

## Forests Without Primates: Primate/Plant Codependency

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Detailed studies of primates and fruiting trees have illustrated that these groups of organisms are involved in a very complex set of interactions, with primates relying on fruiting trees as important food resources and fruiting trees relying on frugivores for seed dispersal. Human activities that influence either primate seed dispersal or fruit production have the potential of having unanticipated effects on the other interactants. Here we evaluate what is known and what we still need to learn to evaluate the long-term consequences of disrupting the interactions between primates and tropical forest trees. We do this by first assessing the potential importance of primates at dispersing the seeds of tropical forest trees. Second, we consider possible consequences of hunting primates on recruitment in tropical tree communities. Third, we address the converse by considering the impacts of decreasing resource availability for primates through either logging or through the extraction of nontimber forest products. Finally, we provide a case study from Kibale National Park, Uganda, that contrasts seedling recruitment in 20 forest fragments in which primate seed dispersers have been dramatically reduced with seedling recruitment in areas that have an intact frugivore community. In comparison to the intact forest, the fragments had lower seedling density and fewer species of seedlings. Furthermore, a greater proportion of the seedlings were from small-seeded species that might not require primates for their dispersal, since they probably can be dispersed by small birds. All of these considerations suggest that disrupting the complex interactions between primates and fruiting trees can potentially have negative and possibly cascading effects on ecosystem processes. *Am. J. Primatol.* 45:127–141, 1998. © 1998 Wiley-Liss, Inc.

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### INTRODUCTION

Recent detailed studies of primates and fruiting trees have illustrated that these groups of organisms are involved in a very complex set of interactions [Tutin et al., 1991, 1996; Chapman & Chapman, 1996]. It is readily apparent that many

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species of primates rely on fruiting trees as important food resources. Researchers have recently begun to assert that these fruiting trees rely on frugivores for seed dispersal and that the maintenance of frugivore populations is critical for the regeneration of tropical forests [Howe, 1984; Pannell, 1989; Chapman et al., 1992; Wrangham et al., 1994; Chapman, 1996; Chapman & Chapman, 1996]. Thus, human activities that influence either primate seed dispersal or fruit production have the potential of having unanticipated effects on the other interactants.

It is widely recognized that the most critical factor endangering primate populations is habitat destruction [Mittermeier & Cheney, 1987], and much effort has been invested into understanding the extent of forest conversion, the factors contributing to its loss, and possible solutions to decrease the rate of destruction. However, human activities that impact primates are not limited to the cutting of trees, and it is clear that a number of these activities are having increasingly negative effects on some primate populations [Redford, 1992; Oates, 1996].

Subsistence and commercial hunting can influence forest animal populations while leaving the physical structure of the forest initially unaltered [Martin, 1983; Peres, 1990; Wilkie et al., 1992; Redford, 1992; Bodmer et al., 1994]. For example, a market survey in two cities in Equatorial Guinea, West Africa, with a combined population size of 107,000 recorded 4,222 primate carcasses being brought to market in 424 days [Fa et al., 1995]. These values are no doubt an underestimate of the total number of primates harvested, since some game is consumed in villages or sold before it gets to market [Colell et al., 1995]. Data from many different Amazonian sites show that, in hunted areas, large primate biomass drops 93.5% when compared with similar unhunted areas [Redford, 1992]. The question must be asked how removing a major proportion of the resident seed-dispersing primate population impacts the regeneration of the fruiting tree community.

Conversely, extractive reserves involving either the harvesting of timber or nontimber forest products can result in a decrease in the resources available to primates. Widespread concern over the destruction of tropical forests has prompted the development of new approaches to rain forest conservation. As a result, extraction-based systems that promise economic benefits to rain-forest inhabitants while leaving the forest standing have become a popular conservation tool [Peters et al., 1989; Redford & Stearman, 1993]. For example, Indian reserves that permit some form of extraction account for 54% of all 459 Amazonian reserves and account for 100.2 million hectares in the Brazilian Amazonia alone [Peres, 1994a]. In Colombia, there are 18 million hectares of Indian reserves and 2.5 million hectares of national parks [Redford, 1992]. An example of an extractive process that directly influences primate numbers involves the palm *Phoenix recclinata* and the Tana River mangabey (*Cercocebus galeritus*). This palm is an important plant species for the people of the lower Tana River, and harvest techniques are often destructive; however, this palm also accounts for up to 62% of the monthly diet of the mangabeys [Kinnaird, 1992].

In this paper, we evaluate what is known and what we still need to learn to evaluate the long-term consequences of disrupting the interactions between primates and tropical forest trees. We do this by first assessing the importance of primates in dispersing seeds of tropical forests. Second, we examine the possible consequences of hunting primates on recruitment in tropical tree communities. Third, we address the converse and consider the impacts of decreasing resource availability for primates through either logging or through the extraction of nontimber forest products. Finally, we provide a case study from Kibale National

Park, Uganda, that contrasts seedling recruitment in forest fragments where primate seed dispersers have been dramatically reduced with seedling recruitment in areas that have an intact primate community.

### HOW IMPORTANT ARE PRIMATES IN DISPERSING SEEDS IN TROPICAL FORESTS?

The more effective primates are at dispersing seeds of tropical trees, the greater the consequence will be of disrupting the interactions between primates and fruiting trees for the maintenance and long-term sustainability of forest ecosystems. Seed dispersal is, however, a complex process involving a number of different steps. To have the greatest ecological impact, primates would have to 1) move large numbers of seeds, 2) not decrease seed viability through their handling of the seeds, and 3) defecate or spit those seeds in locations where they can avoid seed predation (or be suitably secondarily dispersed) and can germinate and grow. Let us evaluate each of these steps in turn.

Early studies of tropical fauna recognized that primates constitute a large proportion of the frugivore biomass in tropical forests [Eisenberg & Thorington, 1973], that they eat large quantities of fruit, and that they defecate or spit out large numbers of seeds [Estrada & Coates-Estrada, 1984; Corlett & Lucas, 1990; Rowell & Mitchell, 1991]. Recently, these initial impressions that primates move large numbers of seeds have been quantified by studies conducted in South America [Garber, 1986; Julliot, 1996], Central America [Estrada & Coates-Estrada, 1984, 1986; Chapman, 1989], and Africa [Gautier-Hion, 1984; Wrangham et al., 1994; Chapman & Chapman, 1996; Lambert, 1997]. For example, in Kibale National Park, Uganda, 98.5% of chimpanzee dung samples contain seeds, with an average of 22 large seeds (>2 mm) per defecation [Wrangham et al., 1994]. The number of large seeds dispersed by the chimpanzee populations is estimated at 369 large seeds/square kilometer/day. Lambert [1997] recently extended this analysis and assessed fruit removal rate of redtail monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), and mangabeys (*Cercocebus albigena*) in Kibale. In a single day, these animals remove approximately 34,000 fruits/square kilometer and disperse 446 seeds/square kilometer. A primate community of northern Costa Rica (*Ateles geoffroyi*, *Alouatta palliata*, *Cebus capucinus*) disperses approximately 5,600 large seeds/square kilometer/day [Chapman, 1989]. Furthermore, one group of howler monkeys (*Alouatta seniculus*) in French Guiana has been shown to disperse more than 1,000,000 seeds/year from approximately 100 plant species [Julliot, 1996].

All of these studies clearly illustrate that primates are dispersing many seeds; however, it may be that other taxonomic groups (e.g., birds) are dispersing as many or more seeds. Because of the diversity of the frugivore community, little information is available that can address this issue. However, through focal observations of individual trees, Chapman and Chapman [1996] quantified the percentage of the fruit crop removed by all diurnal frugivores and found that primates were responsible for 74.8% of the fruits removed from the 12 trees of the six species watched. This suggests that primates not only disperse many seeds but also are responsible for the dispersal of a large proportion of the seeds removed from parent trees of some species.

Evidence suggests that most primate-dispersed seeds are capable of germination. When researchers take seeds from primate dung and attempt to germinate them in controlled settings, results often indicate that the passage through the frugivore's gut improves the rate of germination and reduces latency to ger-

mination. Lieberman et al. [1979] were able to germinate seeds from 59 plant species collected from baboon dung in Ghana, and ingestion improved germination success over that of fresh seeds in three of the four species tested. Garber [1986] experimentally planted seeds defecated by *Saguinus mystax* and *S. fuscicollis* and found a 70% germination success rate. Estrada and Coates-Estrada [1991] documented that the germination success of seeds from dung of the howlers (*Alouatta palliata*) at Los Tuxtlas, Mexico was 57%, an increase of 22% over control seeds collected from the tree. Passage through the chimpanzee gut improved the rate of germination and reduced latency to germination in all ten fruiting tree species tested in the Kibale National Park, Uganda [Wrangham et al., 1994].

The final step for effective seed dispersal requires that defecated or spit seeds must be placed in locations where they can avoid seed predation (or be suitably secondarily dispersed) and can germinate and grow. Examining this final step in the seed-dispersal process has proven very difficult, largely because seed mortality is typically extremely high. For example, Estrada and Coates-Estrada [1991] documented that 59% of the seeds dispersed by howler monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico, disappeared and were presumed to have been killed within 24 h. At Santa Rosa National Park, Costa Rica, 97.9% of the seeds placed at experimental stations had been removed or killed within 70 days [Chapman, 1989]. In Kibale National Park, Uganda, 73% of the seeds placed out on the forest floor had disappeared after 6 months (range = 10–100%) [Chapman & Chapman, 1996]. In all of these studies, rodents are considered to be major seed predators. The majority of the seeds handled by rodents are presumably killed, but detailed studies of the fate of these seeds are lacking. Dung beetles may play a particularly significant role in secondary seed dispersal. Some dung beetles roll or bury primate dung, which can contain seeds (maximum diameter approximately 16 mm [Shepherd, 1996]. Burrowing and ball-rolling dung beetles bury seeds at depths ranging from 1 to >12 cm and may move seeds up to 5 m from the site of deposition [Estrada & Coates Estrada, 1991; Shepherd, 1996]. The removal and burial of these seeds may be beneficial to the trees because the seeds are less likely to be found by rodents.

### WHAT WOULD FORESTS BECOME WITHOUT PRIMATE SEED DISPERSERS?

The removal of primates through hunting may decrease or even eliminate potentially important seed dispersers. Obtaining comprehensive data on the hunting of primates, however, is very difficult [Oates, 1996]. From case studies at particular locations, it is clear that the hunting of wildlife provides a major source of food for many local communities around the globe and that primates are often the target of such hunting activities [South America: Redford, 1992; Bodmer et al., 1988; Peres, 1990; Africa: Martin, 1983; Fa et al., 1995; Fitzgibbon et al., 1995; Johnson, 1996]. For example, Peres [1990] documented that, in a year-and-a-half, one family of rubber tappers in the Brazilian Amazon killed more than 200 woolly monkeys (*Lagothrix lagotricha*), 100 spider monkeys (*Ateles paniscus*), and 80 howlers (*Alouatta seniculus*). Bodmer et al. [1988] reported that approximately 100 primates were harvested in a 12 month period in an area of Peru with approximately 310 inhabitants. Subsistence hunting by 230 inhabitants of three small villages in Ecuador resulted in the killing of approximately 562 woolly monkeys [Yost & Kelley, 1983]. In Arabuko-Sokoke Forest, Kenya (372 km<sup>2</sup>), 1,202 *Cercopithecus mitis* and 683 *Papio cynocephalus* were reported to have been killed

by subsistence hunters in a year [Fitzgibbon et al., 1995]. Martin et al. [1983] found that in Nigeria 50% of the human population ate bushmeat regularly, and bushmeat was popular with all income groups. As dramatic as many of these figures are, most of these data likely represent underestimates of the actual extent of harvest. Harvest estimates from market surveys do not include primates that are consumed in villages (in Zaire 57.1% of primates are eaten in the villages and do not make it to the market, and in Liberia primates were more valuable in rural than urban areas [Lahm, 1993]). Also, interview results will be biased since hunting is officially prohibited in many areas where it occurs [Johnson, 1996].

Most of the studies providing information on the hunting of primates have not been sufficiently detailed to determine whether or not the harvest is sustainable. However, those that have been sufficiently detailed indicate that large-bodied primates are being overharvested in an unsustainable fashion [Bodmer et al., 1994; Fitzgibbon et al., 1995]. Furthermore, comparisons between hunted and unhunted sites suggest that hunting is generally being carried out unsustainably [Peres, 1990, in press; Redford, 1992].

Despite the potential importance of primates as seed dispersers, it is unclear whether their removal by hunting will cause a disruption in the dispersal of the seeds of tropical trees. It is possible that when primate populations reach low levels due to hunting, their role as seed dispersers will simply be taken over by other frugivores. To evaluate this we must know 1) the fate of undispersed seeds, 2) the typical diversity of dispersers visiting tropical trees, and 3) whether nonprimate dispersers can take over the role of primates if they were to be hunted out of an area.

Evidence from a number of studies of specific plant species suggests that seeds not dispersed by frugivores simply fall from the parent's canopy to the ground and have a low probability of surviving [Augsburger, 1984; Sork, 1985; Chapman & Chapman, 1996]. For example, Howe et al. [1985] found that 99.96% of *Virola surinamensis* fruits that drop under the parent are killed within only 12 weeks. Similarly, Schupp [1988] documented 7% survival of *Faramea occidentalis* seeds under the crown of the parent tree in 30 weeks, in comparison to 24% survival 5 m away from the parent tree. Studies such as those by Leigh et al. [1993] and Bierregaard et al. [1992] illustrate the initial loss of tree biodiversity that results when populations are restricted to islands with reduced faunas; however, the time scales over which these studies have been carried out (1913–1980 and 1979 on, respectively) are short relative to the life span of the tree species. In addition, a number of factors are involved in the reduction of species numbers on islands. In general, though, findings support the idea that seed dispersal by frugivores is vital to the maintenance of fruiting tree populations, since the survival of fallen fruit does not appear to be sufficient to maintain populations of many tropical tree species [Howe, 1984; Pannell, 1989; Chapman et al., 1992].

To determine whether the removal of primates by hunting will cause a disruption in the dispersal of tropical trees or if their role will be taken over by some other frugivore, we must know the typical diversity of dispersers attending tropical trees and whether the nonprimate dispersers can subsume the role of primates. Evidence suggests that it is typical for a number of frugivorous species to disperse the fruit of any particular tree species. For example, studies in Gabon illustrate the lack of specificity between frugivores and plant species. Out of 112 fruit species occurring in the diets of ruminants, monkeys, and rodents, 35% were eaten by the three taxa and at least 70% by two taxa [Gautier-Hion et al., 1985]. In 61.5 h of observations of *Trichilia gilgiana*, 22 species were seen eating

fruit from the tree, including two ruminants, nine rodents, ten birds, and two monkey species [Gautier-Hion et al., 1985]. A similar diversity of visitors has been documented from tree watches in Kibale National Park, Uganda [Chapman & Chapman, 1996]. There is one notable exception to these observations: the dispersal of *Cola lizae* seeds by gorillas. It has been documented that gorillas are the only important disperser of this species and that *C. lizae* seeds found in gorilla dung had a high germination success rate [Tutin et al., 1991]. Furthermore, survival of seedlings was significantly better in dung at nest sites than in other areas of the forest [Rogers et al., 1998].

Unfortunately, we do not presently know whether nonprimate dispersers can subsume the role of primates. Furthermore, this information would be extremely difficult to obtain. For tropical fruiting trees that are producing millions of seeds in their lifetime, a disperser that removes only a small number of fruits but places the seeds processed in very favorable locations could theoretically make a large contribution to the propagation of the next generation. To evaluate this issue, we need studies that contrast the distribution of seedlings in areas where the primate community is intact to areas where it has been drastically reduced. However, since the variance in the distribution of seedling types within undisturbed forest is likely great, studies of seedling distributions before and after a primate community has been subjected to hunting may prove most revealing.

#### **WHAT WILL HAPPEN TO PRIMATE POPULATIONS IN EXTRACTIVE RESERVES?**

Few studies have examined the impact of selective logging on primate communities. Furthermore, quantitative comparisons between this small sample of studies are limited because they often employ different methods or do not adequately report the methods used. Studies also vary with respect to extraction regimes and incidental damage levels [Johns, 1988, 1992; Wilkie et al., 1992; White, 1994], the original composition of the primate communities [Bennett & Dahaban, 1995], the proximity to undisturbed refugia and recolonization sources [Bierregaard et al., 1992; Fimbel, 1994a,b], and the length of time between logging and the monitoring of the primate populations. In addition, access provided by the logging operation may or may not have increased the level of hunting [Wilkie et al., 1992; Bennett & Dahaban, 1995; Fa et al., 1995; Oates, 1996]. Such variability between investigations can result in different studies producing very divergent results, even when similar communities are involved and the areas are in close geographical proximity. Two studies in Southeast Asia clearly illustrate this point [Johns, 1992; Bennett & Dahaban, 1995]. Johns [1992] studied the effects of logging on animal populations in dipterocarp forests in Peninsular Malaysia, while Bennett and Dahaban [1995] addressed the same question in dipterocarp forests in Sarawak. The intensity of logging was similar in the two regions (Sarawak: 54% of the trees of at least 10 cm diameter at breast height (DBH) were removed or destroyed [Bennett & Dahaban, 1995]; peninsular Malaysia extraction destroyed 51% [Johns, 1992]). In Sarawak, the logging produced an immediate 35–70% decline in the gibbon and langur populations [Bennett & Dahaban, 1995]. In contrast, the survival of the same genera in peninsular Malaysia was much greater (10% decline to a 74% increase [Johns, 1983]). Bennett and Dahaban [1995] attribute the differences between their study and that of Johns [1983, 1992] to the nutrient rich soils, initially high primate density, and the virtual absence of hunting in peninsular Malaysia, conditions 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, trends would be revealed. Johns and Skorupa [1987] attempted such a test with 37 primate species where population descriptions were available from both undisturbed and disturbed habitats. They discovered that 44% of the variation in species' responses to moderate habitat disturbance could be accounted for by body size and dietary considerations. Smaller species survive disturbance better, and the degree of frugivory was negatively correlated with the ability to survive in degraded habitats. However, they concluded that while this relationship was statistically significant, it provided an insufficient basis to reliably predict how specific species would respond to habitat disturbance. Unfortunately, it is these kinds of predictions that forest managers need to make. The strongest suggestion that this comparative study made was that large-bodied frugivores are the class of primates most vulnerable to habitat disturbance, and three examples are presented: *Ateles*, *Pan*, and *Pongo* [Johns & Skorupa, 1987]. If one looks closely at descriptions of even these three species, exceptions are evident. For example, an *Ateles geoffroyi* population has been described from a severely degraded area that was both intensively logged and grazed by cattle but where hunting is minimal [Chapman et al., 1989]. Similarly, *Pan troglodytes* groups are known to survive in areas that have been logged and almost totally converted to agriculture [Onderdonk, personal observation]. These chimpanzees appear to survive by traveling among the few small remaining forest patches and by raiding crops planted by local farmers [Naughton-Treves, 1996].

The conflicting pieces of evidence revealed by these studies suggest that while resources will be decreased by logging and logging will interrupt other aspects of primate communities' activities, it is very difficult to predict how each species will respond. These observations clearly indicate the need for more detailed studies into the effect of logging on primate populations. However, at this time it seems most prudent to assume that logging operations will typically have negative impacts on primate communities, and means to decrease the extent of these impacts should be investigated.

New approaches to rain-forest conservation have arisen as a result of concern over widespread destruction and the recognition that traditional methods will protect only a small proportion of tropical forests. As a result, extraction of nontimber products, which promise economic benefits while leaving the forest standing, has become a popular conservation tool [Peters et al., 1989; Redford & Stearman, 1993]. Unfortunately, as with logging, there is little quantitative data on the effects of the extraction of nontimber forest products on primate communities. Tropical fruits, which are often items selected for extraction, vary greatly in morphology and nutritional value. Fruits that are nutritious for people and occur in dense stands are commonly harvested [Clement, 1993; Hladik et al., 1993]. Almost without exception, the fruits collected for sale are fruits also eaten by large birds and mammals [Hladik et al., 1993]. However, the impact of such harvesting on primate populations is unknown.

There is evidence indicating that the harvest of some nontimber forest products can be quite extensive. For example, in the markets of Iquitos, Peru, 120 species of wild-harvested fruits are being sold [Vasquez & Gentry, 1989]; some of these species are harvested extensively. The fruits of the palm *Mauritia flexosa* are eaten raw and used to prepare drinks, cakes, and ice cream. *M. flexosa* was common in the area around Iquitos, being found in a common forest type (52.5% of the region near Iquitos) and occurring at high densities (130–250 adults per hectare, with each female producing 450–1,000 fruits per infructescence per year

and three to five infructescences per year). Despite the abundance of the tree in some areas, *M. flexosa* has been rendered locally extinct near human population centers [Vasquez & Gentry, 1989] due to the popularity of the fruits and destructive harvesting techniques. Presently, fruits are being harvested and transported from more than 800 km away from the Iquitos market [Vasquez & Gentry, 1989]. Although the impact of the harvest of *M. flexosa* fruits on local primate populations has not been quantified, it seems likely that it has a negative impact on the primate populations, since a number of primates are described to eat the palm fruits during periods of overall fruit scarcity [Peres, 1994b,c; Phillips, 1993].

Given the extent of harvest that can be associated with extractive reserves, the reality that levels of extraction will increase, and the increased emphasis of such reserves as components of conservation strategies, quantification of the impact of extraction on primate populations is urgently needed to facilitate the construction of informed management plans. However, such studies will be extremely difficult. They naturally will involve comparisons of primate densities in extractive reserves that are being harvested to varying levels. This will facilitate a correlation between harvest intensity and primate population density. However, in addition to such analyses, it would be valuable to compare primate densities in such reserves to densities in undisturbed areas. Contrasting the range of densities in undisturbed areas to that in extractive reserves provides a yardstick with which to evaluate the impact of the extraction process. Studies conducted before and after harvesting will be particularly insightful.

#### **CASE STUDY IN AND AROUND KIBALE NATIONAL PARK, SEEDLING REGENERATION IN INTACT FOREST VS. FOREST FRAGMENTS WITH A REDUCED DISPERSER COMMUNITY**

To provide an initial quantitative assessment of the loss of biodiversity that might result from a significant reduction in populations of seed dispersers, we here evaluate two sets of data from within or near Kibale National Park, Uganda. Previously we attempted to estimate the potential loss in plant biodiversity that would result if all seed dispersers were hunted out of an area and fruit just fell to the forest floor under the parent [Chapman & Chapman, 1996]. This study identified all the seedlings, saplings, and poles growing directly under the canopy of five adult trees of 25 species. For tree species with large fleshy fruits adapted for dispersal by large frugivores, loss of these seed dispersers would affect all species that could not recruit under parent trees. It is difficult to state conclusively whether or not seedlings of a particular species can recruit under adult conspecifics since it is possible that, for some unknown reason, recruitment of a particular species is not occurring in an area or occurs only under specific conditions that arise occasionally over a long time scale. However, the presence or absence of seedlings and saplings under adult conspecifics does provide an initial assessment of the extent of biodiversity loss that might result from a significant reduction in seed-disperser populations. On the basis of the presence or absence of seedlings and saplings under conspecific adults, Chapman and Chapman [1996] estimated that 60% of the 25 tree species sampled could potentially be lost if all frugivores were removed. Since the growth and survival of saplings are often negatively affected by growing under a conspecific adult [Hubbell & Foster, 1990], this estimate may be conservative.

In reality, hunting is likely to cause the local extinction of only a few seed-dispersing species, often only the very largest species, while the majority of the frugivore populations will be reduced in size. Thus, to further investigate seed-



ling recruitment under conditions where frugivore numbers were dramatically reduced, we quantified seedlings found in 20 forest fragments neighboring Kibale National Park (766 km<sup>2</sup>) [Osmaston, 1959; Kingston, 1967; Wing & Buss, 1970; Struhsaker, 1975; Kasenene, 1987; Skorupa, 1988]. An unlogged area within Kibale of approximately 300 ha (compartment K-30) was selected for the study. In addition, since a number of the forest fragments contained significant amounts of swampy valley bottom vegetation, we also sampled areas of valley bottom within this area.

While most of the land outside of the boundaries of the park has been cleared for agriculture, small patches of forest remain in areas that are difficult to farm. These patches are typically either in valley bottoms, where it is too swampy to farm, or along the slopes of hillsides and crater lakes, where it is too steep to farm. The patches we examined were generally less than 10 ha in size, but one larger patch of 130 ha was also sampled (mean patch size (excluding the 130 ha patch) = 4.7 ha, SD = 6.2, range = 0.8–28.7 ha, n = 19). These forest fragments are separated from the National Park by active agricultural land and fallow fields dominated by tall grasses (mean distance to Kibale = 2.8 km, SD = 2.1, range = 0.2–7.2 km). Contrasting the present size and shape of the forest patches with aerial photographs taken in 1959 indicates that the majority of these patches have been isolated for at least the last 30 years, but most have decreased in size and continue to be cleared. To quantify the amount of recent clearing, the number of cut stumps was recorded along 100 m of transect in each patch. Clearing occurred in all patches except two, which were part of a conservation education/tourism project (mean = 90 stumps/hectare, SD = 55.3, range = 0–210). The estimate of clearing could have been artificially inflated in a few patches, however, by using preexisting trails for transects, along which clearing probably occurred at a higher rate than in the patch as a whole.

Of Kibale's six common diurnal primate species, blue monkeys (*Cercopithecus mitis*), redtail monkeys (*Cercopithecus ascanius*), grey-cheeked mangabeys (*Cercocebus albigena*), red colobus (*Procolobus badius*), black-and-white colobus (*Colobus guereza*), and chimpanzees (*Pan troglodytes*), only four were found in the forest patches. Black-and-white colobus and redtail monkeys were the most common species in the patches, being present in 85% and 90% of the areas surveyed, respectively. Red colobus were present in approximately half of the patches (55%), while blue monkeys and grey-cheeked mangabeys were absent from all patches, including the 130 ha patch. While repeat visits to the same patch indicated that black-and-white colobus and red colobus were permanent residents of specific patches, it appeared that redtail monkeys moved among forest fragments. Chimpanzees were seen in only one patch, but evidence of chimpanzees, such as nests and dung, was seen in nine of the 20 patches, suggesting that they move among patches, stopping at any one patch fairly infrequently. At least one species of large frugivorous birds was present at all patches; typically turacos (*Corythaeola cristata*, *Musophaga rossae*, *Tauraco schuetti*) and/or hornbills (*Bycanistes subcylindricus*, *Tockus alboterminatus*) were observed in each of the patches. Thus, two of the largest frugivorous primates, blue monkeys and mangabeys, were completely absent, while the largest frugivore, the chimpanzee, entered a given patch only occasionally. Redtails, the smallest of the frugivorous primates, and the frugivorous birds were only the frugivores regularly present.

Within the patches and in Kibale, seedlings (from germinating seeds to plants 1 m tall) were quantified in 1 m<sup>2</sup> plots every 10 m along 100 m of transect. Plots were placed 2 m off the transect, and successive plots were placed on alternate sides of the transect. All seedlings in the plots were identified and counted. All

trees within a 10 m radius or that had canopies overhanging the sampling site were identified and measured (DBH) to determine whether the seedling probably resulted from a dispersal event or from fruitfall.

We contrasted the density and richness of seedlings that were not under a potential parent tree in five different habitats: two within Kibale (unlogged forest and swampy valley bottoms) and three in different types of forest fragments outside of Kibale (crater lakes, hillsides, and swampy valley bottoms) (Fig. 1). The conditions of the swampy valley bottoms in both the park and the fragments appeared to support few seedlings of only a limited number of species, and thus these habitats are not considered further. The number of seedlings ( $t = 1.459$ ,  $P = 0.179$ ) and species richness ( $t = 0.026$ ,  $P = 0.642$ ) in crater lake fragments did not differ from those in hillside fragments. Therefore, these values were combined and contrasted with those found in the unlogged forest of Kibale. Both seedling density ( $t = 2.962$ ,  $P = 0.006$ ) and the number of species of seedlings ( $t = 2.607$ ,  $P = 0.019$ ) were lower in the forest fragments than in the unlogged areas of Kibale (Fig. 1). The proportion of seedlings that were under a potential parent did not differ between the fragments and the intact forest ( $t = 0.954$ ,  $P = 0.348$ ). This suggests that the ability to regenerate under conspecifics, likely the parent, does not change between the forest fragments and the undisturbed forest.

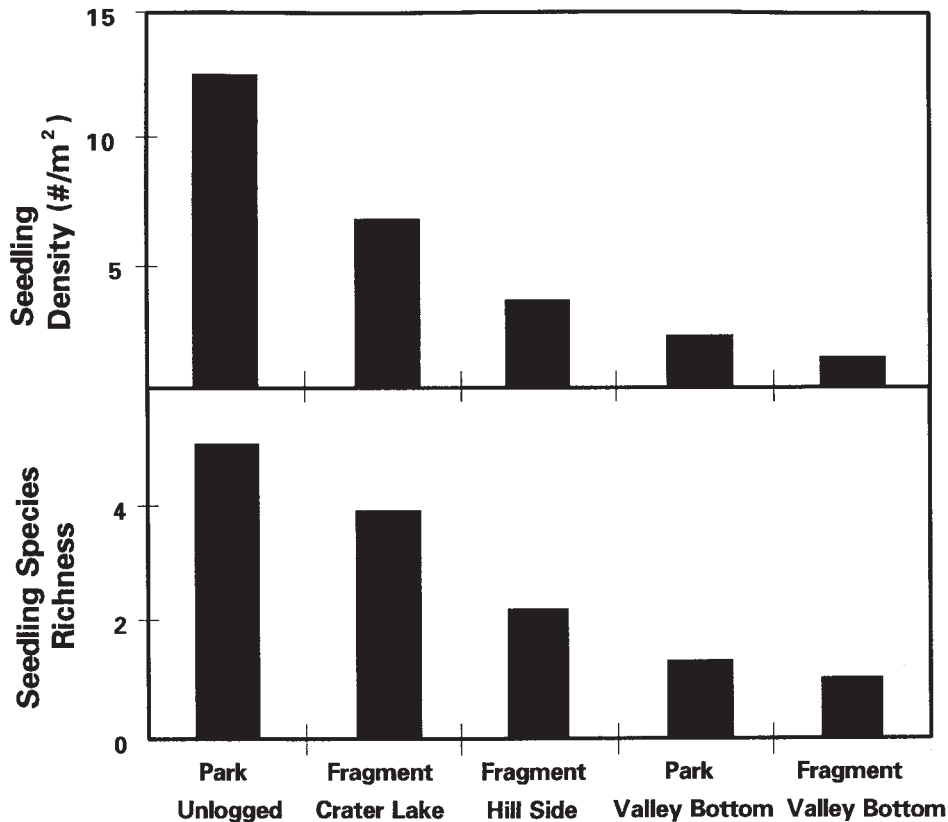


Fig. 1. Density and richness of seedlings (not under or within 10 m of an adult conspecific) in five different habitats: two within Kibale National Park, Uganda (unlogged forested and swampy valley bottoms) and three in forest fragments outside of the National Park (crater lakes, hillsides, and swampy valley bottoms).

This comparison between the fragmented forests with few dispersers and the intact forest with a complete set of dispersers approximates a situation in which some primate frugivores were hunted to local extinction. However, forest fragments differ from continuous forest in which primates have been hunted out in a number of ways. For example, fragmentation may limit the number of pollinators available to a plant and alter fruit set. Stingless bees are important pollinators for species in as many as 30 plant families. Powell and Powell [1985] sampled 15 species of these bees in continuous forest and in isolated fragments in Brazil and found declines in visitation rates by male bees in all forest isolates. Habitat fragmentation dramatically increases the amount of edge relative to the amount of interior habitat, and the microenvironment at a fragment's edge is different from that of the interior (wind, temperature, water availability [Kapos, 1989]). Changes in the microclimate will influence the probability that seeds will germinate and will influence seedling survival and growth. Such factors could contribute to seedling density being lower in fragments than in continuous forest, but other factors may operate in the opposite direction. For example, in an experimental study of seed predation, Burke [1993] demonstrated that seed predation was significantly lower near the forest edge than in interior forest.

If the lower seedling density and richness that we quantified in the fragments were the result of changes in the community of seed dispersers and not due to other consequences of fragmentation, we would expect that large-seeded species would be more dramatically affected than small-seeded species. This prediction is based on the observation that large frugivores are often capable of handling large fruits and seeds that small frugivores are not (e.g., birds are limited by gape width [Howe, 1986]). The average seed diameter of all species found along the transects in either the fragments or in Kibale was determined by measuring seeds collected from parent trees or frugivore dung (largest dimension) or from descriptions from *The Flora of Tropical East Africa* (if a range was given, the mean of the range was used). The average seed size of the combined species lists was 1.08 cm. Of the seedlings found in the forests of Kibale, 22.4% were from species with seed sizes less than the average. In contrast, 83.5% of the seedlings in the fragments were from species with seed sizes less than the average. This suggests that the decrease in the frugivore community found in the forest fragments is related to the decrease in the recruitment of seedlings, particularly for large-seeded species.

In summary, it is clear that primates rely on fruiting trees as important food resources and that primates provide valuable dispersal services to many of these fruiting trees. Primates have been documented to often rely heavily on fruit, to move large numbers of seeds, to be responsible for the dispersal of a large proportion of the seeds produced by some species, typically not to decrease seed viability through their handling of the seeds, and to defecate or spit many seeds in locations where they can germinate and grow. These observations suggest that human activities that influence either primate seed dispersal or fruit production have the potential of having significant effects on the other interactants. The complexity of the interactions between primates and fruiting trees is clearly illustrated with respect to studies on the effects of logging. The conflicting pieces of evidence suggest that while the resource base will be decreased by logging (at least in the short term), it is very difficult to predict how each species will respond. Conversely, subsistence and commercial hunting affect large tracts of forest while leaving their physical structure relatively unaltered, at least initially. The long-term consequences on forest composition of removing primate seed dispersers from such areas is unclear. One can logically argue that since primates

appear to be important seed dispersers, there will be an effect on future forest composition, but the data to substantiate this claim are limited. The case study we provide from Kibale contrasting seedling recruitment in forest fragments in which primate seed dispersers have been dramatically reduced with seedling recruitment in areas which have an intact frugivore community suggests that removing primates will lower seedling density and species richness and will result in a greater proportion of the seedlings being from small-seeded species.

## CONCLUSIONS

1. Obtaining comprehensive data on the hunting of primates is difficult, but it is clear that primates are being harvested in great numbers in many areas of the world. The fact that primates move large numbers of seeds, do not typically decrease seed viability through their handling of the seeds, and defecate or spit seeds in suitable locations suggests that the maintenance of primate populations is critical for the regeneration of tropical forests.

2. Unfortunately, few studies have examined the impact of selective logging on primate communities. Furthermore, quantitative comparisons between this small sample of studies are limited because they vary with respect to extraction and incidental damage levels, the original composition of the primate communities, the proximity to undisturbed refugia and recolonization sources, the length of time between logging and the monitoring, etc. The conflicting pieces of evidence revealed by these studies suggest that while the resource base will be decreased by logging, it is very difficult to predict how each species will respond. At this time it seems most prudent to assume that logging will typically have negative impacts on primate communities, and means to decrease the extent of these impacts should be investigated.

3. Given the extent of harvest that can be associated with extractive reserves, the reality that levels of extraction will rise, and the increased emphasis of such reserves as components of conservation strategies, quantifying the impact of extraction on primate populations is urgently needed to facilitate the construction of informed management plans. However, to date we know little about the impact of extraction of nontimber forest products on primate populations.

4. A case study is presented from Kibale National Park, Uganda, in which we contrast seedling recruitment in 20 forest fragments where primate seed dispersers have been dramatically reduced with seedling recruitment in areas that have an intact frugivore community. The forest fragments had lower seedling density and fewer species of seedlings than the intact forest. Furthermore, in comparison to the intact forest, a greater proportion of the seedlings found in the fragments was from small-seeded species that probably do not depend on primates for their dispersal.

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