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CHAPTER 5

Tropical Dry-Forest Mammals of Palo Verde

ECOLOGY AND CONSERVATION IN A CHANGING LANDSCAPE

Kathryn E. Stoner and Robert M. Timm

MESOAMERICA CONTAINS some of the world's most diverse forests. It has at least 20 major life zones, based on variations of temperature and precipitation that can be broadly summarized in five tropical forest types—dry forest, wet forest, montane forest, coniferous forest, and mangrove swamp (Holdridge et al. 1971). When the Spaniards arrived in the New World, there were perhaps 550,000 km^2 of dry forest on the Pacific side of lowland tropical Mesoamerica. This dry forest occupied as much or more of the Mesoamerican lowlands as did wet forests. Unfortunately, no habitat type in Mesoamerica has been more influenced by humans than the tropical dry forest; today less than 1 percent remains intact, with less than 0.01 percent under protection.

In Costa Rica tropical dry forests occur throughout the Pacific lowlands of Guanacaste Province and adjacent Puntarenas Province from sea level to about 500 m. Costa Rica's dry forest is characterized by a five- to six-month dry season from December through May, an annual precipitation of approximately 1,500 mm, and an average annual temperature higher than 24°C (Maldonado et al. 1995). These dry forests are largely deciduous today and encompass heterogeneous habitats varying in species composition, abundance, rainfall, and soils. These characteristics contribute to creating a harsh and heterogeneous, yet seasonally resource-rich, environment for the native mammals.

Mesoamerica has a diverse mammal fauna that includes elements from both North and South America as well as endemic species. More than 275 species in 28 families are recognized from the region, at least 17.8 percent of which are endemic to Mesoamerica. The mammals of the tropical dry forest are among the most poorly known of any of the bioclimatic life zones. Mammals that inhabit tropical dry-forest areas must be capable of dealing with high temperatures (to 40–41°C), very low precipitation in the dry season, and large fluctuations in the availability

of food resources over time. Most mammals of the dry forest can be characterized as resident generalists that shift their diets to utilize seasonally available food resources, as resident specialists that forage on insects, seeds, or fruit and nectar, or as migrants that occupy dry forests only seasonally and migrate to different habitats during periods of low food availability in search of available food sources.

As in all tropical ecosystems, a wide variety of mammals contribute to the maintenance of dry tropical forests through their role in seed dispersal and pollination (Heithaus et al. 1975; Chapman 1989; Helversen 1993; see chapter 13). Bats visit, and presumably pollinate, at least 14 species of flowers in the tropical dry forest of Palo Verde, and 29 species of fruits are consumed by bats, which in turn disperse their seeds (K. Stoner and R. Timm unpubl. data). In Guanacaste there are two peak periods of flowering activity: one during the long dry season and the other during the middle of the rainy season (Frankie et al. 1974). Primates, many rodents, and several generalist carnivores also are important seed dispersers in Costa Rica's tropical dry forests. Thus the preservation of wildlife and its habitats are interrelated challenges, and conservation efforts in Guanacaste's tropical dry forests need to consider both of these issues together.

DIVERSITY, DISTRIBUTION, AND ENDEMISM

At least 207 species of mammals, including 110 species of bats, have been documented within Costa Rica's borders, and more will undoubtedly be discovered (Timm 1994; Rodríguez and Chinchilla 1996; Timm and LaVal 1998; Timm et al. 1999). The majority of mammals found in Costa Rica's tropical dry forest are distributed northward through Mesoamerica (sometimes as far as western Mexico), and many occur southward into South America. Of the approximately 114 species of mammals originally present in Guanacaste's tropical dry forest, perhaps 110 are still found in this habitat. Bats are by far the most diverse group, with more than 66 species, followed by 11 species of rodents, 7 species of marsupials, 6 species in the weasel family, 5 species of cats, 3 species in the raccoon family, 3 species of primates, 3 species of artiodactyls, 2 species of canids, 2 species of xenarthrans (edentates), 1 rabbit (*Sylvilagus floridanus*), and 1 tapir (*Tapirus bairdii*). Species reaching the southern boundary of their distribution in Costa Rica's dry forest include opossum (*Didelphis virginiana*), gray sac-winged bat (*Balantiopteryx plicata*), gray short-tailed bat (*Carollia subrufa*), long-tongued bat (*Glossophaga leachii*), Salvin's spiny pocket mouse (*Liomys salvini*), slender harvest mouse (*Reithrodontomys gracilis*), harvest mouse (*R. paradoxus*), and hooded skunk (*Mephitis macoura*). Raccoons (*Procyon lotor*), coyotes (*Canis latrans*), Mexican porcupines (*Coendou mexicanus*), and Underwood's long-tongued bats (*Hylonycteris underwoodi*) are found as far south as southwestern Panama. No species reaches the northern limit of its distribution in Costa Rica's dry forest.

Dry forests are believed to be less diverse than wet forests because of the harsh seasonal environment. However, in Costa Rica the documented mammal fauna of the Pacific lowlands consists of 114 species, which is only slightly lower than that of lowland rain forest of La Selva in northeastern Costa Rica, with 123 species (Timm 1994; R. Timm unpubl. data). The dry forest has 66 species of bats and La Selva 67 species. The pattern of lower diversity in tropical dry-forest habitats has been observed in Mexico for other groups of vertebrates (Ceballos 1995) as well as for flora (Gentry 1995).

Most of the resident mammal species of the dry forest are generalists that have a broad diet allowing them to survive changes in food abundance. Some of these generalists include mantled howler monkeys (*Alouatta palliata*), white-faced capuchins (*Cebus capucinus*), white-tailed deer (*Odocoileus virginianus*), coyotes, white-nosed coatis (*Nasua narica*), raccoons, opossums, and some frugivorous bats. Although howler monkeys are mainly folivorous and are selective of the leaves they ingest, they can consume more than 60 different species of plants within any one area (Glander 1978), allowing them sufficient

flexibility to find food throughout the year. During the driest months, when more than 80 percent of the trees have lost their leaves, howlers may still find edible leaves in some of the evergreen species such as *Cecropia peltata* and the wild cashew *Anacardium excelsum*. White-faced capuchins also fare well in the dry forest even when fruit is scarce at the beginning of the rainy season because they then shift their diet to consume mostly insects (Chapman 1988), which are especially abundant at this time (Janzen and Wilson 1983). Capuchins also consume other sources of protein, such as birds' eggs, young birds, and baby coatis. Although white-tailed deer populations in dry forests experience periodic crashes during particularly harsh years, deer are browsers and consume many species of both herbaceous and woody plants and are thus well adapted to cope with the dry tropical forest environment (Vaughan and Rodríguez 1991). Coyotes consume significant amounts of insects, fruits, and grasses in tropical dry forests, and their diet varies seasonally in Costa Rica (Vaughan and Rodríguez 1986), as it does throughout their range. Coatis, raccoons, and opossums are generalists and consume a wide variety of invertebrates (especially insects), fruits, seeds, and smaller vertebrates such as frogs and snakes. Some frugivorous bats, such as Seba's short-tailed fruit bat (*Carollia perspicillata*), consume more insects during periods in which fruit is not available (Fleming 1988; but see the section "Migratory Species" later in this chapter).

Several dry-forest specialists with specific diets are present throughout the year. These include various species of insectivorous bats (funnel-eared bats [*Natalus stramineus*], leaf-chinned bats [*Pteronotus* spp.]), the smaller rodents, and several carnivores. Seasonal migrants that are more abundant during certain periods of the year when specific food sources are present include spider monkeys (*Ateles geoffroyi*) and some nectarivorous (*Glossophaga* spp.) and frugivorous bats (Stoner 2001).

Costa Rica's mammal fauna includes several species that are endemic to the country, including at least six rodents, two shrews, and one bat; these species are found at mid- and high elevations (Timm 1994). All species that historically were found in the dry forest of Costa Rica also were found in the dry forest of adjacent Nicaragua or farther north; thus Costa Rica has no truly endemic dry-forest mammals. However, one species of harvest mouse (*R. paradoxus*) is a dry-forest endemic restricted to the Pacific lowlands of Costa Rica and Nicaragua. In contrast to Costa Rica, tropical dry forests in western Mexico contain as many as 26 endemic mammal species (Ceballos 1995).

EXTIRPATED SPECIES

It is likely that more than 114 mammal species historically were present in the dry forest of Guanacaste. Although most of these can still be found in some areas of this dry forest, several have been extirpated from the Palo Verde region and throughout much of Costa Rica's Pacific lowlands during the past several decades. These include the water opossum (*Chironectes minimus*), giant anteater (*Myrmecophaga tridactyla*), Hoffmann's two-toed sloth (*Choloepus hoffmanni*), the brown-throated three-toed sloth (*Bradypus variegatus*), grison (*Galictis vittata*), southern river otter (*Lutra longicaudis*), white-lipped peccary (*Tayassu pecari*), and Baird's tapir (*Tapirus bairdii*).

Giant anteaters were once found throughout Costa Rica from the Pacific and Caribbean coasts to nearly the highest elevations (Timm et al. 1989). Populations of giant anteaters have been severely reduced throughout their range in the past several decades as a result of overhunting and habitat destruction. Giant anteaters must be considered extremely rare in Costa Rica and in danger of extinction.

Water opossums and southern river otters, and perhaps grisons, require fresh running streams. River otters are still present in Lomas Barbudal, Hacienda Monteverde, on the Corobicí River, and at Parque Nacional Guanacaste. We have historical reports of otters in the Cañas River near its confluence with the Tempisque River, and we suspect that they were found throughout the Tempisque River Basin. Al-

though we have no specific records of water opossums and grisons in Palo Verde, we strongly suspect that they were present historically, as they were widely distributed in both the Pacific and Caribbean lowlands from sea level to mid-elevations. It is likely that stream contamination and erosion caused by both the sugarcane and rice industries in this region contributed significantly to the disappearance of these aquatic and semiaquatic animals from much of the Pacific lowlands.

There have been no observations of white-lipped peccaries or tapirs reported in the Palo Verde region for several decades. David Stewart informed us that during the 1950s tapirs were found only as far west as the vicinity of the Pan American Highway, and neither species was at Palo Verde. Both tapirs and white-lipped peccaries are still found in the tropical dry forest of Parque Nacional Guanacaste, but they are best considered extirpated from the vast majority of the Guanacaste lowlands.

Although we do not have the historical documentation of how widely distributed two-toed sloths and three-toed sloths were in the tropical dry forest, we suspect that they were much more widely distributed when there were larger expanses of mature forest. Mature stands of tropical dry forest would provide a variety of tree species that would be seasonally available for the folivorous sloths as well as cool, shady habitat. Because sloths have a low metabolic rate, maintain a low body temperature, and are imperfect homeotherms (McNab 1985), they may be physiologically less able to survive in the harsh, hotter, drier habitats created by opening up mature stands of tropical dry forest. It is likely that sloths in the dry forest originally occupied riparian habitats that provided both evergreen trees for them to forage on throughout the year and shade for thermoregulation. Forested areas surrounding riparian habitats throughout the Guanacaste lowlands have been largely destroyed owing to the development of agriculture. Costa Rican law prohibits the destruction of habitat within 15 m of rivers (Law No. 7575, Article No. 33); however, this is not enforced, and in most agricultural areas the crops often run up to the rivers' edge.

With such a diverse group of species having disappeared from Palo Verde, it is informative to ask what traits these taxa share that may account for their extirpation or susceptibility. The species that are extirpated are all either highly prized game species that have been eliminated by overhunting (white-lipped peccaries and tapirs) or specialists that either feed on specific foods or have very specific habitat requirements. In general, species that first disappear from a region following alterations are those that have a large body size, low initial population density, large territory size, or narrow habitat tolerance.

ENDANGERED SPECIES

Costa Rica recognizes 13 species of mammals as endangered species in the country—the mantled howler monkey, spider monkey, squirrel monkey (*Saimiri oerstedii*), giant anteater, jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii*), oncilla (*Leopardus tigrinus*), jaguarundi, West Indian manatee (*Trichechus manatus*), white-lipped peccary, and tapir (MINAE 1999). An additional 14 species of mammals are recognized as being found in reduced populations. Of these, 7 are found within the dry forest of Costa Rica—the great false vampire bat (*Vampyrum spectrum*), white-faced capuchin, Hoffmann's two-toed sloth, Deppe's squirrel (*Sciurus deppei*), Underwood's pocket gopher (*Orthogeomys underwoodi*), grison, and southern river otter. Additionally, several species that are especially sensitive to habitat destruction and forest fragmentation include spider monkeys, felids, and predaceous bats of the family Phyllostomidae, subfamily Phyllostominae. Spider monkeys require a large home range because of their dietary preference for ripe fruits (Chapman 1988, 1989). Habitat fragmentation not only necessitates that they must travel farther to find the required ripe fruit resources but also sometimes eliminates arboreal passages that allow access to resources. Felids also require a large home range based on

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their carnivorous diet. The need to pass through open areas in a fragmented landscape makes them more vulnerable to illegal hunting. Previous studies on the predaceous phyllostomine bats have shown that they are sensitive to habitat destruction, and some species are rarely found in disturbed environments (Timm 1994; Schulze et al. 2000). Our data on bat populations in the dry forest suggest that a number of species are rare in this habitat and should be considered as endangered (table 5.1).

MIGRATORY SPECIES

Seasonal migrations along elevational gradients have been well documented for several species of tropical birds and butterflies; however, it only recently has been suggested that migrations may occur in Neotropical bats (Timm and LaVal 2000; Stoner 2001, 2002). The abundance of several species of bats at Palo Verde changes significantly over seasons, suggesting that they shift habitats seasonally or migrate into and out of the region (Stoner 2001).

Bats were mist-netted at Palo Verde approximately once every three weeks from January 1994 through July 1997, for a total of 56 nights. A total of 1,245 individuals representing 47 species were captured at one site, the Guayacán waterhole (10°21′ N, 85°20′ W) (table 5.1). All netting at the waterhole was with ground-level mist nets, which are excellent for sampling most frugivores, nectarivores, and some insectivores but underestimate higher-flying insectivores. Because Palo Verde has a marked dry season, bats are concentrated around waterholes, and sampling there produces a higher number of taxa and greater numbers of individuals than would be expected to be captured at any one site in the surrounding forest. Including our data from netting at Palo Verde, which began in the 1970s and continues to the present, we have captured or observed an additional 12 species in the area, for a total of 59 species.

Significant differences occur in abundances (estimated as bats/m^2FD net × hour) of the most common frugivorous bats over different seasons. The frugivorous Seba's short-tailed fruit bat and the Jamaican fruit-eating bat (*Artibeus jamaicensis*) account for more than 50 percent of the bats captured at this site. An additional 12 species account for 40 percent of captures, whereas the majority of species (33) account for less than 10 percent of total captures, and most of these were captured on fewer than 5 nights of the 56 nights sampled. Excluding the aerial insectivores, of the 10 species captured only once, there were 4 nectarivores, 3 carnivores, 2 gleaning insectivores, and 1 frugivore. Although mist-net data do not accurately sample the abundance of aerial insectivores, they provide useful data for comparing relative abundance of most other bat species within a community. Our mist-netting efforts at Palo Verde suggest that several of the nectarivorous and predaceous bats are found at very low densities, likely a result of disturbance within Palo Verde (i.e., fire and cattle), lack of mature trees, habitat fragmentation surrounding Palo Verde, and lack of forested corridors within the region.

Patterns of capture for some other species of bats also suggest that abundances vary seasonally. The pygmy fruit-eating bat (*Artibeus phaeotis*) and Thomas' fruit-eating bat (*Artibeus watsoni*) were never captured in March, April, May, July, or August. The wrinkled-faced bat (*Centurio senex*) was captured in December (1995), January (1996), and February (1996, 1997) but rarely in August (one individual was captured in August 1995). The insectivorous orange-throated bat (*Micronycteris brachyotis*) was caught from December through April (and two individuals in July), and the tiny big-eared bat (*Micronycteris minuta*) was caught from January through April (and one was captured in June). Although sample sizes for these species were not sufficient to compare statistically, their abundance over seasons and the fact that the same pattern was observed over several years suggest that most of these species are likely moving in and out of the area on a seasonal basis. These patterns of abundance and absence are not one of source/sink because individually marked animals return after months of absence (Stoner 2001).

TABLE 5.1

Abundance of 47 Species of Bats Captured at the Guayacán Water Hole in Palo Verde from January 1994 through July 1997

SPECIES	TOTAL NUMBER CAUGHT	PERCENT OF TOTAL BATS CAUGHT	NUMBER OF NIGHTS CAUGHT	PERCENT OF NIGHTS CAUGHT
Carollia perspicillata	472	37.9	47	84
Artibeus jamaicensis	174	13.9	40	71
Sturnira lilium	111	8.9	33	59
Artibeus lituratus	65	5.2	27	48
Rhogeessa tumida	49	3.9	17	30
Pteronotus davyi	47	3.8	17	30
Glossophaga soricina	43	3.4	17	30
Artibeus phaeotis	38	3.0	21	38
Centurio senex	38	3.0	11	20
Micronycteris brachyotis	37	3.0	15	27
Artibeus watsoni	25	2.0	14	25
Pteronotus parnellii	17	1.4	12	21
Natalus stramineus	16	1.3	9	16
Desmodus rotundus	13	1.0	8	14
Pteronotus gymnonotus	11	0.9	9	16
Trachops cirrhosus	10	0.8	8	14
Micronycteris minuta	9	0.7	8	14
Uroderma bilobatum	7	0.6	2	4
Carollia brevicauda	6	0.5	4	7
Noctilio leporinus	6	0.5	4	7
Platyrrhinus helleri	5	0.4	2	4
Micronycteris microtis	5	0.4	5	9
Carollia castanea	4	0.3	4	7
Lasiurus blossevillii	4	0.3	NA	NA
Vampyressa nymphaea	4	0.3	4	7
Micronycteris nicefori	3	0.2	3	5
Micronycteris schmidtorum	3	0.2	3	5
Chrotopterus auritus	2	0.2	2	4
Diphylla ecaudata	2	0.2	2	4
Tonatia brasiliensis	2	0.2	2	4
Glossophaga commissarisi	1	0.08	1	2

TABLE 5.1 *(continued)*

SPECIES	TOTAL NUMBER CAUGHT	PERCENT OF TOTAL BATS CAUGHT	NUMBER OF NIGHTS CAUGHT	PERCENT OF NIGHTS CAUGHT
Glossophaga leachii	1	0.08	1	2
Pteronotus personatus	1	0.08	1	2
Noctilio albiventris	1	0.08	1	2
Macrophyllum macrophyllum	1	0.08	1	2
Phyllostomus discolor	1	0.08	1	2
Vampyrum spectrum	1	0.08	1	2
Hylonycteris underwoodi	1	0.08	1	2
Carollia subrufa	1	0.08	1	2
Lichonycteris obscura	1	0.08	1	2
Micronycteris hirsuta	1	0.08	1	2
Cyttarops alecto	1	0.08	NA	NA
Rhynchonycteris naso	1	0.08	NA	NA
Saccopteryx bilineata	1	0.08	NA	NA
Myotis elegans	1	0.08	NA	NA
Myotis riparius	1	0.08	NA	NA
Molossus molossus	1	0.08	NA	NA
Balantiopteryx plicata[a]				
Saccopteryx leptura[a]				
Diclidurus albus[a]				
Chiroderma villosum[b]				
Peropteryx kappleri[b]				
Peropteryx macrotis[b]				
Myotis albescens[b]				
Myotis nigricans[b]				
Eumops auripendulus[c]				
Molossus ater[c]				
Molossus pretiosus[c]				
Molossus sinaloae[c]				
Micronycteris sylvestris[d]				
Mimon cozumelae[d]				
Mimon crenulatum[d]				
Tonatia bidens[d]				

TABLE 5.1 *(continued)*

SPECIES	TOTAL NUMBER CAUGHT	PERCENT OF TOTAL BATS CAUGHT	NUMBER OF NIGHTS CAUGHT	PERCENT OF NIGHTS CAUGHT
Tonatia silvicola[d]				
Uroderma magnirostrum[d]				
Vampyrodes caraccioli[d]				
Eumops underwoodi[d]				
Total	1,245			

Note: All data presented in this table are based on 56 nights of netting. Species listed as NA (not applicable) refer to aerial insectivores whose abundance is poorly estimated with mist-netting techniques and thus would be underestimated by our sampling method. Twelve additional species that are listed were observed or captured within the area, and eight additional species listed are expected to occur at Palo Verde (see individual notes).
[a]Bats observed roosting within the area.
[b]Bats captured within the dry forest in the Palo Verde region.
[c]Species detected by their echolocation signals (E. Kalko pers. comm.).
[d]Species that are expected to be found in Palo Verde.

At Palo Verde, Peter's tent-making bat (*Uroderma bilobatum*) also exhibits a seasonal pattern in abundance and reproduction (Timm and Lewis 1991 and subsequent observations by Timm through January 2003). During June and July (mid–rainy season) adult males and females as well as juvenile bats are present in a breeding colony. All adult females captured during the mid–rainy season were either pregnant or lactating. During January and February (dry season), only a couple or in most cases no bats were observed. The few bats that were captured during the dry season were males with testes only moderately developed.

Although we have not yet identified where the bats are moving when they are not in the area, we suspect two areas. The first possibility is that during periods of reduced resource availability bats change habitats to riparian areas within the lowland forest of Guanacaste, possibly near the Bebedero River, Piedras River, or Tempisque River. Another possibility is that bats in the lowland tropical dry forest migrate elevationally to higher areas with more abundant resources during certain seasons.

In addition to bats, some arboreal and terrestrial mammals of the tropical dry forest are migratory. Spider monkeys are present in Palo Verde only during the rainy season and appear to migrate out of the area during the dry season. Fruit availability is strongly seasonal here (Frankie et al. 1974), and the migration of spider monkeys is probably related to the lack of abundant fruit resources during the dry season. Large herds of white-lipped peccaries originally were found in the dry forests of Guanacaste and also were migratory (Janzen 1986). We suspect that the peccary herds would have fed heavily on the seasonally abundant acorns (*Quercus oleoides*) and palm fruits such as *Acrocomia vinifera*, *Attalea butyracea* (= *Scheelea rostrata*), *Bactris major*, and *B. minor*.

FACTORS AFFECTING MAMMALS OF THE TROPICAL DRY FOREST

HUNTING

Hunting and deforestation were the first important influences on the recent distribution and density of mammals of the tropical dry forest, as they were in other areas within the Neotropics. All large and some small mammals in tropical dry forests have been subjected to extreme hunting pressures. The Chorotega, the dominant

pre-Columbian human inhabitants of the Guanacaste lowlands, hunted a wide variety of mammals (Quesada López-Calleja 1980). The most common mammals hunted today as a source of protein in the lowlands of Guanacaste include white-tailed deer, pacas (*Agouti paca*, known in Costa Rica as *tepezcuintle*), collared peccaries (*Pecari tajacu*), armadillos (*Dasypus novemcinctus*), and opossums. Pacas are highly prized but infrequently obtained because they occur in such low numbers. Hunters with whom we have spoken are opportunistic, taking any of the preferred game animals when they are available.

Poaching continues to be one of the most serious problems that threaten Parque Nacional Palo Verde, and this is largely attributed to the lack of guards to protect this approximately 20,000 ha park (Vaughan et al. 1995). White-tailed deer and collared peccaries are the most common animals poached in the park. Most illegal poaching occurs within protected areas such as Palo Verde because these areas provide the best wildlife habitat and consequently the highest densities of game species. In 1997 in the Area de Conservación Tempisque, of the hunters arrested for poaching, approximately three were released for every one that was actually convicted (MINAE 1998). Poaching likely will continue in national parks and other protected areas until more park personnel are available to monitor these areas and stronger laws are enacted and enforced to protect wildlife.

DEFORESTATION AND CONVERSION OF TROPICAL DRY FOREST

The single factor that has most strongly influenced the current distribution and abundance of mammals in the dry forest is land conversion—the loss of tropical dry forest. Conversion of tropical dry forest in Costa Rica has resulted from various activities, including cattle ranching, the timber industry, agricultural development, and the tourism industry (see chapter 21). Regardless of the reasons for deforestation, the result has been the creation of vast expanses of open pastures, agricultural fields, fragmented-forested habitats, and extensive areas in various stages of succession. Hence, large areas of land are only marginally inhabitable by most native species. Opening up forest in the harsh, highly seasonal environment of this area has had additional consequences, including a subsequent increase in dryness, higher temperatures, reduced availability of appropriate forest habitat for both food resources and living space for mammals, and erosion of topsoil, which limits nutrients. The few fragments of dry forest that remain in Costa Rica have all been influenced by the surrounding habitat alterations.

Much of the recent conversion is due to agricultural development, especially sugarcane and rice production. Sugarcane fields, not present in the Guanacaste area until the 1960s, accounted for approximately 16 percent of the area in the basin by 1992–93, and rice and other agricultural crops accounted for an additional 13.9 percent. The lower Tempisque Basin is one of the areas that has been designated by the Ministerio de Agricultura y Ganaderia and the Servicio Nacional de Aguas Subterraneas Riego y Avenamiento as a rice production area, and many pastures and small forest fragments are being converted to rice fields. Because of the extensive rice fields between Palo Verde and Lomas Barbudal, the movement of most terrestrial mammals between these two important reserves is no longer possible.

CATTLE, *JARAGUA*, FIRE, CATTAILS, AND LAND MANAGEMENT

It is our intent here to review briefly the history of cattle use and the introduction of African grasses in the region and to assess their impact on native mammals. In recent years, the use of cattle as a habitat management tool in Palo Verde has been the source of considerable controversy (McCoy 1994; McCoy and Rodríguez 1994; Stern et al. 2002; see chapter 21). Cattle ranching has been important in Guanacaste for more than three centuries, and all of what is now Parque Nacional Palo Verde was a working cattle ranch until the creation of the wildlife refuge in 1977. Cattle were slowly removed from the

refuge during the period 1978–81 (when it was designated a national park); however, some cattle were reintroduced into Palo Verde in 1987 as part of an active management plan to control cattails (*Typha dominguensis*—locally called *enea*), which had expanded dramatically and quickly in the lagoon, effectively eliminating much of the open water needed by waterfowl. In 1991 more cattle were introduced into Palo Verde as part of a management plan to control fires within the park. During the late 1990s, some 1,500 to 6,000 head of cattle were present in the park, with some 600 head in the Palo Verde lagoon and the rest in forested areas and pastures.

One of the earliest ranches in what is now Costa Rica and adjacent Nicaragua was established at Santa Rosa in the late 1500s (Janzen 1986). By 1800, large ranches were present throughout Guanacaste (Boucher et al. 1983). Cattle were raised in Guanacaste primarily for the hides, which were exported to Europe for use as leather; to a lesser extent lard and dried beef also were exported. The *finqueros* (ranch hands) hunted native mammals, especially peccaries, for food and killed jaguars, pumas, and coyotes because they were a threat to livestock.

The rapid deforestation of Costa Rica's dry forest during the 1950s, 1960s, and 1970s, converting mature forest into pastureland, was encouraged by low-interest loans from the national banks, as well as by support from the Agency for International Development and the World Bank (Parsons 1983). During this rapid expansion of the cattle industry, ranchers experimented with several breeds, progressing from the Spanish criollo to various beef breeds, including Herefords, Angus, and Charolais. Today, zebus and Brahman are found throughout the lower elevations of Costa Rica, as well as throughout the Neotropics, because they are well adapted to the hot climate and extremes of rainy and dry seasons and are highly resistant to bites from ticks, flies, and other arthropods.

Jaragua, or African star grass (*Hyparrhenia rufa*), and other African savanna grasses were introduced into Costa Rica in the 1920s as cattle forage because the native Costa Rican grasses are not well adapted for large-scale production in open pastures (Sáenz-Maroto 1955; León S. et al. 1982). The *jaragua*, which came to Central America via Brazil, was introduced into the Palo Verde area from Puntarenas in the 1920s (Sáenz-Maroto 1955; Parsons 1972). As in all C_4 grasses, the nutrient levels of growing stems and leaves during the rainy season are high, and the young grasses provide good forage for cattle (McCammon-Feldman 1980); however, the mature plants during the dry season have little nutritional value (Daubenmire 1972) and are not consumed by cattle. This species is native to the plains of Africa, grows to a height of 2 m or more, and is highly adapted to fires. Throughout the Neotropics, regular burning was, and continues to be, a management strategy to remove mature, nondigestible woody stems during the dry season, promoting growth during the succeeding rainy season. This practice has been the source of numerous uncontrolled fires since its introduction into the area. The fuel provided by this non-native grass allows the fires to burn hotter and to be more destructive than they are by the burning of native vegetation.

C_4 grasses such as *jaragua* grow best in warm, dry conditions, and they mature much more quickly than C_3 grasses. Tall C_4 grasses often become so dense that other plant species are unable to compete. Annual burning of dry aboveground vegetation releases nitrogen, enriching the soil for more dominant C_4 grasses, enhancing their growth and allowing them to outcompete other plant species (Collins et al. 1998). Fires also warm the soil, which favors the growth of C_4 grasses. In temperate prairies of the midwestern United States, annually burned watersheds had the lowest plant species richness, as burning increases the dominance of C_4 grasses and reduces plant species diversity (Collins et al. 1998).

In tropical rain forests of the Amazon Basin, fires have been found to create a positive feedback system whereby periodic burning causes an increase in fuel loading, fire intensity, and fire susceptibility (Cochrane et al. 1999). The first fires characteristically kill only the smaller

trees, especially those with thin bark. Because of fuel buildup, second fires are faster moving and more intense, often killing larger, thicker-barked trees. The long-term effect of recurrent fires in Brazil is to create an open canopy savanna or scrub habitat. In the Mesoamerican dry forest, several tree species with smooth, photosynthetic bark (especially species such as *Bursera simaruba*) are often killed by the first fires. Although some tree species that have bark of medium thickness, such as *Guazuma ulmifolia, Crescentia alata, Byrsonima crassifolia,* and *Curatella americana,* may survive initial burns, continued exposure to surface fires from adjacent pastures eventually penetrates and eliminates the forest (B. Williamson pers. comm.).

Forest fragments have persisted only where they have been protected by humans or by natural firebreaks such as roads and limestone outcrops. Remnant trees, such as *cenizero* (*Samanea saman*) and *guanacaste* (*Enterolobium cyclocarpum*), can be found in pastures, but usually only as older, isolated individuals. Recruits into pastures are limited to a few species, namely, *Byrsonima crassifolia, Crescentia alata, Curatella americana,* and *Guazuma ulmifolia.* These four species are widespread as tree islands throughout the pastures of Mesoamerica and provide some of the few fruits and roost sites available for wildlife in this anthropogenic landscape (Hartshorn 1983).

The development of large-scale cattle ranching in Guanacaste in the early 1900s, combined with the introduction of *jaragua,* not only reduced the available forested habitats for mammals but also stimulated a series of other changes that dramatically affected the remaining habitat and fauna. Previous studies on cattle document that livestock alter ecosystem processes by reducing the cover of herbaceous plants and litter, disturbing and compacting soils, reducing water infiltration rates, and increasing soil erosion (Belsky and Blumenthal 1997). Furthermore, they suggest that forests subjected to grazing pressure are less resilient to natural disturbances such as fire and diseases.

Other direct effects of cattle include competition with native mammalian herbivores (Janzen and Wilson 1983; Robinson and Bolen 1984) and selective grazing on many native plant species. Cattle directly compete with deer for forage, and inadequate habitat may be available for native wildlife because of intensive cattle grazing. A number of previous studies in other habitats demonstrate that competition with cattle may increase annual deer mortality by as much as 40 percent (Robinson and Bolen 1984). Conklin (1987), in a study of several species of plants that are potential browse for cattle at La Pacifica, found that cattle readily consume a large number of native dry-forest trees and shrubs, eating leaves, stems, fruits, and seeds of a wide number of species. Saplings of native species provide excellent protein, nutrients, and crude fiber for cattle, which are able to digest the leaf tannins in native saplings. Unlike *jaragua,* many browse species retain their nutrient levels fairly constantly throughout both the rainy and dry seasons. In contrast, grasses, especially *jaragua,* show significant reduction in digestibility and nutrient levels during the dry season. Native dry-forest trees and shrubs are both more palatable and more nutritious than *jaragua* for grazing by domestic livestock, and free-ranging cattle shift their foraging to native species during the dry season when given the opportunity. Hartshorn (1983: 131) reported that he was "unable to find seedlings or small saplings of *Brosimum alicastrum*" in the inventory plots at Palo Verde after cattle had grazed in the plots. No native mammals of Costa Rica will feed on the stems or leaves of mature *jaragua,* and it is unlikely that even native grazers such as cotton rats (*Sigmodon hispidus*) and eastern cottontail rabbits feed on anything but the youngest shoots.

Our survey efforts in *jaragua* for small mammals have identified only one species of native mammal that can occupy this grass, cotton rats. Daubenmire (1972: 37), in a year-long study on the ecological consequences of converting dry forest to pasturelands near Cañas, noted the lack of mammals (only two rabbits seen) and other

animals in *Hyparrhenia*, stating that "[al]though rodents and insects were present, they were very few in species and numbers and their use of the vegetation [*Hyparrhenia*] was negligible." Cattle also destroy bee nests, especially those of the large, ground-nesting anthophorid bees that are the major pollinators of much of the dry forest (Frankie et al. 1997). We suspect that cattle also will negatively affect the nests of small mammals, as many nests along the periphery of the marsh are at the surface (*Oryzomys* and *Sigmodon* nest at the surface or in aboveground vegetation). The combination of even moderate grazing by cattle and regular burning has an extremely negative impact on rodent populations.

The presence of single-species stands of *jaragua* and of artificially created, open savannalike habitat within the tropical dry forest of Guanacaste has reduced or eliminated the populations of most native dry-forest mammals from those habitats. However, a few species have increased in numbers and distribution with the creation of these grasslands. Cotton rats are much more widespread and abundant in Costa Rica today than they were in the past. Cotton rats are an open-grassland species, and they would have been rare in Guanacaste before the removal of the forests and the introduction of grasses. Other mammals that probably are more common now than before the creation of the open savannalike habitats include opossums, vampire bats, cottontail rabbits, armadillos, coyotes, and gray foxes (*Urocyon cinereoargenteus*).

Controlled cattle grazing potentially may be an effective management tool in reducing the biomass of *jaragua* when cattle are grazed on the growing grass during the rainy season and are then removed. However, the presence of cattle in tropical dry forest will change the structure and composition of that habitat (Stern et al. 2002). Cattle cannot be sustained on *jaragua* throughout the year and must be allowed to forage on other species. Cattle lose weight on a diet consisting solely of *jaragua* during the dry season (D. A. Stewart pers. comm.) because most of the plants' nutrients are stored in the roots and the stems, and leaves are primarily dried cellulose.

Cattle as a management tool for controlling cattails in the Palo Verde marsh have proved ineffective (figs. 5.1–5.3). Although cattle will consume some young, actively growing cattail shoots, they do not consume the mature leaves (D. A. Stewart pers. comm.), and they prefer other species when given the opportunity to feed on them. The explosion of cattails in the marsh began shortly after the transfer of land from a cattle ranch to a national park. At this time, cement gates or weirs that were used in the dry season to maintain water in the lagoon after high tide were abandoned, thus contributing to the flourishing of cattails in the lagoon. Within five years of the change, cattails had eliminated most of the open areas of the marsh, which were critical for waterfowl. Cattle in the marsh primarily feed on floating water hyacinths (*Eichhornia crassipes* and *E. heterosperma*), which are locally called *lirio de agua* or *choreja*, but they will eat a wide variety of species, especially *Pistia stratiotes* (locally called *lechuga*). Cattle will eat young cattails, but they prefer other species. When cattle are allowed to graze in upland areas, they have a significant and detrimental impact on the composition and structure of native forest trees and shrubs. Overgrazing by cattle, the presence of vast areas of *jaragua*, and uncontrolled fires continue to be among the most serious threats to the native flora and fauna in the dry forest of Costa Rica. In recent years, we have observed that in areas where cattle were grazing, most of the smaller saplings had been either consumed or trampled and that there were very few rodents on the forest floor in heavily grazed areas. The use of cattle within Parque Nacional Palo Verde is having a significant negative impact on the regeneration of the forest and on the abundance of native mammals.

PESTICIDE CONTAMINATION

Pesticide contamination is a problem worldwide, and in recent years, with the increase in agricultural development in Guanacaste, it has become

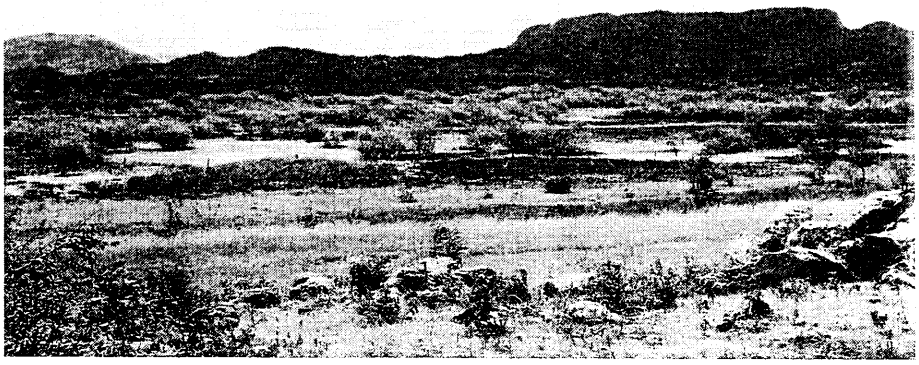

FIGURE 5.1. Laguna Palo Verde in February 1970. The marsh included diverse characteristic aquatic vegetation and open areas between patches of *Parkinsonia aculeata* trees, water hyacinth, water lilies, and bullrush. Large areas of open, shallow water were present. No cattails were visible because they occurred only in small patches along the airstrip (shown in the lower part of photo) near a freshwater spring draining into the marsh. Photograph by Gordon Frankie.

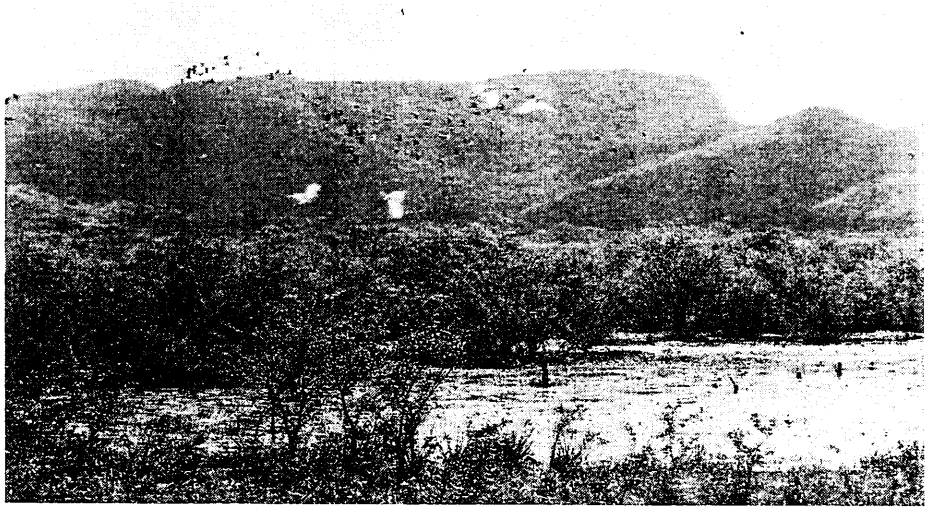

FIGURE 5.2. Laguna Palo Verde in February 1970. A close-up view of the marsh. Photograph by Gordon Frankie.

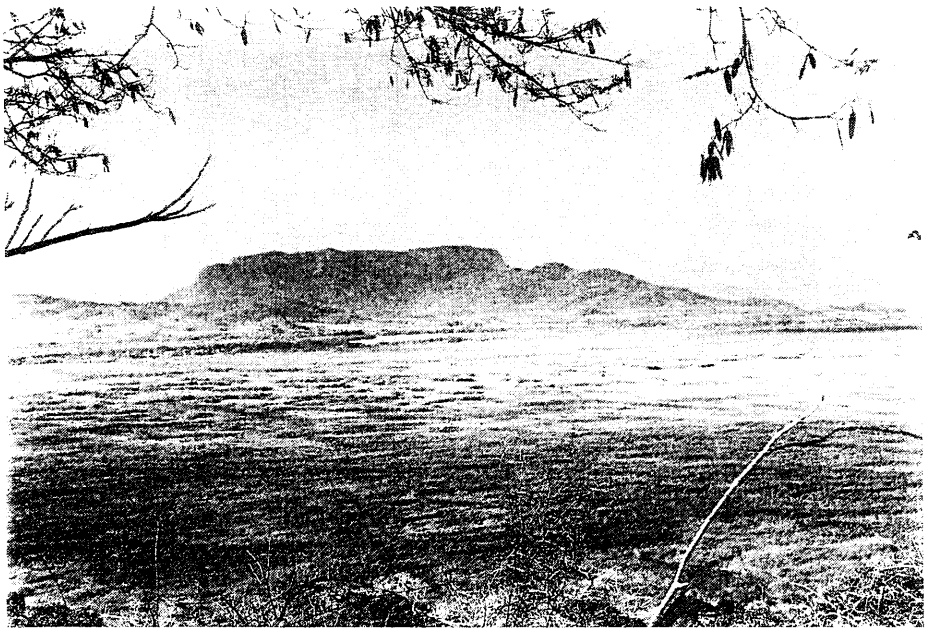

FIGURE 5.3. Laguna Palo Verde in February 2001. Since the mid-1980s, the diversity of both plants and waterfowl has declined dramatically, and the marsh has become choked with cattails (*Typha dominguensis*, Typhaceae) and two aquatic perennial grasses, *Hymenachne amplexicaulis* and *Paspalidium geminatum* (Araceae). Photograph by Robert Timm.

a serious threat to the fauna in this region. Organophosphates and carbamates, the most common insecticides in use today throughout the world, are known as cholinesterase-inhibiting pesticides because they kill by interfering with the enzyme vital for nerve transmission. Organophosphates and carbamates work well against a wide range of insect pests and are often less expensive than many alternatives, which adds to their popularity. In addition to affecting insects, many are acutely (immediately) toxic to most vertebrates and other invertebrates. Because they break down quickly in soil and water, they often need to be applied to crops more than once during the growing season. Organochlorine insecticides, such as DDT, also are very effective in killing a broad range of insects; however, they are slow to break down, remain toxic for a considerable length of time, and accumulate in body fat. Additionally, the long-lived organic pesticides act as endocrine disrupters, mimicking naturally occurring androgens (estrogens), and may be detrimental to mammalian reproductive cycles—for example, by lowering sperm count. Die-offs of both birds and mammals occur even when pesticides are applied responsibly because many animals consume the pesticide, either directly or indirectly. Pesticide residues in the stomachs of poisoned mammals and birds are known to kill predators and scavengers.

Cropdusters in Guanacaste (as well as elsewhere in Costa Rica) have customarily dumped into rivers unused pesticides remaining from aerial spraying, and this practice continues. A number of toxic pesticides have been isolated from the Tempisque River, including aldrin, chlordane, DDT, heptachlor, and lindane (Mata and Blanco 1994). These five insecticides are all organochlorine compounds and are known to cause an increase in cancer incidence in humans and to persist in the environment for many years. Aldrin, chlordane, and heptachlor are cyclodienes that are similar to, but more toxic than, DDT. Chlorinated hydrocarbon pesticides are notorious for their severe effects on nontarget organisms, whereas target species,

particularly many species of insects, develop resistance (Laws 1993). Thirty pesticides have been identified as commonly used in rice fields in the area adjacent to Palo Verde (Robinson 1993). Some of these pesticides are extremely toxic to wildlife (and humans), and their use is illegal in Costa Rica, but they are still available on the black market and are commonly used (Hilje 1988). High levels of pesticide residuals, including organic chlorides and their metabolites, have been found in eggshells of herons that nest on Isla de Pájaros in Parque Nacional Palo Verde (Hidalgo 1986). The effects of agrochemicals on tropical mammals have yet to be studied.

PREDICTIONS AND RECOMMENDATIONS

RESEARCH PRIORITIES FOR DRY-FOREST MAMMALS

Because little is known about the abundance and distribution of most species of mammals in the tropical dry forest, monitoring populations in its many distinct habitats should be a top research priority. In order to identify critical areas for protection and adopt the best strategies for successful conservation, it is imperative to collect basic information about population densities and changes in densities over time within this life zone. This information will help to identify vulnerable species as such and to concentrate research and conservation efforts. Furthermore, monitoring the abundance of mammals within these various habitats throughout the year will help to identify potential migratory patterns; this information, in turn, will help determine which areas to protect as biological corridors connecting tropical dry forest to other habitats. Finally, coordinated efforts should be established between Latin American countries that still have tropical dry forest in order to accumulate information on the distribution and abundance of tropical dry forest mammal species over their entire range.

In addition to documenting the distribution and abundance of dry-forest mammals, it is important to identify ecologically significant species for management and monitoring. Researchers have recognized three categories of species whose interactions in ecosystems are important for providing information about the quality of the habitat: (1) keystone species: species whose disappearance results in the disappearance of several other species; (2) indicator species: species whose population changes are thought to indicate the effects of management activities; and (3) mobile link species: species who are important links to more than one food chain, plant-animal association, or ecosystem (Soulé 1989). Research efforts on mammals in tropical dry forest should concentrate on species that fall into these categories with the goal of conserving both fauna and flora of dry forest regions.

TRAINING AND EDUCATION PROGRAMS FOR PARK PERSONNEL

The implementation of long-term programs for the monitoring and conservation of dry-forest mammals in Costa Rica requires trained professionals working in the national parks. The limited budget that currently supports protected areas in Costa Rica, however, is not sufficient to employ specialized professionals, and most park personnel have no formal training in biology. Creative proposals to increase the budget of national parks should be evaluated, including imposing a tourist tax on hotels with the funds going directly to protected areas (see chapter 21). The goal should be to have at least one specialized, professionally trained biologist working within a protected area to initiate monitoring and conservation programs and train park personnel in fieldwork.

ECONOMIC ALTERNATIVES AND SUSTAINABLE DEVELOPMENT

Although the consensus among conservation biologists is to protect as much land as possible as quickly as possible, the human factor of population expansion and economic needs cannot be easily ignored. Unless conservation programs take into account the needs of human societies, it is unlikely that the goals of long-term conservation will be achieved. Sound economic alternatives need to be provided to rural Costa Ricans

in areas of tropical dry forest if we are to conserve this fragile ecosystem and the mammal fauna that it supports. Alternative means of generating economic benefits beyond the traditional use of the land for timber, agricultural crops, and cattle grazing should be evaluated and encouraged by the Costa Rican government. One possibility is to provide the highest economic incentives for reforestation programs that provide total protection. Under the current forestry policy, programs in which land is devoted to reforestation with plantations and selective logging programs receive larger economic incentives than programs providing total protection (see chapter 21).

It is of utmost importance to encourage research on the sustainable development of ecosystems and to evaluate potential alternative means of land and water exploitation that will have a minimum impact on ecosystems. In particular, in the dry-forest region of Guanacaste, studies evaluating the effects of forest fragmentation, large-scale irrigation projects, and rice cultivation on local mammals should be undertaken. Before sustainable development programs are implemented within or surrounding protected areas, feasibility studies should be conducted in order to estimate not only the economic benefit of the new activity but also the ecological cost to the area. For example, the management plan implemented in Palo Verde using cows within the park was part of a sustainable development plan; unfortunately this activity was implemented without first evaluating the economic benefits or the ecological costs. The economic benefits are at best minimal and the ecological costs high (Mozo 1995; see chapter 21).

PROTECTION, REGENERATION, AND BUFFER AREAS

If the native mammals of Costa Rica's tropical dry forest are to be conserved, additional efforts must be made to protect the forest that remains and allow natural succession to regenerate mature stands of dry forest. Although increased forest regeneration is a positive development, young, regenerating forests do not provide the same environmental benefits for mammalian communities as do old-growth forests. Combined with projects that foster regeneration of degraded areas, continued efforts need to focus on conserving old-growth forests, as many native mammals may be found only in this habitat.

Since dry forests in Costa Rica are largely restricted to protected areas, the habitats immediately surrounding these areas should be evaluated before any type of development is carried out. Buffer areas surrounding national parks and other protected areas theoretically exist in Costa Rica, but little has been done to evaluate or restrict activities in these areas. For example, the agricultural development of rice fields bordering Palo Verde and Lomas Barbudal destroyed the biological corridor that connected them. The potential effect that agricultural development on the borders of the national parks has on native mammal fauna needs to be evaluated more fully.

CONCLUSIONS

No habitat type in Costa Rica (and throughout Mesoamerica) has been more affected by humans than the tropical dry forest. Open pastureland and grazed forested tracts are common habitats within this region today. In recent years rice, sugarcane, and hay fields have replaced natural habitats throughout the Guanacaste region. Palo Verde has lost at least eight species of native mammals to date, and it is likely that more mammals in this habitat will become extinct if efforts are not made to reduce the effects of humans on this ecosystem. Some species of mammals are still abundant at Palo Verde, and a few species (those that live in the savanna) are undoubtedly more abundant today than they were prior to settlement; however, the long-term effects that the fragmented landscape will have on populations of native mammals are still unknown. Because there is no simple solution to guarantee the successful conservation of any particular species or group of species, we suggest a combined effort that includes (1) research; (2) education and training; (3) economic alternatives and evaluation of alternative uses of land

and water; and (4) protection and regeneration of habitats. We believe that such a multifaceted approach will be the most successful way to protect dry-forest mammals and their habitat.

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