

Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content

MICHAEL D. WASSERMAN* and COLIN A. CHAPMAN*†

*Department of Zoology, University of Florida, Gainesville, Florida 32611, USA; and †Wildlife Conservation Society, 185th Street and Southern Boulevard, Bronx, NY 10460, USA

Summary

1. A fundamental ecological question is what determines the abundance of animals? Answering this question is vital in the formulation of effective management plans for endangered or threatened species. However, there are few general hypotheses proposed to account for variation in animal abundance. Studies of folivorous primates are a notable exception. In this group, the protein to fibre ratio of mature leaves is a significant predictor of biomass. However, Dasilva (1992) suggested that the availability of energy may play a critical role in colobine behaviour and ecology.

2. Here we evaluate the importance of food energy content for the red colobus (*Procolobus badius*) and black-and-white colobus (*Colobus guereza*) monkeys of Kibale National Park, Uganda.

3. Energy was found to be of little importance. None of the eight groups studied selected high-energy foods: there was no correlation between food energy content and foraging effort. For all groups, estimates of energy expenditure [daily energy expenditure (DEE) and average daily metabolic needs (ADMN)] were less than estimates of energy consumption. Finally, the average energy content of mature leaves from the 20 most abundant tree species at four sites was not related to colobine biomass.

4. In contrast, the protein and fibre content of foods was important to both colobine species. Seven of the eight groups selected foods with a high-protein, low-fibre content. The average protein to fibre ratio of mature leaves from the 20 most abundant tree species at four sites was correlated positively with colobine biomass.

5. This study provides further validation of the protein to fibre model, suggesting the importance of this model for conservation and management of colobus monkeys, with the potential application to other small mammalian herbivores.

Key-words: calorimetry, *Colobus*, diet choice, Kibale National Park, nutritional ecology.

Journal of Animal Ecology (2003) **72**, 650–659

Introduction

A fundamental issue in ecology is determining factors that regulate animal abundance. A variety of potential factors have been proposed, including external factors such as food resources, weather, predation and disease, and internal conditions such as territoriality and aggressive behaviours (Krebs 1978; Boutin 1990). The importance of understanding determinants of animal abundance has become increasingly vital as ecologists are asked to apply their knowledge to develop informed management plans for endangered or threatened

species. However, understanding and predicting factors that determine the abundance of particular species have proven extremely difficult, and thus there are few general hypotheses addressing this topic. Studies of folivorous primates are a notable exception. 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 colobine populations (see also McKey 1978). Therefore, if easily digestible mature leaves are plentiful in an area when other more preferred foods are lacking, the site may support a relatively large population of colobines (Davies 1994). By measuring overall mature leaf quality as the ratio of protein to fibre, several subsequent studies have found positive correlations between colobine biomass and this index of leaf quality (Waterman *et al.* 1988; Oates *et al.* 1990; Chapman

Correspondence: C.A. Chapman, Department of Zoology, University of Florida, Gainesville, Florida 32611, USA. Tel. +1 352 392 1196; Fax: +1 352 392 3704; E-mail: cchapman@zoo.ufl.edu

et al. 2002). A similar relationship was also found for some folivorous lemurs of Madagascar (Ganzhorn 1992).

Each primate species has a protein threshold below which it cannot maintain bodily functions (Milton 1979; Milton, van Soest & Robertson 1980). As for fibre, there is substantial evidence that colobines can digest some fibre components, but not lignin (Waterman & Choo 1981; Waterman & Kool 1994). Thus, increasing fibre content increases the amount of food ingested that cannot be digested and slows the rate of passage of digesta through the stomach. This reduces the efficiency of bacterial enzyme action, causing a reduction in protein uptake (Milton 1979, 1982, 1998).

While correlative studies suggest that the protein to fibre ratio of available foods may limit colobine populations, there are reasons to be sceptical. This scepticism is based on a number of factors. First, there is controversy over the importance of protein to primates. Oftedal (1991) calculated that even a primate population with low protein digestibility caused by consumption of tannin would require only 7–11% protein on a dry matter basis (DM) for growth and maintenance, and only 14% (DM) for reproduction (note that the impact of tannins on digestibility is not well understood; Mole & Waterman 1985; Waterman & Kool 1994). Because leaves eaten by primates average 12–16% (DM) protein (Glander 1982), Oftedal concluded that it is unlikely that protein deficiency will be a problem for most primates, except for lactating females eating a diet high in tannins. With respect to colobines, protein demand might be even lower, because blood urea can be recycled by secreting it into saliva or diffusing it across the wall of the foregut. This nitrogen source can then be used by microbes for protein synthesis, and the microbes are digested in turn in the small intestine (Kay & Davies 1994).

Secondly, while some studies have found folivorous primates to select foods that are high in protein and low in fibre (Milton 1979, 1998; McKey *et al.* 1981; Davies, Bennett & Waterman 1988; Ganzhorn 1992), other studies have not (Dasilva 1992; two species of lemurs – Ganzhorn 1992).

Finally, scepticism towards the protein to fibre model is warranted because all the studies to date are correlative and based on small sample sizes (i.e. < 12). Some other characteristic of the folivores' foods, that is correlated with protein but not yet identified, may be responsible for maintaining their populations. Along these lines, researchers have often considered the energy content of foods to play a critical role in diet selection (Schoener 1971). Dasilva (1992, 1994) presented evidence that a population of *Colobus polykomos* (Zimmerman) on Tiwai Island, Sierra Leone, was limited seasonally by the availability of energy-rich foods and did not select foods based on protein content. Furthermore, seeds, which had the highest energy content of all parts consumed, were the most preferred food type for this population. Dasilva's findings run

counter to the observation that colobine biomass can be predicted by the protein to fibre ratios in mature leaves and suggest that energy may play a crucial role in colobine nutritional ecology.

Given this controversy, and Dasilva's findings for *C. polykomos*, the objective of this study was to evaluate the importance of food energy content to the red colobus *Procolobus badius* (Kerr) and black-and-white colobus monkeys *C. guereza* (Rüppell) of Kibale National Park, Uganda. We took three approaches. First, we examined if these two colobus monkeys were selecting foods with high energy content and determined if the protein to fibre ratio of their foods was correlated with energy content. This analysis was conducted on eight groups living in different ecological settings and involved over 3000 h of observations conducted over 2 years. Groups were selected to maximize the chances of obtaining variation in the intensity of feeding competition. Thus, groups varied in size (large groups are expected to experience more feeding competition than small) and level of disturbance (groups in more disturbed habitats are expected to experience greater feeding competition). Secondly, to provide a crude evaluation of whether or not the study groups were expending more energy than they were obtaining, we mimicked the analysis of Dasilva (1992), with a few adjustments allowing for a more accurate estimate. This analysis produced rough approximations of energy expenditure and consumption for males and non-reproductive, lactating and pregnant females of each group. Finally, we examined the relationship between colobus biomass and food energy content across four populations representing a range of both biomass and energy availability. This was conducted following the methods used to test the protein/fibre model (Oates *et al.* 1990); the energy content of mature leaves of the 20 most common plants in each habitat were quantified and related to colobine biomass.

Methods

STUDY SITES

The study was conducted in and near Kibale National Park (766 km²), which is located in western Uganda (0° 13'–0° 41' N and 30° 19'–30° 32' E) near the foothills of the Ruwenzori Mountains (Chapman *et al.* 1997; Struhsaker 1997; Chapman & Lambert 2000). Mean annual rainfall in the region is 1734 mm (1990–2000) and rainfall is bimodal, with two rainy seasons generally occurring from March to May and September to November. Relationships between colobus biomass and food energy content were conducted across four sites, each approximately 12 km apart: Sebatoli, Kanyawara (K-30 forestry department), Dura River and Mainaro. Within Kibale there is an elevational gradient from north to south, which corresponds to a north–south increase in temperature and decrease in rainfall and change in forest composition (Struhsaker 1997).

The behavioural component of this study was conducted at the relatively pristine Kanyawara site, a logged site in Kibale (Mikana), and at a forest fragment – Crater Lake Nkuruba. The logged Mikana site is part of the K-14 forestry compartment, but extraction in the observation area was more intense than the whole compartment with estimates of 21 m³/ha or approximately 7.4 stems/ha. Incidental damage in this area was high, and it is estimated that approximately 50% of all trees were destroyed by logging and incidental damage (Struhsaker 1997). Finally, Crater Lake Nkuruba (0°32' N and 30°19' E; 9.2 ha forest, 3 ha lake) is an explosion crater (Chapman *et al.* 1998). Being too steep for agriculture, forest remains on the rim of the crater. However, with improved transportation to the region, clearing for timber, gin brewing, charcoal, brick making and agriculture have become profitable, resulting in the clearing of neighbouring fragments (Chapman *et al.* 2003). Consequently, the black-and-white colobus populations have increased by 320% since 1995, as animals immigrate from cleared fragments.

BEHAVIOURAL OBSERVATIONS

Behavioural observations were made of eight groups to quantify diet and activity budgets, which were used to estimate energy intake and expenditure. Observations were made on two groups of red colobus and on two groups of black-and-white colobus (identified as Big and Small groups) at Kanyawara during dawn to dusk observation for 5 days each month from August 1998 until June 1999. This produced approximately 800 h of observations for each species (red colobus = 3264 feeding scores, black-and-white colobus = 2281). From August 1999 to May 2000, observations were made on one group of each species at Crater Lake Nkuruba (identified as the Fragment group), producing approximately 650 h of observations for each species (red colobus = 1314 feeding scores, black-and-white colobus = 968). From July 1999 to May 2000, we observed one group of each of the species at the logged site (Mikana) for approximately 1000 h (red colobus = 2163 feeding scores, black-and-white colobus = 1558 feeding scores; identified as the Mikana groups). During each half-hour that 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, leaf petiole) were recorded.

At the end of each week of observation, the five most frequently eaten food items for each species were collected. Samples were obtained using a tree-pruning pole to cut down a tree limb, typically from the middle of the tree's canopy. Food items were processed in a fashion that mimicked closely the feeding behaviour of the animals, and only those parts selected by the animals were collected. For example, if the animals ate leaf petioles, the length of petiole typically consumed was collected. Samples were dried in the field either by sun-drying, using a dehydrator that circulated warm

air past the samples, or using a light-bulb heated box containing a series of racks.

CENSUS METHODS

Colobine abundance within Kibale was assessed using line-transect methodology (National Research Council 1981; Chapman, Fedigan & Fedigan 1988; Chapman *et al.* 2000). 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 1997. Censuses were conducted between 07.00 h and 14.00 h at a speed of approximately 1 km per h. Data collected included primate species observed, time of observation, straight-line distance between the animal and observer (estimated visually) and mode of detection. For further details of the census methods used see Chapman *et al.* (2000).

NUTRITIONAL ANALYSES

Dried samples were ground typically to pass through a 1-mm mesh screen using a Wiley mill (a few fruit samples were ground with a coffee grinder). Dry matter was determined by drying a portion of each sample overnight at 105 °C. To determine organic matter, a portion of each sample was then placed in a muffle furnace overnight at 500 °C.

The energy content of samples was determined using bomb calorimetry (0.5 g sample weighed to 0.0001 g) following standard procedure (Parr Instrument Company bomb calorimetry manuals, Paine 1971). Corrections were made for the remaining fuse wire and for the number of calories produced by the formation of nitric acid. The energy content (kJ/g) was expressed on an ash-free organic matter basis (OM). The energy content of 61 colobus foods was determined, and 20 duplicate samples were run to ensure accuracy. The protein (nitrogen) content of the plant parts was assessed using Kjeldahl procedures and fibre was assessed using standard methods (Chapman *et al.* 2002).

ESTIMATES OF ENERGY BUDGETS

We followed the methods used by Dasilva (1992) to estimate the amount of energy that males and non-reproductive, lactating and pregnant females of different colobus groups were obtaining from the environment and expending on a daily basis. These are simple and crude calculations meant to evaluate the possibility that groups could be limited by energy availability. Given the number of assumptions that are made to obtain these estimates, the values should be viewed as preliminary. Clearly, we need detailed studies of the basal metabolic rate of these animals, estimates of energy expenditure using doubly labelled water (Nagy

& Milton 1979), an evaluation of digestion efficiency and a determination of the ingestion rate of various foods.

To estimate energy consumption, we first used behavioural data on the number of hours spent feeding per day and the percentage of time spent feeding on each particular plant part to calculate the number of hours spent feeding on each particular plant part per day. From these values, the amount of each part consumed per day was calculated as:

$$\begin{aligned} \text{(Part) Consumed (g)/day} &= \text{Hours Feeding} \\ &\text{(Part) * 60 min * Dry Mass Feeding Rate (Part) (g/min).} \end{aligned}$$

Feeding rate is difficult to estimate in the field. Kurland & Gaulin (1987) have suggested that a relationship exists between the time spent feeding on leaves and the mass of material ingested. Published values for fresh mass of leaves consumed per minute vary from 1.71 to 6.43 g/min (Dasilva 1992). We used the dry mass feeding rates found in Gaulin & Gaulin (1982) for the 7.3 kg *Alouatta seniculus* (Linnaeus) (average body mass from Harvey & Clutton-Brock 1985). Of the rates available, these seemed the most detailed. However, these rates may underestimate consumption for the black-and-white colobus and red colobus because they are larger than *A. seniculus* (*C. guereza* – 10.5 kg; *P. badius* – 8.2 kg, Harvey & Clutton-Brock 1985). Because rates are listed only for the ingestion of mature and young leaves and ripe and unripe fruit, we used the average rate for all parts for the consumption of other parts. Finally, the total energy consumed per day was determined by summing the product of the amount of the particular plant part consumed per day and the average energy content (DM) for that particular part, for all parts.

Not all energy consumed is available to animals. Watkins, Ullrey & Whetter (1985) estimated that for *C. guereza*, the digestibility of gross energy on a high-fibre diet was 85% (i.e. 15% of the ingested energy is excreted). This value indicates that the colobines are better at digesting low-quality foods than are ruminants, because van Soest (1982) predicts the energy available for growth and activity to be as little as 39%. We assume Watkins's value to be valid for our two colobus species; therefore, we multiply energy estimates from the bomb calorimetry by 85% to provide an estimate of the energy available to the study animals. However, we also determine the level of digestibility at which the monkeys no longer meet their energy demands.

Energy expenditure was evaluated in two ways. First, we estimated the daily energy expenditure (DEE) as twice the basal metabolic rate (BMR; Nagy & Milton 1979; Iwamoto 1988). The BMR we use for both species is based on the work of Müller, Kanau & Maloiy (1983) in which two *C. guereza* males were studied and found to have an average rate of oxygen consumption of 0.285 mL O₂ per gram per hour. This rate was converted to kJ per day by multiplying by the conversion factor 20.08 mass and 24 h. Secondly, we use the equa-

tions of Harvey & Clutton-Brock (1981) to estimate average daily metabolic needs (ADMN), but substituted the calculated BMR based on Müller *et al.* (1983) for the second part of the equation, as it is a more accurate estimate of resting metabolic rate.

$$\text{ADMN (kJ/day)} = \left(\left[\frac{130W^{0.75}}{24 \text{ h}} * S \right] + [\text{BMR (kcal/day)/24 h} * (24 \text{ h} - S)] \right) \times 4.1868 \text{ kJ/kcal},$$

where W = body mass (kg), S = number of active hours each day, and 130W^{0.75} represents active metabolic rate. The behavioural observations for each group were used to estimate the average number of hours the animals were active.

While the time spent travelling is included in the time spent active in the above equation, Harvey & Clutton-Brock (1981) add Tucker's (1970) estimate of travel cost:

$$T = 0.1(10)^E \text{ (kg * km)},$$

where T = travel costs in kcal per kg per km, E = 1.67W^{-0.126} and W = body mass (kg). To calculate the total energy expended per day due to travel, T must then be multiplied by the mean daily distance travelled (Struhsaker & Leland 1987), body mass of the study species, and 4.1868 kJ/kCal.

The arboreal travel that colobus perform (Gebo & Chapman 1995a,b) is probably more expensive than that estimated by Tucker's equation, so the addition of T may still underestimate travel costs. Costs of pregnancy and lactation are generally regarded to increase energy expenditure by 1.25 and 1.5, respectively (Portman 1970). These values are used here, but it should be noted that studies of other animals suggest that lactation costs may be higher (Baile & Forbes 1974).

ANALYSES

To evaluate if the different species/groups were selecting food items high in energy or had large protein to fibre ratios, we used behavioural data to calculate the percentage of foraging effort devoted to particular plant species and part (e.g. leaf petioles of *Markhamia platycalyx*). Subsequently, we attempted to predict foraging effort based on that food's energy and protein/fibre ratio. However, one can consider that these foods are not equally available. Some tree species bearing food items are very abundant in the forest, whereas others are rare. To consider variation in availability for the groups in the unlogged area, we established twelve 200 m × 10 m transects placed randomly along the existing trail system, producing a total sampling area of 2.4 ha (Chapman & Chapman 1997; Chapman *et al.* 1999). All trees with a diameter at breast height (d.b.h.) ≥ 10 cm and within 5 m of the trail were tagged and the d.b.h. recorded. A total of 1171 trees from 67 species were identified. Four similar transects were established in Mikana and ten 60 m × 10 m transects were established

at Crater Lake Nkuruba from the top of the crater to the water's edge. We used a multiple regression technique (partial correlation) to quantify the significance of protein/fibre ratios and energy as predictors of foraging effort when the linear effects of availability were statistically removed.

To examine if the energy content of the foods could limit the size of colobine populations, we quantified colobine biomass and related this to the average energy content of the mature leaves of the 20 most abundant tree species at each of the four sites within Kibale. Tree density (> 10 cm d.b.h.) of these sites was determined using vegetation transects (200 m × 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).

Results

Both species relied most heavily on young leaves regardless of group size or ecological setting (Table 1). The importance of other plant parts in the diets of the two colobus species in the different areas was highly variable. Mature leaves were eaten frequently by groups of both species in the forest fragment. Interestingly, the

black-and-white colobus in the fragment ate ripe fruit for almost 10% of their foraging time. In general, young leaves and flowers had high levels of protein and little fibre; however, there was considerable variation among species (Table 2). For example, the protein to fibre ratio of young leaves ranged from a low of 19 for *Parinari excelsa* to 303 for *Celtis durandii*, whereas the mean for all species eaten by the colobus was 139. As might be expected, fruit (average = 22.4 kJ/g (OM), SD = 1.8) and flowers (22.4 kJ/g (OM), $n = 1$) tended to have a high energy content, although considerable interspecific variation was found in the energy content of the fruit (Table 2). Overall, the energy content of the colobus foods ranged from 18.0 kJ/g (OM) (*Eucalyptus* bark) to 24.4 kJ/g (OM) (*Prunus africana* ripe fruits).

Neither red nor black-and-white colobus selected foods that were high in energy: all eight groups showed no correlation between energy content of their foods and foraging effort ($P > 0.263$ for all groups). In contrast, the protein to fibre ratio was correlated with foraging effort for both red and black-and-white colobus in seven of the eight groups ($P < 0.05$; the group with no correlation was the small group of red colobus from forestry compartment K-30).

When the availability of the different species of food plants were controlled statistically, again seven of the eight groups showed evidence of selection for foods

Table 1. The percentage of total feeding observations that different colobus groups in or near Kibale National Park, Uganda spent eating different plant parts (leaf buds are included in young leaves)

	Ripe fruit	Unripe fruit	Flowers	Young leaves	Mature leaves	Petioles	Bark
Red colobus							
Big	5.0	1.6	3.5	75.6	5.6	7.9	0.3
Small	6.4	2.5	0.8	64.1	13.3	6.4	6.4
Fragment	3.3	4.1	1.8	59.7	22.4	1.6	6.3
Mikana	2.7	2.9	1.8	78.5	7.4	5.8	0.2
Average	4.4	2.8	2.0	69.5	12.2	5.4	3.3
Black-and-white							
Big	0.0	0.0	2.2	84.4	3.6	0.8	0.0
Small	2.4	7.2	0	77.7	5.8	0.4	4.8
Fragment	9.5	2.8	6.2	64.9	14.1	0.8	0.7
Mikana	1.8	8.1	3.4	78.2	5.3	3.1	0.1
Average	3.4	4.5	3.0	76.3	7.2	1.3	1.4

Table 2. The average, standard deviation and sample size of the protein, fibre, and energy content (OM – organic matter basis; DM – dry matter basis) for different plant parts eaten by the colobus monkeys of Kibale National Park, Uganda

	Sample size	Protein/fibre		Energy (OM)*		Energy (DM)*	
		Mean	SD	Mean	SD	Mean	SD
Young leaves	32	138.60	92.11	21.3	0.63	19.4	1.09
Mature leaves	13	88.30	55.30	21.4	0.60	19.5	0.94
Petioles	5	33.50	9.30	18.8	0.37	16.5	0.58
Ripe fruit	3	33.00	16.00	22.4	1.82	21.0	1.30
Bark	2	7.01	0.71	18.0	0.21	15.9	0.54
Unripe fruit	1	15.70		23.0		21.2	
Flowers	1	184.00		22.4		20.4	

*kJ g⁻¹.

Table 3. Rough estimates of the energy expenditure (daily energy expenditure (DEE) and average daily metabolic needs (ADMN)) and consumption (with 85% availability of ingested energy assumed) for four groups of red colobus and four groups of black-and-white colobus monkeys found in or near Kibale National Park, Uganda. All values in kJ/day

Species	Sex	BMR	DEE	ADMN*	Energy consumed**	Energy available**
<i>Procolobus badius</i> ¹	Female	797	1593	1242	13935	11845
	Lactating	1195	2390	1507	13935	11845
	Pregnant	996	1992	1375	13935	11845
	Male	1442	2884	2068	13935	11845
<i>Procolobus badius</i> ²	Female	797	1593	1225	11939	10148
	Lactating	1195	2390	1495	11939	10148
	Pregnant	996	1992	1360	11939	10148
	Male	1442	2884	2044	11939	10148
<i>Procolobus badius</i> ³	Female	797	1593	1232	11009	9358
	Lactating	1195	2390	1500	11009	9358
	Pregnant	996	1992	1366	11009	9358
	Male	1442	2884	2054	11009	9358
<i>Procolobus badius</i> ⁴	Female	797	1593	1196	13084	11121
	Lactating	1195	2390	1475	13084	11121
	Pregnant	996	1992	1336	13084	11121
	Male	1442	2884	2003	13084	11121
<i>Colobus guereza</i> ¹	Female	1270	2541	1734	7199	6120
	Lactating	1906	3811	2202	7199	6120
	Pregnant	1588	3176	1968	7199	6120
	Male	1621	3241	2151	7199	6120
<i>Colobus guereza</i> ²	Female	1270	2541	1715	6725	5716
	Lactating	1906	3811	2190	6725	5716
	Pregnant	1588	3176	1952	6725	5716
	Male	1621	3241	2128	6725	5716
<i>Colobus guereza</i> ³	Female	1270	2541	1688	8099	6884
	Lactating	1906	3811	2174	8099	6884
	Pregnant	1588	3176	1931	8099	6884
	Male	1621	3241	2099	8099	6884
<i>Colobus guereza</i> ⁴	Female	1270	2541	1681	9732	8272
	Lactating	1906	3811	2170	9732	8272
	Pregnant	1588	3176	1926	9732	8272
	Male	1621	3241	2090	9732	8272

*ADMN = $\{[(130W^{0.75}/24) * S] + [(BMR * (0.238846 \text{ kcal/kJ})/24) * (24 - S)] + (T * d * W)\} * (4.1868 \text{ kJ/kcal})$ (Harvey & Clutton-Brock 1981), where W = body weight (kg), S = no. active hours/day, travel costs T (kcal/kg * km) = $0.1(10)^{(1.67W^{0.126})}$ [Tucker 1970], d = distance travelled (km)/day (values for 'd' of 0.535 km for BWC and 0.557 km for RC from Struhsaker & Leland 1987) also for pregnant ADMN *1.25 and for lactating *1.5 (Portman 1970). **Feeding rate estimates used are from *Alouatta seniculus* with mean body weight 7.25 kg from Gaulin & Gaulin (1982): mature leaves: 3.7, young leaves: 1.17, ripe fruit: 6.35, unripe fruit: 3.7, all other parts: 3.5 g dry wt/min. RCMIKANA feed on seeds 0.7% of the time; this value was not used in the calculations. ¹Forestry Compartment K30 Big Group (unlogged), ²K30 Small Group (unlogged), ³Mikana (logged), ⁴Nkuruba (fragment).

high in protein and low in fibre, as indicated by a significant partial correlation coefficient ($P < 0.05$). Only the small red colobus group from K-30 showed no evidence of selecting foods high in protein and low in fibre after controlling for food availability. When the availability of the different species of food plants was removed statistically, again there was no evidence that any of the groups selected foods that were high in energy ($P > 0.442$).

The energy content of the foods of the colobus monkeys was not correlated with their protein content ($P = 0.108$, $n = 43$) or the protein to fibre ratio ($P = 0.357$, $n = 43$).

Calculating an index of activity as the amount of time the groups were active (feeding, travelling, grooming) minus the amount of time inactive (resting) illustrates marked variation, with the largest difference being 41.7% (Fig. 1). Black-and-white colobus were

more inactive than red colobus, and groups in disturbed areas were more inactive than groups in undisturbed habitats.

When comparing both estimates of energy expenditure (DEE and ADMN) to estimates of energy consumption (85% availability), none of the groups are found to be energy deficient (Table 3). Furthermore, for the red colobus, no age/sex class in any group was found to be energy deficient unless digestive efficiency was so low that only 19% of ingested energy was available when comparing to ADMN and 27% or less availability when comparing to DEE. The first age/sex class red colobus to be energy deficient in these cases are the males from the Mikana group. For the black-and-white colobus, a 60% or less availability value must be assumed when comparing ADMN and 33% or less availability value must be assumed with DEE to find

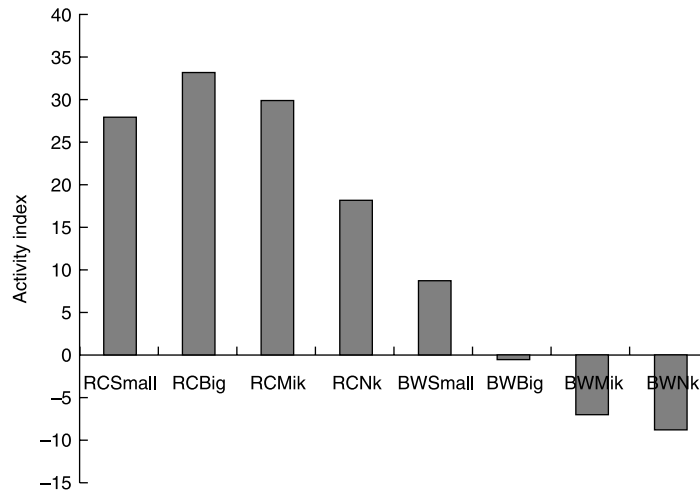


Fig. 1. The level of activity (proportion of time spent active (feeding, travelling, etc.) minus the amount of time spent inactive during the (day) for eight groups of red colobus (*Procolobus badius*) and black-and-white colobus (*Colobus guereza*) living in or near Kibale National Park Uganda (Uganda RCBig – the large group of red colobus at Kanyawara, RCSmall – the small group of red colobus at Kanyawara, RCMik – the group of red colobus in the logged area known as Mikana, RCNk – the red colobus group at Crater Lake Nkuruba; BWBig – the large group of red colobus at Kanyawara, BWSmall – the small group of red colobus at Kanyawara, BWMik – the group of red colobus in the logged area known as Mikana, BWNk – the red colobus group at Crater Lake Nkuruba).

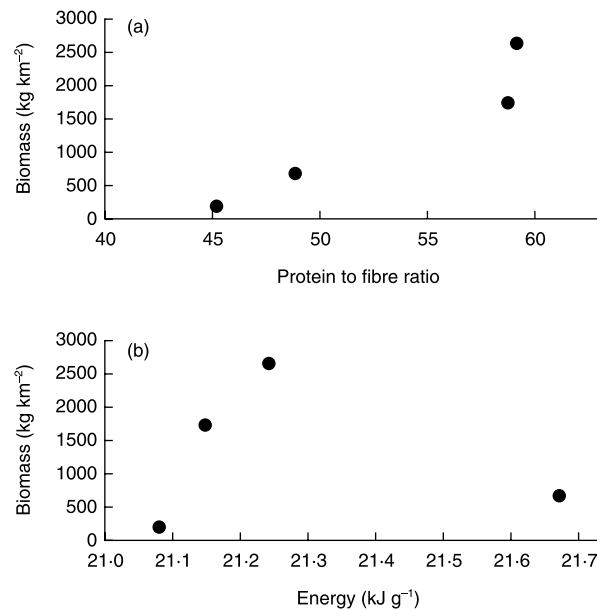


Fig. 2. The relationship between (a) the average protein to fibre ratio and (b) the energy content of the mature leaves from the 20 most abundant tree species at four sites in Kibale National Park, Uganda, and the biomass of red colobus and black-and-white colobus at those sites.

an instance of energy deficiency. Such low estimates of availability seem unrealistic, given current studies (Watkins *et al.* 1985); therefore, these two colobus species do not appear to be energy deficient.

Colobine biomass at the four sites within Kibale varied from 191 kg/km² at the Dura River to 2675 kg/km² at Mainaro in Kibale (mean biomass across sites = 1316 kg/km²). As demonstrated previously (Chapman *et al.* 2002), colobine biomass appears to be related to the average protein to fibre ratio of mature leaves from the 20 most abundant tree species at each site (Fig. 2a).

In contrast, there is no evidence that the biomass at these sites is related to the energy content of mature leaves from the 20 most abundant tree species at these sites (Fig. 2b).

Discussion

Three lines of evidence suggest that neither of the colobine species we studied were limited by energy availability; (1) they did not select food based on energy content; (2) crude estimation of energy gain vs. expenditure

suggested that energy was not limiting; and (3) the biomass of colobus at the four sites in Kibale was not related to the energy content of the available mature leaves. In contrast, seven of eight groups preferred foods that were high in protein and low in fibre, and biomass of colobines could be predicted based on the protein to fibre ratios of the available mature leaves.

These results provide support for Milton's (1979) protein to fibre model, but do not provide evidence to support Dasilva's (1992) suggestion that the colobus monkeys generally suffer from shortages of high energy foods. Why the conclusions of Dasilva's and this study differ is not readily apparent. It may be that the Tiwai Island population of colobus that Dasilva studied had sufficient protein available to them in the seeds they selected (Dasilva 1992), so the need for energy took precedence in limiting population size. However, this is not supported by the observation that the colobus biomass at the Tiwai Island site is relatively low (Oates *et al.* 1990), and it runs counter to the widespread application of the protein to fibre model to account for variation in colobus biomass in Africa (including Tiwai) and South-east Asia (Oates *et al.* 1990). A methodological point worth mentioning is that Harvey & Clutton-Brock's (1981) equation that Dasilva used employs an estimate of basal metabolic rate that is high relative to the actual rate documented by Müller *et al.* (1983) for *C. guereza*. This will overestimate the average daily metabolic needs, as well as DEE, and may therefore suggest energy deficiency when not actually the case. However, it is unlikely that this completely explains the differences among these studies. It may be that our populations of colobus monkeys were able to behaviourally respond to periods when energy was scarce and thus effectively avoid any need to select high energy foods. This idea is supported by the fact that we documented large differences in activity levels among groups. In general, the groups that we would have expected to be experiencing more intense feeding competition (i.e. those groups in the logged area or the forest fragments) tended to be more inactive, potentially conserving energy. If, at times when high energy foods were difficult to find, the groups could easily find foods high in protein and low in fibre without incurring high travel costs, the animals could decrease activity, and thus need not be concerned about the energy content of their foods. The differences between our study and that of Dasilva do highlight the importance of quantifying and understanding factors that may underlie differences in activity patterns (see also Dasilva 1992).

Milton (1979) suggested that for small mammalian herbivores, the protein to fibre ratio may be a good predictor of leaf choice. McKey (1978) 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 colobine populations. In this study we found that for seven of the eight groups observed, the protein to fibre ratio was a good predictor of food choice. However, we have been

collecting quantitative data on colobus foraging in Kibale since 1992, involving over 6000 h of observations. During this time, we have never observed groups to eat mature leaves for extended periods of time (i.e. exclusively for up to a week), as would be suggested if they were a fallback food. Rather, they tend to eat mature leaves during short feeding sessions, typically less than an hour, that occur at widely separated intervals. It may be that we have simply not observed these groups for long enough and that at some time in the future there will be a period when the animals must rely on mature leaves, and such rare events determine the biomass of an area. However, it is also possible that for our populations mature leaves are not 'fallback' foods, eaten when other more preferred foods are unavailable. Following Milton (1979), we suggest that the protein to fibre ratio is a good predictor of food choice in small mammalian herbivores. We suggest that areas that generally have food items that are low in fibre and high in protein are able to support high biomasses of these consumers. Thus, it is not the actual protein to fibre ratio of the mature leaves that is important in influencing biomass, but rather the general availability of high-protein, low-fibre foods. Measuring the mature leaves' protein to fibre ratio may be useful if it correlates with the general availability of high-protein, low-fibre foods.

The influence of the protein to fibre ratio on animal abundance will probably extend beyond the folivorous primates, to include other small mammalian herbivores. Its importance stems from a major problem facing herbivorous animals, the ingestion of long-chain structural polymers that are not hydrolysed easily (McNab 2002). Furthermore, this problem is magnified by size because gut retention time is equivalent to approximately $m^{0.25}$, where m = body mass (McNab 2002). Thus, smaller species have a shorter retention time, causing greater difficulty in meeting nutritional requirements while ingesting relatively high amounts of fibre. Cork (1994) set a size cut-off for fibre tolerance at 15 kg, below which animals become 'fibre-intolerant'. Because of this intolerance, the availability of high-quality foods (low fibre, high nutritional value) becomes ever more important to the health of small herbivores. In our study, we have demonstrated further the importance of protein over other nutritional characters, thereby further defining high-quality folivorous foods as low-fibre, high-protein. With a high-quality folivorous diet possibly being more difficult to obtain or the need for physiological adaptations (i.e. fore-gut fermentation) to deal with fibre, there are few folivores falling under a 15 kg threshold: mainly sloths, primates, hares, rabbits, voles and lemmings (McNab 2002). The abundances of these small folivores are probably the most heavily influenced by the protein to fibre model.

In addition, other small herbivorous mammals may potentially be influenced by this ratio. Studies show that various herbivores select foods high in protein and low in fibre. In the agile wallaby (*Macropus agilis*)

(Gould), a shift in diet occurs from the wet to dry season in response to preferred foods having lower protein and digestibility (higher fibre) in the dry season (Stirrat 2002). Others describe behavioural mechanisms allowing for the ingestion of more protein and less fibre. For example, Lowry (1989) found that the black fruit bat (*Pteropus alecto*) (Temminck) chews the leaves of the tree *Albizia lebbek* (Linnaeus), swallows the liquid extract (which is 36% protein) and spits out the fibrous residue, thus increasing protein and decreasing fibre consumption.

In general, this study provides support for the notion that the protein to fibre ratio is a good predictor of food choice in colobines and for the use of this index of food quality in predicting colobine biomass. The importance of understanding determinants of animal abundance has become increasingly vital, as ecologists are asked to apply their knowledge to develop informed management plans for endangered or threatened species (Chapman & Peres 2001). This study provides support for the use of the protein to fibre model in the conservation and management of colobines, by showing that general food preference is influenced by the protein to fibre ratio, and by finding no evidence to support the alternative hypothesis that colobines are limited by availability of high energy foods. This information could be used by managers in a number of ways. For example, if important food trees used by colobines could be left standing in selective logging operations or if loggers could use directional felling to reduce impact to these trees, for primate species that are negatively impacted by logging their population decline might be less severe or the speed of population recovery might be improved. The results of this study suggest that the tree species targeted for such treatment should provide food items with a high protein to fibre ratio. Energy availability does not appear to be of significant concern in the conservation of black-and-white colobus and red colobus monkeys.

Acknowledgements

Funding for this research was provided by the Wildlife Conservation Society and National Science Foundation (grant number SBR-9617664, SBR-990899) and Michael Wasserman was supported by an REU Supplement and the University Scholars Program at the University of Florida. Permission to conduct this research was given by the Office of the President, Uganda, the National Council for Science and Technology and the Uganda Wildlife Authority. We would like to thank Tom Gillespie and Sophia Balcomb for help with the census work, Karen Bjorndal, Alan Bolten, Matt Burgess, Peter Eliazar, Erin Hauck, Raime Fronstin, Kate Moran and Ada Mayte Santamaria for help with nutritional analysis, Glynn Davies for interesting discussions about protein and energy and Lauren Chapman, Brian McNab, Katie Milton and Sue Boinski for helpful comments on this project.

References

- Baile, C.A. & Forbes, J.M. (1974) Control of feed intake and regulation of energy balance in ruminants. *Physiological Review*, **54**, 160–214.
- Boutin, S. (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. *Canadian Journal of Zoology*, **68**, 203–220.
- Chapman, C.A., Balcomb, S.R., Gillespie, T.R., Skorupa, J. & Struhsaker, T.T. (2000) Long-term effects of logging on African primate communities: a 28 year comparison from Kibale National Park, Uganda. *Conservation Biology*, **14**, 207–217.
- Chapman, C.A. & Chapman, L.J. (1997) Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica*, **29**, 396–412.
- Chapman, C.A., Chapman, L.J., Bjorndal, K.A. & Onderdonk, D.A. (2002) Application of protein to fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology*, **23**, 283–310.
- Chapman, L.J., Chapman, C.A., Crisman, T.L. & Nordlie, F.G. (1998) Dissolved oxygen and thermal regimes of a Ugandan crater lake. *Hydrobiologia*, **385**, 201–211.
- Chapman, C.A., Chapman, L.J., Wrangham, R., Isabirye-Basuta, G. & Ben-David, K. (1997) Spatial and temporal variability in the structure of a tropical forest. *African Journal of Ecology*, **35**, 287–302.
- Chapman, C.A., Fedigan, L.M. & Fedigan, L. (1988) A comparison of transect methods of estimating population densities of Costa Rican primates. *Brenesia*, **30**, 67–80.
- Chapman, C.A. & Lambert, J.E. (2000) Habitat alteration and the conservation of African primates: a case study of Kibale National Park, Uganda. *American Journal of Primatology*, **50**, 169–186.
- Chapman, C.A., Lawes, M.J., Naughton-Treves, L. & Gillespie, T.R. (2003) Primate survival in community-owned forest fragments: are metapopulation models useful amidst intensive use? *Primates in Fragments: Ecology and Conservation* (ed. L.K. Marsh), pp. 63–78. Kluwer Academic/Plenum Publishers, New York.
- Chapman, C.A. & Peres, C. (2001) Primate conservation in the new millennium: the role of scientists. *Evolutionary Anthropology*, **10**, 16–33.
- Chapman, C.A., Wrangham, R.W., Chapman, L.J., Kennard, D.K. & Zanne, A.E. (1999) Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*, **15**, 189–211.
- Cork, S.J. (1994) Digestive constraints on dietary scope in small and moderately-sized mammalian folivores in relation to chemical defenses in temperate and tropical forests. *Plant Defenses Against Mammalian Herbivory* (eds R.T. Palo & C.T. Robbins), pp. 133–166. CRC Press, Boca Raton.
- Dasilva, G.L. (1992) The western black-and-white colobus as a low-energy strategist: activity budget, energy expenditure and energy intake. *Journal of Animal Ecology*, **61**, 79–91.
- Dasilva, G.L. (1994) Diet of *Colobus polykomos* on Tiwai Island: selection of food in relation to its seasonal abundance and nutritional quality. *International Journal of Primatology*, **15**, 1–26.
- Davies, A.G. (1994) Colobine populations. *Colobine Monkeys: Their Ecology, Behaviour and Evolution* (eds A.G. Davies & J.F. Oates), pp. 285–310. Cambridge University Press, Cambridge.
- Davies, A.G., Bennett, E.L. & Waterman, P.G. (1988) Food selection by two South-East Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biological Journal of the Linnean Society*, **34**, 33–56.

- Ganzhorn, J.U. (1992) Leaf chemistry and the biomass of folivorous primates in tropical forests: test of a hypothesis. *Oecologia*, **91**, 540–547.
- Gaulin, S.J.C. & Gaulin, C.K. (1982) Behavioural ecology of *Alouatta seniculus* in Andean cloud forest. *International Journal of Ecology*, **3**, 1–32.
- Gebo, D.L. & Chapman, C.A. (1995a) Positional behaviour in five species of old world monkeys. *American Journal of Physical Anthropology*, **97**, 49–76.
- Gebo, D.L. & Chapman, C.A. (1995b) Habitat, annual, and seasonal effects on positional behavior in red colobus monkeys. *American Journal of Physical Anthropology*, **96**, 73–82.
- Glander, K.E. (1982) The impact of plant secondary compounds on primate feeding behaviour. *Yearbook of Physical Anthropology*, **25**, 1–18.
- Harvey, P.H. & Clutton-Brock, T.H. (1981) Primate home-range size and metabolic needs. *Behavioral Ecology Sociobiology*, **8**, 151–155.
- Harvey, P.H. & Clutton-Brock, T.H. (1985) Life history variation in primates. *Evolution*, **39**, 559–581.
- Iwamoto, T. (1988) Food and energetics of provisioned wild Japanese macaques (*Macaca fuscata*). *Ecology and Behavior of Food-Enhanced Primate Groups* (ed. J. Fa), pp. 79–94. Alan Liss Inc., New York.
- Kay, R.F. & Davies, G. (1994) Digestive physiology. *Colobine Monkeys* (eds A.G. Davies & J.F. Oates), pp. 229–249. Cambridge University Press, Cambridge.
- Krebs, C.J. (1978) A review of the Chitty hypothesis of population regulation. *Canadian Journal of Zoology*, **56**, 2463–2480.
- Kurland, J.A. & Gaulin, S.J.C. (1987) Comparability among measures of primate diets. *Primates*, **28**, 71–77.
- Lowry, J.B. (1989) Green-leaf fractionation by fruit bats: is this feeding behavior a unique nutritional strategy for herbivores? *Australian Wildlife Research*, **16**, 203–206.
- McKey, D.B. (1978) Soils, vegetation, and seed-eating by black colobus monkeys. *The Ecology of Arboreal Folivores* (ed. G.G. Montgomery), pp. 423–437. Smithsonian Institution Press, Washington, DC.
- McKey, D.B., Gartlan, J.S., Waterman, P.G. & Choo, C.M. (1981) Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biological Journal of the Linnean Society*, **16**, 115–146.
- McNab, B.K. (2002) *The Physiological Ecology of Vertebrates*. Cornell University Press, Ithaca, New York.
- Milton, K. (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist*, **114**, 363–378.
- Milton, K. (1982) Dietary quality and demographic regulation in a howler monkey population. *The Ecology of a Tropical Forest* (eds E.G. Leigh, A.S. Rand & D.M. Windsor), pp. 273–289. Smithsonian Institution Press, Washington, DC.
- Milton, K. (1998) Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with the Colobinae. *International Journal of Primatology*, **19**, 513–547.
- Milton, K., van Soest, P.J. & Robertson, J.B. (1980) Digestive efficiencies of wild howler monkeys. *Physiological Zoology*, **53**, 402–409.
- Mole, S. & Waterman, P.G. (1985) Stimulatory effects of tannins and cholic acid on tryptic hydrolysis of proteins: ecological implications. *Journal of Chemical Ecology*, **11**, 1323–1332.
- Müller, E.F., Kanau, J.M.Z. & Maloiy, G.M.O. (1983) A comparative study of basal metabolism in two primate species. *Comparative Biochemical Physiology*, **74**, 319–322.
- Nagy, K.E. & Milton, K. (1979) Energy metabolism and food consumption by wild howler monkeys (*Alouatta palliata*). *Ecology*, **60**, 475–480.
- National Research Council (1981) *Techniques for the Study of Primate Population Ecology*. National Academy Press, Washington, DC.
- Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva, G.L. & Mole, S. (1990) Determinants of variation in tropical forest primate biomass: new evidence from West Africa. *Ecology*, **71**, 328–343.
- Oftedal, O.T. (1991) The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. *Philosophical Transactions of the Royal Society of London B*, **334**, 161–170.
- Paine, R.T. (1971) The measurement and applications of the calorie to ecological problems. *Annual Review of Ecology and Systematics*, **2**, 145–164.
- Portman, O.W. (1970) Nutritional requirements of non-human primates. *Feeding and Nutrition of Non-Human Primates* (ed. R.S. Harris), pp. 87–115. Academic Press, New York.
- Schoener, T.W. (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics*, **2**, 369–404.
- van Soest, P.J. (1982) *Nutritional Ecology of the Ruminant*. O. & E. Books, Inc., Corvallis, Oregon.
- Stirrat, S.C. (2002) Foraging ecology of the agile wallaby (*Macropus agilis*) in the wet-dry tropics. *Wildlife Research*, **29**, 347–361.
- Struhsaker, T.T. (1978) Food habits of five monkey species in the Kibale Forest, Uganda. *Recent Advances in Primatology* (eds D.J. Chivers & J. Herbert), pp. 225–248. Academic Press, New York.
- Struhsaker, T.T. (1997) *Ecology of an African Rain Forest: Logging in Kibale and the Conflict Between Conservation and Exploitation*. University Press of Florida, Gainesville.
- Struhsaker, T.T. & Leland, L. (1987) Colobines: infanticide by adult males. *Primate Societies* (eds B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker), pp. 83–97. University of Chicago Press, Chicago.
- Tucker, V.A. (1970) Energetic cost of locomotion in animals. *Comparative Biochemistry and Physiology*, **34**, 841–846.
- Waterman, P.G. & Choo, G.M. (1981) The effects of digestibility-reducing compounds in leaves on feed selection of some Colobinae. *Malaysian Applied Biology*, **10**, 147–162.
- Waterman, P.G. & Kool, K.M. (1994) Colobine food selection and plant chemistry. *Colobine Monkeys* (eds A.G. Davies & J.F. Oates), pp. 251–284. Cambridge University Press, Cambridge.
- Waterman, P.G., Ross, J.A.M., Bennett, E.L. & Davies, A.G. (1988) A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forest and the influence of leaf chemistry on populations of colobine monkeys in the Old World. *Biological Journal of the Linnean Society*, **34**, 1–32.
- Watkins, B.E., Ullrey, R.E. & Whetter, P.A. (1985) Digestibility of high-fiber biscuit based diet by black and white colobus (*Colobus guereza*). *American Journal of Primatology*, **9**, 137–144.

Received 27 May 2002; accepted 27 March 2003