

Scale Issues in the Study of Primate Foraging: Red Colobus of Kibale National Park

Colin A. Chapman,^{1,2*} Lauren J. Chapman^{1,2}, and Thomas R. Gillespie¹

¹Department of Zoology, University of Florida, Gainesville, Florida 32611

²Wildlife Conservation Society, Bronx, New York 10460

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ABSTRACT Diet data have been used to address a number of theoretical issues. We often calculate the proportion of time spent eating different foods (e.g., fruits, leaves) to place species into dietary categories and contrast morphological or behavioral traits among categories. Yet we have little understanding of how flexible species can be in terms of the plant parts and species consumed. To address this issue, we analyzed data on the diets of red colobus monkeys (*Procolobus badius*) from Kibale National Park, Uganda, to evaluate temporal and spatial variability in the plant parts and species eaten. After considering observer differences and sampling issues, we evaluated how different a group's diet could be if samples were taken in different years. We found that the diet of the same groups showed significant, consistent changes over a 4-year period. For example, the time spent feeding on leaves increased from 56% in 1994 to 76% in 1998. The plant parts and species eaten by eight groups

inhabiting different types of forest (e.g., pristine, logged, riverine) varied among groups. The largest interdemographic difference was seen in the use of young leaves (38%). Dietary differences were also found between groups with overlapping home ranges (41–49% overlap). Different subspecies of *Procolobus badius* also varied in diet; however, this variation was often not of the magnitude documented within Kibale for the same population. The fact that diet can vary considerably over small spatial and short temporal scales within the same species raises the intriguing question as to what level of interspecific difference is biologically significant for addressing particular questions. We conclude that behavioral flexibility blurs our traditional stereotypic assessment of primates; a study of one group that occupies a specific habitat at one point in time may not adequately represent the species. *Am J Phys Anthropol* 117:349–363, 2002.

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Over the last three decades there has been an impressive accumulation of data on diets of wild primates and a growing appreciation for interdemographic variation in diet (Richards, 1974; Struhsaker and Oates, 1975; Chapman and Chapman, 1990, 1999; Davies, 1991; Dasilva, 1992, 1994; Strier, 1994; Davies et al., 1999). For example, while colobine monkeys were initially described as strict folivores (Hill, 1964; Napier, 1970), evidence is steadily accumulating that some populations are not obligate leaf-eaters, and fruits and seeds can constitute a large proportion of their diet (McKey, 1978; Davies et al., 1988, 1999; Yeager, 1989; Dasilva, 1994; Davies, 1994). Similarly, while seasonal variation in diet has been appreciated for some time (Clutton-Brock, 1977; Chapman, 1989; Dasilva, 1994), recent long-term studies are demonstrating strong interannual differences in the composition of a group's diet (Altmann, 1998).

To make generalizations or to formulate theoretical contributions, dietary data have traditionally been used to calculate the average proportion of feeding time devoted to consuming different types of foods, which typically involves some combination of fruits, seeds, leaves, flowers, gums, and insects. Species are then categorized (e.g., frugivore, folivore,

frugivore/insectivore), and contrasts are made among species in different categories (Milton and May, 1976; Clutton-Brock and Harvey, 1977; Terborgh, 1983; Kay, 1984; van Schaik, 1989; Sterck et al., 1997; Koenig et al., 1998). For example, folivores and frugivores have often been compared with respect to behavioral characters such as day range length, home range size, degree of intra- vs. intergroup competition, and ability to withstand habitat disturbance (Clutton-Brock and Harvey, 1977; Harvey et al., 1987; Johns and Skorupa, 1987; Isbell, 1991; Grant et al., 1992, Chapman et al., 1999). Similarly, comparisons are made among species placed into different dietary categories with respect

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*Correspondence to: Colin A. Chapman, Department of Zoology, University of Florida, Gainesville, FL 32611.
E-mail: cachapman@zoo.ufl.edu

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to morphological traits such as dentition (Kay, 1984; Anapol and Lee, 1994) and gastrointestinal tracts (Chivers and Hladik, 1980). Furthermore, diet data have been used to evaluate interspecific interactions, whereby detailed comparisons are made of the plant species and parts eaten (Struhsaker and Oates, 1975; Struhsaker, 1978; Terborgh, 1983; Waser, 1987). A higher degree of overlap in diet in sympatric species is suggested to reflect more intense interspecific competition (for consideration of limitations of such interpretations, see Waser, 1987).

While a few early studies documented that some species have variable diets (Richards, 1974; Rudran, 1978a,b), most theoretical studies that contrasted species placed into dietary categories were made prior to the accumulation of sufficient data to consider spatial and temporal dietary variability. These early studies were limited by the nature of available data, and typically compared investigations of a year or less in duration, conducted in one geographical region.

In this paper, we analyze spatially explicit dietary data on red colobus monkeys (*Procolobus badius*) in Kibale National Park, Uganda. After considering observer differences and sampling issues, we quantify dietary variability, both in terms of plant parts (e.g., fruit, young leaves) and specific plant species and parts. Contrasts are made on the same group among 4 years, among widely separated groups (i.e., eight groups each separated by up to 15 km; some were in relatively pristine habitats, while others were in areas that had experienced various forms of human modification), and between neighboring groups with overlapping home ranges. We evaluate how spatial variation in forest structure and diet can influence how we interpret data on dietary overlap and competition. Next, we take advantage of the fact that Kibale has been the site of a number of previous studies, and examine whether the patterns seen in the red colobus are of a magnitude observed in other primate species. Finally, the magnitude of dietary variation quantified from within Kibale is evaluated with respect to the dietary variability among colobine populations from sites across Africa. These comparisons are used to evaluate how temporal and spatial variation in diet may influence conclusions derived from comparative studies.

METHODS

Study sites

Kibale National Park (766 km²) is located in western Uganda (0°13'–0°41' N and 30°19'–30°32' E) near the foothills of the Ruwenzori Mountains (Fig. 1; Struhsaker, 1975, 1997; Skorupa, 1988; Chapman et al., 1997). The park consists of mature, midaltitude, moist semideciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and plantations of exotic trees (1%; primarily *Cupressus lusii-*

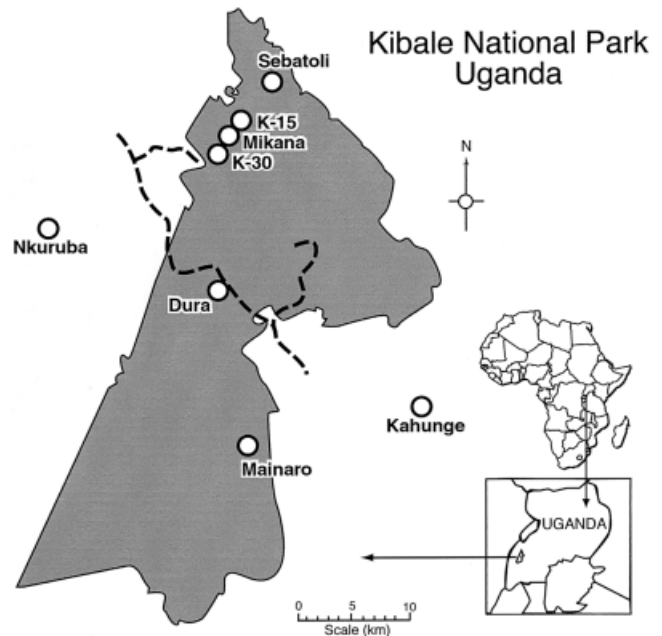


Fig. 1. Map showing location of Kibale National Park, Uganda, and eight sites where diets of red colobus (*Procolobus badius*) were studied.

tanica, *Pinus patula*, *P. caribaea*, and *Eucalyptus* spp.; Chapman and Lambert, 2000). Mean annual rainfall in the region is 1,750 mm (1990–1999, or 1,543 mm from 1903–1999); the mean daily minimum temperature is 15.5°C; and the mean daily maximum temperature is 23.7°C (1990–1999, Chapman and Chapman, unpublished data). Rainfall is bimodal, with two rainy seasons generally occurring from March–May and September–November.

Observations of red colobus were made at eight sites distributed throughout the park or just outside of the park (Fig. 1). Within Kibale, there is an elevational gradient from north to south (1,590 to 920 m), which corresponds to a north to south increase in temperature and decrease in rainfall (Howard, 1991; Struhsaker, 1997). This environmental gradient, other naturally varying abiotic and biotic conditions (e.g., soil type, elephant activity), and varying histories of human modification to the forest have all resulted in the red colobus groups in these eight sites experiencing different environmental conditions.

The most northern site, Sebatoli (elevation, 1,500 m; 1997 rainfall, 1,491 mm), is considered *Parinari* forest by foresters because the spreading crown of *Parinari excelsa* can be distinguished on aerial photographs. The canopy here is dominated by timber trees such as *Parinari excelsa*, *Carapa grandiflora*, *Olea welwitschii*, *Aningeria altissima*, *Strombosia scheffleri*, and *Newtonia buchanani* (Osmaston, 1959). Kibale received National Park status in 1993. Prior to 1993, it was a Forest Reserve, gazetted in 1932, with the goal of providing a sustained production of hardwood timber (Osmaston, 1959; Chapman

and Chapman, 1997; Struhsaker, 1997). As a result, the forest near Sebatoli was commercially logged in the late 1960s. We were unable to obtain information on the level of extraction. However, detailed quantification of stand structure suggests that the level of extraction was similar to or slightly lower than in an area just to the south, K-15 forestry compartment (Chapman and Chapman, unpublished data), in which the harvest averaged 21 m³/ha or approximately 7.4 stems/ha (Skorupa, 1988; Struhsaker, 1997). Incidental damage in the K-15 forestry compartment was much higher, and it is estimated that approximately 50% of all trees were destroyed by logging and incidental damage (Skorupa, 1988; Chapman and Chapman, 1997). Just to the south is the K-14 forestry compartment, a 405-ha forest block that experienced low-intensity selective felling from May–December 1969 (averaging 14 m³/ha or 5.1 stems/ha). Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage (Skorupa, 1988; Struhsaker, 1997). The study group used an area called Mikana that was more heavily exploited than the typical area of this forestry compartment (Chapman and Chapman, 1997).

Kanyawara (K-30 Forestry Compartment, elevation = 1,500 m) is a 282-ha area that has not been commercially harvested. However, prior to 1970, a few large stems (0.03–0.04 trees/ha) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa, 1988; Struhsaker, 1997). At the Dura River (elevation = 1,250 m, 1997 rainfall = 1,500 mm), the forest is no longer considered a *Parinari* forest, as *P. excelsa* and the timber tree species associated with it are relatively rare. *Pterygota mildbraedii*, *Cola gigantea*, *Pipadeniastrum africanum*, and *Chrysophyllum albidum* are the dominant canopy species (Kingston, 1967). Further south at Mainaro (elevation = 1,200 m, 1997 rainfall = 1,394 mm), the forest is dominated by *Cynometra alexandri* and affiliated species (Kingston, 1967). At both the Dura River and Mainaro sites, a few timber trees have been extracted by pitsawyers (approximately 0.1 trees/ha), but this activity has had little impact on the forest. The site furthest to the south is Kahunge (elevation = 1,220 m). This is a more seriously degraded site, as it is outside the park boundaries. The remaining forest has been reduced to a thin strip along the banks of the Mpanga River. Topographic maps from 1959 depict a similar level of forest cover, suggesting that the area has been degraded for several decades.

The last site is to the east of the park, where a series of forest fragments is found within a matrix of small-scale farmland (Onderdonk and Chapman, 2000). These forests are usually in areas unsuitable for agriculture, such as swampy valley bottoms or steep sides of volcanic craters. The group of red colobus inhabiting the forest around Crater Lake Nkuruba was selected for study because the forest

surrounding this crater lake is protected by a conservation education school/ecotourism site we established in 1993. This 9.2-ha patch has relatively intact forest along the steep crater walls and swamp forest to one side. The hunting of primates ceased in the entire region in the early 1960s (Struhsaker, 1975; Skorupa, 1988; Chapman and Onderdonk, 1998). Detailed enumeration of the tree communities in these areas is provided in Chapman et al. (1997) and Onderdonk and Chapman (2000).

Behavioral observations

Behavioral observations of red colobus were made at these eight sites for a total of 3,355 hr (July 1994–June 1999 at Kanyawara K-30 for 2,425 hr; August 1996–May 1997 at K-15 for 85 hr; August 1999–December 1999 at Mikana for 166 hr; July 1996–June 1997 at Sebatoli (248 hr), Dura River (116 hr), and Mainaro (117 hr); July 1995–June 1996 at Kahunge for 58 hr; and August 1999–December 1999 at Crater Lake Nkuruba for 140 hr). Note that the time spent observing some of these groups is small and typically would not be used to describe a species, unless it was a new description (see below for a consideration of sampling effort).

We used an observational method that closely approximates the methods used in a number of previous studies in Kibale (Waser, 1974; Struhsaker, 1975; Butynski, 1990). During each half-hour the observer was with the group, five point samples were made of different individuals. If the animal was feeding, the species and plant part (e.g., fruit, young leaf, and leaf petiole) were recorded. We made an effort to avoid repeatedly sampling particularly conspicuous animals by moving throughout the group when selecting subjects and by sampling animals that were both in clear view and those that were more hidden. These behavioral observations were conducted by L.J.C., C.A.C., volunteers (n = 4) from the United States, and a team of three Ugandan field assistants. The field assistants have worked with us since 1990 and knew the tree species and monkey age-classes prior to the start of the project. The field assistants were supervised by C.A.C. and L.J.C. when they were in the field (27 months) and in their absence by volunteers.

From May 1998–August 1998, T.R.G. conducted intensive observations of a group of 24 (Group 1) for 4 days in 1 week and a group of 48 (Group 2) for 4 days the next week, for a total of 576 hr. Both groups were in the Kanyawara area, close to the Makerere University Biological Field Station. During this period, two observers typically recorded data simultaneously. For all other data sets, only one observer recorded data on a group at one time. Following this study, these groups were watched for 5 days a month from August 1998 until June 1999.

Detailed training was conducted before a new observer started recording diet data. Subsequent to this training, interobserver reliability was assessed by having the new individual observe the foraging

activity of the same animal being watched by C.A.C. (all assistants and volunteers). The first 30 foraging bouts for new observers agreed with those of C.A.C. in >97% of occasions (range, 97–100%; mean, 98.8%). In those instances where there were disagreements, they typically occurred with respect to assessing the stage of maturity (e.g., ripe vs. unripe fruit or mature vs. young leaves, particularly for *Celtis africana*, a species with small leaves).

At locations far from our field camp (e.g., Sebatoli, K-15, Dura River, Mainaro, or Kahunge), observations were made during 2 consecutive days each month. On the first day, an attempt was made to locate the study group early in the morning and follow it until late afternoon. This assisted in locating the same group early the next morning. At Kanyawara (K-30), Mikana, and Nkuruba, observations were made during 5 consecutive days each month (except between July 1996–May 1997 at K-30, when they were made during 2 consecutive days a month).

To evaluate home range overlap between neighboring red colobus groups, the perceived center of mass of the group was plotted on detailed trail maps every 30 min (the grid-like trails were spaced between 50–100 m apart; Waser, 1974; Olupot et al., 1994). From these descriptions of day paths, detailed maps were made of all grids used by the groups, and the home range of the group was considered as the sum of the areas of all grids entered during the study.

To evaluate how small-scale spatial variation in diet can influence our interpretation of dietary overlap, we simultaneously observed neighboring groups of red colobus (Groups 1 and 2) and two groups of black-and-white colobus (*Colobus guereza*, from August 1998–June 1999) that had home ranges that were entirely within the home range of one of the groups of red colobus (Group 1). The two groups of black-and-white colobus were observed for 642 hr (354 hr, Group 1; 288 hr, Group 2), using the same observational approach described for red colobus.

Availability of food trees

To determine the availability of food trees at the different sites, vegetation transects (200 × 10 m) were established at 6 of the 8 study sites (12 transects at Kanyawara K-30, 5 at Kanyawara K-15, and 4 at each of the Dura River, Mainaro, Sebatoli, and Kahunge sites). At Kanyawara (K-30 and K-15), transect location was selected at random from within existing trail systems (Chapman and Chapman, 1997). At the Mainaro, Dura River, and Sebatoli sites, where there were no preexisting trails, transects were established perpendicular to each other at 50–100-m intervals. At Kahunge, transects were placed parallel to the river, because the forest was limited to this thin riverine strip. This regime produced a total sampling area of 6.6 ha (2.4 ha at Kanyawara K-30, 1.0 ha at Kanyawara K-15, and 0.8 ha at Dura River, Mainaro, Sebatoli, and Kahunge). Each tree greater than 10 cm diameter at

breast height (DBH) within 5 m of each side of the trail was individually marked with a numbered aluminum tag and measured (DBH). This produced a sample of 2,432 trees (1,173 trees at Kanyawara K-30, 244 at Kanyawara K-15, 338 trees at Dura River, 293 trees at Mainaro, 322 at Sebatoli, and 62 at Kahunge).

We examined the use of particular plant species relative to availability in even more detail for the neighboring groups of red colobus first observed by T.R.G. For these groups, all trees (>10 cm DBH) of the commonly used species were mapped in detail throughout the groups' home ranges. This was done by searching the area within each of the grids formed by the trail system and recording the number and size of targeted species.

Statistical evaluations

Differences in estimates of primate diets can arise from a number of sources. Here we consider inter-observer differences, short-term sampling differences (i.e., those occurring by sampling different individuals within a day), longer-term sampling differences (from days to years), and differences among groups over increasing spatial scales (from neighboring groups to groups separated by thousands of miles).

When an observer watches a group for a few days a month, she/he is taking a sample of the true diet that is represented by the number of animals observed and the number of observation days. To assess how different one set of observations (a sample) can be from another, we analyzed the detailed behavioral data collected from May 1998–August 1998 by T.R.G. (576 hr) and contrasted the diet obtained from sampling a group on days 1 and 3 vs. days 2 and 4. We calculated the percentage of total feeding time spent eating different plant parts during each of the pair of days and contrasted diets in terms of the most frequently eaten parts (young leaves, mature leaves, leaf petioles) with a paired *t*-test (with arcsine square root transformed data, paired by sampling interval-week). Only the most frequently eaten plant parts were considered, because differences in rarely eaten items will occur simply by chance with a small sample. This analysis assumes that samples taken 12 days apart are independent.

Using the data set collected in the same area (K-30) over 4 years, we examined the effect of sampling at different intensities (i.e., intensely over a short period, or scattered observations over a longer period). To do this, we contrasted a random sample of foraging events vs. a sample of exactly the same size that had a random starting point. We chose a sample equal to 150 hr of observations, a sample size often seen in the literature to describe a species diet. We ran this simulation 30 times, and contrasted the estimated diets using a *t*-test on arcsine square root-transformed data. We also contrasted the diets calculated by each approach against a "true" value with a one-sample *t*-test, where the "true" value was that

calculated from the cumulative data set involving all months of sampling in this area.

Unless otherwise stated, all data concerning analyses of diets used the percentage of time devoted to eating a particular plant part, and the percentage was arcsine square root-transformed. Where appropriate, paired *t*-tests were performed (i.e., if samples were paired by sampling time or group). Interannual dietary differences were assessed by calculating the percentage of feeding time spent eating the most frequently eaten parts (young leaves, mature leaves, leaf petioles) each month and using this as the unit of comparison. We used a Spearman rank correlation to determine if there was a consistent change in diet (% of feeding time devoted to a particular part) over time. Statistical analyses of dietary differences were not made among the widely separated groups, because the monthly sample based on 2 days of observations was viewed to be too small for some groups in some months to accurately represent their diet. However, by pooling months, the effect of a small sample in a particular month is diluted; thus, we consider the diet calculated over a year to be representative.

Interspecific dietary overlap between species or between neighboring groups of the same species was calculated using the following formula:

$$D = \sum S_i$$

where *D* = dietary overlap and *S_i* = percentage of diet shared between two species, evaluated on a plant species and part basis. This formula was first used by Holmes and Pitelka (1968) and has become a standard means of expressing dietary overlap for primates (Struhsaker, 1975; Struhsaker and Oates, 1975; Chapman, 1987; Maisels et al., 1994).

When there are appreciable differences in the mean values of the use of different food items, variation can be evaluated using the coefficient of variation (CV; Sokal and Rohlf, 1981). We use the CV to evaluate variation among groups or time periods in the use of plant parts. The CV was calculated as the standard deviation among groups or time periods for a given dietary component divided by the mean.

RESULTS

Differences in estimating primate diets can arise from a number of sources. Here we consider interobserver differences, short-term sampling differences (i.e., those occurring by sampling different individuals within a day), longer-term sampling differences (from days to years), and differences among groups at increasing spatial scales (from neighboring groups to groups separated by thousands of miles). Differences between new observers and C.A.C. watching the same animal were typically low (range, 97–100% agreement; mean, 98.8%). They typically involved assessing mature vs. immature food items that were rarely a major part of any group's diet at any time (maximum % of feeding time

spent eating mature leaves by different groups within Kibale = 21.0%, mean = 10.3%; ripe vs. unripe fruit not generally considered here as they were not common; however, the maximum feeding time among groups for all stages of fruit = 17.2%). As a result, it is unlikely that interobserver differences in classifying plant items contributed in a major way to the differences observed among groups or within the same group over time.

From May–August 1998 (576 hr), two observers simultaneously collected data on the same groups of red colobus. The data collected by these observers could differ as a result of consistent variation between observers or as a result of their observing different individuals. There were no differences in the percentage of time that the observers recorded the red colobus eating young leaves (paired *t*-test, *t* = 0.979, *P* = 0.350) or leaf petioles (paired *t*-test, *t* = 1.42, *P* = 0.186), but the time recorded feeding on mature leaves did differ (paired *t*-test, *t* = 2.57, *P* = 0.028).

During a 4-day sampling interval, samples taken on days 1 and 3 were not statistically different from those taken on days 2 and 4 with respect to young leaves (paired *t*-test, *t* = 1.17, *P* = 0.266), leaf petioles (paired *t*-test, *t* = 0.138, *P* = 0.195), or mature leaves (paired *t*-test, *t* = 0.352, *P* = 0.732).

We had dietary data on the same groups over a relatively short but intensive study (3 months, groups sampled twice a month) and from a longer, less intensive study (11 months, groups sampled once a month). The plant parts described by these two data sets differ. For example, one group was described as eating young leaves for 50.4% of the time in the short-term study, while the same group was described as eating young leaves for 75.8% of the time in the longer study. This discrepancy may reflect seasonal or interannual variation, but nonetheless suggests caution when generalizing results of short-term studies.

Temporal variation in diet estimations

There were differences among years in the amount of time spent eating different plant parts (Table 1). For example, in 1994, red colobus spent 55.8% of their feeding time eating young leaves, but this increased to 75.8% in 1998. Considering each month as an independent sample revealed that for some plant parts, these interannual differences were significant, while for others they were not (Table 1).

There was also interannual variation in the amount of time spent eating from particular species (Table 2). For example, the red colobus fed on *Albizia grandibracteata* for 10.5% of their feeding time in 1994, but fed on the same species for only 1.2% of their time in 1998 (Table 2). Much of the interannual variation observed in the diets of the red colobus probably reflects interannual differences in food availability. Chapman et al. (1999) examined the phenology of 3,793 trees from 104 species at two

TABLE 1. Percentage of time that a red colobus (*Procolobus badius*) group in Kibale National Park, Uganda, spent feeding on different types of foods during each year of a four years of study¹

Year	Young leaves	Mature leaves	Leaf petiole	Fruit	Flowers	Bark
1994	55.8	13.3	17.8	5.7	2.4	4.5
1995	58.8	10.2	17.0	7.6	1.5	4.2
1996	71.9	2.4	7.2	7.9	1.4	2.6
1998	75.8	5.6	7.8	6.6	3.5	0.3
Largest difference	20.0	10.9	10.6	2.2	2.1	4.2
CV ²	14.9	61.3	46.0	14.4	44.4	66.3
Significance ³	0.077	0.008	0.001	0.130	0.781	0.226

¹ Components do not sum to 100% because of groups eating plant parts that are not listed below. Each year typically goes from August year 1 to July year 2.

² CV, coefficient of variation (standard deviation/mean).

³ Significance values presented represent one-way ANOVA that considers each month of the year as an independent data point. Foraging on mature leaves in year 1 differed from years 3 and 4 ($P < 0.05$, Scheffe post hoc test), while for petiole use, year 1 differed marginally from year 4 ($P = 0.065$). All other contrasts of plant-part use among years were not significantly different.

TABLE 2. Percentage of time spent feeding from the five most important food species in the diet of the red colobus in K-30 in Kibale National Park, Uganda, during each of the years of study (underlined) and their importance in years when they were not in the top five; similar data are also presented for two groups of black-and-white colobus in 1998 that used the same area as the red colobus groups

Species	Red colobus				CV ¹	P ²	Findings	Black-and-white colobus	
	1994	1995	1996	1998				1998	1998
<i>Celtis durandii</i>	<u>11.8</u>	<u>16.3</u>	<u>17.2</u>	<u>21.3</u>	23.4	$P = 0.092$	No difference	<u>31.4</u>	<u>38.3</u>
<i>Strombosia schlefferi</i>	<u>9.5</u>	<u>8.0</u>	<u>10.6</u>	<u>10.2</u>	12.0	$P = 0.966$	No difference	3.0	1.0
<i>Pygeum africana</i>	<u>16.4</u>	<u>11.6</u>	4.5	4.1	64.9	$P = 0.012$	94 differs from 96	<u>11.1</u>	0.3
<i>Markhamia platycalyx</i>	9.3	<u>10.5</u>	6.3	<u>9.0</u>	20.2	$P = 0.244$	No difference	<u>5.4</u>	<u>11.0</u>
<i>Celtis africana</i>	<u>12.2</u>	<u>8.1</u>	<u>6.1</u>	7.5	30.9	$P = 0.058$	No difference	<u>11.4</u>	<u>15.0</u>
<i>Albizzia grandibracteata</i>	<u>10.5</u>	4.2	<u>9.6</u>	1.2	69.5	$P = 0.009$	94 differs from 98	<u>5.4</u>	3.8
<i>Dombeya mukole</i>	1.7	5.0	<u>6.6</u>	<u>6.8</u>	46.9	$P = 0.078$	No differs from 0.4	<u>7.2</u>	
<i>Bosqueia phoberos</i>		1.0	2.9	<u>7.8</u>	118.5	$P < 0.001$	98 differs from all years	0.4	0.4

¹ CV, coefficient of variation (standard deviation/mean).

² ANOVA examines differences among years, with Scheffe post hoc tests examining which particular pairs of years differ.

sites over 76 months and found marked variation among years in the phenology of particular plant species. However, evidence suggests that some of the interannual variation in red colobus diet was not due to differences in food availability. For example, *A. grandibracteata* is a common tree, and the plant parts generally consumed by the red colobus were available in every year of the study at similar levels (Chapman et al., 1999), yet their use of this species was variable (Table 2). Contrasting the CVs for diet components between years and widely separated groups illustrates that variation among years is generally less than variation among widely separated sites.

This large data set allowed an analysis of what sampling effort adequately characterized the diet of a group. A plot of the cumulative diet (i.e., month 1, month 1 + 2, month 1 + 2 + 3, etc.) suggests that variation becomes relatively stable after 6–8 months of sampling. However, the group's diet changed over time (Fig. 2). Specifically, this analysis suggest that over this 45-month study, the amount of time spent eating young leaves increased steadily (Spearman rank $r_{sp} = 0.859$, $P < 0.001$), while the use of petioles ($r_{sp} = -0.995$, $P < 0.001$) and mature leaves ($r_{sp} = 0.646$, $P < 0.001$) declined. Thus, the percentage of feeding time spent eating young

leaves, petioles, and mature leaves showed consistent changes over time (among months 11–20, 21–30, and 31–40: 55.8/68.6/75.7 young leaves, 17.9/8.7/6.1 leaf petioles, and 1.8/4.6/3.0 mature leaves).

This large data set also permitted analysis of the effect of sampling at different intensities. We contrasted the estimation of diet obtained from samples taken over a short but intense period vs. a similarly sized sample obtained over a longer period. The diets derived from these two methods differed with respect to young leaves ($t = -4.72$, $P < 0.001$), leaf petioles ($t = -6.51$, $P < 0.001$), and mature leaves ($t = 5.72$, $P = 0.001$). However, neither method differed significantly from the "true" estimate (the cumulative estimate at the end of the study, $P > 0.150$ in all cases).

Spatial variation in diet

It is often assumed that the diet of one monkey group can be used to reflect all groups within a larger continuous area (e.g., a national park). The data we collected do not support this assumption, both with respect to the plant parts eaten and specific plant species used. There were differences in the amount of time the groups in the eight study areas spent eating different plant parts (Table 3). The largest difference was found in the amount of

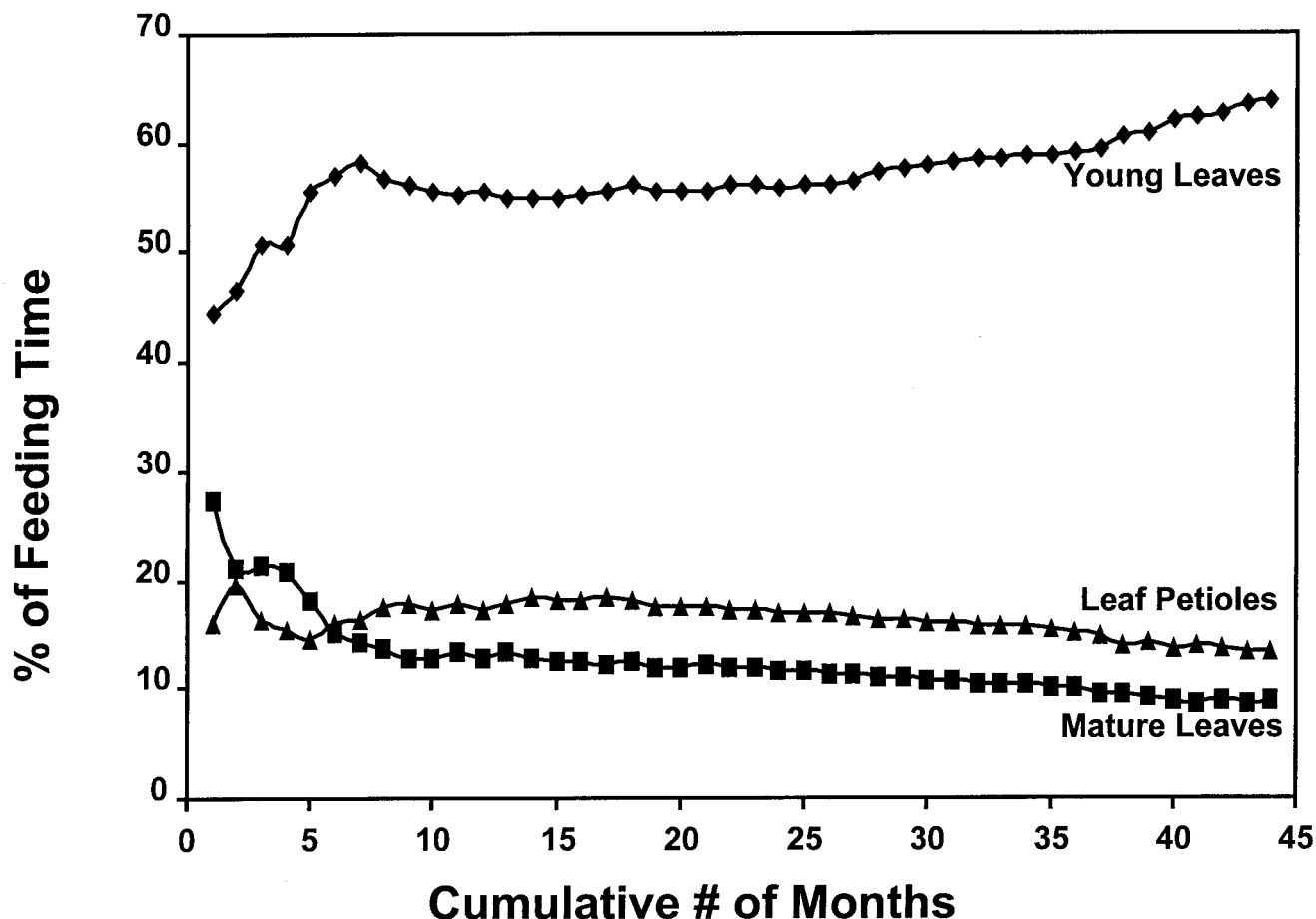


Fig. 2. Plot of diet of red colobus (*Procolobus badius*) studied in Kibale National Park, Uganda, based on an increasing number of months sampled (i.e., month 1, month 1 + 2, month 1 + 2 + 3, etc.).

time spent eating young leaves (38.2% maximum difference). The Kahunge group only spent 48.8% of their feeding time eating young leaves, while the group in the logged area of Mikana ate young leaves for 87.0% of their feeding time. The amount of time eating fruit varied among groups from 1.9–17.2%.

The importance of some plant parts to red colobus diet varied little among groups, while other plant parts exhibited a large degree of variation. The use of flowers by different groups was the most variable relative to its mean (CV = 116%); however, the use of a number of other dietary components was also variable (Table 3).

The plant species that were most important to the different red colobus groups also varied (Table 4). Much of this variation reflected differences in the density of tree species among sites (Table 5, and Chapman et al., 1997). Some foods important to a particular group were only present at one or a limited number of sites. The most poignant example of this is the diet of the red colobus at Kahunge. This group fed on *Acacia kirkii* for 92% of their feeding time, and this tree species was only found at this site. Similarly, *Cynometra alexandri* was eaten by the Mainaro red colobus for 41% of that group's feeding time, and *C. alexandri* is only found in the

south of the park. *Celtis durandii* was important in the diet of red colobus at all sites where it was found. In contrast, *Celtis africana* was only eaten at 6 out of the 7 sites where it was found; it was not eaten at Mainaro despite the fact that it was relatively abundant there (1.3 individuals/ha).

Even when we compared the diets of red colobus groups with overlapping home ranges, we still documented considerable variation in diet, both in terms of the plant parts consumed (Table 6) and the species and parts eaten (Table 7). Group 1 used an area of 26.4 ha, while Group 2 used an area of 21.9 ha. The area of home-range overlap was 10.7 ha, which represents 41% of Group 1's home range and 49% of Group 2's home range. During the days we observed Group 2, it spent 70% of the observation time in this area of overlap, while Group 1 spent 49% of its time in the area of overlap. Despite this degree of home-range overlap, diets differed. For example, Group 1 ate young leaves for 63.9% of the feeding observations, while the second group ate young leaves in 75.8% of the observations. The use of young leaves and mature leaves differed between groups (paired *t*-test, young leaves, $t = 3.52$, $P = 0.004$; mature leaves, $t = 2.43$, $P = 0.032$), and the

TABLE 3. Percentage of feeding time devoted to eating different types of foods by red colobus groups from eight areas in or near Kibale National Park, Uganda, and by neighboring groups sampled at different times¹

Location	Young leaves	Mature leaves	Leaf petiole	Fruit	Flowers	Bark
Sebatoli	72.4	7.4	7.1	6.4	3.3	2.0
K-15	69.8	2.6	5.8	17.2	2.3	0.3
Mikana	87.0	2.0	4.2	3.0	2.2	0.0
K-30	57.6	9.9	14.2	6.7	2.0	4.1
Dura River	65.1	4.6	8.7	13.9	6.2	0.0
Mainaro	57.5	16.2	1.8	10.8	7.2	3.6
Nkuruba	67.3	18.4	2.8	1.9	2.3	6.4
Kahunge	48.8	21.0	0.0	3.1	22.7	2.7
Largest difference	38.2	19.0	14.2	15.3	20.7	6.4
CV ²	17.6	72.2	80.6	70.8	116.6	95.7

Observations of neighboring groups sampled on alternating weeks for 3 months

Small group	56.7	10.2	16.4	7.7	5.7	2.9
Large group ³	50.4	7.6	19.5	3.2	2.5	7.7

Observations of neighboring group samples for 1 week a month for 11 months

Small group	63.9	13.4	6.4	8.9	0.8	6.5
Large group	75.8	5.6	7.9	6.6	3.5	0.3

¹ The components do not sum to 100% because of groups eating plant parts that are not listed below (e.g., the K-30 groups at 3.0% pine needles).

² CV, coefficient of variation (standard deviation/mean).

³ This group ate seeds for 6.74% of the time.

TABLE 4. Percentage of foraging scans involving the top five most frequently eaten plant species (underlined) at each of eight sites and corresponding use at the other sites

Species	Sebatoli	K-15	Mikana	K-30	Dura	Mainaro	Nkuruba	Kahunge	CV ¹
<i>Acacia hockii</i>								<u>91.9</u>	282.8
<i>Celtis durandii</i>	<u>5.4</u>	<u>23.6</u>	<u>19.0</u>	<u>10.4</u>	<u>27.2</u>	<u>6.0</u>			92.3
<i>Celtis africana</i>	4.3	<u>12.2</u>	<u>13.7</u>	<u>9.9</u>	1.5		<u>19.1</u>		94.5
<i>Albizia grandibracteata</i>	1.0	4.1	3.6	8.4	<u>10.8</u>	1.8	<u>14.6</u>	<u>0.68</u>	90.7
<i>Pygeum africanum</i>	<u>5.9</u>	1.7	3.2	<u>13.0</u>		2.4	<u>16.3</u>		115.3
<i>Cynometra alexandri</i>						<u>40.7</u>			282.8
<i>Funtumia latifolia</i>	<u>5.4</u>	<u>8.1</u>	3.1	7.2	<u>12.8</u>	3.0			88.1
<i>Aningeria altissima</i>	<u>8.7</u>	<u>8.7</u>	0.3	0.9	<u>14.9</u>				138.1
<i>Markhamia platycalyx</i>	3.1	<u>10.2</u>	<u>6.1</u>	<u>9.2</u>	1.0		0.9		109.1
<i>Mimusops bagshawei</i>	0.8			0.4	4.6	<u>5.4</u>	<u>16.1</u>		163.2
<i>Strombosia scheffleri</i>	<u>10.9</u>	0.9	2.0	<u>9.2</u>	2.7				135.7
<i>Dombeya mokole</i>		4.1	5.2	3.5			<u>12.8</u>		138.8
<i>Olea welwitschii</i>	5.1	1.5	<u>13.5</u>	3.9			0.2		154.3
<i>Bosqueia phoberos</i>	3.1		2.9	0.8	3.1	<u>5.4</u>	0.9		94.1
<i>Neutonia buchananii</i>	<u>11.2</u>		0.4						271.9
<i>Parinari excelsa</i>			<u>5.3</u>	0.1					276.9
<i>Celtis zenkeri</i>						<u>5.4</u>			282.8
<i>Cola gigantea</i>					<u>5.1</u>				282.8
<i>Sapium ellipticum</i>	1.3			0.1		0.6		<u>0.68</u>	143.8
<i>Bridelia micrantha</i>				1.63				<u>0.68</u>	205.0

¹ CV represents foraging time devoted to each species among sites.

use of bark was marginally different (paired *t*-test, $t = -1.80$, $P = 0.97$).

There were differences between neighboring groups in how much they fed on particular species (Table 7). For example, Group 1 fed on *Celtis durandii* in 7.2% of the feeding records, while Group 2 fed on this species 21.3% of the time. We mapped out all trees (>10 cm DBH) of selected species within the home ranges of each study group to obtain an accurate assessment of availability. From these data, it is evident that some differences in the use of particular species related to availability, but for some species this was clearly not the case. For example, the amount of time that Group 2 spent eating *Albi-*

zzia grandibracteata was only half of the time that Group 1 ate this species, but its density in Group 2's home range was eight times greater than in Group 1's home range (Table 7).

Interpretation of indices of dietary overlap

Struhsaker and Oates (1975) evaluated dietary overlap between groups of red and black-and-white colobus with adjacent home ranges in continuous forests of similar composition. The dietary overlap between these two species was only 7.1%. Calculating dietary overlap in a similar fashion for the two neighboring groups of red colobus (home-range overlap was up to 49%, and up to 70% of the time was

TABLE 5. Density (individuals/ha) of preferred red colobus food trees (top five most eaten species at any of the sites) found at seven sites in or near Kibale National Park, Uganda

Species	Sebatoli	K-15	K-30	Dura	Mainaro	Kahunge
<i>Celtis durandii</i>	2.5 ⁵	33.0 ¹	47.1 ²	63.8 ¹	33.8 ²	
<i>Funtumia latifolia</i>	25.0 ⁵	27.0 ⁵	33.8	43.8 ³	2.5	
<i>Markhamia platycalyx</i>	38.8	43.0 ³	50.0 ⁴	8.8	1.3	
<i>Bosqueia phoberos</i>			50.0	22.5	0.0 ⁴	
<i>Cynometra alexandri</i>					63.8 ¹	
<i>Strombosia scheffleri</i>	36.3 ²	1.0	12.5 ⁵	2.5		
<i>Newtonia buchananii</i>	26.3 ¹	1.0		3.8		
<i>Aningeria altissima</i>	23.8 ³	2.0 ⁴	1.7	2.5 ²		
<i>Mimusops bagshawei</i>	6.3	1.0	3.3	7.5	0.0 ⁴	
<i>Acacia kirkii</i>						20.0 ¹
<i>Celtis africana</i>		7.0 ²	4.2 ³		1.3 ⁵	
<i>Albizia grandibracteata</i>			1.3	1.3 ⁴		10.0 ²
<i>Blighia</i> sp.	7.5	2.0	0.8	1.3		
<i>Cola gigantea</i>				6.3 ⁵		
<i>Prunus africana</i>	2.5 ⁴		0.0 ¹			
<i>Sapium ellipticum</i>	2.5					2.0 ²
Total density	171.3	117.0	204.0	164.0	102.7	32.0
Cumulative DBH	9,496.0	2,759.0	5,548.0	6,708.0	4,747.0	1,765.0

DBH, diameter of a tree measured at breast height.

Superscript numbers indicate the ranking of the top five most eaten species at each site.

TABLE 6. Time spent eating different types of foods by two neighboring groups of red colobus from the tree species comprising 5% of their feeding time and the density of these trees at the time when they were using them¹

Group 1			Group 2		
Species/density	Part eaten	% in diet	Species	Part eaten	% in diet
<i>Prunus africana</i> , 1.6 tree/ha	Young leaves	8.8	<i>Prunus africana</i> , 1.6 tree/ha	Young leaves	6.2
	Mature leaves	6.8		Mature leaves	5.8
	Flowers	2.8		Petioles	1.2
	Bark	2.7		Bark	1.5
	Petioles	0.5		Young leaves	13.2
<i>Strombosia scheffleri</i> , 17.4 tree/ha	Petioles	9.3	<i>Celtis africana</i> , 4.4 tree/ha	Flowers	0.2
	Young leaves	4.0	<i>Strombosia scheffleri</i> , 5.1 tree/ha	Petioles	10.3
	Mature leaves	2.4		Young leaves	2.2
	Flowers	2.1		Mature leaves	0.8
	Bark	0.1		Bark	0.2
Young leaves	8.6	<i>Pinus</i> spp., density unknown		Pine needles	4.8
<i>Funtumia latifolia</i>	Fruit	0.7	<i>Funtumia latifolia</i> , 11.2 tree/ha	Bark	3.2
	Young leaves	4.8		Young leaves	3.0
	Fruit	2.3		Fruit	2.2
	Petioles	0.4		Petioles	0.7
	Flowers	0.2		Flowers	0.1
<i>Acacia pennata</i> , density unknown	Young leaves	7.2	<i>Markhamia platycalyx</i> , 15.7 tree/ha	Petioles	3.5
				Young leaves	1.6
<i>Ficus sansibarica</i> , 0.8 tree/ha	Unripe fruit	3.2	Unidentified vine, density unknown	Seeds	3.9
				Young leaves	0.8
<i>Chrysophyllum</i> sp., 5.5 trees/ha	Young leaves	5.0		Mature leaves	0.1
	Mature leaves	0.2			
	Petioles	0.2			

¹ Data were collected in Kibale National Park, Uganda.

spent in the area of overlap) illustrates that their diet overlapped by 37.3% (Table 8). The dietary overlap between the red colobus and the black-and-white colobus group that had its home range entirely within the home range of the red colobus group was 43.2%.

General patterns of variability

Detailed studies of primates have been conducted in Kibale National Park since the 1970s. Many of

these researchers attempted to make their data comparable to earlier studies by using very similar methodologies. As a result, Kibale offers a unique opportunity to examine whether the variation in diet that we have described for the red colobus is also seen in other species. If one examines the descriptions of plant parts eaten among studies of the same species for the five common diurnal species of Kibale (*P. badius*, *Colobus guereza*, *Cercopithecus ascanius*, *C. mitis*, and *Lophocebus albigena*), it is

TABLE 7. Density and percentage of time spent feeding from some trees used by two neighboring groups of red colobus monkeys at the Kanyawara study area of Kibale National Park, Uganda

Species	Big group			Small group		
	Density	Feeding time	Preference ¹	Density	Feeding time	Preference ¹
<i>Albizzia grandibracteata</i>	16	1.2	0.08	2	3.1	1.55
<i>Bosqueia phoberos</i>	45	7.8	0.17	34	4.1	0.12
<i>Celtis africana</i>	11	7.6	0.69	6	8.1	1.35
<i>Celtis durandii</i>	38	21.3	0.56	22	7.2	0.33
<i>Ficus exasperata</i>	8	2.1	0.26	4	0.5	0.13
<i>Funtumia latifolia</i>	35	8.2	0.23	25	8.9	0.36
<i>Markhamia platycalyx</i>	32	9.0	0.28	16	3.2	0.20
<i>Milletia dura</i>	9	1.3	0.14	1	0.6	0.60
<i>Olea welwitschii</i>	4	0.9	0.23	2	2.2	1.10
<i>Parinari excelsa</i>	2	6.7	3.35	2	8.1	4.05
<i>Dombeya mukole</i>	2	7.5	3.75	1	2.3	2.30
<i>Pygeum africana</i>	1	4.1	4.10	3	17.2	5.73

¹ Preference = feeding time divided by density.

TABLE 8. Comparison of overlap in diet (specific plant species and parts) of red colobus and black-and-white colobus between two different time periods and between neighboring groups of red colobus in Kibale National Park, Uganda

<i>P. badius</i> vs. <i>C. guereza</i>		<i>P. badius</i> vs. <i>C. guereza</i>		<i>P. badius</i> 1 vs. <i>P. badius</i> 2	
Month	Diet overlap	Month	Diet overlap	Month	Diet overlap
April 1971 ¹	7.29	August 1998 ²	44.76	August 1998 ²	38.66
May	3.64	September	41.61	September	36.80
June	4.70	October	25.90	October	5.81
July	3.77	November	27.79	November	38.13
August	4.54	December	72.25	December	46.74
September	15.68	January 1999	37.08	January 1999	62.22
October	12.71	February	36.94	February	25.82
November	2.00	March	44.29	March	32.61
December	13.25	April	66.59	April	60.41
January 1972	3.36	May	34.55	May	25.43
February	9.81				
March	4.30				
Average	7.09		43.18		37.26

¹ The 1971/1972 time period is from Struhsaker and Oates (1975) and involves contrast of groups in slightly different areas.

² The red colobus to black-and-white colobus contrast in 1998/1999 involves groups in the same area.

evident that there is considerable variation (Table 9). For example, Struhsaker (1978) suggested that blue monkeys are primarily frugivorous (45.1% of their foraging time was spent eating fruit), while the study by Butynski (1990) of blue monkeys in the same general area did not support this description (22.1% of their foraging time was spent eating fruit). Variability is also seen with respect to other characters of these species, such as group size, home-range area, and day-range length (Table 9).

There is also considerable variation in the plant parts eaten by different subspecies of *P. badius* from sites across Africa. However, this variation is often not of the magnitude we have documented within Kibale (Table 10). There is also variation in the diet of different populations within the genus *Colobus*. If one contrasts the diet of *P. badius* and with some populations of *Colobus* spp., it is difficult to separate the two genera. Some *Colobus* populations specialize more in eating seeds or young leaves in comparison to red colobus.

DISCUSSION

The fact that different populations of a single species in distinct forests can have different foraging

strategies or social organizations has been recognized for some time (Chambers, 1979; Richards, 1974; but see Sussman, 1987). However, this study reveals considerable variation in red colobus diet over a variety of spatial and temporal scales. This variation exists whether one considers diet in terms of the species and parts eaten or just in terms of the parts consumed. As one might expect, dietary variation was larger among groups that were far apart than between neighboring groups. Annual variation in diet of one group was generally less than variation over any of the spatial scales considered.

Variation in the plant parts eaten by the red colobus of Kibale, other primates in Kibale, or other colobine populations across Africa suggests that dietary variation is often large. The magnitude of this variation suggests that the characterization of species' diet is site- and time-dependent. It was not uncommon for the amount of time spent foraging on specific dietary items to vary by 20% or more, depending on what group or time period was considered. Based on a quantitative review of available data, Richards (1985) considered that primates spend 40–80% of their annual feeding time on 1 of 6 types of foods: insects, gums, fruits, seeds, leaves, and ground herbs. She placed species

TABLE 9. Ecological characteristics reported for some primates of Kibale National Park, Uganda by different researchers¹

Primate species (common name)	Group size	Home range (ha)	Day range (m)	Frugivory	Folivory	Insectivory
<i>Cercopithecus ascanius</i> (redtail monkey)	35 ^b	24.0 ^{b,c}	1,447 ^d	43.7 ^b	16.1 ^b	21.8 ^b
	30–35 ^c			44.6 ^d	34.7 ^d	17.6 ^d
				35.7 ^e	28.2 ^e	31.2 ^e
				55.6 ^f	15.4 ^f	20.6 ^f
<i>Cercopithecus mitis</i> (blue monkeys)	25 ^b	61.0 ^{b,c,h}	1,298 ^b	59.7 ^g	12.9 ^g	14.5 ^g
				45.1 ^{b,h}	20.9 ^{b,h}	19.8 ^{b,h}
	24 ^c	36.4 ^j	1,216 ^j	22.1 ^j	31.4 ^j	39.4 ^j
	21 ^h	253.0 ^l	1,406 ^j	30.1 ^l	22.8 ⁱ	35.9 ⁱ
	15 ^l			39.5 ^k	26.1 ^k	18.3 ^k
<i>Procolobus badius</i> (red colobus)	50 ^{b,c}	35.0 ^{b,c}	650 ^b	5.6 ^b	73.4 ^b	2.6 ^b
	61 ^l			6.4 ^d	86.9 ^d	0.0 ^d
	14 ^m			6.7 ^e	81.7 ^e	0.0 ^e
				13.9 ^f	78.4 ^f	0.0 ^f
				10.8 ^g	75.5 ^g	0.0 ^g
<i>Colobus guereza</i> (black- and-white colobus)	9 ^{b,c,l}	15.1 ⁿ	535 ^b	13.2 ^b	76.4 ^b	0.0 ^b
	11 ⁿ	16.0 ^{b,c}		13.6 ⁿ	77.0 ⁿ	0.0 ⁿ
	8 ^o			8.6 ^v	88.2 ^v	0.0 ^v
	6 ^m					
<i>Lophocebus albigena</i> (mangabey)	15 ^{b,c,p,q}	410.0 ^{b,c}	1,270 ^b	58.8 ^b	5.4 ^b	10.9 ^b
	9 ^r	400.0 ^{+s}		51.6 ^w	7.1 ^w	25.6 ^w
		200.0 ^t		61.1 ^x	12.6 ^x	12.0 ^x
			1,400 ^y	58.0 ^y	10.0 ^y	10.0 ^y

¹ Where several groups were reported, the average value within a given site is presented.

^a Frugivory was quantified as percentage of fruit and seeds in species' diet.

^b Struhsaker (1978, 1980), Kanyawara.

^c Struhsaker and Leland (1979), Kanyawara.

^d Chapman and Chapman (2000), Sebatoli.

^e Chapman and Chapman, unpublished data, Kanyawara.

^f Chapman and Chapman, unpublished data, Dura.

^g Chapman and Chapman, unpublished data, Mainaro.

^h Rudran (1978a).

ⁱ Butynski (1990), Ngogo.

^j Butynski (1990), Kanyawara.

^k Rudran (1978b).

^l Clutton-Brock (1975).

^m Chapman and Chapman, unpublished data, Sebatoli.

ⁿ Oates (1977), Kanyawara (K-30, K-14).

^o Teleen (1994), Kanyawara.

^p Waser and Floody (1974).

^q Olupot et al. (1994), Kanyawara (K-30).

^r Olupot et al. (1994), Kanyawara (K-14).

^s Waser (1975).

^t Olupot (1999), Kanyawara.

^u Olupot (1998).

^v This study, Kanyawara.

^w Barrett (1995), Ngogo.

^x Wallis (1978), Ngogo.

^y Freeland (1977), Ngogo (folivory includes young leaves and flowers).

into dietary categories by this definition. Of the 54 species considered in her review, none were placed in two categories. While all groups of red colobus across all time periods would be considered folivores, groups of blue monkeys studied in Kibale would be classified as frugivores or insectivores, depending on the study (see also *Lophocebus albigena* from Lopé; Tutin, 1999).

Discovering that diet can vary over small spatial scales and short temporal scales to the extent we have documented raises the intriguing question as to what level of difference in diet among populations or species is biologically significant when

addressing particular questions. The answer depends on the question being asked. We consider this issue with respect to inferences made about how diet influences morphology, about dietary overlap, and about how species in different foraging guilds (e.g., frugivore, folivore) are influenced by habitat disturbance.

How diet influences morphology

Understanding what level of difference in diet is biologically significant is particularly important when asking questions that involve contrasts with

TABLE 10. Diets of red and black-and-white colobus from a variety of sites across Africa¹

Red colobus	Young leaves	Mature leaves	Seeds	Fruit pulp	Flowers	Other
<i>P. tholloni</i> (1)	54.3	6.4	30.8	7.1	1.4	
<i>P. badius</i> (2)	31.7	20.2	25.3	5.9	16.1	
<i>P. rufomitrata</i> (3)	52.4	11.5	0.9	24.1	6.2	4.9
<i>P. temminckii</i> (4)	41.5	6.5	18.5	35.9	8.7	7.4
<i>P. temminckii</i> (5)	34.9	11.8	2.9	41.6	8.7	2.9
<i>P. tephrosceles</i> (6)	34.8	44.1	2.8	8.5	6.8	2.9
<i>P. tephrosceles</i> (7)	50.6	23.1	0.8	4.8	11.8	0.0 ²
<i>P. kirkii</i> (8)	46.7	14.6 ³		31.7	10.6	2.3
<i>P. kirkii</i> (8)	53.4	11.9 ⁴		31.2	5.4	1.3
<i>P. tephrosceles</i> (9)	46.8–87.1	2.0–21.0		1.9–17.2	2.0–22.7	
Black-and-white colobus						
<i>C. angolensis</i> (10)	21.2	6.4	49.9	16.8	5.9	
<i>C. angolensis</i> (11)	67.9 ⁵		10.7	21.4		
<i>C. angolensis</i> (12)	24.9	38.9				
<i>C. polykomos</i> (13)	29.9	26.7	33.3	3.2	2.7	4.7
<i>C. satanas</i> (14)	23.0	19.0	58.0			
<i>C. satanas</i> (15)	23.0	3.0	60.1	4.1	5.3	4.4
<i>C. guereza</i> (16)	23.7	29.1	1.2	38.6	0.5	8.1
<i>C. guereza</i> (17)	29.7	28.0	22.0	24.6	2.9	14.5
<i>C. guereza</i> (18)	33.1	19.8	9.3	36.3	7.7	2.1
<i>C. guereza</i> (19)	36.9	24.8	12.0	25.6	8.9	2.6
<i>C. guereza</i> (20)	61.7	12.4	1.0	12.6	2.1	10.2
<i>C. guereza</i> (21)	80.1	5.8	0.1	9.7	0.1	4.2
<i>C. guereza</i> (22)	85.6	3.7	0.2	7.4	2.3	0.8

¹ Democratic Republic of Congo, Maisels et al. (1994). (2) Sierra Leone, Davies et al. (1999). (3) Kenya, Marsh (1981). (4) Senegal, Gatnot (1977). (5) Gambia, Davies (1994). (6) Tanzania, Clutton-Brock (1975). (7) Uganda, Struhsaker (1975). (8) Mturi (1993) (2 groups in same area). (9) This study, range among populations. (10) Democratic Republic of Congo, Maisels et al. (1994). (11) Kenya, Moreno-Black and Maples (1977). (12) Rwanda, Fimbel et al. (unpublished data). (13) Sierra Leone, Dasilva (1992, 1994). (14) Cameroon, McKey et al. (1981), McKey and Waterman (1982). (15) Gabon, Harrison and Hladik (1986). (16) Kakamega, Kenya, Fashing (1999). (17) Ituri Forest, Democratic Republic of Congo, Bocian (1997). (18) Budongo, Uganda, Plumptre and Reynolds (unpublished data) (logged area). (19) Budongo, Uganda, Plumptre and Reynolds (unpublished data) (unlogged area). (20) Kibale, Uganda, Oates (1977). (21) Kibale, Uganda, this study, Group 1. (22) Kibale, Uganda, this study, Group 2.

² 10.4% leaves of unknown age.

³ Includes 7.3 on leaf stalks.

⁴ Includes 5.6 on leaf stalks.

⁵ Young and mature leaves.

respect to traits that are less labile than diet. For example, a major goal of physical anthropology is understanding the extraordinary morphological diversity found within the order Primates. A number of authors have suggested that there are predictable causal relationships between morphology, locomotor behavior, and aspects of the animal's behavior, including diet (Fleagle and Mittermeier, 1980; Gebo, 1992; Gebo and Chapman, 1995a).

In an early comparison of two leaf monkeys (*Trachypithecus obscurus* and *P. melalophos*), Fleagle (1977, 1978) suggested that differences in diet and foraging strategies between two species leads to differences in positional behavior, resulting in differences in muscle mass distribution, arrangement of individual muscles, skeletal proportions, joint mobility, and details of skeletal morphology. The diet differences he discussed between species were similar in magnitude to the differences documented among red colobus in Kibale. Leaves constituted 58% of *Trachypithecus obscurus* feeding observation and 35% of *P. melalophos* observations, a 23% difference (Curtin and Chivers, 1978; Curtin, 1980). The largest difference between any two red colobus groups seen in Kibale was 23.4% (mature leaves, young leaves, and petioles), and young leaf use var-

ied among *P. badius* subspecies by 55.4%. It seems unlikely that the diet of the two species studied by Fleagle (1977, 1978) would be consistently different across their range. Fleagle (1977, 1978) suggested that the diet of *T. obscurus* permitted more sedentary habits and positional behavior that were reflected in their anatomy. However, diets may vary among *T. obscurus* populations, and thus we should consider diet in the context of other selective forces. For example, it may not be the fact that *T. obscurus* eats a large quantity of leaves that leads to their sedentary habitats, but rather it may be that they specialize in particular types of leaves (e.g., high fiber content) that require longer digestion times, or that they are following a time-minimizing strategy (Dasilva, 1992). The recognition that diets can be variable will permit the generation of new testable hypotheses for differences in morphology.

With regard to evaluating studies that compare diet and positional behavior, researchers previously documented considerable annual, seasonal, and habitat variation in positional behavior (Gebo and Chapman, 1995b). This suggests that while positional behavior reflects anatomy, the match may be less deterministic than previously inferred. This adds to the general uncertainty concerning the loco-

motory identity and categorization of primate species. If dietary variation of the magnitude documented here is typical, the match between morphology and diet may be quite loose. This calls for an increased effort to gather data so that we understand the degree of behavioral flexibility associated with particular anatomical traits.

Dietary overlap

The documentation of dietary variation of the magnitude found here leads us to reevaluate studies of dietary overlap, competition, and resource partitioning. With primates, such studies have typically involved interspecific contrasts of groups that occupy different areas or groups of different species studied at different times (Struhsaker and Oates, 1975; Struhsaker, 1978; Waser, 1987). Such contrasts assume that spatial and temporal variation in diet is minimal or at least much less than interspecific variation. Data from Kibale suggest that this may not be the case. Struhsaker and Oates (1975) quantified the dietary overlap between black-and-white and red colobus studied at similar times, but in neighboring areas. They concluded that these two species do not compete because dietary overlap is low. Considering the data that have accumulated since Struhsaker and Oates (1975) and the data presented here, it may be valuable to reassess this interpretation. We studied groups of these species occupying the same area, which reduces variation in the forest structure and phenology experienced by the study animals. We found a 43% overlap in the diet of these two sympatric species. Whether or not this is a "biologically significant" dietary overlap is open to question. Groups were not followed on exactly the same day, and they were typically not using the exact same area. The two neighboring groups of red colobus that we observed had an average home-range overlap of 44%, and these groups had an average monthly dietary overlap of 37%. These examples illustrate that consideration of interspecific interactions and dietary overlap must be made in light of spatial and temporal variation in diet, and should reflect the fact that our categorization of a group's diet represents a sample of the animal's true behavior (for a similar comparison of two sympatric colobines, see Bocian, 1997).

Diet and conservation

Researchers have suggested that species with particular diets are differentially susceptible to different types of human modification. For example, Johns and Skorupa (1987) suggested that species' responses to habitat disturbance could be explained by body size and diet. They found that smaller species survived disturbance better, and the degree of frugivory was negatively correlated with the ability to survive in degraded habitats. Their strongest conclusion was that large-bodied frugivores are most vulnerable to habitat disturbance, and three exam-

ples of large-bodied taxa were presented: *Ateles*, *Pan*, and *Pongo*. However, by scrutinizing evidence on response to disturbance by these three taxa, exceptions are evident. For example, a healthy *Ateles geoffroyi* population has been described from a severely degraded area that was both intensively logged and grazed by cattle, but where hunting was minimal (Chapman et al., 1989). Similarly, *Pan troglodytes* groups are known to survive well in areas that have been logged and almost entirely converted to agriculture (Onderdonk and Chapman, 2000), apparently by traveling between the few small remaining forest fragments and by raiding crops planted by local farmers (Naughton-Treves et al., 1998). Finally, orangutan populations in Sumatra can thrive in protected forests subjected to a high natural disturbance regime (C. van Schaik, personal communication).

It is possible that the failure of the comparative review by Johns and Skorupa (1987) to make reliable predictions was because dietary variability was not considered. For example, Tutin (1999) studied the diet of primates living in forest fragments and continuous forest in Lopé Reserve, Gabon. She found that mangabeys (*Lophocebus albigena*) appeared to rely on fruits and seeds in the continuous forest (65% of their foraging time), but fruits and seeds were eaten less in fragments (29%). The magnitude of this dietary difference places continuous-forest and fragment-dwelling mangabeys into different foraging guilds (following the definition by Richards, 1985). This flexibility may permit mangabeys to live in a variety of habitats (for an example of a species that is not flexible in terms of the plant parts eaten in fragments vs. continuous forest, see Onderdonk and Chapman, 2000). A much broader understanding of dietary flexibility may permit development of simple generalizations that are useful in formulating informed conservation/management plans.

CONCLUSIONS

Behavioral flexibility blurs our traditional stereotypical assessment of primate evolution, whether it is in terms of evolution of positional behavior and anatomy, species interactions, or a variety of other traits. A study of one group that occupies a specific habitat at one point in time may not accurately reflect the species. It may be a marginal population in terms of some character, and we cannot assess this until a number of studies of the same species are conducted. We advocate that increased effort be placed on describing diets of species in different areas and over longer time periods, permitting a characterization of dietary flexibility that can then be used to evaluate evolutionary scenarios.

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LITERATURE CITED

- Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press.
- Anapol F, Lee S. 1994. Morphological adaptation to diet in anthropoid primates. *Am J Phys Anthropol* 94:239–261.
- Barrett L. 1995. Foraging strategies, ranging behaviour and territoriality among grey-cheeked mangabeys in Kibale Forest, Western Uganda. Ph.D. dissertation, University College London.
- Bocian CM. 1997. Niche separation of black-and-white colobus (*Colobus angolensis* and *C. guereza*) in the Ituri forest. Ph.D. thesis, City University of New York.
- Butynski TM. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecol Monogr* 60:1–26.
- Chalmers N. 1979. Social behavior in primates. London: Edward Arnold Press.
- Chapman CA. 1987. Flexibility in diets of three species of Costa Rican Primates. *Folia Primatol* (Basel) 49:90–105.
- Chapman CA. 1989. Ecological constraints on group size in three species of neotropical primates. *Folia Primatol* (Basel) 73:1–9.
- Chapman CA, Chapman LJ. 1990. Dietary variability in primate populations. *Primates* 31:121–128.
- Chapman CA, Chapman LJ. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* 29:396–412.
- Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40:215–232.
- Chapman CA, Chapman LJ. 2000. Constraints on group size in redtail monkeys and red colobus: testing the generality of the ecological constraints model. *Int J Primatol* 21:565–585.
- Chapman CA, Lambert JE. 2000. Habitat alteration and the conservation of African Primates: a case study of Kibale National Park, Uganda. *Am J Primatol* 50:169–186.
- Chapman CA, Onderdonk DA. 1998. Forests without primates: primate/plant codependency. *Am J Primatol* 45:127–141.
- Chapman CA, Chapman LJ, Glander KE. 1989. Primate populations in northwestern Costa Rica: potential for recovery. *Primate Conserv* 10:37–44.
- Chapman CA, Chapman LJ, Wrangham R, Isabirye-Basuta G, Ben-David K. 1997. Spatial and temporal variability in the structure of a tropical forest. *Afr J Ecol* 35:287–302.
- Chapman CA, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *J Trop Ecol* 15:189–211.
- Chivers DJ, Hladik CM. 1980. Morphology of the gastrointestinal tract in primates: comparison with other mammals in relation to diet. *J Morphol* 116:337–386.
- Clutton-Brock TH. 1975. Feeding behaviour of red colobus and black and white colobus in East Africa. *Folia Primatol* (Basel) 23:165–207.
- Clutton-Brock TH. 1977. Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. London: Academic Press. p 539–556.
- Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization. *J Zool Lond* 183:1–39.
- Curtin SH. 1980. Dusky and banded leaf monkeys. In: Chivers DJ, editor. *Malayan forest primates*. New York: Plenum Press. p 107–145.
- Curtin SH, Chivers DJ. 1978. Leaf-eating primates of peninsular Malaysia: the siamang and the dusky leaf-monkey. In: Montgomery GG, editor. *The ecology of arboreal folivores*. Washington, DC: Smithsonian Institution Press. p 441–464.
- Dasilva GL. 1992. The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure, and energy intake. *J Anim Ecol* 61:79–91.
- Dasilva GL. 1994. Diet of *Colobus polykomos* on Tiwai Island: selection of food in relation to its seasonal abundance and nutritional quality. *Int J Primatol* 15:1–26.
- Davies AG. 1991. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern Borneo. *Int J Primatol* 12:119–144.
- Davies AG. 1994. Colobine populations. In: Davies AG, Oates JF, editors. *Colobine monkeys: their ecology, behaviour and evolution*. Cambridge: Cambridge University Press. p 285–310.
- Davies AG, Bennett EL, Waterman PG. 1988. Food selection by two south-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biol J Linn Soc* 34:33–56.
- Davies AG, Oates JF, Dasilva GA. 1999. Patterns of frugivory in three West African colobine monkeys. *Int J Primatol* 20:327–357.
- Fashing PJ. 1999. The behavioural ecology of an African colobine monkey: diet, range use, and patterns of intergroup aggression in eastern black and white colobus monkeys (*Colobus guereza*) Ph.D. thesis, Columbia University.
- Fleagle JG. 1977. Locomotor behavior and muscular anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophus*). *Am J Phys Anthropol* 46:297–308.
- Fleagle JG. 1978. Locomotion, posture, and habitat utilization in two sympatric Malaysian leaf monkeys (*Presbytis obscura* and *Presbytis melalophos*). In: Montgomery GG, editor. *The ecology of arboreal folivores*. Washington, DC: Smithsonian Institution Press. p 243–251.
- Fleagle JG, Mittermeier RA. 1980. Locomotor behavior, body size and comparative ecology of seven Surinam monkeys. *Am J Phys Anthropol* 52:301–314.
- Freeland WJ. 1977. Dynamics of primate parasites. Ph.D. dissertation, University of Michigan, Ann Arbor.
- Gatinot BL. 1977. Le régime alimentaire du colobe bai au Sénégal. *Mammalia* 41:373–402.
- Gebo DL. 1992. Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus*. *Am J Primatol* 26:277–290.
- Gebo DL, Chapman CA. 1995a. Positional behavior in five sympatric old world monkeys. *Am J Phys Anthropol* 97:49–76.
- Gebo DL, Chapman CA. 1995b. Habitat, annual, and seasonal effects on positional behavior in red colobus monkeys. *Am J Phys Anthropol* 96:73–82.
- Grant J, Chapman CA, Richardson K. 1992. Defended versus undefended home range size of mammals. *Behav Ecol Sociobiol* 31:149–161.
- Harrison MJS, Hladik CM. 1986. Un primate granivore: le colobe noir dans la forêt du Gabon, potentialité d'évolution du comportement alimentaire. *Rev Ecol* 41:281–298.
- Harvey PH, Martin RD, Clutton-Brock TH. 1987. Life history in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: Chicago University Press. p 181–196.
- Hill WCO. 1964. The maintenance of langurs (*Colobinae*) in captivity: experiences and some suggestions. *Folia Primatol* (Basel) 2:222–231.
- Holmes RT, Pitelka FA. 1968. Food overlap among coexisting sandpipers on northern Alaskan tundra. *Syst Zool* 17:305–318.
- Howard PC. 1991. Nature conservation in Uganda's tropical forest reserves. Gland, Switzerland: IUCN.
- Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. *Behav Ecol* 2:143–155.
- Johns AD, Skorupa JP. 1987. Responses of rain-forest primates to habitat disturbance: a review. *Int J Primatol* 8:157–191.
- Kay RF. 1984. On the use of anatomical features to infer foraging behavior of extinct primates. In: Rodman PS, Cant JGH, edi-

- tors. Adaptations of foraging in nonhuman primates. New York: Columbia University Press. p 21–53.
- Kingston B. 1967. Working plan for Kibale and Itwara Central Forest Reserves. Entebbe, Uganda: Uganda Forest Department.
- Koenig A, Beise J, Chalise MK, Ganzhorn JU. 1998. When females should contest for food—testing hypotheses about resource density, distribution, size and quality with Hanuman langurs (*Presbytis entellus*). *Behav Ecol Sociobiol* 42:2225–237.
- Maisels F, Gautier-Hion A, Gautier J-P. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. *Int J Primatol* 15:681–701.
- Marsh CW. 1981. Ranging behaviour and its relation to diet selection in Tana River red colobus (*Colobus badius rufomitratu*). *J Zool London* 195:473–492.
- McKey DB. 1978. Soils, vegetation, and seed-eating by black colobus monkeys. In: Montgomery GG, editor. The ecology of arboreal folivores. Washington, DC: Smithsonian Institution Press. p 423–437
- McKey DB, Waterman PG. 1982. Ranging behavior of a group of black colobus (*Colobus satanas*) in the Douala-Edea Reserve, Cameroon. *Folia Primatol (Basel)* 39:264–304.
- McKey DB, Gartlan JS, Waterman PG, Choo CM. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biol J Linn Soc* 16:115–146.
- Milton K, May ML. 1976. Body weight, diet, and home range area in primates. *Nature* 259:459–462.
- Moreno-Black GS, Maples WR. 1977. Differential habitat utilization of four Cercopithecidae in a Kenyan forest. *Folia Primatol (Basel)* 27:85–107.
- Mturi FA. 1993. Ecology of the Zanzibar red colobus monkey, *Colobus badius kirkii* (Gray, 1968), in comparison with other red colobines. In: Lovett JC, Wasser SK, editors. Biogeography and ecology of the rain forest of eastern Africa. Cambridge: Cambridge University Press. p 243–266.
- Napier JR. 1970. Paleocology and catarrhine evolution. In: Napier JR, Napier PH, editors. Old World monkeys: evolution, systematics, and behavior. New York: Academic Press. p 53–95.
- Naughton-Treves L, Treves A, Chapman CA, Wrangham R. 1998. Temporal patterns of crop raiding by primates: linking food availability in croplands and adjacent forest. *J Appl Ecol* 35: 596–606.
- Oates JF. 1977. The guereza and its food. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes. New York: Academic Press. p 275–321.
- Olupot W. 1998. Long-term variation in mangabey (*Cercocebus albigena johnstoni* Lydekker) feeding in Kibale National Park, Uganda. *Afr J Ecol* 36:96–101.
- Olupot W. 1999. Mangabey dispersal and conservation in Kibale National Park, Uganda. Ph.D. thesis, Purdue University.
- Olupot W, Chapman CA, Brown CH, Waser PM. 1994. Mangabey (*Cercocebus albigena*) population density, group size, and ranging: a twenty-year comparison. *Am J Primatol* 32:197–205.
- Onderdonk DA, Chapman CA. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *Int J Primatol* 21:587–611.
- Osmaston HA. 1959. Working plan for the Kibale and Itwara Forests. Entebbe: Uganda Forest Department. 60 p.
- Richards A. 1974. Intra-specific variation in the social organization and ecology of *Propithecus verreauxi*. *Folia Primatol (Basel)* 22:178–207.
- Richards A. 1985. Primates in Nature. New York: W.H. Freeman and Co.
- Rudran R. 1978a. Socioecology of the blue monkey (*Cercopithecus mitis stuhlmannii*) of the Kibale Forest, Uganda. *Smithson Contrib Zool* 249.
- Rudran R. 1978b. Intergroup dietary comparisons and folivorous tendencies of two groups of blue monkeys (*Cercopithecus mitis stuhlmannii*). In: Montgomery GG, editor. The ecology of arboreal folivores. Washington, DC: Smithsonian Institution Press. p 483–503.
- Skorupa JP. 1988. The effect of selective timber harvesting on rain-forest primates in Kibale Forest, Uganda. Ph.D. dissertation, University of California at Davis.
- Sokal RR, Rohlf FJ. 1981. Biometry. San Francisco: Freeman.
- Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291–309.
- Strier KB. 1994. Myth of the typical primate. *Yrbk Phys Anthropol* 37:233–271.
- Struhsaker TT. 1975. The red colobus monkey. Cambridge: University of Chicago Press.
- Struhsaker TT. 1978. Food habits of five monkey species in the Kibale Forest, Uganda. In: Chivers DJ, Herbert J, editors. Recent advances in primatology. Volume 1. Behaviour. New York: Academic Press. p 225–248.
- Struhsaker TT. 1980. Comparison of the behaviour and ecology of red colobus and red-tail monkeys in the Kibale Forest, Uganda. *Afr J Ecol* 18:33–51.
- Struhsaker TT. 1997. Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. Gainesville, FL: University Press of Florida.
- Struhsaker TT, Leland L. 1979. Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. In: Rosenblatt J, Hinde RA, Beer C, Busnel MC, editors. Advances in the study of behavior. Volume 9. New York: Academic Press. p 158–228.
- Struhsaker TT, Oates JF. 1975. Comparison of the behavior and ecology of red colobus and black-and-white colobus monkeys in Uganda: a summary. In: Tuttle RH, editor. Socioecology and psychology of primates. The Hague: Mouton Publishers. p 103–124.
- Sussman RW. 1987. Species-specific dietary patterns in primates and human dietary adaptations. In: Kinzey WG, editor. The evolution of human behavior: primate models. Albany: State University of New York Press. p 151–179.
- Teelen S. 1994. Group size and group structure of guereza, *Colobus guereza occidentalis* (Rochebrune 1886), in the Kibale Forest, Uganda. Diploma, Technischen Universität Braunschweig.
- Terborgh J. 1983. Five New World primates. Princeton: Princeton University Press.
- Tutin CEG. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. *Primates* 40:249–265.
- van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. Comparative socioecology. Cambridge: Blackwell Press. p 195–218.
- Wallis SJ. 1978. The sociology of *Cercocebus albigena johnstoni* (Lydekker): an arboreal, rain forest monkey. Dissertation, University of London.
- Waser PM. 1974. Inter-group interactions in a forest monkey the mangabey *Cercocebus albigena*. Ph.D. dissertation, Rockefeller University, New York.
- Waser PM. 1975. Monthly variation in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lydekker). *E Afr Wildl J* 13:249–263.
- Waser PM. 1987. Interactions among primate species. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker T, editors. Primate societies. Chicago: Chicago University Press. p 210–226.
- Waser PM, Floody O. 1974. Ranging patterns of the mangabey, *Cercocebus albigena*, in the Kibale Forest, Uganda. *Z Tierpsychol* 35:85–101.
- Yeager CP. 1989. Feeding ecology of the proboscis monkey (*Narvalis larvatus*). *Int J Primatol* 10:497–530.