CHAPTER THREE

How Does the Golden Monkey of the Virungas Cope in a Fruit-Scarce Environment?

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INTRODUCTION

Understanding the processes determining the density and distribution of species is one of the primary goals of ecology (Boutin, 1990). The importance of this information has increased with the need to develop informed management plans for endangered or threatened species. With respect to primates, these theoretical issues are critical because the tropical forests they occupy are undergoing rapid

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anthropogenic transformation and modification. For example, countries with primate populations are cumulatively losing approximately 125,000 km^2 of forest annually (Chapman & Peres, 2001). Other populations are being affected by forest degradation (logging and fire) and hunting. However, predicting the responses of particular species has often proved difficult.

The blue monkeys (*Cercopithecus mitis*) of Uganda fit this generalization in that it has proven difficult to predict how they will respond to disturbance or to natural variation in forest structure. For example, blue monkey abundance was severely affected by logging at Kibale National Park, Uganda: 15 years after logging, areas had 20–30% fewer blue monkeys than unlogged areas (Skorupa, 1988) and this trend continues 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). Similarly, within Kibale National Park, blue monkeys are common in the north of the park but their numbers gradually decline toward the south (Chapman & Lambert, 2000). There is no corresponding change in forest structure that explains this gradual decline. Thus, it appears that predicting responses of blue monkeys to disturbance or understanding responses to natural changes in the environment are difficult.

The blue monkey has been characterized as a species capable of occupying a variety of habitat types and forest conditions (Lawes, 1991). This forest species has an extremely wide distribution, extending from the forests of southern Sudan to the Eastern Cape Province in South Africa (Lawes, 1990). It occurs in forests from sea level to over 3000 m. Given this wide distribution, it is surprising that blue monkeys are also one of the most recently derived species within the Cercopithecini (Leakey, 1988; Lernould, 1988; Ruvolo, 1988). Their wide distribution, recent origin, and tendency to generate subspecies are generally attributed to high dispersal ability and their capacity for survival in the fragmented forests that existed at the end of the last glacial period centered on 18,000 BP (Lawes, 1990).

The mechanisms that facilitate blue monkeys' having such a wide distribution are poorly understood. However, a number of studies have suggested that blue monkeys have a broad diet (Rudran, 1978a; Struhsaker, 1978; Gautier-Hion, 1988; Butynski, 1990; Lawes *et al.*, 1990; Chapman *et al.*, 2002). This flexibility allows some populations to turn to a diet with a large leaf component (Beeson, 1989), while others to insects (Rudran, 1978a; Butynski, 1990) or flowers (Schlichte, 1978), when preferred fruit is not available (Lawes, 1991). Their flexible diet appears to have a morphological basis: blue monkeys

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have a significantly larger hindgut (caecum and colon) and the surface area of the small intestine is greater than in vervet monkeys (*Cercopithecus aethiops*; Bruorton & Perrin, 1991) and specialized symbiotic gut microflora (Bruorton *et al.*, 1991). Thus, blue monkeys may have the ability to include a larger amount of fibrous leaf material in their diets than other guenons (Lawes, 1991). A high level of folivory, at least on a seasonal basis, has been noted by a number of studies (Rudran, 1978a; Schlichte, 1978; Beeson, 1989; Lawes, 1991). This should allow blue monkeys to do well in marginal or disturbed habitats, and facilitate their survival in areas where there are seasonal shortages of preferred foods. Although it is generally agreed that blue monkeys have adapted to a broad diet, little is known about the dietary requirements of the species and how populations, in what might be thought of as marginal habitats, are able to meet their nutritional requirements. For example, how do populations occupying areas where fruit is scarce obtain an adequate supply of sugars? Because fruit is often a major energy source sustaining primate populations, the density of fruit-eating primates has been suggested to be limited by the lowest seasonal level of fruit availability (Janson & Emmons, 1990; Janson & Chapman, 1999).

This study compares the nutritional ecology of the golden monkey (*Cercopithecus mitis kandti*) of Mgahinga Gorilla National Park, Uganda, to that of the blue monkey (*C. mitis stuhlmanni*) of Kibale National Park, Uganda, approximately 200 km away. These are two very closely related subspecies, with the golden monkey being isolated in the high elevation forests. Interbreeding between subspecies of *C. mitis* has been described (Kingdon, 1971). Mgahinga is a high elevation site (>3000 m) where fruiting trees are extremely rare and are represented by only a few species (Schaller, 1963, 1964; Kalina, 1991). In contrast, Kibale is a midelevation forest (~1500 m) with a relatively diverse and abundant fruiting tree community (Chapman *et al.*, 1997). We describe the diets of each of these populations and then consider the nutritional quality of the foods eaten with respect to protein, fiber, lipids, sugars, and a series of secondary compounds.

METHODOLOGY

Study Areas

Mgahinga Gorilla National Park (MGNP), Uganda (33 km^2) encompasses the slopes of three volcanoes (Mgahinga, 3474 m; Muhabura, 4127 m; and Sabinyo, 3634 m) and is part of the greater Virunga Conservation Area, which covers 434 km^2 (Figure 1). The park lies in the Albertine rift region, which

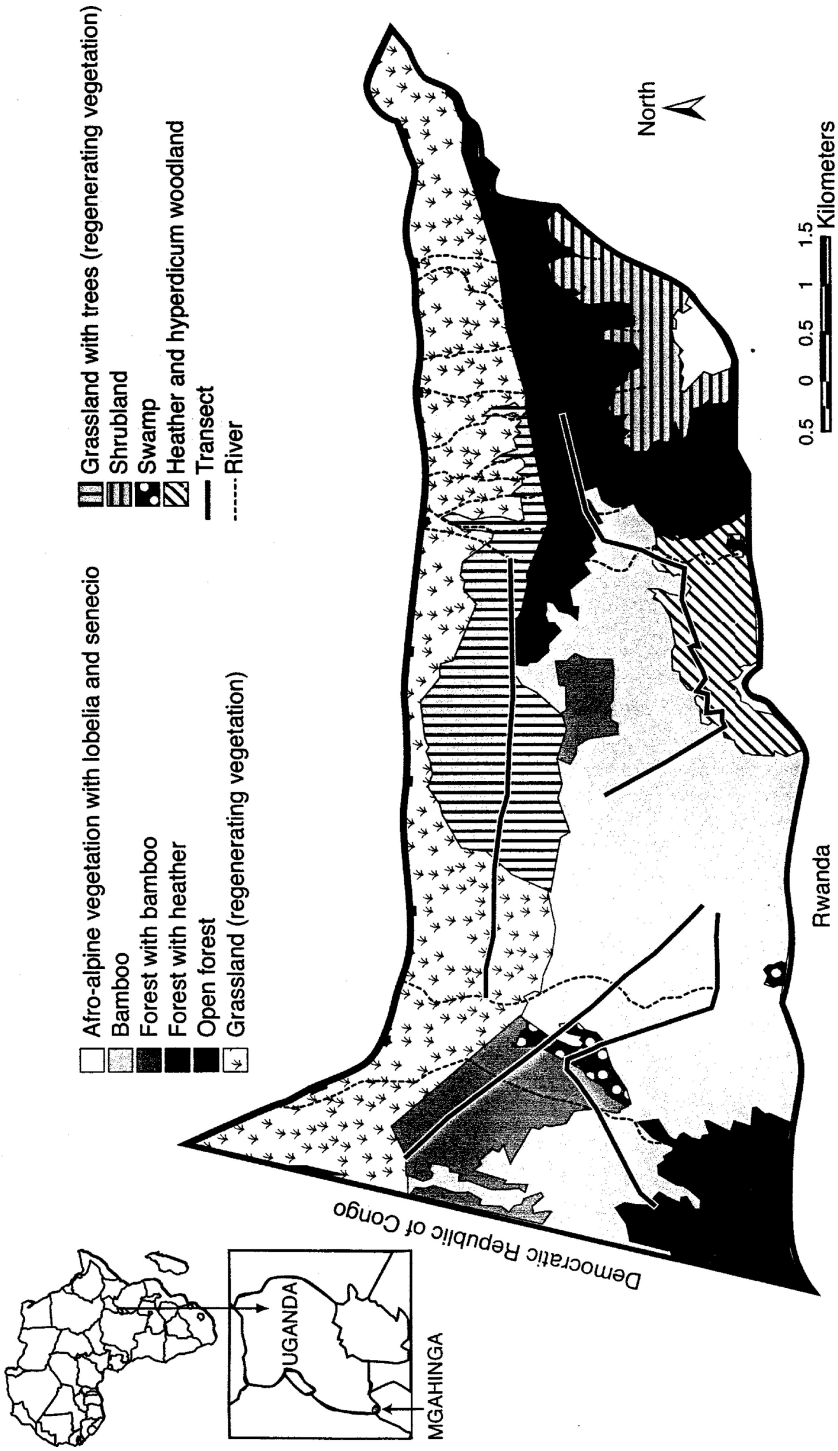

Figure 1. A map of Mgahinga Gorilla National Park, Uganda, illustrating its location within Uganda and the major vegetation types found within the park.

is characterized by a high degree of avian and mammalian endemism (Bibby *et al.*, 1992) owing to its proximity to a glacial forest refugium (Hamilton, 1988). The vegetation types of the park are diverse and are broadly classified into three belts and several zones within the belts (Figure 1). The vegetation belts are alpine, subalpine (ericaceous), and montane forest (Schaller, 1963). The alpine belt is prominent at the highest altitude. The subalpine belt is composed of moorland, montane grassland, and ericaceous zones—the moorland zone being transitional between the ericaceous zone and alpine belt. The ericaceous zone is characterized by the species *Philipa johnstonii*, *Erica arborea*, and *Hypericum revolutum*, which are often densely laden with *Usnea* sp. lichens (Kalina, 1991). The montane forest belt is the most extensive vegetation type, encompassing 40% of the park and is characterized by low tree species diversity (22 species in 2.2 ha, Twinomugisha, 1999). Within this forest belt the most extensive vegetation zone is bamboo (*Arundinaria alpina*). The remaining 33% of the park is covered by grassland and wooded grassland, and was previously under cultivation (Figure 1). The area was declared a National Park in 1991. However, since being gazetted in 1930, it has undergone a number of changes of name, status, size, and management. These changes have had effects on the conservation of the area in terms of habitat degradation and poaching.

Kibale National Park is located in western Uganda near the base of the Rwenzori Mountains (Struhsaker, 1997; Chapman & Lambert, 2000). Kibale is a midaltitude moist evergreen forest that is more diverse than Mgahinga (68 tree species in 4.8 ha; Chapman *et al.*, 1997). The study was conducted at Kanyawara (compartment K-30, ~1500 m elevation). The forest here is considered *Parinari* forest by foresters because of the spreading crowns of *Parinari excelsa*, which can be distinguished on aerial photographs. Canopy codominants include other important timber trees such as *Olea welwitschii*, *Aningeria altissima*, *Strombosia scheffleri*, and *Newtonia buchananii* (Osmaston, 1959; Chapman *et al.*, 1997). Kanyawara receives approximately 1741 mm of rainfall annually (1990–2002), which peaks during two rainy seasons, although rainfall is well dispersed throughout the year, falling on an average of 166 days per year.

Observation of Study Groups

The diet of golden monkeys was quantified during two periods. During the first period (January to September 1998), two already partially habituated groups of golden monkeys were further habituated during the first 2 months. Starting

in March 1998, systematic instantaneous scan samples of feeding behavior were conducted during day-long follows for three consecutive days each month for 7 months. Four scan samples, each lasting 5 min, with 10-min intervals between scans, were conducted each hour on as many individuals as possible. Individuals were observed for 5–10 s and the food item eaten was recorded. During a single 5-min sample period, a feeding observation by any individual on a particular food item was scored only once unless the same individual fed on different parts of the same food plant. Group 1 (Ntebeko group) was followed for 19 days in total, during which 69 h of observations were made. Group 2 (Gatalabana group) was followed for 17 days (85 h). Feeding observations were also recorded opportunistically. Secondary indications (e.g., discarded fruit) were also used, as were interviews of rangers about the foods that they had observed the golden monkey eating. During a second period (January to August 2003) the same methods were used to observe another group for a total of 57 days (485 h). On average, 7 days of observations were conducted each month (range = 3–11 days per month).

Comparative data from Kibale were obtained from Rudran (1978a,b) and Butynski (1990), who collected data using a similar instantaneous scan sample procedure. Butynski (1990) studied five groups of blue monkeys in two subpopulations over a 6-year period (1978–1984). Rudran (1978a,b) studied two groups of blue monkeys between November 1972 and October 1974.

When there are appreciable differences in mean values, variation can be evaluated using the coefficient of variation (CV; Sokal & Rohlf, 1981). We use the CV to evaluate variation in time devoted to different plant parts. The CV was calculated as the standard deviation of the foraging effort devoted to a specific plant part divided by the mean. This value is multiplied by 100 to express the standard deviation as a percentage of the mean.

Plant Collections and Nutritional Analyses

Samples for nutritional analyses were obtained using a tree-pruning pole to cut down limbs, typically from the middle of the tree's canopy. The trees used were located in the same general areas as the groups foraged (with the exception of Group 33, Butynski 1990), but were not necessarily the same tree that the group fed in. No collections were made from trees growing in unusual situations, such as tree fall gaps or forest edges (except for species typically only found in such habitats, such as *Prunus africana* on edges; see Chapman

et al., 2003, for a discussion of sources of variation in nutritional values created by method of collection). Only those food items selected by the animals were collected. For example, if the animals ate leaf petioles, the length of petiole typically consumed was recorded. In Kibale, plant samples were collected at a time when blue monkeys and redtail monkeys (*Cercopithecus ascanius*) were known to be eating these items. Sample collections for the Kibale blue monkeys were part of our long-term studies of the primates of Kibale, and occurred when we were concentrating observations on redtail monkeys (Rode & Chapman, unpublished data).

Samples were dried in the field using a dehydrator that circulated warm air past the samples (the majority of the samples), by using a lightbulb to heat a box containing a series of racks, or by sun drying. All samples were dried at temperatures below 50°C. For samples dried in an oven, the heat setting was at its lowest (37°C). Dried samples were sealed in plastic bags and taken to the University of Florida for analysis.

Dried samples were ground to pass through a 1-mm mesh screen in a Wiley mill (stainless steel). Dry matter mass was determined by drying a portion of each sample overnight at 105°C. Samples were analyzed in duplicate, and replicates were considered acceptable if the relative error was less than 2%. This 2% criterion was applied to dry matter, organic matter, fiber, protein, and saponins.

The protein (nitrogen) content of the plant parts was assessed using Kjeldahl procedures (Horwitz, 1970). Samples were digested using a modification of the aluminum block digestion procedure of Gallaher *et al.* (1975). The digestion mix contained 1.5 g of 9:1 K_2SO_4:$CuSO_4$, and digestion was conducted for at least 4 h at 375 Co using 6 ml of H_2SO_4 and 2 ml of H_2O_2. The nitrogen in the digestate was determined by semiautomated colorimetry (Hambleton, 1977). Measuring total nitrogen provides an estimate of crude protein and traditionally the N content multiplied by 6.25, a conversion factor that has been used as an index of protein levels. A better conversion factor for tropical foliage may be approximately 4.3 (Conklin-Brittain *et al.*, 1999) or 4.4 (Milton and Dintzis, 1981). The 4.3/4.4 conversion factors probably underestimate nitrogen, while the 6.25 overestimates available protein, but it does not necessarily overestimate nitrogen (Conklin-Brittain, *et al.*, 1999). We used a conversion factor of 4.3.

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Fiber (Acid Detergent Fiber [ADF]) was measured using the methods outlined by van Soest (1963) and modified by Goering and van Soest (1970) and

Robertson and van Soest (1980). ADF is a measure of cell wall cellulose and lignin. It has been found to have a strong negative correlation with food selection by some primates (Glander, 1982; Oates *et al.*, 1990). However, ADF is somewhat fermentable, while lignin is not (van Soest, 1982).

The primary components of plant carbohydrates that are easily digestible by mammalian enzymes were quantified using a method that requires differential extractions (80% ethanol) and digestions with colorimetric analysis of filtrates (Hall *et al.*, 1999). This procedure allows an assessment of organic acids and simple sugars (mono- and oligosaccharides). For ease of discussion, we refer to this as an evaluation of sugar content.

Many alkaloids are bitter tasting and perhaps play a role as a feeding deterrent (Harborne, 1993; Roberts and Wink, 1998); however, it has not been demonstrated that primates avoid foods high in alkaloids (Waterman, 1993). The presence of alkaloids was tested using a spot test with Dragendorff's reagent (Waterman, 1993). Dragendorff's reagent is known to sometimes produce false positive results (Waterman, 1993).

Saponins are surfactants and have a "soaplike" foam-forming property in aqueous solutions, hence their name. These compounds are bitter tasting and are found in over 70 plant families. Saponins have been documented to cause bloat in ruminants and have been implicated in diet selection of cattle, but do not influence red colobus diet selection (Chapman & Chapman, 2002). They also have the ability to irritate the digestive tract, and can serve as a steroid hormone precursor (Phillips-Conroy, 1986; Francis *et al.*, 2002). The quantity of saponins present in a 0.25-g sample was indexed using the Froth Test (Fong *et al.*, unpublished guide) using 60 and 1800 s criteria. This relative measure involves shaking the sample in a set fashion and measuring the height of the foam after 60 and 1800 s.

Cyanogenic glycosides are capable of releasing toxic hydrogen cyanide, but their role in deterring herbivory is questionable (Seigler, 1991; Jones, 1998). The presence or absence of hydrogen cyanide was determined by the Feigl–Anger test (Feigl & Anger, 1966; Glander *et al.*, 1989).

To compare the quality of the diet of *C. mitis* at Kibale and Mgahinga, we contrasted the nutritional characteristics in the 10 most frequently eaten foods for two groups of blue monkeys in Kibale (Rudran, 1978a) and the group of golden monkeys studied in 2003. We analyzed 73% of the total possible 210 nutrient–plant combinations (10 species/parts from each of the three populations and seven nutrient/secondary compounds). The majority of the

nutrients/secondary compounds that were not analyzed were from species or parts reported to be eaten by Rudran (1978a,b), but were not observed being eaten during our study and thus were not collected. Percentages were arc-sine square root transformed for correlations between foraging effort and nutritional characteristics. Differences between groups/populations were analyzed taking a univariate (i.e., one-way analysis of variance [ANOVA], contrasting specific nutrients one at a time) and multivariate approaches (i.e., MANOVA contrasting all nutrients in the same analysis). The multivariate approach is somewhat limited, because if one nutrient out of the five continuous nutrients considered (protein, fiber, sugars, lipids, and saponins) could not be measured because of the lack of sample, that species/part had to be dropped from the analysis. Differences in nutrients of the major foods are also illustrated graphically.

RESULTS

Although there are few fruiting tree species in Mgahinga, fruit was a major component of the diet of some golden monkey groups (Table 1). In general, golden monkeys ate fruit less frequently (average 26.3%) than blue monkeys (35.3%); however, fruit eating among blue monkeys at Kibale was highly variable (15–30.1%) and some groups ate less fruit than the average golden monkey group. Two golden monkey groups fed more frequently on young leaves than blue monkey groups from Kibale, but a third golden monkey group used young leaves less frequently than any group from Kibale.

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In terms of the plant parts eaten, the diet of the golden monkeys varied over time and among groups (Table 1). For example, the frequency with which young leaves (including bamboo) were eaten varied among groups from 11.3 to 58.6%, while the use of insects varied from 8.0 to 30.5% (Table 1). Blue monkey diets from Kibale were less variable than those of the golden monkey. The average coefficient of variation for the major plant parts (fruits, young leaves, flowers, and insects) was 31.2% for blue monkeys from Kibale ($n = 6$ groups), 46.4% for all studies of *C. m. stuhlmanni* ($n = 11$), and 68.3% for golden monkeys ($n = 3$).

Au: Add Beeson, 1978, to the list.

Bamboo (*Arundinaria alpina*) was particularly important in the diet of the golden monkeys and they fed on bamboo leaves, culms, and shoots. The group observed in the 2003 field season ate bamboo for an average of 52.4% of their foraging time and in 1 month bamboo foraging constituted 61.7% of their

Table 1. The percentage of foraging effort devoted to different plant parts by diet of different subspecies of *Cercopithecus mitis*

Species	FR	ML[a]	YL	FL	Insect	SD	PT	ST	Other	Source	Study site, country
C. mitis stuhlmanni	54.6	2.3	16.6	3.7	16.8	2.5		1.1	2.4	Cords, 1986	Kakamega Forest, Kenya
C. mitis stuhlmanni	55.8		21.8	4.55	8.6	1.5				Fairgrieve, 1995	Budongo, Uganda
C. mitis stuhlmanni	44.9		29	6.2	9.7	5.9				Fairgrieve, 1995	Budongo, Uganda
C. mitis stuhlmanni	37		14	20	11					Schlichte, 1978	Lake Kivu, DRC
C. mitis stuhlmanni	42.7		19.1	11.7	19.8					Rudran, 1978a,b[b]	Kanyawara, Kibale, Uganda
C. mitis stuhlmanni	30.1		22.8	9.8	35.9					Butynski, 1990	Ngogo, Kibale, Uganda
C. mitis stuhlmani	22.2		34.3	7.4	35.4				0.7	Butynski, 1990	Kanyawara, Kibale, Uganda
C. mitis stuhlmani	28.9		22.4	2.9	45.4				0.4	Butynski, 1990	Kanyawara, Kibale, Uganda
C. mitis stuhlmani	22.1		33.3	7.8	35.1				1.7	Butynski, 1990	Kanyawara, Kibale, Uganda
C. mitis stuhlmani	15		35.4	7.4	41.8				0.4	Butynski, 1990	Kanyawara, Kibale, Uganda
Average[c]	35.3	–	24.9	8.2	25.9	–	–	–	–		
C. mitis erythrarchus	51.7	14.0[d]	11.8[e]	13.4	5.8			0.4	2.8	Lawes, 1991	Cape Vidal, South Africa
C. mitis erythrarchus	59.4		23.9	5.5	<5					Scorer, 1980, in Lawes, 1991	Cyprus, South Africa
Average	55.6	–	17.9	9.45	5.8	–	–	–	–		
C. mitis doggetti	47.4		6.2	6.2	24.9	9.3			6.2	Kaplin, 2001	Nyungwe, Rwanda
C. mitis nyasae	24.2		51.9	17.9	0.3					Beeson, 1987	Zomba, Malawi
C. mitis labiatus	91.1		3	2.1					3.8	Lawes *et al.*, 1990	Ngoye Forest, South Africa
C. mitis kandti	31.1	0.24	47.4	1.38	10.5		0.1	5.8	3.5	This study, Time 1 Group N	Mgahinga, Uganda
C. mitis kandti	36.7	0	11.3	14.0	30.5		0.5	7	0.02	This study, Time 1 Group G	Mgahinga, Uganda
C. mitis kandti	11.0	0	58.6	21.9	8.0		0.08	0.3	0	This study, Time 2	Mgahinga, Uganda
Average	26.3	–	39.1	12.4	16.4	–	–	–	–		

Methods of determining foraging effort vary among studies. FR = fruit; ML = mature leaves; YL = young leaves; FL = flowers; SD = seeds; PT = pith; ST = stems; DRC = Democratic Republic of Congo.

[a] Many studies provide only the total amount of leaves eaten and do not separate young versus old leaves; in this case no information is presented for mature leaves.

[b] Group 1 from February 73 to January 74.

[c] Averages only calculated for parts that were consistently recorded among studies.

[d] Dry leaves included with mature leaves.

[e] Leave buds included with young leaves.

foraging time (see also Aveling, 1984; Kingdon, 1971). No one plant species was this important in the diet of blue monkeys in Kibale: the most frequently eaten plant (*Ficus exasperata*) constituted only 15.1% of a group's foraging effort.

The golden monkey fed on few food sources. In 2003 the golden monkey group fed on between 3 and 12 species of plants in any given month. Over a period of 8 months, only 16 plant species were eaten. Four plant species were added from opportunistic observations. The golden monkey is known to feed on a total of 33 plant species. In contrast, Rudran (1978a) reported that over an annual cycle the blue monkeys at Kibale (group 1) fed on 59 plant species and 101 specific food items.

Comparing the diets of blue monkeys of Kibale and the golden monkeys of Mgahinga to other published accounts of *C. mitis* diets confirms previous assessments of the dietary flexibility of this species (Lawes, 1991). The foraging effort devoted to fruits was as high as 91.1% and as low as 11.0% (Table 1). Similarly the foraging effort devoted to eating leaves was as high as 58.6% and as low as 3%.

Conducting univariate analysis of variance considering each nutritional character one at a time revealed that the diets of golden and blue monkey groups did not differ in terms of any of the continuous nutritional variables (protein, fiber, lipids, sugars, or saponins; $p > 0.1$). Considering this question from a multivariate perspective we contrasted the nutritional content of the most frequently eaten food items among groups using a MANOVA and this analysis revealed no overall effect (Wilks' $\lambda = 0.134$, $F = 1.388$, $p = 0.328$). These patterns were graphically illustrated by producing a three-dimensional plot showing the position of the top 10 foods in relation to their protein, fiber, and lipid contents (Figure 2). This figure illustrates little structuring of the different populations/groups. However, note that bamboo has the highest protein level for the Mgahinga group and is somewhat separated from other foods.

No group had a food item in their top 10 most frequently eaten foods that had cyanogenic glycocides. Of the top 10 most frequently eaten foods by blue monkeys in Kibale, 40% of the species examined tested positive for alkaloids in one group, 60% tested positive in a second group. In the top 10 foods in the diet of the golden monkey group, 50% of the species examined tested positive for alkaloids.

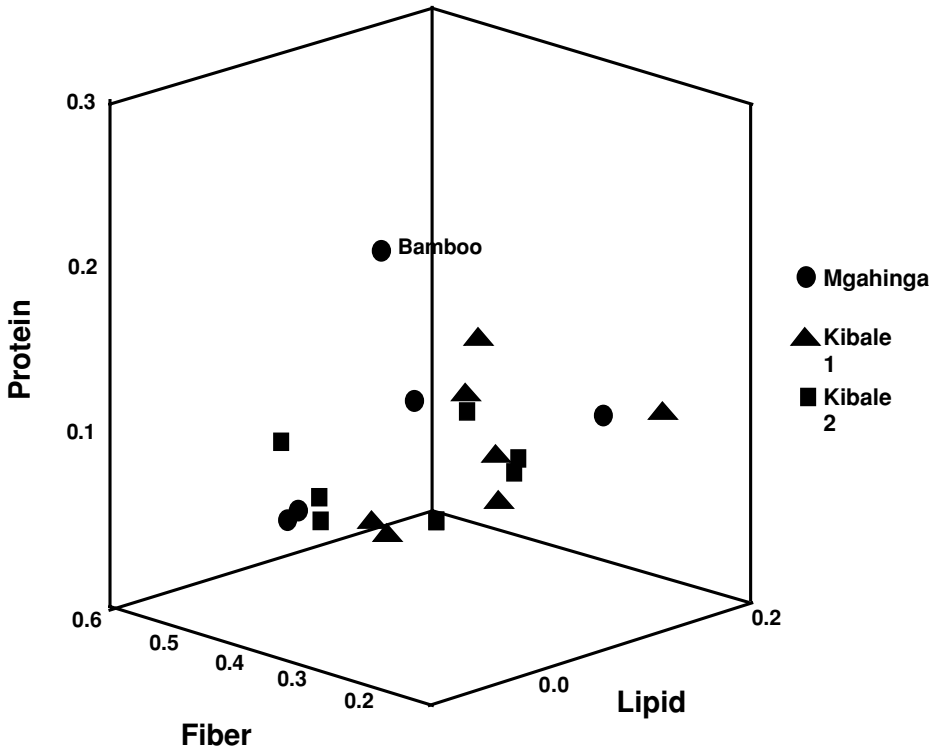

Figure 2. A plot of the nutrient composition of foods eaten by the golden monkey from Mgahinga National Park, Uganda, and two groups of blue monkeys from Kibale National Park, Uganda.

Correlations between foraging effort (the number of point samples observed feeding on an item/all feeding point samples) and nutritional components of the foods suggest that one of the Kibale groups tended to avoid food high in fiber ($r = -0.790$, $p = 0.001$). No other correlation between foraging effort of Kibale blue monkeys and nutritional components of the foods were found. For the Mgahinga group there were no correlations between any of the nutritional components and foraging effort.

Ultimately the quality of an animal's diet affects fecundity and fitness. The adult female-to-infant ratio was contrasted among different subspecies of *C. mitis* (Table 2). Golden monkey groups had a lower infant-to-adult female ratio than blue monkey groups (*C. m. stuhlmanni*), as well as *C. m. erythrarchus* and *C. m. labiatus* groups, suggesting that fewer infants are born into golden monkey groups (Table 3).

Table 2. The age/sex composition of different groups of different subspecies of *Cercopithecus mitis*

Species	Total	AM	AF	Imm.	Inf.	Unk.	Source
C. m. stuhlmanni	45	1	17	18	9	0	Cords, 1986
C. m. stuhlmanni	35	1	19	6	9	0	
C. m. stuhlmanni	34	1	17	11	5	0	
C. m. stuhlmanni	28	1	9	12	3	3	
C. m. stuhlmanni	21	1	9	7	4	0	
Average Kakamega	32.6	1	14.2	10.8	6	0.6	
C. m. stuhlmanni	24	1	11	8	4	0	Rudran, 1978a,b
C. m. stuhlmanni	13	1	5	6	1	0	
C. m. stuhlmanni	27	1	12	11	3	0	
C. m. stuhlmanni	13	1	4	7	1	0	
C. m. stuhlmanni	27	2[a]	9	12	4	0	
C. m. stuhlmanni	17	1	8	7	1	0	Butynski, 1990
C. m. stuhlmanni	11	1	6	3	1	0	
C. m. stuhlmanni	24	1	18	5	0	0	
C. m. stuhlmanni	19	1	8	8	2	0	
C. m. stuhlmanni	18	1	12	3	2	0	
Average Kibale	19.3	1.1	9.3	7	1.9	0	
Average all	23.7	1.1	10.9	8.3	3.3	1.2	
C. m. stulhmanni							
C. m. erythrarchus	26	2	9	13	2	0	McLeod, 2000
C. m. erythrarchus	22	1	7	8	6	0	
C. m. erythrarchus	22	1	8	13	0	0	
Average	23.3	1.3	8	11.3	2.7	0	
C. m labiatus	16	1	6	6	3	0	Lawes *et al.*, 1990
C. m. labiatus	21	1	8	8	4	0	
Average	18.50	1	7	7	3.5	0	
C. m. kandti	41	5[a,b]	11	17	3	4	This study
C. m. kandti	38	1	14	21	2	0	This study
C. m. kandti	41	1	14	26	0	0	This study
Average *C. m. kandti*	40	2.3	13	21.3	1.7	1.3	

Au: add McLeod, 2000, to the list.

AM = adult males; AF = adult females; Imm. = immatures; Inf. = infants; Unk. = unknown.
[a]Sometimes two to five males are seen within 25 m of one another and males who spend a majority of their time away from social groups may join a group during the mating season (Cords, 1986).
[b]Three males, which have been in the group at least for 14 months, were now feeding separately from the group. The remaining subdominant male feeds with the group, but seems to remain on the peripheral.

Table 3. Comparison of group composition data for subspecies of *C. mitis*

Species	Infant-to-adult female ratio
C. m. stuhlmanni (Kibale)	0.2043
C. m. stuhlmanni (Kakamega)	0.4225
C. m. stuhlmanni (all)	0.2988
C. m. labiatus	0.5000
C. m. erythrarchus	0.3333
C. m. kandti	0.1282

DISCUSSION

The density and species richness of fruiting trees at Mgahinga is very low. Despite this fact, the golden monkeys appear to cope well. Some groups focused their feeding effort on a few fruiting species and trees, while other groups relied heavily on flowers and leaves and all groups obtained their protein from bamboo. The overall nutritional characteristics of the foods used by the Mgahinga animals were not different from those foods used by the Kibale groups. This suggests that golden monkeys can substitute nonfruit foods for fruits and still obtain a balanced diet.

In general, fruits are known to provide an easily assimilated source of sugars and energy, but have been suggested to supply inadequate amounts of protein (Gaulin, 1979). This may explain why some populations of *C. mitis* appear to select foods based on their protein content (Beeson, 1989; Lawes, 1991). However, none of the three groups studied here selected foods high in protein (but see discussion of bamboo below). On the other hand, protein is likely readily available from some easily digestible insects, or less readily digestible young leaves (Lawes, 1991). Golden monkeys at Mgahinga consistently fed on bamboo. Bamboo has a relatively high protein content (22% of dry matter), but it is a very poor source of sugars (just trace amounts). Bamboo was eaten in every month of the year and is probably an important source of protein and vital to the survival of golden monkeys in these mountain forests. The importance of bamboo is suggested by the fact that in Mgahinga there were higher sighting rates and densities of golden monkeys in the bamboo zone and in forests with bamboo vegetation types (Twinomugisha *et al.*, 2003).

The golden monkeys obtained their sugars from the few fruits that were available, from flowers, and from the leaves of *Nuxia congesta*, which had higher

levels of sugars (19%) than many fruits eaten by the blue monkeys in Kibale. *Hypericum revolutum* flowers were a particularly important source of sugars (29% of dry weight) and were available and eaten year round. There was no evidence of avoidance of secondary compounds and it may be that plant diet selection is little affected by secondary compounds in these monkeys. Wrangham *et al.* (1998) documented that three cercopithecines (*C. mitis*, *C. ascanius*, and *Lophocebus albigena*) had higher absolute intake levels of secondary compounds than chimpanzees (*Pan troglodytes*), suggesting a high tolerance. Only one of our study groups at Kibale appeared to select foods that were low in fiber, suggesting that fiber is an antifeedant for these animals. In contrast, Conklin-Brittain *et al.* (1998) demonstrated that three species of cercopithecines (*C. mitis*, *C. ascanius*, and *Lophocebus albigena*) had a constant level of intake of the different fiber fractions throughout the year, suggesting that even when they could have avoided eating foods with high fiber content they did not do so. However, if the foods typically eaten by these animals were not high in fiber there may have been no need to avoid such foods. Thus, the role of fiber in cercopithecine diet selection warrants further consideration.

This study confirms the suggestion from a number of studies that *C. mitis* has a very flexible dietary strategy (Rudran, 1978a; Struhsaker, 1978; Gautier-Hion, 1988; Beeson, 1989; Butynski, 1990; Lawes *et al.*, 1990; Lawes, 1991), and cautions against evaluating habitat suitability on the basis of only the availability of different types of foods (e.g., the scarcity of fruit) and without assessing the nutritional value of foods. Golden monkeys appear to be able to obtain an adequate diet by balancing the nutrients they need from a few plant species that are available year-round. Thus they derive their protein from bamboo and their sugars from fruits, flower, and leaves. In addition, the golden monkey group fed on between 3 and 12 plant species in any given month and only 16 plant species were recorded in the diet over the entire study period.

This is not to suggest that the diet of the golden monkey at Mgahinga was optimal in any sense, but merely adequate, and there is evidence to suggest that adopting this diet may have a reproductive cost. Nutrition can affect the age at which a female becomes sexually mature, the ovulatory cycle, the length of time it takes to conceive, interbirth intervals, birth rates, and infant survival (Koenig, 2000). As a result, the relative reproductive success of a population provides information regarding the quality of the population's diet that may integrate a long time frame. Golden monkey groups had a lower infant-to-adult female ratio than any of the other blue monkey subspecies for which data exists,

suggesting that fewer infants are born into these groups (Table 3). While we found no differences in the nutritional quality of the populations' diets, the data on infant-to-adult female ratio may still indicate that golden monkeys are under greater nutritional stress than other subspecies. Thus, further investigation of the cause of the lower infant-to-adult female ratio is warranted, and this should include nutritional elements not evaluated here (e.g., minerals).

Cords (1986) reported that pregnant and lactating female blue monkeys eat 63–83% less fruit than other females and 1.2–3 times as many insects and suggested that this represents the added protein needs associated with childbirth and rearing. The fact that the relative densities of golden monkeys in Mgahinga is highest in the bamboo zone and in forests with bamboo vegetation types (Twinomugisha *et al.*, 2003), that bamboo is a major food item, and that it provides a significant proportion of the group's protein suggests that bamboo is a critical resource for these animals. As a result, efforts should be increased to stop the illegal extraction of bamboo from the national park, and permission for the extraction of bamboo in community-based conservation development projects (Ugandan Wildlife Authority, 1996) should be critically evaluated.

Au: Pls add Ugandan Wildlife Authority, 1996, to the reference list.

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