots of lowland Guanacaste. However, the rotting of large crops of guapinol fruits (*Hymenaea courbaril*) below trees isolated in pasture fencerows is no great ecological puzzle, for the agoutis (*Dasyprocta punctata*) that eat these fruits have been gone from these pastures for two hundred years. In short, as with other organisms, mammal-mammal and mammal-nonmammal interactions become extinct before the participants do. This is especially conspicuous in the interaction-rich habitats of Costa Rica (Janzen 1974; Janzen and Martin 1982).

Although systematists have been contributing to our knowledge of Central American mammalogy for well over one hundred years, it is only in the past twenty years that ecologists have begun asking questions and providing partial answers. We have chosen to orient this essay around a number of such ecological questions, even though speculation may have to serve in lieu of proof.

#### How Diverse Is the Costa Rican Mammal Fauna?

Simpson (1964) found that mammal species richness per unit area increases from Canada through Panama. Subsequently, Fleming (1973a) and Wilson (1974) independently analyzed the same species-richness gradient and found that, if bats are deleted from the analysis, the number of mammal species per unit area remains roughly the same from the central United States to Panama. In short, the increase in species richness with decreasing latitude is attributable almost solely to an increase in the number of bat species. Furthermore, the increase in bat species diversity is primarily due to the large numbers of noninsectivorous species. Frugivores, nectarivores, fish eaters, blood feeders, and carnivores are essentially non-existent in temperate regions but are all well represented

in the Costa Rican fauna. However, a recent analysis of the same gradient (McCoy and Connor 1980) suggests that, if the unit areas studied are larger, other mammal species richness does increase as latitude decreases.

Marsupials are also reasonably diverse in Costa Rica. The Virginia opossum, *Didelphis virginiana*, has Guanacaste as the southern limit of its range. Its more tropical relative, *Didelphis marsupialis*, is found throughout the country (Gardner 1973). These two species are primarily large terrestrial scavengers. There are two medium-sized scansorial omnivores, the four-eyed opossums, *Philander opossum* and *Metachirus nudicaudatus*. Morphologically, *Metachirus* appears to be better adapted for an arboreal existence, with its long limbs and longer tail. The most arboreal marsupial is the woolly opossum, *Caluromys derbianus*. This beautiful little animal is also omnivorous. Three species of small mouse opossums, genus *Marmosa*, are found on the ground and in the undergrowth. They are somewhat shrewlike in appearance and are probably ecological equivalents of insectivores. The most strikingly different marsupial is a water opossum, *Chironectes minimus*. These animals can be seen foraging in small streams throughout the country at lower elevations, and as recently as ten years ago we encountered them in the stream on the campus of the University of Costa Rica in San José.

The order Insectivora is poorly represented in the tropics. Only three species of shrews (*Cryptotis*) occur in Costa Rica, and they are restricted to the interior highlands.

As many as ten species of monkeys and apes can occur sympatrically in a West African rain forest (Booth 1956; Gartlan and Struhsaker 1972), including five species of small prosimians (Charles-Dominique 1974). Wilson has seen three species of prosimians in the same vine tangle in Cameroon. Of the sixteen genera and approximately fifty species of New World monkeys (Mittermeier and Coimbra-Filho 1977), only four occur in Costa Rica. One of these, the squirrel monkey, *Saimiri oerstedii*, is restricted to the Pacific lowlands in the southern part of the country. Capuchins (*Cebus capucinus*) are insectivorous but feed opportunistically on a variety of other things. Spider monkeys (*Ateles geoffroyi*) are wide-ranging aerial acrobats that essentially trapline fruiting trees. Howler monkeys (*Alouatta palliata*), the most conspicuous of the primate fauna, are noisy, sedentary canopy browsers that feed on leaves and fruit. Primate species richness increases rapidly to the south, culminating in Amazonian Brazil, where twenty-two species are listed from an area of 250,000 km<sup>2</sup> (Mittermeier and Coimbra-Filho 1977).

Of the three species of rabbits in Costa Rica, only one (*Sylvilagus brasiliensis*) is wide-ranging. Another has the southern limit of its range in Guanacaste, and the third is a highland endemic.

Although a few square kilometers of desert in the southwestern United States or northern Mexico may have twenty or more species of rodents (Findley et al. 1975), even the most species-rich Costa Rican rain forest contains only about fourteen. This figure is almost equaled by habitat-rich areas of eastern deciduous forest in the United States (Fleming 1973b). Santa Rosa National Park, a mixture of grassland, deciduous forest, rocky ridges, and evergreen riparian forest, boasts only two caviomorphs (agouti and paca), a porcupine (*Coendou mexicanum*), a squirrel (*Sciurus variegatoides*), two rice rats (*Oryzomys*), a climbing rat (*Otodylomys phyllotis*), a spiny pocket mouse (*Liomys salvini*), and a cotton rat (*Sigmodon hispidus*), for a total of nine species (Bonoff and Janzen 1980). Temperate-zone boreal coniferous forests may contain up to ten sciurids (Findley et al. 1975), and Old World tropical rain forests may have as many as nine (Emmons 1975) to twenty-tree (Muul and Liat 1979). All of Costa Rica has only five species of squirrels, and three is the maximum in any one forest.

Pocket gophers (*Macrogeomys*) are represented by only four species, all restricted endemics. Heteromyids, most diverse in arid-temperate and subtropical regions, in Costa Rica are limited to *Heteromys desmarestianus* in wet forests and *Liomys salvini* in dry forests. Although twenty-eight species of cricetine rodents have been recorded from Costa Rica, virtually none are widespread and abundant. The greatest diversity is found in the genus *Oryzomys*, with at least ten species. Several of these ten are arboreal, as are *Tylomys*, *Otodylomys*, and *Nyctomys*. Aquatic mice are represented by two species of *Rheomys*. Costa Rican *Reithrodontomys* (seven species) are mostly restricted highland forms, as are the two *Peromyscus* species. *Scotinomys* are highland mice that are active during the day and that make audible vocalizations.

Costa Rica, like other Neotropical countries, seems to have a depauperate marine mammal fauna. The lack of pinnipeds is not surprising, since they are essentially restricted to temperate and arctic waters (which is probably a reflection of the greater fish abundance in northern near-shore waters). The only exceptions are a population of sea lions (*Zalophus californianus*) on the Galápagos and monk seals in Hawaii and the Mediterranean. The Caribbean monk seal, *Monachus tropicalis*, once occurred on islands off the coast of Honduras but is now extinct (Kenyon 1977). Monk seals are a classic example of large, majestic animals that are incapable of adjusting to man's domination of the environment.

Table 9.1 lists the species of cetaceans that might be expected to occur in Costa Rican waters (J. G. Mead, pers. comm.). Only seven species are recorded from its coastal waters, and two more from nearby Panama.

A viable population of bottle-nosed dolphins (*Tursiops truncatus*) appears to exist in the Caribbean. In October

TABLE 9.1 Marine Mammals Expected in Costa Rican Waters

Scientific Name	Common Name
<i>Tursiops truncatus</i>	Bottle-nose dolphin
<i>Stenella attenuata</i> <sup>a</sup>	Spotted dolphin
<i>S. longirostris</i> <sup>a</sup>	Spinner dolphin
<i>S. coeruleoalbus</i> <sup>a</sup>	Striped dolphin
<i>Delphinus delphis</i> <sup>a</sup>	Common dolphin
<i>Steno bredenesis</i>	Rough-toothed dolphin
<i>Lagenodelphis hosei</i>	Fraser's dolphin
<i>Feresa attenuata</i>	Pygmy killer whale
<i>Peponocephala electra</i> <sup>a</sup>	Melon-headed whale
<i>Lagenorhynchus obliquidens</i>	Pacific white-sided dolphin
<i>Globicephala macrorhyncha</i>	Pilot whale
<i>Pseudorca crassidens</i>	False killer whale
<i>Orcinus orca</i> <sup>c</sup>	Killer whale
<i>Grampus griseus</i> <sup>a</sup>	Risso's dolphin
<i>Physeter catodon</i> <sup>a</sup>	Sperm whale
<i>Kogia simus</i>	Dwarf sperm whale
<i>K. breviceps</i>	Pygmy sperm whale
<i>Ziphius cavirostris</i> <sup>b</sup>	Cuvier's beaked whale
<i>Mesoplodon densirostris</i>	Blainville's beaked whale
<i>M. ginkgodens</i>	Ginkgo-toothed beaked whale
<i>M. carlhubbsi</i> <sup>c</sup>	Hubb's beaked whale
<i>Megaptera novaeanglia</i> <sup>b</sup>	Humpback whale
<i>Balaenoptera acutorostrata</i>	Minke whale
<i>B. physalus</i>	Fin whale
<i>B. edeni</i>	Bryde's whale
<i>B. borealis</i> <sup>c</sup>	Sei whale
<i>B. musculus</i> <sup>c</sup>	Blue whale
<i>Eubalaena glacialis</i> <sup>c</sup>	Right whale

<sup>a</sup> Recorded from Costa Rica.

<sup>b</sup> Recorded from Panama.

<sup>c</sup> Rare possibility.

1976 a mass stranding of more than two hundred melon-headed whales (*Peponocephala electra*) occurred at Playa Tambor, Ballena Bay, on the Nicoya Peninsula. Wilson visited the site and salvaged material for further study, including stomachs containing squid beaks and small fish parts, indicating that the animals had recently fed. The reasons for such mass strandings of apparently healthy animals remain unknown. This species is an apparently widespread pelagic form about which little is known. A similar stranding of about five hundred of these animals occurred in Japan in 1965 (Nishiwaki and Norris 1966).

Bats, edentates, carnivores, and artiodactyls will be discussed in later sections, which focus on the particular ecological problems faced by each. To summarize, the Costa Rican mammalian checklist contains two hundred species, half of which are bats. The fauna is probably not at the equilibrium species number that could be supported by the habitat diversity present before human intervention. The question of human intervention, to be discussed in more detail in a later section, is probably more ancient and complex than previously thought.

### How Do Tropical Mammals Cope with Seasonal Stress?

The climatic rigors of winter have played a large role in shaping ecological responses of extratropical mammals to stressful seasons. The primary problem in these areas is coping with superabundant food supplies during part of the year and greatly reduced or nonexistent resources during another. The two most striking adaptations of this seasonality are hibernation and migration.

In Costa Rica, temperatures in any one zone vary only slightly through the year, and food resources for most mammals are probably little affected by this variation. Moisture regimes are far more variable, and seasonal rainfall patterns undoubtedly affect some kinds of mammals. For most of these animals the time of stress is the dry season, especially in areas like Guanacaste, which has a pronounced five-month dry season. Responses to the dry season are varied, but dormancy is not a viable alternative for tropical mammals for several reasons:

1. Even if a Costa Rican mammal could go dormant for the dry season, its predators and parasites would not, because their food source (the dormant mammal) would still be available. Snakes and other vertebrates adapted to seeking prey in subterranean or intralog burrows would find dormant mammals easy prey. Army ants (*Eciton* spp.) and fire ants (*Solenopsis* spp.) would probably quickly consume a dormant mouse or bat. Poikilothermic ectoparasites would undoubtedly greatly increase their population sizes if released from the normal cleaning and preening exercises of an active host. These are problems not faced by a chilled marmot in a snow-covered burrow in Colorado—winter is on its side, even if some warm-blooded vertebrates are still active in the winter.

2. Dormancy requires stored food reserves, and the warmer the temperatures, the more reserves required per day (e.g., see Janzen and Wilson 1974). It may be physically impossible for a mammal of a given size to carry enough fat to survive an extended period of dormancy at tropical temperatures. This may be why some populations of temperate-zone bats actually migrate northward in search of cold hibernacula, and why lowland Mexican *Myotis velifer* moves into the highlands to hibernate (Villa-R. 1966). McNab (1973) postulated that vampire bats cannot handle more northern climates because they cannot accumulate enough fat to hibernate.

3. Fat accumulation depends on resources being pulsed in such a way that an overabundance is available immediately before the stressful season. Insect densities are highest at the beginning of the tropical rainy season and lowest at the end of the rainy season when insectivorous mammals would need the most food for fat deposition. Although more variable, fruit resources show roughly the same pattern, and most fruits are so nutrient-poor as to make fat deposition physiologically difficult.

Seeds are available during the dry season, but a lull in seed availability occurs at the beginning of the rainy season, a time when massive downpours might render subterranean sites unsuitable for prolonged occupancy. Herbivorous mammals have abundant available resources at the end of the rainy season, but they probably also suffer less shortage during the dry season than it appears, since riparian refugia retain substantial amounts of leafy vegetation.

Some tropical mammals do accumulate fat and use it as a reserve for stressful seasons. Camels, fat-tailed sheep, Brahma cattle, and steatopygous humans are examples. A Brahma bull can live through a 3-month east African dry season largely by metabolizing the fat in its hump, and the camel's legendary ability to survive in the desert may be largely due to the fat stores in its hump. It is probably not an accident that the fat is stored in a lump rather than being spread as a warm coat just under the skin.

4. Highland areas with cooler temperatures might alleviate some of the problems associated with tropical dormancy, especially during the rainy season when week-long periods of little or no insolation or insect activity are common. However, only facultative heterotherms such as some bats are known to undergo periods of torpor in such situations. McNab (1969) found most Neotropical bats he tested, including *Artibeus jamaicensis*, to be homeothermic (constant deep body temperature) endotherms. In contrast, Studier and Wilson (1970) found many tropical species, including *A. jamaicensis* and the other species studied by McNab (1969), to be highly variable in thermoregulatory capabilities; most species showed patterns characteristic of nonhomeothermic endotherms. Recently, Studier and Wilson (1979) showed that these differences are a result of length of time in captivity. *Artibeus jamaicensis* are heterothermic when first captured and quickly become homeothermic in captivity. They suggested that thermoregulation is dependent on the nutritional state of these animals. In the wild, *A. jamaicensis* feeds on fruits that vary seasonally in abundance from scarce to plentiful; individual bats may undergo a natural period of diel torpor, whereas animals kept with free access to food may never go torpid as long as the food supply is constant and plentiful.

Food storage in bulk achieves the accumulation of reserves for a future stressful period while avoiding the problems associated with dormancy. However, hoarding of seeds or other resources, a common practice among many northern heteromyids and sciurids, is uncommon among Costa Rican mammals. *Heteromys desmarestianus* hoards seeds in the rain forest at Finca La Selva (Vandermeer 1979), and *Liomys salvini* does the same in the deciduous forests of Guanacaste (Fleming and Brown 1975). However, both belong to a hoarding family (Het-

eromyidae) that probably evolved the behavior in desert habitats. They are the only heteromyids in a small-rodent fauna of forty-five species. Furthermore, they probably lose a much higher fraction of their hoarded seeds to fungi (Janzen 1979) than do their desert-dwelling relatives and probably depend less on caches than on daily harvesting of new seeds (Fleming 1977b). Certainly, a much smaller proportion of the seeds found in any Costa Rican habitat can be cached in the soil without high losses to fungi and germination than is true with seeds in more northern or more arid areas.

Actually, the stress of a tropical dry season probably is considerably less than that of a northern winter. Food resources may be lowered or changed, but for most mammals they are not eliminated. Many kinds of specialized food resources are available continuously throughout the year. Termites and ants are available for anteaters (though they vary in quantity and quality with season), vertebrate blood is available for vampire bats, and fish are available to fish-eating bats (*Noctilio leporinus*).

Mammals with less restricted diets sometimes switch food resources seasonally. Rodents that feed on seeds in the dry season may become more insectivorous during the rainy season or may take some combination of fruits, buds, flowers, and leaves. *Micronycteris hirsuta*, a bat that forages by foliage gleaning large insects during most of the year, switches to a variety of understory fruits during the dry season (Wilson 1971b). Often, food scarcity in one area may be synchronized with food abundance in other areas. Insect populations on open hillsides are high during the wet season, but very low during the dry season; in adjacent shady riparian habitats, however, insects are abundant during the dry season (Janzen 1973).

Some Costa Rican mammals, like other animals, undoubtedly migrate(d) locally to escape seasonal effects. In areas of deciduous forest traversed by strips of evergreen vegetation along ever-flowing rivers (e.g., ríos Cañas, Corobici, Tempisque, and Potrero, which flow from the volcanic cordillera across Guanacaste to the sea), howler monkeys spread out over the deciduous forest during the rainy season and retreat to the riparian vegetation during the dry season. When there was still forest (and river) at the Ministerio de Agricultura y Ganadería field station on Finca Taboga (1965–70), we saw them lined up perhaps one troop per 0.5 km or less along the Río Higuera in March. It seems likely that the frugivorous and nectarivorous bats that show up in profusion at certain species of trees in flower and fruit in Guanacaste (*Hymenaea courbaril*, *Crescentia alata*, *Bauhinia unguolata* and *B. pauletia*, *Anacardium excelsum*, *Spondias mombin*, *Brosimum alicastrum*, *Piper* spp., *Andira inermis*, and *Ficus* spp.) may move up to tens of kilometers to where stands or populations of these trees are in fruit. Tapirs and peccaries reputedly move into the

*Raphia taedigera* palm swamp around Laguna de Corcovado in Corcovado National Park in the dry season when the palm fruits are falling.

### Why Are So Many Costa Rican Carnivores Frugivorous?

The Costa Rican Carnivora comprise six felids, two canids, six procyonids, and seven mustelids. All except the otter (*Lutra longicaudus*) and mountain lion (*Felis concolor*) are known or alleged to consume large amounts of fruit. When offered bananas, eggs, and meat in a bowl in Santa Rosa National Park, wild hooded skunks (*Mephitis macroura*) take the banana as often as any of the other items. Coyote (*Canis latrans*) feces at Santa Rosa are full of seeds of species such as *Chomelia spinosa*, *Cissus rhombifolia*, *Alibertia edulis*, *Manilkara zapota*, *Ficus* spp., and *Genipa americana*. Tayra (*Eira barbara*) and raccoon (*Procyon lotor*) feces are regularly full of the seeds of a variety of species. Coatis (*Nasua narica*), kinkajous (*Potos flavus*), and olingos (*Bassaricyon sumichrasti*) are widely known as frugivores; coatis even swallow whole fruits as large as *Spondias mombin* (2–3 cm long, 1.5–2 cm diameter) and defecate the nuts whole. Because these animals lack complex stomachs or digestive ceca, all are probably dispersal agents that rarely digest seeds, and we suspect that they carry them for less than 72 h. They are likely to gulp them down with little chewing of the fruit, and therefore fragile seeds that would be ground up by an herbivore's molars may survive the trip through the digestive system of a carnivore. Carnivores often swallow large seeds that a browser would spit out. Whether they are "good" or "bad" dispersal agents, of course, depends on the biology of the plant.

That carnivores should easily become ripe-fruit eaters (but not folivores or green-fruit or seed predators) probably centers on the fact that animal-dispersed ripe fruits are evolutionarily designed to be eaten by vertebrates such as birds, bats, monkeys, tapirs, horses, and agoutis. Given the general similarities of vertebrate digestive systems, it is likely that by producing a fruit that can be eaten by a specific dispersal agent, the fruit becomes edible to many other species as well. Furthermore, part of designing a "good" fruit is not only putting sugars, vitamins, proteins, and lipids in as a reward, but putting them in cellular containers from which they are easily extracted by the correct animals. Because Carnivora have alimentary tracts evolved for extracting nutrients from nearly maximally digestible tissues (compare the ease of digesting a kilo of flesh and fat with the difficulty of digesting a kilo of twigs and leaves), certain kinds of fruits should be the closest thing available to the food believed to be eaten originally by carnivores.

Of course we can turn the question around and note that if the multitude of tree species whose fruits are eaten by Costa Rican (and other tropical) Carnivora grew in

southern Canada, perhaps the northern carnivores would be just as frugivorous as their tropical relatives. Certainly temperate-zone bears, foxes, raccoons, and coyotes eat some species of juicy or fleshy fruits when encountered. Perhaps the "Carnivora" are misnamed; although they obviously have specialized traits for catching and eating prey animals, they may always have been highly frugivorous.

An adjunct of increased frugivory among the carnivores is an increase in the number of arboreal forms. The gray fox (*Urocyon cinereoargenteus*) and tayra (*Eira barbara*) regularly forage in trees. All the procyonids are arboreal to some degree, and kinkajous and olingos are entirely so. All the cats also exhibit arboreality to some extent, though we do not know where they get the fruits (e.g., *Manilkara zapota*) whose seeds appear in their dung.

### Why Do Rat Trappers Become Bat Netters in the Tropics?

The first quarter of this century spanned a period of intense work on the description of the rodent fauna of temperate North America. Mammalogists of this time, such as C. Hart Merriam, Vernon Bailey, Edgar Mearns, E. A. Goldman, and E. W. Nelson, were primarily systematists with a keen eye for natural history. The diversity of the rodent fauna and their relative ease of capture led to a period of descriptive ecological studies during the second quarter of this century. The past thirty years have seen a blossoming of studies dealing with population dynamics and community ecology.

During the first half of the century, work on bats was essentially limited to systematics and anecdotal life-history tidbits. The difficulty of studying nocturnal, volant animals was alleviated somewhat by the discovery that bats could be captured in Japanese mist nets, which had been used for some time to capture birds.

Although early naturalists managed to secure a surprisingly large number of forms of Neotropical bats, they often had only single specimens, which were sent to European museums for description by systematists. These early naturalists were aware of but confused about some of the unusual adaptations of Neotropical bats—witness the number of generic names given to frugivorous species that were mistakenly thought to be vampires (*Vampyrum*, *Vampyrops*, *Vampyressa*, *Vampyriscus*, *Vampyrodes*).

The age of mist netting was already here by the time mammalogists began attempting ecological studies of tropical animals. Students interested in studying small-mammal ecology in the tropics found a rather depauperate rodent fauna that was much more difficult to sample than its temperate-zone counterpart, and an incredibly diverse and interesting bat fauna that could be readily sampled by mist netting.

Although mist nets opened many new paths of inquiry,

they are by no means a perfect sampling technique. Bats are not randomly distributed in the air space, so nets have to be placed where the bats are most likely to encounter them—near roosts, across flyways, over watering areas, or around food sources. Nets are most commonly placed at ground level, so species that routinely fly over or in the forest canopy are less likely to be captured. Many species, especially insectivores, have highly sophisticated echolocation systems that are capable of detecting the nets. Almost all species can learn the location of a net and subsequently avoid it. Often predators are attracted to a net full of noisy bats, and many an opossum has obtained an easy meal from nets that are not closely watched. Students not accustomed to working with bats are easily bitten while trying to extract bats from nets, and the chance of getting rabies from such a bite, though slight, is worrisome to many people.

In spite of these problems, the use of mist nets has furthered knowledge of the Costa Rican bat fauna. That fauna comprises nine families, fifty-two genera, and 103 species. Comparable figures for the United States are four, fifteen, and forty. Ecologically, the diversity is even more striking, because all the United States species are insectivorous, with the exception of a few fruit and nectar feeders that migrate into the extreme southwestern part of the country during the summer. The Costa Rican fauna includes roughly forty-three insectivores, twenty-five frugivores, eleven nectarivores, three blood feeders, two carnivores, one fish eater, and eighteen that feed on some combination of the above. Actually, as details of food habits become better known, an increasing number of these species are relegated to the last category (Gardner 1977).

The most common foraging technique for bats throughout the world is aerial insectivory (Wilson 1973a). These bats, including Costa Rican members of the families Emballonuridae, Mormoopidae, Natalidae, Furipteridae, Thyropteridae, Vespertilionidae, and Molossidae, have highly evolved echolocation systems that allow them to pursue and capture insects on the wing (Novick 1977). More is known about social organization and foraging in emballonurid bats than perhaps any other bat group in Costa Rica, thanks to the excellent work of Bradbury and Vehrencamp (1976a,b, 1977a,b). They studied five species (*Rhynchonycteris naso*, *Saccopteryx leptura*, *Saccopteryx bilineata*, *Balantiopteryx plicata*, and *Peropteryx kappleri*) that divide food resources by a combination of prey size and habitat partitioning. The smaller species tended to forage in groups, whereas the larger ones foraged solitarily; all shifted their foraging areas in response to seasonally changing patterns of insect abundance. Small groups of two to ten bats were the rule of *S. leptura* and *P. kappleri*, five to fifty for *R. naso* and *S. bilineata*, and large colonies with hundreds of individuals for *B. plicata*.

*Rhynchonycteris naso* is one of the smallest (4.5 g) of Costa Rican bats and has unique roosting sites on exposed tree trunks or cliffs, usually adjacent to waterways. The roosting individuals are spaced 2 to 4 cm apart, often in a vertical column. They are cryptically marked with grizzled gray pelage broken by white zigzag lines, and when disturbed they fly off to another of the three to six roost sites used by each colony. The colony maintains a foraging range over the adjacent waterway and socially subdivides the area. Adult breeding females forage together in the center of the range, while younger, non-breeding females and males forage on the periphery and defend the territory against conspecifics from other colonies. The colonies are composed of roughly equal numbers of males and females, but a dominance hierarchy may exist among the males.

*Saccopteryx bilineata* was the first bat species in which a social organization based on harem formation was clearly documented and described (Bradbury and Emmons 1974). Males defend territories, often between the buttresses of large trees. Each territory of about 2 m<sup>2</sup> contains one to eight females. The males have an elaborate repertoire of vocal, visual, and olfactory displays, which they perform regularly at the roosting site.

The family Mormoopidae is a Neotropical endemic, so closely related to the Phyllostomidae that it was formerly considered a subfamily of it (Smith 1972). These bats, represented in Costa Rica by four species of the genus *Pteronotus*, have long been a favorite subject for echolocation studies (Novick 1977), owing in part to their highly specialized, high-intensity systems that combine constant-frequency and frequency-modulated pulses.

The families Natalidae, Furipteridae, and Thyropteridae are also endemic to the Neotropics. *Thyroptera*, the disk-winged bat, is uniquely adapted for roosting in rolled *Heliconia* leaves by adhering to the inner surfaces with suction disks on the wrists and ankles (Findley and Wilson 1974; Wilson and Findley 1977). These small (4 g) bats form colonies of one to nine individuals of mixed sexes and ages, at a density of about four colonies per hectare on the Osa Peninsula. The colonies are socially cohesive, and because of the ephemeral nature of the roost sites each bat must move to a new leaf of the appropriate size (diameter of opening 50 to 100 mm) every few days.

The family Vespertilionidae is cosmopolitan and provides most of the members of temperate-zone bat faunas. Although Costa Rica has twelve species, they are rarely encountered, probably owing to some combination of low numbers and difficulty of capture in mist nets. Half the Costa Rican species belong to the genus *Myotis*, which has about sixty species worldwide and is the most widely distributed genus of mammal other than *Homo*. The two species of *Lasiurus* are migratory but are so little studied in Costa Rica that we do not know if resident

populations also exist. All Costa Rican vespertilionids are aerial insectivores, and most forage in or below the canopy in forested areas.

Free-tailed bats (Molossidae) are also aerial insectivores. They are specialized for fast, high-altitude flight (Findley, Studier, and Wilson 1972) and regularly forage over the forest canopy or above watercourses. Most of the eleven Costa Rican species are rarely encountered, although some species of molossids are commonly found roosting in attics. Although none have been the subject of intensive study in Costa Rica, the Mexican free-tailed bat, *Tadarida brasiliensis*, is a migratory species that has been studied extensively in the United States and intensively at Carlsbad Caverns (Constantine 1967; Geluso, Altenbach, and Wilson 1976; Wilson, Geluso, and Altenbach 1978; Altenbach, Geluso, and Wilson 1979).

The other common foraging pattern for insectivorous bats is foliage gleaning, in which large insects are picked off foliage or the ground. Many members of the phyllostomid subfamily Phyllostominae also feed in this manner. All of these bats possess a suite of morphological characters in common including large ears and short, broad wings. They are capable of slow, highly maneuverable locomotion through the foliage, but how they differentiate between insects and the substrate is unknown.

The two species of noctilionid bats, *Noctilio albiventris* and *N. leporinus*, have foraging patterns that may include some combination of aerial insectivory and foliage gleaning. *Noctilio albiventris* forages along solitary beats about 1 m above the surface of watercourses. The bats appear to be catching insects mainly from the air, but their enlarged hind feet suggest that they may occasionally take insects or small fish from the water surface. *Macrophyllum macrophyllum*, a phyllostomine, forages in similar areas and may do the same (Gardner 1977). The fishing bat, *N. leporinus*, has carried this behavior a step further and specializes in plucking small fish off or from near the water surface. It forages over fresh and salt water.

Other phyllostomines have evolved a similar behavior in foraging over land. *Tonatia* and *Mimon* foliage glean large insects but may occasionally take small vertebrates such as lizards. *Trachops cirrhosus* also foliage gleans but appears to be specialized for capturing frogs from the forest floor (M. Tuttle, pers. comm.). The next logical step is seen in the carnivores, including *Phyllostomus hastatus*, *Chrotopterus auritus*, and especially *Vampyrus spectrum*. Vehrencamp, Stiles, and Bradbury (1977) radio tracked *V. spectrum* foraging in deciduous woodlands in Guanacaste. The bats' primary prey was sleeping birds, and the authors speculated that olfaction might be used in locating the prey. The bats appeared to focus on birds sleeping in the vegetation rather than in holes, and

they took birds weighing 20 to 150 g. Many of the prey items either roosted communally or had a strong odor.

The final major foraging type is found in the vampire bats, family Desmodontidae, of which there are three in Costa Rica. The common vampire, *Desmodus rotundus*, has received the most attention (McNab 1973; Turner 1975). Although probably originally adapted to feed on large wild mammals such as deer, tapir, and peccaries, vampire bats have found a plentiful new source of food in man's livestock. Turner's (1975) study at La Pacifica in Guanacaste outlines basic details of their life history and documents prey preferences that include calves and estrous females, and even swiss over brahma cattle. These preferences were probably due to the increased exposure of the preferred types while sleeping but may also have to do with blood chemistry.

*Desmodus* shows a variety of interesting adaptations for its unique mode of life, including locomotory abilities on the ground that are unmatched by other bats (Altenbach 1979). These bats have highly developed senses of olfaction (Schmidt 1973) and vision (Chase 1972) but only a low-intensity echolocation system (Novick 1977). The dentition is highly specialized; the incisors are enlarged for scooping out a small piece of flesh, and the cheek teeth are almost vestigial (Phillips, Grimes, and Forman 1977). The saliva contains anticoagulants that keep the blood flowing once a bite is made (DiSanto 1960). The digestive tract is modified to deal with large quantities of blood (15 ml per day), which is low in carbohydrates and fat but high in protein. This causes rapid excretion of highly concentrated urine after the bats have returned to the roost and concomitant water-balance problems (McFarland and Wimsatt 1969).

Vampire bats are a problem to livestock producers, owing both to direct effects of blood loss on the animals and to indirect complications such as infection from the bites and disease potential, especially paralytic rabies. Rabies-control programs have been undertaken in many Latin American countries, and these normally include destruction of vampire populations. Thus man has given vampire bats a double dose of environmental determinism—first by introducing livestock that caused vampire populations to increase greatly and then by controlling selected populations because they interfere with man's activities. In a captive colony at the Cincinnati Zoological Gardens, Mills (1980) observed colony mates feeding a female, which had recently given birth, by carrying blood from a bowl and then regurgitating it. On one occasion when the baby bat was a few weeks old but still nursing, the mother regurgitated blood herself and allowed the baby to feed from her mouth.

*Diaemus youngii*, a close relative of *Desmodus*, feeds primarily on birds (Sazima and Uieda 1980). These bats are adept at sneaking along the underside of a branch to a roosting bird, biting it on the toe or leg, and feeding.

This species seems to be rare in Costa Rica, although specimens have been taken at Finca La Pacifica in Guanacaste (Gardner, Laval, and Wilson 1970) and at Santa Rosa National Park (T. Fleming, pers. comm.).

The third species of vampire bat, *Diphylla ecaudata*, is also rare in Costa Rica, although it is known from the Osa Peninsula (Starrett 1976) and we have taken specimens at Finca Palo Verde in Guanacaste. This species also feeds on bird blood (Gardner 1977).

Frugivorous species in Costa Rica belong primarily to the phyllostomid subfamilies Stenodermatinae and Carolliinae. Most of these species roost in small groups or solitarily in the foliage. Some species modify roosting sites by cutting leaves to make tents. Included here are *Uroderma bilobatum*, *Artibeus jamaicensis*, *Artibeus phaeotis*, *A. watsoni*, and *Ectophylla alba* (Foster and Timm 1976). *Ectophylla alba* is one of the few species that is nearly all white. These tiny bats roost in small groups on the underside of *Heliconia* leaves, which they modify into tents by cutting holes along both sides of the midrib (Timm and Mortimer 1976). They have an unusual layer of subcutaneous melanin covering the skull that may provide some of the protection that would be supplied by darker skin (Gardner and Wilson 1971).

*Artibeus jamaicensis* is among the better studied of Neotropical bats (Morrison 1978a,b, 1979; Janzen et al. 1976; Fleming 1971). These bats are particularly fond of figs, and much of their natural history has been worked out on fig-rich Barro Colorado Island in Panama. Males defend harems of four to eleven in tree hollows. Morrison (1978a) used radio tracking to follow their nightly routine of flying to a fig tree, plucking a fruit, and flying up to several hundred meters away to hang up and eat it. They then return for another, taking up to ten figs a night by this pattern. A feeding roost can be recognized by the pile of chewed fragments of figs that accumulates underneath. We have seen areas on Barro Colorado where the ground was littered with such piles over many square meters. These bats eat more figs than they need for caloric reasons, and they produce urine that is extremely dilute compared with that of most mammals (E. H. Studier, pers. comm.). This suggests that they may be processing extra fruit to obtain sufficient quantities of some trace mineral or other necessary nutrient that is in short supply, such as salt or protein. It is a mystery why they fly far from the fruit tree to eat the fruit.

The subfamily Carolliinae has one genus, *Carollia*, with four species in Costa Rica. *Carollia perspicillata* has been the subject of intensive studies of foraging behavior at Santa Rosa National Park (Heithaus and Fleming 1978). These bats tend to roost in colonies of more than one hundred individuals in small caves, although some individuals roost in hollow trees or solitarily in the vegetation. From these day roosts, the bats fly an average 1.6 km to feeding areas, and they average another 1.5 km in

moving back and forth between two to six such feeding areas. *Piper* spp. compose over 50% of the diet, and night roosts are usually 30–40 m from food plants. The bats average thirty to forty trips a night between food source and night roost. This pattern is not unlike that described for *Artibeus jamaicensis* in feeding on figs (Morrison 1978a), except that *Artibeus* makes fewer trips with larger fruits over longer distances (and see Janzen et al. 1976).

Nectarivorous bats in Costa Rica belong primarily to the phyllostomid subfamily Glossophaginae. These bats, with characteristically elongated rostra and tongues and reduced dentition, hover in front of flowers to feed on nectar and pollen. The most common species throughout the country is *Glossophaga soricina*, a second-growth forest species that feeds on fruit and occasional insects as well as nectar (Howell and Burch 1974; Gardner 1977). At least one phyllostomine, *Phyllostomus discolor*, also feeds heavily on nectar and pollen (Gardner 1977). Heithaus, Fleming, and Opler (1975) found considerable amounts of pollen on the frugivorous species *Artibeus jamaicensis*, *A. lituratus*, *A. phaeotis*, *Sturnira lilium*, and *Carollia perspicillata*. Their data suggest seasonal shifts between frugivory in the wet season and nectarivory in the dry season. Heithaus, Opler, and Baker (1974) contrasted the visitation patterns of the large *Phyllostomus discolor* and small *Glossophaga soricina* to *Bauhinia paulletia* patches at Finca La Pacifica. Individuals of *Phyllostomus discolor* forage in groups, grasp branches high on the plant and pull the flowers down, drain the nectar well, and seem to concentrate on *Bauhinia*. Individuals of *Glossophaga soricina* forage singly, hover in front of both high and low flowers, take small amounts of nectar, and seem to be less specialized on *Bauhinia*.

This diversity of resource use in bats makes it possible to compare and contrast faunas from different parts of the world. Analytical zoogeographers normally do this by comparing overlap values calculated on the basis of taxa shared between regions (Simpson 1964; Wilson 1974). This type of analysis shows the Neotropical bat fauna to be most closely related to the Nearctic one, a finding that is not surprising, since the common worldwide pattern is for contiguous areas to be most alike (Wilson 1973a). However, a similar analysis based on trophic diversity yields the ecologically more satisfying finding that the Neotropical fauna is most like the Australian, Oriental, and Ethiopian ones and least like the Nearctic and Palearctic ones (Wilson 1973a).

This trophic diversity of bats is correlated with a number of morphological features. One of the more interesting correlations is between food habits or foraging type and brain size (Eisenberg and Wilson 1979). The lowest brain/body weight ratios are found in the aerial insectivores and the highest in frugivores and nec-

tarivores. Foliage gleaners, fishing and vampire bats, and carnivores are somewhat intermediate in brain size.

Aerial insectivores have brains almost as small as those of extant primitive members of the order Insectivora. Presumably, bats evolved from terrestrial insectivores, and brain-size modifications have accompanied shifts in foraging behaviors and food habits. Perhaps foraging for flying insects can be accomplished by a fairly stereotyped behavioral pattern based heavily on echolocation. Fruit-feeders, on the other hand, may require larger brains to integrate inputs from a variety of sensory modalities used in locating and feeding on seasonally pulsed, localized food resources. They not only must know where to find food today, but must census the habitat well enough to know where to find it tomorrow and next week as well. The same process has been postulated for orangutans (Hrdy and Bennett 1979).

These correlations cut across phylogenetic lines in such a way as to make parallelism unlikely. Costa Rican phyllostomids have brain/body-weight ratios comparable to those of Old World pteropodids, or flying foxes, which also feed on fruit and nectar. Similarly, the low ratios seen in New World aerial insectivores are found in endemic Old World groups as well.

Before leaving the bats, we should briefly discuss some of the interesting demographic patterns that are beginning to surface. Small terrestrial mammals tend to reach sexual maturity in a few months, and they have large litters, short gestation periods, several litters per year and live for only a year or two. In contrast, most bats require several months to a year to reach sexual maturity, have gestation periods of 2–6 months, have one offspring per litter, often have only one or two litters per year, and may live up to 30 years (Keen and Hitchcock 1980).

Reproductive patterns of Costa Rican bats show four basic patterns that may be thought of as a continuum (Wilson 1973b). The basic types of cycle for temperate-zone species is to produce only one litter per year at a time when food resources are plentiful. This pattern is seen in many insectivorous species in Costa Rica (Wilson and Findley 1971; Mares and Wilson 1971; Fleming, Hooper, and Wilson 1972; Bradbury and Vehrencamp 1977b). These bats tend to time reproductive events so that the young are weaned at the time of maximum food availability (usually early in the rainy season).

Most frugivorous and nectarivorous species have two litters per year (Wilson 1979). Some insectivorous species may have this pattern if they are inhabitants that have more stable food resources (Bradbury and Vehrencamp 1977b). The typical pattern in the frugivorous and nectarivorous species is to wean the first young at the beginning of the rainy season, undergo postpartum estrus, and wean a second young later in the rainy season. A period of sexual diapause then follows. This usually lasts for a

few months, and then the cycle begins again. An interesting variation on this pattern is seen in *Artibeus jamaicensis* (Fleming 1971). These bats undergo postpartum estrus after the second litter, but the implanted blastocyst develops very slowly through the end of the rainy season until the dry season. Then development accelerates, and the young bat is ready for weaning at the normal time the first litter of the year is weaned in other bat species.

*Myotis nigricans*, a small insectivorous vespertilionid, has the third pattern, seasonal polyestry. Up to three litters are produced in succession each year, with a short sexual diapause at the end of the rainy season (Wilson and Findley 1970; Wilson 1971a).

The fourth pattern, aseasonal polyestry, is found in vampires, *Desmodus rotundus* (Wilson 1979). These bats enjoy a relatively stable food source, and in most areas they tend to reproduce throughout the year. However, the long gestation period (6–7 months) and lactation period (3–9 months) may mean that individual females are producing fewer than two young per year anyway (Schmidt and Manske 1973).

In short, bat reproductive cycles seem to be strongly influenced by food availability, which is in turn strongly correlated with seasonal rainfall patterns. Most evidence suggests that reproduction patterns are directed toward weaning young at the most favorable times, and that the stresses of gestation and lactation are less critical than might otherwise be supposed (Fleming, Hooper, and Wilson 1972; Bradbury and Vehrencamp 1977b; Wilson 1979).

### What Is Especially Tropical about the Costa Rican Mammalian Fauna?

Monkeys, anteaters, sloths, and noninsectivorous bats are the ecologically unique tropical mammals found in Costa Rica. Small Costa Rican rodents do not seem to be different in any major way from extratropical counterparts. Agoutis and pacas might seem to be candidates, but their large size, small litters, extensive parental care, and great longevity are to some degree paralleled by temperate-zone rodents such as beavers and porcupines. Armadillos, peccaries, frugivorous procyonids, and marsupials all range well into extratropical habitats. Aside from a slight tendency toward the increased frugivory already discussed, tropical carnivores are rather unexceptional.

### ANTEATERS

Mammals that largely eat ants and termites are found around the world in the tropics, and rarely outside (cf. Bequaert 1922) (though bears approximate this dietary habit with ants at certain times of year). Each major type of anteater—echidnas, pangolins, armadillo, armadillo, anteaters—is probably independently evolved. They are

all nearly toothless, have long sticky tongues, and have large digging claws on powerful feet. Anteaters are probably missing from the extratropical regions because of the absence of large termite colonies (Y. Lubin, pers. comm.) and because large ant colonies are generally inaccessible during the winter.

The three Costa Rican anteaters are distinctive. The giant anteater (*Myrmecophaga tridactyla*) is a large (20 kg) terrestrial forest dweller. Tamanduas (*Tamandua mexicana*) are medium-sized and scansorial. They are the anteaters most frequently encountered in Costa Rica and are equally at home on the ground or in trees. The smallest species, the silky anteater (*Cyclopes didactylus*), is almost totally arboreal and is rarely seen.

### SLOTHS

The two species of sloths are *Bradypus variegatus*, the three-toed sloth, and *Choloepus hoffmani*, the two-toed sloth. Both are highly specialized for a low intake rate of highly indigestible food, namely mature leaves of forest trees. Sloths use fewer resources per day than most mammals and have a suite of corresponding characteristics such as their proverbial lethargic behavior, long interdefecation periods, and variable, nearly poikilothermic, body temperature (Goffart 1971; Montgomery and Sunquist 1978).

*Bradypus* is more commonly seen because it is active during the day, whereas *Choloepus* is nocturnal and spends the daylight hours asleep, often in dense masses of leaves (Montgomery and Sunquist 1978). Both have exceptionally thick fur. *Bradypus* occurs at a density of 8.5 per hectare on Barro Colorado Island, a very high density for a Neotropical large mammal (Montgomery and Sunquist 1975). Each animal occupies a home range of less than 2 ha and may use fifty trees of up to thirty species, feeding on mature and young leaves. Food passage is so slow that rates must be measured in days rather than hours. Sloths descend from the canopy about once a week to defecate. Although analyses are unavailable, sloth feces probably contain a highly concentrated residue of indigestible secondary compounds (lignins, tannins, etc.).

Mother sloths carry the young for a few months after weaning, giving them the opportunity to learn individual trees. Then the mother disperses, leaving the home range to the offspring. This unique dispersal system probably minimizes intraspecific fighting over food (Montgomery and Sunquist 1978).

Although sloths do not occur in the Old World, the arboreal folivore habit occurs in a variety of primates, and in Australia it is seen in koalas and phalangerids. The absence of sloths from the temperate zone may be due to thermoregulatory problems that are also shaped by their food habits.

## MONKEYS

The four species of Costa Rican monkeys were discussed earlier. Primates are another group essentially restricted to the tropics, and their absence from the temperate zone is not really surprising. Humans are the only contemporary primates that do conspicuously well in many extratropical habitats, and they are obviously using more than their own flesh and blood to deal with these habitats. One of humanity's truly unique traits is the propensity and ability to store and dispense large stores of food for the bad season. It is tempting to argue that northern winters would be just too hard on arboreal monkeys in terms of exposure, food availability, and predator avoidance. However, it should be noted that there is a lightly subsidized population of howler monkeys apparently surviving in a deciduous French woodland. Although the vine-free northern forests might appear to be poor substrate, monkeys seem to move quite well in tropical forests poor in vine entanglement. We suspect that the lack of year-round food availability would be the real problem for an arboreal extratropical primate. A very fat monkey might make it through a northern winter, but its arboreal mobility would be severely reduced, and sheltering sites would be very scarce.

For all the mammals discussed above it is obvious that no single trait is keeping them out of extratropical habitats, nor is there any single habitat characteristic that is an absolute barrier. For example, all the mammal groups discussed show the ability in some of their species or populations to withstand some cold or desiccation. Competition with other animals is a commonly suggested explanation of why they are missing from extratropical habitats. Whether direct, indirect, or diffuse in nature, the question of competition is simply unexplored.

To turn this question around, we also note that there are a number of extratropical mammals that do not range into the tropics in general and Costa Rica specifically. Bears are missing, and it is easy to blame their absence on an absence of large pulses of highly edible food types (big acorn crops, salmon runs, blueberry crops, winter-killed deer, etc.). The social cursorial carnivores seem to require much greater big game populations than now occur in Costa Rican forests. The social rodents (beaver, muskrats, marmots, prairie dogs) seem to lack large natural stands of highly edible plants (though capybaras are fair analogues to beaver and muskrats). The same may be said of the large cervids. However, if the Pleistocene megafauna had not disappeared it is possible that they would have helped keep more grassland open, thereby generating habitat for themselves and smaller grassland forms.

**What Happened to the Pleistocene Megafauna?**

There are several reasons to believe that the fauna of large mammals that ranged over North America from ten

to sixty thousand years ago was also present in Costa Rican forests. First there are Pleistocene horse fossils (*Equus fraternus*) from a variety of Costa Rican sites, including Guanacaste Province (L. Gómez, pers. comm.), where contemporary horses do very well. The same applies to gomphotheres (Snarskis, Gamboa, and Fonseca 1977; L. Gómez, pers. comm.). There is even a single ground sloth record from the San Carlos region of northern Costa Rica (L. Gómez, pers. comm.). If those animals were present, it is possible that some of their carnivorous and herbivorous associates were also present. Second, Venezuela and Mexico contain many more fossils of these groups, including sites of kills by ancient humans (Bryan et al. 1978). Judging from the very broad habitat ranges of contemporary large mammals in Africa, it is likely that animals that occurred in southern North America and northern South America also occurred in Costa Rica. Third, horses and cattle maintain solid breeding populations, even when left much to themselves, in a variety of Costa Rican habitats (including nearly pure forest in Corcovado National Park and Guanacaste).

Assuming that the big mammals were here, where did they go? There is no reason to believe that all of Costa Rica underwent any dramatic climate change ten thousand years ago. Martin (1973) postulated that Pleistocene hunters, rapidly descending on a naive set of large mammals, quickly extinguished the species that were slow to learn and whose traits were especially vulnerable to human hunting methods. The scarcity of fossil beds in the tropics make this type of speculation difficult to substantiate. However, part of the problem is that the tropics seem to be generally unsuitable for fossil preservation. A dead horse or cow on the rain-forest floor is represented by nothing but a skull in less than a year, and only the teeth remain after that. The same applies to larger mammals in deciduous forest, once the rainy season comes. One of us (Janzen) has observed that nothing but teeth and skull fragments were left of an elephant 7 months after it died in a Cameroon rain forest; only natural scavengers processed it. At a similar site an elephant 2 years after death had only the decomposing molars remaining. The wet tropics are notoriously poor sites for animal preservation as fossils, and observing the high speed of decomposition on land or in water makes it obvious why.

Why do we care? Certainly extinctions of animals occur all the time, and this change is an integral part of the evolutionary process. However, it seems possible that the "natural" habitats studied today in Costa Rica have undergone ten thousand years of ecological adjustments among the surviving fauna and flora, but many of the possible evolutionary changes have not yet occurred. The habitats should be liberally sprinkled with anachronisms, such as sizable crops of big-seeded large fleshy fruits that are not consumed by the contemporary mammals. Also,

spines and other mechanical and chemical defenses of vegetative parts are widespread, but from what are they protecting the plants (Janzen and Martin 1982)? For example, the large fruits of *Enterolobium cyclocarpum*, *Pithecellobium saman*, *Hymenaea courbaril*, *Annona purpurea*, *Sapranthus palanga*, *Cassia grandis*, *Acacia farnesiana*, *Crescentia alata*, and *Guazuma ulmifolia* are only part of the Guanacaste species that are eaten by horses and cattle and probably were originally dispersed by the Pleistocene megafauna. These plants probably have different distributions and densities among habitats now that their major dispersal agents are missing. In fact, a mixed grassland-forest, populated by range cattle and horses, is probably a more "natural" habitat for these plants than the pre-Columbian pure forest habitats being protected by Costa Rican parks.

### How Good Are Costa Rican Mammals as Seed Dispersers?

Seed dispersal by Costa Rican mammals appears rather simple. Mammals eat fruits and spit or defecate the seeds elsewhere, or they carry the seeds off to eat later (cache and scatter hoard) but for various reasons do not eat them. However, to illustrate the deceptive nature of this simplistic view, a few of the high points of an ongoing study of horses, spiny pocket mice, and guanacaste seeds in Santa Rosa National Park are mentioned below.

Horses avidly eat the newly fallen fruits of the guanacaste tree (*Enterolobium cyclocarpum*), and the ungerminated seeds appear in the dung (Janzen 1981c). These later germinate to produce healthy seedlings. However, when the horse is chewing the fruits, it spits out 40–60% of the seeds (Janzen 1981b). Some of these seeds have been nicked by the horse's molars; this raises the immediate germination percentage upon contact with moist soil from about 3% to 10–15% for most seed crops. However, the spit seeds are left below the parent tree, where their almost certain fate is to be eaten by spiny pocket mice (*Liomys salvini*) if the tree is growing in forest. Beginning on the second day after the seeds are swallowed, a very small percentage of the seeds appear each day in the dung until about day 10–15, depending on the horse. Then, after weeks, occasional further seeds appear. The seeds in the dung are in three states. About 90% are ungerminated and do not germinate if placed in water; they are alive but unscarified. About 1–3% of the seeds are soft, just beginning to germinate, and still alive; they produce seedlings growing out of the dung (their fate to be determined by habitat, season, dung-beetle activity, and microsite exposure of the dung). An equal percentage of the defecated seeds are soft, recently germinated, and killed by the horse's digestive processes. The bulk of the seeds swallowed by horses never appear in the dung, and it appears that they are either digested or remain (in the cecum?) for many months. Seed-coat frag-

ments occur frequently in the dung, but indigestible buttons used as controls remained in the horse for months.

As implied above, defecation in dung of even some guanacaste seeds does not mean that the horse is a "good" guanacaste seed disperser. When horse dung with guanacaste seeds in it is left in Santa Rosa National Park deciduous forest, the spiny pocket mice find it in 1–2 nights and eat the seeds. The rate at which they find dung-free seeds is substantially less. However, if the dung is dropped in open grassland several hundred meters or more from forest, seeds placed in it germinate unmolested (though the seedlings are on occasion eaten by *Sigmodon hispidus*). We do not as yet know the fate of these guanacaste seedlings in open grassland, but fire and dry-season desiccation must take a heavy toll. When cattle consume guanacaste fruits, they spit out fewer than 5% of the seeds and pass nearly all the rest undamaged and ungerminated within 10 days; as many as half of these seeds may appear in the dung on day 4–5. The tapir (*Tapirus bairdii*) eats many fewer guanacaste fruits, spits about as many seeds as do horses, digests at least 70% of the seeds it swallows, but defecates in water (Janzen 1981a). By doing the latter it not only places the seeds in a *Liomys*-free habitat, but substantially increases the chance that the seedling will end up on a relatively competition-free and water-rich gravel bar or riverbank (a habitat often occupied by guanacaste trees).

If there are no large mammals present to eat the newly fallen guanacaste fruits, they lie indehiscent through the remaining 1–2 months of the dry season and then rot open during the first 2 months of the rainy season. In grassland, the seeds simply become part of the soil seed bank and occasionally germinate in later years as the hard seed coat is scarified by soil chemical reactions. In forest the pods are opened by the resident *Liomys* population and the seeds are taken off to an underground burrow (though some are eaten on the spot). If they happen to be just starting to germinate, they are peeled of their seed coats and eaten directly. In the laboratory, an adult mouse can maintain its body weight on a pure diet of about 10–13 germinating seeds per day for at least a month (Hallwachs and Janzen 1983). If ungerminated, some are eaten directly by chewing off the seed coat at one end and gnawing through the extremely hard seed contents; a mouse can maintain its body weight on a pure diet of about 6–7 such seeds per day, again for a month. A highly variable number of the hard seeds are also notched at an end, in one to four places; these germinate immediately when placed in water or moist soil, and the mouse then eats them (W. Hallwachs, pers. comm.). What we do not yet know is the fate of guanacaste seeds that the mouse caches below ground but then loses because it dies or cannot relocate them.

As mentioned earlier, spiny pocket mice are avid collectors of guanacaste seeds (as well as other species of

seeds) from horse dung (Janzen 1982*b,c*). If forty piles of dung (a normal adult horse dung pat is about 1.5 kg) are placed out in the forest with twenty guanacaste seeds buried in the center of each, it is normal for the *Liomys* in the upland forests of Santa Rosa National Park to get all the seeds the first night. The size of the dung pat has little effect; twenty to five hundred seeds buried in the center of as much as 15 kg of horse dung are 99–100% discovered and removed the first or second night. Cattle dung, a more liquid and more caustic substrate, sometimes retains its seeds as long as 4 days in the face of active *Liomys* seed harvesting. Guanacaste seeds placed in the same forest, but without dung associated, sometimes remain as long as a week before they are removed. In certain circumstances horse dung is a more effective trap bait than oatmeal or peanut butter, though for this to occur, there must have been seed-enriched horse dung in the area previously.

All seed-eating and frugivorous mammals probably function as seed dispersers for some species of Costa Rican plant. However, there are many variables peculiar to the seed and the animal. Fruits of *Spondias mombin* are eaten whole by coatis, spider monkeys, and howler monkeys; the large nuts are defecated within 1–2 days. Horses and a captive tapir, however, avidly chew the fruit pulp off the nut and spit it out (below the parent tree in nature). Agoutis also eat the pulp and then sometimes bury the nuts (Smythe 1978).

Many animals eat figs, and it appears that the seeds are generally too small to be ground up. *Artibeus* bats are champion fig eaters (Morrison 1978*a*; Janzen 1979), but their seed dispersal is complex. They carry a fig from the parent tree to a feeding roost tens of meters away (and see their similar treatment of Guanacaste *Andira* fruits, Janzen et al. 1976) and bite pieces out of the fig wall and inner seed-floret mix. After chewing this mix and pressing out the juices, they spit it out as a pellet. These pellets may accumulate by the hundreds below a single bat's feeding roost, and each contains an average of about one viable seed (the remaining seeds are empty shells, since fig wasps long ago emerged from them). However, while feeding on the fig, the bat is somehow removing a small number of only viable seeds along with the juices. These come out in the feces, and a single fecal load may contain as many as fifty of these good seeds. These fecal pellets are dropped in widely scattered areas on the vegetation and ground, as well as at the feeding roost.

After collecting dung of many species of Costa Rican mammals in many habitats, we are left with the general impression that mammals generate widely scattered, diffuse seed shadows, but that these often contain intense small peaks and contour lines (e.g., 55,000 *Piper auritum* seeds below one bat feeding roost in Corcovado National Park; Janzen 1978*a*). It is commonplace to

come upon a pile of monkey feces containing several hundred seeds of *Genipa americana*, *Chomelia spinosa*, or *Alibertia edulis* in Santa Rosa National Park. On the other hand, we suspect that there is much greater seed mortality by mammalian dispersal agents than generally realized. Peccaries almost never pass entire seeds and are adept at cracking those that require as much as several hundred pounds pressure to break (e.g., Janzen and Higgins 1979; Kiltie 1979). Tapir dung almost never contains viable seeds, but seed coat fragments are common in it. Deer customarily spit out all seeds except the very smallest. Even mice such as *Oryzomys*, *Sigmodon*, and *Liomys* ground up the minute seeds in such fruits as *Muntingia calabura* and *Ficus* spp. as well as defecating some whole seeds (W. Hallwachs, pers. comm.).

In interpreting mammal dispersal of seeds, extreme caution must be used for two other reasons. First, as implied above in the interaction of mammals with guanacaste seeds, the detailed site of seed defecation matters, as does the fact that the seeds are marked with a conspicuous odor flag for a while after defecation. Second, many mammals eat seeds while still in the milk stage and are thus seed predators rather than dispersers. Monkeys and squirrels are heavy offenders. Further, in addition to killing seeds directly, when they pick immature fruits and eat some of the seeds, the remaining seeds often die even if untouched.

#### What Are the Special Costa Rican Challenges to a Mammal?

With respect to the gross traits of the physical environment, Costa Rica is about as hospitable as any tropical country. Snow has never been recorded there. Although nighttime temperatures may drop as low as  $-3^{\circ}\text{C}$  on the tops of the taller mountain ranges, the coldest daylight temperatures are in the range of  $5-15^{\circ}\text{C}$ . These extremes do not appear to be much of an instantaneous challenge for a warm-blooded animal. However, the impact of a physical environmental challenge, such as a drop in temperature, is also a function of the temperature regime in which the animal normally lives. It may well be that apparently small temperature extremes encountered by a Costa Rican mammal in moving over elevational gradients, extremes that seem minor to those of us accustomed to extratropical fluctuations, are severe challenges (Janzen 1967).

Although Costa Rica has (had) extensive areas of deciduous forest, these differ strongly from similar deciduous forest in Mexico and Venezuela in that the lowlands of Guanacaste are crossed at frequent intervals by ever-flowing rivers off the Pacific slopes of the volcanoes. These linear oases are dry-season sites of mammal concentration of water, shade, fruit and foliage, and animal prey. During the Pleistocene this riparian vegetation

probably experienced the same heavy usage as is currently experienced by riparian vegetation in eastern Africa during the dry season. Of course the dry season means a shortage of water for most mammals and thereby restricts their movements, but the challenge is not as severe as it would be if moist habitats were not nearby and if certain remnants of the rainy season did not persist. There are tree holes with drinking water (Glander 1978), many trees with juicy fruits (based on the groundwater supply accumulated during the rains), and local springs and surfacings of underground streams. One such water-hole in Santa Rosa National Park contains a volume of about 8 liters of water at any one time and is daily visited by several deer, five to fifteen coatis, five to fifteen peccaries, two to five agoutis, five to twenty white-faced monkeys, and numerous birds.

On the other hand, the frequent rainy season rains undoubtedly render many underground cavities inhospitable for mammal nests and sleeping sites. Logs and dead standing trees rot rapidly and are often waterlogged. Dry cavities, especially large ones, are probably in short supply in many areas.

In contrast to the physical environment, there are a number of fairly drastic biotic challenges to a Costa Rican mammal in comparison with, for example, those faced in the eastern deciduous forests of North America. Ants are probably one of the worst. Both army ants and various solenopsines (e.g., *Solenopsis* fire ants) are killers of live-trapped small rodents in rain-forest sites and may be a major source of nestling mortality for those that nest on, in, or near the ground. Even arboreal nesting will not help mammals escape the climbing army ants such as *Eciton burchelli*. Ants are quick to occupy small carcasses (Cornaby 1974) and probably keep small carnivores away. Snakes are of course a predation threat to small and medium-sized mammals in all forests, but Costa Rican forests contain a much greater array of sizes and foraging types of snakes than do extratropical forests. Boa constrictors take animals as large as coatis (e.g., Janzen 1970), and the large vipers take animals agouti-sized and smaller. Whether predation pressure by birds and predaceous mammals is more intense in a Costa Rican forest than in an extratropical forest is unknown. Although the tropics are often thought of as more "disease-ridden" for humans and their livestock, there is no compelling natural-history information that we know of to indicate that this is also true for Costa Rican wild mammals. There has never been a comparative survey of the parasites or diseases of animals found in both northern and Costa Rican habitats.

It is tempting to suggest that food for herbivores is generally less edible in Costa Rica forests than in extratropical ones, but this generalization is probably too broad to be useful (or true). The large northern coniferous

and fagaceous forests produce highly edible seed crops compared with the mix of secondary-compound-rich seeds found on the floor of a tropical forest. However, it is hard to compare these forests because of the highly pulsed nature of the northern seeds as compared with the more uniform production of tropical seeds (Janzen 1971, 1978b). There are certainly a large number of species of foliage that large browsing herbivores reject in tropical forests (e.g., Janzen 1982a; Glander 1975), but northern forests likewise have species of plants consistently rejected by deer, elk, moose, and such. Perhaps after we have much more browsing data for tropical tapirs, horses, peccaries, and white-tailed deer we will be able to make a more reliable statement.

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