RESEARCH ARTICLES

Habitat Alteration and the Conservation of African Primates: Case Study of Kibale National Park, Uganda

COLIN A. CHAPMAN[1,2*] AND JOANNA E. LAMBERT[2]
[1]*Department of Zoology, University of Florida, Gainesville*
[2]*Wildlife Conservation Society, Bronx, New York*
[3]*Department of Anthropology, University of Oregon, Eugene*

Tropical forests and the animals they support are being threatened by accelerating rates of forest conversion and degradation. In a continually fluctuating sociopolitical world, it is often impossible to protect areas from such conversion until the political environment is suitable to pursue conservation goals, by which time, the forests have often been converted to other uses. This reality suggests a need for inquiry into which primate species can persist after different types of disturbances and how quickly primate communities can recover from disturbance. Here we examine the persistence of primate populations in disturbed habitats by providing a case study of patterns of primate abundance in areas of Kibale National Park (766 km^2), Uganda, that have been modified by different types and intensities of human activities, primarily commercial logging and agricultural clearing. Distributional surveys at 24 sites and detailed line-transect censuses at six sites demonstrate that primate populations in Kibale are often high and suggest that patterns of population change associated with disturbance are complex. Analysis of the land use coverage of Kibale reveals that abandoned farms (10.3%) and degraded forest (8.7%) now cover 146 km^2. Unfortunately, we do not know what proportion of the farms were established on areas that were forest versus grassland. However, if the areas that are now abandoned farms were all once forested, this means that 79 km^2 of forest has been lost. Based on density estimates from nearby sites, this would represent a loss of 52,612 monkeys and 200 chimpanzees. Populations would also have been affected by the degradation of the 66 km^2 (8.7%) of forest. These estimates of the potential reductions in the primate populations that could have resulted from forest clearing and degradation illustrate the importance of protecting land. A review of the literature illustrates that the biomass of primates found within Kibale is very high in comparison to other locations and thus illustrates the importance of Kibale to regional conservation. Am. J. Primatol. 50:169–185, 2000.   © 2000 Wiley-Liss, Inc.

*Correspondence to: Colin A. Chapman, Department of Zoology, University of Florida, Gainesville, FL. E-mail: cachapman@zoo.ufl.edu

INTRODUCTION

Tropical forests and the animals they support are being threatened by accelerating rates of forest conversion and degradation [Lanly, 1982; Brown & Lugo, 1990; Struhsaker, 1997]. In a continually fluctuating sociopolitical world, it is often impossible to protect areas from such conversion until the political environment is suitable to pursue conservation goals, by which time, the forests have often been converted to other uses. Indeed, there are repeated examples of legally protected areas suffering serious degradation during periods of political or economic instability [Hart et al., 1996; Chapman et al., 1999]. For example, the northern part of Taï National Park (730 km^2), which comprises 21% of the total park area, was temporarily de-gazetted and is now heavily impacted by human agricultural activity [IUCN, 1987]. Similarly, Bia National Park in Ghana was gazetted in 1974 to include 306 km^2, reduced in 1979 to 230 km^2, and further reduced to 78 km^2 in 1980. The area excised from the park has been classified as a Game Production Reserve [IUCN, 1987; now called a Resource Reserve) and has now been largely opened up to timber exploitation.

Throughout the tropical world, less than 5% of rain forests are legally protected from human exploitation [Redford, 1992; Oates, 1996]. Furthermore, many tropical species are locally endemic or are rare and patchily distributed [Struhsaker, 1975; Richards, 1996]. Such restricted distributions predispose many tropical forest species to increased risk of extinction, simply because their range may not fall within a protected area [Terborgh, 1992]. Consequently, national parks and reserves, even if effectively protected, will fail to conserve many species. As a result, the conservation of many tropical species will depend on the capacity of disturbed forests to support their populations [Struhsaker, 1997]. More than 90% of all primate species occur in the tropical forests of Asia, Africa, and South and Central America [Mittermeier & Cheney, 1987], and these forests are being heavily impacted. Thus, information on the effect of various types of forest degradation on primates and on the form and speed with which their populations recover from disturbance is vital to allow managers to construct informed conservation plans. However, little is known about the process of forest regeneration in different tropical areas of the world (particularly in Africa). Moreover, studies have primarily focused on understanding variation in recovery of plant communities, largely ignoring how animal populations recover [Uhl, 1987; Chapman & Chapman, 1999].

Kibale National Park, Uganda (766 km^2), provides an excellent opportunity to investigate the impact of forest degradation and recovery on primate populations. This park has had a complicated history of human impacts, both in terms of commercial logging and agricultural clearing. With respect to commercial logging, Kibale forest received National Park status in 1993. Prior to this date, it was a Forest Reserve established between 1926 and 1932 with the goal of providing a sustained production of hardwood timber [Osmaston, 1959; Struhsaker, 1997]. A polycyclic felling cycle of 70 years was initiated, and it was recommended that the canopy be opened up by approximately 50% through the harvest of trees over 1.52 m in girth [Kingston, 1967]. This history of logging has led to varying degrees of disturbance among sites [Struhsaker, 1997].

The clearing of land for agriculture has occurred primarily in the south of the park in an area known as the southern corridor, particularly in the Kibale

Forest Corridor Game Reserve, which links Kibale with Queen Elizabeth National Park. This game reserve was managed by a separate government agency from the rest of the reserve and had an area of 340 km^2, of which 134 km^2 had dual status and lay within the Forest Reserve and Game Reserve [van Orsdol, 1986; MISR, 1989; Howard, 1991; Struhsaker, 1997].

As early as 1971, illegal destruction and encroachment occurred in the corridor. In 1976, some 30 eviction orders were issued but were never carried out. In 1983, the government again ordered settlers out of these encroached areas, and by 1984, it was estimated that 60% of the forest plots and 30% of the grassland plots had been abandoned. However, the situation soon reverted to the prior state and encroachment increased. On April 1, 1992, the government ordered settlers off the land, and with the aid of a United Nations Program resettled all encroachers [MISR, 1989]. Estimates of the number of people residing in the southern corridor vary dramatically. Based on aerial surveys counting houses, van Orsdol [1986] estimated that 8,800 people were living in the southern corridor. A national census carried out in 1980 indicated that as many as 17,000 people were residing in Kibale. Baranga [1991] estimated 40,000 people, MISR [1989] reported some 60,000 people, and after the resettlement, the National Environmental Management Authority [1997] estimated that 30,000 households, or approximately 170,000 people, were residing in Kibale. The extreme variance in these estimates (8,800 to 170,000) illustrates the need for careful research prior to the initiation of resettlement programs. Based on our surveys conducted just after the resettlement program was completed, it is our impression that most of these estimates are high and it seems likely that the larger estimates were politically and economically motivated. However, whichever estimate one chooses, it is evident that a large number of people were residing in the southern corridor.

The history of human impact in Kibale is a complicated one—not an uncommon story for many tropical forests. The fact that there are areas of this park that are now in a state of recovery from previous human impact allows for an examination into how primate populations are able to persist in the face of different types of disturbance. Our objective in this paper is to provide a case study that documents patterns of primate abundance in areas of Kibale that have been modified by different types and intensities of human activities: commercial logging and agricultural clearing. We address three issues: 1) What is the extent of degradation that has occurred in Kibale over the last two decades? 2) What is the current pattern of distribution and abundance of the six common diurnal primates. (3) Does this pattern provide insights into which primate species are able to persist in the face of these disturbances?

METHODS

Study Sites

Two types of surveys were conducted: 1) distributional surveys to determine the presence or absence of primate species in given areas and 2) intensive line transect surveys to quantify densities of primate groups at six specific sites. Although Kibale is home to 13 species of primates, both of these surveys only consider the six common diurnal primates: red colobus (*Procolobus badius*), black-and-white colobus (*Colobus guereza*), redtail monkeys (*Cercopithecus ascanius*), blue monkeys (*Cercopithecus mitis*), grey-cheeked mangabeys (*Lophocebus albigena*), and chimpanzees (*Pan troglodytes*). The sites for the distribu-
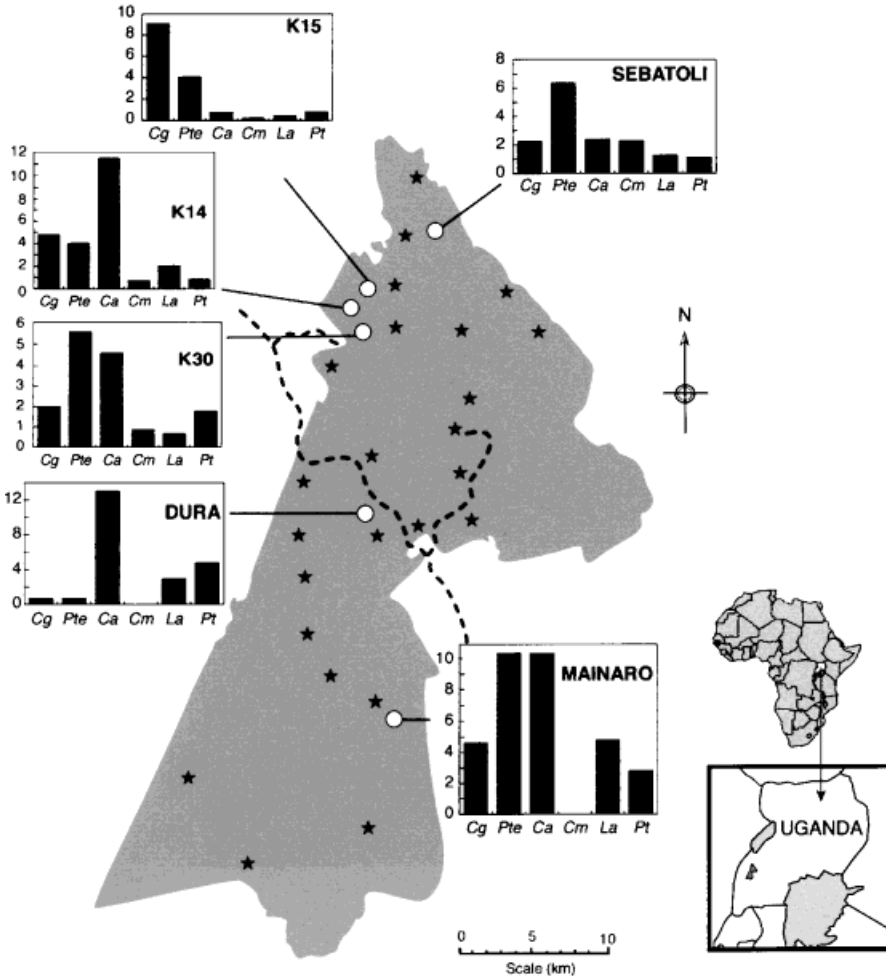
Fig. 1. A map of Kibale National Park, Uganda showing the location of the 6 sites where detailed transect surveys were conducted and the 24 sites were a distributional survey was conducted. Also, depicted is the group density for the monkeys (groups/km^2), and nest density for chimpanzee derived from nest counts (number of nests/km^2/day). Dotted lines are the major dirt roads that provide access to the park.

tional survey were spread throughout the park (Fig. 1). Some of these locations were visited many times (e.g., the site near the field station where detailed behavioral observations were being conducted), while other sites were in distant, inaccessible, parts of the park and were visited only once. More areas were visited in the north of the park than in the south because prior to 1993 it was unsafe to travel into the southern corridor because of the encroachment, and since 1996 there has been intermittent rebel activity in the south.

The six intensively studied sites were distributed along a north-south gradient, and each of the sites was selected to represent a particular region of the park and a particular management history (Fig. 1). The most northern site, Sebatoli (elevation 1,500 m) was commercially logged in the late 1960s. While we were unable to obtain information on the level of extraction, detailed quantification of stand structure suggests that the level of extraction was similar to or

slightly lower than the site just to the south (K-15 forestry compartment; Chapman & Chapman, unpublished data, see below).

Three sites were near the Kanyawara study site (elevation 1,500 m), the location of Makerere University Biological Field Station. The first, K-15 is a 347 ha section of forest that experienced heavy selective felling from September 1968 through April 1969. Total harvest averaged 21 m^3/ha or approximately 7.4 stems/ha [Skorupa, 1988; Struhsaker, 1997], but incidental damage was much higher. It is estimated that approximately 50% of all trees in compartment K-15 were destroyed by logging and incidental damage [Kasenene, 1987; Skorupa, 1988; Chapman & Chapman, 1997]. The damage caused by this intensity of logging is very spatially heterogenous. Today in the K-15 compartment areas exist that are as large as 100 m by 100 m where there are few or no large trees and the vegetation is dominated by herbaceous vegetation. However, such intensely disturbed areas can be adjacent to areas where few or no trees were extracted and the forest is relatively intact. A total of 18 tree species were harvested, with nine species contributing more than 95% of the harvest volume [Kasenene, 1987; Skorupa, 1988]. Many of the harvested tree species provided primates with food. For example, of the nine species that contributed more than 95% of the harvest volume, all were red colobus food trees [Skorupa, 1988; Struhsaker, 1997].

Forestry compartment K-14, a 405 ha forest block, was lightly and selectively harvested from May through December 1969 (averaging 14 m^3/ha or 5.1 stems/ha). Twenty-three tree species were harvested, with nine species accounting for 94% harvest volume. Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage [Skorupa, 1988; Struhsaker, 1997].

K-30 is a 282 ha area that has not been commercially harvested. However, prior to 1970, a few large stems (0.03 to 0.04 trees/ha) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest [Skorupa & Kasenene, 1984; Skorupa, 1988; Struhsaker, 1997].

At the Dura River (elevation 1250 m) and Mainaro (elevation 1200 m) sites, a few timber trees have been extracted by pitsawyers (approximately 0.1 trees/ha), but this has had little impact on the forest. The Mainaro site is located in the southern corridor, where the majority of the agricultural encroachment occurred. At this site and further to the south, there is a strip of forest that ranges from 1 to 7 km wide through which the Dura River flows. Much of this forest is bordered by abandoned agricultural lands, or grasslands that have existed at least since the turn of the century [Howard, 1991].

Within Kibale, there is an elevational gradient from north to south, which corresponds to a north to south increase in temperature and decrease in rainfall [Howard, 1991; Struhsaker, 1997]. Corresponding to these changes, the vegetation at these different sites varies [Chapman et al., 1997]. Foresters have classified the forest at Sebatoli and Kanyawara as *Parinari* forest, distinguished on photo aspect maps by large spreading crowns of *Parinari excelsa* [Kingston, 1967; Skorupa, 1988]. The species associated with *P. excelsa* change between these two sites. At Sebatoli, the major sub-dominant is *Carapa grandiflora.* Near Kanyawara co-dominants included *Aningeria altissima, Olea welwitschii, Newtonia buchananii,* and *Chrysophyllum gorungosanum.* These assemblages are thought to represent climax forests between 1,370 m and 1,525 m [Osmaston, 1959]. At Dura River these species are less common; *Pterygota mildbraedii, Cola gigantea, Pipadeniastrum africanum,* and *Chrysophyllum albidum* are the dominant tree species. Further south at Mainaro, the forest is dominated by *Cynometra alexandri*

and its affiliated species. Detailed enumeration of the tree community of these areas is provided by Chapman et al. [1997] and Chapman and Chapman [1999].

Quantification of the Land Cover

To determine the extent of deforestation and the amount of suitable forest habitat for primates in Kibale, we digitized land use cover maps produced by the Forest Department and the Norwegian Forestry Society for the National Biomass Study. These 1:50,000 maps were derived from manual interpretation of SPOT satellite imagery taken between February 1989 and December 1992 combined with some Landsat and aerial photographs from early 1995. These maps were verified through extensive, systematic field surveys. On these maps, the following land use categories were depicted: forest, grassland, farmland, degraded forest, woodland, lake, wetland, broadleaf plantation, conifer plantation, seasonal grassland, seasonal woodland, and seasonal bushland. In this classification, commercially logged forest was included in the broader category of "forest." Degraded forests were areas from which much of the canopy cover had been removed, and the areas were dominated by secondary growth.

None of the common forest dwelling primates included in the census were seen to use woodland or grassland, unless it was immediately adjacent to forest. Thus, for these species we only considered forest and degraded forest as suitable habitat. For chimpanzees this may underestimate available area, since some communities make foraging excursions into woodland and grassland. Baboons (*Papio anubis*) and vervet monkeys (*Chlorocebus aethiops)* were frequently seen in woodland and grassland habitats, but we did not estimate their densities.

The six areas in which detailed transect surveys were conducted represented larger zones that included adjacent forest. Thus, the number of primates in Kibale was estimated as the sum of the density of each primate species in a particular zone multiplied by the amount of suitable habitat in that zone. In this analysis, Sebatoli represented habitat north of 70000 N, K-15 and K-14 values were averaged and used to represent habitat between 70000 N and 60000 N, K-30 represented habitat between 60000 N and 55000 N, the Dura River represented between 55000, and 50000 N, and Mainaro represented habitat south of 50000 N.

Survey and Density Estimation

For the distributional survey, we recorded the presence or absence of each of the common diurnal primate species in different regions by traveling to an area and searching throughout the day for primates. As indicated previously, some of these locations were visited many times, while other, more distant sites were visited only once (Fig. 1). These surveys were conducted at various intervals between March 1990 and August 1998. In the south of the park, searches were typically made both in the degraded areas and adjoining less disturbed forested areas.

Primate group densities at the six focal sites were assessed using line-transect methods [Struhsaker, 1975, 1997; National Research Council, 1981; Defler & Pintor, 1985; Skorupa, 1987; Chapman et al., 1988; Whitesides et al., 1988]. All species examined are large-bodied and diurnal; the subset of primates for which the line-transect method is thought to be appropriate for estimating densities [National Research Council, 1981]. Primate censuses along transects approximately 4 km long were initiated in June 1996. Data were collected biweekly at K-30 (n=26), K-14 (n=26), K-15 (n=24), and Dura (n=23) and once a month at Sebatoli (n=14) and

Mainaro (n=10). Rebel activity prevented us from sampling at Mainaro in January, February, and April of 1997. The census was conducted by C. Chapman, L. Chapman, S. Balcomb, volunteers, and field assistants following line-transect procedures previously used in Kibale [Struhsaker, 1975; National Research Council, 1981; Skorupa, 1988; Butynski, 1990; Struhsaker, 1997]. Censuses were conducted between 0700 hr and 1400 hr at a speed of approximately 1 km per hr. Data collected included primate species observed, time of observation, straight line distance between the animal and observer (visually estimated), and mode of detection. At the beginning of the study observers trained together to estimate observer to animal distance. Variation between observers in sighting estimates was assessed at the end of the study. While particular estimates could be inaccurate, overestimates of distances tended to be countered by underestimates.

A variety of methods have been proposed for estimating primate density using transect data and considerable controversy exists regarding the accuracy of these different methods [Burnham et al., 1980; Chapman et al., 1988; Skorupa, 1988]. Given this controversy and the difficulty of obtaining the sample size needed to use computer programs such as "Distance" [Buckland et al., 1993], we relied on empirical criteria for selecting the best method. Ghiglieri [1979, 1984], Struhsaker [National Research Council, 1981], and Skorupa [1988] concluded that a modified Kelker [1945] method produced the best empirical results for primates at Kibale. Following these recommendations, we plotted the distance at 10 m intervals and used a 50% cut-off rule to select the sighting distance. If X_i is the number of sightings in distance class i for a given species, the last distance considered was at the end of the first class such that X_{i+1}/X_i and X_{i+2}/X_i were both equal to 0.50 or less. We used the observer to animal sighting distance, rather than perpendicular distance, because empirical data indicate that perpendicular distance underestimates transect width for forest dwelling primates [National Research Council, 1981; Whitesides et al., 1988; Chapman et al., 1988; Struhsaker, 1997]. Thus, the density of groups was calculated as the number of groups sighted within the truncated sighting distance divided by the area sampled (length of the census route times the truncated distance for animal sighting distance.

Obtaining reliable group counts of forest dwelling primates is extremely difficult as inactive animals are often hard to locate and, when groups are traveling, animals often take different pathways which are difficult for an observer located at one site to see. As a result a considerable effort was placed on counting groups in each area. Each month between July 1996 and May 1998, two observers spent 2 days at each site following groups and attempting to obtain accurate counts. Counts were rarely attempted when a group was stationary, rather the best counts were obtained when a group was moving and crossing a gap in the forest, the river (Dura, Sebatoli, and Mainaro), or a road (Kanyawara and Dura). Repeat counts were made of the same group to ensure accuracy and to document changes in group size over the year long period. Groups were identified either by individually recognizable animals or by matching the group count to previous ones. In addition, counts were made opportunistically while observers were collecting behavioral data and groups were seen to cross a road or river. For each site, the estimate of group density derived from the transect survey was multiplied by the average group size for that site to determine the density of individuals. Thus, if particular habitat modification influences group size [Struhsaker,1997; Skorupa, 1988], this effect was taken into consideration when calculating the density of individuals.

It is widely acknowledged that chimpanzee density is difficult to determine [Marchesi et al., 1995; Plumptre & Reynolds, 1996]. Direct counts of social groups from line-transect methods [Struhsaker, 1975, 1997] are known to underestimate

chimpanzee density since apes, as large bodied mammals, occur at relatively low densities and unhabituated chimpanzees often flee before they are detected by observers [Ghiglieri, 1979, 1984; Tutin & Fernandez, 1984; Skorupa, 1988]. Alternatively, nest counts have been used as a measure of chimpanzee density [Ghiglieri, 1984; Tutin & Fernandez, 1984; Skorupa, 1988; White, 1994; Hashimoto, 1995; Plumptre & Reynolds, 1996; Hall et al., 1998] and it is widely asserted that this is the most practical and reliable method [Skorupa, 1988; Hashimoto, 1995; Plumptre & Reynolds, 1997]. Along each of the 4 km census routes, new chimpanzee nests were flagged perpendicular to their location along the transects and the following were recorded: perpendicular distance from the transect to the nest, the height of the nest, the age-class of the nest, and the tree species in which the nest was located. This methodology is equivalent to the marked nest counts following Plumptre & Reynolds [1996]. Chimpanzee nest density was calculated based on the total number of nests seen per km^2 per day [White, 1994; Plumptre & Reynolds, 1996; see Hashimoto, 1995; Plumptre & Reynolds, 1996 for a comparison of chimpanzee nest density techniques). Assuming that the chimpanzees at these sites make one nest a day [Ghiglieri, 1979, 1984], the value produced by this method is equivalent to density of individuals of nest building age. Transect width was calculated following Skorupa [1988].

To estimate the biomass of the primates, adult male and female body weight were collected from the literature (using data on wild caught animals where possible). The populations were assumed to have an equal sex ratio, and half of the members of a group were assumed to be juveniles that were half the weight of the adult.

RESULTS

Quantification of Land Cover

Forest (57.9%) and grassland (14.6%) were the most extensive habitats in Kibale. Grasslands were much more common in the southern sections of the national park than in the northern areas. Woodlands were prevalent in the far south of the park, but they only covered 5.8% of the total park's surface area. Wetlands and lakes comprised 2.2% of the park and were distributed throughout the area. Plantations, primarily conifers, planted in the 1960s on grasslands [Osmaston, 1959; Kingston, 1967] and constitute 1.0% of the park's area [Struhsaker et al., 1989; Chapman & Chapman, 1996; Struhsaker, 1997; Zanne, 1998]. These plantations are primarily found in the northern sections of the park near Sebatoli and in the more central areas around Kanyawara. Abandoned farms (10.3%) and degraded forest (8.7%; largely representing secondary forest associated with agricultural encroachment) cover 146 km^2. Seventy-six percent of these degraded lands were found in the southern corridor.

Primate Survey and Density Estimation

In the distributional survey, we visited 24 sites distributed throughout the park (Fig. 1). At 11 (46%) of these sites all six of the common diurnal primate species were observed. In seven (29%) of southern sites all species were seen except blue monkeys. Most intriguingly, blue monkeys were common in the north of the park but were at such a low density that they were not seen in 134 km of transects walked at Dura and Mainaro. At five (21%) of the remaining sites, it is believed that all species were present, but the duration of the sampling was too short to locate them. For these sites, this claim was substantiated by talking to

park guards and local villagers. At the remaining site, Lake Kabaleka in the southwest corner of the park, only redtail monkeys, black-and-white colobus, vervet monkeys, and baboons were seen. At this site there is a thin strip of forest surrounding the lake, and this forest is separated from other forests by approximately 6 km of grassland. Vervet monkeys and baboons were more abundant in the southern sections of the park than in the north. Baboons were more abundant in areas near grasslands. Vervet monkeys were frequently seen in the very far south of the park; however they were extremely rare in the north (e.g., to our knowledge only two male vervet monkeys have been seen in Kanyawara in 29 years; T.T. Struhsaker personal communication and CAC personal observation).

Despite the broad distribution of most of the common diurnal primates throughout the park, patterns of abundance varied dramatically among species and sites (Table 1, Fig. 1). In the transect component of the study, 97 census walks were conducted for a total of approximately 388 km. The two colobine species were present at all sites. The lowest density that was recorded for both these species was at the undisturbed Dura River site. Mangabeys were found throughout the forested sections of the park, but were most abundant in the two most southern sites. Blue monkeys were common in the north of the park, but their numbers progressively decline as one travels south. Redtail monkeys were abundant in all areas except the most heavily logged sites. Many of these patterns of distribution are not easily interpreted in light of basic forest structure. For example, it is difficult to see how changes in the tree community composition could explain the decline in blue monkey abundance from the north to the south. Similarly, red colobus and black-and-white colobus were found at the lowest density at the Dura River site; a location that has not been disturbed and harbors a well developed and diverse forest (Chapman and Chapman [1999], Struhsaker [1975], and Clutton-Brock [1975] report higher densities near this site in the 1970s).

Differences in density between logged and unlogged areas reveal conflicting patterns with respect to the effect of logging on primate abundance. Chimpanzees were the only species to consistently occur at lower densities in logged areas than in unlogged areas. Redtails had lower densities in heavily logged areas, but not in lightly logged areas. Red colobus show a decline in density between the unlogged K-30 site and the neighboring logged sites at K-14 and K-15; however, they were abundant at Sebatoli, a logged site to the far north. Black-and-white colobus were found at their lowest density at Dura River, which is an unlogged, relatively pristine site and were abundant at the logged sites. Documenting a pattern of the effect of logging on blue monkeys is confounded by their tendency to decline in abundance from the north to the south of the park.

TABLE I. Group Densities of the Common Primates in Different Areas of Kibale National Park[a]

Species	Sebatoli	K-15	K-14	K-30	Dura	Mainaro
C. guereza	2.05	9.12	4.83	2.00	0.79	3.85
P. tephrosceles	6.53	4.43	4.35	5.50	0.53	10.25
C. ascanius	2.53	1.04	11.48	4.83	12.19	10.25
C. mitis	2.53	0.35	0.91	1.00	0[b]	0[b]
L. albigena	1.97	0.87	2.41	1.13	3.29	5.13
P. troglodytes	1.12	0.82	0.86	1.78	4.81	2.83

[a]Density estimates for the monkeys were derived from line transect surveys (groups/km^2), while chimpanzee density was derived from nest counts (number of nests/km^2/day).
[b]Known to be present in the area but not seen during the transect censuses.

The majority (76%) of the agricultural encroachment (farm and degraded forest land use categories) occurred in the south of the park in the area represented by Mainaro. This area had relatively large populations of all species, except blue monkeys that were present in the area, but were not seen on the line-transect survey.

Because of the difficulty of obtaining accurate counts of primate groups, we have focused on estimating differences in the density of primate groups. In doing so, we have assumed that group size is equal among sites. However, intraspecific variation in group size has been extensively documented [Struhsaker & Leland, 1979; Chapman, 1989]. Kibale has been the site of numerous investigations of primate behavior and ecology that provide detailed counts of primate groups in different areas. For example, Butynski [1990] documented that blue monkey group size decreased by 52% from K-14 to K-30. Oates [1974] reported that black-and-white colobus group size was 25% smaller in K-14 as compared to K-30. Olupot (personal communication) found that mangabey group sizes decreased by 21% between K-14 and K-30 and by 36% between K-15 and K-30. Based on repeat counts made during this study, we made a crude estimate of the number of individuals for each species in the park and their biomass (Table 2). However, these estimates should be interpreted with caution until more detailed counts of habituated groups can be obtained.

A review of the literature illustrates that the biomass of primates found within Kibale is high (Table 3) in comparison to other locations. What the primate biomass would have been had the park not been disturbed remains uncertain. Nonetheless, the current biomass estimate illustrates the importance of this park to regional primate conservation efforts.

DISCUSSION

The objective of this study was to provide information on which primate populations are able to persist in areas that had experienced different types and intensities of human disturbance. Such information is important for assessing the value of protected areas that have been degraded or of regenerating habitats outside of protected areas. We assess this objective in two types of human modified landscapes: degraded agricultural land and commercially logged areas.

Abandoned farms (10.3%) and degraded forest (8.7%) now cover 19% of the park. Unfortunately, we do not know what proportion of the farms were established on areas that were forest vs. grassland. However, if the areas that are now abandoned farms were all once forested, this means that 79 km^2 of forest has been lost. Based on density estimates from nearby sites, this would represent a loss of 52,612 monkeys and 200 chimpanzees. Populations would also have been affected by the degradation of the 66 km^2 (8.7%) of forest. The only species

TABLE II. The Density (Individuals/km^2) and Total Population Size of the Common Primates in Kibale National Park

Species	Density (ind./km^2)	Total population size
C. guereza	26	13,228
P. tephrosceles	159	80,675
C. ascanius	184	92,945
C. mitis	6	3,133
L. albigena	45	22,607
P. troglodytes	3	1,527
Total	423	214,114

TABLE III. Estimates of Primate Biomass and Primate Community Richness at
Selected Forest Sites (Biomass = kg/km^2)

Site	Biomass	Frugivore biomass	Folivore biomass	Number of species	Source[a]
Asia					
Kutai Nature Reserve, Borneo	335	273	82	7	1
Kuala Lompat, Malaysia	933	596	337	6	2
Ketambe, Sumatra	837	702	135	6	3
Sepilok, Sabah	268	184	83	6	4
Africa					
Kibale National Park, Uganda	2,330	1,116	1,214	13	5
Kibale National Park, Uganda	1,954	754	1,200	11	6
Tai, Cote d'lvoire	802	244	558	9	7
Tiwai Island, Sierra Leone	1,379	786	600	11	8
Douala-Edea, Cameroon	409	198	217	7	9
Lope Reserve, Gabon	319	228	91	8	10
Budongo Forest Reserve, Uganda	545	262	284	5	11
Ituri Forest, Zaire	710	402	308	12	12
South/Central America					
Manu National Park, Peru	636	456	180	11	13
Urucu River, Amasonas, Brazil	381	344	37	13	14
Barro Colorado Island, Panama	445	29	416	5	15
Raleighvallen, Suriname	251	157	94	8	16
La Macarena, Columbia	235	88	235	7	17
Santa Rose, Costa Rica	327	181	146	3	18
Los Tuxtlas, Mexico	171	161	11	2	19
Madagascar					
Morondava N5, Madagascar	685	247	438	7	20
Morondava CS7, Madagascar	583	357	226	7	20
Ampijoroa, Madagascar	771	444	327	7	20
Ankarana, Madagascar	346	165	181	10	20
Analamazaotra, Madagascar	375	208	167	11	20
Ranomafana, Madagascar	290	249	41	12	20

[a]1 Rodman, 1978; Rodman personal communication, Waser, 1987. 2 Terborgh and van Schaik, 1987; Raemaekers and Chivers, 1980. 3 Terborgh and van Schaik, 1987. 4 Oates et al., 1990; Davies et al., 1988. 5 This Study and Chapman et al. in press to include other species (e.g., nocturnal primates) weights from Stuhsaker and Leland, 1987; Wrangham et al., 1994, Cords, 1987; Jones and Bush, 1988; Weisenseal et al., 1993; and Harvey et al., 1987; Does not include baboons or vervet monkeys. 6 Butynski, 1990 (Ngogo); see also estimates in Struhsaker 1997 and Pope, 1996. 7 Terborgh and van Schaik, 1987; Galat and Galat-Luong, 1985 with *Pan* added from Bouliere, 1985. 8 Oates et al., 1990 (mid-point in range used). 9 Oates et al., 1990. 10 White, 1994 (mean of five neighboring sites). 11 Plumptre et al., 1994a,b (density, unlogged forest only), Harvey et al., 1997 (weights assuming 50/50 sex ratio and 1/2 group immature weighing 1/2 adult). 12 Thomas, 1991 (density). 13 Terborgh, 1983 and Symington, 1988 for *Ateles belzebuth*, Harvey et al., 1987 (weights). 14 Peres, 1993. 15 Glanz, 1982; Eisenberg and Thorington, 1973. 16 Mittermeier and van Roosmalen, 1981 (body weights adjusted). 17 Klein and Klein, 1977 (densities, midpoints of ranges), Harvey et al., 1987 (weights assuming 50/50 sex ratio and 1/2 group immature weighing 1/2 adult). 18 Chapman, 1988, 1990, Glander et al., 1991, Chapman unpublished. 19 Estrada and Coates-Estrada, 1985. 20 Ganzhorn, 1992.

seen to use degraded forests were the red colobus, black-and-white colobus, red tails, and chimpanzees. This pattern of habitat use is supported by the fact that black-and-white colobus and redtails are frequently observed in forest fragments outside Kibale National Park, and red colobus and chimpanzees are occasionally seen using such habitats [Onderdonk, 1998]. In contrast, blue monkeys and mangabeys have never been seen in forest fragments outside of Kibale and are currently rarely seen near the forest edge [Onderdonk, 1998; Chapman & Onderdonk, 1998].

Despite these reductions in primate number, primate abundance is still relatively high within the remaining forests in the southern corridor. Unfortunately, it is difficult to evaluate the long-term implications of these data. First, deforestation for agriculture may initially cause population densities to rise in remaining forests as animals are concentrated in these refugia. It may take a number of years before population densities decline to the density the area can support because of reproductive failure. For example, Struhsaker [1976] found that it was nearly 10 years after the loss of approximately 90% of a major food resource before a statistically significant decline in the vervet monkeys of Amboseli, Kenya could be detected. In *Cynometra* forest in the Ituri, Thomas [1991] documented red colobus density to be 80% lower than our *Cynometra* study site, suggesting the density near Mainaro may be artificially high. Secondly, 76% of the degraded lands occurred in the southern corridor; however we lack information on primate populations in this area prior to disturbance. Much of the forest in the southern corridor is a monodominant *Cynometra* forest, a forest type very different from other areas of the park. However, in spite of these cautionary considerations, at present the density of primates in the southern corridor suggests that degraded areas that regain protected status could play important roles in conservation of particular species.

With respect to logging, the most appropriate comparison is that between the unlogged K-30, the lightly logged K-14, and the heavily logged K-15 sites. Struhsaker [1975, 1997] and Skorupa [1988] made detailed comparisons of these areas in the 1970s and 1980s and our findings echo their results [see also Chapman et al., in press.]. Heavy intensity logging corresponds to a decline in primate group density in all species except black-and-white colobus. Light intensity logging is associated with increased abundance of black-and-white colobus and redtail monkeys. Compared to unlogged areas red colobus and blue monkeys decline in abundance in lightly logged areas, but the decline is less that that associated with heavily logged areas. While differences in group size and changes in social organization associated with logging [Skorupa, 1988; Struhsaker, 1997] must be considered, these results suggest that light intensity logging may, in some instances, be compatible with primate conservation. However, high intensity logging, which is typical for most logging operations throughout Africa, is incompatible with primate conservation.

The findings from our study offer a number of lessons for projects attempting to assess impacts of human modifications on primate populations. First, there is often a high degree of natural spatial variation in the abundance of animal populations that can obscure contrasts between a control site (e.g., undisturbed) and a treatment site (e.g., disturbed). For example, if one simply contrasted the abundance of blue monkeys in K-30 (high density) and Mainaro (low density), it would be logical to conclude that agricultural encroachment leads to declines in blue monkey densities. However, by adding additional sites and through the distributional survey, it is evident that there is a general decline in blue monkey abundance as one travels from the north of the park to the south. This is a natural pattern that seems to be unrelated to human modification (Lwanga, 1987). Similar conflicting results would be found with red colobus and black-and-white colobus. Second, this study illustrates the importance of having before and after disturbance data, as well as the importance of careful selection of control sites. One approach that is commonly used in assessments is to contrast primate abundance in a human-impacted area with a neighboring control area that has not been altered [Struhsaker, 1975, 1997; Weisenseel, et al. 1993; Fimbel, 1994a,b; Plumptre & Reynolds, 1994a,b; Bennett & Dahaban, 1995]. The assumption is that the control and treatment areas had the same primate densities prior to

disturbance. The unlogged site at Kanyawara is only 3 km from the K-15 logged site and 9 km from the Sebatoli site. The general composition of the tree community at Sebatoli differs only modestly from that at Kanyawara [Chapman et al., 1997]. However, the density of red colobus at Sebatoli is approximately twice that of the K-15 site that was logged to a similar intensity, and the density of blue monkeys at Sebatoli is twice that of any other location. Clearly, in this case there is a confounding variable beyond that of disturbance regime, suggesting that control and treatment site should be selected to be as similar as possible before logging. Alternatively, one can collect data before and after a disturbance [Johns, 1986, 1988, 1992, 1997] or examine how population sizes change when a population is suspected to be recovering [Chapman et al., in press]. These sorts of studies may reveal more precise information, but this precision comes at the extremely high cost of long-term monitoring (i.e., more than 10 years). For some species, logging will not result in immediate death of individuals but may suppress reproduction. For such species it may take a number of years after logging before a significant decline in populations can be detected [Skorupa, 1988; Struhsaker, 1976, 1997]. Third, this study highlights the importance of long-term monitoring of populations. For example, we have no way of knowing if the estimated population densities in the southern corridor represent densities that the forest can support, or if they represent elevated densities resulting from immigration of animals into the remaining forest from degraded forest. Only by monitoring this population over the next decade will this become clear.

As with all censuses that attempt to estimate primate numbers over large areas, the reliance on the actual density values for particular species should be made with caution, since the calculations used will multiply any error. For example, if redtail monkey average group size at the Dura River was estimated at 25 instead of 18.4, it would change the estimate of the number of individuals in this section of the park by 12,529 animals. This can be further illustrated by comparing our estimate of densities in the section of Kibale represented by the Dura site to those of Struhsaker [1997] from the nearby Ngogo site. If, instead of using the Dura site to represent the area, we used an average of the Dura and Ngogo sites, and assumed that population sizes have not changed at Ngogo since Struhsaker's surveys (which J. Mitani et al. in unpublished data indicates is not the case), it would change the overall estimate of primate numbers in Kibale by only 1%. However, particular species would be affected dramatically (e.g., red colobus numbers would be estimated to be 14% greater). Considering these limitations, the best management tool will be to continue to monitor the areas, allowing the detection of relative changes over time.

The results obtained from this case study in Kibale suggest that incorporating degraded lands into management of primate populations may be an important conservation strategy. However, we should employ caution in generalizing these results. In Kibale, hunting of primates ceased in the early 1960's [Struhsaker, 1975; Skorupa, 1988]. This differs from many areas of Africa where hunting is a serious concern and tends to be associated with logging activities and agricultural encroachment [Wilkie et al., 1992, 1998; Fa et al., 1995; Chapman et al., 1999]. Even light levels of hunting can seriously affect species that have slow reproductive rates, such as chimpanzees. In addition, studies for other regions have reported findings that appear to conflict with the trends documented in Kibale. Plumptre & Reynolds [1994a] conclude that *C. mitis*, *C. ascanius*, and *C. guereza* benefit from heavy logging and arboricide treatment in Budongo Forest Reserve, Uganda. In Kibale heavy logging negatively affects all species, except *C. guereza*. [Struhsaker, 1975, 1997; Skorupa, 1988; Chapman et al., in press,

this study]. Similarly, mangabeys commonly occur in forest patches in Lopé, Gabon [Tutin et al., 1997], and blue monkeys often reside in patches near Budongo Forest Reserve Uganda [Fairgrieve, 1995], but neither of these species are found in the patches that surround Kibale [Onderdonk, 1998]. These contradicting findings call for more studies on effects of different types of disturbance on primates.

CONCLUSIONS

1. A detailed analysis of land use coverage of Kibale National Park, Uganda reveals that during the years of political and economic instability farmers encroaching into the area that is now National Park degraded 79 km^2 of forested land.

2. Distributional surveys at 24 sites and detailed line-transect censuses at six sites demonstrate that primate abundance in Kibale is high and that relationships between primate abundance and habitat disturbance are complex. Understanding the effect of disturbance on primate communities requires careful selection of control sites and documentation of primate abundance over a number of sites in the area.

3. Calculating the potential reduction in the primate populations that could have resulted from forest clearing and degradation clearly illustrates the importance of protecting land.

4. A review of the literature suggests that the biomass of primates in Kibale is high relative to other locations, illustrating the importance of Kibale to regional conservation.

ACKNOWLEDGMENTS

REFERENCES

Baranga, J. 1991. Kibale Forest Game Corridor: man or wildlife? In: Saunders DA, Hobbs RJ, editors. Nature conservation: the role of corridors. London: Surrey Beatty and Sons. p 371–375.

Bennett EL, Dahaban Z. 1995.Wildlife responses to disturbances in Sarawak and their implications for forest management. p 66–86. In: ecology, conservation, and management of southeast asian rainforests. Primack RB, Lovejoy TE, editors. New Haven: Yale University Press.

Boulière F. 1985. Primate communities: their structure and role in tropical ecosystems. Int J Primatol 6:1–26.

Brown S, Lugo AE. 1990. Tropical secondary forests. J Tropical Ecol 6:1–32.

Buckland ST, Anderson DR, Burnham KP, Laake JL. 1993. Distance sampling: estimating abundance of biological populations. London: Chapman & Hall.

Burnham KP, Anderson DR, Laake JL. 1980. Estimation of density from line-transect sampling of biological populations. Wildlife Monogr 72.

Butynski TM. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. Ecol Monogr 60:1–26.

Chapman CA. 1988. Patterns of foraging and range use by three species of neotropical primates. Primates 29:177–194.

Chapman CA. 1989. Ecological constraints on group size in three species of neotropical primates. Folia Primatol 73:1–9.

Chapman CA. 1990. Association patterns of

male and female spider monkeys: the influence of ecology and sex on social organization. Behav Ecol Sociobiol 26:409–414.

Chapman CA, Balcomb, S.R, Gillespie, T, Skorupa, J, Struhsaker, T.T. Long-term effects of logging on African primate communities: a 28 year comparison from Kibale National Park, Uganda. Conserv Biol, in press.

Chapman CA, Chapman LJ. 1996. Exotic tree plantations and the regeneration of natural forest in Kibale National Park, Uganda. Conserv Biol 76:253–257.

Chapman CA, Chapman LJ. 1999. Forest restoration in abandoned agricultural land: a case study from East Africa. Conserv Biol 13:1301–1311.

Chapman CA, Chapman LJ. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. Biotropica 29:396–412.

Chapman CA, Chapman LJ, Wrangham R, Isabirye-Basuta G, Ben-David K. 1997. Spatial and temporal variability in the structure of a tropical forest. African J Ecol 35:287–302, 1997.

Chapman CA, Fedigan LM, Fedigan L. 1988. A comparison of transect methods of estimating population densities of Costa Rican primates. Brenesia 30:67–80.

Chapman CA, Gautier-Hion A, Oates JF, Onderdonk DA. 1999. African primate communities: determinants of structure and threats to survival. In: Fleagle JG, Janson CH, Reed K, editors. Primate communities. Cambridge: Cambridge University Press, 1–37.

Chapman CA, Onderdonk DA. 1998. Forests without primates: primate/plant codependency. Am J Primatol 45:127–141.

Clutton-Brock TH. 1975. Feeding behaviour of red colobus and black and white colobus in East Africa. Folia Primatol 23:165–207.

Cords M. 1987. Forest guenons and patas monkeys: male-male competition in one-male groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 98–111.

Davies AG, Bennett EL, Waterman PG. 1988. Food selection by two southeast Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. Biol J Linnean Soc 34:33–56, 1988.

Defler TR, Pintor D. 1985. Censusing primates by transect in a forest of known primate density. Int J Primatol 6:243–259.

Eisenberg JF, Thorington, Jr RW. 1973. A preliminary analysis of a neotropical mammal fauna. Biotropica 5:150–161.

Estrada A, Coates-Estrada R. 1985. A preliminary study of resource overlap between howling monkeys (*Alouatta palliata*) and other arboreal mammals in the tropical rain forest of Los Tuxtlas, Mexico. Am J Primatol 9:27–37.

Fa JE, Juste J, del Val J.P, Castroviejo J. 1995. Impact of market hunting on mammal species in Equatorial Guinea. Conserv Biol 9:1107–1115.

Fairgrieve C. 1995. The comparative ecology of blue monkeys (*cercopithecus mitis stuhlmannii*) in logged and unlogged forest, budongo forest reserve uganda: the effects of logging on habitat and population density. Ph.D. dissertation. Edinburgh, Scotland: University of Edinburgh.

Fimbel C. 1994a. Ecological correlates of species success in modified habitats may be disturbance- and site-specific: the primates of Tiwai Island. Conserv Biol 8:106–113.

Fimbel C. 1994b. The relative use of abandoned farm clearings and old forest habitats by primates and a forest antelope at Tiwai, Sierra Leone, West Africa. Biol Conserv 70:277–286.

Galat G, Galat-Luong A. 1985. La communaute de primates diurnes de la foret de Tai, Cote d'Ivoire. Revue D'ecologia (Terre Et Vie) 40:3–32.

Ganzhorn JU. 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests: test of a hypothesis. Oecologia 91:540–547.

Ghiglieri MP. 1979. The socioecology of chimpanzees in kibale forest, Uganda. Ph.D. dissertation. Davis: University of California.

Ghiglieri, M.P. 1984. The chimpanzees of kibale forest. New York: Columbia University Press.

Glander K, Fedigan LM, Fedigan L, Chapman CA. 1991. Field methods for capture and measurement of three monkey species in Costa Rica. Folia Primatol 57:70–82.

Glanz WE. 1982. The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. In: Leigh, Jr EG, Rand AS, Windsor DM, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes.Washington, D.C.: Smithsonian Institution Press. p 455–468.

Hall JS, White LJT, Inogwabini B, Omari I, Simons Morland H, Williamson EA, Saltonstall K, Walsh P, Sikubwabo C, Bonny D, Kiswele KP, Vedder A, Freeman K. 1998. Survey of Grauer's gorillas (*Gorilla gorilla graueri*) and Eastern chimpanzees (*Pan troglodytes schweinfurthi*) in the Kahuzi-Biega National Park lowland sector and adjacent forest in Eastern Democratic Republic of Congo. Int J Primatol 19:201–235.

Hart TB, Hart JA, Hall J. 1996. Conservation in the declining nation state: a view from Eastern Zaire. Conserv Biol 10:685–686.

Harvey, P.H, Martin, R.D, Clutton-Brock, T.H. 1987. Life histories in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press, p 181–196.

Hashimoto C. 1995. Population census of the chimpanzees in the Kalinzu Forest, Uganda: comparison between methods with nest counts. Primates 36:477–488.

Howard PC. 1991. Nature conservation in uganda's tropical forest reserves. Gland, Switzerland: IUCN.

IUCN. 1987. IUCN directory of afrotropical protected areas. Gland, Switzerland: IUCN.

Johns AD. 1986. Effects of selective logging on the behavioral ecology of West Malaysian primates. Ecology 67:684–694.

Johns AD. 1988. Effects of "selective" timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. Biotropica 20:31–37.

Johns AD. 1992. Vertebrate responses to selective logging: implications for the design of logging systems. Philos Trans R Soc Lond B 335:437–442.

Johns AG. 1997. Timber production and biodiversity conservation in tropical rain forests. Cambridge: Cambridge University Press.

Jones WT, Bush BB. 1988. Darting and marking techniques for an arboreal forest monkey, *Cercopithecus ascanius*. Am J Primatol 14:83–89.

Kasenene JM. 1987. The influence of mechanized selective logging, felling intensity and gap-size on the regeneration of a tropical moist forest in the Kibale Forest Reserve, Uganda. Ph.D. dissertation. Michigan: Michigan State University.

Kelker GH. 1945. Measurement and interpretation of forces that determine populations of managed deer. Ph.D. dissertation. Ann Arbor, Michigan: University of Michigan.

Kingston B. 1967. Working plan for kibale and itwara central forest reserves. Entebbe, Uganda, Uganda Forest Department, 1967.

Klein LL, Klein D. 1997. Feeding behavior of the Columbian spider monkey, In: Clutton-Brock TH, editor. Primate ecology. London: Academic Press. p153–181.

Lanly JP. 1982. Tropical forest resources. Forestry Paper 30, Rome, Italy: United Nations Food and Agriculture Organization.

Lwanga JS. Group fission in blue monkeys (*Cercopithecus mitis stuhlmanni*): effect on the socioecology in Kibale Forest, Uganda. M.Sc. Thesis. Kampala, Uganda: Makerere University.

Marchesi P, Marchesi N, Fruth B, Boesch C. 1995. Census and distribution of chimpanzees in Cote D'Ivoire. Primates 36:591–607.

MISR (Makerere Institute for Social Research). 1989. Settlement in forest reserves game reserves and national parks. Kampala, Uganda: Makerere University Press.

Mittermeier, R.A, Cheney, D.L. 1987. Conservation of primates and their habitats. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 477–490.

Mittermeier RA, van Roosmalen MGM. 1981. Preliminary observations on habitat utilization and diet in eight Surinam monkeys. Folia Primatol 36:1–39.

National Environment Management Authority (NEMA). 1997. Kabarole district environment profile. Kampala, Uganda: NEMA.

National Research Council. 1981. Techniques for the study of primate population ecology. Washington, D.C.: National Academy Press.

Oates JF. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. Austral J Ecol 21:1–9.

Oates JF 1974. The ecology and behaviour of the black and white colobus monkey (*Colobus guereza* ruppell) in east africa. Ph.D. dissertation. London: University of London.

Oates JF, Davies AG, Delson E. 1996. The diversity of living colobines. In: Colobine monkeys: their ecology, behaviour and evolution. Davies AG Oates JF, editors. Cambridge: Cambridge University Press. p 45–73.

Oates JF, Whitesides GH, Davies AG, Waterman PG, Green SM, Dasilva GL, Mole S. 1990. Determinants of variation in tropical forest primate biomass: new evidence from West Africa. Ecology. 71:328–343.

Onderdonk DA. 1998. Coping with forest fragmentation: the primates of kibale national park, uganda. M.Sc. thesis. Gainesville, FL: University of Florida.

van Orsdol KG. 1986. Agricultural encroachment in Uganda's Kibale Forest. Oryx 20:115–117.

Osmaston HA. 1959. Working plan for the kibale and itwara forests. Entebbe, Uganda: Uganda Forest Department.

Peres CA. 1993. Structure and spatial organization of an Amazonian terre firme primate community. J Tropical Ecol 9:259–276.

Plumptre AJ, Reynolds V. 1994a. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. J Appl Ecol 31:631–641.

Plumptre AJ, Reynolds V. 1994b. the contribution of fruit eating primates to seed dispersal and natural regeneration after selective logging: Final report of ODA (R4738).

Plumptre AJ, Reynolds V. 1996. Censusing chimpanzees in the Budongo Forest, Uganda. Int J Primatol 17:85–99.

Plumptre AJ, Reynolds V. 1997. Nesting behavior of chimpanzees: implications for censuses. Int J Primatol 18:475–485.

Pope TR. 1996. Socioecology, population fragmentation, and patterns of genetic loss in endangered primates. In: Avise JC, Hamrick JL, editors. Conservation genetics: case histories from nature. New York: Chapman and Hall. p 119–159.

Raemaekers, J, Chivers, D.J. 1980. Socioecology of Malayan forest primates. In: Chivers DJ, editor. Malayan forest primates: ten years study in tropical rain forest. New York: Plenum Press. p 29–61.

Redford KH. 1992. The empty forest. Bioscience 42:412–422.

Richards PW. 1996. The tropical rain forest (2nd edition). Cambridge, England: Cambridge University Press.

Rodman PS. 1978. Diets, densities, and distributions of Bornean primates In: Montgomery GG, editor. The ecology of arboreal folivores. Washington, D.C.: Smithsonian Institution Press. p 465–478.

Skorupa JP. 1987. Do line-transect surveys systematically underestimate primate densities in logged forests? Am J Primatol 13:1–9.

Skorupa JP. 1988. The effect of selective timber harvesting on rain-forest primates in Kibale Forest, Uganda. Ph.D. dissertation: University of California, Davis.

Skorupa JP, Kasenene JM. 1984. Tropical forest management: can rates of natural treefalls help guide us? Oryx 18:96–101.

Struhsaker TT. 1975. The red colobus monkey. Chicago: University of Chicago Press.

Struhsaker TT. 1976. A further decline in numbers of Amboseli vervet monkeys. Biotropica 8:211–214.

Struhsaker TT. 1997. Ecology of an african rain forest: logging in kibale and the conflict between conservation and exploitation. Gainesville, Florida: The University Presses of Florida.

Struhsaker TT, Kasenene JM, Gaither Jr. JC, Larsen N, Musango S, Bancroft R. 1989. Tree mortality in the Kibale Forest, Uganda: a case study of dieback in a tropical rainforest adjacent to exotic conifer plantations. Forest Ecol Manage 29:165–185.

Struhsaker TT, Leland L. 1979. Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. p 158–228. In: Advances in the study of behaviour, Vol 9. Rosenblatt J, Hinde RA, Beer C, Busnel MC, editors. New York: Academic Press.

Symington M. 1988. Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. Am J Primatol 15:45–67.

Terborgh J. 1983. Five new world primates. Princeton: Princeton University Press.

Terborgh J. 1992. Diversity and the tropical rain forest. New York: Scientific American Library.

Terborgh J, van Schaik CP. 1987. Convergence vs. nonconvergence in primate communities. p 205–226. In: Organization of communities, past and present. Gee JHR, Giller PS, editors. Oxford, England: Blackwell Scientific Publications.

Thomas SC. 1991. Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. Biotropica 23:68–83.

Tutin CEG, Fernandez M. 1984. Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. Am J Primatol 6:313–336, 1984.

Tutin CEG, White LJT, Mackanga-Missandzou A. 1997. The use by rain forest mammals of natural forest fragments in an equatorial African savanna. Conserv Biol 11:1190–1203.

Uhl C. 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J Ecol 75:377–407.

Waser PM. 1987. Interactions among primate species. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: Chicago University Press. p 210–226.

Weisenseel K, Chapman CA, Chapman LJ. 1993. Nocturnal primates of Kibale Forest: effects of selective logging on prosimian densities, Primates 34:445–450.

White LJT. 1994. The effects of commercial mechanized selective logging on a transect in lowland rainforest in the Lopé Reserve, Gabon. J Tropical Ecol 10:313–322.

Whitesides GH, Oates JF, Green SM, Kluberdanz RP. 1988.

Estimating primate densities from transects in a West African rain forest: a comparison of techniques. J Anim Ecol 57:345–367.

Wilkie, D.S, Sidle, J.G, Boundzanga, G.C. 1992. Mechanized logging, market hunting, and a bank loan in Congo. Conserv Biol 6:570–580.

Wilkie DA, Curran B, Tshombe R, Morelli GA. 1998. Modeling sustainability of subsistence farming and hunting in the Ituri Forest of Zaire. Conserv Biol 12:137–147.

Wrangham, R.W, Chapman, C.A, Chapman, L.J. 1994. Seed dispersal by forest chimpanzees in Uganda. J Tropical Ecol 10:355–368.

Zanne AE. 1998. Expediting indigenous tree regeneration in African grasslands: plantations and the effects of distance and isolation from seed sources. M.Sc. thesis. Gainesville, Florida: University of Florida.