

Primate Conservation in the New Millennium: The Role of Scientists

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For nearly three decades, the academic community has clearly recognized that many primate populations are severely threatened by human activities.¹⁻³ In 1983, Wolfheim⁴ estimated that more than 50% of all primate species faced some form of threat. Over a decade later, the Primate Specialist Group of the Species Survival Commission of the World Conservation Union⁵ estimated that half of the world's 250 species of primates were of serious conservation concern. In a recent review of the current status of primate communities, Wright and Jernvall⁶ commented that it was an achievement for primate conservationists that we had not lost any species in the last millennium. It is ironic that the first documented extinction of a widely recognized primate taxon occurred just as we entered the new millennium.⁷ Based on surveys in Ghana and Cote d'Ivoire, Oates and colleagues⁷ have failed to find any surviving populations of Miss Waldron's red colobus (*Procolobus badius waldroni*), a primate taxon endemic to this region and one that some authorities consider worthy of species status. Because 96 primate species are now considered to be critically endangered or endangered,^{6,8,9} much must be done in the near future to ensure that extinction curves do not lag behind tropical deforestation and high levels of commercial and subsistence hunting.¹⁰

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In this article we use new data to review the major threats facing primate populations and assess probable declines and local extinctions. Subsequently, we outline some of the approaches currently advocated for primate protection (Fig. 1). Finally, we draw on our experiences in regions of the world under very different contexts of threat to make recommendations on the types of information that will be needed to construct informed management plans and discuss the role scientists can play in formulating these plans.

MAJOR THREATS

Habitat Modification

Deforestation

Ninety percent of all primate species are found in tropical regions and depend on rapidly disappearing forests (Fig. 2).¹¹ A recent report by the Food and Agriculture Organization of the United Nations¹² provides the latest figures on worldwide forest cover, making it possible to estimate the fate

of primate populations in different regions. For developing countries, the FAO defines deforestation as the depletion of tree cover in closed-canopy forests to less than 10%, a canopy thinning threshold that is almost certainly incompatible with the survival of most strictly arboreal primates.

For countries harboring primates, statistics from the Food and Agriculture Organization indicate that there are 18,910,280 km² of forest. Forest loss between 1980 and 1995 was 10.5% for Africa, 9.7% for Latin America and the Caribbean, and 6.4% for

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Asia and Oceania. Countries with primate populations are losing 125,140 km² of forest annually. This is an area greater than Mississippi (122,335 km²) or just smaller than Greece (131,985 km²). The highest losses have occurred in countries with large expanses of tropical forest; they included average annual conversions of 25,540 km² in Brazil, 10,840 km² in Indonesia, and 7,400 km² in the Democratic Republic of Congo (Fig. 3). If one looks at which countries are losing the greatest proportion of remain-

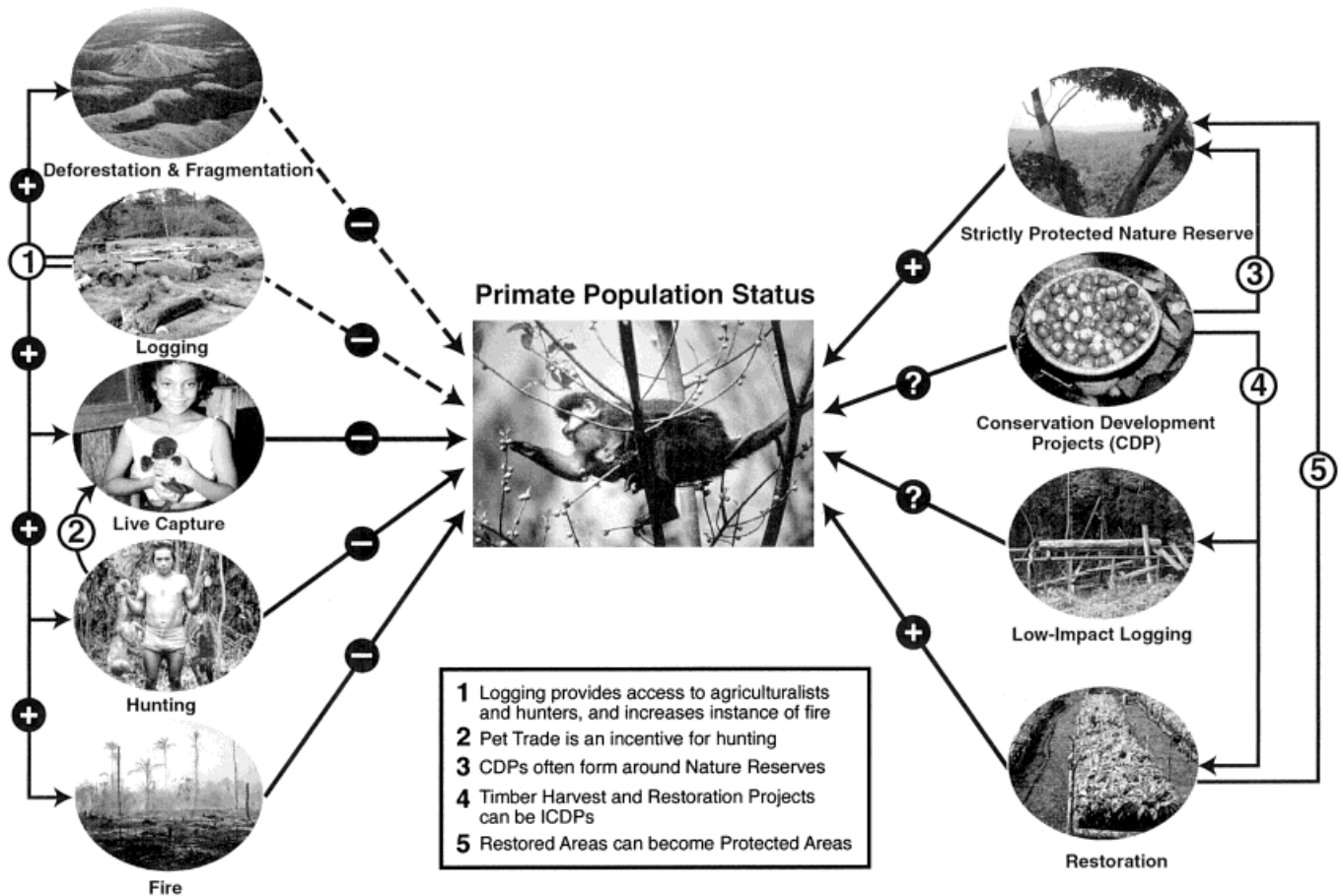


Figure 1. The major threats facing primate populations, interactions among those threats, and approaches advocated to mitigate those threats. + signs indicate positive association (that is, an increase in one component will lead to an increase in the next; – signs indicate a negative association; ? indicates that the association is largely unknown; straight lines indicate direct effects (increase in hunting leads to fewer primates); and a dashed line represents indirect effects (for example, logging decreases trees, which decreases primate food supply, which lowers primate abundance). All photographs are by the authors with the exception of that of the redtail monkey, which was taken by Lisa Leland.

ing forest cover, the top four countries are the Philippines (annual deforestation rate 3.87%), El Salvador (3.81%), Costa Rica (3.29%), and Sierra Leone (3.28%). Growing external debts place strong pressures on governments to encourage timber harvesting and increased agricultural activity. For example, each year the countries of sub-Saharan Africa return a mean of 58% of their Gross National Product in repayment of foreign debts that can be as high as 241% of GNP.¹³

Chapman¹⁴ reviewed density and biomass estimates for the best-studied primate field sites around the world. These values indicate an average global primate density of 257 individuals/km² and a biomass of 979 kg/km². Because many of these sites were selected because of their high primate

abundance, these figures may overestimate the typical primate density. On the other hand, these estimates often exclude nocturnal species, such as galagos, or wide-ranging species such as mandrills. Despite such limitations, these are the best estimates available to calculate primate population declines. We estimate that the amount of forest habitat lost each year would support approximately 32 million primates corresponding to a biomass of 123,000 tons.

Economic valuation of wildlife and other non timber forest products is often considered to be an inherent component of future conservation strategies under the “use it or lose it” paradigm of tropical conservation.^{15,16} The consumption and sale of wild game meat is a common practice

throughout the humid tropics. Because game meat can be seen as a market commodity, one can calculate a dollar value for the 123,000 tons of primate biomass being lost each year. Considering only yields of edible meat (i.e., muscle mass and edible viscera for different species mean = 55% of body mass Martins¹⁷ and C. Peres and H. Nascimento unpublished data), this represents a loss of 68,000 tons. In economic terms, assuming the mean substitution value of \$2.14/kg¹⁸ for bovine beef purchased in small Amazonian settlements,¹⁸ this would represent a mean annual market value of \$146 million lost to deforestation alone. The more meaningful calculation that should be made is what the annual economic loss would be if these populations had been harvested

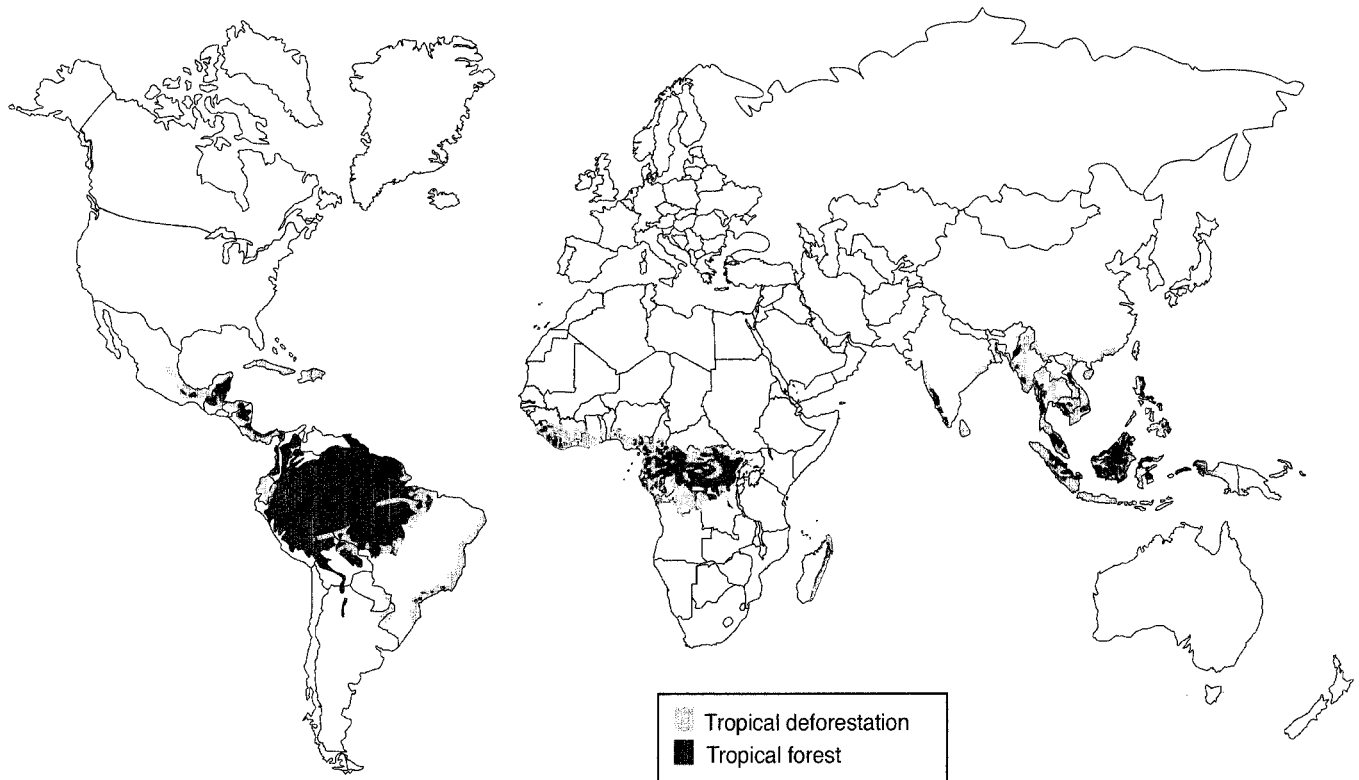


Figure 2. Map of the world illustrating the major regions of moist and wet forest, and the extent of deforestation in these areas. (Adapted from National Geographic Atlas of the World, 1992).

sustainably. However, sustainable harvest rates are extremely low and have not been empirically derived for most primate species. For many species, no harvest would be suitable because their populations are already threatened.

Timber extraction

Tropical deforestation appears to be driven primarily by frontier expansion of subsistence agriculture and large economic development programs involving resettlement, agriculture, and infrastructure.¹² However, primate population declines are typically preempted by hunting and logging activity well before the coup de grâce of deforestation is delivered. According to the definition of the Food and Agriculture Organization, selective logging is not considered to be deforestation because it does not decrease forest cover to less than 10% of its original level. It is estimated that between 5 and 6 million ha of tropical forests are logged each year; approximately a third of the area that is completely deforested.¹⁹ To put this in

perspective, this area is approximately equal to West Virginia (62,470 km²) or Ireland (68,895 km²). The total area of forest that is either selectively logged or deforested is approximately 185,000 km².

Few studies have examined the impacts of selective logging on pri-

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mate communities. Also, comparisons among studies are limited because investigators often have failed to employ comparable methods or to adequately report their methods. Studies also vary with respect to extraction re-

gimes and incidental damage levels,^{20–23} original composition of the primate communities,²⁴ proximity to undisturbed refugia and recolonization sources,^{25–27} and time lag between logging and the monitoring of the primate populations.^{28–31} In addition, access provided by logging operations may or may not have increased the synergistic effects of hunting.^{22,24,32–34} Such variability has led to different conclusions even with respect to study areas in close geographical proximity and sites with similar species assemblages. For example, Johns²¹ studied the effects of logging on primate populations in dipterocarp forests in Peninsular Malaysia, while Bennett and Dahaban²⁴ addressed the same question in dipterocarp forests in the Bornean state of Sarawak. The intensity of logging was similar in the two regions. In Peninsular Malaysia, extraction removed or destroyed 51% of the trees of at least 10 cm diameter at breast height (DBH) while in Sarawak 54% were destroyed. In Sarawak, the logging produced an immediate 35% to 70% decline in the gib-

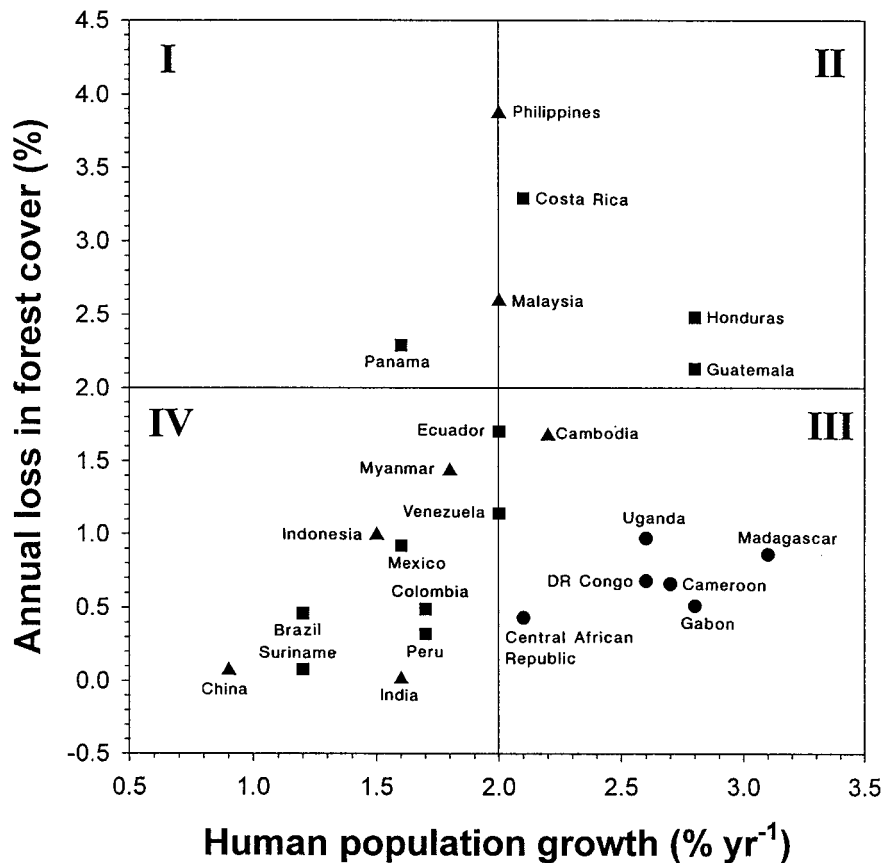


Figure 3. The annual loss of forest cover and human population growth for select countries harboring wild primate populations (data from the Food and Agriculture Organization, 1999).¹² On average, future projections for existing primate populations are most pessimistic for countries in quadrant II, whereas those in quadrant IV are perhaps the most optimistic. Solid squares, circles, and triangles indicate countries in the neotropics, Africa (including Madagascar), and southern Asia, respectively.

bon and langur populations. In contrast, the survival of the same genera in peninsular Malaysia was much greater (10% decline in abundance to a 74% increase). Bennett and Dahaban²⁴ attributed the differences between their findings and those of Johns^{21,35} to the nutrient-rich soils, initially higher primate densities, and virtual absence of hunting in Peninsular Malaysia, conditions that are quite different from those in Sarawak.

One might argue that examples such as these are simply exceptions to general trends, and that if one employed good comparative methodologies across a range of species and study sites, real trends would be uncovered. Johns and Skorupa³⁶ attempted such a test with 37 primate species for which population descriptions were available from both undisturbed and disturbed habitats. They

found that 44% of the variation in species' responses to moderate habitat disturbance could be accounted for by body size and diet: smaller species survived disturbance better and the degree of frugivory was negatively correlated with survival in degraded habitats. Their strongest conclusion was that large-bodied frugivores are most vulnerable to habitat disturbance, and three examples of large-bodied taxa were presented: *Ateles*, *Pan*, and *Pongo*. However, if one scrutinizes evidence on response to disturbance by these three taxa, exceptions are evident. For example, a healthy *Ateles geoffroyi* population has been described in a severely degraded area that was both intensively logged and grazed by cattle, but where hunting was minimal.³⁷ Similarly, *Pan troglodytes* groups are known to survive well in areas that have been logged and

almost entirely converted to agriculture,³⁸ apparently doing so by traveling between the few small remaining forest fragments and raiding crops planted by local farmers.³⁹ Orangutan populations in Sumatra can thrive in protected forests that have been subjected to a high natural disturbance regime (C. van Schaik, personal communication).

The conflicting results obtained by Johns²¹ and Bennett and Dahaban,²⁴ the lack of reliable predictions derived from comparative studies such as that by Johns and Skorupa,³⁶ and the many variables that researchers have suggested to influence how populations respond to logging clearly cry out for the use of a multiple regression approach. Unfortunately, given the large number of variables proposed to influence the responses of primate species and the relatively few studies that have addressed this issue using comparable methodology, we will probably have to wait until more data are collected before such statistical approaches yield reliable predictions.

Most sustainable logging regimes call for some sort of rotation: the area is logged, left to recover for a specified period, often 30 to 50 years, and then logged again. If timber extraction is to be compatible with the persistence of primates, populations must recover from the initial disturbance and return to somewhere near their former densities within a shorter cycle than the typical interval between consecutive logging operations. Few studies have followed primate populations in logged areas over a sufficiently long period to address this issue. However, Chapman and coworkers³¹ have determined the density of five primate species three times over a 28-year period in logged areas of Kibale National Park, Uganda. Species differed markedly in their response to the logging. Moreover, species that declined following logging differed in their pattern of recovery. For species that were negatively affected by logging, it was expected that, given enough time and forest recovery, their populations would increase. The most dramatic exception to this expectation was that group densities of blue monkeys (*Cercocebus mitis*) and redtail monkeys

(*C. ascanius*) in a heavily logged area actually declined between a census conducted 18 years after logging and the final census 28 years after logging. Red colobus (*Procolobus badius*) populations were recovering in the heavily logged areas, but their rate of increase was very slow (0.005 groups/km² per year). In contrast, black-and-white colobus appeared to do well in some disturbed habitats and were found at higher group densities in logged areas than in unlogged areas. There was no evidence of an increase in mangabey group density in the heavily logged area since the time of logging. Indeed, there was a tendency for their numbers to be lower in heavily logged areas than in lightly logged ones. Groups in logged areas had fewer infants and individual animals weighed less.^{31,40} Evidence also suggests that these forests are not regenerating at the expected rate.⁴¹ Even if logged areas are left to regenerate in the complete absence of agricultural encroachment and hunting, some primate populations will be much reduced from their undisturbed levels by the time the area is eventually scheduled to be reharvested.

Fire

With the proliferation of forest fires throughout southeast Asia^{42,43} and South America,^{44–46} and the media coverage that they have incited, it has recently been recognized that wildfires are having significant impacts on tropical ecosystems that were previously immune to fires. The prevailing idea concerning fire ecology in tropical forests is that natural fires are relatively rare, and that today the majority of fires are either induced or aggravated by humans.^{47,48} Determining the amount of tropical forest recently burned from conventional satellite imagery is, at best, difficult¹² because many fires are restricted to the understory, leaving much of the canopy relatively intact.^{45,46} Obtaining representative figures for the amount of tropical forest that burns annually is further complicated by the fact that there is large year-to-year variability in the extent of fires, which are primarily mediated by supra-annual El Niño events. Therefore, we simply illustrate the potential magni-

tude of forest fires rather than attempting to estimate the tropical forest area burned each year. The United Nations Food and Agriculture Organization¹² estimates a forest area of 2 million ha in Brazil and 4 million ha in Indonesia burned in 1997 and 1998. From December 1997 to April 1998, more than 13,000 fires burned in Nicaragua, destroying vegetation on more than 800,000 ha of land.¹² These estimates appear to be extremely conservative. At least 1 million ha of intact forests burned in the State of Roraima alone following the 1997–1998 El Niño dry season.⁴⁹ At this time, almost half of the forest cover in the entire Brazilian Amazon (1,550,000

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km²) had already completely exhausted its ground-water supply to a depth of at least 10 m, and were therefore highly inflammable.⁴⁵

The effect of current fires on wildlife, including primates, is largely unknown. However, it is safe to speculate that many animals are killed directly by heat stress and smoke asphyxiation or subsequently as a result of a degraded resource base or loss of foraging habitat. Individuals of territorial species fleeing to unburned areas will encounter aggression from residents and may subsequently be in-

jured or killed. While sampling vegetation plots in central Amazonian areas affected by ground fires, Peres⁴⁶ noted several signs of direct casualties, including skeletal remains of marmosets (*Callithrix humeralifer*). Only a small subset of the original primate assemblage in this area, including small-bodied taxa such as marmosets and titi monkeys (*Callicebus hoffmannsi*), which tend to thrive in disturbed forest, was able to persist in burned areas 10 to 15 months after the fires (C. Peres, T. Haugaasen, and J. Barlow, unpublished data). Estimates of undisturbed forest cover in parts of eastern Amazonia declined from 65% to 6% once selectively logged and burned areas were excluded.⁵⁰ In addition, by integrating the effects of drought and logging on forest susceptibility to fire, Nepstad and coworkers⁴⁵ estimated that 400,000 km² of Brazilian Amazonian forest would be moderately to highly susceptible to fires by the end of the 1999 dry season. Hydrological models based on the amount of forest edge along the highly fragmented deforestation arch of southern Amazonia predict that most small and medium-sized forest fragments will be consumed by both understory and canopy fires in the foreseeable future (M. Cochrane, personal communication).

In Indonesia, there is widespread consensus that the 1997–1998 fires will mark the beginning of a steeper downward trend in the already declining population of Bornean orangutans (*Pongo pygmaeus*). Some Indonesian primates were not as heavily affected by the 1982–1983 fires as they are by the 1997–1998 fires because they were able to switch to other foods from favored fruit sources that had succumbed to high levels of damage. Leighton⁵¹ reported that both pig-tailed macaques (*Macaca nemestrina*) and gibbons (*Hylobates muelleri*) took advantage of the population explosions of wood-boring insects immediately after the fires. He detected no change in the behavior or activity of two gibbon families that he had studied prior to the fires. On the other hand, leaf-eating monkeys (*Presbytis* spp.) were very difficult to find after the fires and still were at low densities six years later. Proboscis monkeys

(*Nasalis larvatus*) are a threatened species found almost exclusively in riverine and coastal habitats. Because riverine forest was heavily affected by the 1997–1998 fires, this species has probably lost a greater percentage of its remaining habitat than has any other primate species in Borneo (C. Yeager, personal communication). However, this species maintained its populations in mangrove forest,⁵² a vegetation type not heavily damaged by the fires. Western tarsiers (*Tarsius bancanus*) and slow loris (*Nycticebus coucang*) were extirpated or extremely reduced in number as of 1986.⁵² Seven years after the fires, natural succession favored figs, lianas, and other fruit species important to primates.⁵³ This bodes well for the recovery of most primate populations if these areas are not burned a second time.

Conservation biologists often evaluate the most immediate conservation needs based on what has happened in the last decade or so. However, there is evidence that fire has shaped some primate communities for thousands of years. For example, Madagascar harbors a unique and diverse primate community, but paleontological studies have shown that one-third of the lemur species have already gone extinct.^{54,55} Many of these extinctions probably resulted from the loss of forest, which began on a large scale when Indonesian settlers used fire to remove forest and create swidden fields, starting in 600 A.D. Forest loss was greatly accelerated when zebu cattle were introduced in 1000 A.D. and fire was used to maintain and increase grazing areas.⁵⁶ Today the use of fire on Madagascar has become a cultural habit, so that fires burn forests even when there is no El Niño event.

Hunting

Subsistence and commercial hunting can have a profound impact on forest animal populations while leaving the physical structure of the original forest largely unaltered.^{22,57–61} Obtaining comprehensive data on the impact of game harvest on primate populations is very difficult (but see Oates³³ and Peres⁶²). From case studies at particular locations, it is clear

that wildlife harvest provides a major source of food for many local communities around the globe, and that primates are often prime targets, especially in South America^{58,62–64} and Africa.^{32,57,65,66} For example, a market survey in two cities in Equatorial Guinea, West Africa, having a combined population size of 107,000, recorded 4,222 primate carcasses on sale over 424 days.³² Peres⁵⁸ documented that a single family of rubber

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230 inhabitants of three small Huaorani villages in Ecuador resulted in the killing of approximately 562 woolly monkeys.⁶⁷ In Arabuko-Sokoke Forest, Kenya (372 km²), 1,202 blue monkeys and 683 baboons (*Papio cynocephalus*) were reported to have been killed by subsistence hunters in a year.⁶⁵ Martin⁵⁷ found that 50% of the Nigerian population ate bush meat regularly, and that bush meat was popular with all income groups. The market for bush meat is not restricted to the tropical countries where the animals originate. In Brussels, a tremendous amount of bush meat flown in from Africa is consumed as a prestige food, mostly by expatriate Africans (P. Wright, personal communication).

As dramatic as these figures are, they probably underestimate actual hunting-induced mortality. Harvest estimates from market surveys do not include primates that are consumed in villages. In the Democratic Republic of Congo, 57% of primates are eaten in the villages and do not make it to the market; in Liberia, primates were more valuable in rural than urban areas.^{68,69} Also, interview results are often biased because hunting is officially prohibited in many areas where it occurs.⁶⁶ Moreover, animals lethally wounded by hunters in the forest often cannot be retrieved and are thus not included in village-based harvest estimates, which are based on the number of carcasses intercepted. This is particularly typical of Amazonian atelines, which often remain secured to the upper canopy by their prehensile tails and thus are inaccessible to hunters long after rigor mortis has set in.⁷⁰

In the only large-scale study of the effects of subsistence hunting on vertebrates, Peres^{18,71} used transect censuses conducted over 10 years to examine the effects of hunting on vertebrate community structure at 25 Amazonian forest sites. He found that vertebrate biomass was highly correlated with hunting pressure. At unharvested and lightly hunted 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. This study also summarized new

information on the average annual number of animals consumed per capita in the Amazon. Peres calculated the total game harvest in the Brazilian Amazon by multiplying these values by the size of the zero-income rural population in the entire region. Using the values presented for primates, we estimate that 3.8 million primates are consumed annually in the Brazilian Amazon (range in estimates, 2.2 to 5.4 million), which represents a total biomass harvest of 16,092 tons and a mean annual market value of \$34.4 million.

It is difficult to make similar estimates of bush meat harvest for other parts of the world, because there are few studies in Africa or Asia that quantify the number of primates taken per annum by local groups (but see Fa and Peres⁷²). It is also likely to be more difficult to extrapolate across cultural groups in Africa and Asia. However, the probable magnitude of the exploitation can be considered in light of the population density, the percent of the population that is rural, and the amount of forest that the rural population has access to (Fig. 3). In contrast to the rural population density of the Brazilian Amazon (1.61 people/km²,¹⁸) the latest statistics of the Food and Agricultural Organization indicate that there are 406 million people living in a rural setting in primate-habitat countries in Africa. These people retain the use of 5,161,040 km² of forest, resulting in a population density of 78.7 people/km² of forest. This figure is even higher in Central America, where there are few large remaining forest tracts (84.7 rural persons/km² of forest), and is highest in Asia, where there are 420 people/km² of forest. These figures assume that all rural people have access to and extract forest resources, which is unlikely to be true for many countries. Even so, they provide a somber illustration of the likelihood that African and Asian forests will be heavily exploited for bush meat, given their higher human population densities and more fragmented forest landscape.⁷²

The international live-capture and trade of primates was dramatically reduced with ratification of the Convention of Trade in Endangered Species of Wild Flora and Fauna in 1973.

Countries that signed this accord agreed to ban commercial trade in endangered species and monitor trade in other species that may become endangered. In 1968, prior to ratification, the United States imported 113,714 primates. In contrast, in 1983 the United States imported only 13,148 primates.^{4,11} Presently 122 countries are parties to this treaty. South Korea, Vietnam, and St. Kitts/Nevis are the most recent countries to sign.⁷³ Unfortunately, live trade is still a threat to some endangered species, particularly the great apes, because high prices for illegally obtained animals still provide huge incentives.

It is a common tradition among many cultural groups to keep juvenile primates as pets. Many of these animals are seen as byproducts or bonuses of meat hunting. This creates the incentive for selective harvesting of lactating females of the target-species to obtain the infants for pets. Even a small added incentive to capture some species will aggravate mortality pressure.

While international trade of most primate species is not threatening many populations, national trade of primates is a concern. It is a common tradition among many cultural groups to keep juvenile primates as pets. Many of these animals are seen as byproducts or bonuses of meat hunting.¹¹ This creates the incentive for selective harvesting of lactating females of the target-species to obtain the infants for pets.⁷⁰ Even a small added incentive to capture some spe-

cies will aggravate mortality pressure. For example, captive primates are found in most villages and small towns of Brazilian Amazonia, where a small but significant proportion of households have pet monkeys, often *Lagothrix*, *Ateles*, *Cebus*, *Saimiri*, *Saguinus*, and *Callithrix* (C. Peres, personal observation). This could translate into at least 45,327 monkey pets held captive at any one time throughout the region if we conservatively estimate an average ratio of 1:30 rural households containing at least one pet monkey. Mortality of wild-caught infant and juvenile primates in the aftermath of encounters with hunters is likely to be very high, even if they survive the fall and transportation traumas, because of the sudden loss of their mothers and exposure to poor conditions and diet in captivity. This generates a high turnover of pet monkeys and provides further incentive for additional flow of animals from natural populations. Based on interviews with hunters along the Juruá, Tefé, Uruçú, and Purús rivers of western Brazilian Amazonia, it has been estimated that, on average, at least 10 lactating females are sacrificed for every infant woolly monkey surviving to be brought to the nearest town.⁷⁰

THE ROLE OF SCIENTISTS

Scientists at academic institutions have traditionally contributed to conservation efforts by either providing information^{74,75} or by educating people, and thereby increasing public awareness and interest. Here we outline some general issues concerning approaches to studies of primate conservation, offer perspectives on the value of different types of information that academics can provide to conservation efforts, and discuss critical questions that need to be addressed with respect to primate population threats.

General Issues Related to Studying Primate Conservation

Effective programs promoting primate conservation must operate at larger spatial and temporal scales than those typically addressed by a single scientist. For example, to eval-

uate a conservation effort one must typically embrace the geographic range of an endangered taxon or a watershed that needs protecting, as well as a temporal scale that includes a number of generations of a target species or of sufficient length to monitor ecosystem change.

There is little question that, whenever possible, replicated controlled field experiments are always desirable.⁷⁴ However, when dealing with long-lived, often endangered species, it usually is not ethical or feasible to conduct controlled perturbation experiments on processes such as the effects of hunting or logging. Furthermore, even if such experiments were ethical, obtaining the needed sample size for experiments conducted at the appropriate spatial and temporal scale would be very difficult. Responses to dramatic changes in the environment are often slow. For example, Struhsaker⁷⁶ documented that it was nearly 10 years after the loss of approximately 90% of a major food resource that a statistically significant decline could be detected in the vervet monkeys (*Chlorocebus aethiops*) of Amboseli National Park, Kenya. Thus, narrowly defined experiments are likely to have limited value in quantifying the effects of hunting, logging, or fire on primate populations.

In many cases, it may be possible to advance our understanding of primate responses to disturbance by explicitly designing contrasts between sites that have experienced specific types of habitat modifications. For example, in an attempt to see how similar primate communities responded to perturbations at the level of habitats or populations, Onderdonk and Chapman³⁸ studied the primates in forest fragments near Kibale National Park, Uganda to permit explicit comparison with the study of Tutin et al.⁷⁷ from Lopé, Gabon. This comparison revealed that mangabeys were present at similar densities in forest fragments and in continuous forest at Lopé, while they were absent from fragments around Kibale. Furthermore, all primate species from Lopé were found to some degree in forest fragments, while two Kibale species, mangabeys and blue monkeys, were absent from the neighboring frag-

ments. We could eliminate methodological differences as the reason for the documented differences, permitting the formulation of hypotheses to account for these discrepancies. For example, at Kibale the matrix surrounding forest fragments is often actively used by people, while at Lopé humans are absent from the surrounding matrix. This encourages researchers to select for future studies sites that would permit them to test the hypothesis that the nature of the matrix in which the fragments are found is important in determining the use of fragments by primates, as has been documented for other forest vertebrate taxa.⁷⁸

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In addition to permitting the formulation of hypotheses to account for inter-site differences, there are other benefits of such explicit comparisons. First, they allow the researcher to test the generality of the results obtained from one site. For example, the results from Lopé could not be generalized to predict how the primate community at Kibale would respond. Second, conducting additional studies of the same phenomenon builds a baseline data set, which, in the future, would allow a correlative approach to understanding the impacts of different types of human modification.⁷⁹ To achieve this second objective, it is es-

sential that the same methods be used in all studies addressing similar questions.

Before we turn to the specific research questions that are called for to investigate specific types of human modifications, let us raise one final general issue. Traditionally, primate studies have been conducted in relatively undisturbed areas and have focused on a single species. It is thought that in these undisturbed, typically un hunted areas, primates will express their natural behavior.⁸⁰ However, remaining faithful to this traditional approach may not serve the interests of primate conservation. First of all, less than 5% of tropical forests worldwide are legally protected from human exploitation, and in many countries the amount of protected area is far less.^{33,59,81,82} For example, paleontological studies have shown that one-third of the lemur species in Madagascar are already extinct,^{54,55} yet less than 3% of the island has protected status.⁸³ As a result, conducting further studies in these last strongholds of prime primate habitat may not tell us a great deal about the general patterns. Furthermore, many tropical primate species are locally endemic or rare and patchily distributed.^{84,85} Such restricted distributions predispose many tropical forest species to an increased risk of extinction when habitats are modified⁸⁶ because limited species ranges often fail to overlap with a protected area. Thus, studies restricted entirely to nature reserves cannot evaluate the status of such species. Second, by conducting only single-species investigations, it will not be possible to understand interactive effects at the community level. For example, if a specific type of habitat modification reduces the abundance of one species, a second competing species might be expected to increase in abundance as the result of density compensation.⁸⁷ Few studies have quantified density compensation in primate communities.^{88,89} Peres and Dolman⁸⁹ sought evidence for density compensation in neotropical primate assemblages using data from 56 hunted and nonhunted forest sites of Amazonia and the Guianan shield. They found that although hunting was highly selective toward

large-bodied species that had been drastically reduced in numbers, this was only partially offset by increases in the abundance of smaller taxa.

A conflict intrinsic to situations in which academics contribute to conservation efforts involves instances in which the information needed to make conservation advancements is seen to be excessively descriptive as in, for example, a census of an endangered species. In these circumstances, colleagues in our departments, but in slightly different fields, may not see the value of such efforts. The importance of this issue should not be played down because it proves a strong selective pressure against such activities (for example, they rarely count toward tenure or promotion). However, with creative thought this need not become an issue as long as it is possible to resolve the challenge of combining descriptive information that is useful for conservation with theoretical advancements. For example, population survey data can be made relevant to ecological theory, such as tests of density compensation and cascading effects of the removal of seed dispersers. There also is no reason why this situation cannot change. If articles are published in well-respected peer reviewed journals, a tenure and promotion committee cannot object. Thus, editors of well-respected, high-impact journals should seriously consider good-quality papers with a stronger conservation focus.

One of the strongest factors that may motivate academic communities to appreciate efforts of their faculty to participate in conservation efforts is the huge overhead that these efforts can generate. However, the rigid structure of academic life currently restricts this potential. Development agencies funding such efforts operate on rigid deadlines that are not subject to change because of the teaching schedules of faculty members. If universities and colleges are to take advantage of the overhead that will result from their faculty leading conservation and development programs, flexibility must be built into the system. This flexibility must operate at all levels, including not just the full professor who has developed a reputation in this area, but also

include the young assistant professor who is just becoming involved with conservation and development projects.

Information Needed to Address Questions on Habitat Modification

Deforestation and habitat fragmentation

The statistics we have presented on deforestation rates and resulting losses of forest primates illustrate the need for studies on the impact of habitat conversion. If agriculturists or

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livestock enterprises have unlimited access to forests, the landscape will probably become dominated by farms and cattle pastures with some relict forest fragments in economically marginal areas. This calls for studies of responses to forest fragmentation.

As previously illustrated by contrasting studies in forest fragments in Lopé, Gabon^{77,90} and Kibale, Uganda,³⁸ it is currently difficult to predict which species or functional groups (for example, frugivore or folivore) will survive in forest fragments or what their density will be in those fragments. Similar examples can be

found in studies that have examined the density of spider monkeys (*Ateles* spp.) in forest fragments in South and Central America. For example, studies at the Minimum Critical Size of Ecosystems project in the Brazilian Amazon found spider monkeys to be absent even from the largest (100 ha) patches.⁹¹ Estrada and Coates-Estrada⁹² found spider monkeys in only 8% of the 126 forest fragments they surveyed in southern Mexico. In contrast, spider monkeys were found in approximately half (17 of 37) of the forest fragments in another site in Mexico⁹³ and were abundant in dry forest fragments in Costa Rica as long as hunting was controlled.³⁷ Managers need to be able to predict which species will survive in forest fragments in order to identify which species are most threatened by deforestation. This calls for further studies describing the structure of primate communities in forest fragments. Furthermore, the contrast between Kibale and Lopé suggests that the nature of the surrounding habitat matrix may be important in predicting which species will persist in fragments.

Some species readily move between fragments, using habitat corridors, while others do not.^{94,95} Understanding which species or what types of species can use corridors of different types will permit managers to predict future extinction rates in increasingly isolated forest fragments. The complexity of this issue is illustrated by the fact that near Kibale redtail monkeys frequently move between forest fragments, using available forest corridors and crossing un forested areas, whereas blue monkeys, which have a similar diet and social organization, do not use these corridors. In contrast, blue monkeys often reside in fragments near Budongo Forest Reserve, Uganda, and likely travel between fragments.⁹⁶

As in the case of the mangabeys at Lopé,⁷⁷ primate densities in forest patches sometimes are similar to those in continuous forest. In other cases, patches support much higher densities of primates than do nearby continuous forests (black-and-white colobus³⁸). Identifying the critical resources in fragments may suggest management options. For example, if

particular tree species prove to be a critical resource, managers could encourage local people not to harvest this species. Such studies should take a community-wide perspective because an increase in the density of one species in forest fragments, as was seen with the black-and-white colobus, may represent density compensation.

Most forest fragments lie outside protected areas and are owned by local agriculturists. As a result, the success of any management program will depend on the cooperation of the local people. In settings where a forest fragment is surrounded by agricultural, rather than cattle land, it will be difficult to obtain the cooperation of the local people if the primates are raiding crops.⁹⁷ As a result, understanding crop raiding, including the factors that encourage it, its temporal dynamics, and the means to regulate it, will be critical in formulating management plans for fragmented landscapes.

Timber extraction

Discrepancies among studies examining the effects of timber extraction on primates illustrate that moving beyond context-dependent case studies will be difficult. Given this, a profitable avenue for future research may be to investigate the determinants of primate density in undisturbed forests. Variation in primate density has typically been attributed to one of three major factors: food resource availability, predation, and disease or parasites. While there has been considerable interest in identifying the role played by parasites and disease in the demographic processes of host populations,^{98,99} there is only scant evidence that they regulate primate populations.^{100–104} However, disease and parasites can clearly cause short-term reductions in population size.^{105,106} For example, a 50% decline in the population of howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama, between 1933 and 1951 was attributed to yellow fever.¹⁰⁵ However, within eight years this population had exceeded its pre-epidemic numbers. There is also evidence that predators can cause severe temporary reduction in population size. Isbell¹⁰⁷ documented a substantial short-term

increase in the predation rate by leopards on vervet monkeys (*Chlorocebus aethiops*) in Amboseli National Park, Kenya. That predation rate, which had been, on average, at least 11% between 1977 and 1986, increased to at least 45% in 1987, possibly because of an increase in the leopard population. However, documented cases of predators taking significant proportions of primate groups are rare.^{108–112}

While the evidence for pathogens, parasites, or predators regulating primate populations is scant, a growing body of evidence suggests that the nature of the food supply can determine animal density. In an early review of population regulation, Lack¹¹³ suggested that although many factors influence population density, food resources are most commonly a regulating factor.^{114–117} In the simplest and most general sense, it is possible to explore whether or not food resources can regulate primate populations by examining single sites at which food supply has changed over time. For example, vervet populations in Amboseli, Kenya, declined 43% between 1964 and 1975 with a natural reduction in their food resources.⁷⁶ Similar examples are evident from other long-term studies, among them the baboons (*Papio anubis*) of Amboseli¹¹⁸ and the toque macaques (*Macaca sinica*) of Sri Lanka.¹¹⁹

Evidence from West Africa suggests that timber trees can contribute disproportionately to the diets of some primate species, indicating that logging could have severe impacts on these species unless they have extremely flexible diets. In Bia National Park, Ghana, it was found that 43% of the plant species in the diet of red colobus were from commercially valuable timber species. Diana monkeys (*Cercopithecus diana*) and black-and-white colobus also fed heavily on timber trees (20% and 25%, respectively).¹²⁰ Nine tree species contributed more than 95% of the harvest volume from an area of Kibale that was logged before it was declared a National Park, and the red colobus relied on all of these species for food.^{121–123} Similar comparative data are generally unavailable from other parts of the world.

Researchers have sometimes been

very successful at explaining variation in the abundance of a single species or a small group of species based on indices of food availability. For example, by contrasting a number of sites across Southeast Asia, Mather, as described by Janson and Chapman,¹²⁴ found a nearly perfect ($r = 0.99$) correlation between the biomass of gibbons (including siamangs) and the proportion of trees that were gibbon food trees. A particularly attractive system for studying determinants of primate abundance involves colobine monkeys. McKey¹²⁵ was the first to suggest that year-round availability of digestible mature leaves, which colobus monkeys eat when preferred foods are unavailable, limits the size of colobine populations. Several subsequent studies found positive correlations between colobine biomass and an index of leaf quality, the ratio of protein to fiber.^{126–128} A similar relationship was found between the quality of leaves and the biomass of folivorous primates in both Madagascar¹²⁹ and neotropical forests from southern Mexico to northern Argentina.¹³⁰ Milton, van Soest, and Robertson¹³¹ provided a physiological explanation for the importance of protein-to-fiber ratios. Each primate species has a protein threshold below which it cannot meet its protein requirements. If protein intake falls below this threshold, then the animal will suffer a negative nitrogen balance and eventually die. Increasing the fiber content of the diet an animal eats slows the passage rate of digesta through the stomach as the efficiency of bacterial enzyme action is reduced, thus reducing protein uptake.^{132–134} If trees bearing leaves that have low fiber and high protein prove to be consistently important for colobine monkeys, it may be possible to implement sound conservation policies based on simple nutritional information. If trees that were important to the colobines could be left standing in selective logging operations, or if loggers could use directional felling to reduce impact on important food trees, the decline of colobine population following logging might be lessened or the rate of population recovery might be improved.

The management of keystone species has been put forward as a mech-

anism to maintain biodiversity.¹³⁵ A keystone species is one that has far greater impacts on many other species than might be expected from its numbers or biomass.^{136,137} From this definition, it is clear that if keystone plant resources could be identified and kept undamaged during a logging operation, the negative impacts of logging on primate populations could be reduced. Peres¹³⁸ considers that, from a vertebrate's perspective, keystone plants are those that produce reliable, low-redundancy resources that are consumed by a large number of the vertebrate species with which they coexist. When considering these criteria with respect to frugivores, very few plants studied to date reliably produce resources that are both nonredundant (that is, they cannot be replaced by something else with few detrimental consequences to consumer species) and that are consumed by a large proportion of the frugivorous assemblage, regardless of the resource abundance.¹³⁸ Despite the questionable evidence currently available, we believe that keystone mutualisms remain highly plausible. Further work on the primate populations in areas with harvested and unharvested populations of plants that are candidates for designation as keystone plant species is therefore urgently needed.

Surface fires

There are almost no data available to make conservation recommendations with regard to the effects of understory wildfires on primate populations (but see Peres,¹⁸ Kinnaird and O'Brien,⁴³ and Saleh¹³⁹). Basic descriptive data on the impacts of different types of fires on primate populations and on forest structure and composition are therefore critically needed. In particular, we need information on which species are most severely affected and how, and which life-history and ecological traits enhance or prevent recolonization of previously burned areas from adjacent unburned patches. In the future, catastrophic wildfires in tropical forests will be aggravated by the synergistic effects of climate change, increasingly strong El Niño-mediated dry seasons, and anthropogenic forest disturbance, such as selective logging, which generates greater densities of canopy gaps, more

rapid drying, and the amount of dead wood that can burn.^{44,140} Information is needed to determine how logging or previous fires affect the probability of additional fires, as well as the consequences of recurrent fires on forests and primates. If most arthropod foraging substrates in the understory and some canopy trees are selectively eliminated by wildfires,¹⁸ what are the long-term consequences of the reduced resource availability? With the increasing frequency and severity of El Niño dry seasons,¹⁴¹ wildfires are likely to become one of the most powerful agents of change in tropical forest biotas. Countries like Madagascar provide a poignant example of what can happen with uncontrolled burning. There, 66% of the original forest has been de-

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stroyed.¹⁴² Much of this forest was burned and converted to grassland for cattle. Now areas that were forest support invasive, unpalatable grass.⁵⁶

Information Needed to Address Questions on Hunting

Many case studies indicate that large numbers of primates are being hunted in different regions.^{18,22,32,57,59,143} In demographic terms, this primate harvest is almost invariably unsustainable: it can reach into the core of even the largest and least accessible nature reserves, even in vast regions of tropical forests.⁸⁰ Information on hunting levels in different regions, particularly Asia, and on whether or not it is being

conducted at a sustainable level, is needed if we are to understand which primate populations are most threatened. We can build on an extensive wildlife literature to determine what functional groups and life-history characters are most susceptible to over-harvest.¹⁴⁴ Generalizations as to the types of animals that are most susceptible will be particularly useful so that results can be extrapolated to broader regions.

To rally interest in primate conservation from fields as distant from primatology as, for instance, forestry, it will be useful to understand the cascading effects of primate removal on forest dynamics. One of the strongest arguments for primate protection may be that their removal might reduce regeneration of the trees that are dependent on primate seed dispersal.^{145–147} Seeds not dispersed by frugivores simply fall from the parent's canopy to the ground and have a low probability of survival.^{148,149} For example, Howe, Schupp, and Westley¹⁵⁰ found that 99.96% of *Virola surinamensis* fruits that drop under the parent are killed within only 12 weeks. To date, only a few studies have examined the effects of removing seed dispersers. Wright and coworkers¹⁵¹ explored how hunting alters seed dispersal, seed predation, and seedling recruitment for two palms, *Attalea butyraceae* and *Astrocaryum standleyanum*, in Panama. They found that where hunters had not reduced mammal numbers, most seeds were dispersed away from the parent palms, but were subsequently eaten by rodents. Where hunters had reduced mammal abundance, few seeds were dispersed, but these tended to escape rodent predation. Thus, seedling density increased by 30% to 500% at heavily hunted sites as compared to un hunted sites. In contrast, Asquith and colleagues¹⁵² demonstrated that the presence of agoutis (*Dasyprocta*) was necessary for dispersal and recruitment of *Hymenaea courbaril*. (For similar examples, see Chapman, Chapman, and Wrangham¹⁴⁷ and Peres and Baider¹⁵³).

We know of only three studies that have contrasted the outcome of seedling regeneration under different levels of hunting pressure or reduced

seed disperser abundance. These studies revealed very different outcomes. At the community level, seedling density in disturbed forest was indistinguishable from, greater than, or less than in the undisturbed forests of Panama,¹⁵¹ Mexico,¹⁵⁴ and Uganda.⁸² It may be that the outcome of increased hunting pressure depends on the target species hunted. For example, at an overhunted site in Panama where seedling density was increased, hunting was removing large-seed predators like agouti and paca (*Agouti paca*). In contrast, at a site in Uganda where seedling density was decreased when frugivores were reduced, there were no large-bodied seed predators.

Research on the effect of removing large-bodied primate seed dispersers may be particularly critical in managing the forests of Madagascar. The present-day Malagasy fauna lacks many of the mammalian frugivores, such as ungulates and large rodents, and avian frugivores such as hornbills and guans, frugivores, which are playing important roles as seed dispersers in other Old and New World forests. Furthermore, large frugivorous bats such as *Pteropus* and *Eidolon* are not found in the montane wet forest.^{155,156} This suggests that large-seeded rainforest trees may be particularly dependent on the seed-dispersal service performed by the lemurs.

Information Needed to Evaluate Proposed Solutions

One way of viewing management schemes proposed for primate conservation is that they represent simple, typically non-replicated quasi-experiments set under a constantly changing social, economic, and cultural backdrop. Furthermore, different people viewing these experiments will see different desired outcomes. For example, development agencies financing conservation efforts may evaluate the success of the experiment in terms of financial gain accrued to the region. From a conservation perspective, the only defensible outcome is the long-term maintenance of biodiversity. This conservation perspective may often run counter to other demands on resources, so that compro-

mises may have to be made for social, political, or economic reasons. It must be recognized, however, that these are compromises. For example, encouraging ecotourism in an area may provide a financial mechanism for the protection of primate populations, but it does this at some long-term cost to conservation in terms, for example, of increased habitat disturbance, a net increase in human migrants into economically favorable areas, and perhaps disease transmission.

If one agrees that management schemes represent simple experiments, then their outcome must be evaluated and monitored. Academics

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can provide valuable information by evaluating conservation efforts that can be considered to fall into one of three types: traditional protection schemes and conservation development programs, extractive reserves, and new opportunities relating to forestry, climate change, and restoration.

Evaluate traditional protection schemes and conservation development programs

A myriad of attempts have been made to protect primates and their habitats, ranging from programs that provide strict protection of primate

populations in protected areas to those advocating that conservation goals can be met through development.^{157,158} There is little question that well-protected parks and nature reserves can conserve plant and animal populations, but they must operate in a setting that facilitates their long-term existence. Many protected areas have either decreased in size over time or have had their status downgraded to allow exploitation. In western Brazilian Amazonia, for example, a considerable portion of the Serra do Divisor National Park was annexed to a neighboring extractive reserve that will not necessarily serve the interests of primate conservation (C. Peres, personal observation). The 770 km² northern part of Tai National Park, 21% of the total park area, was temporarily ceded for exploitation and has now been heavily affected.¹⁵⁹ Similarly, Bia National Park in Ghana was gazetted in 1974 to include 306 km², then reduced to 230 km² in 1979, and further reduced to 78 km² in 1980. The area excised from the park has been reclassified as a Game Production Reserve (now called a Resource Reserve¹⁵⁹) and largely opened up to timber exploitation. Evaluations of factors leading to change in park status and ways of preventing it would be extremely useful and could provide donor agencies with guidelines to help fund national park services.

Scientists can play a significant role in evaluating park design. What minimum park size is necessary for particular primate species? Given environmental heterogeneity, what shape and mosaic of adjacent habitats are most appropriate for a park? How should the balance be set between a single large park that may not encompass all habitat types versus smaller parks that include more habitat types? In light of source-sink dynamics and metapopulation models, which species are most likely to move between parks connected by natural dispersal corridors?

It was only two decades ago that academics first advocated that an effective population size of 500 individuals would be sufficient for the long-term maintenance of genetic variability,^{160,161} and this figure was quickly adopted by management au-

thorities.¹⁶² Fifteen years after this initial guideline was proposed, Lande¹⁶³ demonstrated that 5,000 would be more appropriate. Many parks are simply too small to support 5,000 individuals of the larger or naturally rare primate species. This challenges researchers to verify this 5,000 rule and to discover ways to “cheat the rule” by doing such things as promoting dispersal through corridors. The number of avenues of research that this change in perspective calls for is enormous.

Projects claiming to meet conservation goals through rural development have met with varying results, mostly negative.¹⁶⁴ These projects are often very complex because a variety of social variables are affected by development programs, which have long-term cascading effects on the environment. This is illustrated by the simple example of the taungya system, a system used to increase forest regeneration after logging. In the first attempt to implement this system, in Nigeria in 1945, local farmers were allocated land after logging, provided they subsequently planted and tended timber species along with their crops, and then moved on.^{165,166} The offer of “free land” resulted in the immigration of large numbers of people to the project area. The forestry departments were unable to provide seedlings to all these immigrants, and the system degraded to the point that, as the State Forestry Department stated, that it had become “a peasant shifting cultivation system that could eventually liquidate the forest reserves.”

Several authors have suggested taking advantage of the huge international ecotourism market, estimated in 1993 to be 1.4 thousand million in the United States alone, to enhance the value of intact wildlands, thereby promoting their conservation.^{167–169} However, projects that have been evaluated to date have demonstrated that this approach has variable success.¹⁷⁰ For example, the reserves associated with two rain-forest tourist lodges in southeastern Amazonian Peru have lost much of their land to encroachment from settlers.¹⁶⁷ In contrast, the tourism profit obtained at Ranamafana National Park in Madagascar ap-

pears to have benefited conservation of the area.

Kremen, Merenlender, and Murphy¹⁷¹ evaluated 36 projects that had attempted to integrate conservation and development. Only five of these projects demonstrated a positive contribution to wildlife conservation. Such projects make the assumption that planned rural development will automatically lead to conservation success.^{157,171} There is little evidence to support this assumption, and there are a number of case studies to illustrate that the reverse can be true.¹⁶⁶ Natural resources and conservation

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areas in the tropics continue to be lost despite enormous expenditure of foreign aid for development and conservation.¹⁷² Unfortunately, although it is clear that many integrated conservation and development projects have not performed as envisioned, and in many cases the conservation situation actually has become worse, the problem in evaluating these projects is that there is no suitable control for comparison. We do not know what the conservation situation would have been if such programs had not been initiated. For example, in Uganda a

number of integrated conservation and development projects were initiated only after funding to maintain a suitably equipped park guard force became impossible. We do not know what the situation in these parks would have been like if different alternatives had been attempted. However, long-term researchers working in the tropics are often in a unique position to document the successes and failures that do occur.

Different tropical regions are in different stages of economic development. Thus, some areas are already experiencing what represent future projections for other areas. Given this, it may be useful to anticipate biodiversity threats to more pristine study areas on the basis of more degraded sites elsewhere. From this perspective, African and Asian forests, where human population densities outside parks can be very high (200 to 400 people/km²), offer insights into the future of South American parks.⁷² If it is appropriate to use African or Asian forests as models, it may provide managers in South America time to evaluate the types of measures that should be instigated now to safeguard wildlife in the future. However, caution must be used when deciding in which direction comparisons are appropriate. For example, models of extractive reserves developed in South America have been employed in African National Parks.¹⁷³ However, human population density surrounding the South American forest reserves is approximately 100 times lower than in Africa. Without careful consideration of how greater human densities will inflate resource demand and the need for greater park monitoring and regulation, it is unrealistic to apply conservation approaches developed in South America to Africa. Similarly, it may be inappropriate to apply models derived from African countries with rich soils to Madagascar, which has poor soils.⁸³ In Madagascar the population density is only 27.2 people/km², yet the damage to the environment is great.¹²

Evaluate extractive reserves

Widespread concern over tropical deforestation has prompted the development of new approaches to rain for-

est conservation. As a result, extraction-based systems that promise economic benefits to forest dwellers while leaving the forest standing have become popular in conservation.^{15,174} The potential importance of this approach is evident when one considers that Indian reserves that permit some form of extraction account for 54% of all 459 Amazonian forest reserves and 100.2 million ha in Brazilian Amazonia alone.¹⁷⁵ In Colombia there are 18 million ha of Indian reserves and 2.5 million ha of national parks.⁵⁹ However, extractive reserves can reduce food resources available to primates, even if the harvest is entirely restricted to nontimber forest products.

Fruits that are nutritious for people and that occur in dense stands are commonly harvested.¹⁷⁷ Almost without exception, the fruits collected for sale are those also eaten by primates,¹⁷⁷ yet the impact of this harvest on primate populations remains unknown. There is evidence that harvest of some nontimber forest products can be quite extensive. For example, in Iquitos, Peru, 120 species of wild-harvested fruits are marketed,¹⁷⁸ some of which are harvested extensively. Of particular interest are fruits of the palm *Mauritia flexuosa*, which are eaten raw and used to prepare drinks, cakes, and ice cream. *Mauritia flexuosa* is found in monodominant stands known as aguajales (130 to 250 adults per ha), which account for 52.5% of the area near Iquitos. Adult females of this large arborescent palm typically produce 450 to 1,000 fruits per infructescence per year, with three to five infructescences occurring per year. Despite the abundance and fecundity of the tree, *M. flexuosa* has been rendered locally extinct near human population centers due to popularity of the fruits and destructive harvesting techniques.¹⁷⁸ Presently, fruits are being harvested and transported from more than 800 km away from Iquitos.¹⁷⁸ Although this has not been investigated, the *M. flexuosa* fruit harvest may be detrimental to primate populations because a number of primates eat the palm fruits during periods of fruit scarcity.^{179–181} Similarly, ungulate populations are also likely to be affected because they feed on fruits of *M. flexuosa* and other arborescent

palms that are destructively harvested elsewhere in Amazonia.¹⁸² Another example of an extractive process affecting primate numbers involves the palm *Phoenix reclinata* and the Tana River mangabey (*Cercocebus galeritus*). This palm is an important plant species for people of the lower Tana River, and harvest techniques are often destructive. This palm accounts for up to 62% of the monthly diet of the mangabeys.¹⁸³ The extent of harvest that can be associated with extractive reserves, the reality that levels of extraction will increase with larger human populations, and the increased emphasis on such reserves as a conservation strategy calls for quan-

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tification of the impact of extraction on primate populations.

Evaluate new opportunities: forestry, climate change, and restoration

Policy makers and forest managers are responding to changing national and international priorities. This was reflected in commitments made at the United Nations Conference on Environment and Development in 1992, in which measures were agreed on that are aimed toward sustainable management of forests.¹² As a result of these changes, a sector of the forestry community is now open to sugges-

tions regarding more ecologically benign harvest protocols. If it is possible to change forestry toward more sustainable, less deleterious practices, this presents an opportunity to protect wildlife populations. However, to take advantage of this opportunity, information must be made available with regard to the types of forestry-management techniques that will be most beneficial to primate populations.

Similar opportunities are arising because of changes in how developed countries are responding to global warming. Over the last century, the concentrations of greenhouse gases have increased, largely as a result of fossil-fuel combustion and land-use conversion. Net carbon dioxide emissions from changes in land use, primarily tropical deforestation, currently contribute approximately 20% of global anthropogenic CO₂ emissions.¹² Carbon sources and sinks from deforestation and abandonment of agricultural lands in large tropical forest regions like the Brazilian Amazon are nearly balanced, but with an interannual variability of ± 0.2 PgC yr⁻¹.¹⁸⁴ Forest growth serves as a means to sequester carbon from the atmosphere. The Kyoto Protocol of the Framework Convention on Climate Change in 1997 provides industrialized countries with incentives to invest in forestry activities that increase carbon sequestration and reduce carbon emissions. At this conference, it was agreed to achieve a 6% reduction in carbon production by 2012. These developments have led to a keen interest in studies of timber certification, reduced-impact logging programs, and forest restoration.^{185,186} Some of these programs are extensive. Presently there are between 20 and 40 million ha of tropical forests that either have been certified or are being seriously considered by certification programs (F.E. Putz, personal communication). The area of forest plantation in the world has been increasing over the past two decades, and this trend is expected to continue. For example, Vietnam recently announced plans for the restoration of 5 million ha of forest land, of which 3 million ha will be plantations. The reported afforestation rate in the

tropics and subtropics in 1995 was 3 million ha per year.¹² In Uganda there is a 10-year project funded by Dutch power companies to reforest 150,000 ha in two national parks with indigenous trees.¹⁸⁷ Although it takes a long time to regrow a tropical forest, such projects represent opportunities to recover some ecosystem functions, such as carbon and water storage, and perhaps to protect primate populations, as well as offer new avenues for scientists to contribute to conservation.

CONCLUSIONS

While it is clear that primate populations have been deleteriously affected by human agricultural activity over the last two millennia and by hunting for much longer,^{10,90,188,189} it is also clear that this next century will bring an even greater potential for change. The severity of this situation has been widely recognized for the last three decades. What has changed is the opportunities available to long-term researchers to contribute to conservation efforts. The future offers a great opportunity for academics to contribute to primate conservation by documenting patterns of change, understanding the cascading effects of primate removal, predicting how different functional guilds will be affected by different types of human activities, understanding mechanisms determining primate abundance, and evaluating different conservation approaches. From an intellectual perspective, many of the items in this renewed research agenda may be at odds with those traditionally addressed over the last three decades of primate field studies, which have typically focused on the behavioral ecology of single species within protected areas. Primatologists will, however, increasingly be forced to consider the choices between “business as usual” or studies that can be defined as useful from a conservation viewpoint.

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What has changed is the opportunities available to long-term researchers to contribute to conservation efforts. The future offers a great opportunity for academics to contribute to primate conservation by documenting patterns of change, understanding the cascading effects of primate removal, predicting how different functional guilds will be affected by different types of human activities, understanding mechanisms determining primate abundance, and evaluating different conservation approaches.

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