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Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds[☆]

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Abstract

The diet selection of two groups of red colobus monkeys (*Procolobus badius*) in Kibale National Park, Uganda are considered with respect to protein, fiber, digestibility, alkaloids, total phenolics, tannins, saponins, and cyanogenic glycosides. Both groups selected young leaves over mature leaves and young leaves had more protein, were more digestible, and had a higher protein to fiber ratio than mature leaves. Young and mature leaves did not differ with respect to secondary compounds. There were no differences in the phytochemical factors examined between frequently eaten foods and leaves that red colobus were never known to eat, but were relatively common in the environment. Regression analyses predicting foraging effort from the phytochemical components of the large group's diet revealed selection for only one factor, foods that are high in protein and low in fiber, when differences in food tree availability were taken into consideration. A similar analysis with the small group did not suggest selection or avoidance of foods with respect to any of the factors considered. Previous studies have found the biomass of folivorous primates to be related to the ratio of protein to fiber concentration of mature leaves in the environment. These investigations have considered variation in folivore biomass and forest composition among sites separated by hundreds of kilometers; however, large variation in folivore abundance occurs over much smaller spatial scales. In Kibale National Park the average protein to fiber ratio of the mature leaves of the 20 most abundant tree species predicted the biomass of red colobus among four neighboring sites. We examined the generality of this relationship by adding our biomass and leaf chemistry values to previously published values; 62% of the variance in colobine biomass was explained by variation in the protein to fiber ratios of mature leaves at the sites. There was no evidence that red colobus avoided plants with high levels of secondary compounds. In fact, one of the most preferred trees (*Prunus africana*) was the species with the highest levels of cyanogenic glycosides, and the highest saponin levels were found in the young leaves of *Albizia grandibracteata*, the sixth and fourth most preferred plant species for the large and small groups, respectively.

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1. Introduction

Comparative physiology has provided a template to understand nutritional niches of domesticated and wild animals (Stevens and Hume, 1995). However, studies of the diet choice in wild animals have illustrated that selection, although based on phytochemical factors, is a very complex process. For example, closely related species with similar anatomy and presumably physiology can exhibit very different foraging strategies (Struhsaker and Oates, 1975). Also, within a single population researchers have documented large variation in diet choice among individuals or group that would not likely be due to variation in physiology (Chapman et al., 2002; Chapman, 1987; Davies et al., 1999).

Some of this complexity may be comprehended by more fully understanding nutritional aspects of diet choice and physiological variation. For example, the ingestion of one diet item can affect the digestion of another item (associated effects; Robbins, 1983; Bjorndal, 1991). Thus, the analysis of each diet item in isolation, as is done by most nutritional ecological studies, can be misleading. Similarly, the understanding of physiological responses to different diets may help us understand the complexity illustrated in diet choice studies of wild populations. For example, a variety of omnivorous fish, birds, and mammals have been shown to alter glucose absorption depending on the concentration of carbohydrates in their diets (Karasov and Diamond, 1988). Microtine rodents have been shown to increase their small intestine and caecal capacity in response diet quality (Gross et al., 1985; Lee and Houston, 1993). Finally, unique physiological adaptations allow some animals to live on diets that one would think would be unpalatable. For example, proline-rich proteins that have an affinity for tannins have been found in the saliva of various mammals and may reverse the detrimental effects of tannins (Mehansho et al., 1987; Mole et al., 1990). These sorts of flexible physiological responses may account for much of the variation seen in the diet choice of wild populations.

Identifying the chemical basis of diet selection is critical to understanding a species' nutritional requirements. And, understanding nutritional requirements permits managers to provide adequate nutrition for captive animals. This is becoming increasingly important as conservation biologists

are turning to captive breeding programs to assist in the survival of endangered species. Furthermore, a more complete understanding of an endangered species' nutritional requirements can assist in the development of sound conservation and management policies. For example, if tree species that were important to frugivorous or folivorous species could be left standing in selective logging operations or if loggers could use directional felling techniques to reduce impact to these species, populations decline following logging might be lower and/or the speed of population recovery might be more rapid.

A valuable first step to understand a species' nutritional requirements is to describe the food items selected relative to their availability and to identify phytochemical components that are associated with preferred and avoided foods. For example, if it can be demonstrated that a species frequently ingests toxic plant compounds known to target specific physiological pathways, then it is of value to explore the possibility that the species has mechanisms to render the toxic compounds ineffective.

From this perspective, the first objective of this study was to describe the diet choice of two groups of red colobus monkey (*Procolobus badius*) in Kibale National Park, Uganda. We examined how protein, fiber, digestibility, alkaloids, total phenolics, tannins, saponins, and cyanogenic glycosides influence diet choice. We observed two groups to examine the generality of our findings; namely was a correlation identified with one group also found with the second group. The second objective was to use information on diet choice to understand variation in the biomass of red colobus that exists within the national park. Red colobus are an endangered arboreal folivore (Struhsaker, 1975) that possess a specialized ruminant-like digestive system with a sacculated stomach, where bacteria digest cellulose (Bauchop, 1978; Chivers, 1994; Kay and Davies, 1994; Milton, 1998). At first inspection, the food items for an arboreal folivore living in a tropical forest might appear to be readily available; leaves of tropical forest trees are very abundant. However, when primates eat foliage they are very selective of species and plant parts, feeding primarily on young leaves of only a few species.

Protein and fiber content of foods are known to be important to leaf-eating monkeys. McKey (1978), Milton (1979) proposed that year-round

availability of digestible mature leaves, which are used by colobus monkeys when other more preferred foods are unavailable, limits the size of folivorous monkey populations. Thus, if easily digestible mature leaves are plentiful in an area during periods when other more preferred foods are lacking, the site can support a relatively large population of colobines (Davies, 1994). By measuring overall mature leaf acceptability as the ratio of protein to fiber, several subsequent studies have found positive correlations between Asian and African colobine biomass and this index of leaf quality (Waterman et al., 1988; Oates et al., 1990; Davies, 1994). A similar relationship was found between the quality of leaves and the biomass of the folivorous lemurs of Madagascar (Ganzhorn, 1992; see Peres (1997) for a similar argument to explain variation in primate density among 20 Amazonian sites and Emmons (1984) for a similar discussion for Amazonian mammals). To date, all studies examining the limits of colobine biomass have been made among areas separated by hundreds or thousands of kilometers, yet primate densities can vary markedly over small spatial or temporal scales (e.g. within one forest; Butynski, 1990; Chapman and Fedigan, 1990; Chapman and Chapman, 1999, or within one site over time Struhsaker, 1976; Marsh, 1986; Bronikowski and Altmann, 1996). Over a small spatial scale differences in plant communities or in many factors influencing investment in anti-feedants should be smaller than among sites separated by hundreds or thousands of kilometers (e.g. soil type, seasonality, deciduousness: Janzen, 1975; Feeny, 1976; Coley, 1983; Janzen and Waterman, 1984; however, the proportion of a community, that is, colonizers can change). Here we examine if this protein-to-fiber hypothesis can explain variation in the biomass of red colobus among sites within the same forest.

Milton (1979), Milton et al. (1980) provided a physiological explanation for the importance of protein to fiber ratios. Each primate species has a protein threshold below which it cannot meet the protein required for bodily functions. If protein intake falls below this threshold, then the animal will suffer a negative nitrogen balance and eventually die. While there is substantial evidence that colobines can digest some fiber components, they cannot digest lignin (Waterman and Choo, 1981; Waterman and Kool, 1994). Increasing fiber content increases the amount of food ingested that the animals cannot digest and slows the rate of passage

of digesta through the stomach as the efficiency of bacterial enzyme action is reduced, thus reducing protein uptake (Milton, 1979, 1982, 1998). A number of studies of arboreal folivores have found leaf selection to be influenced by protein and fiber content, supporting the importance of protein and fiber levels in their diet (e.g. *Alouatta palliata*—Milton, 1979, 1998; *Presbytis johnii* (just selection for easily digestible material)—Oates et al., 1980; Waterman and Choo, 1981; *Presbytis rubicunda* Davies et al., 1988; *Colobus satanas* McKey et al., 1981; 10 out of 12 populations (8 species) of lemurs Ganzhorn, 1992; *Procolobus badius* and *Colobus satanas*, and *Presbytis johnii* (just selection for easily digestible material) Waterman and Choo, 1981).

Unfortunately, the role of secondary plant compounds in colobine digestion is not well known. The gut flora of these animals may enable them to detoxify some toxins that would otherwise act as dietary deterrents (Oates et al., 1980; Waterman, 1984; Waterman et al., 1988). For example, McKey et al. (1981) found that black colobus (*Colobus satanas*) can consume appreciable quantities of the alkaloid-rich leaves of *Rawolfia vomitoria* that would be lethal to non-adapted folivores. Furthermore, when indices of plant secondary compounds are included with protein to fiber ratios to predict biomass, the predictive power of the relationship is generally not greatly improved over the use of protein to fiber ratios alone (Oates et al., 1990). The lack of evidence that secondary plant compounds are a dietary deterrent in colobines may to some degree represent the compounds considered to date; namely those compounds that human observers would consider bitter, astringent, or poisonous. Waterman et al. (1988) and Kay and Davies (1994) suggest that colobines avoid eating the foliage of certain plant families because they contain compounds that kill bacteria and would lower the efficiency of their gut flora. We evaluate the diet choice of red colobus with respect to alkaloids, total phenolics, tannins, saponins, and cyanogenic glycosides; the latter two have not been widely considered with respect to primate diet selection.

2. Methods

2.1. 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 (Struhsaker, 1975, 1997; Skorupa, 1988; Chapman et al., 1997). The park consists of mature, mid-altitude, moist semi-deciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and plantations of exotic trees (1%; primarily *Cupressus lusitanica*, *Pinus patula*, *P. caribaea*, and *Eucalyptus* spp.; Chapman and Lambert, 2000). Mean annual rainfall in the region is 1750 mm (1990–1999, or 1543 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 to May and September to November. The behavioral component of this study was conducted at the Kanyawara site (forestry compartments K30 and K14). Comparisons of red colobus biomass with the mature leaf chemistry was conducted at four sites that are each approximately 15 km apart: Sebatoli, Kanyawara, Dura River, and Mainaro (see Chapman et al., 1997; Chapman and Lambert, 2000 for a description of the different sites).

2.2. Behavioral observations

Behavioral observations were made on two groups of red colobus (24 and 48 members; subsequently called the small and large groups) during dawn to dusk observation periods for 5 days each month from August 1998 until June 1999, producing approximately 800 h of observations. Each group had several recognizable individuals allowing verification of group identity. We used an observational method that 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. Often the observer had to wait for a number of minutes to determine what a less observable animal was doing. These behavioral observations were conducted by LC, CC, and a

team of three Ugandan field assistants. The field assistants have worked with us since 1990 and knew the tree species, the observational technique, and monkey age classes prior to the start of the project.

2.3. Abundance of red colobus

The abundance of red colobus was assessed using line-transect methodology (National Research Council, 1981; Chapman et al., 1988, 2000; Whitesides et al., 1988). Censuses along transects approximately 4 km long were initiated in June 1996. Data were collected biweekly at Kanyawara ($n=26$) and Dura ($n=23$), and once a month at Sebatoli ($n=14$) and Mainaro ($n=10$). Rebel activity prevented us from sampling at Mainaro in January, February, and April of 1997. Censuses were conducted between 07:00 and 14:00 h at a speed of approximately 1 km/h. Data collected included primate species observed, time of observation, straight-line distance between the animal and observer (visually estimated), and mode of detection. At the beginning of the study, observers trained to estimate observer to animal distance. Variation among observers in sighting estimates was assessed at the end of the study. While particular estimates could be inaccurate, overestimates of distances tended to be countered by underestimates.

A variety of methods have been proposed for estimating primate density using transect data, and considerable controversy exists regarding the accuracy of these different methods (Burnham et al., 1980; Chapman et al., 1988; Skorupa, 1988). Given this controversy, we relied on empirical criteria for selecting the best method. Ghiglieri (1979, 1984), Struhsaker (National Research Council, 1981), and Skorupa (1988) concluded that a modified Kelker (1945) method using observer to animal sighting distance produced the best empirical results for primates at Kibale. Following these recommendations, we pooled data from census areas where sighting distance did not differ (ANOVA) and plotted the distance at 10-m intervals. This permitted us to estimate the animal sighting distance for each species. We used a 50% cut-off rule to select the sighting distance (Chapman et al., 2000).

Obtaining reliable group counts of forest-dwelling primates is extremely difficult, because inactive animals are often hard to locate and traveling

animals often take different pathways. As a result, a considerable effort was placed on counting groups in each area. Each month between July 1996 and May 1998 (22 months), two observers spent 2 days at each site simply following groups and attempting to get counts. Counts were rarely attempted when a group was stationary; the best counts were obtained when a group was crossing a gap in the forest canopy. Repeat counts were made of the same group to ensure accuracy. Groups were identified either by recognizing individuals or by matching the group count to previous ones. In addition, counts were made opportunistically when we were collecting behavioral data and groups were seen to cross a road or river. To estimate the biomass of the colobines, adult male and female body mass were taken from Struhsaker (1978). The composition of the groups as determined through the group counts was used to estimate biomass for each region. Subadult and juvenile weights were assumed to be half that of adults.

2.4. Nutritional analyses

For each of the two groups watched in the behavioral component of this study, the five most frequently eaten food items were collected each month. Samples were obtained using a tree-pruning pole to cut down a tree limb. Items were processed in a fashion that closely mimicked the feeding behavior of the study animals, and only those parts selected by the red colobus were collected. For example, if the animals only ate the tip of the leaf, only leaf tips were collected or if they were eating the petiole, the length of petiole typically consumed was collected. A selection of mature and young leaves from relatively abundant tree species that the red colobus were never seen to eat were also collected for comparison. After collection, food items were dried, stored in sealed plastic bags, and transported to the University of Florida. Dried samples were ground to pass through a 1-mm mesh screen in a Wiley mill. Dry matter was determined by drying a portion of each sample overnight at 105 °C. Samples were analyzed in duplicate, and replicates for analyses were considered acceptable if the relative error was less than 2%.

The protein (nitrogen) content of the plant parts was assessed using Kjeldahl procedures (Horowitz, 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 °C using 6 ml of H_2SO_4 and 2 ml H_2O_2 . The nitrogen in the digestate was determined by semiautomated colorimetry (Hambleton, 1977). Measuring total nitrogen provides an estimate of crude protein (protein levels = $N \times 6.25$; Maynard and Loosli, 1969). A better conversion factor for tropical foliage may be 4.4 tropical plant samples (Milton and Dintzis, 1981) or 4.3 (Conklin-Brittain et al., 1999). However, we used the 6.25 factor so that our results would be comparable to previous studies (Gartlan et al., 1980; Waterman et al., 1988; Oates et al., 1990; Davies, 1994).

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, which are refractory components of fiber. ADF has been found to have a strong negative correlation with food selection by primates (Glander, 1982; Oates et al., 1990). However, ADF is somewhat fermentable, while lignin is not (van Soest, 1982).

We assessed digestibility using a procedure that is commonly used in cattle forage analysis (Moore and Mott, 1974) and make the assumption that the efficiency of digestion using cattle rumen fluid will be correlated with the efficiency of red colobus digestion. The sample is first incubated with rumen microorganisms for 48 h and then it is incubated with an acid-pepsin solution.

Many alkaloids are bitter tasting and perhaps play a role as a feeding deterrent or damage the microbial community of colobine stomachs (Harborne, 1993; Roberts and Wink, 1998); however, most studies have not demonstrated that colobines avoid food items high in alkaloids (Waterman, 1993). The presence of alkaloids was tested using a spot test with Dragendorff's reagent (Waterman, 1993).

Saponins are surfactants, and have a 'soapy' foam-forming property in aqueous solutions, hence their name. They also have the ability to hemolyse red blood cells when injected, irritate the digestive tract, and can serve as a steroid hormone precursor (Phillips-Conroy, 1986). These compounds are bitter tasting, and are found in over 70 plant families. Most importantly, saponins have been documented to cause bloat in ruminants and have been impli-

cated in diet selection of cattle. Given the ruminant-like digestive system of colobines, it is intriguing to consider if saponins are important in colobine diet selection. To our knowledge, the role of this compound in colobine diet selection has not been investigated. The quantity of saponins present in a sample was indexed using the Froth Test (Fong et al., unpublished lab guide) using a 60-s and a 300-min criteria.

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

Tannins are naturally occurring water-soluble phenolic compounds that have the ability to precipitate alkaloids, gelatin, and proteins. Tannins produce an astringent and unpalatable taste that may deter herbivory. Tannin and total phenolic estimates were derived from the study of Dominy (2001) on a subset of the plants eaten by the red colobus groups; assessment of these compounds were not made on mature leaves or the leaves from relatively abundant tree species that the red colobus were never seen to eat. The radial diffusion assay described by Hagerman (1988) and modified by Dominy (2001) was used to determine relative differences in total tannin concentrations among samples. Tannin measures were expressed as equivalents to an 8-point standard curve based on crude quebracho tannin. Levels of total phenolics were measured by the Prussian blue test (Price and Butler, 1977 as modified by Dominy, 2001).

2.5. Statistical analyses

We took three approaches to explore the chemical basis of diet selection for red colobus. First, since red colobus are known to prefer young leaves over mature leaves (Struhsaker, 1975; supported by our data, see below), we contrasted the chemical constituents between young and old leaves of plants that red colobus eat. Differences were quantified with a paired *t*-test (paired by species).

Second, we compared frequently eaten foods, which were considered the five most frequently eaten food items collected each month for each group, to leaves that red colobus were never, or extremely rarely, known to eat but were relatively

common in the environment (see Yeager et al., 1997 for a similar analysis).

Third, we used behavioral data to calculate the percentage of foraging effort devoted to particular plant species and parts (e.g. the leaf petioles of *Markhamia platycalyx*). Subsequently, we attempted to predict the feeding effort based on that food's chemical constituents. However, one must consider that these foods are not equally available. Some tree species bearing food items are very abundant in the forest, while others are rare. To consider availability, we established twelve 200 × 10 m² transects placed randomly along the existing trail system, producing a total sampling area of 2.4 ha. All trees with a diameter at breast height (DBH) ≥ 10 cm and within 5 m of the trail were tagged and the DBH recorded. A total of 1171 trees from 67 species were identified. We used a multiple regression technique to quantify the significance of particular phytochemical component (e.g. fiber) as predictors of foraging effort, when effects of availability were statistically removed using partial correlations.

Dietary overlap between the two neighboring groups 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).

To meet the second objective of examining nutritional constraints that could limit the size of colobine populations and to test Milton's (1979) protein to fiber hypothesis, we quantified colobine biomass and related this to the average protein to fiber ratio of mature leaves of the 20 most abundant tree species at each of the four sites. Tree density (> 10 cm DBH) at each site was determined using vegetation transects (200 m by 10 m). This regime produced a total sampling area of 4.8 ha (2.4 ha at Kanyawara, and 0.8 ha at Dura River, Mainaro, and Sebatoli) and produced a sample of 2126 trees (1173 trees at Kanyawara, 338 trees at Dura River, 293 trees at Mainaro, and 322 at Sebatoli). The difficulty in testing the generality of the relationship between protein to fiber ratios and colobine abundance is primarily

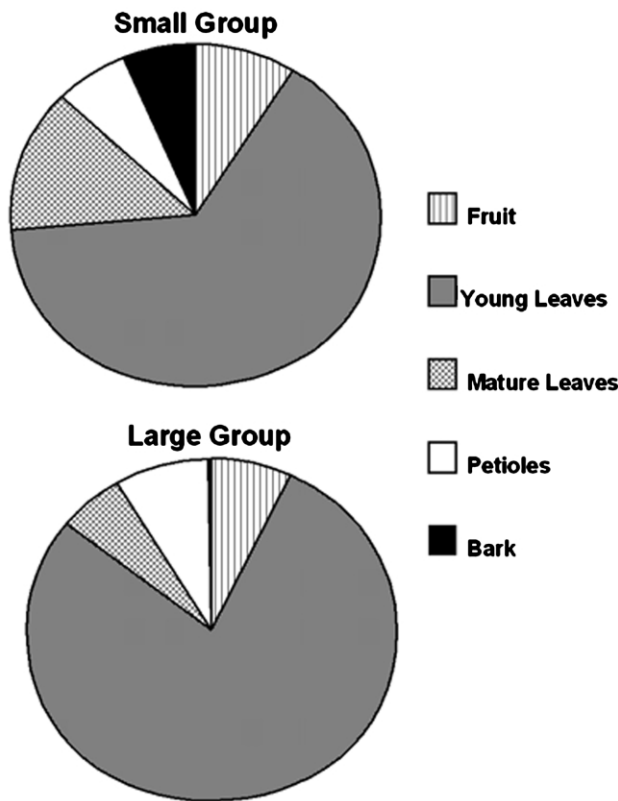


Fig. 1. The diet in terms of plant parts eaten for two groups of red colobus monkeys (*Procolobus badius*) studied in Kibale National Park, Uganda. For simplicity sake feeding on leaf buds were considered in the young leaf category, ripe and unripe fruit were combined into one category, and feeding on flowers was omitted since it constituted only 0.8 and 3.5% of the groups feeding time.

logistical: censusing arboreal primates is difficult and should be done over many months, and determining the protein and fiber content for 20 species at each site is time consuming. We are therefore limited in the strength of our test because we only have four sites, thus a simple graphical analysis is presented. When using literature data to test the generality of the relationship between protein to fiber ratios and colobine biomass and when considering just the sites considered here indexing availability by tree size, chemical values are weighted mean percentages of dry mass, standardized to the species basal area to account for different proportions of the flora being sampled at each site. The weighted values were calculated from $\Sigma(P_i \times X_i) / \Sigma P_i$ where P_i is the proportion of the basal area contributed by species i and X_i is the chemical measure for species i . This figure is standardized to 100%. Excluding the four new sites from Kibale, all chemical and biomass data are from Oates et al. (1990).

3. Results

3.1. Red colobus diet

Both groups of red colobus relied heavily on young leaves, but also fed on a variety of other plant parts (Fig. 1). There were differences between neighboring groups in how much they fed on particular species (Table 1). For example, the small group fed on *Celtis durandii* in 7.2% of the feeding records, while the large group fed on this species 21.3% of the time. We mapped out all

Table 1

Density (individuals per ha) and percentage of time (proportion of the total number of foraging scans) 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	Large group			Small group		
	Density	Feeding time	Preference	Density	Feeding time	Preference
<i>Albizia 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>Prunus africana</i>	1	4.1	4.10	3	17.2	5.73

Preference = Feeding time/Density.

Table 2

The difference in phytochemical factors between foods frequently eaten by red colobus monkeys and leaves that red colobus were never or extremely rarely known to eat but were relatively common in the environment

	Small group	Big group
Protein	$t=0.292, P=0.775$	$t=0.330, P=0.746$
Digestibility	$t=0.349, P=0.729$	$t=0.392, P=0.865$
Fiber	$t=0.80, P=0.936$	$t=0.60, P=0.952$
Protein to fiber ratio	$t=0.294, P=0.773$	$t=4.63, P=0.650$
Saponins	$t=0.375, P=0.710$	$t=0.333, P=0.741$
Alkaloids	Mann–Whitney $P=0.428$	Mann–Whitney $P=0.756$
Cyanogenic glycosides	Mann–Whitney $P=0.417$	Mann–Whitney $P=0.440$

trees (> 10 cm DBH) of selected species within the home ranges of each group to obtain an accurate assessment of availability (Gillespie and Chapman, 2001). From these data, it was evident that some of the differences in use of particular species were related to availability; but for some species, this was clearly not the case. For example, the amount of time that the large group spent eating *Albizia grandibracteata* was only half of the time that the small group ate this species, but its density in the large group's home range was eight times greater than in the other group's home range (Table 1).

These differences existed despite the fact that the red colobus groups had home ranges that overlapped extensively. The small group used an area of 26.4 ha, while the large group used an area of 21.9 ha. The area of home-range overlap was 10.7 ha, which represents 41% of the small group's home range and 49% of the large group's home range. During our observations, the large group spent 70% of its time in the area of overlap, while the small group spent 49% of its time in the shared area. Despite this high degree of home range overlap, diets differed, overlapping by only 37.3%.

3.2. Young vs. mature leaves

For the 23 species for which we had samples of mature and young leaves, young leaves were eaten more frequently than mature leaves (paired t -test $t=3.486, P=0.001$), had more protein ($t=4.179, P<0.001$), were more digestible ($t=1.921, P=0.034$), and had a higher protein to fiber ratio ($t=3.581, P=0.001$). There was no indication that young and mature leaves differed with respect to alkaloids (Wilcoxon signed rank test $P=0.480$), cyanogenic glycosides (Wilcoxon signed rank test $P=0.317$), or saponins ($t=0.865, P=0.339$).

3.3. Frequently eaten foods vs. not eaten foods

There were no differences in any of the phytochemical factors considered between frequently eaten foods (the five most frequently eaten food items collected each month for each group) and young and mature leaves that red colobus were never or extremely rarely known to eat, but were relatively common in the environment (Table 2).

3.4. Predicting preference from phytochemical factors

To identify significant phytochemical predictors of foraging effort we first examined the relationship between foraging effort and each of seven factors (protein, fiber, protein to fiber ratio, digestibility, saponins, tannins and total phenolics), after statistically controlling for the effects of food tree density using partial correlation. Each factor was considered in an independent partial correlation analysis. Protein to fiber ratio (Fig. 2) was the only significant predictor of foraging effort (after controlling for the effects of food tree density). Protein, fiber (considered independently), digestibility, total phenolics, tannins, and saponin content were not significant predictors (Fig. 2).

We examined interactive effects of the different phytochemical components using a multiple regression including a suite of phytochemical factors to predict foraging effort. This was done in two ways: based on those plant species and parts where protein/fiber, digestibility, and saponin content were determined (large sample) or considering those plant species where these factors plus their tannin and total phenolic content were estimated (smaller sample). For the large group, the analysis of the larger sample indicated the protein to fiber ratio as the only significant predictor (partial $r=$

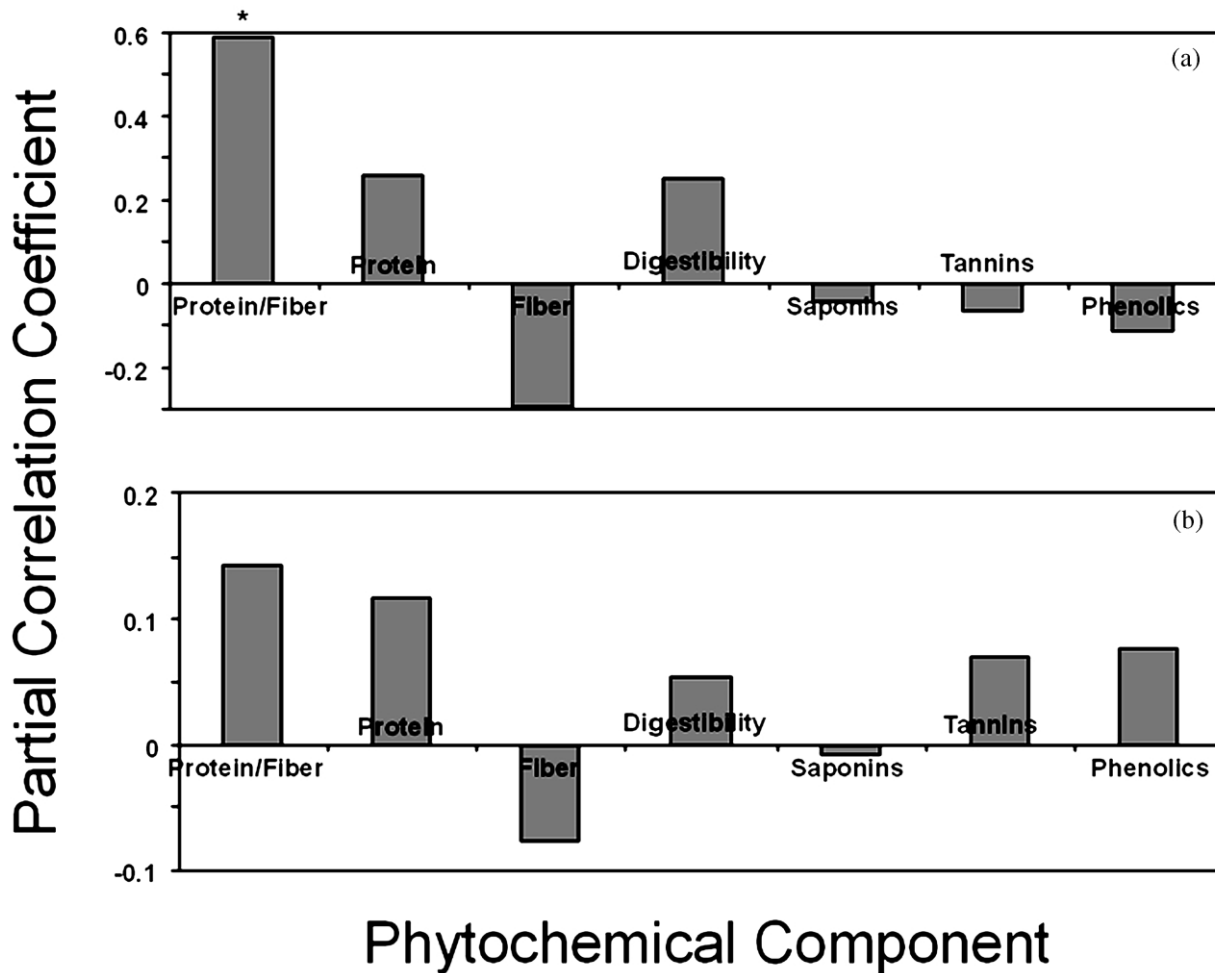


Fig. 2. (a) The relationships between foraging effort and phytochemical components of the large red colobus (*Procolobus badius*) group when the effects of the density of the food trees are statistically controlled (partial correlation coefficients) and (b) the same relationship for the small group. * indicates significance ($P < 0.05$).

0.552, $P = 0.017$), and this relationship explained 50% of the variance in foraging effort ($r^2 = 0.499$, $P = 0.020$; $n = 21$ species/parts). In the second analysis ($n = 14$ species/parts), 77% of the variance in foraging effort could be accounted for ($r^2 = 0.773$, $P = 0.047$), and again the only factor to have a significant partial correlation coefficient was the protein to fiber ratio (partial $r = 0.69$, $P = 0.040$).

For the small group, none of the phytochemical factors were related to foraging effort when each was considered independently after controlling for food tree density (Fig. 2). The multiple regression considering the larger number of phytochemical factors was not significant ($r^2 = 0.145$, $P = 0.398$; $n = 30$ species/parts). The regression considering

the smaller number of phytochemical factors approached significance ($r^2 = 0.760$, $P = 0.056$) with saponins and tannins appearing to influence diet selection (partial correlations—tannins partial $r = 0.566$, $P = 0.018$, saponins partial $r = 0.553$, $P = 0.020$; $n = 14$ species/parts).

The difference between groups with respect to the importance of the protein to fiber ratio deserves further attention. The larger group fed on the young leaves of *C. durandii* for 21.3% of the time they were seen foraging. Young leaves of *C. durandii* has the highest protein to fiber ratio of any plant part eaten; in fact it is 35% high than the next species/part. If *C. durandii* is excluded from the analysis, none of the dietary components considered significantly explained variation in for-

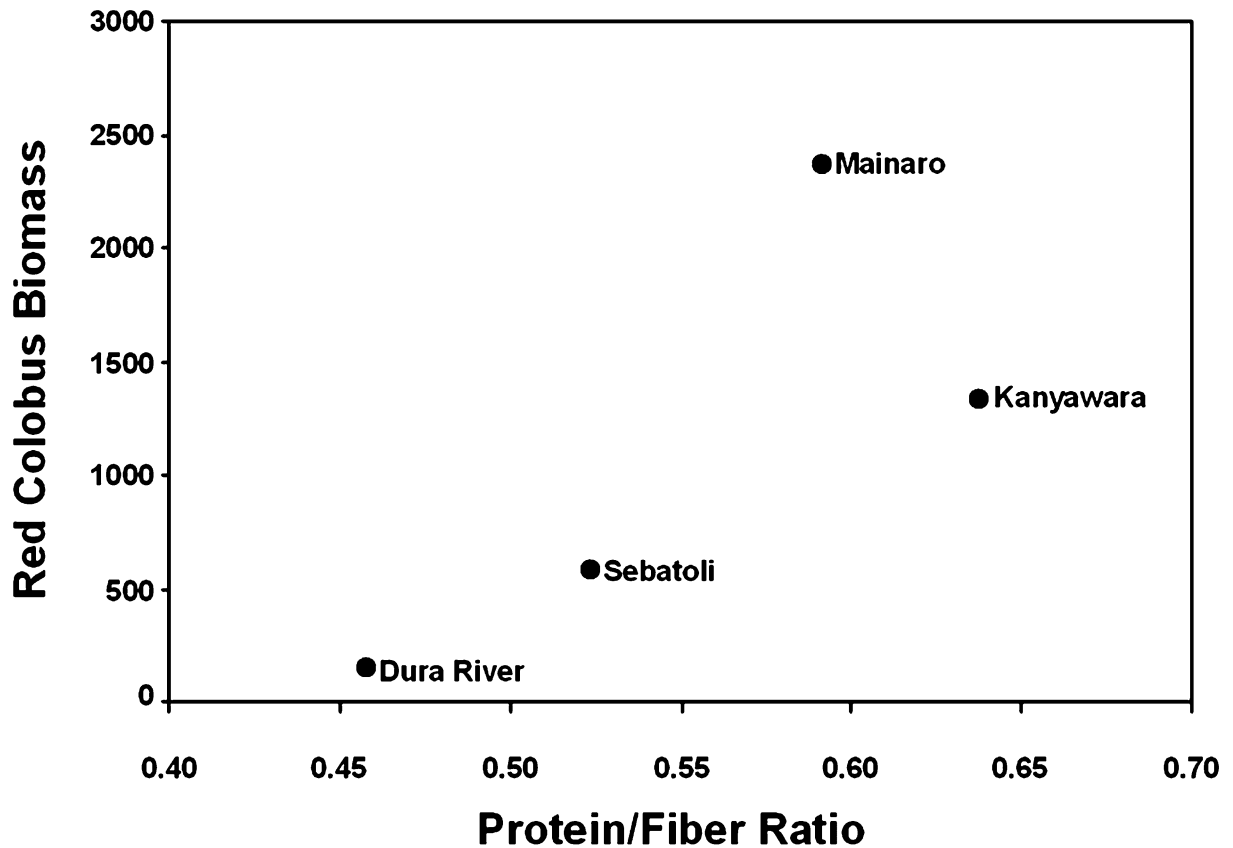


Fig. 3. The relationship between the average protein to fiber ratio of the mature leaves from the 20 most abundant tree species at four sites in Kibale National Park, Uganda, and the biomass of red colobus (*Procolobus badius*) at those sites.

aging effort and the multiple regression considering all phytochemical factors was not significant (smaller sample $r^2=0.118$, $P=0.736$, larger sample $r^2=0.479$, $P=0.540$).

3.5. Protein/fiber ratios and biomass

The variation in the mature leaf protein to fiber ratios among tree species was considerable (range=0.25–1.09). There was a marginally significant difference in the protein to fiber ratios among sites ($F=2.237$, $P=0.091$, $n=80$ mature leaf samples; mean protein to fiber ratio—Sebatoli=0.488, Kanyawara=0.588, Dura River=0.461, Mainaro=0.592). For some tree species, protein to fiber ratios varied little among sites, while for other species, this ratio showed a great deal of inter-site variation. We used a paired t -test (paired by species) to contrast protein to fiber ratios among pairs of sites. Mainaro had a higher average protein to fiber ratio than Sebatoli ($t=3.78$, $P=$

0.032, $n=4$ species) and Dura River ($t=2.34$, $P=0.041$, $n=11$ species) and a marginally higher ratio than Kanyawara ($t=2.00$, $P=0.086$, $n=8$ species). Other comparisons did not reveal significant differences (Dura River to Kanyawara $t=1.37$, $P=0.214$, $n=8$ species; Dura River to Sebatoli $t=0.909$, $P=0.398$, $n=7$ species; Kanyawara to Sebatoli ($t=0.36$, $P=0.735$, $n=6$ species)).

Considering these four sites, colobine biomass appears to be related to the average protein to fiber ratio of the 20 most abundant tree species at each site (Fig. 3). This relationship is evident giving each tree of the size classes measured an equal weighting regardless of size (Fig. 3) or if the chemical values are standardized to the species basal area (i.e. larger trees contribute more than smaller ones; Fig. 4).

On average, red colobus were only observed feeding on half of the 20 most abundant trees at each site (range among sites 45–55%). Feeding

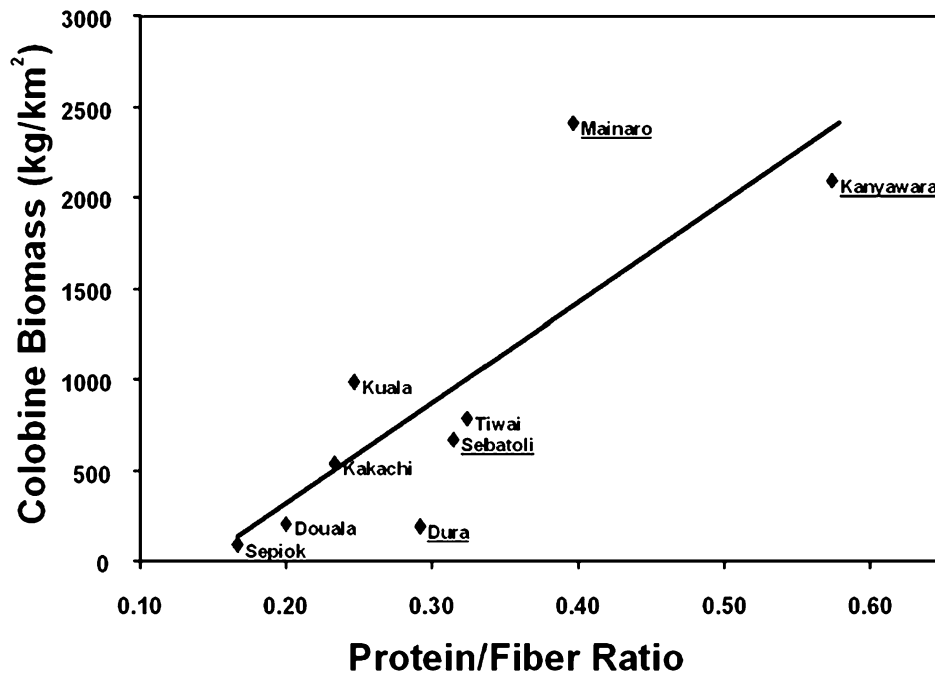


Fig. 4. The relationship between mature leaf chemistry and colobine biomass at rainforest sites in Africa and Asia. Chemical values are weighted mean percentages of dry mass, standardized to the species basal area to account for different proportions of the flora being sampled at each site. The weighted values were calculated from $\Sigma(P_i \times X_i) / \Sigma P_i$ where P_i is the proportion of the basal area contributed by species i and X_i is the chemical measure for species i . This figure is standardized to 100%. Excluding the four new sites from Kibale (which are underlined), all chemical and biomass data are from Oates et al. (1990). Note the Kibale values are for red (*Procolobus badius*) and black-and-white colobus (*Colobus guereza*).

on items from these tree species constituted an average of 58.8% of their feeding time (Sebatoli, 50.4%, Kanyawara 55.3%, Dura River 62.6, Mainaro 67.0%). The mean protein to fiber ratios of those trees on which red colobus fed (0.55) did not differ significantly from those that they did not eat (0.52, $t=0.696$, d.f. = 78, $P=0.489$).

Around the world, colobine biomass and leaf chemistry have been quantified at nine sites. This permits an examination of the predictive power of the relationship between protein to fiber ratios and colobine abundance. Oates et al. (1990) presented six sites, and we have an additional four sites; however, one of those sites is shared between the two data sets, Kanyawara. For this site we take the mean of the previous values provided by Struhsaker and Waterman (presented in Oates et al., 1990) and our new values. If a range of biomass values was given for a site, the mean of the range was used in the regression. Colobine biomass varied from 84 kg/km² at Sepilok, Malaysia to 2675 kg/km² at Mainaro in Kibale (mean biomass across sites = 910 kg/km²). The protein/

fiber ratios reported in these studies showed a similar degree of variation (mean = 0.306, range 0.167–0.577). Colobine biomass at the nine sites could be predicted from the protein to fiber ratios of the mature leaves ($r^2=0.616$, $P=0.012$; Fig. 4). This relationship is also significant using a nonparametric approach ($r_s=0.800$, $P=0.01$).

4. Discussion

The fact that red colobus selected young leaves over mature leaves and that there are consistent phytochemical differences between these leaf stages, suggests that their diet choice is determined by the chemical constituents of their foods (see also Baranga, 1982, 1983). However, the fact that there were no detectable differences between frequently eaten foods and not eaten leaves with respect to any of the factors considered, suggests that the selection process is complex. This complexity is also indicated by the fact that when we attempted to predict foraging effort based on the different nutritional components and secondary compounds,

we only found one significant relationship and this was only with one of the two groups. This group selected foods that were high in protein and low in fiber. When we looked at the actual plants they were selecting, it is clear that this relationship was largely driven by the use of only one tree species; *C. durandii*. A previous behavioral study suggests that these two groups of red colobus experience different levels of feeding competition (Gillespie and Chapman, 2001). This earlier study found that the large group responded to a decline in the abundance of food by increasing its day range and speed of travel, presumably so that it could locate additional food sources. However, the small group did not change its ranging patterns in response to changes in food availability. This suggests that the members of the large group were experiencing feeding competition, while members of the small group were not. The differences among previous studies with respect to whether or not selection for high protein, low fiber food was evident may be a function of the level of feeding competition that the study group or population was experiencing (selection for *Alouatta palliata*—Milton, 1979, 1998; *Presbytis rubicunda* Davies et al., 1988; *Colobus satanas* McKey et al., 1981; 10 out of 12 populations (8 species) of lemurs Ganzhorn, 1992; no selection *C. polykomos* Dasilva, 1992, 1994).

The differences in factors influencing diet choice between the two groups of red colobus and the variability in diet over time and space (Chapman et al., 2002), indicates that caution must be used when attempting to make generalizations based on a single diet choice study. Similarly, diet choice studies conducted on captive animals that involve the choice among high quality diets that only vary with respect to particular compounds (e.g. toxin level), may not reflect the decision rules of wild populations that are experiencing feeding competition.

There was no evidence that red colobus avoided plants with high levels of secondary compounds. In fact one of the most preferred trees (*Prunus africana*) was the species with the highest levels of cyanogenic glycosides. This was true both for the large group that appeared to be experiencing feeding competition and for the small group that did not. It seems likely that the red colobus have physiological mechanisms to avoid the negative effects of these compounds. It may be that the gut flora of these animals enables them to detoxify some toxins that would otherwise act as dietary

deterrents (Oates et al., 1980; Waterman, 1984; Waterman et al., 1988). However, there was no evidence that red colobus avoided plant species with compounds (saponins) that have been shown to influence diet choice in domestic animals with similar digestive systems. In fact, the species with the highest saponin levels in its young leaves (*Albizia grandibracteata*) was the sixth and fourth most preferred plant species for the large and small groups, respectively.

Both our data on diet selection and the fact that colobine biomass within Kibale National Park can be predicted by the protein to fiber ratio of mature leaves in their environment, indicates the importance of protein and fiber to these animals. Digestible mature leaves that are rich in protein and low in fiber have been suggested to maintain colobine biomass when other more preferred foods are unavailable (McKey, 1978; Milton, 1979; Oates et al., 1990; Davies et al., 1999). This study adds to our previous understanding of determinants of colobine biomass by documenting that this relationship holds when comparisons are made both among sites scattered across the continent and among populations within a single forest. Given the inaccuracies associated with the estimation of primate densities, the means of collecting mature leaves (by basal area—Oates et al., 1990, this study; density—this study, or haphazardly—Ganzhorn, 1992), and the fact that many of the colobine species depend on mature leaves of lianas to support them through periods of food scarcity and that liana density is not quantified (Davies, 1991; Dasilva, 1994), it is surprising that 62% of the variance in colobine biomass among the nine sites can be explained by this relationship. Furthermore, the whole notion that protein to fiber ratio could predict colobus biomass assumes that all populations experience a season shortage of preferred foods and must fall back to eating mature leaves; some populations may not experience this shortage, as suggested by the diet selection of the small group of red colobus studied here.

Understanding and predicting factors that determine the abundance of particular animal species has proven extremely difficult, and there have been few direct tests of general hypotheses proposed to account for variation in abundance. A notable exception is this protein/fiber model for predicting the biomass of folivorous primates. Our study suggests that this model is a useful estimator of folivore carrying capacity, as the model can

make reliable predictions on a variety of spatial scales. However, the information available to date may not be sufficient to convince managers to use this information. This skepticism is based on a number of factors. First, to date, all studies draw their conclusions based on correlations among a small number of populations (i.e. <10), and it is conceivable that it may not be the protein to fiber ratio that is important, but something correlated with this ratio. Secondly, as previously mentioned, there is controversy over the importance of protein to primates (Ofstedal, 1991). Finally, previous studies have not demonstrated that the populations used for the correlations are at equilibrium. If some populations are not at the carrying capacity because a factor, such as a disease, has temporarily reduced their numbers, then correlations of food availability and/or quality and colobine biomass may be spurious. Predators (Isbell, 1990) and disease/parasites (Milton, 1996) are well known to cause short-term reduction in primate population size. While these are valid concerns, this is one of the few situations where there is a general model that can account for variation in primate abundance. This calls for further investigations into possible nutritional limits to colobine populations.

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