

7 The Immediate Impact of Selective Logging on Rwenzori Angolan Colobus (*Colobus angolensis ruwenzorii*) at Lake Nabugabo, Uganda

Julie A. Teichroeb, Gregory R. Bridgett, Amélie Corriveau and Dennis Twinomugisha

7.1 Personal Narrative

With my strong interest in animal behaviour, I (JAT) started my undergraduate career in biology, but ended up completing a Bachelor of Science in biological anthropology at the University of Calgary after my discovery that this was the area where primate behaviour was most intensively studied. I went on to do my Master of Arts with Jim Paterson and my PhD with Pascale Sicotte in primatology at the University of Calgary, engaging in fieldwork on ursine colobus monkeys (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana for both degrees. Many questions interested me throughout my graduate career, especially understanding how an animal's resources influenced their grouping patterns and their relationships with other individuals in their group. This was, after all, the heyday of testing socioecological models. Though more difficult to study in long-lived animals like primates, I was also intrigued with how sexual selection had acted on primates and what the effects might be in terms of morphological adaptations in males, female mate choice and sexual conflict. My PhD dissertation ended up focusing on both the social and the ecological factors controlling group size and group composition in ursine colobus.

Working in West Africa over the 10 years it took to complete my graduate degrees, I became acutely aware of all the conservation challenges facing wildlife there. When I started travelling to Ghana in 2000, it was rare to see large forest trees still standing, and when you did find areas where forest had been preserved, large animals were never seen and even birds were relatively rare. The bushmeat trade was (and is) also a serious problem, decimating wildlife in the region. Hunters were found lining the roads near any forested area, holding up dead monkeys by their tails or displaying other animals, hoping that passing motorists would be interested in buying the meat. Larger animals were already so scarce that most hunters had only forest snails or grasscutters (bush rats) for sale.

BFMS seemed like a sanctuary to both humans and monkeys in comparison with what I would normally see driving through Ghana. The two monkey species present, the ursine colobus and Campbell's mona monkeys (*Cercopithecus campbelli lowei*),

were protected by traditional religious beliefs that saw them as the children of two local gods. This hunting taboo was bolstered with laws prohibiting their killing and officers from the Ghana Wildlife Division stationed at the site. The forest surrounding the village, though less protected than the monkeys, contained a sacred grove area and still had many tall forest trees, including huge mahoganies (*Khaya grandifoliola*) and giant strangler figs (*Ficus ottoniifolia*, *F. polita*). It was a place where I could follow the monkeys without them fleeing due to past hunting pressure. I did not focus on questions of conservation while working there, but the fact that BFMS is made up of a series of relatively small forest fragments, hemmed in by agriculture, had to be a consideration in my work. Population density for the colobus was high within these forest fragments and dispersing beyond them was not really a viable option for the monkeys. On one particular day, while working in the forest in my first year in Ghana, Tania Saj and I saw two mona monkeys die because they were poisoned by proponents of a local Christian sect, who had hunted and eaten monkeys at BFMS in the past. It struck me at that moment that even where conservation seems to be working, changing circumstances and beliefs can reverse progress very quickly.

My postdoctoral work took me to McGill University to work with Colin Chapman at his new field site, Lake Nabugabo in Uganda. He chose this site specifically because it was not a national park and thus the vervet monkeys (*Chlorocebus pygerythrus*) could be studied for their abilities to survive in an anthropogenically modified landscape. The abundance of vervet monkeys and the unprotected status of the area also meant that we could get permission to do some foraging experiments on this population. I had begun to be quite interested in how animals detected food and chose their travel paths through their complicated habitat. By providing small amounts of food to the vervets in specific ways and patterns, I could begin to understand their perceptive abilities and their decision-making processes in greater detail.

It was difficult to watch the vervets interact in such varied ways with the people of Nabugabo. While tourists, the staff of the tourist lodges and fishermen often fed the monkeys, they would also act quite aggressively towards them. The vervets also raided local crops and came into direct conflict with farmers and the dogs of local people. Our field assistants watched many vervets die from violent assaults by both people and dogs, as well as incidents of mass poisoning. It was that first year at Nabugabo that I realised that my future research programme was always going to have to incorporate questions on how the monkeys were adapting to increasing anthropogenic pressure.

During my first year in Uganda, I became aware of a rare colobus monkey population living in the tall forest fragments around Nabugabo. This population was the montane subspecies of Rwenzori Angolan colobus (*Colobus angolensis ruwenzorii*) about which little was known, especially in low-altitude forest. I began to habituate part of this population in 2013 and continue to have students and a team of field assistants follow this fluid 'supertroop'. Again, my research was focused on a primate population living in forest fragments with a far from secure future.

My habituated animals were in a fragment, mostly contained in a forest reserve, and thus the government of Uganda could decide at any time to utilise the resources there. That is indeed what happened in March 2014, when logging began in the area. Despite the fact that most of my original research interests lay elsewhere, it has become impossible to study primates in the wild without some focus on how human impacts on the environment are affecting them.

7.2 Introduction

Habitat loss is the most pervasive threat facing primate populations today (Chapman & Peres, 2001; Estrada et al., 2017). Tropical forests, which contain 90 per cent of the world's primates, are specifically at risk (Hansen et al., 2013; Mittermeier & Cheney, 1987) and logging and wood harvesting now threaten 60 per cent of primate species (Estrada et al., 2017). Deforestation due to timber extraction is occurring at alarming rates worldwide and the threat is increasing as global demand for timber grows (Malhi et al., 2014). The subsequent habitat modifications after timber extraction will inevitably impact primates, forcing them to live in human-altered environments (Barbier et al., 1994; Lewis et al., 2015). It is understood that primate populations occupying tropical forest habitat will decrease following widespread deforestation. It has also been proposed by Cowlshaw (1999) that even primate populations that have survived the deforestation of their habitat may still incur an 'extinction debt', in that they are experiencing a lag-time until population collapse. Using the species/area curve and examining populations of forest primates across Africa, Cowlshaw (1999) found that current populations could be expected to decrease in size due to historical deforestation; however, as these populations are also experiencing ongoing deforestation, their extinction risk is exacerbated. The lag-time between habitat modification and eventual population extinction means that synergistic factors such as hunting, edge effects, fires, climate change and disease work together to decrease animal populations and cause their extinction in association with deforestation (Brook et al., 2008; Chapman & Peres, 2001).

Studies on the effects of selective logging on primates fail to present as clear a picture as studies on complete deforestation. Selective logging is typically defined as the harvesting of less than 10 per cent of trees in a forest, which allows for forest regeneration post-logging (Johns & Skorupa, 1987). Selective logging has become a common practice in the tropics (Asner et al., 2009); however, it often acts as a gateway leading to other forms of disturbance (Edwards et al., 2014; Lewis et al., 2015; Mayor et al., 2015). An extensive review of the effects of selective logging on various primate populations occupying a variety of forest habitats, conducted by Johns and Skorupa (1987), has shown idiosyncratic results, some of which may be due to logging defined as 'selective' showing great variability in the actual amount of destruction (from 5 to more than 70 per cent). Chapman and Peres (2001) point to the fact that trees not targeted for logging can still be damaged, impacting the actual number of trees lost. Furthermore, similar habitats with similar populations of primates experiencing equivalent rates of destruction have resulted in markedly

different population effects of selective logging due to differences in initial primate densities and the levels of human impact on these populations pre- and post-logging. Primate responses to logging appear to be species-specific and dependent on the type and level of disturbance, as well as the responses of the ecosystem after logging (Fimbel, 1994; Johns & Skorupa, 1987). Multiple factors, including size and spacing of remaining forest fragments, availability and density of important food sources, the overall degree of damage, species' ability to move between fragments, and the amount of hunting pressure following disturbance, will all impact a species' ability to survive locally.

Despite the variation across populations, some general patterns of the impact of selective logging are evident. Body size and diet are typically assumed to be the most predictive of a primate's ability to survive habitat disturbance. However, Johns and Skorupa (1987) found that body size is only predictive when the effects of diet are controlled. Diet type alone was considered to be predictive as it was found that the level of frugivory in a primate's diet negatively correlated with a species' survival ratio following forest disturbance. These results indicate that large-bodied frugivores, particularly the members of the genera *Ateles*, *Pan* and *Pongo*, are most at risk following disturbance, while smaller-bodied primates and primates with more folivorous diets have an increased chance of survival in selectively logged habitats.

Based on the folivorous diet of colobine monkeys, one might expect these species to successfully inhabit selectively logged areas, but numerous studies have once again presented a more complicated picture. Guerezas (*Colobus guereza*) appear to maintain abundant populations in logged habitat (Skorupa, 1986), and this species was actually found at higher densities in lightly logged compared to unlogged areas, indicating that logged forest may be preferred habitat (Chapman et al., 2000; Plumptre & Reynolds, 1994). Johns and Skorupa (1987) describe guerezas as a 'light-loving' species that can benefit from the higher temperatures in logged habitats where more energy can be directed to digestion, allowing them to exploit a lower-quality leafy diet. Conversely, closely related black colobus (*C. satanus*) and red colobus monkeys (*Procolobus badius*) have been found to be more abundant in undisturbed forest and to respond negatively to logging, perhaps as a result of more specialised diets (Johns & Skorupa, 1987; McKey, 1978; Struhsaker, 1972). Unsurprisingly, the dietary flexibility of a species coupled with the abundance of specific food types post-logging can alter its ability to survive disturbances. Studies thus need to take into account local conditions to explain the responses of different species to selective logging. Colobus monkeys also typically face a great deal of hunting pressure due to their large size, and have been shown to be vulnerable to being hunted to depletion due to their conspicuous nature (Johns & Skorupa, 1987; Oates et al., 2000). With increased access by people to disturbed forests and the changes in canopy height and makeup (Bennett & Dahaban, 1995), colobus could be even more susceptible than other primate groups to hunting pressure following selective logging.

The difficulty of finding broad-scale patterns of the effect of selective logging on primates is compounded by variation in methodologies between studies and the fact

that studies often lack comparable data on the same forest areas and primate populations both pre- and post-logging. It is common to compare primate populations living in logged areas to those in nearby unlogged areas (e.g. Chapman et al., 2000; Plumptre & Reynolds, 1994). Johns and Johns (1995) point out the critical importance of studying single populations of the same species prior to logging, during logging, and throughout the regeneration of the forest post-logging.

In this study, we examined the immediate ecological changes caused by small-scale, selective logging in a forest fragment, Manwa Forest Reserve, at Lake Nabugabo, Uganda. We also determined the effect of logging on the density, activity budget, diet and subgroup sizes of Rwenzori Angolan colobus (*Colobus angolensis ruwenzorii*). This subspecies of Angolan colobus is vulnerable to extinction according to the IUCN (Kingdon et al., 2008). We collected pre- and post-logging data on the structure of the forest, the numbers of colobus present, and the behaviour of one large colobus group. We predicted that: (1) since logging does not usually kill primates (Struhsaker, 1997) and because the extraction was at low levels and done without heavy machinery, changes to colobus densities would not be apparent immediately after logging; (2) the colobus activity budgets would show more resting and less feeding and moving after selective logging due to lowered food availability, as has been seen in other primate populations immediately after selective logging (Johns, 1986); (3) the diet of the colobus would include fewer of the tree species targeted by logging (umbrella tree, *Maesopsis eminii*). Logging has been shown to decrease fruit availability but lead to increased young leaf growth (Johns, 1983); we therefore also predicted that (4) colobus would show a reduction in time spent feeding on fruit (Johns & Skorupa, 1987), with a corresponding increase in leaf eating (Ganzhorn, 1995; Johns, 1986) post-logging. (5) Finally, we also predicted that the colobus would form smaller subgroup sizes than in pre-logging periods because of reduced food availability (e.g. Johns, 1986; Johns & Johns, 1995). Though we are unable to test this hypothesis currently, we also propose that downstream effects of logging may be apparent after several years, with lowered recruitment of juveniles for the colobus ranging in logged areas, due to a loss of important food trees (Johns, 1992; Struhsaker, 1997).

7.3 Methods

This study was conducted at Lake Nabugabo, Masaka District, central Uganda (0°22'–12°S and 31°54'E). Lake Nabugabo is a small lake (8.2 × 5 km) at an elevation of 1136 m, lying to the west of the large Lake Victoria. The landscape surrounding the lake consists mostly of swamps, with the north and west sides also including a mixed habitat of wetlands, grasslands, patches of tall forest, degraded forest, farmers' fields, and a few buildings (Chapman et al., 2016). One of these patches of tall forest adjacent to the trading centres of Bukumbula and Nabugabo is partly made up of the ~280 ha Manwa Forest Reserve. Rwenzori Angolan colobus inhabit this forest and the adjacent fragments. This subspecies forms large permanent groups of >300 individuals in montane areas (Fashing et al., 2007; Fimbel et al., 2001), but at

lowland sites, like Nabugabo, subgroups of variable size show fission–fusion behaviour and have been referred to as ‘supertroops’ (Oates, 1974). Pre-logging data were collected on the structure of the forest, the numbers of colobus present and the behaviour of a large fluid supertroop of colobus in 2013 and the beginning of 2014. Selective logging took place in Manwa Forest Reserve beginning on 26 March 2014. Ninety loggers in six teams entered the forest to log *Maesopsis eminii* trees ≥ 40 cm diameter at breast height (DBH) using hand and pit saws. The local community protested the logging, with representatives travelling to Kampala to discuss the issue with the Ugandan environment minister. After these protests, logging ceased after only one month. We collected post-logging data on changes to the forest, colobus numbers and behaviour beginning in July 2014.

7.3.1 Ecological Survey

As part of a long-term study on the behavioural ecology of Rwenzori Angolan colobus, pre-logging data were collected on the structure of the forest and the numbers of colobus present in the large forest fragment (140 ha were sampled, of which just over half is within the forest reserve boundary) at Lake Nabugabo from 19 April to 29 June 2013. Though the entire forest fragment is not included within Manwa Forest Reserve where logging occurred, to consistently compare pre- and post-logging data we include data from the whole 140 ha that we sampled (Table 7.1). Colobus subgroups were found throughout the entire forest fragment and the ones studied (Troop FG) were usually found within the reserve.

Line-transect surveys (Whitesides et al., 1988) were used to assess both the ecology of the forest and the abundance of primate populations. First, the perimeter of the forest was mapped using a GPS, then 32 parallel, straight-line transects were cut at 100 m intervals through the forest fragment. Transects varied in length (Table 7.1) and were cut either until the edge of the fragment was reached or we moved into the swamp on the northwest side of the forest and standing water became more than 30 cm deep. Ecological assessment was done by identifying and measuring all trees ≥ 10 cm DBH within 5 m on each side of the transects. For trees with multiple stems ≥ 10 cm DBH, we measured all stems and consolidated them by taking the square root of the sum of all squared DBHs (Nature Conservation Practice, 2006). Trees were identified to the species level with the assistance of a knowledgeable local botanist (Matovu Ponsiano). The percentage of canopy cover was estimated every 50 m along transects. On each transect, a scan was taken to assess average canopy height and one tree that represented this height was measured using a clinometer. In addition to the ecological survey, we examined the amount of disturbance to the forest by noting all instances of human activity (stumps, charcoal pits, cut branches, etc.) present within 5 m on either side of all transects.

Post-logging ecological surveys were carried out in July 2014 by rewalking the existing 32 pre-logging transects and noting any new disturbance caused by the loggers. We recorded, measured and identified the species of new stumps within 5 m on either side of transects, determining whether the trees were cut by loggers or by

Table 7.1 Pre-logging tree composition and occurrence of logging on transects at Lake Nabugabo, Uganda

Transect	Length (m)	Number of stems ≥ 10 cm DBH*	Mean DBH (cm)	Logging?	# Trees logged	Mean stump diameter (cm)
1	73	39	18.6	N		
2	86	42	24.3	N		
3	67	27	27.3	N		
4	527	236	23.7	N		
5	98	21	23.6	N		
6	190	61	21.7	N		
7	120	61	22.5	N		
8	73	76	20.1	N		
9	43	37	21.9	N		
10 [‡]	140	36	22	N		
11	170	55	26.9	Y	5	32.4
12	626	216	25	Y	+	
13	337	105	25.8	Y	+	
14	29	13	22.5	Y	1	39
15	140	61	22.9	Y	+	
16	110	52	26	N		
17	100	39	28.1	N		
18	290	105	22.4	Y	+	
19	300	103	22.7	N		
20	359	116	23.4	Y	5	34.7
21	459	167	26.1	Y	+	
22	498	212	27.7	Y	12	33.5
23	548	208	25.5	N		
24	615	285	25.3	Y	+	
25	671	259	29.9	Y	3	30.3
26	509	234	27.8	Y	9	35.7
27	602	199	27.5	Y	+	
28	524	173	28.8	Y	1	51.6
29	527	149	31.4	Y	7	30.8
30	432	128	32.3	Y	2	29
31	252	73	31.8	Y	1	40
32	187	43	33.3	N		

* Pre-logging stems within 5 m of either side of the transect.

† Logging just off transect.

‡ Transects 1–10 were located outside of Manwa Forest Reserve where no logging took place.

local people gathering firewood and building supplies. We additionally noted when logging had occurred just off transects (Table 7.1). Incidental damage to living trees caused by the felling of large trees for timber and damage caused by the construction of logging camps were also recorded when possible. Canopy coverage was again estimated every 50 m along transects in post-logging surveys.

7.3.2 Primate Surveys

Pre-logging primate surveys were done in a single day using the 32 parallel transects. Beginning early in the morning on 5 June 2013, researchers, in four teams of two, walked slowly (~1 kmh) and quietly along parallel transects at the same time until the end was reached. Observers then turned around and walked quietly back to the starting point so that two sweeps of each transect were done to identify and count the primates seen. When primate groups were detected, their location along the transect was noted, as well as the time, species, distance from the observer, sighting angle, approximate distance to the first animal encountered and the average height of the group (Anderson et al., 2007a; Buckland et al., 2001; Whitesides et al., 1988). Additional data gathered included the main group behaviour when encountered, number of animals seen, age and sex class of animals observed, approximate group spread, presence of other species, which side of the transect the group was encountered on and whether the count was considered accurate or incomplete. After each set of sweeps along transects, the research teams met outside the forest to collate results and discuss observations to ensure the accuracy of the data and avoid the double-counting of groups (Anderson et al., 2007b). The four teams of observers then moved to the next four parallel transects and began walking them at the same time. This process was repeated until all transects had been walked.

A post-logging primate survey was carried out over several days in July 2014. Due to time constraints, a large team was not assembled in post-logging surveys and two observers concurrently completed the primate survey and the ecological survey. Two observers walked quietly at about 1 kmh on the existing 32 parallel transects, recording both damage to the forest and any primates seen. Two sweeps were again done for each transect, and when primates were encountered the same information was recorded as for the pre-logging survey. Sampling effort, in terms of walks along transects, was the same in pre- and post-logging surveys; however, because post-logging primate surveys were done over a number of days rather than all on the same day, the possibility of double-counting the same groups was higher. We do not think that this affected our results because the groups that were encountered on successive days in the post-logging survey were in areas of the forest fragment that were distant from one another. Though vervet monkeys and red-tailed monkeys (*Cercopithecus ascanius*) were also encountered in both primate surveys, here we only report data on Rwenzori Angolan colobus.

7.3.3 Behavioural Data

After the initial primate survey in 2013, a large, fluid supertroop of Rwenzori Angolan colobus was chosen for habituation and continued behavioural monitoring (Troop FG). Local field assistants were trained in teams of two to conduct follows of this supertroop (often found in subgroups of differing size) for six days per month. Follows began in July 2013 and continued until March 2014, when logging began. Follows started again in July 2014 after the loggers had left the forest and the

monkeys had returned to their former range. With some variability, follows generally began at 7:30 a.m. and continued until 4:30 p.m. Field assistants collected scan samples (Altmann, 1974) via the frequency method (Struhsaker, 1975) every 30 minutes for up to five individuals, recording age and sex class, identity (if known), activity, food item and species (if feeding), distance and age and sex class of the nearest-neighbour, and a GPS point of the subgroup location. Observers moved around the subgroup between scans in an attempt to ensure that the same individuals were not scanned in successive samples. A count of the subgroup and the age and sex class composition was recorded at least once during each follow, as well as whether or not it was deemed a good count. Observers noted any fission and fusion events with other subgroups *ad libitum*. When the subgroup being followed underwent fissioning, observers stayed with either the largest subgroup or the one that contained the most known individuals.

We compared the behaviour of the Rwenzori Angolan colobus supertroop pre- and post-logging by examining data on activity budget, diet and subgroup sizes. To ensure a valid comparison and avoid both seasonal effects on these behaviours and interindividual differences in data collection between researchers, we used a matched sample of data from July to September 2013 (pre-logging) and July to September 2014 (post-logging) that was collected by the same observation team (M. Ponsiano and L. Katwere). After these restrictions to ensure comparable samples, we were left with 11 days of pre-logging data (835 scans of individuals) to compare with 11 days of post-logging data (815 scans of individuals).

7.3.4 Data Analyses

For our pre-logging ecological assessment of the forest, we calculated the total stems present, number of tree species, dominant tree species, average tree height (m), mean DBH (cm), stem density (#/ha), basal area (m^2/ha) and canopy cover. Total stems were calculated by adding up all the trees enumerated along our 10 m wide transects (total area covered 9.702 ha) and extrapolating this to the entire 140 ha sampled. The dominant tree species was the most common species (≥ 10 cm DBH) enumerated along transects. The basal area for the forest was calculated by determining the area covered by each sampled tree ($A = \pi r^2$), then adding these together and dividing by the number of hectares sampled. Canopy cover estimates were averaged for each transect. Comparisons between pre- and post-logging data were possible for total stems, stem density, and canopy cover, so these were recalculated for our post-logging ecological survey. Statistical comparisons of these three measures were done with data from each transect using Wilcoxon signed rank tests and paired *t*-tests, with use of parametric and non-parametric tests dependent on sample size.

From the primate survey data, we calculated the group density of colobus seen along the transects in the pre- and post-logging periods for comparison. Colobus group densities were calculated using the reliable distance-to-animal method, where the width of the transect was the maximum reliable observer-animal distance from the transect (Struhsaker, 1981; equation 7.1).

$$\text{Group density} = \frac{\Sigma \text{ group sightings}}{2(\text{length} \times \text{width of one side of transect in km})} \quad (7.1)$$

Though the Whitesides method (Whitesides et al., 1988) has been shown to be more accurate for primate survey data (Fashing & Cords, 2000), this method could not be used here because it requires species- and site-specific mean group spreads and group sizes, of which samples of ≥ 30 are considered reasonable (Whitesides et al., 1988). Our colobus surveys led to 26 sightings where group spread and size values were attained. Given that we are comparing group densities at the same site over time, rather than between sites and researchers, the reliable distance-to-animal method should be sufficient. We acknowledge, however, that the main issue with the calculation of group density for Rwenzori Angolan colobus at Nabugabo is that the fission–fusion behaviour of this subspecies makes different size groupings possible over short time periods.

Activity budget was analysed by comparing daily proportions of scans spent feeding, resting, moving or socialising with Mann–Whitney U tests between pre- and post-logging periods. Subgroup size counts each day that were deemed ‘good counts’ by observers were also compared for these two periods with Mann–Whitney U tests. We extracted diet data on plant part and species from scans in which individuals were feeding. The daily proportions of scans spent feeding on different plant parts were compared for the pre- and post-logging periods with Mann–Whitney U tests. Data were analysed using R version 3.2.0 (R Core Team, 2015).

7.4 Results

7.4.1 Changes to the Forest as a Result of Logging

In the pre-logging ecological survey, the forest was found to contain 60 tree species with an average height of 22.95 m, and the dominant tree species was *Pseudospondias microcarpa*. Logging should not have changed these characteristics because *Maesopsis eminii* was targeted and a small percentage of trees were logged. Pre-logging analyses showed that the total stems (≥ 10 cm DBH) present within the 140 ha sampled was 53 471. Post-logging, the number of stems logged along transects (9.702 ha) was 46, for an estimated loss of 664 trees within the 140 ha (Table 7.1). Thus, post-logging, total stem number was estimated at 52 807 for a loss of only 1.2 per cent; however, statistical comparison of the number of stems ≥ 10 cm DBH along logged transects showed that this was a significant decrease (Wilcoxon signed rank: $N = 17$, $Z = 2.78$, $p = 0.005$). Mean DBH in the forest in the pre-logging period was 26.31 cm and basal area was 26.96 m²/ha. Larger trees were the ones removed by loggers (mean stump diameter: 33.97 cm), so presumably mean DBH and basal area had decreased slightly in the post-logging period; however, we did not reassess the DBH of all trees along transects post-logging due to time constraints. Logging led to an overall reduction in stem density from 374.3 stems/ha in the pre-logging period to 371.9 stems/ha post-logging, which was not significantly different when including logged and unlogged transects (paired t -test: $N = 32$, $t = 0.11$,

$p = 0.91$). Mean canopy cover in the pre-logging period was 77.4 per cent and post-logging it was 73.6 per cent. Canopy coverage decreased on most transects where logging occurred compared to pre-logging coverage, leading to a significant difference (Wilcoxon signed rank: $N = 14$, $Z = 3.03$, $p = 0.002$), while there was no difference on transects without logging ($N = 14$, $Z = -1.37$, $p = 0.17$).

This logging operation was supposed to exclusively target *M. eminii* trees ≥ 40 cm DBH; however, only 42.9 per cent of logged stumps enumerated on transects (18/42) were identified as this species, with a mean stump diameter of 44.5 cm. A stump diameter of just over 44 cm indicates that the DBH of these trees was likely often less than 40 cm. At least five species other than *M. eminii* were also cut (including *Funtumia latifolia*, *Newtonia buchananii*, *Pycnanthus angolensis*, *Beilschmiedia ugandensis* and *Sieberiana holckii*; mean stump diameter 35.8 cm) and the loggers damaged several areas building camps (Figure 7.1a). Since some of these trees may have been cut for the building of pit saws and camps (Figure 7.1a, b), it is not known whether the boles of trees other than *M. eminii* were removed for timber. However, the larger size of the *F. latifolia* stems (mean stump diameter = 40 cm) suggests that this species was removed for timber. The felling of the largest trees ($N = 3$) did a fair amount of incidental damage, with a mean of 3.33 other large trees damaged by being either knocked down or having most of their canopies ripped off.

7.4.2 Colobus Densities Pre-Logging and Post-Logging

Local field assistants at Nabugabo reported that Rwenzori Angolan colobus were not seen, nor was any loud calling heard, during the logging operation. Colobus had returned to their former range in the logged areas of the forest by July 2014, two and a half months after logging ceased, which we confirmed with the observation of 14 known individuals. Due to the fission–fusion of subgroups and the transient nature of groups in this population, comparing pre- and post-logging group densities is difficult, but we did see a change from 4.37 groups/km² to 2.43 groups/km². In the



Figure 7.1 (a) Logger camp and (b) pit saws abandoned after logging at Lake Nabugabo.

pre-logging survey we counted 93 colobus in nine groups, while in the post-logging survey we counted 54 individuals in five groups.

7.4.3 Post-Logging Impacts on Colobus Behaviour

The mean daily subgroup size for supertroop FG in the pre-logging period from July to September 2013 was 153.3 individuals ($N = 8$ days with good group counts), while in the post-logging period from July through September 2014, it was 166 ($N = 7$ days). There was no significant difference in daily totals for subgroup size between these two periods (Mann–Whitney U : $N_{\text{pre}} = 8$, $N_{\text{post}} = 7$, $U = 38$, $p = 0.27$).

Activity budget in the pre-logging period was 23.7 per cent feeding, 41.8 per cent resting, 24.7 per cent moving, 4.6 per cent socialising and 4.8 per cent other. In the post-logging period the activity budget changed to 17.4 per cent feeding, 48.1 per cent resting, 20.6 per cent moving, 9.6 per cent socialising, and 4.3 per cent other (Figure 7.2). This resulted in less feeding and moving and more resting and socialising than in the pre-logging period (Mann–Whitney U : feeding, $N_{\text{pre}} = 11$, $N_{\text{post}} = 11$, $U = 19$, $p = 0.007$; moving, $N_{\text{pre}} = 11$, $N_{\text{post}} = 11$, $U = 30$, $p = 0.049$; resting, $N_{\text{pre}} = 11$, $N_{\text{post}} = 11$, $U = 97$, $p = 0.018$; social, $N_{\text{pre}} = 11$, $N_{\text{post}} = 11$, $U = 100$, $p = 0.011$; other, $N_{\text{pre}} = 11$, $N_{\text{post}} = 11$, $U = 49.5$, $p = 0.49$).

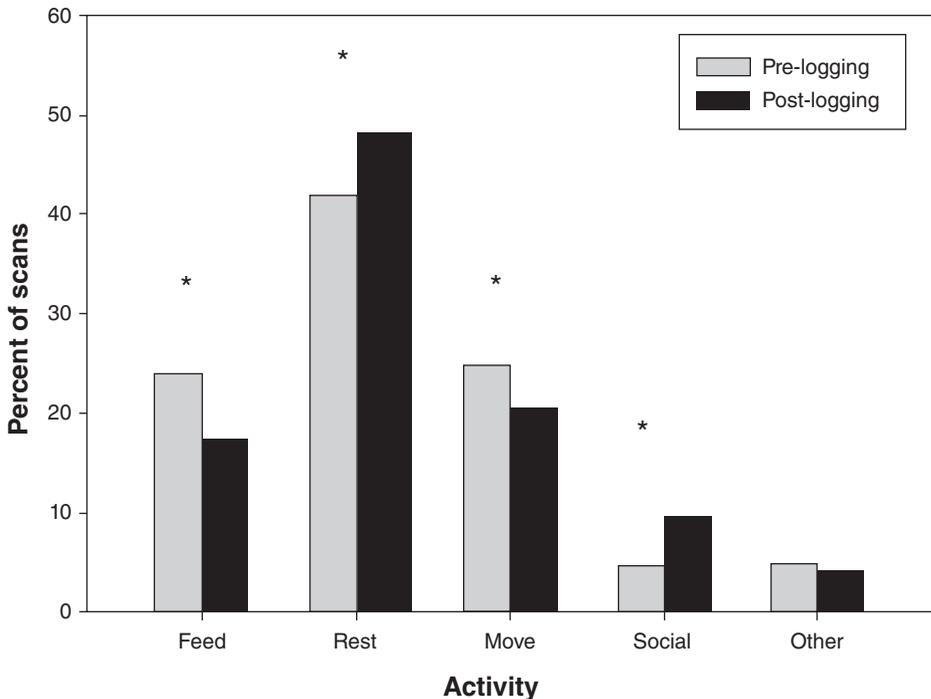


Figure 7.2 Activity budget of Rwenzori Angolan colobus (*Colobus angolensis ruwenzorii*) in July to September 2013 (pre-logging) and July to September 2014 (post-logging) at Lake Nabugabo. Stars indicate significant differences.

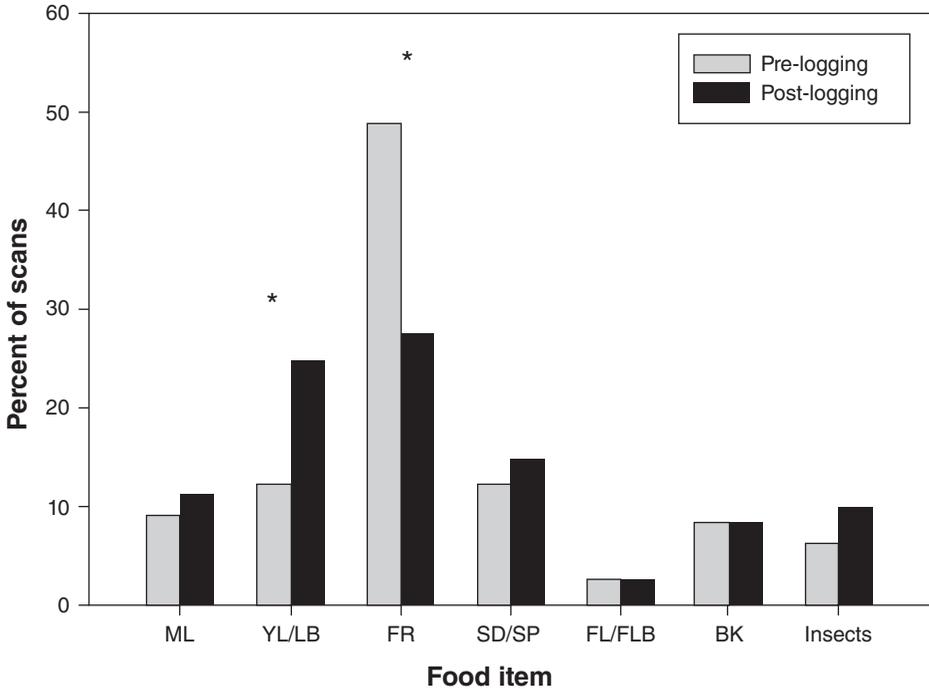


Figure 7.3 Diet of Rwenzori Angolan colobus (*Colobus angolensis ruwenzorii*) in July to September 2013 (pre-logging) and July to September 2014 (post-logging) at Lake Nabugabo. Abbreviations: ML mature leaves, YL/LB young leaves/leaf buds, FR fruit, SD/SP seeds/seed pods, FL/FLB flowers/flower buds, BK bark. Stars indicate significant differences.

The diet in the pre-logging period was made up of 8.9 per cent mature leaves, 12.1 per cent young leaves/leaf buds, 48.9 per cent fruit, 12.1 per cent seeds/seed pods, 2.6 per cent flowers/flower buds, 8.4 per cent bark and 6.3 per cent insects. In the post-logging period, the diet consisted of 11.3 per cent mature leaves, 24.8 per cent young leaves/leaf buds, 27.7 per cent fruit, 14.9 per cent seeds/seed pods, 2.8 per cent flowers/flower buds, 8.5 per cent bark and 9.9 per cent insects (Figure 7.3). Significant differences were seen in the greater post-logging intake of young leaves/leaf buds and smaller consumption of fruit compared to the pre-logging period (Mann-Whitney U : mature leaves, $N_{pre} = 11$, $N_{post} = 11$, $U = 77.5$, $p = 0.28$; young leaves/leaf buds, $N_{pre} = 11$, $N_{post} = 11$, $U = 105$, $p = 0.004$; fruit, $N_{pre} = 11$, $N_{post} = 11$, $U = 3$, $p = 0.0002$; seeds/seed pods, $N_{pre} = 11$, $N_{post} = 11$, $U = 74.5$, $p = 0.37$; flowers/flower buds, $N_{pre} = 11$, $N_{post} = 11$, $U = 64.5$, $p = 0.82$; bark, $N_{pre} = 11$, $N_{post} = 11$, $U = 56$, $p = 0.79$; insects, $N_{pre} = 11$, $N_{post} = 11$, $U = 88.5$, $p = 0.07$).

In terms of important tree species in the diet, there were five species that each made up at least 5 per cent of the diet in the pre-logging period, with *M. eminii* the most eaten at 21.5 per cent of the diet. Post-logging this increased to six species each making up at least 5 per cent of the diet, and while *M. eminii* was still important, its contribution to the diet dropped to 7.8 per cent (Table 7.2). In pre-logging feeding on

Table 7.2 Food species most frequently eaten* by Rwenzori Angolan colobus July through September 2013 and 2014 (before and after logging) at Lake Nabugabo, Uganda

Pre-logging food species	Percentage of diet	Post-logging food species	Percentage of diet
<i>Maesopsis eminii</i>	21.5	<i>Maesopsis eminii</i>	7.8
<i>Antiaris toxicaria</i>	9.1	<i>Antiaris toxicaria</i>	7.8
<i>Pseudospondias microcarpa</i>	6.5	<i>Pseudospondias microcarpa</i>	7.0
<i>Newtonia buchananii</i>	5.9	<i>Newtonia buchananii</i>	5.5
<i>Pycnanthus angolensis</i>	5.4	<i>Pycnanthus angolensis</i>	5.5
		<i>Macaranga schweinfurthii</i>	5.5

* Species making up at least 5 per cent of the diet.

M. eminii, 86.8 per cent of samples were fruit, 7.9 per cent were young leaves and 5.3 per cent were mature leaves. In the post-logging period, 50 per cent of feeding on *M. eminii* was on fruits, 40 per cent was on young leaves and 10 per cent was on mature leaves. Overall, 36.3 per cent of fruit feeding in the pre-logging period was on *M. eminii* and this dropped to 13.5 per cent post-logging.

7.5 Discussion

The small scale of the logging that was done at Nabugabo in March 2014 was likely due to both community protests that halted logging prematurely and the small size of the forest reserve. Had the forest been larger, it is unlikely that traditional logging methods would have been employed and roads and heavy logging machinery would have led to much greater damage (e.g. Cannon et al., 1994; Douglas et al., 1992; Gullison & Hardner, 1993; Uhl & Vieira, 1989). Logging done by hand is usually much less damaging than that done with heavy machinery (Putz et al., 2001); loggers at Nabugabo cut logs into planks at pit saws before carrying them out of the forest on foot, so large trees were not hauled out on roads. Subsequent attempts to collect firewood on a commercial scale from the forest (by firewood dealers from the nearest town, Masaka), which would have aggravated degradation, were also foiled by the local community.

The behaviour of the Rwenzori Angolan colobus at Nabugabo during logging conformed to that observed in other primates: the animals fled the area of active logging but returned to their former range once logging ceased (Arnhem et al., 2008; Johns, 1986; White & Tutin, 2001). We suspect that the colobus at Nabugabo fled to safe spots in adjoining forest along the Juma River (just outside of the forest reserve boundaries) where no logging occurred. The tendency for animals to flee areas where active habitat disturbance is occurring can cause them to move into ranges that are already occupied by conspecifics, leading to increased territorial aggression (White & Tutin, 2001). Given the large-scale fission–fusion events that we have observed among subgroups of Rwenzori Angolan colobus and the extremely large groups seen

in montane areas (Fashing et al., 2007), we suspect that, despite temporal variation in which individuals maintain association, the whole population of the forest fragment may sometimes coalesce. If this is the case, it would mean that the colobus could gather together, for a period of time, in one part of the forest without suffering heightened territorial aggression.

Two and a half months after logging at Lake Nabugabo, our results suggest a decrease in the numbers of Rwenzori Angolan colobus. Though our study group had returned to its previous range, the overall population size may have decreased or some colobus that fled logging may have yet to return. It is also possible that the colobus densities had not changed but that there were more group fissions in the pre-logging period or that our slightly different survey methods between the pre- and post-logging periods led to spurious results. Although counting the overall number of individuals is difficult in fission–fusion species (Chapman et al., 1993), we found that colobus subgroup sizes remained the same compared to a matched pre-logging sample. This may be an indication that colobus densities did not change; however, primates tend to maintain their species-specific social organisation (i.e. group sizes and compositions) even in the face of substantial decreases in population density (Cowlshaw & Dunbar, 2000).

Direct mortality due to logging is not common in primates, but a decreased food supply after logging could potentially lead to lowered recruitment of infants in the long term (Johns, 1992; Struhsaker, 1997). Even when species targeted by selective logging are not key food resources, primate food sources can be negatively affected due to a high degree of unintended incidental damage (Skorupa, 1986). At Nabugabo, the targeted tree species (*M. eminii*) was actually the top food item in the colobus diet. Thus, despite the relatively small amount of damage that was done by the logging, we still saw some of the predicted changes in colobus behaviour. Compared to the pre-logging period, our focal supertroop of colobus changed their diet in the post-logging period. The logged tree species, *M. eminii*, decreased in importance in the diet, likely due to the reduction in the availability of this species caused by logging. The consumption of fruit decreased after logging while young leaves/buds and mature leaves became more important. While phenology data are not available, young leaves were observed in abundance after logging due to the opening up of some areas of the canopy. Fruit may also have been less available due to the felling of important fruit trees and subsequent disturbance (Felton et al., 2003; Johns, 1983; 1986; Johns & Skorupa, 1987). The targeted tree species, *M. eminii*, made up a lot of the fruit feeding before logging, but far less afterwards when young leaves were eaten more from this species and, overall, it was consumed less. That being said, without phenology data we cannot be entirely certain that dietary changes were an effect of logging and not just due to changes in overall food availability; however, we tried to mitigate this potential issue by analysing matching seasonal samples from before and after logging.

It is difficult to say whether these changes in the diet of our study troop will have eventual detrimental effects on infant recruitment. Fruit is considered a high-quality food source (Felton et al., 2009; Isbell, 1991; Wrangham, 1980) that allows

population growth. However, young leaves are also often easily digested and have high amounts of protein (Ganzhorn, 1995; Ganzhorn & Wright, 1994; Rothman et al., 2006). The increased availability of new leaves provided by more sun exposure and colonising plants after logging has been cited as the reason that the guereza populations at Kibale National Park and Budongo Forest Reserve in Uganda have responded positively to logging (Chapman et al., 2000; Plumptre & Reynolds, 1994; Skorupa, 1986). After some disturbance, even mature leaves may become higher quality because sun exposure can increase protein and simple sugars, while fibre remains the same (Behie & Pavelka, 2012; Ganzhorn, 1995). Indeed, folivores often fare better than frugivores when their habitat is disturbed (Johns & Skorupa, 1987), though there is a lot of variability in the responses of folivores to logging (Struhsaker, 1972). Thus, the possibility remains that Rwenzori Angolan colobus at Nabugabo will not be affected negatively by the little logging that was done and, in fact, that they may respond positively.

We did find that the activity budget of Rwenzori Angolan colobus at Nabugabo showed all of the changes that were predicted by prior research on the effect of logging in other species. Johns (1986) found that white-handed gibbons (*Hylobates lar*) and banded leaf monkeys (*Presbytis melalophos*) both decreased the time that they fed and travelled and increased the time spent resting following selective logging in Malaysia. Notably, the percentage of trees cut at the site studied by Johns (1986) was also low (3.3 per cent), but incidental damage due to felling and mechanised log transportation caused a total loss of 50.9 per cent of the trees ≥ 30 cm DBH, much greater than the damage done at Nabugabo. Based on Johns' (1986) findings, we predicted a decrease in moving and feeding and an increase in resting after logging for Rwenzori Angolan colobus, all of which we found. We also saw an increase in social behaviour after logging, though subgroup sizes were not any larger. Decreased moving and feeding for the colobus after logging at Nabugabo could be explained by several factors: (1) given that their top food species was the target of loggers, lowered overall food availability may have led to less feeding and decreased energy output (Milton, 1980; Raemaekers, 1978; Waser, 1975); (2) the greater proportion of leaves in the diet post-logging may have necessitated greater resting to digest the associated cellulose and hemicellulose (Dasilva, 1992; Waterman & Choo, 1981); (3) alternatively, if fewer trees were producing high-quality leaves after logging, the monkeys may have been able to get enough food in fewer locations without searching widely (Behie & Pavelka, 2005); and/or (4) the decreased canopy cover in the post-logging period could have disrupted travel routes for this arboreal species (Cheyne et al., 2013; Johns, 1986; Putz et al., 2001).

The increased social behaviour that we found post-logging could be a reflection of the animals having more time available for grooming and playing due to the decrease in moving and feeding. Alternatively, the stress caused by the logging and the subsequent decrease in food could have triggered an increase in social grooming. In several other animal species, females increased their grooming of infants and one another after stressful events (reviewed by Liu et al., 1997 and Taylor et al., 2000). Our data support the idea that increased sociality in Rwenzori Angolan colobus at

Nabugabo post-logging was simply a result of having more time available. Time spent grooming pre- and post-logging was the same and the increase in social behaviour post-logging was actually due to an increase in time spent playing.

Selectively logged forests tend to retain high conservation value (Mayor et al., 2015), and if logging is not resumed at Nabugabo recovery from this episode of logging will likely be relatively fast. Twenty-five years after logging at Kibale National Park, Uganda, Chapman and Chapman (1997) found that, compared with unlogged areas, lightly logged areas showed similar growth of small trees and greater growth rates for large trees. Another ten years after this initial study, lightly logged areas also had greater tree recruitment than either unlogged or heavily logged areas (Chapman & Chapman, 2004). At Nabugabo, the current dominance of a pioneer species, *M. eminii*, and other species like *Funtumia latifolia* strongly suggests that the forest is under recovery from a past destructive episode. The presence of these species may facilitate forest recovery.

One of the main reasons why primate populations often do not recover after logging, despite being relatively resilient to changes in their habitat (Johns, 1992; Plumptre & Reynolds, 1994), is that logging opens up the forest to access by hunters (Bennett & Dahaban, 1995; Remis & Jost Robinson, 2012). Hunting can actually be a greater threat than logging because it can persist long after logging has ceased (Brodie et al., 2014). At Nabugabo, the location and fragmented nature of the forest means that it is already open to hunters, but luckily primates are not currently targeted in this area as ungulates are the preferred bushmeat species.

7.6 Conclusions and Future Directions

This study shows that even a short logging episode, in which a small number of trees are targeted and logs are removed without the use of machinery, can still cause significant changes to the behaviour of an arboreal primate species. Though the damage done did not appear to have a great immediate effect on colobus numbers and survival, the animals changed their diet and their activity budget in the post-logging period. Our long-term study of Troop FG and the forest at Nabugabo will allow us to document whether these changes have future impacts on this population. Will the dietary change and the activity budget modifications eventually influence infant recruitment? How will the forest recover from this episode of selective logging? These are questions we aim to tackle. In addition, the small nature of the forest fragment that we work in and the increasing anthropogenic pressure from local people that need fuelwood and other resources is a constant threat. What does the future hold for animals impacted by humans to such a degree? Almost all zoologists are facing this question and current and future primatologists will need to adapt their interests to understand primate responses to a multitude of threats. Only by understanding species-specific responses to varied conditions can we begin to reverse the situation. Given the response of the community at Nabugabo to the threats to the forest, we are very hopeful for the future of the forest wildlife there. We hope to build positive community attitudes by expanding our team of local field assistants in the

next few years and training others to identify birds and butterflies, which will give them employment leading tourists into the forest. In addition, we hope to further build the skills of promising residents of Nabugabo and surrounding areas by helping them further their education. Conservation has been truly positively impacted in primate-habitat countries when nationals have gone on to get PhDs in related fields and make a difference in their own countries (e.g. Strier & Boubli, 2006).

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