

RESEARCH ARTICLE

Predicting Folivorous Primate Abundance: Validation of a Nutritional Model

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Understanding the determinants of animal abundance has become more vital as ecologists are increasingly asked to apply their knowledge to the construction of informed management plans. However, there are few general models available to explain variation in abundance. Some notable exceptions are studies of folivorous primates, in which the protein-to-fiber ratio of foods has been shown to predict biomass. Here we examine the generality of Milton's [American Naturalist 114:363–378, 1979] protein/fiber model by providing a detailed analysis of diet selection in black-and-white colobus monkeys (*Colobus guereza*), and applying the model to populations shown to be stable; an assumption not previously examined. Based on observations of two groups of black-and-white colobus in Kibale National Park, Uganda, and one group in a forest fragment, we documented that the animals selected young leaves that had more protein, were more digestible, and had a higher protein-to-fiber ratio than mature leaves. The mature leaves did not differ from young leaves with respect to secondary compounds or mineral content (with the exceptions of copper and zinc). All of the colobus groups selected foods with a high protein-to-fiber ratios. However, one group also selected more digestible foods, and in another group, foraging efforts were positively related to zinc and negatively related to potassium. Previous studies that examined Milton's protein/fiber model did not demonstrate that the study populations were stable. If some populations were not at carrying capacity, then the correlations drawn between food availability and/or quality and folivore biomass may have been spurious. To address this issue, we censused a series of forest fragments in 1995 and again in 2000.

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We found that the populations in these fragments had declined from 165 in 1995 to 119 animals in 2000. However, based on evidence of population stability and lack of forest disturbance, we concluded that five of the original populations were stable. The biomass of these populations was related to the protein-to-fiber ratio of the fragment's trees. Combining our data with published data, we demonstrate that the protein-to-fiber ratios of mature leaves available to these folivorous primates accounted for 87% of the variance in their biomass. *Am. J. Primatol.* 62:55–69, 2004. © 2004 Wiley-Liss, Inc.

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INTRODUCTION

A fundamental issue in ecology is the determination of important factors that affect the density of animal populations [Boutin, 1990]. The importance of understanding the determinants of animal abundance has increased with the need to develop informed management plans for endangered and threatened species. With respect to primates, these theoretical issues are critical because the tropical forests these animals occupy are undergoing a rapid anthropogenic transformation [National Research Council, 1992]. Cumulatively, countries with primate populations are losing approximately 125,000 km² of forest annually [Chapman & Peres, 2001]. Other populations are affected by forest degradation (logging and fire) and hunting. However, it is extremely difficult to understand and predict the factors that affect the abundance of a particular primate species. Numerous studies of forest primates have revealed a high degree of intersite variation in density [Waterman et al., 1988; Oates et al., 1990; Ganzhorn, 1992; Chapman & Chapman, 1999], but few direct tests of general hypotheses have been proposed to account for this variation. Some notable exceptions are studies of folivorous primates. Milton [1979] proposed that the protein-to-fiber ratio was a good predictor of leaf choice [see also McKey, 1978]. By measuring overall mature leaf acceptability as the ratio of protein to fiber, several subsequent studies have found positive correlations between colobine biomass and this index of leaf quality on both local [Chapman et al., 2002a; Ganzhorn, 2002] and regional [Waterman et al., 1988; Oates et al., 1990] scales. Milton [1979, 1998] and Milton et al. [1980] proposed a physiological explanation for the importance of protein-to-fiber ratios in regulating population densities.

While these correlative studies and this physiological explanation suggest that the protein-to-fiber ratio in foods is a limiting factor in folivorous primate populations, the available data are likely insufficient to confidently use this model to construct management plans. Our skepticism is based on a number of factors. First, to date, studies have been correlative and based on a small number of populations (i.e., less than 12). It may not be the protein-to-fiber ratio that is important, but something correlated with this ratio. For example, Dasilva [1992] found that a population of *Colobus polykomos* was seasonally limited by the availability of suitable energy-rich foods, and did not select foods with high protein content. Similarly, there is evidence that some populations of red colobus (*Procolobus badius*) may be limited by the availability of certain minerals (e.g., sodium [Rode et al., 2003]). Second, there is controversy over the importance of protein in primates. Oftedal [1991] calculated that even where low protein

digestibility due to effects of tannins occurred, a primate would require only 7–11% protein on a dry-matter basis for growth and maintenance, and only 14% for reproduction (however, it should be noted that the influence of tannins is not well understood [Waterman & Kool, 1994]). Since leaves eaten by primates average 12–16% protein [Glander, 1982], and these leaves are readily available Oftedal [1991], concluded that protein deficiency is not a problem for most primates. Protein demand may be even lower in colobines, since it is possible that blood urea is recycled by secretion into saliva or diffusion across the wall of the foregut, as has been demonstrated in other folivores [Kay & Davies, 1994]. This nitrogen source could be used by microbes for protein synthesis, which would in turn be digested in the small intestine. Third, previous studies did not demonstrate that the study populations were stable. If some populations were not at carrying capacity because some factor had temporarily reduced their numbers, then the correlations drawn between food availability and/or quality and folivore biomass may have been spurious. It is well known that predators [Isbell, 1990] and disease/parasites [Milton, 1996] can cause short-term reductions in the size of primate populations. While including populations not at carrying capacity would likely lead to finding a nonsignificant relationship, this issue still warrants consideration. Finally, Milton's protein/fiber model has not been examined under different situations in forests that have been degraded by human activities.

While these are reasons to be skeptical about applying Milton's protein/fiber model to manage colobine populations, this is one of the few situations in which a general hypothesis exists to account for variation in primate abundance. This calls for further investigation of the nutritional factors that limit colobine populations.

The objective of this study was to first examine diet selection in three groups of black-and-white colobus monkeys (*Colobus guereza*) to gain a general understanding of their dietary requirements. We considered diet selection with regard to protein, fiber, digestibility, secondary compounds (saponins, alkaloids, and cyanogenic glycosides), and minerals. Second, we evaluated the generality of the protein/fiber model for "stable" populations. In the foothills of the Rwenzori Mountains adjacent to Kibale National Park, Uganda, there are a series of crater lakes with forested rims that support colobus populations. These crater lakes offer the opportunity for a natural experiment in that they vary in extent and tree composition, and one can investigate how this variation influences primate populations. In 1995, we surveyed primate communities in 20 of these forest fragments to determine the abundance of black-and-white colobus, the presence or absence of other primates, tree species composition, patch size, and distance to the nearest patch [Onderdonk & Chapman, 2000]. The fragments were resurveyed in 2000. For those black-and-white colobus populations that appeared to be stable, we examined the relationship between the protein-to-fiber ratios of the most abundant trees and colobine biomass.

MATERIALS AND METHODS

Study Site

The primates in 20 crater lake forest fragments were censused from May to August 1995 [Onderdonk & Chapman, 2000], and 19 fragments were recensused in May to November 2000. These forest fragments neighbor Kibale National Park, Uganda (766 km², 0 13'–0 41' N and 30 19'–30 32' E). Kibale is a mid-altitude, moist evergreen forest that receives approximately 1,749 mm of rainfall annually (1990–2001), primarily during two rainy seasons [Chapman & Lambert, 2000]. Before this area was cleared for agriculture, there probably was continuous

forest throughout the region. The forests and wildlife of western Uganda have been influenced by human activities for some time, but these activities have intensified over the past 50 years [Naughton-Treves, 1999].

Surveying Primate Fragment Occupancy and Fragment Characters

In 1995, forest fragments were selected if they had clearly defined boundaries, were isolated from other fragments or tracts of forest by ≥ 50 m, and were small enough that all black-and-white colobus groups could be counted. Twenty fragments were visited in the first survey. One large fragment (130 ha) was surveyed in 1995; however, since a complete count of all black-and-white colobus was not obtained in 1995, it was not resurveyed. In the first survey, the following parameters were measured: primate species present, black-and-white colobus group size and composition, tree species richness, area of the fragment, and distance to the nearest fragment [Onderdonk & Chapman, 2000]. The 20 fragments ranged from 0.8 to 130 ha, but most were < 10 ha (mean excluding the largest 130-ha fragment = 4.7 ha). We determined which primate species were present over 2–4 days, and for each group of black-and-white colobus encountered we determined size and composition (following Oates [1974]).

In the survey conducted in 2000, the same parameters were measured, with the exceptions of distance to the next fragment and fragment size, and changes in the condition of the fragments were noted. From long-term research at one fragment (Lake Nkuruba) [Chapman et al., 1998], we know that redbelt monkeys and chimpanzees frequently move among fragments, while the colobines display much more site fidelity and rarely move among fragments (and then do so only to colonize).

In 17 of the 19 fragments, we identified and measured all trees that were > 10 cm in diameter at breast height (DBH). When the trees were on extremely steep sides of the craters, we visually estimated their size (error in visual estimation = $\pm 3.8\%$). Since colobus rarely feed in small trees [Gillespie & Chapman, 2001], this represents a nearly complete inventory of all potential food sources. We also counted all tree stumps that remained after harvest by local people. For most tree species, after the tree is cut the stump will remain for several years; therefore, we used this inventory of tree stumps as an index of fragment change, which we applied when we considered whether the fragment's forest structure was stable.

Behavioral Observations

Dietary data were gathered during dawn to dusk observations on 4 days each month from July 1998 to June 1999 for two groups of black-and-white colobus in the unlogged forest in Kibale (~ 600 hr), and from August 1999 to April 2000 for a forest fragment group at Crater Lake Nkuruba (~ 330 hr). During each half hour, five-point samples were made of different individuals. If the animal was feeding, the species and plant part were recorded. We avoided repeatedly sampling conspicuous animals by moving throughout the group, and by sampling animals that were in clear view as well as those that were more hidden.

Nutritional Analyses

For each group, the five most frequently eaten food items were collected each month. Samples were obtained by using a tree-pruning pole to cut down a tree limb from the middle of the tree's canopy. Items were processed in a fashion that closely mimicked the animal's feeding behavior, and only plant parts selected by

the black-and-white colobus were collected. For example, if they were eating the petiole, the length of petiole typically consumed was collected. For some statistical approaches (see below), mature and young leaves were collected from the same tree. Samples were dried in the field either by sun-drying, using a dehydrator that circulated warm air past the samples, or by a light-bulb-heated box containing a series of racks. Dried samples were stored in sealed plastic bags until they were transported to the University of Florida for analysis. The samples were dried thoroughly to avoid mold. We ensured that all of the samples were dried below 50°C by putting Max/Min thermometers in with the drying samples. Samples were dried in the drying oven at its lowest heat setting (37°C). A selection of mature and young leaves from relatively abundant tree species that the colobus were not seen to eat were also collected for comparison (see statistical analysis below). To test the protein/fiber model, we collected mature leaves from the 20 species that made up the greatest basal area in each fragment, regardless of whether they were eaten by the colobus (following Oates et al. [1990]).

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. The samples were analyzed in duplicate, and replicates for analyses were considered acceptable if the relative error was <2%.

The protein (nitrogen) content of the plant parts was assessed using Kjeldahl procedures. 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 K₂SO₄:CuSO₄, and digestion was conducted for at least 4 hr at 375°C using 6 ml of H₂SO₄ and 2 ml H₂O₂. The nitrogen in the digestate was determined by semiautomated colorimetry. The measurement of total nitrogen provides an estimate of crude protein (protein levels = N × 6.25). A better conversion factor for tropical foliage may be just over 4 [Milton & Dintzis, 1981]. However, we used the 6.25 factor so that our results would be comparable to those of previous studies [Waterman et al., 1988; Oates et al., 1990]. Acid detergent fiber (ADF) was measured using the methods of van Soest [1963]. ADF is a measure of cell wall cellulose and lignin. ADF has been found to have a strong negative correlation with food selection in some primates [Glander, 1982; Oates et al., 1990]. We assessed digestibility using a procedure that is commonly used in cattle forage analysis [Moore & Mott, 1974]. We made the assumption that digestion efficiency determined from cattle rumen fluid would be correlated with colobus digestion efficiency. The sample was first incubated with rumen microorganisms for 48 hr and then incubated in an acid-pepsin solution for 44 hr.

Many alkaloids are bitter-tasting and may serve to deter feeding and/or damage the microbial community of colobine stomachs. The presence of alkaloids was tested using a spot test with Dragendorff's reagent [Waterman, 1993]. Saponins are surfactants, and have a "soaplike" foam-forming property in aqueous solutions (hence their name). They also have the ability to hemolyze red blood cells when injected, irritate the digestive tract, and 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 implicated in diet selection of cattle. Given that colobines are also forestomach fermenters [Milton, 1998], it is intriguing to consider that saponins may also be important in colobine diet selection. 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 data), which involves mixing the sample with deionized water, shaking the sample, and measuring the froth formed after set

intervals (60 sec and 300 sec). Cyanogenic glycosides are capable of releasing toxic hydrogen cyanide; however, their role in plant food selection is largely unknown [Jones, 1998]. The presence or absence of hydrogen cyanide was determined by the Feigl-Anger test [Feigl & Anger, 1966].

The preparation for mineral analysis and the protocol for analysis with an atomic absorption spectrophotometer followed procedures outlined by Miles et al. [2001]. Sample concentrations of each element were determined by comparing the absorbancy to a standard linear regression using three standard points for each element. Concentrations were corrected based on two blanks run per each set of 60 samples. Additionally, a sample of known mineral concentration (certified National Bureau of Standards citrus leaves SRM-1572) was run with each set of samples to ensure that values obtained from the atomic absorption spectrophotometer were accurate [National Bureau of Standards, 1982; National Institute of Standards and Technology, 1982]. We tested each sample for eight minerals: iron (Fe), copper (Cu), manganese (Mn), zinc (Zn), sodium (Na), potassium (K), magnesium (Mg), and calcium (Ca). Multiple samples were run for most colobus foods, and the results were averaged to obtain a single mineral value for each food item.

Statistical Analyses

We took three approaches to explore the chemical basis of diet selection in the colobus. First, since black-and-white colobus are known to prefer young leaves over mature leaves [Oates, 1974], we compared the chemical constituents of young and old leaves of plants eaten by colobus. Differences were quantified with a paired *t*-test (paired by species) to evaluate the variance between young and mature leaves without considering the variance among species. Second, we compared the five most frequently eaten foods in each month, for each group, with leaves that the colobus were never (or extremely rarely) known to eat but that were relatively common in the environment. Since the rarely eaten foods were often mature leaves, we conducted a similar analysis comparing frequently eaten young leaves with young leaves that were never or rarely eaten but are common in the environment. Third, we used behavioral data to calculate the percentage of foraging effort devoted to particular plant species and parts, and attempted to predict the feeding effort based on that food's chemical constituents. As regards the latter analysis, 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 estimate food plant availability, we established 12 transects (200 m × 10 m) placed randomly along the existing trail system in Kibale National Park (Kanyawara), for 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 identified, and the DBH was recorded. A total of 1,171 trees from 67 species were identified. To determine the density of each tree species at Crater Lake Nkuruba, 10 transects (~60 × 10 m) were systematically established around the rim of the crater from the crater rim to the lake's edge. We used a multiple regression technique to quantify the significance of particular phytochemical components as predictors of foraging effort, when linear effects of availability were statistically removed using partial correlations.

To test the generality of the protein/fiber model for black-and-white colobus populations that our recensus indicated were stable, we calculated a weighted protein/fiber index using the data from the inventory and measurements of trees in the fragment. Following Oates et al. [1990], the weighted protein-to-fiber ratio

values were calculated from $\Sigma (P_i + X_i) / \Sigma P_i$, 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 value is standardized to 100%. To estimate the biomass of the colobus, the composition of the groups was determined through group counts, and subadult and juvenile weights were assumed to be half that of adults. A one-tailed test was used to evaluate the correlation predicting biomass.

RESULTS

Diet Choice

The diets of the black-and-white groups were characterized from 3,249 foraging records. For all groups, young leaves were the most commonly eaten plant part (Table I). However, the group in the forest fragment fed on mature leaves more often than did groups within the park. Surprisingly, the fragment group spent 9.5% of the foraging scans eating ripe fruit—primarily guava (*Psidium guajava*, a species introduced from South America). One of the groups in Kibale fed on bark for 3.8% of the time. *Prunus africana* was the species from which this group primarily ate bark, and this species was not available in the other group’s unlogged home range.

The black-and-white colobus ate both mature and young leaves from 13 species of trees. Young leaves of this species were eaten more frequently than mature leaves (paired t -test, $t = 2.602$, $P = 0.026$), had more protein ($t = 4.713$, $P = 0.003$), were more digestible ($t = 2.933$, $P = 0.026$), and had a higher protein-to-fiber ratio ($t = 3.706$, $P = 0.014$). There was no indication that young and mature leaves differed with respect to saponins ($t = 1.321$, $P = 0.235$). Of the species examined, two species tested positive for alkaloids and one species tested positive for cyanogenic glycosides. The tests results from the mature and young leaves of these species were identical. Thus, there was no indication that young leaves were less protected by secondary compounds than mature leaves. With the exceptions of copper ($t = 2.780$, $P = 0.02$) and zinc ($t = 7.664$, $P < 0.001$), there were no differences in the mineral content of young and mature leaves.

There were a variety of differences in phytochemical constituents between frequently eaten foods (the five most frequently eaten food items collected each month for each group) and young and mature leaves that the black-and-white colobus were not known to eat, but were relatively common in the environment

TABLE I. Foraging Effort (% of Foraging Scans) Devoted to Different Plant Parts by Black-and-White Colobus Groups in Unlogged Forest (Groups 1 and 2) in Kibale National Park, Uganda and a Crater Lake Forest Fragment Outside the Park

Food item	Unlogged (1)	Unlogged (2)	Fragment
Ripe fruit	0.00	2.40	9.54
Unripe fruit	0.00	7.20	2.80
Flower	2.22	0.13	6.22
Young leaf	83.91	77.65	64.94
Mature leaf	3.64	5.81	14.11
Leaf petiole	0.81	0.38	0.83
Leaf bud	0.54	1.01	0.00
Bark	0.00	3.79	0.73
Other	0.00	0.00	0.62
Total	1485	792	964

(Table II). For all three groups, the frequently-eaten foods had higher levels of saponins, zinc, and iron. For the two groups in Kibale, the frequently-eaten foods had more protein, were more digestible, and had higher protein-to-fiber ratios than the nonconsumed foods. Foods that were frequently eaten by the group in the forest fragment had less fiber and had protein-to-fiber ratios that were marginally higher than the foods that were rarely eaten, but there were no differences in the protein or digestibility levels. The pattern of differences between frequently eaten young leaves and rarely eaten young leaves was similar to that for all foods, with the exception that there were no differences in digestibility (Table II).

We used behavioral data to calculate the percentage of foraging effort devoted to particular plant species and parts. Subsequently, we attempted to predict feeding effort based on that food's chemical composition, partialling out food availability. All groups appeared to select foods with high protein-to-fiber ratios (Fig. 1). One group in the unlogged forest selected more digestible foods. With respect to minerals, partial correlation analysis indicated that foraging effort for one group in the unlogged forest was positively related to zinc and negatively related to potassium.

Predicting Biomass for Fragments With Stable Populations

Of the 16 fragments that supported resident populations of black-and-white colobus in 1995, three had been cleared by 2000. The fragments that were cleared had supported five groups of black-and-white colobus (31 individuals). In 1995 we counted 165 black-and-white colobus, while in 2000 only 119 animals were seen. In five fragments there were relatively small changes in the populations

TABLE II. The Difference in Phytochemical Factors Between Foods Frequently Eaten by Black-and-White Colobus Monkeys and Foods That Were Never or Extremely Rarely Known to Eaten but Were Relatively Common in the Environment for Two Groups in Unlogged Forest and One in a Forest Fragment*

	Unlogged 1		Unlogged 2		Fragment	
Protein	More	$P = 0.007/0.027$	More	$P \leq 0.001/0.001$	-	$P = 0.996/0.566$
Digestibility	More	$P = 0.041/0.224$	More	$P = 0.002/0.076$	-	$P = 0.730/0.725$
Fiber		$P = 0.299/0.396$	Less	$P = 0.005/0.053$	Less	$P = 0.011/0.006$
Protein to fiber ratio	Higher	$P = 0.001/0.016$	Higher	$P \leq 0.001/0.002$	Higher	$P = 0.089/0.067$
Saponin	More	$P = 0.013/0.005$	More	$P = 0.003/0.006$	More	$P \leq 0.001/0.028$
Copper	-	$P = 0.359/0.728$	More	$P = 0.044/0.059$	-	$P = 0.633/0.600$
Manganese	-	$P = 0.136/0.082$	-	$P = 0.072/0.039$	-	$P = 0.263/0.196$
Zinc	More	$P \leq 0.001/0.107$	More	$P = 0.018/0.005$	More	$P \leq 0.001/0.020$
Iron	More	$P \leq 0.001/<0.001$	More	$P \leq 0.001/<0.001$	More	$P = 0.001/0.006$
Sodium	-	$P = 0.769/0.085$	-	$P = 0.839/0.052$	-	$P = 0.668/0.393$
Magnesium	-	$P = 0.855/0.294$	-	$P = 0.366/0.178$	-	$P = 0.770/0.155$
Potassium	-	$P = 0.969/0.770$	-	$P = 0.335/0.096$	-	$P = 0.457/0.932$
Calcium	-	$P = 0.298/0.191$	-	$P = 0.773/0.198$	-	$P = 0.395/0.884$
Sample size consumed		40/15		19/10		22/5
Sample size not consumed		18/10		30/20		30/25

*The first probability level presented is all foods, while the second is just young leaves.

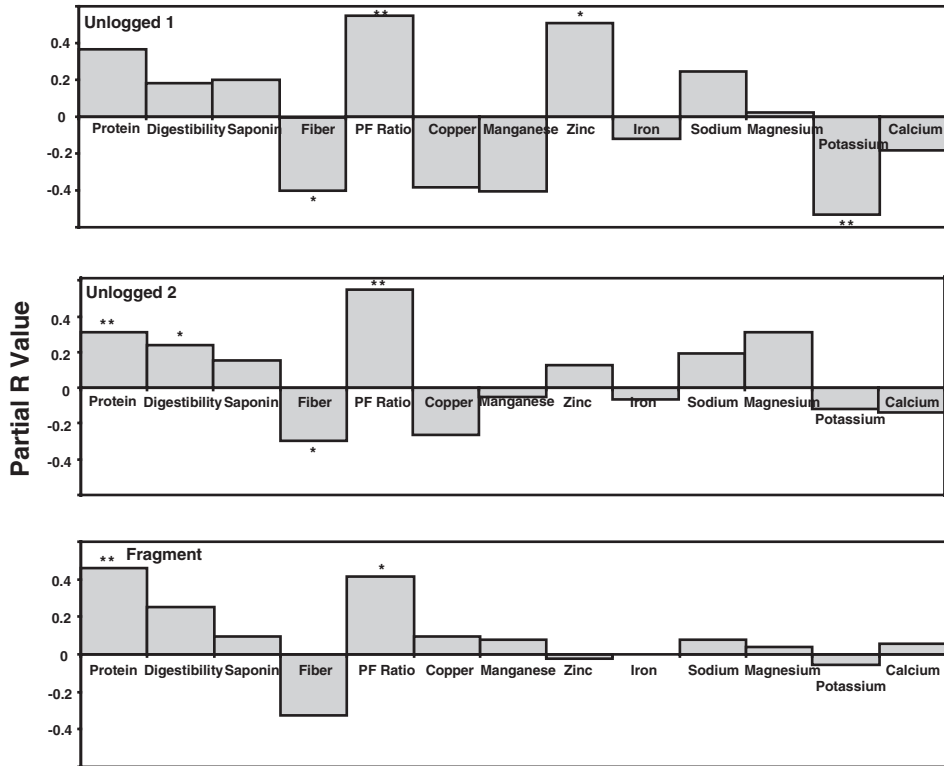


Fig. 1. The relationships between foraging effort and nutrient components in three groups of black-and-white colobus (*Colobus guereza*: two from unlogged forest and one from a forest fragment) when the effects of the density of the food trees are statistically controlled (partial correlation coefficients). * $P < 0.05$, ** $P < 0.01$.

(mean = -5.4%, range = -20% to 18%) and there was limited evidence of forest clearing. In the following analyses, these populations are considered stable. This categorization seemed reasonable since most fragments had only one or two groups, and on average there were 9.8 animals in each fragment (considering both time periods); thus a change of 10% often would represent the birth or death of one animal. There were no resident red colobus populations in the five fragments that were considered stable.

The biomass of the black-and-white colobus in the five forest fragments considered to be stable was correlated with the protein-to-fiber ratio of the fragment's trees ($r^2 = 0.730$, $P = 0.033$, $n = 5$; Fig. 2). In this evaluation, we determined the protein-to-fiber ratio of the majority of the resources in each fragment (proportion of the fragment's basal area sampled, mean = 91.4%, range = 89.2–97.5, SD = 4.5, $n = 5$).

Colobine biomass and leaf chemistry were previously quantified at nine other sites [Oates et al., 1990; Chapman et al., 2002a], which enabled us to examine the predictive power of the relationship between protein-to-fiber ratios and colobine abundance. Colobine biomass varied from 84 kg/km² at Sepilok, Malaysia, to 13,160 kg/km² in one of the fragments outside of Kibale (mean biomass across sites = 3,405 kg/km², $n = 14$). The protein/fiber ratios reported in these studies showed a similar degree of variation (mean = 0.41, range = 0.17–0.71, $n = 14$).

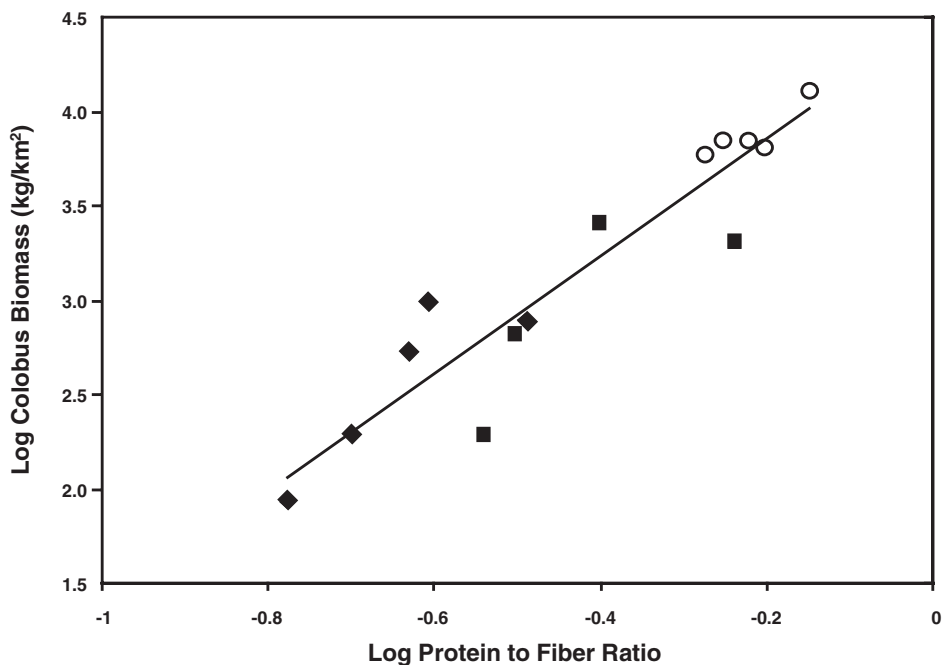


Fig. 2. The relationship between mature leaf chemistry and colobine biomass at rainforest sites in Africa and Asia. Chemical values are weighted mean percentages of dry mass, standardized to the species' basal area to account for different proportions of the flora being sampled at each site. The weighted values were calculated from $\sum (P_i + X_i) / \sum P_i$, 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%. Diamonds are sites from around the world [Oates et al., 1990], squares are forest sites within Kibale National Park, Uganda [Chapman et al., 2002a], and open circles are the forest fragments examined in the current study.

Colobine biomass (log transformed) at the 14 sites (including the five sites presented here) could be predicted with a significant level of confidence from the protein-to-fiber ratios of the site's mature leaves ($r^2 = 0.869$, $P < 0.001$; Fig. 2).

Compared to previous studies, the colobus in the forest fragments of Western Uganda have high biomass and protein-to-fiber ratios. This may reflect the successional state of these fragments. Coley [1983] demonstrated that canopy gaps are typically colonized by climbers and fast-growing pioneer tree species, the leaves of which generally have more protein, less fiber, and a lower phenolic content than the leaves of persistent canopy tree species. To evaluate this with respect to the forest fragments near Kibale, we categorized the habitat preference of as many tree species as possible ($n = 47$) in terms of forest, small gap, and large gap/edge. The protein-to-fiber ratio of large gap/edge species ($n = 20$) in this sample was greater than that of forest species ($n = 18$, $F = 3.55$, $P = 0.038$, Scheffe $P = 0.039$), but not of small gap species ($n = 9$, Scheffe $P = 0.767$).

DISCUSSION

Three lines of evidence suggest that the protein and fiber levels in potential foods are important for colobus populations. First, groups in both undisturbed and fragmented forests selected foods that had high protein-to-fiber ratios. Second, the protein-to-fiber ratio was a significant predictor of the biomass of

populations in forest fragments that were stable. Third, for all populations in which this information has been collected, the protein-to-fiber ratio of potential foods is related to colobine biomass.

It is somewhat surprising that researchers have been able to repeatedly and reliably predict colobine biomass with this index of the quality of food a habitat provides. This is particularly interesting considering the inadequacies of census methodology, the fact that lianas are not evaluated, and the fact that researchers are measuring the protein-to-fiber ratio of mature leaves (colobines rarely eat mature leaves). Milton [1979] suggested that for small mammalian herbivores, the protein-to-fiber ratio may be a good predictor of leaf choice. Building on that work, Davies [1994] suggested that the year-round availability of digestible mature leaves with high protein-to-fiber ratios, which are used by colobus species when other, more preferred foods are unavailable, serves to limit the size of colobine populations. We have been collecting quantitative data on red colobus foraging in Kibale since 1992, involving over 6,000 hr of observations and data on black-and-white colobus at various intervals involving 1,400 hr of observation. During this time, we have never observed groups to eat mature leaves for extended periods of time (i.e., almost exclusively for up to a week), as would be expected if they were a fallback food. It may be that we have simply not observed these groups long enough, and that at some time in the future there will be a period when the animals must rely on mature leaves, and that such rare events determine biomass. However, it seems more likely that these colobus at Kibale do not need to eat mature leaves, since young leaves are always readily available. In the last 3 years there has been no month where young leaves eaten by colobus monkeys were not available (289 trees monitored monthly), nor any month when *Celtis durandii* young leaves—a particularly important food for both species—were not available (11 trees monitored monthly). The fact that we found a relationship between the protein-to-fiber ratio of mature leaves at Kibale and colobus biomass does not necessarily indicate that high-quality mature leaves are an important fallback food, as suggested by Davies [1994]. Rather, the protein-to-fiber ratio of mature leaves in an area may be correlated with the protein-to-fiber ratio of foods in general, and particularly young leaves. This is supported by the fact that in the sample of leaves from Kibale, we found that the protein-to-fiber ratio of mature leaves and young leaves were strongly correlated ($r=0.837$, $P<0.001$). Thus, measuring the protein-to-fiber ratio of mature leaves may be useful because it often correlates with the general availability of high-protein, low-fiber young leaves, and thus is a useful index of habitat quality for colobus monkeys.

The findings that colobus biomass was high in the fragments, and the average protein-to-fiber ratios of the large gap/edge species was higher than that of forest species support the observation made by Oates [1996] that moderate forest disturbance, such as selective logging or low-intensity bush-fallow agriculture, can increase rather than decrease the density of some folivorous primates in the absence of hunting. The importance of the protein and fiber content of foods in driving this relationship is supported by the observations of Ganzhorn [1995]. He found that trees that received increased light as a result of canopy opening associated with logging produced leaves with a higher protein-to-fiber ratio. Such nutritional changes associated with human disturbance are likely to be modified by changes in the predator and competitor communities, locomotor costs, risk of disease and parasitism, etc. For example, T. Gillespie and C. Chapman (unpublished data) quantified changes in parasite load and the risk of infection associated with different types of habitat modification, including logging and

fragmentation; however, the changes they documented varied depending of whether the species examined was a folivore or a frugivore. In the logged sites, this change in parasite load and risk of infection is evident even 30 years after the logging occurred.

Such species-specific responses to changes that accompany habitat disturbance may account for differences in the responses of black-and-white and red colobus to disturbance. Chapman et al. [2000] conducted censuses over a 28-year period to quantify the long-term effects of both low- and high-intensity selective logging on the density of the five common primates in Kibale. With respect to the two colobine species in the park, they found that red colobus populations were recovering in the heavily logged areas; however, the rate of increase appeared to be slow (0.005 groups/km²/year) and the population density in the logged areas was much lower than in the unlogged areas. In contrast, the black-and-white colobus appeared to do well in these disturbed habitats, and they were found at higher group densities in the logged areas than the unlogged area. This difference exists even though these two species have similar diets and a preference for foods with high protein-to-fiber ratios [Chapman & Chapman, 2002]. We also found that these two colobine species are responding differently to fragmentation. In contrast to the black-and-white colobus, red colobus were found in more fragments in the 2000 census than in the 1995 census, and the ratio of adult females to infants was much higher compared to the black-and-white colobus. Since the fragments have degraded over the last 5 years, it is not immediately apparent why their numbers would increase (as indicated by the increased number of fragments they occupy). It is unlikely that they are just now colonizing the fragments, since the fragments have existed for decades. It is possible that the fragments are operating as a sink, and excess animals from Kibale emigrate to the fragments—only to do poorly in the long term. However, the ratio of adult females to infants does not support this idea.

In general, this study provides support for the notion that the protein-to-fiber ratio is a good predictor of food choice in colobines, and encourages the use of this index in predicting colobine biomass. This information could be used by managers in a number of ways. For example, if trees that are important to the colobines could be left standing in selective logging operations, or if loggers could use directional felling to reduce the impact on important food trees, the population declines of primate species that are negatively impacted by logging might be lessened or the speed of population recovery improved by adopting such proactive measures. The results of this study suggest that tree species that should be targeted for colobus conservation should have leaves with a high protein-to-fiber ratio. Furthermore, the trees should be relatively abundant and of the species frequently eaten by colobus. In Kibale, such a tree would be *Celtis durandii*. The mature leaves of this tree have one of the highest protein-to-fiber ratios of the species examined. It is a relatively common tree (mean density among sites = 36.8 individuals per ha) that has some young leaves in most, if not all, months of the year, and both red colobus and black-and-white colobus feed heavily on this species during many months of the year.

The ideas should be applied cautiously in terms of conservation, since there is still a great deal we do not understand about how colobines respond to disturbance. For example, why do the red colobus of Kibale appear to be dramatically negatively affected by logging, while the black-and-white colobus numbers appear to increase following logging [Struhsaker, 1997; Chapman et al., 2000]? This is surprising given the high levels of dietary overlap observed in these species. Struhsaker and Oates [1975] evaluated dietary overlap between groups of

red and black-and-white colobus with adjacent home ranges in continuous forests of similar composition, and concluded that it was low (7.1%). Chapman et al. [2002b] examined the dietary overlap between a red colobus group and a black-and-white colobus group that had its home range entirely within the home range of the red colobus group, and calculated it to be 43.2%. Struhsaker and Oates [1975] found that black-and-white colobus had a monotonous diet in which the study group fed largely on young leaves of *C. durandii*, and suggested that this represented a significant difference between the species. However, recent studies [Chapman et al., 2002b] have revealed that some red colobus populations have much more monotonous diets than those described by Struhsaker and Oates [1975] for black-and-white colobus, and that other populations can at times rely heavily on young leaves of *C. durandii*.

It remains to be determined why the populations of red colobus are increasing in the fragments (as indicated by the number of fragments occupied), while the black-and-white colobus numbers are declining? These are resident populations with little (if any movement) among fragments, so it is the characters of each fragment that should be determining abundance. The populations of black-and-white colobus are declining in fragments both with and without red colobus, and with and without *C. durandii*, so competition is probably not a key determining factor. Population density may be under the influence of additional factors that interact with nutrition, such as disease and/or parasites [Milton, 1996]. At the present time, these ideas should only be applied when the costs of making an error are minimal. For instance, in the example presented above, if an area is going to be logged, maintaining trees with a high protein-to-fiber ratio is not likely to be a decision that will negatively effect colobus monkeys, even if the population in the specific area does not respond as predicted.

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