Long-Term Effects of Logging on African Primate Communities: a 28-Year Comparison From Kibale National Park, Uganda

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Abstract: *If logging is to be compatible with primate conservation, primate populations must be expected to recover from the disturbance and eventually return to their former densities. Surveys conducted over 28 years were used to quantify the long-term effects of both low- and high-intensity selective logging on the density of the five common primates in Kibale National Park, Uganda. The most dramatic exception to the expectation that primate populations will recover following logging was that group densities of* Cercopithecus mitis *and* C. ascanius *in the heavily logged area continued to decline decades after logging.* Procolobus tephrosceles *populations were recovering in the heavily logged areas, but the rate of increase appeared to be slow (0.005 groups/km² per year).* Colobus guereza *appeared to do well in some disturbed habitats and were found at higher group densities in the logged areas than in the unlogged area. There was no evidence of an increase in* Lophocebus albigena *group density in the heavily logged area since the time of logging, and there was a tendency for its population to be lower in heavily logged areas than in lightly logged areas. In contrast to the findings from the heavily logged area, none of the species were found at a lower group density in the lightly logged area than in the unlogged area, and group densities in this area were not changing at a statistically significant rate. The results of our study suggest that, in this region, low-intensity selective logging could be one component of conservation plans for primates; high-intensity logging, however, which is typical of most logging operations throughout Africa, is incompatible with primate conservation.*

Efectos de Largo Plaza de la Tala en Comunidades de Primates Africanos: Una Comparación de 28 Años en el Parque Nacional Kibale, Uganda

Resumen: *Si se espera que la tala sea compatible con la conservación de primates, se deberá esperar que las poblaciones de primates se recuperen de las perturbaciones y que eventualmente retornen a sus densidades previas. Utilizamos estimaciones llevadas a cabo a lo largo de 28 años para cuantificar los efectos a largo plazo de la tala selectiva tanto de baja como de alta intensidad en la densidad de los cinco primates comunes presentes en el Parque Nacional Kibale, Uganda. La mas dramática excepción a las expectativas de que las poblaciones de primates se recuperarían posteriormente a la tala fue el hecho de que las densidades de grupos de* Cercopithecus mitis *y* C. ascanius *en un área fuertemente talada continúan disminuyendo aún décadas después fuertemente taladas; sin embargo, la tasa de incremento parece ser lenta (0.005 grupos/km² por año).* Colobus guereza *aparenta estar bien en ciertos hábitats perturbados y fuéron encontrados en mas altas*

densidades de grupo en las áreas taladas que en las áreas no taladas. No hubo evidencia de un incremento en densidades de grupo de Lophocebus albigena *en las áreas altamente taladas a partir del tiempo de tala y se observó una tendencia en la densidad de sus poblaciones a ser más baja en áreas fuertemente taladas que en las áreas ligeramente taladas. En contraste con los resultados de las áreas altamente taladas, ninguna de las especies presentó densidades de grupo más bajas en las zonas ligeramente taladas que en las zonas sin tala, y las densidades de grupo en esta área no cambiaron a una tasa estadísticamente significativa. Los resultados de este estudio sugieren que en esta región la tala selectiva de baja intensidad podría ser un componente de los planes de conservación para primates; sin embargo, la tala de alta intensidad, que es típica en la mayoría de las operaciones de tala a lo largo de Africa, es incompatible con la conservación de primates.*

Introduction

Although they cover only 6% of Earth's arable surface, tropical forests account for nearly 50% of all known species (National Research Council 1992). The future of these highly diverse ecosystems is threatened by escalating rates of forest conversion and degradation (Johns & Skorupa 1987; Struhsaker 1987; Brown & Lugo 1990). Less than 5% of tropical forests are legally protected from human exploitation, and many of these legally protected areas are subjected to illegal exploitation (Redford 1992; Oates 1996; Chapman & Onderdonk 1998; Chapman et al. 1999*a*). 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 an increased risk of extinction when habitats are modified (Terborgh 1992) because national parks and reserves, even if effectively protected, cannot conserve species whose ranges do not fall within a protected area. As a result, conservation of many tropical forest species depends on the capacity of disturbed forests to support their populations. Because all forms of extractive exploitation result in biological loss and ecosystem change, knowledge of how particular species are affected by extraction and an understanding of their speed of recovery from disturbance are essential for developing sound conservation and management plans for disturbed forest habitats. The most prevalent form of disturbed forest habitat with conservation potential is selectively logged forest (Skorupa 1988; Frumhoff 1995; Struhsaker 1997).

Although a number of studies have examined the effects of selective logging on primate populations, the majority have been limited by methodological shortcomings. Some studies have been conducted soon after logging has occurred (Plumptre & Reynolds 1994; Bennett & Dahaban 1995; Ganzhorn 1995; Rao & van Schaik 1997) and may be inappropriate for examining the effect of logging on primate communities because habitat modification often lowers recruitment but does not usually kill primates (Struhsaker 1997). Thus, in many cases, declines in primate populations become evident only years after logging (Skorupa 1988). For example, Struh-

saker (1976) documented that it was nearly 10 years after the loss of approximately 90% of a major food resource that a statistically significant decline in vervet monkeys (*Cercopithecus aethiops*) at Amboseli, Kenya, could be detected. Most other studies have not had data on primate abundance from before and after logging and thus use neighboring unlogged sites to compare with the logged site (but see Grieser-Johns & Grieser-Johns 1995). This approach cannot take into account natural variation in primate abundance within undisturbed forest (Johns 1986; Chapman & Chapman 1999).

The generalizations that can be drawn from investigations of the effects of logging are limited because primate densities at the study sites are affected by confounding factors such as hunting (Mittermeier & Coimbra-Filho 1977; Wilkie et al. 1992, 1998; Oates 1996; Struhsaker 1997; Rosenbaum et al. 1998). Furthermore, few of these studies examine the effects of more than one intensity of logging on the primate community in question (but see Struhsaker 1975, 1997; Skorupa 1988). Studies examining the effects of variable intensities of logging over several decades, preferably with data collection before and after logging, are needed for researchers to discern how selective logging affects primate populations.

Our objective was to examine the long-term effects of selective logging on density of the five most common diurnal primate species of Kibale National Park, Uganda. To meet this objective, censuses were conducted over 28 years to (1) compare primate group densities between unlogged, lightly logged, and heavily logged areas and (2) evaluate the recovery of primate populations following logging. Most logging regimes call for some sort of rotation: the area is logged, left to recover for a specified period, often 30–50 years, and logged again. We suggest that if logged areas are to be compatible with primate conservation, primate populations must recover from the initial disturbance and return to their former densities over a period of time shorter than the typical period between logging rotations. Our investigation proposes explanations for similarities and differences in primate densities between unlogged, lightly logged, and heavily logged sites and suggests sustainable logging practices at Kibale and other similar forests.

Methods

Study Site

Kibale National Park ($766 km^2$) is located in western Uganda (lat $0°13'$–$0°41'$ N, long $30°19'$–$30°32'$ E) near the foothills of the Ruwenzori Mountains and contains moist evergreen forest (Struhsaker 1975, 1997; Skorupa 1988; Chapman et al. 1997; Chapman et al. 1999b). Mean annual rainfall (measured at Kanyawara) is 1664 mm (1974–1996); mean daily minimum and maximum temperatures are 15.5°C and 23.7°C (1990–1996).

Kibale forest received national park status in 1993, prior to which it was a forest reserve, gazetted in 1932, with the stated goal of providing a sustained production of hardwood timber (Osmaston 1959). A polycyclic felling cycle of 70 years was initiated, and it was recommended that logging open the canopy by approximately 50% through the harvest of trees >1.52 m in girth (Kingston 1967). This history of logging has led to varying degrees of disturbance among sites. We conducted our study in three areas, or forestry compartments, two of which had been logged to different intensities in the late 1960s and one of which was unlogged.

The K-15 forestry compartment is a 347-ha section of forest that experienced high-intensity, 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 (Skorupa 1988; Chapman & Chapman 1997). A total of 18 tree species were harvested, with 9 species contributing more than 95% of the harvest volume (Kasenene 1987; Skorupa 1988). Many of the tree species harvested provided primates with food. For example, of the 9 species that contributed more than 95% of the harvest volume, all were red colobus *Procolobus tephrosceles* food trees (Skorupa 1988; Struhsaker 1997).

Forestry compartment K-14, a 405-ha forest block, experienced low-intensity selective felling 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% of before-harvest volume. Approximately 25% of all trees in K-14 were destroyed by logging and incidental damage (Skorupa 1988; Struhsaker 1997).

The K-30 compartment is a 282-ha area that has not been commercially harvested. Prior to 1970, however, a few large stems (0.03–0.04 trees/ha) were removed by pitsawyers. This extremely low level of extraction seems to have had little effect on the structure and composition of the forest (Skorupa & Kasenene 1984; Skorupa 1988; Struhsaker 1997). Hence, compartment K-30 serves as a control plot for some of our comparisons. As a control, we are assuming that differences between the un-logged K-30 compartment and the logged compartments (K-14, K-15) are due only to the effects of logging. This is not ideal because some variation in primate density could be due to naturally occurring variation in forest structure (Chapman et al. 1997). These compartments, however, are arranged in a north-south continuous sequence (map in Struhsaker 1997), and there are few marked differences between the compartments in terms of physical characters that influence forest structure (e.g., slope), with the exception that K-15 has more swamp than K-30 (Struhsaker 1997). *C. guereza* are apparently more abundant near swamps.

Kanyawara has been protected from human exploitation since the 1970s, and the hunting of primates ceased in the region in the early 1960s (Struhsaker 1975; Skorupa 1988). The site's primates have been well studied, with close to 30 years of primate research and substantial background information on the majority of primate species present (Struhsaker 1997). For these reasons, a number of primate groups are habituated, encounter rate is high, and long-term data are available on several groups for most primate species.

Primate Density

Primate densities were assessed by line-transect method (Struhsaker 1975; National Research Council 1981; Defler & Pintor 1985; Skorupa 1987; Chapman et al. 1988; Whitesides et al. 1988; Weisenseel et al. 1993). 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).

We conducted primate censuses in each of the forestry compartments (K-30, K-14, K-15) from February 1980 to December 1981 (J.P.S.) and from July 1996 to June 1997 (C.A.C., S.R.B., and field assistants) and in the unlogged forestry compartment from August 1970 to October 1976 (T.T.S.). An effort was made to use equivalent census techniques in each of the time periods. Identical census routes were walked bi-weekly or monthly for each compartment in all periods censused (Table 1). Censuses were conducted between 0700 hours and 1400 hours at a speed of approximately 1 km per hour. Data collected for all census periods (except 1970–1974) included primate species observed, time of observation, straight-line distance between the animal and observer (visually estimated), and mode of detection. During the 1970–1974 censuses, observer-to-animal distance was not estimated; consequently, censuses during this time period were not used in calculations of group densities (45 census walks), but they were used in calculations of relative abundance. At the beginning of the 1996–1997 study, observers were trained together to estimate observer-to-animal distance. Variation among observers in sighting estimates was assessed at the end of

Table 1.   Characteristics of census routes used at Kibale National Park, Uganda, 1970–1976, 1980–1981, and 1996–1997.

	Unlogged			Lightly logged		Heavily logged	
	70–76	*80–81*	*96–97*	*80–81*	*96–97*	*80–81*	*96–97*
Route length (km)	4.0	4.0	4.0	3.6	3.6	4.0	4.0
Survey walks	61	28	25	27	23	26	24
Kilometers surveyed	245	112	100	97.2	82.8	104	96

the study. Although 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 their accuracy (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 pooled data from census areas where sighting distance did not differ (analysis of variance) and plotted the distance at 10-m intervals. This permitted us to estimate the animal sighting distance for each species. We 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; 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). The raw data were obtained for each sample period and analyzed by identical methods, so the density estimates differ from previously published estimates where methods differ (e.g., Skorupa [1988] corrected sighting distance for average group spread, whereas we did not make this correction).

To evaluate whether primate densities estimated for different time periods or forestry compartments were significantly different, we calculated the density of each species for each time the census route was sampled and used these as independent sample points. Nonparametric Kruskal-Wallis tests were used when three compartments or time periods were being compared. When significant differences were detected with this test, we used post-hoc Mann-Whitney tests to determine which

pairs of the categories differed (Day & Quinn 1989). When two time periods or forestry compartments were being compared, Mann-Whitney tests were used.

Relative Abundance

One of the reasons for calculating the width of the transect is to standardize the areas sampled by different observers at the different time periods. This is suggested to eliminate biases that could be caused by an observer's ability during one period to detect groups at different distances than a second observer at a subsequent period, such as might occur with changes in visibility due to logging or regeneration. But this does not address the possibility that there is interobserver variation in the ability of the observers to accurately estimate distance. We can evaluate the accuracy and reliability of distance estimations during one period (see above, Skorupa 1988; Struhsaker 1997), but we cannot evaluate them between time periods. To assess the possible errors in interpretations that this could cause, we calculated changes in a relative abundance measure: the number of groups seen per kilometer of census trail walked. This method does not take into account differences in visibility between periods or differences in the ability of the observers to detect animals, and does not correct for visibility differences between logged and unlogged compartments. In the heavily logged area, regeneration of the understory vegetation following logging has likely decreased visibility, and apparent decreases in primate abundance over time may in fact reflect decreases in visibility. We have no way of evaluating the ability of the different observers to detect primate groups. We calculated both group density and relative abundance because where both estimates agreed we could have more confidence that the trend observed was real.

Results

Primate Density

Over the three periods, 214 census walks were conducted over a total of 837 km (Table 1). In the 1980–1981 time period, higher group densities of *P. tephrosceles* were found in the unlogged and lightly logged areas than in the heavily logged areas (Table 2). In con-

Table 2. Mean group densities for primate species in three areas (unlogged, lightly logged, and heavily logged) of Kibale National Park, Uganda, during 1980–1981 and 1996–1997 census periods. [a]

	Group densities (groups/km^2)				
Species	*unlogged*	*lightly logged*	*heavily logged*	p[b]	*Post-hoc tests*[c]
1980–1981					
P. tephrosceles Red colobus	5.46	5.78	3.08	0.007	H < L & U
C. guereza Black and white colobus	0.89	3.31	4.81	<0.001	all sites differ
C. ascanius Redtail monkey	5.58	7.03	2.21	<0.001	H < L & U
C. mitis Blue monkey	2.53	2.06	1.71	0.224	
L. albigena Grey-cheeked mangabey	1.04	1.03	0.27	0.142	
1996–1997					
P. tephrosceles	5.50	4.35	4.43	0.265	
C. guereza	2.00	4.83	9.12	0.001	all sites differ
C. ascanius	4.83	11.48	1.04	<0.001	H < L & U
C. mitis	1.00	0.91	0.35	0.304	
L. albigena	1.13	2.41	0.87	0.065	

[a]*The values reported here differ slightly from those reported by Skorupa (1988) and Struhsaker (1975, 1997). These differences result from our recalculating the strip width from the original data collected based on the criteria outlined in our methods. This recalculation was necessary to ensure that the same methods were used to calculate strip width during all three time periods.*
[b]*Values based on Kruskal-Wallis test.*
[c]*Post-hoc tests reveal differences between pairs of sites (U, unlogged; L, lightly logged; H, heavily logged).*

trast, *C. guereza* group densities differed significantly between all sites, with the heavily logged area having more groups than the lightly logged area, which had more groups than the unlogged area. For *C. ascanius*, group density was higher in the unlogged and lightly logged areas than in the heavily logged areas. For *C. mitis* and *L. albigena* there were no significant differences between the areas, but these species both occur at low densities, so the power of this statistical test is low. For the 1996–1997 census period, the relationships among compartments were the same with two exceptions: *P. tephrosceles* abundance did not differ between the different areas, and *L. albigena* was found to be marginally more abundant in the lightly logged area than in the heavily logged area (Table 2).

We made comparisons within each forestry compartment among the three census periods (1974–1976, 1980–1981, and 1996–1997) to test the prediction that primate populations would increase in the logged areas over time. Except for *C. mitis*, all species showed no change in group density in the unlogged forest between the censuses (Table 3). *C. mitis* showed lower group densities during the 1996–1997 census than during the other two census periods. In the lightly logged forest, *L. albigena* showed marginally significant increases in group density between the 1980–1981 and 1996–1997 census periods. All other species showed no change in density between the 1980–1981 and 1996–1997 censuses. In the heavily logged forest, *C. guereza* showed a

marginally significant increase in group density between the 1980–1981 and 1996–1997 censuses, whereas *C. ascanius* and *C. mitis* populations declined between the 1980–1981 and 1996–1997 census periods. *L. albigena* showed no change in group density between the 1980–1981 and 1996–1997 censuses within the heavily logged area.

These comparisons make a number of assumptions likely to be true to varying degrees (see Struhsaker [1997] for a discussion of inherent problems of evaluating primate populations). Because of the difficulty of obtaining accurate counts of the number of individuals in each primate group during the line-transect censuses, researchers are forced to examine differences in group density and not individual density. Thus, it is typically assumed that the size of groups is equal between the areas being compared, but extensive documentation exists for intraspecific variation in group size (Chapman 1989; Struhsaker 1997). Detailed group counts in different areas of Kibale indicate that in general groups in logged areas are smaller than groups in unlogged areas (an average of 13.1% and 14.2% smaller for heavily and lightly logged areas, respectively; Table 4). Furthermore, Skorupa (1988) also documented that logging can affect the social system of a species. He noted that in heavily logged areas *P. tephrosceles* sometimes adopts a fission-fusion social organization in which a social group splits into small foraging subgroups that can be separated by several hundred meters. During a census, these subgroups

Table 3.   Mean group densities for primate species in the unlogged forest of Kibale National Park, Uganda, for each census period (1974–1976, 1980–1981, and 1996–1997) and for the lightly logged and heavily logged areas for the 1980–1981 and 1996–1997 censuses.[a]

Species	Densities (groups/km²)			p[b]	Post hoc[c]
	1974–1976	*1980–1981*	*1996–1997*		
Unlogged (K-30)					
P. tephrosceles	5.36	5.46	5.50	0.935	
C. guereza	0.91	0.89	2.00	0.390	
C. ascanius	3.80	5.58	4.83	0.528	
C. mitis	2.45	2.25	1.00	0.012	74,80 > 96
L. albigena	0.37	1.04	1.13	0.216	
Lightly logged (K-14)					
P. tephrosceles		5.78	4.35	0.196	
C. guereza		3.31	4.83	0.383	
C. ascanius		7.03	11.48	0.260	
C. mitis		2.06	0.91	0.304	
L. albigena		1.03	2.41	0.098	
Heavily logged (K-15)					
P. tephrosceles		3.08	4.43	0.678	
C. guereza		4.81	9.12	0.051	
C. ascanius		2.21	1.04	0.006	
C. mitis		1.71	0.35	<0.001	
L. albigena		0.27	0.87	0.715	

[a]*The values reported here differ slightly from those reported by Skorupa (1988) and Struhsaker (1975, 1997). These differences result from our recalculating the strip width from the original data collected based on the criteria outlined in our methods. This recalculation was necessary to ensure that the same methods were used to calculate strip width during all three time periods.*
[b]*For the unlogged forest p values are based on Kruskal-Wallis tests that examine whether there are differences between any of the populations across time. For the lightly and heavily logged forest, p values are based on Mann-Whitney tests that compare differences between time periods.*
[c]*Mann-Whitney U post-hoc tests were used to detect which pairs of years differ.*

would be considered separate groups. Groups in unlogged or lightly logged areas have not been seen to form such subgroups. Skorupa (1988) calculated that this bias would result in line-transect surveys overestimating *P. tephrosceles* density in logged areas by 25% (see also Struhsaker 1997).

Relative Abundance

Within the unlogged forest, significant differences existed between time periods for *P. tephrosceles, C. guereza*, and *L. albigena*, but the populations were not consistently decreasing or increasing (Table 5). These differences may be due to interobserver differences and/or to real changes. In contrast, *C. ascanius* and *C. mitis* showed fairly consistent declines in relative abundance since 1970. In the lightly logged forestry compartment, the relative abundance of *P. tephrosceles* declined significantly between the 1980–1981 and 1996–1997 censuses (there was also a decline in their abundance in the unlogged area at this time). In the heavily logged area the relative abundance of all species except *L. albigena* declined between the 1980–1981 cen-

Table 4.   Average group size in sections of Kibale National Park, Uganda, that have been logged to different intensities.[a]

Species (reference)	Unlogged	Heavily logged (% change)[b]	Lightly logged (% change)[b]
C. guereza			
(this study)	9.2	9.1 (−1.1)	9.7 (+5.4)
(Oates 1974; Skorupa 1988)	10.5	—	7.9 (−24.8)
P. tephrosceles			
(this study)	40	30 (−25.0)	41 (+2.5)
(Struhsaker 1975; Skorupa 1988)	50	—	47 (−6.0)
L. albigena			
(Olupot Unpub)	17.1	11 (−35.7)	13.5 (−21.1)
C. mitis			
(Butynski, 1990)	23.6	—	12.2 (−48.3)
Average percent change		−13.1	−14.2

[a]*Estimates of group size involve repeat counts of individually recognizable groups.*
[b]*The percent decrease (−) or increase (+) of the group size in that area from the unlogged forest.*

Table 5. Relative abundance of primates (number of groups seen per kilometer walked) in the unlogged forest of Kibale National Park, Uganda, for each census period (1970–1972, 1974–1976, 1980–1981, 1996–1997) and in the lightly logged and heavily logged areas for the 1980–1981 and 1996–1997 censuses.

Species	Relative abundance				p[a]	Post-hoc[b]
	1970–1972	*1974–1976*	*1980–1981*	*1996–1997*		
Unlogged (K-30)						
P. tephrosceles	0.960	0.813	1.063	0.56	<0.001	70,74 dif[c] 80,96
C. guereza	0.233	0.109	0.107	0.15	0.037	70>74, 80
C. ascanius	0.733	0.547	0.589	0.31	<0.001	70,74,dif[c] 80,96
C. mitis	0.443	0.391	0.366	0.08	<0.001	70,74 dif[c] 80,96
L. albigena	0.097	0.031	0.152	0.09	0.023	70<80
Lightly logged (K-14)						
P. tephrosceles			0.710	0.459	0.014	
C. guereza			0.504	0.314	0.093	
C. ascanius			0.525	0.556	0.944	
C. mitis			0.195	0.072	0.104	
L. albigena			0.113	0.181	0.169	
Heavily logged (K-15)						
P. tephrosceles			0.567	0.292	0.002	
C. guereza			1.144	0.542	<0.001	
C. ascanius			0.589	0.094	0.001	
C. mitis			0.337	0.021	<0.001	
L. albigena			0.048	0.073	0.78	

[a] *For the unlogged forest,* p *values are based on Kruskal-Wallis tests that examine whether there are differences between any of the populations across time. For the lightly and heavily logged forest,* p *values are based on Mann-Whitney tests that compare differences between time periods.*
[b] *Mann-Whitney* U *post-hoc tests are used to detect which pairs of years differ.*
[c] *There is a statistically significant difference.*

sus and the 1996–1997 census. The likely reason for this apparent decline is that visibility has declined in this area as the 2–3 m tall understory vegetation has become more dense.

Discussion

The significance of this study is not in documenting differences between logged and unlogged areas, many of which were reported in 1975 (Struhsaker 1975). Rather, it is in the fact that many of the differences found between the heavily logged and the unlogged areas have not diminished over the decades that the forest and primates have had to recover. If logging is to be compatible with primate conservation, primate populations must be expected to recover from the disturbance and eventually return to their former densities. The most dramatic exceptions to this expectation were that group densities of *C. mitis* and *C. ascanius* in the heavily logged area continued to decline decades after logging (Table 3). For *C. mitis*, however, this contrast must be interpreted with caution because their density also declined in the unlogged forest at this time. *P. tephrosceles* populations were recovering in the heavily logged areas, but the rate of increase appeared to be slow (0.005 groups/km² per year; Table 3). If one considers that the average group size in the unlogged area was 40 animals, whereas in the logged area groups contained on average 30 members,

populations in the unlogged area were still 65% larger than in the logged area (unlogged areas: 5.50 groups/km² × 40 individuals/group = 220 individuals/km²; logged: 4.43 groups/km² × 30 individuals/group = 133 individuals/km²). Considering Skorupa's (1988) observations that in heavily logged areas *P. tephrosceles* groups often split into small foraging subgroups, the difference between the logged and unlogged areas was likely even greater. *C. guereza* group density in the heavily logged forest was both higher than the unlogged forest (Table 2) and had increased since the surveys in the 1980s (Table 3). *C. guereza* group size differed by only 1% between unlogged and heavily logged areas. This could mean either that reproductive rates for *C. guereza* were higher in the logged forest than the unlogged forest or that *C. guereza* groups were moving into the logged forest because it is preferred habitat (e.g., more young leaves available due to increased light; Ganzhorn 1995). There was no evidence of an increase in *L. albigena* group density between the 1980–1981 and 1996–1997 censuses in the heavily logged area, and there was a tendency for their population to be lower in heavily logged areas. In addition, group size in the heavily logged area was 35.7% less than in the unlogged area and groups in these areas are known to regularly divide into small foraging subgroups (W. Olupot, unpublished data). Based on the capture of 31 male *L. albigena*, Olupot (unpublished data) documented that males in the logged areas weighed significantly less than males in the unlogged

area and suggested that logging negatively affects their body condition. Based on these results it seems logical to suggest that *L. albigena* in heavily logged areas may have reduced reproductive rates. In marked contrast to the findings from the heavily logged area, none of the species were found at a lower group density in the lightly logged area than in the unlogged area, and group densities in this area did not change at a statistically significant rate.

The analysis of relative abundance supported all of the differences indicated by analyses of group densities and also revealed additional differences between the census periods. These differences may depict real density changes, differences in visibility (which has likely occurred as the vegetation has changed), or differences in observer abilities. None of these possibilities are mutually exclusive. In the heavily logged area the relative abundance of all species except *L. albigena* declined between the 1980–1981 census and the 1996–1997 census. The most likely reason for this apparent decline is that visibility had declined in this area as understory vegetation became more dense. The changes in relative abundance in the unlogged and lightly logged area warrant further investigation, particularly the apparent consistent decline in *C. ascanius* between 1974 and 1997 in the unlogged forest and the decline in *P. tephrosceles* in the lightly logged and unlogged areas between 1980 and 1997. (Similar declines in *P. tephrosceles* have been documented at a site 12 km south, J. C. Mitani, T.T.S., and J. S. Lwanga, unpublished data.) Research is particularly critical for *P. tephrosceles*, which is an endangered species of critical concern because its distribution is patchy. Long-term monitoring of known groups would provide the most detailed and useful information about how these populations are changing.

With studies such as this one, it is difficult to conclusively attribute any documented changes to the effects of logging. Because primates are long-lived and population responses are slow, investigations of the effect of logging must be conducted over biologically relevant time scales (i.e., decades). Over such lengthy periods, however, the environment in the control site will not necessarily be stable. In Kibale, for example, there is evidence that the tree community in the unlogged area has changed over the last few decades. To examine temporal variation in the tree composition over a 20-year period, Chapman et al. (1997) replicated a sampling regime that was carried out in the early 1970s on the floristic composition of the unlogged site we studied. Although no human intervention occurred in this area between the early 1970s and 1992, there were marked changes in the densities of some tree species. Twenty-seven percent of the identified species increased in abundance, 33% decreased, and 40% remained relatively unchanged. Not only could the forest of control sites be changing, but primate abundance could be affected by

factors other than logging and forest regeneration. The explicit assumptions being made when a logged site is contrasted to an unlogged control site is that the unlogged population is at equilibrium and that the logged population is either at equilibrium or increasing in step with forest regeneration. Diseases and parasites, however, can clearly cause short-term reductions in population size (Collias & Southwick 1952; Work et al. 1957). For example, yellow fever was implicated as the cause of a 50% decline in the howler monkey (*Alouatta palliata*) population on Barro Colorado Island, Panama, between 1933 and 1951 (Collias & Southwick 1952; Milton 1996). As with disease, there is evidence that predators can cause a severe temporary reduction in population size. Isbell (1990) documented a substantial increase in the rate of predation by leopards on vervet monkeys in Amboseli National Park, Kenya. Between 1977 and 1986, the average vervet monkey predation rate was at least 11%, whereas in 1987 this rate increased to at least 45%. The general decline in *C. mitis* documented in our study in all compartments suggests that their populations are not at equilibrium. Similarly, red colobus numbers at some sites in Kibale may be temporarily below carrying capacity due to disease (Chapman & Chapman 1999). Finally, when a study spans a number of decades there are always methodological considerations that limit one's ability to attribute change in primate populations to logging. The clearest example of this is when we compared relative abundance of primates in the heavily logged habitat over time; the abundance of most species appeared to decline.

For studies such as ours to be valuable from a conservation or management perspective, they must support generalizations that can be accurately applied to a number of species in many regions. Unfortunately, our ability to generalize about the effects of selective logging on primates is limited. This is because few studies have examined the effect of selective logging on primate communities, and many of the studies that have done so have employed different methods or do not adequately report their methods (Johns 1997). Furthermore, studies vary with respect to extraction regimes and incidental damage levels (Johns 1988, 1992; Wilkie et al. 1992; White 1994; Struhsaker 1997), original composition of the primate communities (Struhsaker 1975; Bennett & Dahaban 1995), proximity to undisturbed refugia and recolonization sources (Bierregaard et al. 1992; Fimbel 1994a, 1994b), and length of time between logging and monitoring of the primate populations (Struhsaker 1997). In addition, access provided by the logging operation may have increased the level of hunting (Wilkie et al. 1992; Bennett & Dahaban 1995; Fa et al. 1995; Oates 1996; Struhsaker 1997). Such variability between investigations can produce divergent results, even when similar communities are involved and the areas are in close proximity. Two studies in Southeast Asia clearly illus-

trate this point (Johns 1992; Bennett & Dahaban 1995). Johns (1992) studied the effects of logging on animal populations in dipterocarp forests in Peninsular Malaysia, whereas Bennett and Dahaban (1995) addressed the same questions in dipterocarp forests in Sarawak. The intensity of logging was similar in the two regions. Fifty-four percent of the trees of at least 10 cm dbh (diameter at breast height) were removed or destroyed in Sarawak (Bennett & Dahaban 1995), and in Peninsular Malaysia extraction destroyed 51% of the trees (Johns 1992). In Sarawak the logging resulted in a 35–70% decline in the gibbon (*Hylobates muelleri*) and langur (*Presbytis*) populations (Bennett & Dahaban 1995). In contrast, the survival of the same genera in peninsular Malaysia was much greater, ranging from a 10% decline to a 74% increase (Johns 1983). Bennett and Dahaban (1995) attribute the differences between their study and that of Johns (1983, 1986, 1992) to the nutrient-rich soils, initially high primate density, and virtual absence of hunting in peninsular Malaysia, conditions different from those in Sarawak. Furthermore, the responses of these communities to logging may also reflect differences in the length of time it takes different species to respond to habitat change. For instance, breeding of all four monkey species in West Malaysia was depressed 6 years after logging (Johns 1992). Such a decline may have occurred more rapidly at the site studied by Bennett and Dahaban (1995).

The population declines associated with logging are probably caused at least partially by a reduction in food availability (Skorupa 1988; Oates 1996). For primates, reduction in food availability has been documented to lead to increased infant and juvenile mortality (Struhsaker 1976; Altmann et al. 1977; Dittus 1977; Skorupa 1988). Several studies suggest that low-intensity logging (5–20% of trees destroyed) can be compatible with primate conservation (Johns & Skorupa 1987; Skorupa 1988; Ganzhorn 1995; Oates 1996; Struhsaker 1997). For example, Ganzhorn (1995) demonstrated that low-intensity logging of forest in Madagascar (affecting <10% of the forest surface) corresponds with an increase in abundance of all lemur species (significantly so for three out of seven species). This increase was associated with increased exposure of the remaining trees to sunlight, which led to an increase in the abundance of fruit that could be used by the frugivorous lemurs and an increase in the quality of the leaves eaten by the folivorous species. In areas that are heavily logged, such changes may not be evident, and intense logging may be incompatible with primate conservation. For example, Skorupa (1988) demonstrated that in Kibale the annual fruiting intensity was 26% lower in heavily logged forest than in unlogged forests.

Although the importance of food resources is clear, it seems likely that a number of other variables will covary with a decline in food availability. For example, removing food trees through logging will also open the canopy, thereby reducing potential canopy pathways and increasing energetic demands, risk of falling, and perhaps risk of predation (Marsh et al. 1987; Gebo & Chapman 1995). Furthermore, reduction of food availability associated with logging may decrease animals condition and increase their vulnerability to disease or parasites (Milton 1996).

It was surprising to find that 28 years after logging the densities of two of the frugivorous-insectivorous primate species (*C. ascanius* & *C. mitis*) were still declining in the heavily logged area. This suggests that for these species the quality of this heavily logged area is decreasing, not increasing as expected. Chapman and Chapman (1997) quantified forest regeneration in the same Kibale forest compartments we examined 25 years after logging. The lightly logged compartment had annual increases in dbh equivalent to those of the unlogged area for small tree classes and showed elevated growth rates among large tree classes. In contrast, growth rates in the heavily logged forest were lower than those for the unlogged area. In addition, tree density for all size classes was lower and seedling mortality was higher for the heavily logged area than for the unlogged area. Death rates of trees >10 cm dbh in the heavily logged area were higher than for any other area (see also Kasenene 1987; Skorupa 1988). Thus, it appears that recruitment and growth processes are following a different trajectory for the heavily versus the lightly logged sites, and it is not unreasonable to speculate that the quality of the heavily logged area is actually decreasing for *C. ascanius* and *C. mitis.* Because of a lack of aggressive colonizing tree species, the presence of an aggressive herb community, and increased elephant activity in areas with large canopy gaps, heavily logged areas at Kibale appear to be slow to regenerate and often seem to remain in a state of arrested development (Struhsaker et al. 1996; Chapman & Chapman 1997; Struhsaker 1997; Chapman et al. 1999*b*).

The results of our study suggest that in this region low-intensity selective logging could be one component of conservation plans for primates, whereas heavy logging is incompatible with primate conservation. This is encouraging because it suggests that conservation biologists could work with foresters to make conservation advances in the extensive area outside national parks. The general applicability of our suggestions, however, needs to be verified through further investigations. Our findings may be specific to Kibale (e.g., the nature of the regeneration), or they may be strongly influenced by specific uncontrolled factors. For example, the lightly logged area abutted the unlogged area, and this proximity may have facilitated regeneration or allowed animals to make excursions into this area at stressful times. Future studies may lead to recommendations regarding how to form a mosaic of logged and unlogged areas or how to leave unlogged forest islands within a logged landscape.

Such considerations and difficulties in comparing the findings from Kibale to the findings at other sites indicate that our understanding of how primates respond to timber harvests of different intensity is in its infancy. Our comprehension of how logging practices and forest regeneration influence primate densities will be improved by more long-term studies of the issue at a greater number of sites and detailed studies of the regeneration of the plant community after different intensities of harvest.

Acknowledgments

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