

Female Red Colobus Monkeys Maintain Their Densities Through Flexible Feeding Strategies in Logged Forests in Kibale National Park, Uganda

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ABSTRACT Behavioral flexibility allows primates to cope with environmental variability. Quantifying primate responses to human habitat modifications allows an effective means of assessing coping mechanisms. Within Kibale National Park, Uganda, logging led to reduced primate food availability that still exists almost 50 years after the harvest. Following the predictions of the ideal free distribution theory, primate densities are expected to decrease in areas of lower resource availability so that the resources available per individual are equivalent in logged and old-growth areas. However, counter to what would be predicted by the ideal free distribution theory, red colobus monkeys (*Procolobus rufomitratus*) occur at similar densities in logged and old-growth areas of Kibale. This suggests that either the ecological differences between the two areas are not sufficient to impact red colobus densities or that animals in logged areas are compensating to changes in resource

availability by using different foraging strategies. To test between these hypotheses, we examined four groups of red colobus, two in logged and two in old-growth forests, and compared feeding behavior, feeding tree size, and tree productivity. Females in logged areas fed on resources from a greater number of plant species, fed on fewer resources from each species, and spent more time feeding than those in old-growth areas. By expanding their diet, females in logged areas effectively increased the resources available to them, which may contribute to their ability to maintain similar densities to females in old-growth areas. These findings have implications for an evolutionary understanding of how species deal with environmental change and considerations for conservation practices that determine what areas should be prioritized for protection. *Am J Phys Anthropol* 154:52–60, 2014. © 2014 Wiley Periodicals, Inc.

Primate species often consume a variety of resources (e.g., Garber, 1987; Chapman et al., 2002; Rothman et al., 2007; Ryan et al., 2012) and environmental changes, such as deforestation and climate change, can lead to even greater dietary variability (Chapman and Chapman, 1990; Rode et al., 2006). This has important implications for applying foraging theories to primate behavioral ecology (Garber, 1987; Chapman, 1988; Janson and Chapman, 1999). For example, optimal foraging theory was originally proposed by MacArthur and Pianka (1966) and Emlen (1966) to explain the energy that predators gain from capturing prey compared to the energy or time expended in acquiring prey. The theory was used to understand spatial and temporal variation in diet (Belovsky, 1981; Houle et al., 2006; Pyke, 1984). However, because primates have such variable diets and are rarely dietary specialists, feeding strategies are more complicated than typically considered by optimal foraging theory (Garber, 1987; Janson, 2007). Thus, understanding primate foraging strategies through an optimal foraging perspective is challenging (but see Sayers et al., 2010). The ideal free distribution theory was proposed by Fretwell and Lucas (1969) to describe how populations distribute themselves among variable habitats and, in a simplified version dealing only with

food, predicts that the number of individuals in an area will be proportional to the foraging gains, such that a decrease in resources (foraging gains) should lead to a decrease in consumer numbers (Pulliam and Caraco, 1984). However, this prediction is not always upheld and factors, such as predators, territoriality, and disease, can

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impact the distribution of consumers (Fretwell and Lucas, 1969; Cowlshaw, 1997; Stephens and Stevens, 2001; Nunn and Altizer, 2006; Grove, 2012). Furthermore, since primates can adopt variable diets, individuals may use new foraging strategies in areas with altered resource availability, allowing them to obtain consistent foraging gains by alternative means. For example, Nakagawa (1990) provided evidence that Japanese monkeys (*Macaca fuscata*) sometimes fed in less crowded patches of lower quality food, rather than on higher quality foods in crowded patches, because the net benefit for these two were equal.

Examining between-group behavioral variation compared to the overall expected norm for a population allows the quantification of behavioral plasticity (Komer, 1997; Pigliucci, 2001) and on small spatial scales, where phylogeny is likely not an important issue, it allows an evaluation of strategies to cope with ecological variation. For example, logged areas of Kibale National Park, Uganda (hereafter Kibale), have significantly fewer red colobus (*Procolobus rufomitratu*s) food resources compared to old-growth areas (Chapman et al., 2010a, 2010b). Unfortunately, the disturbed open areas of the logged forest are not regenerating with young trees as expected; instead, they are being colonized by shrubs that directly compete with regenerating red colobus food trees (Paul et al., 2004; Lawes and Chapman, 2006). Based on a food-oriented version of the ideal free distribution, population densities of red colobus should be lower in heavily logged areas. However, there is no significant difference in red colobus densities between heavily logged and old-growth areas (Struhsaker, 1997, 2010; Chapman et al., 2010b). Chapman et al. (2010b) did not find differences in red colobus densities between the forestry compartments for a study analyzing 238 transects spanning 1,104 km of Kibale over 25 years. These findings are not consistent with standard applications (i.e., those dealing with only food resources) of the ideal free distribution model. This suggests that either the ecological differences between the two areas are not sufficient to affect red colobus population density, or that red colobus use different strategies in heavily-logged areas to maintain their densities.

Here, we examine dietary and behavioral differences in female red colobus living in different areas of Kibale to test if females have a plastic behavioral response to variation in food availability created by logging. There is already a strong database of red colobus feeding behaviors in Kibale; however, this is the first study to provide a detailed examination of identified focal animal behaviors across two different habitats at this site. The long-term database of red colobus densities and forest ecology in Kibale make this an ideal site and subject to examine differences in feeding ecology across habitats. Furthermore, this allows us to test the ideal free distribution in a folivorous primate species. A plastic behavioral response may allow red colobus to maintain a positive energy balance and have equivalent reproductive output as females in old-growth areas. Under this model, individuals in degraded environments should show behavioral plasticity in feeding behaviors and should expand their diet to include a greater variety of foods than seen for red colobus in old-growth forest (optimal diet model by Schoener, 1971; Charnov, 1976), which would effectively increase their resource availability and thus support an equivalent biomass of individuals under the

ideal free distribution. Specifically, (1) females were predicted to eat a more diverse diet in terms of plant species in the logged areas compared to the old-growth areas and (2) as the result of having a more diverse diet, the top foods of females in logged areas should constitute a smaller proportion of their total diet than females in old-growth forest. Additionally, (3) females in the logged areas were expected to spend more time feeding than females in old-growth areas. By expanding on the ideal free distribution model to include behavioral plasticity, females are expected to diversify their diet in areas where resources are low, which would effectively increase the availability of resources, and result in equivalent densities in both logged and old-growth forests. Alternatively, (4) if the reason population densities remain similar between logged and old-growth areas is because there are insufficient ecological differences between the habitats, we expect female red colobus in the logged areas to use similar foraging strategies to those in the old-growth areas. We focus on female red colobus feeding ecology because maintaining a positive energy balance is particularly important for females due to its close relationship to ovarian function, pregnancy maintenance, and lactation (Ellison, 1990; Wade and Schneider, 1992; Sherry, 2002; Tardif et al., 2005; Miller et al., 2006; Emery Thompson et al., 2007). Though we recognize the need for males to also maintain a positive energy balance, demands on reproductive females are greater and therefore they were the subjects of this research.

METHODS

Study site and animals

Research was conducted in the forest near Makerere University Biological Field Station (MUBFS) in Kibale (795 km²; 0°13'–0°41'N, 30°19'–30°32'E). Kibale is a mid-altitude, moist evergreen forest that receives 1,696 mm of rainfall annually (1990–2011; Chapman unpublished data; Chapman and Lambert, 2000; Stampone et al., 2011). Kibale provides a valuable setting for examining the impact of habitat disturbance on foraging strategies in primates because both the forest and the primate populations have been studied for over 40 years. Forestry compartment K-30 is old-growth forest that was never commercially logged (Chapman et al., 2010a; Struhsaker, 2010), while K-15 was heavily logged and 50% of the trees were cut or indirectly killed (Kasenene, 1987; Skorupa, 1988; Chapman and Chapman, 1997, 2004). The K-13 area was heavily logged and poisoned with arboricide (Struhsaker, 1997; Oates, 1999). Logging activities that took place during the late 1960s and early 1970s have resulted in large gaps in the canopy that persist today (Gebo and Chapman, 1995; Lawes and Chapman, 2006). Four tree species (*Pouteria altissima*, *Lovoa swynnertonii*, *Strombosia scheffleri*, and *Parinari excelsa*) consisting of approximately 25% of red colobus feeding time in old-growth forest at Kibale (Struhsaker, 1978, 1997) are also considered high value timber and were heavily targeted during logging (Kingston, 1967).

Red colobus are endangered folivorous primates (Struhsaker and Leland, 1987; Chapman et al., 2006a, 2006b; 2007, 2010b; Gillespie and Chapman, 2006; Struhsaker, 2010). They live in multi-male, multi-female groups where females typically disperse out of their natal groups (Struhsaker, 2010; Miyamoto et al., 2013).

TABLE 1. Composition of the four red colobus (*Procolobus rufomitratus*) groups studied in Kibale National Park, Uganda

	Logged Group 1	Logged Group 2	Old-growth Group 1	Old-growth Group 2
Adult males	8	4	9	11
Adult females	22	14	15	22
Subadults	3	3	2	4
Juveniles	8	10	1	23
Infants	10	6	7	13
Total	51	37	34	73
Infant/adult female ratio	0.45	0.43	0.47	0.59

Females reach sexual maturity between 38 and 46 months (Struhsaker and Leland, 1987). Males reach sexual maturity between 35 and 58 months (Struhsaker and Leland, 1987) and form a loose dominance hierarchy (Struhsaker and Leland, 1979, 1987; Korstjens, 2001; Miyamoto et al., 2013). Female reproduction is characterized by a gestation of approximately 5 months and an interbirth interval of just over 2 years (Struhsaker, 1975; Struhsaker and Leland, 1987). Females may be particularly susceptible to habitat changes, and resultant changes in food availability as indicated by the fact that in forest fragments ($N = 11$) neighboring Kibale, the ratio of red colobus infants to adult females decreased from 0.31 to 0.19 from 2000 to 2003 and animals in fragments have high cortisol concentrations compared to individuals in the park (Chapman et al., 2006b).

Research design

Four groups of red colobus, with similar infant-to-adult female ratios, were simultaneously observed; two groups ranged in old-growth areas of K-30 and two groups ranged in the heavily logged areas of K-13 and K-15 (Table 1). Each focal group was followed from 8:00 am to 4:00 pm 6 days a week from July 2009 to May 2010. Five individually recognizable focal females (adult, parous females without infants) were selected from each group and observed on a rotating basis until they gave birth, at which time a new adult female without an infant was selected to enter the rotation. Sample sizes of focal females differ slightly among groups because additional females were added when prior focal females gave birth. On the rare occasion that a focal female was out of sight for longer than 1 h (<3% of focal follows), another focal female was followed for the remainder of the day. Instantaneous focal animal behavioral samples were collected on the focal female every 10 minutes. The female's activities

(foraging, feeding, traveling, resting, mating, and grooming), the identity, distance, and activity of her nearest neighbor, and any other individuals within 5 m were recorded. Data were collected by a team of local field assistants and weekly interobserver reliability tests were conducted to ensure the data collection was standardized.

Feeding observations included the plant species and plant part (e.g., young leaf and leaf petiole) consumed. Each day, two feeding trees were selected and measured for each group: the first tree the focal female was seen feeding in the morning and the second tree that she was seen feeding in the afternoon were tagged and scored. A visual estimate of the percentage (0, 25, 50, or 100%) of fruit, young leaves, mature leaves, and flowers was recorded. Diameter at breast height (DBH), a visual estimate of tree height, and crown size [visual estimates of length, width, and height (m)] of these trees were also recorded (Chapman et al., 1992).

To get a clearer estimate of food availability for red colobus in each area, we created a proxy for food availability by multiplying the average crown size of specific species by the density of trees. To get a specific food availability index for each type of food, we also multiplied this number by the percent of the crown that contained any particular food type (e.g., young leaves). Thus, we combined the crown volume and young leaf production of the top 10 food trees measured with data on densities from the areas (Chapman and Chapman, 1997; Chapman et al., 1997). Levene's test for equality of variances was used to evaluate the use of parametric statistics and when variance were unequal, Wilcoxon rank-sum tests were used (female behaviors in logged vs. old-growth areas).

RESULTS

Females in logged areas eat a more diverse diet compared to females in old-growth areas

Overall, female red colobus were observed eating food from 62 species of plants. As predicted, females in the two groups in the logged area had a more diverse diet (42 and 43 different species), whereas females in the old-growth groups fed from fewer tree species (29 and 34; Tables 3 and 4; $F = 5.084$; $df = 13$; $P < 0.001$) despite there being the same plant species available in both areas (Struhsaker, 1997). Both groups in each area fed from many of the same species (Table 2). There were 30 species that made up the 90% of feeding observations for all groups. In the logged areas, the two study groups fed on many of the same foods (overlapping in 28 of these 30 species), and in the old-growth area, both groups fed

TABLE 2. The most common tree species used by red colobus (*Procolobus rufomitratus*; percentage of each tree species relative to overall feeding tree records for each group)

Tree species	Family	Logged 1	Logged 2	Old-growth 1	Old-growth 2
<i>Albizia grandibracteata</i>	Fabaceae	11	7	7	0
<i>Celtis africana</i>	Cannabaceae	0	0	16	7
<i>Celtis durandii</i>	Cannabaceae	0	0	7	7
<i>Dombeya mukole</i>	Malvaceae	0	0	8	12
<i>Funtumia latifolia</i>	Apocynaceae	11	12	7	0
<i>Markhamia lutea</i>	Bignoniaceae	0	0	13	11
<i>Millettia dura</i>	Fabaceae	7	8	8	8
<i>Prunus africana</i>	Rosaceae	12	0	0	0
<i>Strombosia scheffleri</i>	Strombosiaceae	7	10	8	20
<i>Trilepsium madagascariense</i>	Moraceae	0	0	14	8
Other		52	63	12	27

from 24 of the 30 plant species. Across all groups, leaves were the most common plant part eaten (55–75% of the diet), followed by leaf petioles (15–30% of the diet). Within the old-growth area, neither group was seen eating fruit; however, both groups in the logged area ate fruits (making up 1–5% of their diet), including fruits from *Ficus* spp and *S. scheffleri*. Individuals in the logged areas ate both fruit and leaves from a variety of fig species (*Ficus* spp.), making up 9.5% of feeding observations, while fig species only accounted for 0.25% of feeding observations for individuals living in the old-growth areas. *S. scheffleri* was one of the top 10 food trees in all four groups; however, only the groups in the logged areas ate the fruits from this species.

As a result of having a more diverse diet, the top foods of females in logged areas constitute a smaller proportion of their diet than for females in old-growth forest

Females in the logged groups fed on each species as a lower proportion of their overall diet. The top 10 tree species accounted for 61.6 and 57.9% of the diet in the logged groups (Fig. 1), but the top 10 trees made up 72.6 and 69.7% of the diet in the old-growth groups, respectively (Table 2).

Females in the logged areas spend more time feeding than females in old-growth areas

Females had different activity budgets in logged ($N = 15$ individuals) versus old-growth ($N = 12$ individuals) areas (Table 3). Females in logged areas spent more time feeding than in old-growth areas ($Z = -3.15$, $x_{\text{logged}} = 47.65$, $\text{stdev}_{\text{logged}} = 9.5$, $x_{\text{old growth}} = 32$, $\text{stdev}_{\text{old growth}} = 7.67$; $P = 0.0021$). Resting was observed less in logged areas than in old-growth areas ($Z = 3.7816$,

$P = 0.0004$). Similarly, traveling was observed less in logged areas than in old-growth areas ($Z = 2.22$, $P = 0.0180$). All grooming behaviors make up a small percentage of the overall activity budget in all groups (less than 8%; Table 3); however, allogrooming was observed less in logged areas than in old-growth areas ($Z = 3.05$, $P = 0.0030$).

Female red colobus in old-growth and logged areas have different foraging strategies suggesting significant ecological differences between these areas

Data from tagged feeding trees illustrate differences in feeding ecology between logged and old-growth areas of Kibale, suggesting ecological differences (Table 2). The most common species that were tagged as feeding trees among all four groups were: *Albizia grandibractata* (4.7% in old growth, 8.5% in logged), *Trilepsium madagascariense* (9.5% in old growth, 0% in logged), *Celtis africana* (9.9% in old growth, 3.6% in logged), *Celtis durandii* (6.9% in old growth, 5.2% in logged), *Dombeya mukoke* (9.9% in old growth, 0.7% in logged), *Funtumia latifolia* (3.5% in old growth, 11.5% in logged), *Markhamia lutea* (11.6% in old growth, 3.9% in logged), *Milletia dura* (8.2% in old growth, 7.9% in logged), *Prunus africana* (0.4% in old growth, 5.2% in logged), and *S. scheffleri* (14.2% in old growth, 8.9% in logged). These constituted 73–88% of the feeding trees for groups living in the old-growth area, but only 37–48% of the feeding trees of those in the logged area. Similar to the behavioral data, the feeding tree data showed that individuals in the logged area had a more diverse diet (29–30 species vs. 20–24 in old-growth areas), thus, each species made up a smaller percentage of their overall diet (Fig. 1). Each major feeding tree species made up 12% or less of the feeding trees selected by individuals in logged areas; whereas, each tree species made up 16–20% in the old-growth area. Overall, there were significant differences between the feeding time devoted to the tagged trees evaluated in the logged and old-growth areas ($F = 4.695$; $df = 12$; $P < 0.001$).

Evidence suggests that there are sufficient ecological differences between old-growth and logged areas to make adopting different foraging strategies profitable. For example, some red colobus food trees differed in size. *S. scheffleri* trees were smaller (DBH) in the logged area as compared to the old-growth areas ($t = -3.430$, $df = 53$, $n_{\text{logged}} = 24$, $n_{\text{old growth}} = 31$, $P = 0.001$, $x_{\text{logged}} = 38.51$ cm DBH, $x_{\text{old growth}} = 68.91$ cm DBH, $\text{stdev}_{\text{logged}} = 22.00241$, $\text{stdev}_{\text{old growth}} = 38.81331$). *Strombosia* also had a smaller crown area (length \times height \times width m) in the logged areas ($t = -4.302$, $df = 48.799$, $P < 0.000$,

TABLE 3. Activity budgets of female red colobus (*Procolobus rufomitratu*s) in the logged and old-growth areas of Kibale National Park

Activity	Logged growth (%)	Old-growth (%)	Snaith and Chapman		
			Struhsaker (1975) (%)	Struhsaker (2008) (%)	Struhsaker (2010) (%)
Feeding	46	35	44.5	40–51	30–50
Resting	34	39	34.8	25–30	30–40
Traveling	14	18	9.2	16–29	7–11
Allogroom	4	6	5.3	5–10	2–8
Self-groom	2	2	NA	NA	NA

All observations were collected simultaneously for all groups. Activity budgets of focal females (percentage of overall activity budget).

TABLE 4. Densities of red colobus monkeys (*Procolobus rufomitratu*s) in different areas of Africa

Species	Density	Group size	Habitat	Citation
<i>P. temminckii</i>	105 individuals/km ²	32.08	Open Forest	Gatinot (1975)
<i>P. temminckii</i>	433 individuals/km ²	32.08	Dense Riverine Forest	Gatinot (1975)
<i>P. temminckii</i>	225 individuals/km ²	26.5	Mosaic (largely undisturbed)	Starin (1991)
<i>P. badius</i>	112 individuals/km ²	52.25	Old growth	Calculated by Struhsaker (2010) from Korstjens (2001)
<i>P. tephrosceles</i>	160 individuals/km ²	40	Old growth	Calculated from Chapman et al. (2010b)
<i>P. tephrosceles</i>	160 individuals/km ²	40	Heavily logged	Calculated from Chapman et al. (2010b)

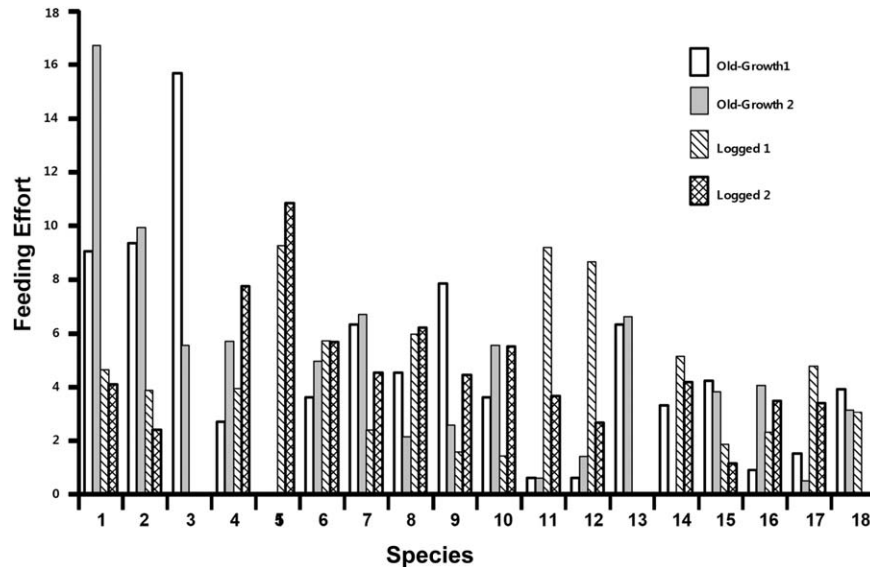


Fig. 1. The species that made up over 10% of the combined feeding time of the four red colobus groups in Kibale National Park, Uganda (1 = *Strombosia scheffleri*; 2 = *Markhamia lutea*; 3 = *Trilepsium madagascariense*; 4 = *Funtumia latifolia*; 5 = *Acacia* sp.; 6 = *Millettia dura*; 7 = *Celtis durandii*; 8 = *Albizia grandibracteata*; 9 = *Celtis africana*; 10 = *Mimusops bagshawei*; 11 = *Prunus africana*; 12 = *Urella* sp.; 13 = *Dombeya mukole*; 14 = *Olea capensis*; 15 = *Pouteria altissima*; 16 = *Parinari excelsa*; 17 = *Newtonia buchananii*; 18 = unknown vine 1.

$x_{\text{logged}} = 27.52 \text{ m}^3$, $x_{\text{old growth}} = 38.84 \text{ m}^3$, $\text{stdev}_{\text{logged}} = 6.923$, $\text{stdev}_{\text{old growth}} = 12.354$). *Albizia grandibracteata* trees were larger in DBH ($t = 2.567$, $df = 34$, $P = 0.015$) and crown size ($t = 3.39$, $df = 35$, $P = 0.002$) in the logged areas ($N = 26$, $x_1 = 47$, $\text{stdev} = 22.814$ and $= 33.92$, $\text{stdev} = 12.076$, respectively) compared to the old-growth areas ($N = 10$, $x_1 = 27.5$, $\text{stdev} = 11.336$ and $x_2 = 19.91$, $\text{stdev} = 9.762$, respectively). These data only explain the differences between feeding trees that have been selected by red colobus, not the overall differences in food availability between different habitats in Kibale. However, previous research (Struhsaker, 1997; Snaith and Chapman, 2008; Chapman et al., 2010a) provide evidence of the overall differences in tree densities and food availability between logged and old-growth areas.

There were no differences in the amount of flowers or young leaves present on the red colobus selected feeding trees between the logged and old-growth forests ($n_{\text{logged}} = 132$, $n_{\text{old growth}} = 107$, sample sizes are the same for all feeding tree analyses; flowers: $t = 1.827$, $df = 236.482$, $P = 0.069$, $x_{\text{logged}} = 7.01$, $x_{\text{old growth}} = 3.27$, $\text{stdev}_{\text{logged}} = 17.829$, $\text{stdev}_{\text{old growth}} = 13.772$; young leaves: $t = -0.505$, $df = 206.018$, $P = 0.614$, $x_{\text{logged}} = 41.86$, $x_{\text{old growth}} = 43.22$, $\text{stdev}_{\text{logged}} = 18.661$, $\text{stdev}_{\text{old growth}} = 22.405$). However, there were significantly more fruits and mature leaves on trees in the logged versus old-growth areas (fruits: $t = 3.788$, $df = 200.179$, $P < 0.000$, $x_{\text{logged}} = 7.01$, $x_{\text{old growth}} = 1.64$, $\text{stdev}_{\text{logged}} = 14.261$, $\text{stdev}_{\text{old growth}} = 7.097$; mature leaves: $t = 2.053$, $df = 211.622$, $P = 0.041$, $x_{\text{logged}} = 56.25$, $x_{\text{old growth}} = 49.30$, $\text{stdev}_{\text{logged}} = 24.002$, $\text{stdev}_{\text{old growth}} = 27.570$). This does not represent the overall differences in food availability between the logged and old-growth areas, but rather differences in food availability on selected red colobus feeding trees. However, because there are fewer trees in the logged areas (Chapman and Chapman, 1997; Struhsaker, 1997; Chapman et al., 2010a), the amount of young leaves and flowers are expected to be lower in logged areas. Thus, combining food estimates

based on feeding tree measurements with tree densities reveal differences in food availability between logged and old-growth areas. Of the top 10 food trees, 5 tree species were found in the vegetation plots monitored by CAC (Chapman et al., 2002). Not only were *Strombosia* trees smaller, they also occurred at a lower density in logged areas (1 tree/ha compared to 12.5 trees/ha). Density multiplied by crown volume and % young leaves results in an index of food index of only 8.6 for *Strombosia* foods in logged areas compared to 117.5 in old-growth areas. Using this same method, *C. durandii* index of food availability index is 482.5 in logged and 747.2 in old growth, *Markhamia* and *Funtumia* indices of food are similar in logged (345.4 for *Markhamia* and 189.0 for *Funtumia*) and old-growth areas (360.6 for *Markhamia* and 168.92 for *Funtumia*), and *C. africana* food availability index is actually higher in logged areas (105.4) compared to old-growth areas (54.0).

DISCUSSION

Population densities change in relation to changes in food availability (i.e., Fretwell and Lucas, 1969; Pulliam and Caraco, 1984). Anthropogenic changes to primate habitats impact primate populations by changing the availability, density, abundance, and distribution of plant species (Marsh, 2003; Chapman et al., 2006a, 2006b; Ratsimbazafy, 2007). For example, red-tail monkey (*Cercopithecus ascanius*) food in Kibale was three times less abundant in heavily logged than old-growth areas (Rode et al., 2006) and these differences corresponded to lower densities, smaller group size, fewer polyspecific associations, and more home range overlap for redtails in the heavily logged areas than old-growth areas (Rode et al., 2006).

Red colobus densities differ across Africa, which is attributed to differences in habitat quality (Table 4; Gatinot, 1975; Struhsaker et al., 2004; Galat Luong and Galat, 2005). In our study however, while the density of food trees differ between logged and old-growth areas,

the red colobus of Kibale occur at similar densities. This goes against the predictions of the food oriented version of the ideal free distribution model and thus requires explanation. We proposed that this discrepancy between theory and the empirical data could be because the logging activities in Kibale were insufficient to impact red colobus or that red colobus behavioral plasticity permits them to adjust to living in these degraded habitats, thus effectively expanding their resource base and maintaining an ideal free distribution. Our results support the latter. We found that female red colobus in degraded habitats fed from a higher number of plant species, increased the time spent feeding, and fed on species that had not been previously recorded in the red colobus diet (despite their availability).

Behavioral flexibility has been suggested to help to maintain densities following disturbance in other studies of red colobus. Galat Luong and Galat (2005) found that after 30 years of logging, the forest they studied in Senegal was reduced by 50%, which resulted in a 30% reduction in tree species diversity; however, red colobus (*Procolobus badius temmincki*) numbers only decreased by 17%. These researchers argued that the population made 5 major behavioral changes that allowed them to cope with habitat degradation: (1) frugivory, (2) terrestriality, (3) polyspecific associations with green monkeys (*Cercopithecus sabaeus*), (4) frequenting more open habitats, and (5) using mangrove forest for refuge and foraging. Ruffed lemurs (*Varecia varecia*) living in degraded habitats diversified their diet to include different types of fruits compared to those in pristine habitats (Ratsimbazafy, 2007). Also, increases in population densities of mantled howler monkeys (*Alouatta palliata*) in forest fragments of less than 10 ha in size were associated with more diverse diets and incorporating new foods compared to groups living at lower densities in larger forest areas (Cristobal-Azkarate and Arroyo-Rodriguez, 2007).

This pattern of primate diet expansion has also been documented in the human fossil record (Flannery, 1969; Stiner, 2002; Stiner and Munro, 2002). Flannery (1969) described the diet expansion of humans in the Pleistocene as part of the "Broad Spectrum Revolution" in which populations began using different types of resources, including hunting small game. Stiner and Munro (2002) proposed that there were even earlier shifts in the diet that can be documented from including animals in the diet that were easy to capture and later transitions into harder-to-capture animals (as opposed to looking at what taxonomic groups were being eaten). The current study in combination with evidence from the human fossil record and previous work done on howler monkeys, green monkeys, and red colobus monkeys suggests that diet expansion is a common primate response to ecological stressors. Furthermore, it shows that behavioral changes may allow primates to adjust without restructuring their dentition or other anatomy.

Previous studies also have shown that individuals in disturbed habitats have different activity budgets than individuals in undisturbed areas (Altmann and Muruthi, 1988; Eley et al., 1989; Isbell and Young, 1993; Wong and Sicotte, 2007; Silva and Ferrari, 2009; Boyle and Smith, 2010). For example, baboons (Iwamoto and Dunbar, 1983; Altmann and Muruthi, 1988; Eley et al., 1989), gorillas (Watts, 1988), and bonnet macaques (Singh and Vinathe, 1990) spent more time foraging and feeding in degraded areas than individuals living in

high-quality habitats. Female red colobus monkeys in logged and old-growth areas of Kibale also differed in their behaviors, despite similar overall behavioral patterns. As predicted, females in logged areas spent significantly more time feeding than females in old-growth areas and reduced energy expenditure by spending less time on all other activities than females in the old-growth areas. It is notable that the red colobus did not travel more as may be expected when animals must search for food resources; however, this suggests that their behavioral strategy to maintain a positive energy balance is to reduce energy spent traveling to specific resources and instead expand their diet to foods that are readily available. This pattern of reduced travel in poor habitats has also been documented in ruffed lemurs (Ratsimbazafy, 2007).

The increase in feeding time may be the result of having lower quality foods. Females in logged areas fed from a different range of species than females in old-growth areas. Thus, females in logged areas may spend more time feeding to maintain energy intake despite different resource availability. Individuals living in the logged areas ate fruit; whereas, individuals in the old-growth areas never did. A similar increase in fruit eating was observed by Galat Luong and Galat (2005) in logged forests in Senegal. It should be remembered that given the digestive system of the red colobus and the necessity to maintain a particular pH in the gut, fruit is not necessarily a high-quality food; in fact it is likely much less suitable than high-quality young leaves (Davies et al., 1988; Waterman and Kool, 1995; Danish et al., 2006).

Understanding how wild populations respond to degraded habitats is important for understanding interspecific variation, for conservation management planning, and for hypothesizing about the role of the environment in past speciation events (Kennedy and Gray, 1993; Soule et al., 2005). By building on previous studies examining habitat quality and primate food availability within and around Kibale (Chapman et al., 2004; Chapman et al., 2006a; Rode et al., 2006; Emery Thompson et al., 2007), our results can help to inform conservation policy and management practices for this ecosystem. Specifically, these results suggest that red colobus are able to adjust to degraded habitats when there are alternative resources for them and when the habitat is stable. This contributes to our understanding of why red colobus in logged areas of Kibale are able to maintain densities similar to those in old-growth areas, but red colobus in forest fragments are not. These results also support the benefits of protecting forested land, even if it has been degraded previously. Determining under what conditions the endangered red colobus can be flexible and survive is fundamental to determining effective conservation management strategies for Kibale.

Like several previous studies (Galat Luong and Galat, 2005; Cristobal-Azkarate and Arroyo-Rodriguez, 2007; Ratsimbazafy, 2007), our study demonstrates that individuals in disturbed habitats are able to cope by adjusting their foraging strategies; this has significant implications for evolutionary theory and conservation practices where it is necessary to prioritize the protection of different habitats. Additional studies which examine the nutrient content of the foods being eaten in each area (particularly protein availability relative to fiber; Chapman and Chapman, 2002), the nutritional

requirements of red colobus, male energy budgets in different habitats, evaluations of trees species available in each area, sensory basis of food selection, cognitive aspects of foraging, handling time of food resources, travel time/distance between food patches, predation danger, parasite presence, and behavioral observations of differences in time spent on specific activities will help to illuminate the role that food availability has on these feeding differences (Rothman et al., 2012). Furthermore, examining the toxins in the foods that red colobus are feeding on could explain why additional species are being eaten in such small portions in the logged areas. It could be related to the detoxification limitation hypothesis (Freeland and Janzen, 1974; Freeland, 1991), which can help explain feeding behaviors in folivores (reviewed in Marsh et al., 2006). The detoxification limitation hypothesis explains why mammalian herbivores may not be able to specialize in one plant food because of the inability to detoxify plant secondary compounds at a sufficient rate (Freeland and Janzen, 1974). An understanding of the impact of logging on endangered primate populations is essential for management practices and can provide insight into the response of species to ecological changes throughout evolution.

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