The Empty Forest

Many large animals are already ecologically extinct in vast areas of neotropical forest where the vegetation still appears intact

Kent H. Redford

The world conservation community has focused much of its attention on the plight of tropical forests. Many authors have lamented the loss of forest cover and the destruction of the forest and speculated on the extent of the tropical forest left intact. Throughout the discussion, tall, majestic, tropical trees are used as a symbol for the complete set of animal and plant species found in tropical forests. Trees are also being used by some conservation biologists, park planners, and others to represent the entire tropical forest biota and as a measure of conservation worth.

The presence of soaring, buttressed tropical trees, however, does not guarantee the presence of resident fauna. Often trees remain in a forest that human activities have emptied of many of its large animals. The absence of these animals has profound implications, one of which is that a forest can be destroyed by humans from within as well as from without.

Until recently, human influence on tropical forests through such activities as burning, swidden agriculture, and hunting was regarded by ecologists as of such low impact that it was negligible, as important but confined to areas of human settlement, or as confined to rapacious colonizers de-

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> We must not let a forest full of trees fool us into believing all is well

stroying the forest from the outside. In any case, ecologists looked for study sites that would allow for examination of "natural" processes uncontaminated by anthropogenic effects. Data from botany, archaeology, and anthropology collected in many parts of the world are showing, however, that anthropogenic effects are ubiquitous and that the sought-after virgin habitat may not exist. Flenley (1979), for example, has documented widespread human effects on tropical forests throughout the equatorial regions.

The relatively recent arrival of humans in the western hemisphere has not lessened the overall impact our species has had on neotropical forests. From the forests of Mexico through Panama, and the montane forests of Colombia to Ecuador, scientists have documented the ways in which pre-Columbian humans altered the presence, extent, and structure of forests. The forests of the Amazon basin were also extensively altered by human activities. In fact, Balée (1989) has recently suggested that at least 11.8% of the *terra firme* forests of the Brazilian Amazon, almost 400,000 km^2, show continuing effects of past human interference.

With few exceptions, researchers have concentrated on direct alteration of vegetation, not discussing the ways in which human activities have affected the animals of tropical forest ecosystems. In this article, I expand the focus to include defaunation of tropical forests, concentrating on the forests of the Amazon basin, and I show that the long-term preservation of tropical forest vegetation will not be possible if the forest fauna is not also preserved.

Indirect defaunation

Humans can devastate a fauna by indirect or direct means. Indirect defaunation is the destruction of a fauna through human activity not aimed specifically at animals. In tropical forests, habitat destruction is the most common of these practices—not surprisingly, many forest animals cannot survive without forest. A less-often-considered type of habitat destruction occurs when animals are absent from an area of otherwise excellent habitat because some critical area elsewhere, such as a nesting beach, was destroyed. This problem affects animals including migratory birds, beach-nesting turtles, and white-lipped peccary (*Tayassu pecari*) herds.

There are many other types of indirect defaunation. One of the most important is probably the effect of forest-extraction activities by humans. For example, logging can remove fruit-bearing trees and destroy nesting and other critical areas.

Less obvious are the effects that stem from the much-publicized ex-

traction of forest fruits and nuts. Almost without exception, the fruits collected for sale are fruits also eaten by large birds and mammals (Redford et al. in press). However, the extent to which animal species can survive with reduced availability of fruits and nuts is unknown.

A recent article by Vásquez and Gentry (1989) documented the huge number of fruits from wild trees collected by humans for sale in Amazonian markets. One of the major fruits in this market was that from *Mauritia* palms—the only food of the macaw *Ara manilata* (Roth 1984) and the most important fruit in the diet of the tapir (Bodmer 1990). The enormous quantities of Brazil nuts removed from a patch of tropical forest undoubtedly affect the animals that otherwise would have fed on those nuts. The extractive activities also remove nutrients from the ecosystem.

Indirect defaunation can also take place through the effects of subsistence or commercial hunting and fishing that remove potential prey from tropical forests, thereby affecting predators, scavengers, and the animals that depend on them (Thiollay 1984). As Emmons (1987) and Jorgenson and Redford (in press) have pointed out, every major prey species of the jaguar is intensively hunted by humans. In these cases, it seems clear that the removal from tropical forests of food for human consumption reduces the capacity of those forests to support many animals.

Finally, many of the by-products of modern human activities are important contributors to indirect defaunation. These byproducts include mercury and sediment contamination of fish (Martinelli et al. 1988); smoke, which especially affects pollinators (Lovejoy et al. 1984); and an increase of edge habitat in the forest (Malcolm 1991).

Direct defaunation

The indirect effects of human activity on defaunation, important as they are, have arisen chiefly in recent decades. The effects of direct defaunation, the deliberate killing of animals, has a much longer history in the Amazon forests—a history that coincides with the presence of humans in the area. Direct defaunation can be di-
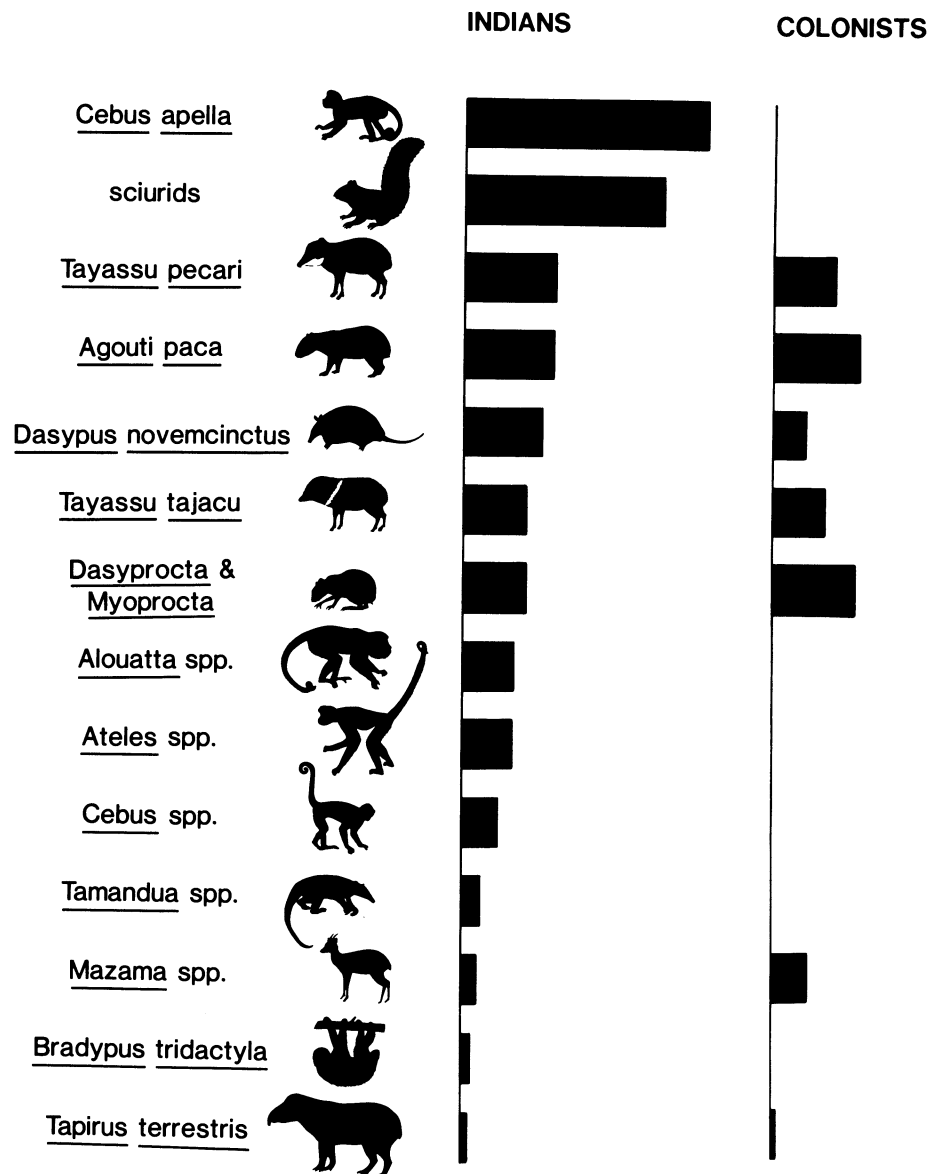

Figure 1. Importance of mammals to contemporary Indian and colonist hunters (only considered were those species found in a minimum of five Indian studies and three colonist studies). Bars denote the number of individuals of that taxon killed per hunter per year. To give an idea of scale, there were approximately 2.5 individual *Cebus apella* monkeys killed by Indians per consumer per year and approximately 0.05 *Tapirus*. (Data from Redford and Robinson 1987.)

vided into two categories: subsistence hunting and commercial hunting.

Subsistence hunting. In many parts of the world, wildlife serves as a major source of food for local peoples. In Latin America, game is a vital protein and fat source to many groups living outside of urban areas. As a general rule, wildlife is most important to Indian groups that depend on game meat for subsistence. It is of lesser importance, though still important, to settlers of European descent who have lived for decades in tropical forests but have recourse to domestic animals. It is also of lesser importance to colonists recently arrived to Amazonian forests, who frequently are unfamiliar with hunting and have access to other sources of meat.

A wide variety of wildlife is hunted for food by humans. The Maraca Indians of Colombia, for example, take at least 51 species of birds, including 10 species of hummingbirds (Ruddle 1970). Hunters generally take more mammals than birds and

INDIANS　　　　　　　　**COLONISTS**

Penelope spp.

Ramphastos spp.

Crax spp.

Psophia spp.

Crypturellus spp.

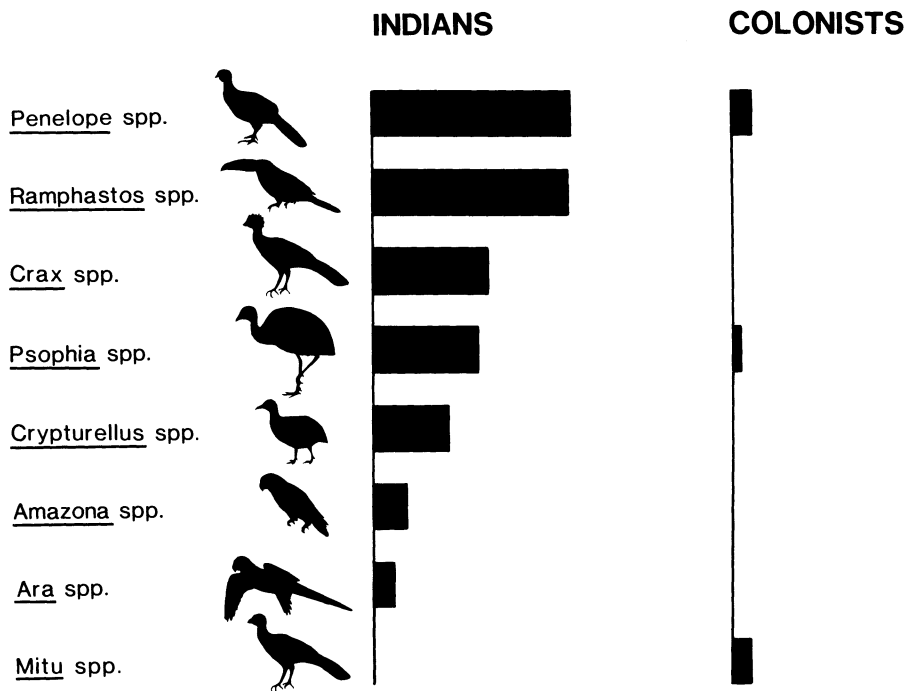Amazona spp.

Ara spp.

Mitu spp.

Figure 2. Importance of birds to contemporary Indian and colonist hunters (only considered were those species found in a minimum of five Indian studies and two colonist studies). Bars denote the number of individuals of that taxon killed per hunter per year. To give an idea of scale, there were approximately 0.9 individual *Penelope* guans killed by Indians per consumer per year and approximately 0.09 *Ara*. (Data from Redford and Robinson 1987.)

more birds than reptiles (Redford and Robinson 1987).

Throughout Amazonia and Latin America, indigenous hunters usually kill only a few of the many types of mammals and birds present. Of the mammals, monkeys, peccaries, deer, armadillos, and large rodents like paca and capybara are frequently hunted; and, of the birds, the most common prey are guans and curassows, toucans, trumpeters, and macaws. The number of species hunted by nonnative peoples is even more restricted. Figures 1 and 2 show the differences in the range of mammal and bird species taken by Indians and colonists.

The numbers of animals taken by subsistence hunters can be large. In less than a year, the 230 inhabitants of three Waorani villages in Ecuador killed 3165 mammals, birds, and reptiles (Yost and Kelley 1983). This total included 562 woolly monkeys (*Lagothrix lagothricha*), 313 Cuvier's toucan (*Ramphastos cuvieri*), and 152 white-lipped peccary. Not all subsistence hunting is of this intensity.

I have estimated the number of mammals killed in one year by the rural population of Amazonian Brazil. In 1980, there were an estimated 2,847,000 people living outside of cities in an area of 3,581,180 km² (FIBGE 1982). I multiplied this number of consumers by the per capita per annum consumption values derived from studies of colonist hunting (Redford and Robinson 1987). The resulting figure, 14 million individual mammals killed each year, suggests the staggering extent of subsistence hunting. Adding birds and reptiles, the number of game animals killed each year in Amazonian Brazil probably reaches 19 million animals. The number of animals fatally wounded or killed could reach 57 million animals a year.

Commercial hunting. The second major cause of direct defaunation is commercial hunting. The killing of animals in Amazon forests by Europeans for commercial purposes has been going on since soon after their discovery of the continent. This trade has involved many different species

and has shifted from group to group as market demand and availability have changed (Figure 3; c.f. Redford and Robinson 1991). Even before Europeans arrived in the Americas, animals and their products were traded. Among the Incas, adult caiman and anacondas were transported from the Amazonian lowlands up to the Andean city of Cuzco for use in menageries (Lathrap 1975). Nonetheless, trade in wildlife did not assume major proportions until Europeans arrived.

EDIBLE PRODUCTS. As early as the seventeenth century, the commercial harvesting of manatees for meat began (Redford and Robinson 1991). Until the mid-1900s, the average annual catch of these *Trichechus inunguis* in the Amazon was at least several thousand animals. Two other important commercialized sources of meat are caiman and river turtles. Caiman of several species, but principally of the genus *Caiman*, have been, and still are, an important source of meat in some areas of the Amazon basin, with the current trade in meat estimated at 21,500 to 32,000 animals annually.

The first European to navigate the Amazon River found many Indian villages with hundreds of penned turtles (mostly *Podocnemis expansa*). Despite ferocious exploitation for meat and eggs, female *P. expansa* continued to gather near nesting beaches and be plentiful enough through the 1850s to impede river traffic on the Madeira.

Turtle eggs have been heavily exploited for industrial and nutritional purposes. In the Amazon basin, the eggs of *P. expansa* were so abundant and in such great demand that an industry developed to process them. Oil from the eggs was used for cooking and lighting, and as early as the eighteenth century royal decree controlled the lucrative harvest in Brazil. In 1719, 192,000 pounds of oil, equaling approximately 24 million eggs, were produced from the upper Amazon; as late as the 1860s, at least 48 million eggs yearly were harvested to supply the industry. In many areas, giant river turtles have been virtually eliminated, and there is still heavy predation on their eggs wherever and whenever they can be found.

Although no longer available on the scale once observed, game is still readily obtained in many local markets. Castro et al. (1975–1976) reported the meat of 24 species of wildlife, including six species of primates, for sale in the markets of Iquitos, Peru. They estimate that the inhabitants of the Peruvian department of Loreto, which includes the city of Iquitos, kill 370,000 monkeys annually for consumption and sale.

The difference between commercial and subsistence hunting is becoming increasingly blurred. For example, in a study of the ungulate harvest in one watershed near Iquitos, Peru, lumbermen hunting to supply their camps with food accounted for 51% of the ungulate harvest, illegal commercial hunters for 11%, and subsistence hunters for only 38% (Bodmer et al. 1988).

LEATHER. The earliest European commercial exploitation of wildlife for nonedible products was the use of leather, particularly that made from deer hides. Most of the recent market for leather has been luxury items such as purses, gloves, and expensive shoes and overcoats. The principal animals killed for this trade are peccaries, capybara, and various species of reptiles.

Peccary leather has always been popular, particularly in Europe and Japan. Between 1946 and 1966, more than 2 million collared peccary (*Tayassu tajacu*) skins and 800,000 white-lipped peccary skins were exported from Iquitos, Peru, alone. Capybara are another source of high-quality leather. Between 1960 and 1969, almost 500,000 capybara skins were exported from the Brazilian Amazon. Trade in these species continues today, although at substantially reduced levels.

The most important wildlife in the leather industry at present are the reptiles, principally the crocodilians. During the peak of the trade in the 1950s and 1960s, five to ten million crocodilian skins were reported as traded annually worldwide, with the actual figure probably much higher. The extent of the trade is staggering: for example, in Venezuela during 1930 and 1931, 3000–4000 caiman skins were being sold daily, and between 1951 and 1980 Colombia legally exported almost 12 million

Caiman sclerops skins.

MAMMALIAN SKINS. Just as was the case with leather, large-scale commercialization of skins was brought to Latin America by the Europeans. Both trades are directed at the luxury markets in Europe, Japan, and North America. The skin trade has always focused on a relatively few species. The trade in skins originating in the Amazon basin has been well documented and has concentrated on giant otter (*Pteronura brasiliensis*), river otter (*Lutra longicaudis*), jaguar (*Panthera onca*), and ocelot (*Felis pardalis*). Much smaller numbers of *Felis wiedii* and *Felis tigrina* skins are also traded.

The trade in cat skins began with jaguars at the end of the last century.

In the 1960s, apparently in response to overexploitation of jaguar and the concomitant decrease in numbers, the cat trade shifted to the smaller species.

The period between the end of the Second World War and the early 1970s was the golden era of the trade in skins originating from the Amazon Basin (McGrath 1986). In the 20 years since 1946, the Amazon River port of Iquitos, Peru, exported 22,644 giant otter skins, 90,574 river otter skins, 12,704 jaguar skins, and 138,102 ocelot skins. The value of skins caused people to move into sparsely inhabited areas and devote tremendous effort to commercial hunting. For example, one family of hunters in the Ecuadorian Amazon
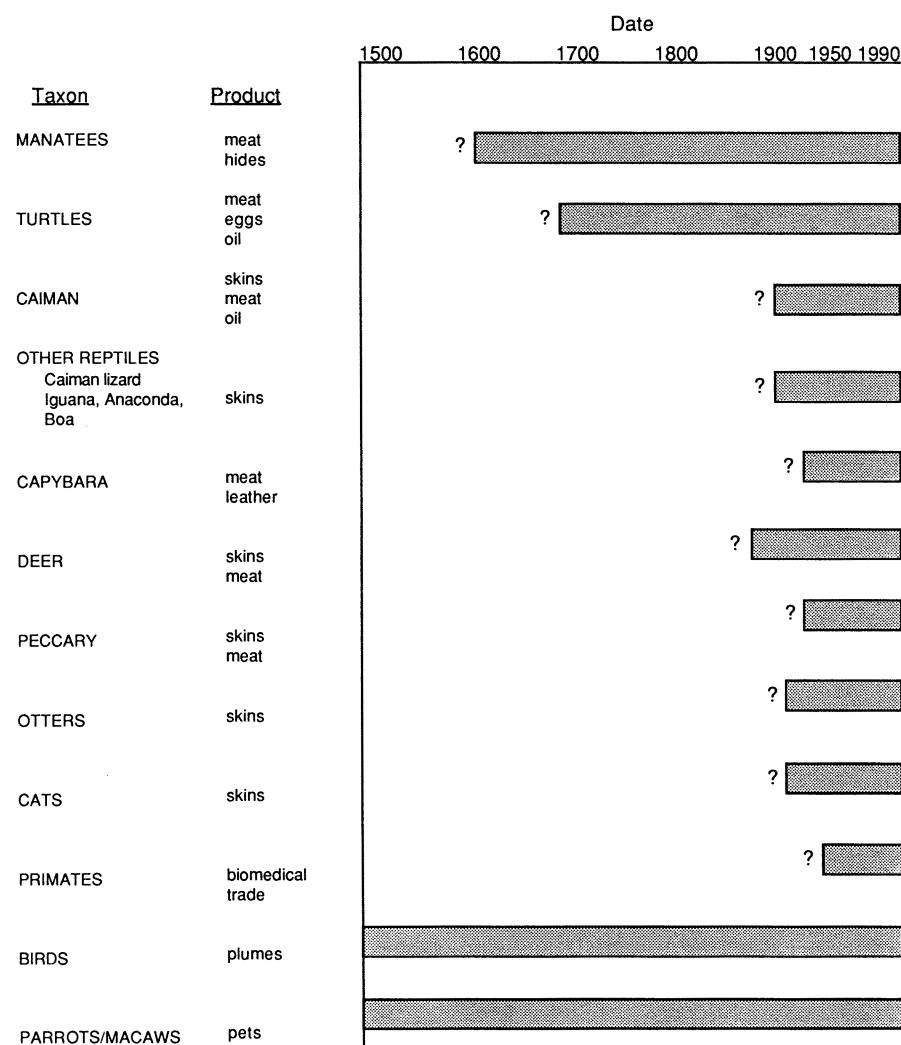

Figure 3. Commercial exploitation of fauna in the Amazon since the time of European discovery.
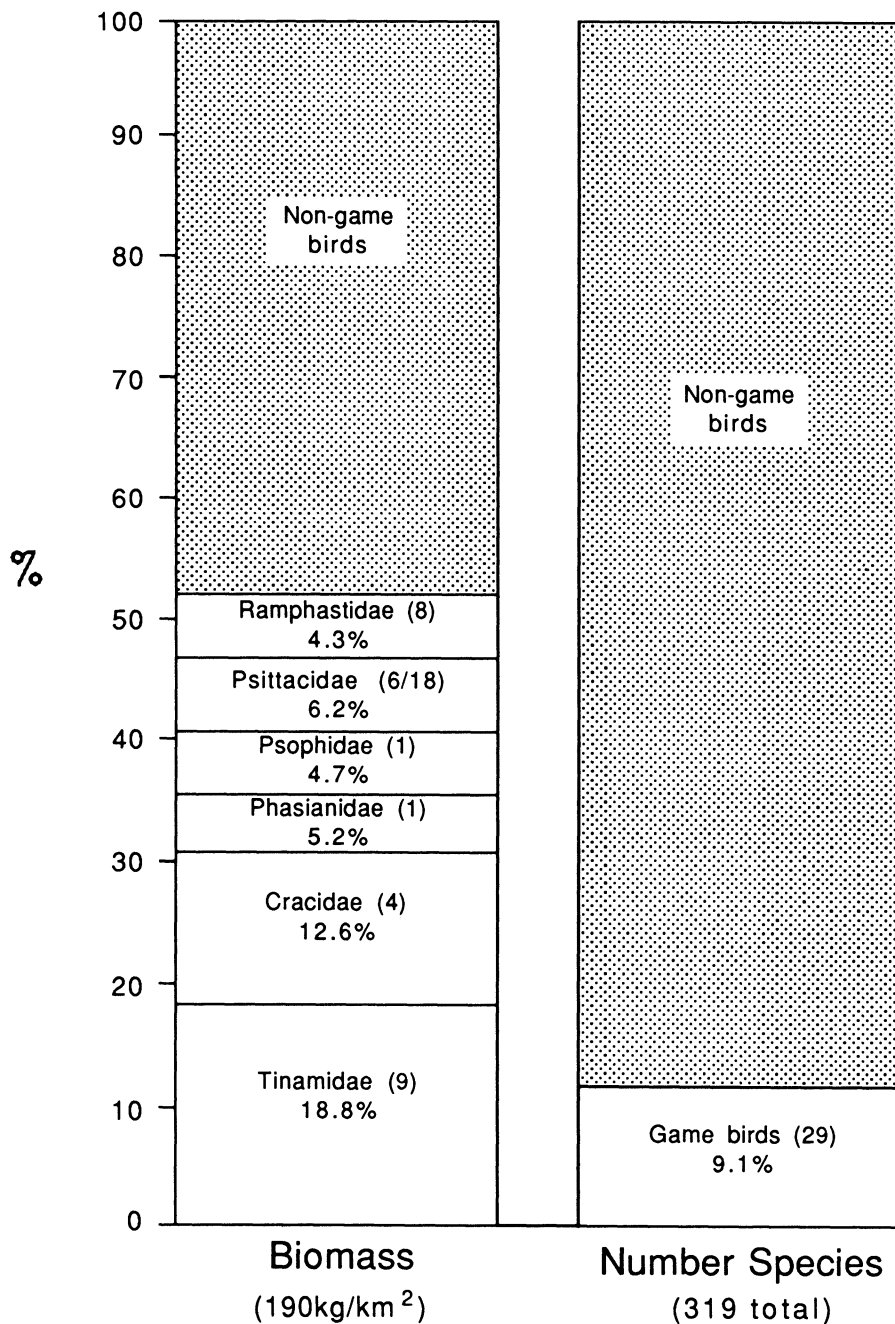
Figure 4. Avian diversity in Amazonian Peru. Numbers in parentheses are numbers of species in taxon. (Data from Terborgh et al. 1990.)

killed an estimated 10,000 small spotted cats in a 15-year period (Paz y Miño C. 1988).

FEATHERS. Much less well-studied is the exploitation of birds for their feathers. Although currently out of fashion, feathers were once important elements in women's fashion. The trade concentrated on egrets and herons. At the height of the feather frenzy, premium feathers went for $5 per plume or $28 per ounce in New York. Between 1899 and 1920, South America (principally Argentina, Brazil, and Venezuela) exported 15,000 kg of egret and heron feathers, representing an estimated 12–15 million individuals of smaller species of birds and 3–4.5 million larger ones.

BODY COUNTS. In interpreting the numbers of individual animals involved in the commercial trade emanating from the Amazon, previous authors used either the number reportedly exported at various ports of exit or the number imported at various ports of entry. From the perspective of an ecologist, however, what is of interest is the total number of individual animals removed from ecosystems in the course of commercial trade. For each animal that makes it into the import/export trade, many others are killed.

The number of animals actually killed is unknown, but from the limited data it seems reasonable to estimate that for each animal entered as an export statistic approximately three additional individuals die. These animals may be wounded by the hunter or the hunter's dogs or traps and escape to die later; the skin may be damaged either in the course of the hunt or in processing or storage; the animal may be too small and is discarded either by the hunter or the buyer; or a lactating female may be killed and her infant dies as a result of her death. In the case of the live animal trade, the mortality in transport to the point of final sale is even higher (Grimwood 1968).

To illustrate the number of animals involved in the commercial wildlife trade, Table 1 lists the number exported between 1962 and 1967 from the Amazonian port of Iquitos. Using the correction factor of three, the total number of animals killed would be almost 5 million, or approximately 800,000 animals per year or one animal for each square kilometer of the Peruvian Amazon each year.

Table 1. Animals and animal skins exported from Iquitos, Peru, 1962–1967. (From Redford and Robinson 1991.)

Animals	Number of individuals exported
Live monkeys	183,664
Skins	
Caiman	
Melanosuchus	47,616
Caiman	101,641
Mammals	
Capybara (*Hydrochaeris*)	67,575
Otter (*Lutra*)	47,851
Giant otter (*Pteronura*)	2529
Ocelot (*Felis pardalis*)	61,499
Margay (*Felis wiedii*)	9565
Jaguar (*Panthera*)	5345
Collared peccary (*Tayassu tajacu*)	690,210
White-lipped peccary (*Tayassu pecari*)	239,472
Deer (*Mazama*)	169,775
Total	1,626,751

It is important to realize that subsistence and commercial hunting occur simultaneously. As a means of providing a first approximation of the combined effects of these two types of hunting, at least in the 1960s and 1970s, I have extrapolated the above estimate to the 3,581,180 km² Brazilian Amazonian states. This calculation yields an estimate of 4 million animals killed for commercial purposes per year, which may be combined with an estimated 19 million killed each year for subsistence. Therefore, approximately 23 million animals are killed per year in the Brazilian Amazonian states. If the correction factor for fatal wounding is applied to subsistence hunting as well, the total reaches 60 million. Given the increase in human population in the Brazilian Amazon since 1980, this total undoubtedly is an underestimate of current kill rates.

Which animals are killed by hunters?

Before attempting to assess the impact of the removal of such large numbers of animals from Amazonian forests, it is necessary to consider several factors. First, the most commonly taken game animals are almost always the largest members of their group and usually the largest species in the forest. Hunters prefer birds and mammals of large body size. The only large mammals not commonly hunted for food (felids and otters) are hunted for their pelts. Large wading birds and raptors are the only large birds not commonly hunted for food.

Second, large animals, although represented by relatively few species, are major contributors to the overall biomass. The best data available to illustrate this point comes from the work done at Cocha Cashu Biological Station in Manu National Park, Peru (Janson and Emmons 1990, Terborgh et al. 1990). Of the 319 bird species recorded at this site, 9% are commonly hunted (Redford in press, Redford and Robinson 1987). However, these 29 species make up 52% of the total avian biomass (Figure 4).

This pattern is even more striking for the mammals, for which data are available only for nonvolant species. Of the 67 total species, 18% of the species are commonly hunted. These
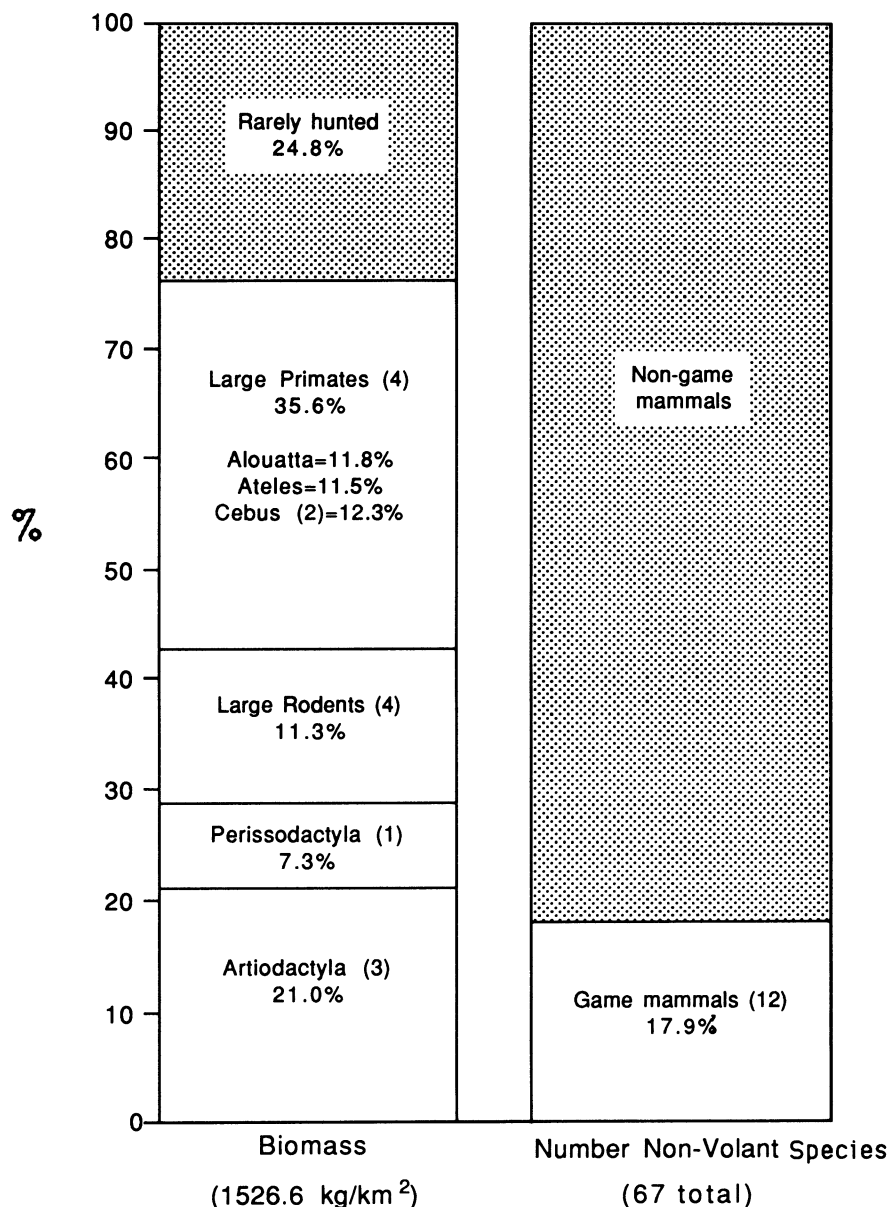

Figure 5. Nonvolant mammalian diversity in Amazonian Peru. Numbers in parentheses are numbers of species in taxon. (Data from Terborgh et al. 1986 and Janson and Emmons 1990.)

12 species make up 75% of the mammalian biomass (Figure 5). To show that the Manu site is not atypical of neotropical forest sites, Figure 6 compares mammalian biomass data from three other nonhunted sites. Clearly, species that are preferred game make up a large proportion of the biomass in unhunted sites.

Third, and as a result, if hunting affects the abundance of game species, areas that have been hunted should show decreases in density and therefore biomass of these species. A review of the available data of effects of hunting shows that under condi-

tions of moderate hunting, densities of nonprimate mammalian game species decreased 80.7% when compared with similar, unhunted sites. Under hunting conditions described by the authors as heavy, nonprimate mammal densities decreased 93.7% compared with similar, unhunted sites (for details, see Redford in press).

Due to the greater amount of data on primates, a similar comparison of the effect of hunting on primates can include both density and biomass. Data from many different Amazonian sites show that in hunted areas large primate biomass drops 93.5% when
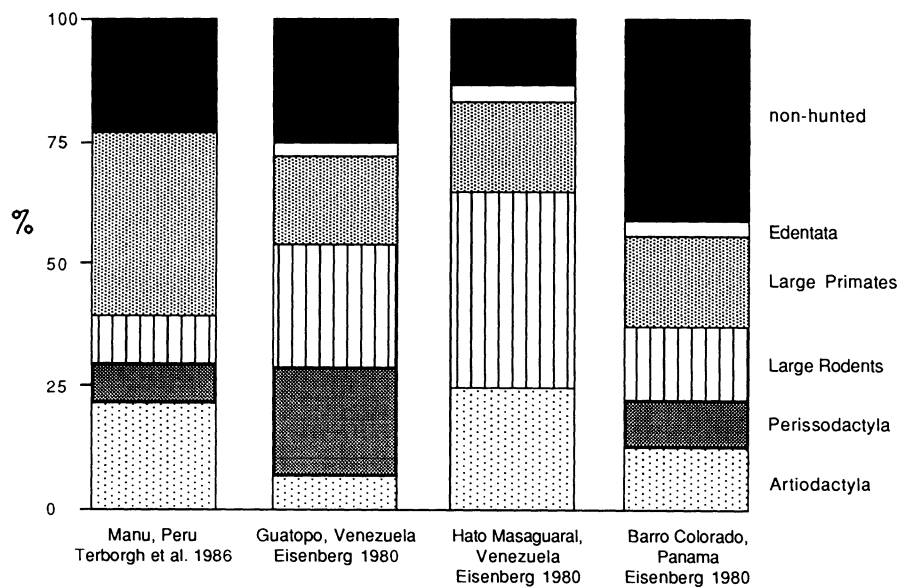
Figure 6. Biomass of game mammals as a proportion of total mammal biomass at four neotropical sites. Only the animals indicated in black are not hunted.

1990) shows that 69.5% of the game bird biomass is composed of fruit-eating species. This total would increase to 96.2% with the inclusion of the curassow (*Mitu*), which some experts believe is also primarily frugivorous.[1]

Many of the most important commercial food fish in the tropical forest are also large fruit-eating species. Many of these frugivores are involved in seed dispersal, seed predation, and the structuring of tropical forests.

The ecology of game animals and of their absence

Although many ecologists have documented the important roles played by large animals in seed dispersal, seed predation, herbivory, pollination, and predation, until recently few have considered the role of large animals in tropical forests and what would happen if they were removed from the system (Emmons 1989, Janson and Emmons 1990, Terborgh 1988). Some ecologists have stated that removal of some individual species from an ecosystem would probably not have any substantial effects on the remaining species (c.f. Feinsinger 1983). Some studies, however, have not only documented the existence of keystone species but also have demonstrated what happens when such species are extirpated. Recently, Brown and Heske (1990) have shown that the removal of a guild of kangaroo rats from an experimental plot in the southwestern United States resulted in major changes in the vegetation structure.

Such clear-cut cases are not known from neotropical areas, but there is a growing body of work suggesting that in this ecosystem large vertebrates may perform important ecological roles and that their absence will result in a changed forest (Janzen 1988). Such a conclusion has been reached for paleotropical settings and in comparisons between the Pleistocene and the present, but it has not been made explicit for neotropical settings. Studies that shed light on the ecological functions of large neotropical verte-

compared with similar unhunted areas, and large primate density drops 80.7% (Table 2). In fact, Freese et al. (1982) have stated that "predation by humans is clearly one of the most important factors affecting monkey densities in most of the Peruvian and Bolivian Amazon, and probably elsewhere in South America" (p. 82).

A similar comparison made for game birds shows a drop of 73.5% of original density under moderate hunting and of 94.6% under heavy hunting. Similar conclusions were reached by Terborgh et al. (1990) when comparing Panamanian and Peruvian avian biomass. Finally, Thiollay (1986) showed that in comparing a hunted forest site with an unhunted forest site in French Guiana, avian game species biomass decreased from

50.9% to 26.8% of the total avian biomass.

A fourth factor that must be considered before assessing the effects of the removal of large numbers of animals from Amazonian forests is that in tropical forests many of the largest animals, both terrestrial and arboreal, are frugivores. Turning again to the Cocha Cashu data, 84% of the game-mammal biomass is composed of fruit-eating species, according to a calculation taking the biomass of the most commonly hunted mammalian taxa and considering frugivore-omnivores, frugivore-granivores, and frugivore-herbivores as frugivores (data from Robinson and Redford 1986).

A similar analysis of the game birds (food habit data from Terborgh et al.

Table 2. Impact of hunting on large primates in Amazonia. Means (standard deviations) are given.

a	Primate biomass* (kg/km²)	Large primate percentage of total primate biomass*	Number of sites
Unhunted	363.8(314.3)	64.5(11.4)	9
Hunted	23.8 (38.1)	19.6(29.6)	19

b	Primate density† (individuals/km²)	Large primate percentage of total primate density†	Number of sites
Unhunted	34.1 (10.8)	33.8(16.3)	7
Hunted	6.6 (5.8)	8.1(10.0)	8

*Data from Peres 1990, Freese et al. 1982, and C. Mitchell and E. Raez Luna (unpublished results, 1991, Wildlife Conservation International).
†Data from Peres 1990 and C. Mitchell and E. Raez Luna (unpublished results, 1991, Wildlife Conservation International).

brates fall into three categories: herbivory and seed predation, seed dispersal, and predation.

Herbivory and seed predation. In Mexico, Dirzo and Miranda (1990) compared two tropical forests, one with its full complement of large mammals (peccaries, deer, and tapir) and another in which these species had been extirpated by hunters. There were striking differences between the two forests. The hunted forest was typified by seedling carpets, piles of uneaten rotting fruits and seeds, and herbs and seedlings undamaged by mammalian herbivores—phenomena much less evident in the unhunted forest.

A second example comes from work done comparing seed and seedling predation, tree recruitment, and rodent populations on Barro Colorado Island, Panama, with adjoining mainland areas (De Steven and Putz 1984, Glanz 1990). On the island, ocelots and other large mammalian predators are absent, with agouti (*Dasyprocta*) and squirrel populations high compared with the mainland, where not only felids, but also humans, have reduced the population of these rodents. Predation of seeds and seedlings of several canopy trees on Barro Colorado Island is much higher than on the mainland due to high populations of seed-eating mammals on the island. In an elegant study of small (1–4 ha) islands in an artificial lake in Panama, Putz et al. (1990) showed that, in the absence of seed-eating mammals, trees with large seeds had a distinct advantage over those with small seeds and came to dominate the small forest patches in less than 75 years.

Other important seed predators are peccaries, deer, and tapirs (Bodmer 1989); these species consume an enormous number of seeds, particularly those from palms. These ungulates, especially the white-lipped peccary with its large group size, were probably important elements in affecting forest composition and structure but now are very rare.

Seed dispersal. Many authors have documented the important role played by large birds and terrestrial mammals in the dispersal of the seeds of tropical plants. Based on his work

in Panama, Howe (1984) stated that "animal-mediated dispersal is certain to be critical for the demographic recruitment of many or most tropical forest species" (p. 266).

Large birds, particularly the toucans and cracids, are among the most important seed dispersers. Many of the species of cracids, particularly the curassows, are among the species whose local populations are most rapidly depleted by hunting. They are also slow to reproduce, with the average cracid requiring at least six years to replace itself in the population (Silva and Strahl 1991). Because of the cracids' importance as seed dispersers and susceptibility to hunting, Silva and Strahl have suggested that "human impact on the Cracidae may have irreversible long-term effects on the biology of neotropical forest ecosystems" (p. 51).

The other group of important large seed dispersers are the primates, particularly the woolly and spider monkeys. In a study in Surinam, spider monkeys were shown to disperse seeds 93.5% of the times they fed on fruit and apparently served as the only dispersal agent for several tree species (von Roosmalen 1985). Defler (1989) has shown a similar pattern for woolly monkeys. Like curassows, spider and woolly monkeys are highly prized game animals and are rapidly hunted out of a forest (Peres 1990). In the absence of such large primates, many species of plants may experience severely altered seed dispersal patterns.

Interestingly, agoutis in addition to being major seed predators also serve as seed dispersal agents. It seems that at lower densities they are important dispersal agents for large-seeded trees (c.f. Forget 1991, Hallwachs 1986); in their absence, at least some trees would become locally extinct.

Another important group of seed dispersers is tropical fish. Fish apparently disperse seeds of at least nine plant families (Goulding et al. 1988). Many of the fish seed-dispersers are important food fish and are heavily pursued by both subsistence and commercial fishers.

Gentry (1983) has shown, in the neotropics, that areas of higher rainfall have higher tree diversity and that much of the overall increase in plant diversity accompanying this higher

rainfall is due to the addition of bird-dispersed and mammal-dispersed tree species. In addition, he shows that wind-dispersed species tend to be wide-ranging, whereas mammal-dispersed species tend to be localized in distribution. For example, 43% of the tree species found at Río Palenque were presumably dispersed by large, nonvolant mammals, and 50% of these are endemic to coastal Ecuador or to Ecuador and adjacent Colombia, whereas only one mammal-dispersed species ranges throughout tropical America. Given these facts, the loss of large vertebrate dispersers, which has undoubtedly occurred in much of this area, would affect not only local populations of trees, but in many cases it might result in the extinction of tree species with only localized distributions, resulting in a loss of diversity of plant species much greater than expected.

Predation. The role played by predators in structuring communities has been well studied in marine and intertidal systems. This work has shown that predators can increase the overall species diversity in a community by decreasing the abundance of smaller predators and competing herbivores and by reducing dominance of plant prey species.

Such research has not been conducted in neotropical forests, but biologists working in various locations have observed that a decrease in abundance of large predatory mammals is correlated with the increase in abundance of medium-sized terrestrial mammals, particularly agoutis (Glanz 1990, Janson and Emmons 1990). Absence of large predators such as jaguars, pumas, and ocelots also seems to result in more uneven densities of prey species (Emmons 1987). Da Fonseca and Robinson (1990) suggested that the absence of ocelots in forest patches was the reason for large numbers of opossums and consequent lower small rodent densities.

Intact communities of large cats are rare in neotropical forests. Even where there has been no hunting of these animals for their skins, there has usually been game hunting focused on the species that are primary prey species of the large cats. Large raptors are likewise affected as they eat pri-

and mammals, an indication of the ecological roles played by these species is possible. These examples make clear the importance of fruit-eating vertebrates in structuring and maintaining tropical forests. What exactly will happen as a result of the loss of the game animals is not clear. Some cases, as on Barro Colorado Island and in the Mexican forests, provide hints as to these consequences—the resulting forest will be determined by a complicated mix of more predation on some species, less on others, and the rarification or extinction of still others. What further complicates our ability to predict outcomes is the fact that humans have been altering tropical forests all along. What has changed is the intensity and scale.

Ecological extinction. During the height of the skin trade, many animals with valuable skins were killed. Since the collapse of the skin trade, tropical forest peoples have continued to hunt many of these animals because their meat is appreciated. The result of this widescale human activity has been the reduction or extinction of local game populations in virtually all areas of Amazonia.

Conservation biologists are by definition concerned about extinction. Yet, as Estes et al. (1989) point out, there are several types of extinction: global extinction, local extinction, and ecological extinction. Ecological extinction is defined as "the reduction of a species to such low abundance that although it is still present in the community it no longer interacts significantly with other species" (p. 253). Although of tremendous importance, conservationists ignore the widespread nature of ecological extinction in neotropical forests, focusing instead on demographic extinction (extinction of a population or deme) and calculations of minimal viable population sizes.

Even if jaguars, woolly monkeys, or large curassows have not gone extinct in the wild, their populations may have been reduced to such an extent that they no longer perform their ecological functions. What is needed is movement beyond the genetically based concern with demographic size to a new emphasis on minimum ecologically operational population size that incorporates in-
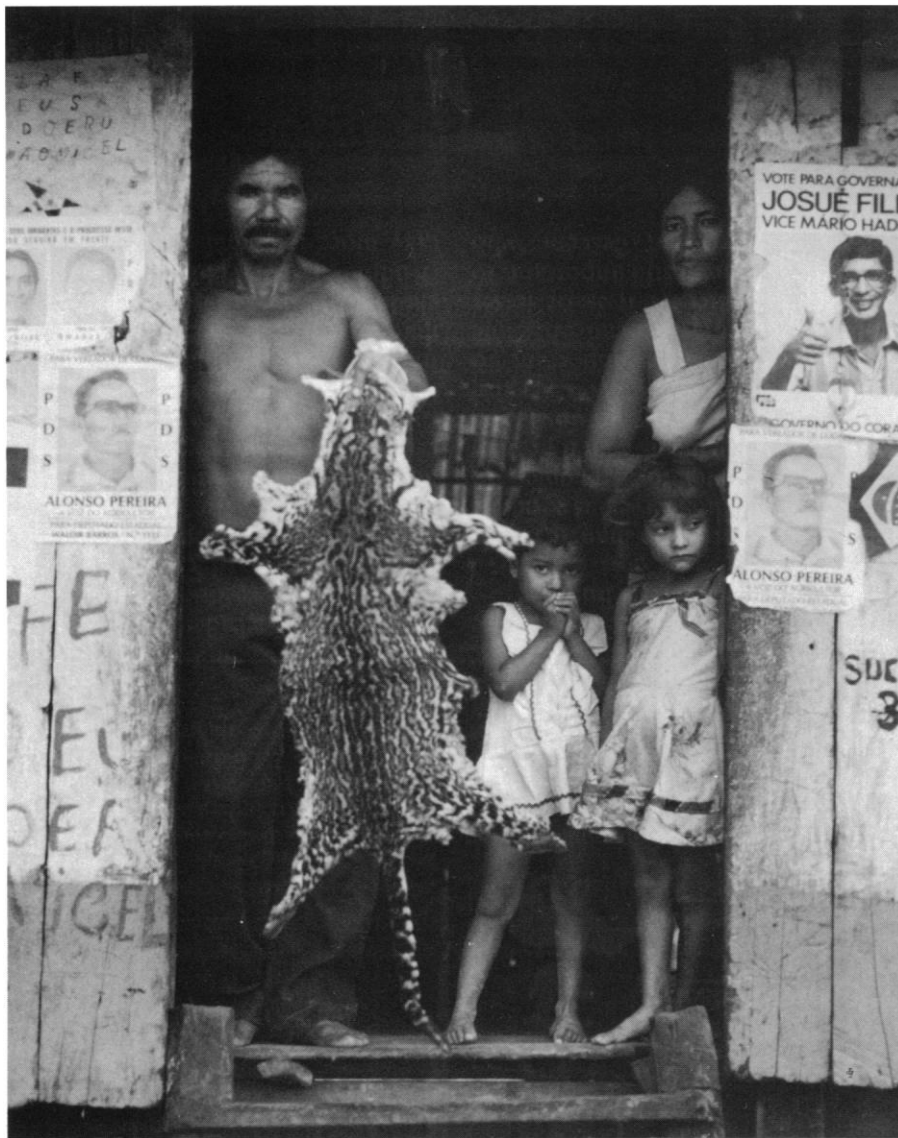

Figure 7. A group of Brazilians living along the Amazon River display an ocelot skin. Photo: Kent H. Redford.

marily animals that are major game species for humans.

There has been much less work done on the effects of large mammalian and reptilian predators on neotropical aquatic ecosystems. Yet this guild has probably been the one most heavily affected by human hunting. For example, an estimated 3 million caiman, river otters, and giant otters were removed from from Brazil, Colombia, and Peru between 1962 and 1969.[2] Grimwood (1968) calculated that, based on the home-range of river otters, the mid-1960s commercial harvesting of river otters in Peru

resulted in the elimination of adult otters from more than 20,000 km of waterway per year. Both black caiman and giant otters, the two largest carnivores in neotropical freshwater ecosystems, have also been eliminated from many areas. The effects of the loss of these two predators is unknown, although Fittkau (1970, 1973 in Best 1984) has speculated that caiman serve an important function in nutrient transfer from terrestrial to aquatic ecosystems and that their absence is correlated with a decrease in the diversity and biomass of fishes.

By examining studies of herbivory, seed predation, seed dispersal, and predation by large neotropical birds

[2]K. H. Redford, 1992, unpublished results.

teractions between plant and animal species.

The animals that are the most popular game species, and the ones whose populations have most likely become ecologically extinct, include the most important predators, the large-seed dispersers, and the seed predators in neotropical forests (Janson and Emmons 1990). These large animals provide what Terborgh (1988) has referred to as a "stabilizing function." Black caiman, jaguars, and harpy eagles maintain the incredible diversity of tropical forests through indirect effects, "the propagation of perturbations through one or more trophic levels in an ecosystem, so that consequences are felt in organisms that may seem far removed, both ecologically and taxonomically, from the subjects of the perturbation" (Terborgh 1988, p. 402).

Humans are among the most severely affected species. The effects of hunting on large animals are not just of concern to those interested in jaguars and bird-watching. Hunting is a tremendously important source of nutrition for millions of neotropical forest-dwelling humans—a "subsidy from nature" (c.f. Hecht et al. 1988) without which many other so-called sustainable activities, such as rubber tapping, would not take place. As Peres (1990) has shown, in one year and a half, one family of rubber tappers in the Brazilian Amazon killed more than 200 woolly monkeys, 100 spider monkeys, and 80 howlers. As many are beginning to realize, game is becoming rare in many areas inhabited by rubber tappers, affecting not only the game animals, but also the ability of the people to live in the forest. Animals are important not only as food for humans, but also as pollinators and dispersers of economically important plant species, as regulators of pest populations, and as providers of myriad other ecological services.

Hunting affects not only game species, but also local densities of non-game species. In a study of the bird communities in hunted and unhunted forests of French Guiana, Thiollay (1986) showed that hunting significantly reduced the species richness, diversity, density, and biomass of game birds. Hunting was also correlated with decreased densities of rap-tors and insectivores, as well as a threefold decrease in the biomass of frugivores.

Integrating humans, hunting, and conservation

Almost every remaining piece of neotropical forest has been affected by humans during pre-Columbian times, during the rubber-boom era, during the golden era of the skin trade, or more recently by gold miners, timber extractors, ranchers, and farmers. Even where no sign of human habitation is to be found, rubber trees show the unmistakable signs of having once been tapped, piles of open Brazil nut shells show the telltale mark of a machete, and bones of caiman killed for their skins whiten on the beaches.

Today, hunting is an integral part of all forest-based activities, be it lumbering, fishing, or medicinal plant collection. For those living in the forest, hunting is an essential component of feeding a family; for those venturing into the forest to collect forest products, it is also a necessary subsistence activity.

In virtually all areas of neotropical forest, game animal populations have already been affected by human hunting. This pattern continues as human populations grow and forest exploitation increases. The trend in recent years has been to increase the amount of land allocated to multiple-use areas—including Indian lands, Man and the Biosphere Programme reserves, extractive reserves, faunal production areas, and national forests—and to keep at a much lower level the amount of land dedicated to national parks and other traditional conservation units. This pattern in the neotropics is illustrated by Brazil, which has 74 million hectares in all categories of Indian lands, compared with 13 million hectares in all categories of conservation units, and by Colombia, which has 18 million hectares in Indian reserves and 2.5 million hectares in Natural National Parks (sources in Redford in press).

As with other subsidies from nature, game has been undervalued, understudied, and ignored by the conservation and development communities. For example, in the World Bank's 1978 list of benefits from the forest, game does not even appear (Myers 1988).

Conclusions

In tropical forests, large animals are important not only as food for people but also as integral ecological components of forested ecosystems. If these ecosystems are to continue as forests, providing all of the financial, ecological and aesthetic benefits currently desired, then animals must not be ignored. Many large animals have already gone ecologically extinct in vast areas of neotropical forest—areas with large, towering tropical trees, lush ferns, and beautiful orchids.

We must not let a forest full of trees fool us into believing that all is well. Many of these forests are "living dead" (Janzen 1988), and, although satellites passing overhead may reassuringly register them as forest, they are empty of much of the faunal richness valued by humans. An empty forest is a doomed forest.

Acknowledgments

References cited

Balée, W. 1989. The culture of Amazonian forests. Pages 1–21 in D. A. Posey and W. Balée, eds. *Resource Management in Amazonia: Indigenous and Folk Strategies.* New York Botanical Gardens, Bronx, NY.

Best, R. C. 1984. The aquatic mammals and reptiles of the Amazon. Pages 371–412 in H. Sioli, ed. *The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and its Basin.* Dr. W. Junk, Boston.

Bodmer, R. E. 1989. Ungulate biomass in relation to feeding strategy within Amazonian forests. *Oecologia* 81: 547–550.

———. 1990. Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). *J. Zool.* 222: 121–128.

Bodmer, R. E., T. G. Fang, and L. M. Ibañez. 1988. Ungulate management and conservation in the Peruvian Amazon. *Biol. Conserv.* 45: 303–310.

Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705–1707.

Castro, N., J. Revilla, and M. Neville 1975–1976. Carne de monte como una fuente de proteínas en Iquitos, con referencia especial a monos. *Revista Forestal del Peru* 6: 19–32.

da Fonseca, G. A. B., and J. G. Robinson. 1990. Forest size and structure: competitive and predatory effects on small mammal communities. *Biol. Conserv.* 53: 265–294.

Defler, T. 1989. Recorrido y uso del espacio en un grupo de *Lagothrix lagothricha* (Primates: Cebidae) mono lanudo churuco en la Amazonía Colombiana. *Trianea (Colombia)* 3: 183–205.

De Steven, D., and F. E. Putz. 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. *Oikos* 43: 207–216.

Dirzo, R., and A. Miranda. 1990. Contemporary neotropical defaunation and forest structure, function, and diversity—a sequel to John Terborgh. *Conserv. Biol.* 4: 444–447.

Emmons, L. H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behav. Ecol. Sociobiol.* 20: 271–283.

———. 1989. Tropical rainforests: why they have so many species and how we may lose this biodiversity without cutting a single tree. *Orion Nature Quarterly* 8(3): 8–14.

Estes, J. A., D. O. Duggins, and G. B. Rathbun. 1989. The ecology of extinctions in kelp forest communities. *Conserv. Biol.* 3: 252–264.

Feinsinger, P. 1983. Coevolution and pollination. Pages 282–310 in D. J. Futuyma and M. Slatkin, eds. *Coevolution.* Sinauer Associates, Sunderland, MA.

Flenley, J. R. 1979. *The Equatorial Rainforest: A Geological History.* Butterworths, London.

Forget, P. M. 1991. Seed-dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. *J. Trop. Ecol.* 6: 459–468.

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

Fund. Inst. Bras. Geogr. Estat. (FIBGE). 1982. *Anuario Estatistico do Brasil.* FIBGE, Rio de Janeiro, Brazil.

Gentry, A. H. 1983. Dispersal ecology and diversity in neotropical forest communities. *Sonderbd. Naturwiss. Ver. Hambg.* 7: 303–314.

Glanz, W. E. 1990. Neotropical mammal densities: how unusual is the Barro Colorado Island, Panama, community? Pages 287–313 in A. H. Gentry, ed. *Four Neotropical Rainforests.* Yale University Press, New Haven, CT.

Goulding, M., M. L. Carvalho, and E.G. Ferreira. 1988. *Rio Negro: Rich Life in Poor Water.* SPB Academic Publ., The Hague, The Netherlands.

Grimwood, I. R. 1968. *Notes on the Distribution and Status of Some Peruvian Mammals.*

American Committee for International Wild Life Protection, Bronx, NY.

Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). Pages 285–304 in A. Estrada and T. H. Fleming, eds. *Frugivores and Seed Dispersal.* Dr. W. Junk Publ., Dordrecht, The Netherlands.

Hecht, S. B., A. Anderson, and P. May. 1988. The subsidy from nature: shifting cultivation, successional palm forests and rural development. *Hum. Org.* 47: 25–35.

Howe, H. F. 1984. Implications of seed dispersal by animals for tropical reserve management. *Biol. Conserv.* 30: 261–281.

Janson, C. H., and L. H. Emmons. 1990. Ecological structure of the nonflying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. Pages 314–338 in A. H. Gentry, ed. *Four Neotropical Forests.* Yale University Press, New Haven, CT.

Janzen, D. H. 1988. Management of habitat fragments in a tropical dry forest: growth. *Ann. Mo. Bot. Gard.* 75: 105–116.

Jorgenson, J., and K. H. Redford. In press. Humans and big cats as predators in the neotropics. *Symposium of the Zoological Society of London No. 65.* Oxford University Press, New York.

Lathrap, D. W. 1975. The antiquity and importance of long-distance trade relationships in the moist tropics of Pre-Columbian South America. *World Archaeology* 5: 170–186.

Lovejoy, T. E., J. M. Rankin, R. O. Bierregaard Jr., K. S. Brown Jr., L. H. Emmons, and M. E. Van der Voort. 1984. Ecosystem decay of Amazon forest remnants. Pages 295–325 in M. H. Nitecki, ed. *Extinctions.* University of Chicago Press, Chicago.

Malcolm, J. R. 1991. The small mammals of Amazonian forest fragments: patterns and process. Ph.D. dissertation, University of Florida.

Martinelli, L. A., J. R. Ferreira, B. R. Forsberg, and R. L. Victoria. 1988. Mercury contamination in the Amazon. *Ambio* 17: 252–254.

McGrath, D. G. 1986. The animal products trade in the Brazilian Amazon. Unpublished report to World Wildlife Fund, Washington, DC.

Myers, N. 1988. Tropical forests: much more than stocks of wood. *J. Trop. Ecol.* 4: 209–221.

Paz y Miño C., G. 1988. Notas sobre la cacería y la conservación de los félidos en la Amazonía Ecuatoriana. *Fundación "Simon Bolivar" (Quito, Ecuador) Boletín Científico* Año II(3).

Peres, C. A. 1990. Effects of hunting on western Amazonian primate communities. *Biol. Conserv.* 54: 47–59.

Putz, F. E., E. G. Leigh Jr., and S. J. Wright. 1990. Solitary confinement in Panama. *Garden* March/April 1990: 18–23.

Redford, K. H. In press. Hunting in neotropical forests: a subsidy from nature. In M. Hladik, ed. *Nutrition in Tropical Forests.* UNESCO,

Paris.

Redford, K.H., B. Klein, and C. Murcia. In press. The incorporation of game animals into small scale agroforestry systems in the neotropics. In K. H. Redford and C. Padoch, eds. *Conservation of Neotropical Forests: Building from Traditional Resource Use.* Columbia University Press, New York.

Redford, K. H., and J. G. Robinson. 1987. The game of choice: patterns of Indian and colonist hunting in the neotropics. *Am. Anthropol.* 89: 650–667.

———. 1991. Subsistence and commercial uses of wildlife in Latin America. Pages 6–23 in J. G. Robinson and K. H. Redford, eds. *Neotropical Wildlife Use and Conservation.* University of Chicago Press, Chicago.

Robinson, J. G., and K. H. Redford. 1986. Body size, diet and population density of neotropical forest mammals. *Am. Nat.* 128: 665–680.

Roth, P. 1984. Repartição do habitat entre Psitacídeos simpátricos no sul da Amazonia. *Acta Amazonica* 14: 175–221.

Ruddle, K. 1970. The hunting technology of the Maraca Indians. *Anthropologica* 25: 21–63.

Silva, J. L., and S. D. Strahl. 1991. Human impact on populations of chachalacas, guans, and curassows (Galliformes: Cracidae) in Venezuela. Pages 37–52 in J. G. Robinson and K. H. Redford, eds. *Neotropical Wildlife Use and Conservation.* University of Chicago Press, Chicago.

Terborgh, J. 1988. The big things that run the world: a sequel to E. O. Wilson. *Conserv. Biol.* 2: 402–403.

Terborgh, J., L. H. Emmons, and C. Freese. 1986. La fauna silvestre de la Amazonía: el despilfarro de un recurso renovable. *Boletín de Lima (Perú)* 46: 77–85.

Terborgh, J., S. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. *Ecol. Monogr.* 60: 213–238.

Thiollay, J. 1984. Raptor community structure of a primary rain forest in French Guiana and effect of human hunting pressure. *Raptor Res.* 18: 117–122.

Thiollay, J. M. 1986. Structure comparee du peuplement avien dans trois sites de foret primaire en Guyane. *Rev. Ecol.* 41: 59–105.

Vasquez, R., and A. H. Gentry. 1989. Use and misuse of forest-harvested fruits in the Iquitos area. *Conserv. Biol.* 3: 350–361.

von Roosmalen, M. 1985. Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta Amazonica* 15 (3/4) suppl.

Yost, J., and P. Kelley. 1983. Shotguns, blowguns, and spears: the analysis of technological efficiency. Pages 189–224 in R. B. Hames and W. T. Vickers, eds. *Adaptive Responses of Native Amazonians.* Academic Press, New York.