Behavioral Patterns of Colobus in Logged and Unlogged Forests

The Conservation Value of Harvested Forests

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INTRODUCTION

Although tropical forests cover only 6% of Earth's arable surface, they account for nearly 50% of all known species (National Research Council, 1992). Despite this diversity, these systems are increasingly threatened, as exemplified by a recent Food and Agriculture Organization report (FAO, 1999) which indicates that tropical countries are losing 127,300 km^2 of forest annually; this does not consider the vast area being selectively logged (~55,000 km^2; FAO, 1990) or the forests degraded by fire (Laurance, 1999; Nepstad *et al.*, 1999;

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Chapman & Peres, 2001). Furthermore, many tropical species are locally endemic or rare and patchily distributed (Struhsaker, 1975; Richards, 1996). Such restricted distributions predispose many species to increased risks of extinction (Terborgh, 1992) since they are less likely to be found inside national parks and reserves. As a result, conservation of many tropical forest species will depend on the capacity of disturbed forests to support their populations. Since 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 the mechanisms leading to this response are essential for developing sound conservation and management plans for disturbed forests. The most prevalent form of disturbed forest with conservation potential is selectively logged forest (Frumhoff, 1995; Struhsaker, 1997).

Primates are valuable subjects for examining the effects of logging. Most species are relatively easy to census and a great deal is known about their natural history. Furthermore, many primate species are endangered or threatened, making it critical that threats to their survival are better understood. Unfortunately, deriving generalizations about how primate populations respond to logging has proven to be difficult. Although a number of studies have examined the effects of selective logging on primate populations, the strength of the conclusions drawn is questionable. First, some studies were conducted soon after logging occurred (Plumptre & Reynolds, 1994; Bennett & Dahaban, 1995; Ganzhorn, 1995; Rao & van Schaik, 1997). Such studies may be inappropriate for examining the impact of logging on primate communities since habitat modification often lowers recruitment but does not usually kill primates (Struhsaker, 1997). Thus, in many cases, declines in primate populations will not appear until years after logging has occurred. Most other studies have not had data on primate abundance from before and after logging, and thus use neighboring unlogged sites to contrast to the logged site (for an exception, see Grieser Johns & Grieser Johns, 1995). This approach suffers by not taking into account natural variation in primate abundance within undisturbed forest (Johns, 1986; Chapman & Chapman, 1999). In addition, primate densities at many study sites are affected by confounding factors such as hunting (Wilkie et al., 1992, 1998; Oates, 1996; Struhsaker, 1997; Rosenbaum et al., 1998).

Primate studies have illustrated that variability in factors such as the intensity of timber extraction, associated hunting pressure, the nature of the habitat being studied, and even the methods used to conduct the study can lead to divergent results. As such, it is difficult to modify management plans based on existing

studies. Two studies exemplify this divergence of results. Johns (1992) studied the effects of logging on animal populations in dipterocarp forests in Peninsular Malaysia, while Bennett and Dahaban (1995) addressed the same question in dipterocarp forests in Sabah. The intensity of logging was similar in the two regions. In Sabah, the logging produced an immediate 35–70% decline in the gibbon (*Hylobates muelleri*) and langur populations (*Presbytis* spp.; Bennett & Dahaban, 1995). In contrast, survival of the same genera in Peninsular Malaysia was much greater (10% decline to an increase of 74%; Johns, 1983). Bennett and Dahaban (1995) attribute the differences between their study and that of Johns (1983, 1992) to the nutrient-rich soils, initial high primate density, and virtual absence of hunting in Peninsular Malaysia, conditions quite different from those in Sabah.

As a second example, blue monkeys (*Cercopithecus mitis*) appeared to be severely impacted by logging at Kibale National Park, Uganda. Fifteen years after logging, areas had 20–30% fewer blue monkeys than unlogged areas (Skorupa, 1988), and this pattern continues to become more extreme to this day (Chapman *et al.*, 2000). In contrast, in Budongo Forest Reserve, Uganda, blue monkeys are 3.7 times more abundant in logged areas than in unlogged areas (Plumptre & Reynolds, 1994).

One might argue that examples such as these are simply exceptions to general trends, and, if good comparative methodologies were employed across a range of species and study sites, patterns would emerge. Johns and Skorupa (1987) attempted such a test with 37 primate species having populations from both undisturbed and disturbed habitats. They discovered that 44% of the variation in species' responses to moderate habitat disturbance could be accounted for by body size and dietary considerations. Body size and degree of frugivory were both negatively correlated with survival ability in degraded habitats. However, they concluded that while this relationship was statistically significant, it provided an insufficient basis to reliably predict how specific species would respond to disturbance. Unfortunately, it is these kinds of predictions that forest managers must make. The strongest suggestion that this comparative study was able to make was that large-bodied frugivores are the class of primates most vulnerable to habitat disturbance, and three examples were presented: *Ateles*, *Pan*, and *Pongo* (Johns & Skorupa, 1987). Unfortunately, if one looks closely at descriptions of even these three species, exceptions are evident. For example, an *Ateles geoffroyi* population has been described to be relatively abundant in a severely degraded area that was both intensively logged and grazed by cattle

(Chapman *et al.*, 1989). Similarly, *Pan troglodytes* groups are known to survive in areas that have been logged and almost totally converted to agriculture (Onderdonk & Chapman, 2000). These chimpanzees appear to survive by traveling between the few small remaining forest patches and by raiding crops planted by local farmers (Naughton-Treves, 1996).

As a result, predicting the effect of logging on particular primate species has proven difficult. On the basis of this perspective, the objective of this paper is to use a comparison of the behavior of the black-and-white (*Colobus guereza*) and red colobus (*Procolobus badius*) in logged and unlogged areas of Kibale National Park, Uganda, to provide insights into responses to logging. We selected these two species because they appear to respond differently to logging, while there are theoretical reasons to suggest that their biomass is determined by the same factors. The density of red colobus in a heavily logged area of Kibale was approximately half that of an adjacent unlogged area a decade after logging, while there were 5 times more black-and-white colobus in this logged area than in the unlogged area (Skorupa, 1988; Struhsaker, 1997; Chapman *et al.*, 2000). This difference exists despite the fact that these two colobus species are of similar size (red colobus and black-and-white colobus both weigh 8.8 kg; Struhsaker and Leland 1979), have similar locomotory patterns (Gebo & Chapman, 1995), have similar day ranges (red colobus 648 m/day, black-and-white colobus 535 m/day; Struhsaker & Oates, 1975), and have similar diets (Chapman *et al.*, 2000a,b). Furthermore, the two species respond differently to logging despite the fact that the biomass of both species can be predicted by the protein-to-fiber ratios of potential foods at sites within the park (Chapman *et al.*, 2000). Since the tree species that first colonize after logging have higher protein-to-fiber ratios than forest species, the response of the red colobus is not expected (Chapman *et al.*, 2005).

Here we contrast the activity budgets, travel costs, percentage of time in mixed-species groups, and diet between two groups of each species in unlogged forest and one group in the logged forest. We consider two groups in the unlogged forest to provide a better understanding of the natural variation that can exist in the variables considered. In the unlogged forest, we selected groups that varied in size, since many of the parameters we were contrasting are known to vary as a function of group size. This comparison is conducted approximately 30 years after the logging was completed. Most logging regimes call for some sort of rotation: the area is logged, it is left to recover for a specified period, often 30–50 years, and then it is logged again. We suggest that if logged areas are to be

compatible with primate conservation, primate populations must recover from the initial disturbance, and their behavioral patterns should be similar prior to the time that the area would be scheduled to be reharvested. If a similar comparison was conducted at some time prior to this (i.e., only a few years after logging), it is likely that the findings would differ from those reported here.

METHODOLOGY

Study Site

Kibale National Park (795 km^2) is located in western Uganda (0°13′–0°41′ N and 30°19′–30°32′ E) near the foothills of the Ruwenzori Mountains (Struhsaker, 1975, 1997; Skorupa, 1988; Chapman et al., 1997). The park consists of mature, midaltitude, moist semideciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and plantations of exotic trees (Chapman & Lambert, 2000). Mean annual rainfall in the region is 1749 mm (1990–2001, or 1547 mm for 1903–2001); the mean daily minimum temperature is 14.87°C, and the mean daily maximum temperature is 20.18°C (1990–2001). There are distinct wet and dry seasons that are bimodal in distribution. May to August and December to February tend to be drier than other months (Chapman et al., 1999).

We contrasted the behavior of groups of both species living in areas that had been heavily logged to groups in an unlogged section of forest. The logged forest experienced heavy selective felling in 1969. The harvest averaged 21 m^3/ha or approximately 7.4 stems/ha (Skorupa, 1988; Struhsaker, 1997). Incidental damage in the area was high, and it is estimated that approximately 50% of all trees were destroyed by logging and incidental damage (Skorupa, 1988). The unlogged area had not been commercially harvested; however, prior to 1970, a few large stems (0.03–0.04 trees/ha) were removed by pit-sawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa, 1988; Struhsaker, 1997).

Censuses conducted over a 17-year period have been used to quantify the long-term effects of high-intensity selective logging on the density of the five common primates in these areas (Chapman et al., 2000). Red colobus populations were recovering in the heavily logged areas; however, the rate of increase appeared to be slow (0.005 groups/km^2 per year). Black-and-white colobus appeared to do well in some disturbed habitats and were found at higher group

densities in the logged areas compared to the unlogged area. Group densities of blue monkeys (*Cercopithecus mitis*) and redtail monkeys (*C. ascanius*) in the heavily logged area were low and continued to decline decades after logging. There was no evidence of changes in mangabey (*Lophocebus albigena*) group density in the heavily logged area since the time of logging.

Behavioral Observations

Behavioral observations were made 4 days each month on two groups of each species in the unlogged forest between August 1998 and June 1999 (except March). The black-and-white colobus groups were of similar size (Group 1 = 9, Group 2 = 6), while the red colobus groups differed substantially in size (Group 1 = 48, Group 2 = 24). The groups are subsequently called the big and small groups. This sampling resulted in approximately 650 h of observations on black-and-white colobus, and 700 h of observations on red colobus. One group of each species was observed in the logged area for 5 days a month between July 1999 and May 2000 (except July and August, when they were watched for 4 days), producing approximately 500 h of observations for each species. The red colobus group contained 34 individuals, while the black-and-white group contained 7 individuals.

During each half hour, the observer was with the group, five point samples were made of different individuals. If the animal was feeding, the species and plant part (e.g., fruit, young leaf, and leaf petiole) were recorded. We made an effort to avoid repeatedly sampling particularly conspicuous animals by moving throughout the group when selecting subjects and by sampling animals that were both in clear view and those that were more hidden. At the end of each half hour, we estimated the distance the group had traveled and the group spread, and we determined if the group was in association with other primates. Distance traveled was estimated as the straight-line distance between the center of mass of the group in the previous 30-min sample to the current center of mass. Distance estimations were assisted by travel routes plotted on detailed trail maps in which trails were only 50–100 m apart. Given that it was sometime difficult to locate groups predawn, data was often not recorded until 0730 or 0800 h. As a result, daily distance traveled was calculated as the distance moved between 0800 and 1700 h. Days when follows were shorter than this (e.g., groups could not be found until after 0800 h) were excluded from the analysis. Group spread was estimated by having one observer frequently walk from the

perceived center of mass of the group to where no additional animals could be seen. The observer would walk perpendicular to the direction of group travel. If the study group was within 50 m of another primate species, it was considered to be in a mixed-species association.

These behavioral observations were conducted by CC, Lauren Chapman, and a team of three Ugandan field assistants. The field assistants have worked with CC and LC since 1990 and knew the tree species and monkey age classes prior to the start of the project. The field assistants were supervised by CC and LC when they were in the field and in their absence by project directors. Detailed training was conducted prior to when a new observer started recording data. Subsequent to this training, interobserver reliability was assessed by having the new individual observe the activity of the same animal being watched by CC (all assistants and volunteers). The first 30 foraging bouts for new observers agreed with those of CC in >97% of the occasions (range = 97–100%, mean = 98.8%). In those instances where there were disagreements, they typically occurred with respect to assessing the stage of maturity (i.e., ripe versus unripe fruit or mature vs. young leaves, particularly for *Celtis africana*—a species with small leaves).

Food Tree Density

To evaluate if the groups in the logged area used foods that were less preferred than groups in the unlogged area, the density of food trees was estimated by establishing four permanent vegetation plots (200 by 10 m) in the home range of the study groups. Each tree with a diameter at breast height (DBH) >10 cm within 5 m of each side of the trail was individually marked with a numbered aluminum tag and measured (DBH).

Statistical Evaluations

We constructed monthly profiles of behavioral variables (i.e., activity budgets, proportion of time in mixed-species groups, distance traveled, group spread, and dietary profiles (i.e., % of scans eating different plant parts) and con-trasted groups in logged and unlogged areas using one-way analysis of variance, with each month considered as an independent sample. Where appropriate we arcsine-square-root-transformed proportional data. In addition to this analysis, we attempted to control for seasonal variation by pairing samples by month and

contrasting groups using a paired t-test. Since mixed-species association with a particular species was often rare and 4–5 days of observations were made each month, the sample size was not thought to be sufficient to accurately depict particular associations. Hence, for analysis of mixed-species associations, only the overall level of association is compared statistically (i.e., time in association with any primate).

RESULTS

For both species there were significant differences among groups in the amount of time spent feeding and traveling, while the amount of time resting did not differ (Figure 1, statistical comparisons in the figure legend). However, in all cases, the activity level of the groups in the logged area was intermediate between the two groups observed in the unlogged area. Thus, the differences in activity budgets cannot be attributed to the effects of logging. When we controlled for seasonal variation in activity pattern by pairing samples by month and contrasting groups using a paired t-test, for both species there were the same number of significant differences between the groups in the logged and unlogged areas as between the two groups in the unlogged area. This supports the previous analysis and suggests that observed differences in activity budgets cannot be attributed to the effects of logging.

The average distance traveled each day between 0800 and 1700 h by the different groups revealed similar, but not identical, patterns to the time spent traveling. For red colobus ($F = 21.65$, $P < 0.001$), the group in the logged forest (mean distance = 123 m) traveled less than the large group in the unlogged forest (232 m), and the small group in the unlogged forest (142 m) traveled shorter distances each day than the large group in the unlogged forest ($P < 0.001$ in all cases). However, there was no significant difference between the group in the logged forest and the small group. For black-and-white colobus ($F = 7.32$, $P = 0.001$), the large group in the unlogged forest (138 m) traveled farther than either of the other groups (unlogged small 83 m, $P = 0.01$, logged 83.5 m, $P = 0.003$).

Group spread differed among all groups for both species (black-and-white colobus, $F = 194.6$, $P < 0.001$; red colobus, $F = 254.03$, $P < 0.001$). The large groups in the unlogged area (black-and-white colobus 21.0 m, red colobus 63.5 m) were more spread out than small groups in the unlogged area (17.0 m, 47.8 m) or the groups in the logged area (12.0 m, 39.5 m). The small groups in
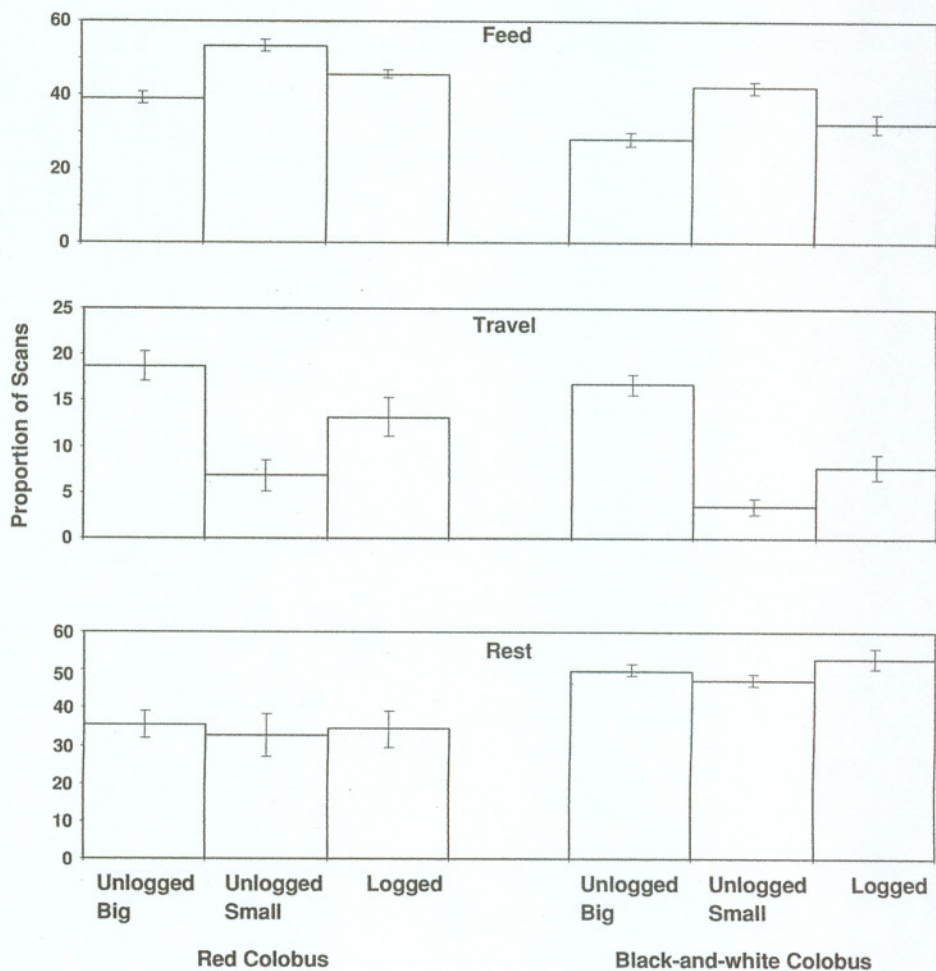
Figure 1. The average proportion of scans each month (+SE) that groups of red colobus and black-and-white colobus in Kibale National Park, Uganda, spent engaged in feeding, resting, and traveling. Black-and-white colobus: Feeding $F = 11.91$, $P < 0.001$, Scheffe post hoc tests logged versus unlogged big $P = 0.344$, logged versus unlogged small $P = 0.008$, unlogged big versus unlogged small $P \leq 0.001$; Travel $F = 30.49$, $P < 0.001$, Scheffe post hoc tests logged versus unlogged big $P ¡ 0.001$, logged versus unlogged small $P = 0.048$, unlogged big versus unlogged small $P ¡ 0.001$; Rest $F = 2.15$, $P = 0.137$. Red colobus: Feeding $F = 20.29$, $P < 0.001$, Scheffe post hoc tests logged versus unlogged big $P = 0.018$, logged versus unlogged small $P = 0.006$, unlogged big versus unlogged small $P \leq 0.001$; Travel $F = 9.64$, $P = 0.001$, Scheffe post hoc tests logged versus unlogged big $P = 0.121$, logged versus unlogged small $P = 0.072$, unlogged big versus unlogged small $P = 0.001$; Rest $F = 0.84$, $P = 0.442$.
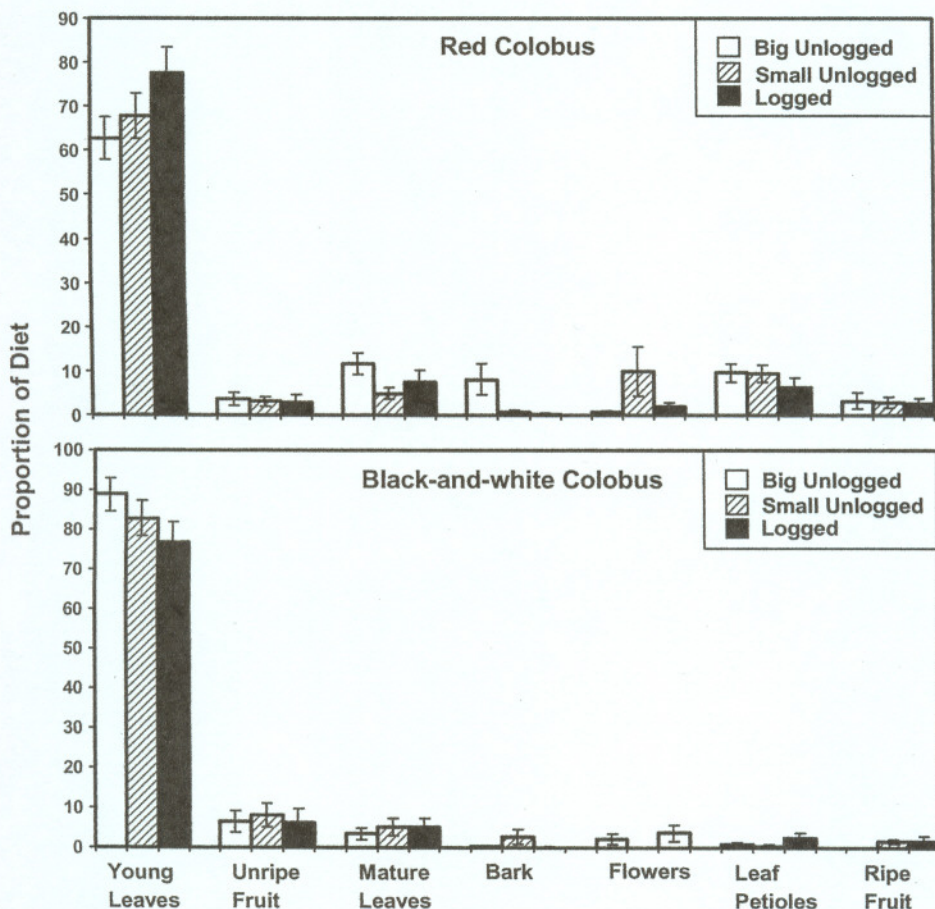
Figure 2. The average proportion of foraging scans each month (+SE) that groups of red colobus and black-and-white colobus in Kibale National Park, Uganda, spent eating different plant parts. Black-and-white colobus nonsignificant in all comparisons. Red colobus nonsignificant in all comparisons, except bark $F = 4.22$, $P = 0.023$.

the unlogged forest had a smaller group spread than the groups in the logged area (Scheffe, $P < 0.001$ for both species).

There were no differences in the diets of the different groups of black-and-white colobus in terms of the plant parts eaten ($P > 0.122$; Figure 2). All groups relied most heavily on young leaves (77–82% of all foraging scans). In contrast, there were differences in the diets of the red colobus among groups. The large group of red colobus in the unlogged area spent more time eating bark (primarily *Prunus africana*) than either of the other groups ($F = 4.218$, $P = 0.023$). Similarly, there was a marginal difference in the time spent eating

young leaves between the large group in the unlogged area and the group in the logged area, with the group in the logged area spending more time eating young leaves. Since young leaves are nutritionally one of the best foods that red colobus eat (Chapman & Chapman, 2002), this difference does not suggest that the group in the logged area is eating poorer quality food. In contrast, this may represent a cost associated with large group size in red colobus (Gillespie & Chapman, 2001).

Given the heterogeneity in forest composition of tropical forests over short spatial scales, it is not surprising that the diets of the different groups differed with respect to the species and part consumed (Table 1). For all groups, *Celtis durandii* and *Celtis africana* young leaves were frequently eaten as these species were two of the top four most eaten items for all groups and the top two for 4 of the groups. *Celtis durandii* seems to be most important as it remained the top food for 5 of the 6 groups despite its density decreasing to one-third the unlogged value in the logged forest. Other than these two species, it is difficult to determine how logging altered the diet selection and preference of the animals. For example, while *Olea welwitschii* was one of the species targeted in the logging operation, its current density in the logged and unlogged areas are the same (1.3 individuals/ha). Despite the fact that its density is equivalent in both areas, the red colobus groups in the unlogged area never or rarely ate this tree's young leaves, while the group in the logged area fed on its young leaves extensively (7.8%, Table 1). The density of *Strombosia scheffleri* is also the same in the different areas, but red colobus fed on it less (2.7%) in the logged area than either group in the unlogged forest (5.3 and 4.6%). Therefore, for species that had identical availability in both forests, some species are used more frequently in the logged forest, while others are eaten more in the unlogged forest, making general trends unapparent. To further exemplify the inconsistent effect of logging on the colobus diets, the density of 11 food species decreased from unlogged to logged areas, 13 increased, and 10 stayed approximately the same.

When examining the diet richness (defined as the number of foods consisting of 1% or more of each colobus' diet), trends differ between the two colobus. For the black-and-white colobus, the small group had the richest diet with 16 foods, followed by the logged group, which fed on 14, and the big group fed on 11 foods. Similarly, the small red colobus group had the richest diet with 24 foods; however, in contrast to the black-and-white colobus, the big group fed on more foods (20) than the logged group (18). As for rare food feeding

Table 1. The proportion of all foraging scans that the red and black-and-white colobus of Kibale in logged and unlogged forests spent eating different species and parts

Species (Part)	BWC Big Unlogged	BWC Small Unlogged	BWC Logged	RC Big Unlogged	RC Small Unlogged	RC Logged	Unlogged Density/ha	Logged Density/ha
Celtis durandii (YL)	31.6	26.3	20.6	18.3	5.3	12.3	47.5	16.3
Celtis africana (YL)	12.8	11.1	13.4	6.8	7.9	8.8	13.8	17.5
Albizia grandibracteata (YL)	3.5	5.2	12.7	1.1	3.0	5.5	1.3	2.5
Markhamia platycalyx (YL)	9.6	4.8	2.9	4.1	1.9	6.1	58.8	16.3
Dombeya mukole (YL)	7.0	0.4	2.8	7.1	2.2	4.4	5.0	6.3
Olea capensis (YL)	4.6	1.1	6.9	0.9	0.0	7.8	1.3	1.3
Strombosia scheffleri (YL)	2.8	2.8	0.0	5.3	4.6	2.7	11.3	11.3
Prunus africana (YL)	0.3	6.7	1.0	1.6	4.5	3.1	1.3	2.5
Parinari excelsa (YL)	0.4	2.4	1.9	6.4	7.7	5.5	1.3	2.5
Celtis durandii (UF)	0.0	3.3	7.1	1.2	1.3	3.6	47.5	16.3
Funtumia africana (YL)	1.3	4.2	0.7	2.9	4.6	2.7	45.0	15.0
Millettia dura (YL)	1.8	0.5	6.0	1.1	0.6	6.0	1.3	11.3
Trilepsium madagascariensis (YL)	0.4	0.4	0.3	7.4	3.9	2.1	48.8	23.8
Prunus africana (ML)	0.0	3.7	0.2	2.1	7.4	0.2	1.3	2.5
Funtumia africana (RF)	0.0	0.5	0.0	3.9	4.2	0.7	45.0	15.0

Ficus brachylepis (YL)	3.6	1.5	0.0	2.1	1.1	0.8	2.5	1.3
Markhamia platycalyx (Petiole)	0.7	0.4	0.3	4.6	1.1	1.7	58.8	16.3
Strombosia scheffleri (Petiole)	0.1	2.8	0.0	2.9	1.6	1.2	11.3	11.3
Diospyros abyssinica (YL)	2.0	1.5	0.2	0.0	0.1	2.9	26.3	35.0
Chrysophyllum spp. (YL)	0.1	2.7	0.0	1.3	1.9	0.0	1.3	1.3
Celtis durandii (ML)	0.8	0.5	1.8	0.0	0.6	0.9	47.5	16.3
Celtis durandii (FL)	0.9	0.0	1.7	1.0	0.0	0.9	47.5	16.3
Macaranga schweinfurthii (YL)	0.0	1.4	0.0	0.5	2.1	0.0	1.3	1.3
Prunus africana (RF)	0.0	0.8	0.0	0.1	2.7	0.0	1.3	2.5
Celtis africana (ML)	0.0	0.1	0.8	0.0	0.3	1.7	13.8	17.5
Prunus africana (Bark)	0.0	0.0	0.1	0.0	2.3	0.1	1.3	2.5
Mimusops bagshawei (YL)	0.0	0.0	0.0	0.3	1.7	0.5	1.3	1.3
Diospyros abyssinica (RF)	0.0	0.0	1.7	0.0	0.0	0.4	26.3	35.0
Funtumia africana (FL)	0.2	0.0	0.0	1.0	0.0	0.3	45.0	15.0
Balanites wilsoniana (YL)	0.0	0.3	0.0	0.0	1.1	0.0	1.3	1.3
Pancovia sp. (YL)	0.0	0.0	0.0	0.2	1.1	0.0	1.3	1.3
Fagaropsis angolensis (Petiole)	0.0	0.0	0.2	0.0	0.0	1.0	3.8	8.8
Spathodea campanulata (YL)	0.0	0.0	1.1	0.0	0.1	0.0	1.3	1.3
Pancovia sp. (Petiole)	0.0	0.0	0.0	0.0	1.1	0.0	1.3	1.3

(defined as a food that consists of 1% or more of the diet and is not fed on by the other two groups within that colobus species), the small group of red colobus in the unlogged area fed on seven rare foods, the group in the logged area fed on four, and the big group in the unlogged area fed on two rare foods. Within the black-and-white colobus groups, the small and logged groups fed on four rare foods, and the big group fed on no rare foods.

The average amount of time that the different groups spent in association with another primate species differed among black-and-white colobus groups ($F = 5.00$, $P = 0.014$), but not red colobus groups ($F = 2.06$, $P = 0.146$; Figure 3). In the unlogged area, the large group of black-and-white colobus spent more time in association than the small group (Scheffe $= 0.014$), but the
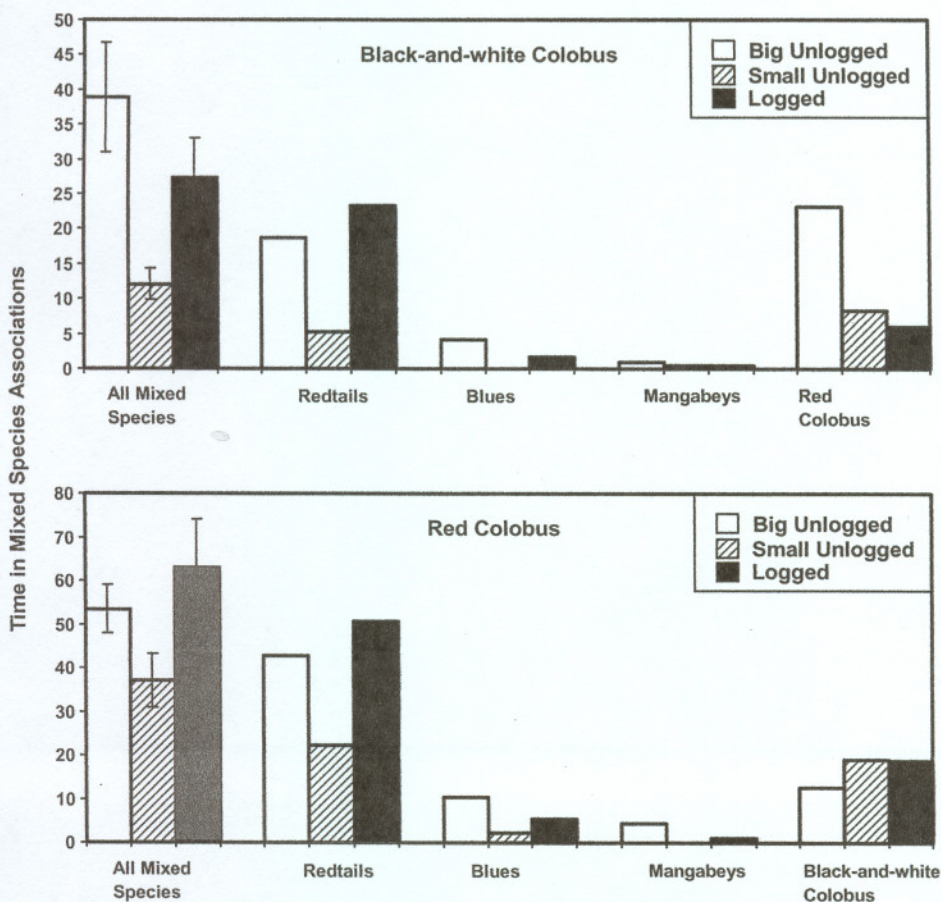

Figure 3. The time spent in mixed-species association by groups of red colobus and black-and-white colobus in Kibale National Park, Uganda.

time the other groups spent in association did not differ ($P > 0.228$). However, since the amount of time black-and-white colobus spend in association has been shown not to differ from random (Chapman & Chapman, 2000a), the biological significance of the difference found is questionable.

DISCUSSION

The differences in activity budgets, group spread, diet, mixed-species associations, and distance traveled do not suggest that the ecological differences between the logged and unlogged areas are creating large differences in the behavior of these two colobine species 30 years after logging. In contrast, the differences that were documented support the claim that group size is a strong determinant of many aspects of colobine behavior (Gillespie & Chapman, 2001). Large groups are thought to deplete food patches more rapidly, which alters foraging behavior and increases travel time (Janson & Goldsmith, 1995; Chapman & Chapman, 2000b).

Onderdonk and Chapman (2000) documented that the activity budget of a group of black-and-white colobus in a forest fragment that was an order of magnitude smaller than their typical home range was similar to a similarly sized group in the continuous forest. This study, in combination to the results obtained here, suggests that colobus groups in what one would expect to be stressful habitats (logged forest, fragments) are not spending more time traveling or feeding, as might be expected if they were forced to search harder for food or to eat lower quality foods. It may be that the densities and group sizes of the populations have been adjusted so that the animals are distributed between the logged and unlogged forest and among groups in a pattern that would represent an ideal free distribution (Fretwell & Lucas, 1970). Thus, where food resources are scarce, there are fewer animals to compete over those resources and those animals are in smaller groups. Therefore, the amount of resource available per individual is constant across habitats. In support of this, Teelen (1994) censused black-and-white colobus groups in the heavily logged and unlogged areas where we worked. She found that the average group size was 6.4 animals in the heavily logged area and 8.1 in the unlogged area. Struhsaker (1997) reported that the black-and-white colobus groups in lightly logged forest were 25% smaller than in the adjacent unlogged forest (7.9 vs. 10.5). Chapman et al. (2000) documented a 25% reduction in group size in red colobus between the heavily logged and unlogged areas of Kibale.

The smaller group size in degraded habitats is consistent with other studies of black-and-white colobus in forest fragments. Oates (1977) found smaller group size (modal size 7, $n = 2$) at Chobe, Uganda, a site consisting of patchy riparian forest, than in Kibale (modal size 9, $n = 7$). Similarly, Dunbar (1977) found that groups in Bole Valley, Ethiopia, in gully patches were smaller than groups in riverine forest, although this difference was not significant. In examining the relationship between habitat quality and black-and-white colobus group size across sites, Dunbar (1987) found that groups are significantly larger in more forested habitats.

The apparent relationship between colobine group size and habitat degradation suggests that the animals may be adjusting group size to the ecological conditions of the degraded habitat in such a fashion as to maintain relatively similar activity budget, travel costs, etc. It is generally held that group size is a trade-off between costs of reduced foraging efficiency and benefits of reduced predation risk (Chapman *et al.*, 1995; Janson & Goldsmith, 1995). As group size increases, reduced foraging efficiency of individuals requires them to travel farther to meet their nutritional requirements (the ecological constraints model; Chapman & Chapman, 2000b). For a group in a logged habitat, increasing foraging area may be too costly because it would involve traveling long distances between suitable feeding sites. Thus, the size of a group in degraded habitats may be constrained by the resources available.

The most recent survey in Kibale demonstrates that red colobus density is slightly higher in the unlogged forest than the heavily logged forest (unlogged = 5.5 groups/km^2, logged = 4.4 groups/km^2), while the density of black-and-white colobus is much higher in the heavily logged forest (unlogged = 2.0 groups/km^2, logged = 9.1 groups/km^2). The lower density of red colobus would presumably also reduce competition, possibly facilitating the maintenance of similar behavioral patterns in logged and unlogged forests. The fact that the black-and-white colobus are found at high density in the logged forest in comparison to the unlogged forest would increase competition and thus one would expect behavioral patterns to diverge. This may be offset by the reduction in group size; however, this explanation is somewhat unsatisfactory, as the reduction in group size between logged and unlogged areas is similar for these two species. Thus, the different response of the two colobine species to logging requires further investigation.

Primates have frequently been described forming mixed-species groups (Cords, 1987). These groups involve two or more species associating together

and coordinating activities for a number of hours or days and these associations are often argued to have adaptive functions. Benefits of mixed-species associations are controversial, but studies in Kibale have emphasized the role they can play with respect to decreasing predation risk through increased detection of predators and predator defense (Struhsaker, 1981; Chapman & Chapman, 1996, 2000a). Similarly, research in Tai National Park, Ivory Coast, has experimentally demonstrated that these associations may function to reduce predation risk (Bshary & Nöe, 1997a,b; Nöe & Bshary, 1997). Playbacks of chimpanzee (*Pan troglodytes*) hoot recordings induced formation of new associations and extended the duration of existing associations.

In censuses, Struhsaker (1975, 1981, 1997) documented that red colobus were in associations with other primates in unlogged forest 65% of the time, but only in association in heavily logged forest 36% of the time, while black-and-white colobus associated with other primates in the unlogged area 37% of the time and in the logged area 29% of the time. The levels of association we documented for red colobus in the heavily logged forest was much higher (60%) and for the black-and-white the level was reduced (12%). However, we also documented large differences between groups within a habitat type in the percentage of time spent in association. For example, the big black-and-white colobus group spent 39% of its time in association, while the small group was with other primates only 27% of the time. This suggests that estimates of percentage of time in association from observations of single groups may not represent the population as a whole. The differences between Struhsaker's finding and those reported here may reflect the fact that our study was conducted many years after the logging, while the previous study was closer to the time of logging.

Despite this, it is somewhat surprising that the colobus could maintain high levels of mixed-species associations in the logged forest. Given the fact that primate density is much lower in the logged forest (Chapman *et al.*, 2000), this would suggest the animals are actively seeking out other monkeys to associate with. Since the density of food trees are lower, the costs of these associations will be elevated in the logged area (Chapman & Chapman, 2000a). That red colobus are associating more in the logged area suggests that the benefits of association may be great in this habitat. It would be consistent with these observations to suggest that red colobus are reacting to an increased risk of predation in logged forest by associating more when the costs are greater.

The fact that few differences were documented in the behavioral patterns of the two colobus species between logged and unlogged areas 30 years after

logging suggests that mechanisms are present that facilitate their use of degraded forests. This mechanism may in part involve a reduction of group size to allow a decrease in feeding competition. These findings suggest that with respect to behavioral patterns, logged forest has considerable value for colobines. However, a number of issues remain to be resolved before the conservation value of logged forests are understood. For example, why is the density response to logging so different between these two colobus species? Why is the nature of forest recovery following logging in Kibale so slow (Struhsaker *et al.*, 1996; Chapman and Chapman 2004)? Why is the population growth rate of black-and-white colobus in the last decade much greater than that of red colobus (Chapman and Chapman 2004)? How will cascading consequences of logging affect the colobus? For example, if cercopithecine abundance continues to decline, a point may be reached where it is impossible to maintain the current level of mixed-species association, which may result in increased predation risk. Until such questions can be answered for colobines and many other species, caution should be used in following the lead of many conservation and development agencies that are suggesting that the conservation of many tropical forest species will depend on the capacity of disturbed forests to support their populations. If conservation funding is limited, it may be that conserving disturbed forests could be at the detriment of protected area management.

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