Chapter 15
Impacts of Subsistence Game Hunting on Amazonian Primates

Benoit de Thoisy, Cécile Richard-Hansen, and Carlos A. Peres

15.1 Introduction

Human and nonhuman primates have coexisted as predator and prey in all major tropical forest regions for millennia. Coexistence has often been mystical, with widespread taboos and avoidance (Cormier 2006), but primates have usually contributed prominently to human diets. Drastic declines of several large-bodied primate species were but one consequence of human colonization of several major islands and continents, and hunting probably contributed to prehistorical extinctions of megafauna, such as the giant lemurs of Madagascar (e.g. *Palaeopropithecus ingens* and *Pachylemur insignis*) following the earliest human arrivals, 2,000 years ago (Burney 1999; Burney et al. 2004; Perez et al. 2005). In the New World, hunting of primates and other vertebrates has been reported since at least the earliest Mayan period (Vaughan 1993), and most likely drove several large-bodied taxa to extinction, such as the mega-*Brachyteles* of the Brazilian Atlantic forest (Cartelle and Hartwig 1996).

In contemporary times, monkeys and apes are still a key part of the traditional diets of most tropical forest dwellers. In many communities, socio-cultural and religious taboos may limit predation of some species, but consumption of primate meat remains frequent and widespread in most tribal and non-tribal territories throughout the humid tropics. In the Paleotropics, lemurs are hunted in Madagascar (Garcia and Goodman 2003) and game harvest severely threatens several species (Bollen and Donati 2006). Gibbons, pig-tailed macaques and white-fronted leaf monkeys are regularly consumed in Indonesian Borneo (Wadley et al. 1997), where current levels of hunting, combined with pressures on forest habitats, have resulted in dramatic declines of the endemic Hose's leaf monkey (Nijman 2004). In China, hunting pressure is one of the main drivers of local extinctions of western black-crested gibbons (Jiang et al. 2006). Isolated populations of primate species in India, including the threatened Nilgiri langur and the lion-tailed macaque are also hunted by local

B. de Thoisy (✉)
Kwata NGO, Association Kwata, "Study and conservation of Guianan Wildlife", French Guiana
e-mail: thoisy@nplus.gf

communities for subsistence purposes (Madhusudan and Karanth 2002; Kumara and Singh 2004).

African primates face severe threats from widespread subsistence and commercial hunting in addition to habitat loss (Oates 1996; Cowlishaw 1999), exposing the so-called "bushmeat crisis" (Milner-Gulland et al. 2003). These threats are particularly acute in apes for which dramatic population losses due to commercial hunting are now evident (Walsh et al. 2003). Monkeys are also hunted by local rural communities for subsistence or commerce, resulting in unsustainable harvests in Côte d'Ivoire (Refish and Koné 2005), Zaïre and Congo (Wilkie et al. 1998), Cameroon (Muchaal and Ngandjui 1999), Tanzania (Fusari and Carpaneto 2000), and Mozambique (Fusari and Carpaneto 2006).

In Brazilian Amazonia, large primates are among the most threatened mammal species, and this is primarily driven by widespread hunting pressure (Peres 1990; Costa et al. 2005). However, ethnographic studies have rarely focused specifically on the relationships between humans and their platyrrhine primate prey, with a few notable exceptions (Shepard 2002; Cormier 2003). In many game harvest studies of Indian and *caboclo* settlements, primates are generally cited as one of the top-ranking orders of mammals in terms of numeric offtake (Peres 2000a, Jerozolimski and Peres 2003). Among 40 Amerindian groups for which reliable data on harvests were available, 30 hunted solely cebids, and only 10 hunted both cebids and callitrichids (Cormier 2006). In most cases, hunting is for meat and restricted to household subsistence purposes, but smaller monkeys can also be killed for ornamental purposes or captured as pets (Mittermeier 1991; Shepard 2002).

In this chapter, we first review the impacts of hunting on neotropical primate communities. Secondly, we describe the hunting patterns of Amazonian indigenous groups, and attempt to identify factors that regulate primate offtakes. To illustrate interactions between primate populations and hunting pressure exerted by traditional communities, we consider results from two cases studies based on a standardized series of line-transect surveys. The first includes an extensive network of over 70 forest sites censused throughout the lowland Amazon basin. The second used a similar methodology to census 41 French Guianan sites spread across the entire country. We present comparisons of primate richness and abundance between remote and hunted sites, as well as hunting practices in survey sites, and their observed impacts on primate populations. We also consider the future of Amazonian primates by exploring the relationship between traditional game harvest practices and population viability. Finally, we consider the need for further fieldwork to inform the imperative challenge to protect primate populations and their habitats.

15.2 Effects of Hunting on Primates

Some 230 of the 625 living primate species are threatened. Nearly one-third of the 202 Neotropical primate species are vulnerable, endangered or critically endangered, and hunting has been identified as a major cause of decline in the Northern

Muriqui *Brachyteles hypoxanthus* and the Brown spider monkey *Ateles hybridus brunneus*, two of the three South American species among the world's 25 most endangered primate species (Mittermeier et al. 2005). It is well established that species vulnerability to a well-identified extinction risk is inexorably related to species life history traits. Among the most common threats, primate species exhibiting low ecological flexibility are often vulnerable to forest habitat disturbance, whereas large-bodied species are more susceptible to hunting (Peres 1999; Isaac and Cowlishaw 2004).

Population declines and local extinctions in relation to direct human exploitation are widely reported in South and Central America, including Guyana (Sussman et al. 1995; Lehman 2000), Venezuela (Urbani 2006), Peru and Bolivia (Freese et al. 1982), French Guiana (de Thoisy et al. 2005), and Brazilian Amazonia (Peres 1990, 1997a, 1999, 2000a; Lopes and Ferrari 2000; Haugaasen and Peres 2005; Peres and Palacios 2007). Large cebids are usually the first target species, and consequently the most dramatically affected. For instance, a single family of rubber tappers in a remote forest site of western Brazilian Amazonia killed more than 200 woolly monkeys (*Lagothrix lagotricha*), 100 spider monkeys (*Ateles paniscus*), and 80 howlers (*Alouatta seniculus*) over a period of 18 months (Peres 1991). As dramatic as these figures are, they likely underestimate actual hunting-induced mortality. For instance, harvest estimates from market surveys do not include primates that are consumed in villages. In the Democratic Republic of Congo, 57.1% of primates are consumed in the villages and do not make it to the market, and in Liberia, primates were more valuable in rural than in urban areas (Lahm 1993; Colell et al. 1995). Also, interview results are often biased, since hunting and/or sale is officially prohibited in many areas where it occurs (Johnson 1996; Richard-Hansen and Hansen 2004; de Thoisy et al. 2005). Finally, animals lethally wounded by hunters in the forest often cannot be retrieved and are thus not included in village-based harvest estimates based on the number of carcasses intercepted. For example, this is particularly typical of all Amazonian atelines which often remain secured to the upper canopy by their prehensile tails, hence becoming inaccessible to hunters long after *rigor mortis* sets in (Peres 1991). Ohl et al. (2007) estimated that incorporating collateral mortality increased the impact of hunting by Matsigenka Indians on ateline primates in the Peruvian Amazon by 14–18%, depending on the species and hunting practices.

Hunted primate populations initially face a numerical reduction in reproductive individuals. Among large-bodied species, frugivores are frequently the most rapidly affected by harvests (Peres and Palacios 2007), perhaps because populations are more susceptible to fluctuations in resource supplies (Peres 1991; Ferrari et al. 1999). However, other biological or behavioral effects can also contribute to population declines. For instance, disturbance by hunters wielding fire-weapons may result in more cryptic behavior and less active foraging, which may have negative consequences to patterns of group dispersal (Johns and Skorupa 1987). Additional pressures on habitat and smaller group sizes may result in a break-down of social structure (Young and Isbell 1994), poor body condition (e.g., Olupot 2000) and direct demographic effects, including elevated infant mortality (Johns 1991) and decreased juvenile survival and

mean adult body weight (Milner et al. 2007). Despite the importance of genetic diversity for long-term population viability, the effects of recent human-induced population declines remain difficult to demonstrate, since genetic structures revealed with molecular markers can be driven by ancient demographic events that confound the signature of more recent population collapses (Harris et al. 2002). Evidence of lower breeder genetic diversity associated with population depletion through hunting is therefore scarce in mammals (but see Larson et al. 2002). Human-induced population collapses resulting in changes in population genetic structure has been revealed in Orangutans only (Goossens et al. 2006). In contrast, recent molecular surveys in large cebids (*Alouatta* and *Lagothrix*) may have exposed recent population bottlenecks, but these events were considered much older than the contemporary threats (Ruiz-Garcia 2005). Finally, population declines induced by hunting can be aggravated by the ravages of infectious diseases, such as Ebola hemorrhagic fever, as demonstrated in great apes in west Africa (Bermejo et al. 2006), but this has not been evidenced in Neotropical species.

   Population declines can also result in marked effects on the dynamics of forest habitats as primates play a key role in many ecosystem processes. Their ecological traits, including dietary and habitat specialization, can help predict major extinction processes that would result from species extinctions. However, predicted effects of species loss in the neotropics—where species tend to share their main ecological functions with other mammals (Jernvall and Wright 1998)—would result in lesser impacts on ecosystems than in the paleotropics. Harvesting of key seed-dispersal agents, such as howlers, spider monkeys and woolly monkeys likely limit the quality and extent of seed deposition patterns (Nuñez-Iturri and Howe 2007; Stoner et al. 2007). Consequently the proportion of seeds dispersed is negatively affected, and may result in lower level of seedling recruitment, as tentatively demonstrated in several neotropical forest sites (Peres and van Roosmalen 2002; Serio-Silva and Rico-Gray 2002; Ratiarison and Forget 2005; Nuñez-Iturri and Howe 2007; Russo et al. 2006). This can also depress the gene flow and genetic diversity of plant populations facing a dramatic reduction in the aggregate pool of effective seed dispersal agents (Pacheco and Simonetti 2000).

15.3 Indigenous Groups and Hunting Practices in South America

Direct pressures on primate species depend on a complex set of interactions between historical, cultural, socioeconomic, and spatial factors related to the use of hunting catchment areas by neighboring communities, and/or other land uses within a given region (e.g., mining, logging) which may exacerbate local demand for wild game meat.

15.3.1 The Role of Primates in the Diet of Native Amazonians

The relative importance of wildlife meat and fish to Amazonian settlements is widely variable, ranging from 2 to 10% of the dietary protein intake of colonist

groups along the Transamazon highway to 100% in the most isolated Amerindian populations (Redford and Robinson 1991). Primates are often the numerically dominant prey items harvested by indigenous groups throughout Amazonia, ranking higher than any other order of mammals (e.g., de Souza-Mazurek et al. 2000; Peres and Nascimento 2006). In French Guiana, primates represent the numerically dominant prey species (14–26% of prey items) harvested by Amerindian hunter-gatherer communities, below large ungulates (de Thoisy et al. 2005; Richard-Hansen et al. 2006). Conversely, as previously noted for Suriname (Mittermeier 1991), primates represent only around 10% of prey items captured by Bushnegro communities living along the main Maroni river of French Guiana, far below ungulates, rodents, birds and even xenarthrans. "Colonists" generally hunt fewer primates, and prefer large rodents and ungulates, mainly because these species resemble domestic livestock (Redford and Robinson 1987, but *see* Jerozolimski and Peres 2003). For instance, primates are not the principal source of game meat for extractive communities in the Jaú National Park, Brazilian Amazonia, who preferentially harvest ungulates and aquatic prey such, including fish and turtles (Barnett et al. 2002). In a small isolated non-tribal village of central French Guiana, ungulates, terrestrial frugivorous birds and rodents were the most frequently harvested prey (Richard-Hansen et al. 2004). More widely, primate biomass accounts for no more than 5% of total game biomass harvested by mixed communities in northern French Guiana, although, according to Creole tradition, some primate species are still regularly hunted for certain festive ceremonial occasions. This is particularly the case during the fruiting season, when food is abundant and animals become fat (Cormier 2006). On the other hand, primate meat was generally avoided by "white" people mainly because of their physical similarity to humans. This has been noted for other Amerindian groups elsewhere, but in other cases, primates were the favorite food *because* of this similarity (Mittermeier 1991; Cormier 2006).

Hunters largely target large-bodied species, such as *Ateles paniscus*, *Alouatta seniculus* and *Lagothrix lagotricha*, rather than small-bodied species (Peres 1990, Bodmer 1995, Shepard 2002; Franzen 2006). However, preferred midsized species, such as sakis and bearded sakis (*Pithecia* spp. and *Chiropotes* spp.) and capuchins (*Cebus* spp.), and even small-bodied species, such as squirrel monkeys (*Saimiri* spp.) and tamarins (*Saguinus* spp.) may be killed in far greater numbers than larger-bodied species regardless of the abundance of the latter. For example, 203 brown capuchins and 99 bearded saki monkeys were consumed in a single eastern Amazonian Indian village (Kayapó of A'Ukre) over 525 days of sampling, whereas only three howler monkeys were killed in the same period (Peres and Nascimento 2006). For the Waimiri Atroari Indians of central Amazonia, spider monkeys, tapirs and peccaries are also key target species (de Souza-Mazurek et al. 2000). Similarly, in Amerindian territories of southern French Guiana, howler monkeys, spider monkeys, and capuchin monkeys are also preferred target species (Renoux 1998; Richard-Hansen et al. 2006). In Manu National Park (Peru), Matsigenka tribal hunters show a clear preference for *Ateles* and *Lagothrix*, whereas smaller species are harvested either by young boys, and/or by adults returning from

hunting trips empty-handed (Shepard 2002; Ohl et al. 2007). In the Yasuni National Park (Ecuador), Huaorani hunters also preferentially target howlers and spider monkeys (Franzen 2006).

15.3.2 What Regulates Harvests in Traditional Communities?

Considerations by ethnographers of Ameridian communities as "managers" of natural forest resources is an old debate fraught with difficulties (Balée 1989). Taboos and avoidance may involve all monkey species occurring in the catchment area of a community, but few communities avoid all primate species (Cormier 2006). Avoidance may be related to prey type and consumer status. For instance, communities may limit the consumption of some species (e.g., howler monkeys, uakaries) because of their similarity to humans (Cormier 2003; Kracke 1978). For others, avoidance may be related to age, gender, and reproductive and heath status of consumers. However, the cultural basis of prey avoidance may be entirely unrelated to conservation concerns over the status of prey populations. In some Amerindian communities, adult female *Ateles paniscus* dominate the harvest of this species (85–97%) and are strongly selected over males, since males of this species are not considered to be good enough to eat (e.g., Souza-Mazurek et al. 2000; Richard-Hansen et al. 2006). Conversely, brown capuchin kills may show a strong male-biased skew (25–35% of females only), which could be attributed to either the confrontational behavior of dominant males in the presence of hunters or an unbalanced sex-ratio in the population (Richard-Hansen et al. 2006).

Cultural limitation on the amount of forest and aquatic resources harvested (e.g., game, fish, non-timber plant products) are reported in Wayapi Indians and explained in terms of the fear of resource "wasting" and of "taking too much" (Renoux 1998). This may be interpreted as a conservation strategy, but this may be entirely unrelated to a proactive and conscious assessment of the risk of overharvesting. Similarly, Matsigenka Indians, who believe in the revenge of game spirits, report that the Saangarte spirits may hide animals when overhunting occurs (Shepard 2002). On the other hand, technological constraints may lead to overharvesting of females. For instance, Matsigenka bow hunters, who may prefer adult males, primarily kill female primates which often move slower and make easier targets (Shepard 2002). Other socioeconomic factors can limit the extent and intensity of hunting activities. Access to technology (outboard motors) fuel, and ammunition have a direct impact on hunting patterns, and consequently on harvests of monkey populations. Traditional livelihoods are often affected by infrastructure development and cash income. In some cases, smaller amounts of bushmeat in diets may be simply explained by a reduction of wildlife densities, changes in population structures, and/or cultural and economic changes influencing food preferences (Ayres et al. 1991). In Ecuador, for instance, roads provide wide accesses to large forest areas for Huaorani hunters, and allow persistent harvests of sensitive species such as spider monkeys (Franzen 2006). Improvement of socioeconomic conditions can also contribute to a

decrease in subsistence hunting pressure (Jorgenson 2000), and depletion of primate populations by hunters may also result in shifts to alternative game species. Similar changes have been recorded in southern French Guiana: a comparison of harvests in the same area at two periods (1976–1977 and 1994–1995) showed decreased game harvests, related to either a decrease in the densities of target species or a shift to alternative resources (Renoux 1998).

15.4 Impact of Hunting on Primates: Two Cases Studies

Here we briefly illustrate the predominant impacts of subsistence or commercial hunting on neotropical primate populations. For this purpose, results of surveys conducted throughout lowland Amazonia (Peres 1990, 1999, 2000a,b; Peres and Palacios 2007) and in French Guiana (de Thoisy et al. 2005, 2006; C. Richard-Hansen, unpubl. data) are summarized in relation to local levels hunting pressure. These represent the most extensive studies anywhere in the tropics on the effects of hunting on forest primates using standardized line-transect censuses.

15.4.1 Lowland Amazonia

Humans have been hunting primates and other forest vertebrates in Amazonia since the arrival of the earliest paleoindians >10,000 years BP, but consumption greatly increased following the first rubber boom in the late 19th century. Exploitation of primate meat by tribal and nontribal Amazonians has increased due to larger numbers of consumers, a greater spatial dispersion of these consumers, local scarcity of alternative sources of protein, changes in hunting technology, and because primates are often a preferred food. Peres (1999, 2000a,b) found that assemblage-wide primate biomass was strongly negatively correlated with hunting pressure, although, this effect size is also a function of forest habitat productivity and soil fertility (Peres 1997b, 1999, 2000a; Peres and Dolman 2000). At unhunted and lightly hunted forest sites, the densities of the three ateline genera, which are preferred targets of hunters, were consistently higher than those at moderately to heavily hunted sites. Peres and Palacios (2007) provide the first comprehensive large-scale meta-analysis of changes in vertebrate population densities in a large number of hunted and unhunted, but otherwise undisturbed, neotropical forest sites that takes into account differences in site productivity. Considering the variation in abundance among primate species at 101 Amazonian forest sites, population responses ranged from small-bodied species that on average more than doubled their abundance at higher levels of hunting pressure (cf. Peres and Dolman 2000), to midsized to large-bodied species that declined to less than half their abundance in intensively hunted sites. In the extreme, mean population densities of *Lagothrix* and *Ateles* in heavily hunted sites were only 1.8% and 8.7% of those in unhunted, but otherwise comparable, forest sites. Indeed, even moderate levels of hunting pressure can drive

large atelines to local extinction, as documented in a number of forest sites surveyed throughout the Brazilian Amazon (Peres and Palacios 2007).

Peres (2000a) summarized new information on the average annual offtake of all game animals consumed by the rural, and usually unwaged, population of Brazilian Amazonia. Total game harvest throughout the region was estimated by multiplying species-specific per capita consumption rates by the size of the zero-income rural population across the entire region retaining forest cover. On the basis of estimates for primates, 3.8 million individuals are consumed annually in the Brazilian Amazon (range in estimates: 2.2–5.4 million), which represents a total biomass harvest of 16,092 tons. This is likely severely underestimated because it does not consider the fraction of lethally wounded animals that fail to be captured by hunters. Hunting rates are unsustainably high for several Amazonian primate species, often averaging over three times the maximum rate that could be sustained by a stable population (Peres 2000b). As a consequence, healthy population sizes of several large-bodied species can only be found in areas that are either effectively protected (e.g., strictly protected reserves and private forest set-asides) or extremely inaccessible to game hunters (Peres and Lake 2003).

This poses the difficult question as to what fraction of the original geographic range of different species still retains demographically viable populations. The extent of hunting-induced range contraction of several large-bodied taxa can be significant even in forest areas that remain relatively intact in terms of structural habitat disturbance detectable from satellite imagery (Peres et al. 2006). This is ecologically significant for all species regardless of geographic range size, but most serious for those range-restricted species, that are endemic to small parts of Amazonia. For example, the yellow-tailed woolly monkey, *Oreonax* (formerly *Lagothrix*) *flavicauda*, is endemic to the cloud forests of the Peruvian Andes at elevations of 1,700–2,700 m (Butchart et al. 1995). The remoteness of these areas had by default protected this species until the 1950s but since then agricultural colonization, road building projects, and logging have encroached relentlessly on its range (Leo Luna 1987). Yellow tails, like all woolly monkeys, are easy, attractive targets for hunters (Butchart et al. 1995). From the mid-1970s to the mid-1980s, at least 600 individuals had been killed by peasants and several populations had been driven to local extinction (Leo Luna 1987). Consequently, the estimated total population size of this monotypic genus is perhaps fewer than 250 animals placing it as critically endangered in the IUCN Red List (2006). Yellow-tailed woolly monkeys and other large-bodied primates endemic to small areas are obvious candidates for global extinction in the foreseeable future unless the largest remaining populations can be protected in reserves that are effectively protected from poachers.

In sum, the vast remaining forest cover that extends unbroken throughout the Amazon basin belies a scenario of partial to complete defaunation of large-bodied primates even in many relatively inaccessible areas that appear to remain structurally intact (Peres et al. 2006). These areas can no longer be considered as pristine primary forests because some key components of their large-vertebrate fauna have already been reduced to a pale shadow of their formerly intact condition (Peres and Lake 2003).

15.4.2 The Guianas

The Guianan shield is one of the largest pristine neotropical rainforest block and a floristically distinctive province compared to the Amazonian basin (Lindeman and Mori 1989). About 70 non-flying mammal species, including nine primates, are recorded in this region. This species richness is relatively low compared to western Amazonia, which may be explained by environmental unfavorableness, related to, for example, nutrient-poor soils (Emmons 1984). Eighty percent of the region is covered by uplands moist forests. The alluvial coastal plain covered by marsh forests, savannas, transition forests, herbaceous swamps and is rather narrow on this part of the Guianan shield (de Granville 1988). Compared to other neotropical countries, the forest conservation status of eastern Venezuela, Guyana, Suriname, French Guiana, and the Brazilian state of Amapá is still rather favorable, but recent increases of demographic pressures and a recent gold mining rush (Hammond et al. 2007) are serious threats on terrestrial biodiversity. French Guiana benefits from recent but extensive knowledge of primate communities in relation to habitats patterns. Eight primates species occur in the country: the red howler monkey *Alouatta seniculus macconnelli*, the black spider monkey *Ateles paniscus paniscus*, the tuffted capuchin *Cebus apella apella*, the wedge-capped capuchin *Cebus olivaceus castaneus*, the white-faced saki *Pithecia pithecia pithecia*, the bearded saki *Chiropotes satanas satanas*, the common squirrel monkey *Saimiri sciureus sciureus* and the golden handed tamarin *Saguinus midas midas*. All the species have a large distribution, except the bearded saki which is restricted to the south of the country. The spider monkey and the two sakis are protected by law, whereas other species can be hunted for subsistence use only. Primate hunting is widespread in French Guiana. In short, all human communities, whether or not indigenous, may hunt monkeys, either for subsistence or trade. Although prohibited, sales of monkey meat are common. Moreover, legal regulation of hunting is actually in course, resulting in widespread and often unsustainable game harvests, for instance in tapir (de Thoisy and Renoux 2004) and large primates (de Thoisy et al. 2005).

This case study provides a wide overview of the structure of primate communities in relation to hunting pressure and other features of sites. We examined patterns of primate richness and abundance at 41 forest sites (surveyed by BT and CRH) in relation to hunting pressure (classified as nil, medium or heavy), the type of game harvest (area hunted for traditional uses, or harvested by mixed communities facing other forms of disturbance such as logging), the other pressures on survey area (e.g., fragmentation), and forest vegetation types, including upland moist forest with or without pronounced relief, with low/high and continuous/discontinuous canopy (Fig, 15.1). In ten sites hunted by Amerindian and/or mixed communities, game harvests were monitored for 5 to 14 months. Among these sites, the number of hunters ranged from 13 to 105, and the size of the catchment area ranged from 225 to 1,250 km^2. Ethnographic and ecological data then provide an opportunity to relate the intensity of hunting pressure and local socioeconomic patterns to their effects on primate communities.
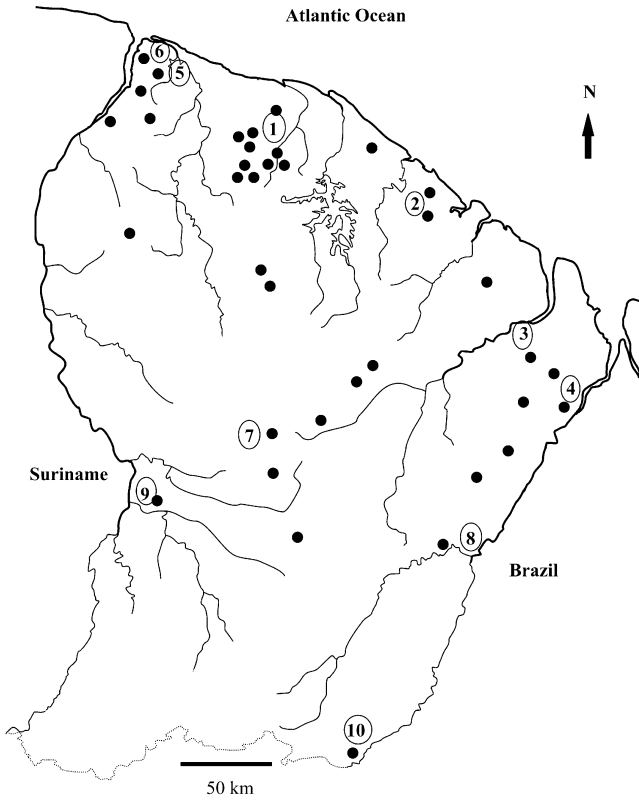
Fig. 15.1 Location of sites where primate surveys were implemented (*dots*) and where harvests were monitored (*numbers*)

The number of primate species per site ranged from as few as two in the most disturbed habitats, with tamarins and white-faced sakis dominating these communities, to as many as six species (howlers, spider monkeys, tufted and wedge-capped capuchins, white-faced sakis and tamarins) in pristine forests. Population abundance, expressed as the number of sightings of large primate species per km of transect walked was negatively correlated with levels of hunting pressure in the case of brown capuchins, howlers, and spider monkeys. A Canonical Correspondance Analysis (Fig. 15.2) provides an overview of the relationships between species richness and abundances and site descriptors. The axis 1 explained 72% of the variability in the multivariate pattern of species composition, with coordinates describing hunting and other habitat pressures being equivalent to 0.85 and 0.82. The abundance coordinates for large Cebids were $-1.60, -0.69, -0.75$ for spider monkeys, howler monkeys and capuchins, respectively, and the primate species richness coordinate amounting to -0.62. This symmetric distribution of primate community patterns on
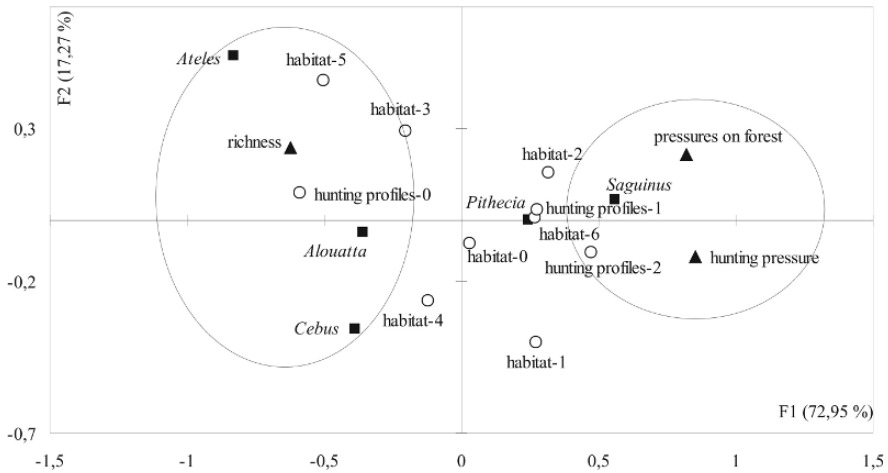
Fig. 15.2 Canonical Correspondance Analysis showing the relationships between primate species richness and abundance and the characteristics of 41 forest sites scattered across French Guiana. The negative relationship between hunting and habitat pressure and the richness and abundance of large-bodied species can be illustrated by their diametrically opposite multivariate responses

one hand, and threats on populations on the other hand, clearly underlines the relationships between levels of game harvests and population abundances of large frugivorous primates. Group sizes were also significantly affected by hunting pressure in the case of howler monkeys. For example, the mean ($\pm$ SD) group size recorded in unhunted, moderately, and heavily hunted areas was 4.6 $\pm$ 1.5, 3.8 $\pm$ 1.5, and 3.6 $\pm$ 2.0 individuals, respectively (Kruskall-Wallis test: H_{obs} = 10.7, p = 0.001). In contrast, abundances of small-bodied insectivorous/frugivorous species, such as the golden-handed tamarin, may be positively correlated with level of disturbance (Fig. 15.2).

The relative contribution of primate meat in the total harvest (primates vs. other game species) was highly variable among sites, ranging from less than 1% to more than 20% (Table 15.1). The proportion of primates in the overall harvest of prey species recorded depended not only on hunter preferences but also on local game abundances. For instance, in the northern French Guianan Amerindian settlements of Awala Yalimapo and Macouria, where threats on fauna were clearly important, harvest of primates were low in comparison to that observed at sites where Amerindian communities did not share their catchment areas. But even in the most remote southern part of the country, we found evidence of large primate depletion in all forest sites surveyed in the vicinity of large, isolated villages, and consequently even small-bodied species (golden-handed tamarins, squirrel monkeys) were hunted (Table 15.1). In contrast, the ethnic origin of hunters (i.e., indigenous vs. mixed communities) and the forest type had no detectable effect on the degree to which different primate populations were depleted. Primates were mainly hunted during "expeditions", rather than day hunts. On the other hand, we found that single-day

Table 15.1 Primate hunting at ten sites in French Guiana, including the ethnic group using the area, main use of game, estimates of game biomass harvested, and maximum sustainable harvest thresholds. Numbers refer to Fig. 15.1

Forest sites:	Local community	Use of game meat	Primate biomass/ total game biomass (%)	Primate biomass removed (kg/hunter /year/100 km²)[1]	Number of primates taken/year	Sustainable threshold of species[2]
1. Counami	mixed	subsistence	1.9	0.5	Apa:1	Apa: 12
					Ase: 10	Ase: 22
					Cap:5	Cap: 24
2. Macouria	Amerindians	commerce, subsistence	6.4	1.5	Ase: 39	Ase: 11
					Cap: 52	Cap: 56
					Col: 7	Col: nd[3]
					Ppi: 4	Ppi: 20
3. Régina	mixed	commerce	0.5	0.2	Apa: 8	Apa: 23
					Cap: 14	Cap: 58
4. St Georges	mixed	commerce	0.3	0.2	Apa: 1	Apa: 46
					Ase: 6	Ase: 83
					Cap: 22	Cap: 117
5. Mana	mixed	commerce, subsistence	19.6	5.8	Ase: 28	Ase: 8
					Cap: 40	Cap: 9
					Ppi: 24	Ppi: 7
					Ssc: 28	Ssc: 9
6. Yalimapo	Amerindians	subsistence	1.2	0.7	Cap: 8	Cap: 12
					Col: 4	Col: nd
7. Saül	mixed	subsistence	3.5	7.8	Apa: 3	Apa: 5
					Cap: 3	Cap: 19
8. Camopi	Amerindians	subsistence	22.4	9.1	Apa: 132	Apa: 40
					Ase: 252	Ase: 72
					Cap: 220	Cap: 27
					Ppi: 16	Ppi: 36
					Ssc: 16	Ssc: nd
					Smi: 4	Smi: 370
9. Elahé	Amerindians	subsistence	12.6	29.9	Apa: 52	Apa: nd
					Ase: 56	Ase: 5
					Cap: 32	Cap: 5
					Col: 24	Col: 4
					Ppi: 4	Ppi: 4
					Ssc: 12	Ssc: nd
10. Trois Sauts	Amerindians	subsistence	9.9	6.4	Apa: 48	Apa: nd
					Ase: 65	Ase: 5
					Cap: 293	Cap: nd
					Ppi: 17	Ppi: nd
					Ssc: 7	Ssc: nd
					Smi: 29	Smi: 132

[1] this variable allows comparisons of the hunting effort across communities with different number of hunters and different sizes of catchment areas.
[2] Apa = *Ateles paniscus*; Ase = *Alouatta seniculus*; Cap = *Cebus apella*; Col = *Cebus olivaceus*; Ppi = *Pithecia pithecia*; Ssc = *Saimiri sciureus*, Smi = *Saguinus midas*.
[3] nd = not determined, species not observed during surveys.

hunting trips were more profitable per unit of hunting effort than any given day of a multiple-day hunting expedition, regardless of the site, hunting method and the measure of yield considered (e.g., number or biomass of prey items captured per hunter-hour). It therefore appears that hunting effort allocated to multi-day expeditions in infrequently hunted areas primarily attempts to maximize yield of preferred (and locally depleted) prey species rather than the overall bag size (or biomass) of all potential prey species. The alternation of day hunting trips with expeditions farther afield lasting several days is cited in many hunting studies of native Amazonians (Smith 1976; Stearman 1990; Vickers 1991; Peres and Nascimento 2006). Beyond the social role of these expeditions, they represent a quest for preferred game species such as large primates which are already depleted in core hunting areas. From a wildlife management perspective, these expeditions are also extremely important because they disperse hunting activities into larger catchments, thereby diluting their impact on a per area basis. In French Guiana, Amerindians of French nationality have access to medical and social assistance and receive financial government aid, which guarantees them a regular cash income that can be used to purchase pirogues, motors, gasoline and firearms. Communities that have greater access to government handouts can easily enlarge their hunting areas, thus reducing the hunting impact even where human population density is high. Large primates are still hunted during long-range day trips, but these rely on motorboats which considerably expand the catchment area. However, these hunting zones are mainly located along major rivers, which still border very large source areas. In the most remote villages, access to money and fuel is limited, and hunters on foot can only reach a more restricted area surrounding the village in which sensitive wildlife populations have already collapsed. In these cases, hunting yields are typically very low and large primates are rarely killed.

To conclude, hunting pressure in French Guiana is a major factor explaining the variation in both the species richness and density of primate populations, as well as other vertebrate groups (de Thoisy et al. 2006). As shown in several sites of lowland Amazonia (Peres and Lake 2003), we found evidence of large primate depletion as soon as new areas become accessible to hunters. The potential roles of other factors related to habitat structure and quality (i.e., topography, geology, soil types, forest types) still remain difficult to demonstrate unambiguously, but the effects of harvests are much stronger and may obscure those of other environmental variables. The recent gold rush over the last decade (Hammond et al. 2007) resulted in a cryptic but exponentially growing harvest of sensitive species. With the newly decreed French Guiana National Park, the country presently contains a comprehensive and well- configured network of protected areas, contributing with a major role as wildlife refugia, which are likely to operate as source populations for large-bodied species. However, this National Park controversially remains legally open to hunting practices by tribal communities, under the policy rationale that both scientific monitoring and respect for aborigine livelihoods are part of the solution for nature resource conservation in inhabited Amazonian forests.

15.5 The Sustainability of Traditional Practices and the Future of Amazonian Primates

We now consider the question of whether subsistence hunting practices could coexist with viable prey populations of species characterized by slow life-histories such as primates. Sustainability of game hunting depends on the target species, game preferences, access to alternative sources of meat, either domestic or wild, and other uses of forest areas (e.g., logging) with potential direct or indirect impacts on wildlife populations. Predicted estimates of maximum sustainable yields suggest that harvest rates in most of Amazonia need not to be very high before they begin to drive primate populations to precipitous declines (Peres 2000a). In particular, *Ateles* and *Lagothrix* populations are almost always overhunted, whereas *Alouatta* and *Cebus* can sometimes be defined as sustainably exploited (Hill and Padwe 2000; Mena et al. 2000). However, midsized primates, including sakis, bearded sakis and capuchins, are typically harvested at rates exceeding their replacement capacity (Peres 1999; Bodmer and Robinson 2004). Based on data from French Guiana, we evaluated the degree to which traditional hunting practices could be considered to be sustainable using the Robinson and Redford offtake model. Briefly, unsustainable harvests are above a threshold expressed as the annual number of animals captured per unit area and calculated as the population density of any given species times the size of the catchment area x 0.03 (Robinson 2000). Surveys were conducted within hunting catchment areas, and population densities were calculated using the Leopold method (*see* de Thoisy 2000). This method is controversial because it is suspected to overestimate population densities (Brockelman and Ali 1987; Gonzales-Solis et al. 1996; Richard-Hansen and Niel 2005). Calculated sustainable offtake thresholds are therefore also consequently overestimated, resulting in a conservative diagnostic of when observed harvests exceed maximum sustainable harvests. Even in the sparsely populated southern part of the country, where only traditional Amerindian communities harvest wildlife, observed harvests were far above the predicted thresholds for the three largest primate species, capuchins, howlers and spider monkeys. In the north of the country, harvests by the Amerindian community of Macouria were also above thresholds, although harvests by other northern communities, either Amerindian or mixed, were below the critical thresholds (Table 15.1) (Fig. 15.3). This apparent under-harvesting, however, could be interpreted as an example of inevitably small offtakes of previously depleted game populations, rather than a sustainable harvest per se. In Saül, a non-native isolated village in the central part of French Guiana, crude numbers of harvested mammals generally appear to be below their maximum sustainable harvest level. However, the percentage of production harvested as estimated from local abundance estimates based on line-transect censuses was far above the maximum sustainable level for *Ateles paniscus*, and the observed percentage of offtake (Robinson 2000) was also at the maximum predicted level. Levels of meat intake were not so high, but local wildlife densities were very low, and far below the 80% of carrying capacity required to meet a safe hunting strategy (Bodmer and Robinson 2004).
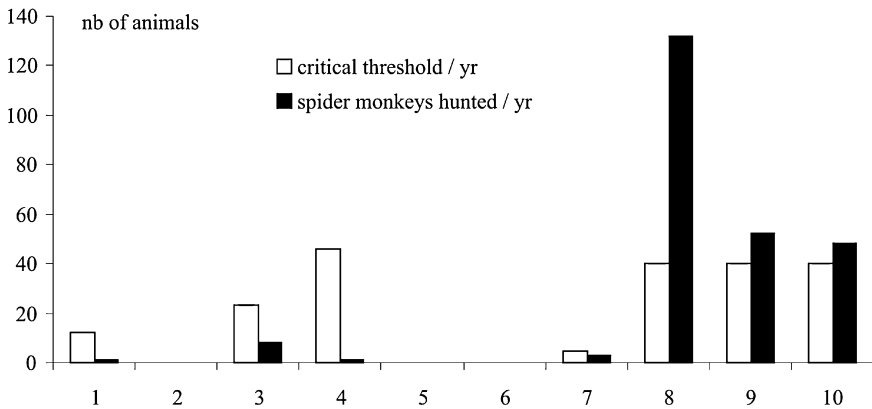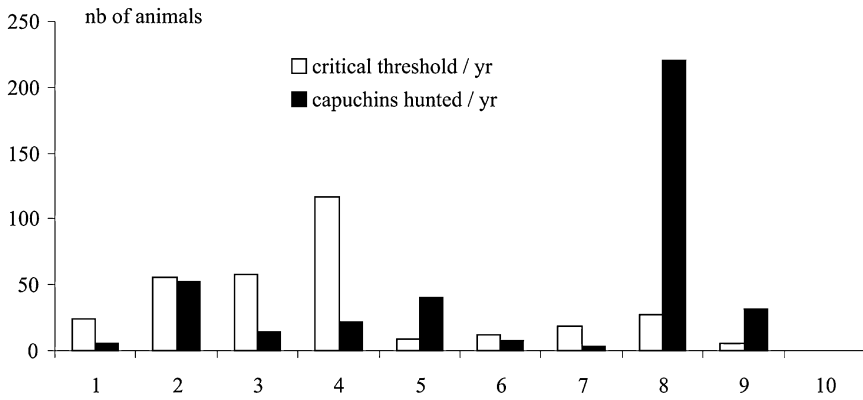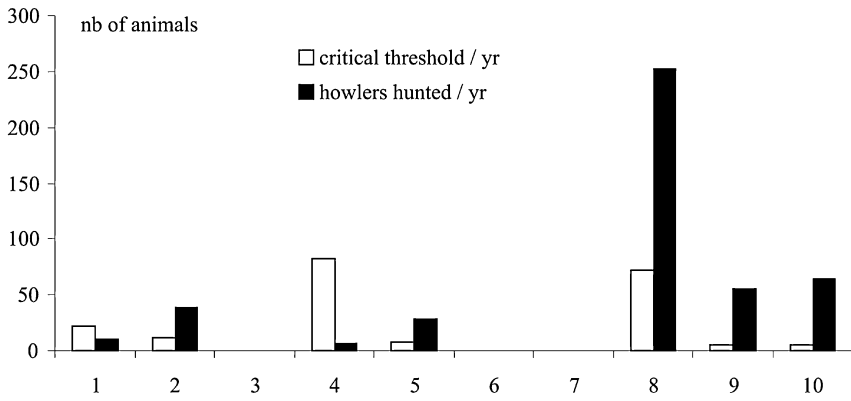
Fig. 15.3 Comparison of annual harvests and calculated maximum sustainable offtakes for three species in 10 French Guianan forest sites: the red howler monkey *Alouatta seniculus* (*above*), the brown capuchin *Cebus apella* (*middle*), and the black spider monkey *Ateles paniscus* (*below*). This is only a ratio of recorded harvests *vs.* thresholds for the three main species, on the ten sites. Numbers of sites refers to Table 15.1 and Fig. 15.1

In Peru, harvests of *Ateles paniscus* and *Cebus apella* by native subsistence hunters were close to, if not above, the predicted maximum sustainable offtakes, although the number of *Lagothrix lagotricha* and *Alouatta seniculus* kills were below the thresholds. Nevertheless surveys did not reveal any dramatic decrease in the abundance of target species (Alvard et al. 1997). Similarly, a study of a Siona-Secoya Indian community in Ecuador suggests no long-term large-scale depletion of primate populations driven by subsistence hunting (Vickers 1991). In contrast the use of long expeditions to hunt primates, as recorded in the Matsigenka communities in Peruvian Amazonia (Shepard 2002) and at some Indian villages of southern French Guiana (Richard-Hansen et al. 2006) suggests that these species are becoming scarce in the vicinities of villages, which was confirmed by line-transect censuses within core hunting areas (but *see* Ohl et al. 2007). Similar evidence of faunal depletion around indigenous settlements has been reported in Amazonia (de Souza-Mazurek et al. 2000, Peres and Nascimento 2006) and in Ecuador (Franzen 2006). However, the use of large hunting areas may also result in misinterpretation of hunting sustainability models, since faunal densities recorded in a small portion of the area may not reflect the entire area. This could be the case for some southern French Guianan villages, where surveys were conducted within the core of the hunting area near the villages, whereas most primate kills were obtained much farther from the settlement. This can partly explain the striking discrepancies between actual harvests and estimates of sustainable harvest thresholds (Fig. 15.2). Indeed, considering the mean primate population densities calculated on the basis of data from other areas subjected to moderate hunting pressure (e.g., Saül), harvests would appear to be sustainable for capuchins and howlers. Also, since these communities hunt across vast expanses of continuous habitats, there is a crucial need to include the non-hunted areas surrounding harvested areas to enable a better consideration of faunal dynamics according to different source-sink scenarios (Novaro et al. 2000).

The potential impact of traditional harvests on wild primate populations is concealed by a wide range of other concurrent pressures on forest habitat, which can confound assessments of the effects of hunting. Other stakeholders, including miners, loggers, and small farmers, may share an economic interest in harvest areas exploited by traditional communities, and often use the same target species. This may result in both interethnic conflicts and overharvesting, that cannot be attributed solely to the practices of traditional forest dwellers. Efficient conservation action plans targeting highly sensitive species will also require a wider ecological and socioeconomic research agenda, if they can claim to take into account the needs of traditional peoples. Field procedures to record population trends, population dynamics between source and sink areas, and harvest sustainability have to be improved. Ecological complexity models that can explicitly consider species distributions and abundances are a limiting factor for monitoring populations, with expected consequences on the reliability of sustainability indexes. Since habitat fragmentation is also a growing threat to forest species, the effectiveness of reserve corridors and importance of reserve design (Peres and Terborgh 1995; Ferrari et al. 1999; Azevado-Ramos et al. 2006) to maintain baseline patterns of faunal dispersal have to be better understood. Also, further work needs to be undertaken to better assess

the ability of primate species to co-exist with other forest land uses implemented by local communities (e.g., agroforestry, ecotourism). Second, in many human-occupied protected areas, the protection of primate species cannot be effectively implemented without a "conservation community" approach (Hackel 1999). Long standing cultural and economic knowledge is necessary to propose realistic alternatives to primates hunting. For example, the Baboon Sanctuary project in Belize successfully promotes the "non-extractive" utilization of primates by local communities (Alexander 2000). Game harvest is an extractive activity that provides income not only for the hunters but also for the communities (Hill 2002); effective conservation plans will require economic returns to local communities. Scientific and charismatic value of the primates should help to promote conservation and fund-raising (Alexander 2000), some of which may help communities. Finally, no conservation plan can be implemented without the knowledge of the cost of long-term losses of depleting natural resources.

Combined with a significant role in the symbolism related to wild species, non-human primates are a widely used source of protein for Amerindian communities throughout Amazonia (Cormier 2006; Shepard 2002). Food choices vary among Amazonian communities, and the importance of primate meat in local diets is highly variable at a regional scale. Although most studies of tribal communities conclude that, with traditional use of space and respect for cultural beliefs, harvests are presumably sustainable, the status of primate populations in relation to traditional hunting pressure is inherently complicated by the fact that indigenous hunting interacts with other threats, such as road building, logging, and hunting by nontribal immigrants. Questions have been raised about the opportunity to maintain such traditions in forest landscapes increasingly facing other threats. In forest areas facing a high degree of hunting pressure, particularly where catchment areas are shared by several neighboring communities, we found that Amerindian communities are unable to harvest primates and other game species sustainably, even though very similar communities that are isolated in more remote areas can exercise sustainable harvests. Indeed, as densities of target species including ungulates and large gamebirds decrease, and hunting pressure on primates is expected to increase, there is a high risk of overharvesting several sensitive species (de Thoisy and Renoux 2004; de Thoisy et al. 2005). Our analysis of primate communities in French Guiana and concomitant studies on game hunting show that most primates are simply unable to coexist with poorly regulated hunting practices, even for the most benign subsistence purposes, as soon as human population densities increase. This is clearly at odds with the widespread belief that traditional aborigine communities share an intuitive and time-tested ability to ensure the sustainable use of natural resources. In most cases, apparently harmonious coexistence between indigenous groups and forest wildlife is more related to low densities of the indigenous population, and hence small offtakes exerted under conditions of negligible habitat changes, rather than an active body of adaptive knowledge guiding a successful resource management system. In addition, indigenous population growth is often inevitable, thus, placing greater pressures on natural resources, including sensitive game populations. Reconciling the subsistence needs of local peoples and the requirements of wild primate

populations will therefore, always remain a difficult challenge. However, a renewed focus on the demarcation of indigenous territories, and subsequent enforcement of territorial rights, can provide adequate incentives for long-term resource management, particularly if successful partnerships can be implemented with conservation organizations (McSweeney 2005; Schwartzmann and Zimmerman 2005).

15.6 Summary

For millenia, coexistence between human and nonhuman primates has been mystical in all tropical forest regions. Many primate populations have, however, contributed to human diets, often resulting in drastic declines of several species. Although socio-cultural and religious taboos may still limit predation in contemporary times, harvesting of primate populations remains a frequent occurrence throughout the humid tropics. Population declines and local extinctions in relation to direct human exploitation are widely reported in South and Central America, with large-bodied species as the first target species being the most dramatically affected. We illustrate the relationships between offtakes by local communities and wild primate populations using two cases studies. Subsistence hunting has affected game populations throughout lowland Amazonia, with profound consequences to the size structure of primate assemblages, affecting even some of the most remote parts of the region. In French Guiana, the richness of primate communities and the abundance of large cebids were negatively correlated with levels of hunting pressure. Monitoring of harvests by both native and non-native communities revealed that the relative contribution of primate meat to the total harvest was highly variable, ranging from less than 1% to more than 20%. As shown in previous studies, predicted estimates of maximum sustainable yields suggest that harvests need not be very high before they begin to drive primate populations to precipitous declines. Although most studies of tribal communities conclude that, with traditional use of space and respect for cultural beliefs, harvests may be sustainable for some species, the status of primate populations facing subsistence hunting pressure by indigenous groups is profoundly complicated by the fact that harvests interact with other threats, such as road building, logging, and additive hunting by nontribal immigrants. All Amazonian studies show that most primates are simply unable to coexist with unregulated hunting, even for the most benign subsistence purposes, as soon as human population densities increase. We therefore question the widespread belief that traditional communities share an intuitive wisdom to ensure the sustainable use of natural resources. In most cases, harmonious coexistence between indigenous groups and forest wildlife is more related to low densities of the indigenous population and small offtakes exerted on habitats with negligible changes, rather than an active adaptive body of knowledge guiding a successful resource management system. Reconciling the subsistence needs of local peoples and the requirements of primate populations will therefore always remain a difficult challenge. However, demarcation of indigenous territories and subsequent enforcement of territorial rights can

provide adequate incentives for long-term resource management. Efficient conservation action plans designed for sensitive species and respect for traditional cultures will also require further research and policy action. Ecological studies should include improved monitoring of population trends and the dynamics between source and sink areas. Finally, long-standing socioeconomic knowledge will be necessary to propose viable alternatives to primate hunting, and a "conservation community" approach should be promoted, with efficient economic returns to local communities.

References

Alexander, S. E. 2000. Resident attitudes toward conservation and Black howler monkeys in Belize: the Community Baboon Sanctuary. Environmental Conservation 27:341–350.

Alvard, M. S., Robinson, J. G., Redford, K. H., and Kaplan, H. 1997. The sustainability of subsistence hunting in the Neotropics. Conservation Biology 11:977–982.

Ayres, J. M., Lima, L. M., Martins, E. S., and Barreiros J. L. K. 1991. On the track of the road: changes in subsistence hunting in a Brazilian Amazonian village. In J. G. Robinson and K. H. Redford (eds), *Neotropical Wildife Use and Conservation* (pp 82–92). Chicago: University of Chicago Press.

Azevado-Ramos, C., Domingues do Amaral, B., Nepstad, D. C., Filho, B. S., and Nasi, R. 2006. Integrating ecosystem management, protected areas, and mammal conservation in the Brazilian Amazon. Ecology and Society 11:art 17.

Balée, W. 1989. The culture of Amazonian forests. Advances in Economic Botany 7:1–21.

Barnett, A. A., Borges, S. H., de Castilho, C. V., Neri, F. M., and Shapley, R. L. 2002. Primates of the Jaú national park, Amazonas, Brazil. Neotropical Primates 10:65–70.

Bermejo, M., Rodriguez, J. D., Illera, G., Barroso, A., Vila, C., and Walsh, P. D. 2006. Ebola outbreak killed 5000 gorillas. Science 314:1564.

Bodmer, R. E. 1995. Managing Amazonian wildlife: biological correlates of game choice by detribalized hunters. Ecological Applications 5:872–877.

Bodmer, R., and Robinson, J. 2004. Evaluating the sustainability of hunting in the neotropics. In K. Silvius, R. Bodmer and J. Fragoso (eds.), *People in nature: wildlife conservation in South and Central America* (pp. 299–323). New York: Columbia University Press.

Bollen, A., and Donati, G. 2006. Conservation status of the littoral forest of south-eastern Madagascar: a review. Oryx 40:57–66.

Brockelman, W. Y., and Ali, R. 1987. Methods of surveying and sampling forest primate populations. In C. W. Marsh and R. A. Mittermeier (eds.), *Primate Conservation in the Tropical Rain Forest* (pp. 23–42).New York: Alan R. Liss, Inc.

Burney, D. A. 1999. Rates, patterns, and the processes of landscape transformation and extinction in Madagascar. In R. D. E. MacPhee (ed.), *Extinctions in Near Time: Causes, Contexts, and Consequences* (pp. 145–164). New York: Plenum Press.

Burney, D. A, Burney, L. P., Godfrey, L. R., Junters, W. J., Goodman, S. M., Wright, H. T., and Jull, A. J. 2004. A chronology for late prehistoric Madagascar. Journal of Human Evolution 47:25–53.

Butchart, S. H. M., Barnes, R., Davies, C. W. N., Fernandez, M., and Seddon, N. 1995. Observations of two threatened primates in the Peruvian Andes. Primate Conservation 1:15–19.

Cartelle, C., and Hartwig, W. C. 1996. A new extinct primate among the Pleistocene megafauna of Bahia, Brazil. Proceedings of the National Academy of Sciences 93:6405–6409.

Colell, M., Maté, C., and Fa, J. E. 1995. Hunting among Moka Bubis: dynamics of faunal exploitation at the village level. Biodiversity and Conservation 3:939–950.

Cormier, L. A. 2003. Kinship with monkeys: the Guajà foragers of Eastern Amazonia. New York: Colombia University Press.

Cormier, L. A. 2006. A preliminary review of neotropical primates in the subsistence and symbolism of indigenous lowland South American people. Ecological and Environmental Anthropology 2:14–32.

Costa, L. P., Leite, Y. L. R., Mendes S. L., and Ditchfield, A. D. 2005. Mammal conservation in Brazil. Conservation Biology 19:672–679.

Cowlishaw, G. 1999. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. Conservation Biology 13:1183–1193.

de Granville, J. J. 1988. Phytogeographical characteristics of the Guianan forests. Taxon 37: 578–594.

de Thoisy, B. 2000. Line-transects: sampling application to a rainforest in French Guiana. Mammalia 64:101–112.

de Thoisy, B., and Renoux, F. 2004. Status of the lowland tapir in French Guiana: hunting pressure and threats on habitats. Second International Tapir Symposium, TSG/SSC/IUCN, Panama.

de Thoisy, B., Renoux, F., and Julliot, C. 2005. Hunting in northern French Guiana and its impacts on primates communities. Oryx 39:149–157.

de Thoisy, B., Brosse, S., Richard-Hansen, C., and Thierron, V. 2006. Rapid evaluation of relationships between impacts of forest anthropic activities and threats on biodiversity in French Guiana. VII Congresso Internacional sobre manejo de fauna silvestre na Amazônia e América latina. Ilhéus, Bahia, Brasil.

De Souza-Mazurek R. M., Pedrinho, T., Feliciano, X., Hilário, W., Gerôncio, S., and Marcelo, E. 2000. Subsistence hunting among the Waimiri Atroari Indians in central Amazonia, Brazil. Biodiversity and Conservation 9:579–596.

Emmons, L. H. 1984. Geographic variation in densities and diversities of non flying mammals in Amazonia. Biotropica 16:210–222.

Ferrari, S. F., Emidio-Silva, C., Aperecida Lopes, M., and Bobadilla, U. L. 1999. Bearded sakis in South-eastern Amazonia – back from the brink? Oryx 33:346–351.

Franzen, M. 2006. Evaluating the sustainability of hunting: a comparison of harvest profiles across three Huaorani communities. Environmental Conservation 33:36–45.

Freese, C. H., Heltne, P. G., Castro, N., and Whitesides, G. 1982. Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distribution. International Journal of Primatology 3:53–90.

Fusari, A., and Carpaneto, G. M. 2000. Subsistence hunting and bushmeat exploitation in central-western Tanzania. Biodiversity and Conservation 9:1571–1585.

Fusari A., and Carpaneto, G. M. 2006. Subsistence hunting and conservation issues in the game reserve of Gile, Mozambique. Biodiversity and Conservation 15:2477–2495.

Garcia, G., and Goodman, S. M. 2003. Hunting of protected animals in the Parc National d'Ankarafantsika, north-western Madagascar. Oryx 37:115–118.

Goossens, B., Chikhi, L., Ancrenaz, M., Lackman-Ancrenaz, I., Andau, P., and Brudford M. W. 2006. Genetic signature of anthropogenic population collapse in Orang Utans. PLoS Biology 4:e25.

Gonzales-Solis, J., Mateos, E., Manosa, S., Ontanon, M., Gonzlez-Martin, M. and Guix, J. C. 1996. Abundance estimates of primates in an Atlantic rainforest area of southeastern Brazil. Mammalia 60:488–491.

Hackel, J. D. 1999. Community conservation and the future of Africa's wildife. Conservation Biology 13:726–734.

Hammond, D. S., Gond, V., de Thoisy, B., Forget P. M., and DeDijn, B. 2007. Causes and consequences of a tropical forest gold rush in the Guiana Shield, South America. Ambio 36:661–670.

Harris, R. B., Wall, W. A., and Allendorf, F. W. 2002. Genetic consequences of hunting: what do we know and what should we do? Wildlife Society Bulletin 30:634–643.

Haugaasen, T., and Peres, C. A. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. American Journal of Primatology 67:243–258.

Hill, C. M. 2002. Primate conservation and local communities – ethical issues and debates. American Anthropologist 104:1184–1194.

Hill, K., and Padwe, J. 2000. Sustainability of Aché hunting in the Mbaracayu reserve, Paraguay. In J. G. Robinson and E. L. Bennett (eds.), *Hunting for Sustainability in Tropical Forests* (pp. 79–105). New York: Columbia University Press.

Isaac, N. J. B., and Cowlishaw, G. 2004. How species respond to multiple extinction threats. Proceedings Royal Society of London B 271:1135–1141.

IUCN. 2006. 2006 IUCN Red List of Threatened Species. www.redlist.org. Accessed October 2006.

Jernvall, J., and Wright, P. C. 1998. Diversity components of impending primate extinctions. Proc. Natl Acad. Sci. 95:11279–11283.

Jerozolimski, A., and Peres, C. A. 2003. Bringing home the biggest bacon: a cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. Biological Conservation 111: 415–425.

Jiang, X., Luo, Z., Zhao, S., Li, R, and Liu, C. 2006. Status and distribution pattern of black crested gibbon (*Nomascus concolor jingdongensis*) in Wuliang Mountains, Yunnan, China: implication for conservation. Primates 47:264–271.

Johns, A. D. 1991. Forest disturbance and Amazonian primates. In H. O. Box (ed.), *Primate Responses to Environmental Changes* (pp. 115–135). London: Chapman and Hall.

Johns A. D., and Skorupa, J. P. 1987. Responses of rain-forest primates to habitat disturbance: a review. American Journal of Primatology 8:157–192.

Johnson, K. 1996. Hunting in the Budongo Forest, Uganda. Swara Jan–Feb:24–27.

Jorgenson, J. P. 2000. Wildlife conservation and game harvest by Maya hunters in Quintina Roo, Mexico. In J. G. Robinson and E. L. Bennett (eds.), *Hunting for Sustainability in Tropical Forests*, (pp. 251–266). New York: Colombia University Press.

Kracke, W. H. 1978. Force and persuasion, leadership in an Amazonian society. Chicago: University of Chicago Press.

Kumara, H. N., and Singh, M. 2004. The influence of differing hunting practices on the relative abundance of mammals in two rainforest areas of the Western Ghats, India. Oryx 38:321–327.

Lahm, S. A. 1993. Utilization of forest resources and local variation of wildlife populations in Northeastern Gabon. In C. M. Hladik, A. Hladik, O. F. Linarea, H. Pagezy, A. Semple and M. Hadley (eds.), *Tropical Forest, People and Food* (pp. 213–226). Paris: Parthenon Publishing Group.

Larson, S., Jameson, R., Bodkin, J., Staedler, M., and Bentzen, P. 2002. Microsatellite DNA and mitochondrial DNA variation in remnant and translocated sea otter (*Enhydra lutris*) populations. Journal of Mammalogy 83:893–906.

Lehman, S. M. 2000. Primate community structure in Guyana: a biogeographic analysis. International Journal of Primatology 21:333–351.

Leo Luna, M. 1987. Primate conservation in Peru: a case study of the yellow-tailed woolly monkey. Primate Conservation 8:122–123.

Lindeman, J. C., and Mori, S. A. 1989. The Guianas. In D. G. Campbell and H. D Hammond (eds.), *Floristic Inventories of Tropical Countries: The Status of Plants Systematics, Collections and Vegatation, Plus Recommendations for the Future* (pp. 375–390). New York: New York Botanical Garden.

Lopes, M. A., and Ferrari, S. F. 2000. Effects of human colonization on the abundance and diversity of mammals in eastern Brazilian Amazonia. Conservation Biology 14:1658–1665.

Madhusudan, M. D., and Karanth, K. U. 2002. Local hunting and the conservation of large mammals in India. Ambio 31:49–54.

McSweeney, K. 2005. Indigenous population growth in the lowland Neotropics: social science insights for biodiversity. Conservation Biology 19:1375–1384.

Mena, V. P., Stallings, J. R., Regalado, B. J., and Cueva, L. R. 2000. The sustainability of current hunting practices by the Huaorani. In J. G. Robinson and E. L. Bennett (eds.), *Hunting for Sustainability in Tropical Forests* (pp. 57–78). New York: Columbia University Press.

Milner-Gulland, E. J., Bennett, E. L. and the SCB 2002. Annual Conference Wild Meat Group. 2003. Wild meat: the bigger picture. Trends on Ecology and Evolution 18:351–357.

Milner, J. M., Nilsen, E. B., and Andreassen H. P. 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:36–47.

Mittermeier, R. A. 1991. Hunting and its effects on wild primate populations in Suriname. In J. G. Robinson and K. H. Redford (eds.), *Neotropical Wildlife Use and Conservation*, (pp. 93–106). Chicago, University of Chicago Press.

Mittermeier, R. A., Valladares-Pádua, C., Rylands, A. B, Eudey, A. A, Butynski, T. M., Jörg, U. Ganzhorn, J. U., Rebecca Kormos, R., Aguiar J. M., and Walker, S. 2005. The World's 25 Most Endangered Primates 2004–2006. IUCN/Primate Specialist Group and International Primatological Society.

Muchaal, P. K., and Ngandjui, G. 1999. Impact of village hunting on wildlife populations in the Western Dja Reserve, Cameroon. Conservation Biology 13:385–396.

Nijman, V. 2004. Effects of habitat disturbance and hunting on the density and the biomass of the endemic Hose's leaf monkey *Presbytis hosei* (Thomas, 1889) (Mammalia: Primates: Cercopithecidae) in east Borneo. Contributions to Zoology 73:art4.

Novaro, A. J., Redford, K. H. and Bodmer, R. E. 2000. Effect of hunting in source-sink systems in the Neotropics. Conservation Biology 14:713–721.

Nuñez-Iturri, G., and Howe, H. F. 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rainforest in western Amazonia. Biotropica 39:348–354.

Oates, J. F. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. Australian Journal of Ecology 21:1–9.

Ohl-Schacherer, J., Shepard, G. H., Kaplan, H., Peres, C. A., Levi, T; Yu, D.W. 2007. The sustainability of subsistence hunting by Matsigenka Native communities in Manu National Park, Peru. Conservation Biology 21:1174–1185

Olupot, W. 2000. Mass differences among male Mangabey monkeys inhabiting logged and unlogged forest compartments. Conservation Biology 14:833–843.

Pacheco, L. F, and Simonetti, J. A. 2000. Genetic structure of a Mimosoid tree deprived of its sed disperser, the spider monkey. Conservation Biology 14:1766–1775.

Peres, C. A. 1990. Effects of hunting on western Amazonian primate communities. Biological Conservation 54:47–59.

Peres, C. A. 1991. Humboldt's woolly monkeys decimated by hunting in Amazonia. Oryx 25: 89–95.

Peres, C. A. 1997a. Primate community structure at twenty western Amazonian flooded and unflooded forests. Journal of Tropical Ecology 13:381–405.

Peres, C. A. 1997b. Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: a case study of howler monkeys (*Alouatta* spp.). Folia Primatologica 68:199–222.

Peres, C. A. 1999. Effects of hunting and habitat quality on Amazonian primate communities. In J. G. Fleagle, C. Janson and K.E. Reed (eds.), *Primate Communities* (pp. 268–283). Cambridge: Cambridge University Press.

Peres, C. A. 2000a. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conservation Biology 14:240–253.

Peres, C. A. 2000b. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. In J. G. Robinson and E. L. Bennett (eds.), *Hunting for Sustainability in Tropical Forests* (pp. 31–57). New York: Columbia University Press.

Peres, C. A., and Terborgh, J. W. 1995. Amazonian nature reserves: an analysis of the defensibility status of existing conservation units and design criteria for the future. Conservation Biology 9:34–46.

Peres, C. A., and Dolman, P. 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and non-hunted Amazonian forests of varying productivity. Oecologia 122:175–189.

Peres, C. A., and van Roosmalen, M. 2002. Patterns of primate frugivory in Amazonia and the Guianan shield: implications to the demography of large-seeded plants in overhunted tropical forests. In D. Levey, W. Silva and M. Galetti (eds.) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (pp. 407–423). Oxford: CABI International.

Peres, C. A., and Lake, I. R. 2003. Extent of nontimber resource extraction in tropical forests: accessibility, to game vertebrates by hunters in the Amazon basin. Conservation Biology 17: 1–17.

Peres, C. A., and Nascimento, H. S. 2006. Impact of game hunting by the Kayapó of southeastern Amazonia: implications for wildlife conservation in Amazonian indigenous reserves. Biodiversity and Conservation 15:2627–2653.

Peres, C.A, Barlow, J., and Laurance, W. 2006. Detecting anthropogenic disturbance in tropical forests. Trends in Ecology and Evolution 21:227–229.

Peres, C. A., and Palacios, E. 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. Biotropica 39:304–315.

Perez, V., Godfrey, L. R., Nowak-Kemp, M., Burney, D. A., Ratsimbazafy, J., and Vasey, N. 2005. Evidence of early butchery of giant lemurs in Madagascar. Journal of Human Evolution 49:722–742.

Ratiarison, S., and Forget, P. M. 2005. Frugivores and seed removal at *Tetragastris altissima* (Burseraceae) in a fragmented forested landscape of French Guiana. Journal of Tropical Ecology 21:1–8

Redford, K. H., and Robinson, J. G. 1987. The game of choice: patterns of Indian and colonist hunting in the Neotropics. American Anthropologist 89:650–667.

Redford, K. H., and Robinson, J. G. 1991. Subsistence and commercial uses of wildlife in Latin America. In J. G. Robinson and K. H. Redford (eds.), *Neotropical Willdife Use and Conservation* (pp. 6–23). Chicago: University of Chicago Press.

Refish, J., and Koné, I. 2005. Impacts of commercial hunting on monkey populations in the Taï region, Côte d'Ivoire. Biotropica 37:136–144.

Renoux, F. 1998. Se nourrir à Trois Sauts: analyse diachronique de la prédation chez les Wayãpi du Haut-Oyapock. Journal d'Agriculture Traditionnelle et de Botanique Appliquée 40: 167–180.

Richard-Hansen, C., and Hansen. E. 2004. Hunting and wildlife management in French Guiana: current aspects and future prospects. In K. Silvius, R. Bodmer and J. Fragoso (eds.), *People in Nature: Wildlife Conservation in south and central America* (pp. 400–410). New York, Columbia University Press.

Richard-Hansen, C., Khazraie, K., Mauffrey, J.-F., and Gaucher, P. 2004. Pratiques de chasse dans un village isolé du centre de la Guyane: Evaluation de l'impact sur les populations animales. 6th International Wildlife Ranching Symposium, 6–9 juillet, Paris.

Richard-Hansen, C., and Niel, C. 2005. "Estimer les faibles densités d'espèces chassées en Guyane avec peu d'observations: Proposition de calcul d'une "largeur effective de comptage" (Effective Strip Width, ou ESW) spécifique." ONCFS, Rapport scientifique 2004:22–27.

Richard-Hansen, C., Gaucher, P., Maillard, J.-F., and Ulitzka, M. 2006. Análisis comparativa de la cacería en tres pueblos de comunidades indígenas en Guyana Francesa. VII Congreso Internacional sobre Manejo de Fauna Silvestre en la Amazonía y Latinoamérica, Ilhéus, Brazil.

Robinson, J. G. 2000. Calculating maximum sustainable harvests and percentage offtakes. In J. G. Robinson and E. L. Bennett (eds.), *Hunting for Sustainability in Tropical Forests* (pp. 521–524). New York: Colombia University Press.

Ruiz-Garcia, M. 2005. The use of several microsatellite loci applied to 13 neotropical primate revealed a strong recent bootleneck event in the woolly monkey (*Lagothrix lagothricha*) in Colombia. Primate Report 71:27–55.

Russo, S. E., Portnoy, S., and Augspurger C. K. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. Ecology 87:3160–3174

Schwartzmann, S., and Zimmerman, B. 2005. Conservation alliances with indigenous people of the Amazon. Conservation Biology 19:721–727.

Serio-Silva, J. C., and Rico-Gray, V. 2002. Interacting effects of forest fragmentation and howler monkey foraging on germination and dispersal of figs. Oryx 36:266–271.

Shepard, G. H. 2002. Primates in Matsigenka subsistence and World view. In A. Fuentes and D. Wolfe (eds.), Primates Face to Face: *The Conservation Implications of Human-Non Human Primate Interconnections* (pp. 101–136). Cambridge: Cambridge University Press.

Smith, N. J. H. 1976. Utilization of game along Brazil's Transamazon Highway. Acta Amazonica 6:455–466.

Stearman, A. M. 1990. The effects of settler incursion on fish and game resources of the Yuqui, a native Amazonian society of eastern Bolivia. Human Organization 49:373–385.

Stoner, K. E., Vulinec, K., Wright, S. J., and Peres, C. A. 2007. Hunting and plant community dynamics in tropical forests: a synthesis. Biotropica 39:385–392.

Sussman, R. W, and Phillips-Conroy, J. E. 1995. Survey of the distribution and density of primates of Guyana. International Journal of Primatology 16:761–791.

Urbani, B. 2006. A survey of primate populations in Northeastern Venezuelan Guayana. Primate Conservation 20:47–52.

Vaughan, C. 1993. Human population and wildlife: a Central American focus. Transactions of the 58th North American Wildlife and Natural Resources Conferences.

Vickers, W. T. 1991. Hunting yields and game composition over ten years in an Amazon Indian territory. In J. G. Robinson and K. H. Redford (eds.), *Neotropical Willdife Use and Conservation* (pp. 53–81). Chicago: University of Chicago Press.

Wadley, R. L., Carol, J., Pierce Colfer, C. J. P., and Hood, I. G. 1997. Hunting primates and managing forests: the case of Iban Forest Farmers in Indonesian Borneo. Human Ecology 25:243–271.

Walsh, P. D., Abernethy, K. A., Bermejo, M., Beyers, R., de Watcher, P., Akou, M. E., Huljbregts, B., Mambounga, D. I., Toham, A. K., Kilbourn, A. M., Lahm, S. A., Latour, S., Maisels, F., Mbina, C., Mihindou, Y., Oblang, S. N., Effa, E. N., Starkey, M. P., Telfer, P., Thibault, M., Tutin, C. E. G., White, L. J. T., and Wilkie, D. S. 2003. Catastrophic ape decline in western equatorial Africa. Nature 422:611–614.

Wilkie, D. S., Curran, B., Tshombe, R, and Morelli, G. A. 1998. Modeling the sustainability of subsistence farming and hunting in the Ituri Forest of Zaire. Conservation Biology 12:137–147.

Young, T. P., and Isbell, L. A 1994. Minimum group size and other conservation lessons exemplified by a declining primate population. Biological Conservation 68:129–134.