

Influence of Plant and Soil Chemistry on Food Selection, Ranging Patterns, and Biomass of *Colobus guereza* in Kakamega Forest, Kenya

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*Nutritional factors are among the most important influences on primate food choice. We examined the influence of macronutrients, minerals, and secondary compounds on leaf choices by members of a foli-frugivorous population of eastern black-and-white colobus—or guerezas (*Colobus guereza*)—inhabiting the Kakamega Forest, Kenya. Macronutrients exerted a complex influence on guereza leaf choice at Kakamega. At a broad level, protein content was the primary factor determining whether or not guerezas consumed specific leaf items, with eaten leaves at or above a protein threshold of ca. 14% dry matter. However, a finer grade analysis considering the selection ratios of only items eaten revealed that fiber played a much greater role than protein in influencing the rates at which different items were eaten relative to their abundance in the forest. Most minerals did not appear to influence leaf choice, though guerezas did exhibit strong selectivity for leaves rich in zinc. Guerezas avoided most leaves high in secondary compounds, though their top food item (*Prunus africana* mature leaves) contained some of the highest condensed tannin concentrations of any leaves in their diet. Kakamega*

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guerezas periodically traveled great distances to exploit rare foods (bark from exotic Myrtaceae trees and soil) outside their normal home ranges. Our results suggest that these journeys were driven by the fact that these rare foods contained exceptionally high sodium concentrations, a mineral believed to be deficient in the guereza's usual diet. Lastly, our results are consistent with the pattern established across other Paleotropical rain forests in which colobine biomass can be predicted by the protein-to-fiber ratio in mature leaves. Of the 8 rain forests for which the relevant data are available, Kakamega features the second highest mature leaf protein-to-fiber ratio as well as the second highest colobine biomass.

KEY WORDS: colobines; macronutrients; minerals; protein-to-fiber ratio; secondary compounds.

INTRODUCTION

As eclectic omnivores typically occurring in species-rich tropical environments, most primates must choose between a great many potential food items (Harding, 1981). These choices are influenced by a variety of ecological, morphological, and physiological factors including patterns of food abundance and distribution (Oates, 1987), intra- and inter-specific food competition (Janson, 1988; Waser, 1987), risk of predation (Miller, 2002), body size (Gaulin, 1979), gut morphology (Chivers, 1994; Milton, 1998), energetic requirements (Dasilva, 1992), macronutrient and mineral requirements (Silver *et al.*, 2000; Yeager *et al.*, 1997), and ability to cope with secondary compounds (Glander, 1982). Because food is essential to survival and reproduction, natural selection is expected to exert a strong influence on the food choices of animals, favoring either individuals that maximize their net intake rates of energy or those that optimize the mix of nutrients they consume while foraging (Pyke *et al.*, 1977; Stephens and Krebs, 1986; Westoby, 1974). Indeed, empirical studies have demonstrated that disparities in food intake and foraging efficiency within groups of several primate taxa are associated with interindividual differences in reproductive success (Altmann, 1991; van Noordwijk and van Schaik, 1987, 1999; Whitten, 1983). The strong selective pressure on primate food choice suggests that patterns of food selection observed during studies of wild primates are adaptive and can provide important insights into primate evolutionary ecology (Altmann, 1998; Milton, 1993).

Nutritional factors are among the most powerful influences on food choice, posing several challenges that primates must overcome if they are to obtain suitable diets. First, few individual plant food items contain adequate concentrations of all the major essential nutrients (protein, fats, carbohydrates, water, vitamins, and minerals), forcing most primates to forage

widely for a variety of food items from many species (Milton, 1993; Richard, 1985). Second, primates must take fiber content into account when selecting food items. Items with high concentrations of fibrous components (particularly lignin, cellulose, and hemicellulose) are difficult to digest and many primates avoid them (Milton, 1979; Rogers *et al.*, 1990; Yeager *et al.*, 1997). Third, primates, especially those feeding heavily on leaves or seeds, must cope with the fact that many plants produce secondary compounds intended to deter herbivores from consuming them (Freeland and Janzen, 1974; Glander, 1982). Many primates largely avoid these compounds, including tannins, which bind with proteins to reduce the digestibility of foods, and alkaloids, which act as toxins that disrupt metabolic processes, while other primates have evolved specialized digestive physiologies that allow them to consume some secondary compounds (Lambert, 1998). Because the tropical forests where most primates live are so diverse and each potential food item has its own distinctive combination of essential nutrients, fiber, and secondary compounds, the effects of nutritional variables on food choice can be complex.

Researchers have studied the influence of nutrition on food choice in primates most intensively in the Colobinae (Chapman *et al.*, 2004; Davies *et al.*, 1988; Kool, 1992; McKey *et al.*, 1981; Mowry *et al.*, 1996; Oates, 1980; Yeager *et al.*, 1997). Colobines are primarily arboreal monkeys living in Africa and Asia that are characterized by a digestive physiology unique among the primates (Chivers, 1994; Oates and Davies, 1994). They possess an enlarged, sacculated forestomach containing large quantities of anaerobic bacteria, protozoa, and fungi that ferment ingested food items (Kay and Davies, 1994). The capacity for microbial fermentation in the forestomach offers colobines unusually acute abilities to extract nutrients contained within the fibrous cell walls of plants and to detoxify some plant secondary compounds (Kay and Davies, 1994). Though originally believed to be an adaptation solely to the challenges of a leafy diet, forestomach fermentation also allows colobines to exploit foods such as seeds that are also often rich in secondary compounds (Chivers, 1994). In fact, in recent decades, researchers have upended the traditional view of colobines as obligate leaf-eaters and it is now clear that many colobines are capable of expanding beyond the specialist folivore niche to consume large quantities of whole fruit, seeds, or lichen on a seasonal or even annual basis (Kirkpatrick, 1998; McKey, 1978; Starin, 1991). Still, leaves make substantial contributions to the diets of nearly all colobines (Fashing, 2006; Kirkpatrick, 2006) and their fundamental importance to colobines is reflected in the robust link that has been established between the protein-to-fiber ratio in mature leaves and colobine biomass across forests in the Paleotropics (Waterman and Kool, 1994).

One colobine species known to exhibit considerable dietary flexibility is the eastern black-and-white colobus or guereza (*Colobus guereza*). Guerezas subsist heavily on leaves at some sites (Kibale, Uganda: Chapman *et al.*, 2004; Harris, 2005; Oates, 1977a; Ituri, D.R. Congo: Bocian, 1997) and on a more varied diet of leaves and whole fruits or seeds at others (Kakamega, Kenya: Fashing, 2001b; Dja, Cameroon: Poulsen *et al.*, 2002; Budongo, Uganda: A. Plumptre, *unpub. data*). Researchers have studied the influence of nutritional factors on food choice among guerezas only at the sites where they are most folivorous (Kibale: Baranga, 1982, 1983; Chapman *et al.*, 2002, 2003, 2004; Oates, 1978; Oates *et al.*, 1977; Rode *et al.*, 2003; Wasserman and Chapman, 2003; Ituri: Bocian, 1997). At these sites, levels of protein (Bocian, 1997; Chapman *et al.*, 2004); fiber (Chapman *et al.*, 2004); tannins (Oates *et al.*, 1977); and several minerals including zinc, manganese, and sodium (Oates, 1978; Rode *et al.*, 2003) in food items appear to affect food choice. Sodium content also appears to exert a powerful influence on the ranging patterns of guerezas at Kibale, causing them to travel long distances intermittently to access sodium-rich swamp plants and *Eucalyptus* sp. (Myrtaceae) trees believed to make up for sodium deficiencies in their normal diet (Harris, 2005; Oates, 1978; Rode *et al.*, 2003).

We examine the relationship between nutritional variables and food choice in a guereza population in Kakamega Forest, Kenya that consumes a more varied diet than guerezas at previous study sites. In particular, we explore how different macronutrients, minerals, and secondary compounds influence their leaf choices, and compare our results to those from studies of other colobines, including the more folivorous guereza populations at Kibale and Ituri. Like their conspecifics at Kibale, Kakamega guerezas also embark on periodic long journeys to reach rare resources, specifically the bark of 2 exotic tree species (*Callistemon* sp. and *Eucalyptus* sp.) in the Myrtaceae family and a patch of bare soil under a rest house on the edge of the forest (Fashing, 2001a,b). We therefore also examine whether this bark and soil might be important sources of sodium or other minerals poorly represented in the foliage component of the guereza's diet at Kakamega. Lastly, we examine whether results from Kakamega are consistent with the pattern across other Paleotropical forests in which colobine biomass can be predicted by the protein-to-fiber ratio in mature leaves.

METHODS

Study Site and Population

Kakamega Forest is located *ca.* 40 km NW of Lake Victoria and is the last remaining Guineo-Congolian rain forest in Kenya. Kakamega is

fragmented into 6 blocks, the largest of which covers 85 km² and includes our study site of Isecheno (BIOTA, 2004). Isecheno (elev. 1580 m) is characterized by an unusually high density and biomass of trees in the Moraceae family (Fashing, 1999, 2001b). The study area has undergone varying levels of human disturbance including past selective logging and current illegal harvesting of small trees for poles, liana cutting, and honey collection (Fashing *et al.*, 2004). Mean yearly rainfall is 2215 mm at Isecheno, and mean monthly maximum temperatures vary from 18° C to 29° C while mean monthly minimum temperatures vary from 11° C to 21° C (Cords, 1987).

Fashing has studied the guereza population at Isecheno since 1993. Guerezas at this site live at a higher density (150 ind/km²) and biomass (1035 kg/km²) and in larger groups (mean = 13, $n = 5$) than other guereza populations inhabiting large rain forest blocks (Fashing, 2001a; Fashing and Cords, 2000). Based on a dietary study of 2 groups occupying adjacent home ranges (T: 11 members; O: 7 members), they are also one of the most frugivorous populations of guerezas studied (Fashing, 2001b). In fact, Isecheno guerezas select fruit over young leaves even when both are available (Fashing, 2001b). Most of the fruits Isecheno guerezas consume are from species in the Moraceae family (Fashing, 2001b). During periods of fruit scarcity at Isecheno, guerezas increase their leaf consumption, with the mature leaves of *Prunus africana* (Rosaceae) acting as their primary fallback food (Fashing, 2004).

Tree Community Composition

To determine the density and biomass of the different tree species and families available to groups T and O, we established a series of 8 transects following preexisting trails that passed through their home ranges. We recorded tree species identity and girth at breast height (GBH) for all trees ≥ 20 cm GBH that had trunks ≤ 5 m from the center of the transect (Fashing, 2001b). We then converted GBH to diameter at breast height (DBH) and calculated basal area (BA) per ha as an estimate of foliar biomass (Fashing, 2001b; Kool, 1993) for each tree species in the home ranges of T and O.

Guereza Diet

We collected feeding data on 5 consecutive dawn-to-dusk study days each month for T and O from March 1997 to February 1998. On these days, we conducted activity scan samples of 5-min duration at 15-min intervals on

up to the first 6 visible adults or juveniles and all visible infants ≥ 2 mo old. We recorded activities as rest, feed, move, or social, and if a subject was feeding at the time of a scan, we recorded the plant species and food item upon which it was feeding. We designated food items as leaf buds, young leaves, mature leaves, unclassified leaves, whole fruit, seeds, flowers, bark, or unidentified (Fashing, 2001b).

We calculated selection ratios for species eaten by groups T and O as a means of measuring dietary selectivity. Because basal area-based methods of calculating selection ratios provide a better index of the amount of food available to primates than stem density-based methods (Kool, 1989), we calculated selection ratio by dividing the percentage of the annual feeding time spent feeding on a particular species-specific food item by the percentage of the total basal area in the forest contributed by that species (Fashing, 2001b).

Plant Sample Collection and Processing

We collected leaf, bark, and soil samples at Isecheno in August 1998. We collected samples from trees only from large individuals assumed to be reproductively mature. A local tree climber procured samples, generally from lower strata of the upper canopy, and we dried them in the sun for several days. We stored dried samples in paper bags until we conducted lab analyses for macronutrients and secondary compounds in 2001 and for minerals in 2003.

We collected mature leaf samples from 20 species (19 trees, 1 climbing vine), 11 of which guerezas exploited for their mature leaves (Appendix I.A). In the 14 cases in which young leaves were available on the same plant, we also collected young leaf samples. Guerezas were known to feed on young leaves from 11 of these 14 species. The leaf (mature and young) samples we collected accounted for 74% of the total leaves guerezas consumed (Fashing, 2001b). We collected bark samples from individuals of 2 tree species that guerezas from several groups traveled long distances to exploit. Together these species accounted for 79% of the bark that guerezas consumed (Fashing, 2001b). We collected soil from 1 location beneath a tourist guest house raised on stilts that bordered the forest where on numerous occasions we observed several colobus groups consuming soil (Fashing, 2001b).

Though we collected samples from a substantial percentage of the items in the guereza's diet, our sampling regimen had several limitations. First, because we collected all of the samples during a single month, we could not account for seasonal variation in nutritional quality within food

items and for how this temporal variability may have affected food choice (Chapman *et al.*, 2003; Worman and Chapman, 2005). Second, because we collected most of our samples from a single tree of each species, we were unable to control for any interindividual variability in nutritional quality within tree species (Chapman *et al.*, 2003). Nevertheless, the fact that we uncovered a number of significant relationships between nutritional variables and food choice that are consistent with those of previous colobine studies suggests that any biases introduced into our study by our limited sampling regimen were not overly powerful.

Macronutrient, Mineral, and Secondary Compound Analysis

We transported samples to Dierenfeld's nutrition laboratory at the Bronx Zoo, weighed each sample to the nearest 0.1 g, then ensured that the samples were completely dry by placing them in a forced-draft oven at $<60^{\circ}\text{C}$ until constant weight to determine moisture content. We then used an inexpensive Oster coffee grinder to mill samples into a fine powder consisting of as uniform particles as possible and stored them in sealable plastic bags at room temperature until analysis. We measured absolute dry matter (DM) by drying samples at 100°C , and corrected all macronutrient data to a 100% DM basis. We analyzed them for crude protein (CP), acid detergent fiber (ADF), neutral detergent fiber (NDF), sulfuric acid lignin, hemicellulose (HC), cellulose (CEL), and ash content. We calculated CP content by multiplying total nitrogen by 6.25 using a macro-Kjeldahl method with a Cu catalyst (Cunniff, 1996). We conducted analyses of the fibrous components of plant cell walls (ADF, NDF, lignin, HC, and CEL) per the methods of Van Soest *et al.* (1991).

Members of the Animal Toxicology Laboratory at the University of Pennsylvania Veterinary School conducted assays for minerals in our samples via spectroscopy using standard methods (Cunniff, 1996). They assayed 5 macrominerals (Ca, K, Mg, Na, P) and 5 trace elements (Co, Cu, Fe, Mn, Zn) and reported the measurements in mg/kg.

We assayed samples for secondary compounds, specifically condensed tannins (CTs) and alkaloids, in Mowry's laboratory at Berry College. Assay procedures followed those of Remis *et al.* (2001) and Powzyk and Mowry (2003). We prepared extractions for CTs using 50% methanol and estimated CTs as proanthocyanidins using a butanol-HCl technique (Remis *et al.*, 2001). To ensure comparability with previous studies (Waterman and Kool, 1994), we used quebracho tannin as the standard for CTs and expressed CTs as percentage dry mass quebracho tannin equivalents (% QTE). CT values can surpass 100% when a given sample is more reactive than an equivalent amount of quebracho tannin (Remis *et al.*, 2001).

We determined whether alkaloids were present in our samples using Dragendorff's and iodoplatinate reagents. We extracted 100 mg of each sample in 10 ml of 95% ethanol at room temperature for 24–36 h. Next, we thoroughly dried the extract and added equal portions of petroleum ether and water. Once 2 distinct layers formed, we spotted several drops of the aqueous bottom layer on 2 pieces of filter paper. We then sprayed Dragendorff's reagent on 1 paper and iodoplatinate reagent on the other. The paper turning orange in the case of Dragendorff's reagent or purple in the case of iodoplatinate reagent indicated the presence of alkaloids. Samples had to react to both reagents for us to consider them to be alkaloid positive.

Data Analysis

Before analyzing our data, we combined feeding records initially categorized as leaf buds and young leaves into a single young leaves category. We also recategorized unclassified leaves as mature leaves owing to strong circumstantial evidence gathered during the study that most unclassified leaves were mature (Fashing, 2004). When dividing food items into eaten and not eaten, we considered items eaten if they contributed $\geq 0.10\%$ to the annual diet, i.e., if ≥ 2 individuals ate the item or the same individual ate the item on ≥ 2 separate occasions.

Because most of our data passed Kolmogorov-Smirnov tests for normality, we used primarily parametric statistics for the tests described here. If data were not normally distributed, we log transformed the data and retested for normality before applying parametric analyses to them. As an initial examination of the nutritional variables influencing guereza food choice, we compared the macronutrient, mineral, and condensed tannin concentrations of eaten vs. not eaten leaf items via independent sample *t*-tests. Next, we used Pearson correlations to explore the relationship between the percentage contribution of leaf food items to our study groups' diets and macronutrient, mineral, and condensed tannin concentrations. Lastly, we used Pearson correlations to examine the relationship between the selection ratio of leaf food items and macronutrient, mineral, and condensed tannin concentrations. This latter approach was the most informative measure of choice for the various phytochemicals because it took into account both the differential abundance of tree species in the forest and the frequencies at which subjects consumed different species-specific leaf food items (Williams-Guillen, 2003).

We also constructed a Pearson correlation matrix with our mineral data to examine the extent to which concentrations of different minerals were related to one another in food items. We did not attempt to estimate

the overall content of specific macronutrients and minerals (Rode *et al.*, 2003) in the guereza's diet at Kakamega because a substantial proportion of their diet consists of whole fruit (37%), a category for which we did not collect samples for nutritional analysis.

After establishing that the results of our analyses were consistent for both T and O when analyzed individually, we pooled data from the 2 groups for all subsequent analyses. The results of the pooled analyses are what we present here.

Lastly, we estimated overall mature leaf protein-to-fiber ratio for Kakamega and compared it to previously published values for 7 other forests per the methods of Waterman *et al.* (1988). Specifically, we calculated a weighted mean CP:ADF ratio for the 19 tree species on which we conducted mature leaf chemistry analyses at Kakamega. We calculated weighted values for CP and ADF via the formula: $\sum(P_i \times X_i) / \sum P_i$, where P_i represents the proportion of the basal area accounted for by species i and X_i represents the chemical measure for species i . Because researchers have evaluated different proportions of the tree flora at different sites, we standardized the final weighted value to 100% of the basal area. We used weighted values for the other 7 sites from Oates *et al.* (1990) and Waterman and Kool (1994).

RESULTS

Dietary Composition

The diet of Kakamega guerezas consisted of 23.7% young leaves, 29.1% mature leaves, 37.4% whole fruits, 1.2% seeds, 0.5% flowers, 2.5% bark, and 5.7% unclassified items. Guerezas consumed soil occasionally as well, though never during a feeding scan. Eighty percent of their diet came from only 10 plant species (Table I). Mature leaves of *Prunus africana* made by far the greatest contribution to the annual diet (16.1%) and had the highest selection ratio (6.0) of any species-specific leaf food item (Tables I and II). Other species-specific leaf food items for which guerezas exhibited strong selection were mature leaves of *Alangium chinense* (3.2), young leaves of *Zanthoxylum gillettii* (2.7), young leaves of *Teclea nobilis* (2.3), and young leaves of *Alangium chinense* (2.0).

Eaten vs. Not Eaten Leaves

Leaf items that were eaten are significantly higher in CP ($t = -2.893$, $df = 31$, $p = .007$) than those that were not eaten (Fig. 1). The CP/ADF

Table 1. Top 10 plant species in the diet of *Colobus guereza* in Kakamega Forest, Kenya from March 1997 to February 1998

Plant species	Family	Young leaves	Mature leaves	Fruit	Seeds	Flowers	Bark	Uid	Total
<i>Prunus africana</i>	Rosaceae	2.91	16.11			.05	.03	.12	19.21
<i>Trilepisium madagascariense</i>	Moraceae		.19	9.92				1.55	11.66
<i>Ficus exasperata</i>	Moraceae	1.27	.54	8.01				.29	10.11
<i>Teclea nobilis</i>	Rutaceae	1.39	.05	6.02			.25	1.04	8.75
<i>Celtis africana</i>	Ulmaceae	7.24	.79				.10	.05	8.17
<i>Antiaris toxicaria</i>	Moraceae			8.04				.10	8.14
<i>Piper guineense</i>	Piperaceae	.39	3.73					.03	4.14
<i>Morus mesozygia</i>	Moraceae	3.45		.52				.07	4.04
<i>Albizia gummifera</i>	Mimosaceae	2.75	.15		1.00		.08	.03	3.99
<i>Celtis gompophylla</i>	Ulmaceae	.74	1.01						1.74
Totals		20.14	22.57	32.51	1.00	.05	.46	3.28	79.95

Note. Values represent the percentages of total feeding scans ($n = 4254$) during which we observed each item being consumed.

ratio is also significantly higher for eaten than for not eaten leaf items ($t = -2.346$, $df = 31$, $p = .026$). Concentrations of ADF ($t = .793$, $df = 31$, $p = .434$), NDF ($t = .570$, $df = 31$, $p = .573$), lignin ($t = 1.167$, $df = 31$, $p = .252$), hemicellulose ($t = -.330$, $df = 31$, $p = .744$), cellulose ($t = .029$, $df = 31$, $p = .977$), and ash ($t = .068$, $df = 31$, $p = .946$) do not differ between eaten and not eaten leaf items.

Leaf items that were eaten are significantly higher in Zn ($t = -3.010$, $df = 30.9$, $p = .005$) and Cu ($t = -2.000$, $df = 31$, $p = .054$) than leaf items that were not eaten (Fig. 2). However, only the choice for items high in Zn appears to be biologically significant because the marginally significant value for Cu appears to be driven by a correlation between Zn and Cu content (see below). There is also a trend toward Mn being lower in leaves that were eaten than in those that were not eaten ($t = 1.929$, $df = 14.5$, $p = .073$; Fig. 2). There is no difference between eaten and not eaten leaf items in their concentrations of Na ($t = .961$, $df = 31$, $p = .344$), K ($t = .069$, $df = 31$, $p = .945$), Mg ($t = .142$, $df = 31$, $p = .888$), Ca ($t = .807$, $df = 31$, $p = .426$), Fe ($t = .697$, $df = 31$, $p = .491$), P ($t = -1.643$, $df = 31$, $p = .110$), and Co ($t = .677$, $df = 31$, $p = .503$).

Table II. Contributions to the annual diet and selection ratios of leaf food items of *Colobus guereza* collected in Kakamega Forest for chemical analyses

Plant species	Family	Food item	% of Annual diet	Selection ratio
<i>Prunus africana</i>	Rosaceae	Mature leaves	16.11	5.97
<i>Celtis africana</i>	Ulmaceae	Young leaves	7.24	1.14
<i>Piper guineense</i>	Piperaceae	Mature leaves	3.73	NA ^a
<i>Prunus africana</i>	Rosaceae	Young leaves	2.91	1.08
<i>Teclea nobilis</i>	Rutaceae	Young leaves	1.39	2.32
<i>Zanthoxylum gillettii</i>	Rutaceae	Young leaves	1.08	2.70
<i>Celtis gomphophylla</i>	Ulmaceae	Mature leaves	0.98	1.63
<i>Olea capensis</i>	Oleaceae	Mature leaves	0.96	0.43
<i>Celtis africana</i>	Ulmaceae	Mature leaves	0.79	0.12
<i>Celtis gomphophylla</i>	Ulmaceae	Young leaves	0.74	1.23
<i>Ficus exasperata</i>	Moraceae	Mature leaves	0.54	0.03
<i>Markhamia lutea</i>	Bignoniaceae	Young leaves	0.48	0.40
<i>Strombosia scheffleri</i>	Olacaceae	Mature leaves	0.44	0.24
<i>Piper guineense</i>	Piperaceae	Young leaves	0.39	NA ^a
<i>Zanthoxylum gillettii</i>	Rutaceae	Mature leaves	0.33	0.83
<i>Alangium chinense</i>	Alangiaceae	Mature leaves	0.19	3.17
<i>Trilepisium</i>	Moraceae	Mature leaves	0.19	0.02
<i>madagascariense</i>				
<i>Albizia gummifera</i>	Mimosaceae	Mature leaves	0.15	0.02
<i>Markhamia lutea</i>	Bignoniaceae	Mature leaves	0.14	0.12
<i>Alangium chinense</i>	Alangiaceae	Young leaves	0.12	2.00

^aThe basal area value necessary to calculate selection ratio could not be determined because *Piper guineense* is a climber, not a tree.

Among leaf items that were eaten, there are significant positive correlations between Cu and Zn, P and Zn, Ca and Fe, Ca and Mg, Cu and P, Fe and Mg, K and P, and Cu and K (Table III), and a trend toward a correlation between K and Zn.

Condensed tannins (% QTE) occur at significantly lower levels in leaves that were eaten than in leaves that were not eaten ($t = 2.176$, $df = 31$, $p = .037$; Fig. 1). We detected no alkaloids in any of the eaten or not eaten leaves.

Relationship Between Feeding Selectivity and Nutritional Variables in Leaves

Percentages of time spent feeding on species-specific leaf food items are not significantly correlated with any of the macronutrient, mineral, or secondary compound measures (Table IV). However, the potential influence of differences in food tree species abundance on food choice

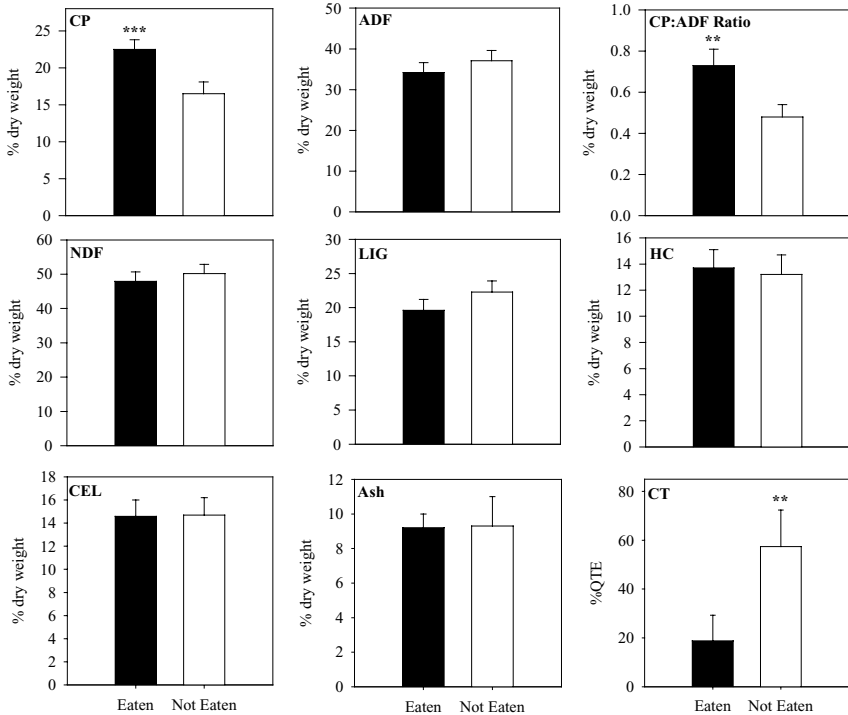


Fig. 1. Comparison of mean macronutrient and condensed tannin concentrations in eaten ($n = 20$) vs. not eaten ($n = 13$) leaf food items for *Colobus guereza* in Kakamega Forest. Significance: * $p < .10$; ** $p < .05$; *** $p < .01$.

are not considered in the above correlations, which may therefore be insufficiently precise to identify relationships between food selection and macronutrients, minerals, or secondary compounds (Williams-Guillen, 2003). Indeed, if selection ratios for species-specific leaf food items are employed instead of percentage contributions to the diet, significant negative correlations emerge between selection and ADF ($r = -.696$, $n = 18$, $p = .001$), NDF ($r = -.666$, $n = 18$, $p = .003$), lignin ($r = -.557$, $n = 18$, $p = .016$), and cellulose ($r = -.539$, $n = 18$, $p = .021$) (Table IV). Further, selection ratio and CP/ADF ratio correlate significantly ($r = .516$, $n = 18$, $p = .028$). Among minerals, only selection ratio and Zn ($r = .517$, $n = 18$, $p = .028$) correlate significantly. There is no relationship between selection ratio and condensed tannin content ($r = -.273$, $n = 18$, $p = .273$).

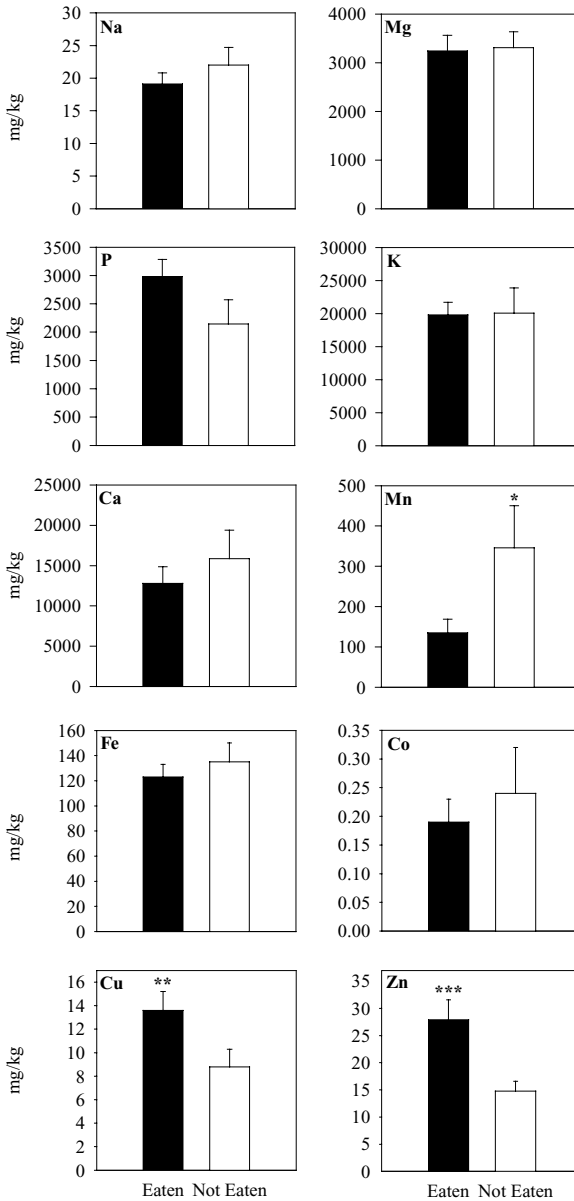


Fig. 2. Comparison of mean mineral concentrations in eaten ($n = 20$) vs. not eaten ($n = 13$) leaf food items for *Colobus guereza* in Kakamega Forest. Significance: * $p < .10$; ** $p < .05$; *** $p < .01$.

Table III. Pearson correlation (r) matrix of minerals in leaf food items ($n = 20$ items from 13 species) consumed by guerezas at Kakamega

Mineral	Na	Mg	P	K	Ca	Mn	Fe	Co	Cu	Zn
Na	–									
Mg	.115	–								
P	–.251	.079	–							
K	–.041	.199	.529**	–						
Ca	–.021	.735***	–.116	–.193	–					
Mn	.200	–.004	–.300	–.312	.003	–				
Fe	.229	.665***	.150	.019	.739***	.185	–			
Co	–.003	–.164	–.026	–.147	–.238	–.052	–.259	–		
Cu	–.311	–.034	.708***	.526**	–.235	–.211	–.035	.095	–	
Zn	–.208	–.138	.767***	.403*	–.362	–.360	–.101	.161	.811***	–

*Significant at $p \leq .10$; ** $p \leq .05$; *** $p \leq .01$.

Nutritional Properties of Bark and Soil Compared to Leaves

Bark and soil that guerezas ate had much lower values for several important macronutrient variables, e.g., CP, CP/ADF ratio, than leaf food items (Table V). However, concentrations of several minerals were far higher in the bark and soil guerezas consumed than in their leaf food items. In particular, mean Na values for barks of *Callistemon* and *Eucalyptus* and for soil were all much higher than the mean Na value for leaf food items (Table V). In fact, the leaf food item (young leaves of *Strombosia schefleri*) with the highest Na concentration was still 49 times lower in Na than the bark of *Callistemon*, 15 times lower in Na than the bark of *Eucalyptus*, and 18 times lower in Na than soil (Appendix I.B). Further, barks of *Callistemon* and *Eucalyptus* were both more than twice as high in Ca than the mean for leaf food items (Table V), though there were individual leaf food items, e.g., young leaves of *Celtis africana*, that were comparably high in Ca (Appendix I.B). Soil and bark of *Eucalyptus* were both many times higher in Mn than the average leaf food item (Table V), though the fact that the leaves guerezas consumed are nearly significantly lower in Mn than those they avoided suggests they probably were not eating soil and bark of *Eucalyptus* for their high Mn content. Soil also had unusually high concentrations of Co, Cu, Fe, and Zn relative to leaf food items (Table V).

Comparison of Protein-to-Fiber Ratio and Colobine Biomass Between Kakamega and Other Sites

Previous reviews demonstrated a significant positive correlation between CP/ADF ratio and colobine biomass across Paleotropical rain forests (Chapman *et al.*, 2002; Waterman and Kool, 1994). We add an eighth forest,

Table IV. Pearson correlations (r) between selectivity indices [1] percent contribution to the annual diet and 2) selection ratio] and macronutrient, mineral, and secondary compound content of leaf food items ($n = 20$)

A. Macronutrients and condensed tannins	CP	ADF	CP:ADF	NDF	Lignin	HC	CEL	Ash	CT
% in diet	.172	.133	.090	.042	-.010	-.199	.233	.024	-.344
Selection ratio ^a	.172	-.696***	.516**	-.666***	-.557**	-.196	-.539**	-.044	-.273
B. Minerals									
	Na	Mg	P	K	Ca	Mn	Fe	Co	Cu
% in diet	-.219	-.276	-.104	-.124	-.166	.194	-.191	-.095	.180
Selection ratio ^a	-.052	-.074	.357	.370	-.241	-.237	-.175	.051	.178

Note. Significant at * $p < .10$; ** $p < .05$; *** $p < .01$.

^aCorrelations based on only 18 leaf food items because we could not calculate basal-area based selection ratios for the young leaves and mature leaves of the climber *Piper guineense*.

Table V. Mean macronutrient (% DM) and mineral content (mg/kg) of leaves, bark, and soil eaten by guerezas at Kakamega

Variable	Leaves ^a	Bark ^b	Soil ^c
CP	23	2	1
ADF	34	50	NA ^d
CP:ADF	.73	.05	NA ^d
NDF	48	75	NA ^d
LIG	20	31	NA ^d
HC	14	25	NA ^d
CEL	15	20	NA ^d
Ash	9	9	92
Na	19	889	505
Mg	3240	2289	466
P	2980	207	218
K	19,812	4699	812
Ca	12,789	27,959	12,307
Mn	135	675	1109
Fe	123	316	96,961
Co	.19	.47	11
Cu	14	2	61
Zn	28	14	78

^a*n* = 20 leaf food items from 13 species.

^b*n* = 2 species.

^c*n* = 1 sample.

^dFiber values for soil are not reported owing to logistical difficulties inherent in accurately assaying soil fiber content.

Kakamega, to this comparison and consider whether the pattern of CP/ADF ratio predicting biomass still holds. With both the second highest mature leaf CP/ADF ratio (.48) and the second highest colobine biomass (1035 kg/km²: Fashing and Cords, 2000), Kakamega fits the protein-to-fiber model for colobine biomass well (Fig. 3). The addition of Kakamega slightly strengthens the Spearman rank correlation coefficient ($r_s = .898$, $n = 8$, $p = .002$ vs. $r_s = .847$, $n = 7$, $p = .016$), and slightly weakens the Pearson correlation coefficient ($r = .799$, $n = 8$, $p = .017$ vs. $r = .859$, $n = 7$, $p = .013$), between CP/ADF ratio and colobine biomass in Paleotropical rain forests. Regardless of the type of correlation chosen for analysis, however, the relationship between CP/ADF ratio and colobine biomass remains clearly significant ($p < .02$ in both cases) after the addition of Kakamega.

DISCUSSION

Influence of Macronutrients on Guereza Leaf Choice at Kakamega

Macronutrients had a complex influence on leaf choice by guerezas at Kakamega. At a broad level, protein content was the primary factor

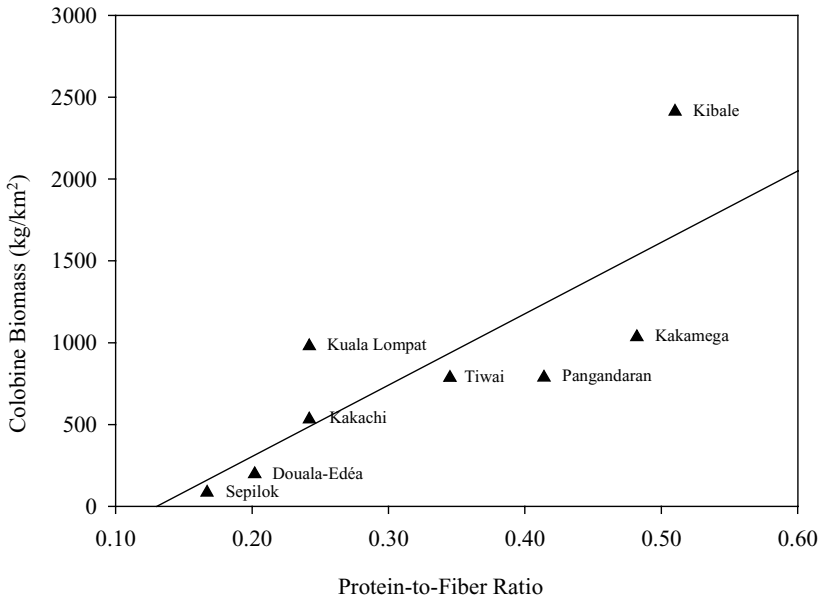


Fig. 3. Relationship between mature leaf protein-to-fiber ratio and colobine biomass across 8 Paleotropical rain forest sites.

determining whether guerezas consumed specific leaf items. In particular, leaves guerezas ate are significantly higher in protein than uneaten leaves, and there was a protein threshold of *ca.* 14% DM that leaves had to reach to be considered edible by guerezas (Appendix I.A). Mowry *et al.* (1996) reported a similar leaf protein threshold (*ca.* 13%) for red colobus (*Ptilocolobus rufomitratus*) in gallery forests along the Tana River in Kenya. However, despite the initial importance of protein levels to determining whether Kakamega guerezas ate specific leaf items, a finer grade analysis considering the selection ratios of only items eaten revealed that fibrous components played a much greater role than protein in influencing the rates at which subjects ate different items relative to their abundance in the forest. Specifically, among leaf food items, guerezas exhibited strong selectivity for items that were low in ADF, NDF, cellulose, and lignin, with little regard for protein levels of these items.

Our results are consistent with previous evidence that the most consistent macronutrient predictor of colobine food choice is fiber content. In all but a few populations (*Colobus angolensis*: Maisels *et al.*, 1994; *C. guereza*: Bocian, 1997; *C. polykomos*: Dasilva, 1994), colobines exhibit a preference for food items (especially leaves) that are low in fiber (*C. guereza*: Chapman

et al., 2004; this study; *C. satanas*: McKey *et al.*, 1981; *Nasalis larvatus*: Yeager *et al.*, 1997; *Ptilocolobus rufomitratu*s: Mowry *et al.*, 1996; *Pi. tephrosceles*: Chapman and Chapman, 2002; *Presbytis johnii*: Oates *et al.*, 1980; *Pr. rubicunda*: Davies *et al.*, 1988; *Procolobus verus*: Oates, 1988; *Trachypithecus auratus*: Kool, 1992). This pattern might initially seem surprising in light of the renowned ability of colobines to use forestomach fermentation to extract nutrients from the fibrous cell walls of plants (Bauchop, 1978; Bauchop and Martucci, 1968; Watkins *et al.*, 1985). However, extensive reliance on the extraction of nutrients from high-fiber foodstuffs requires long gut retention times, a luxury probably unavailable to colobines owing to their relatively small body—and thus gut—sizes (Kay and Davies, 1994). While large-bodied ruminants such as cows and buffaloes have the capacious guts necessary to focus on fibrous, low-energy foodstuffs, colobines appear to require a more selective feeding strategy that limits their reliance on foregut fermentation as a source of nutrients.

Influence of Minerals on Guereza Leaf Choice at Kakamega

Most minerals do not appear to exert a strong influence on leaf choice by Kakamega guerezas, a pattern similar to that which Rode *et al.* (2003) described previously for food items Kibale guerezas consumed. This result is not unexpected because the foliage available to wild primates is believed to be generally high in most minerals relative to recommended dietary requirements (Milton, 2003), thereby rendering it unnecessary in most cases for primates to base dietary decisions on mineral content. However, at least 1 notable exception to this pattern appears to exist for guerezas. Kakamega guerezas exhibited marked selection for leaves high in Zn—not only were the leaves that guerezas consumed significantly higher in Zn than those they did not eat, but even among only the leaves they consumed, there is a significant correlation between selection ratio and Zn content. Though Zn content in leaf food items also correlates significantly with Cu, P, and K content, the fact that Zn was the only mineral significantly selected for suggests that Zn was the primary mineral influencing guereza leaf choices at Kakamega. Further, because Cu, P, and K do not adversely affect the bioavailability, i.e., proportion that is absorbed and used, of Zn (King and Keen, 1999), negative interactions with other minerals in the diet are unlikely to play large roles in driving the selection for Zn.

Kibale guerezas also select for plant foods with high Zn content (Rode *et al.*, 2003). This consistent selection by guerezas for plants rich in Zn is interesting because most leaves at Kakamega and Kibale far exceed the NRC

(2003) recommendation for Zn content (13 mg/kg) in catarrhine food items (Appendix I.B). Based on evidence from the wild, it appears that the generalized NRC recommendations for Zn consumption by catarrhines may be too low for guerezas. This finding is of particular relevance to captive managers of guerezas because Zn is essential to proper metabolic functioning and deficiencies can have myriad adverse effects, including stunted growth, reproductive failure, immune deficiencies, and impaired cognitive function (King and Keen, 1999).

Influence of Secondary Compounds on Guereza Leaf Choice at Kakamega

The food choices of many animals are constrained by the secondary compounds that plants produce as chemical defenses against herbivory (Bryant *et al.*, 1992; Coley, 1983). Researchers believe colobines are somewhat buffered against the adverse effects of some secondary compounds because of their specialized digestive morphology. For example, microbial flora in the colobine forestomach are thought to be capable of detoxifying alkaloids that render food items unpalatable for other herbivores (Waterman and Kool, 1994). Indeed, several colobines, including *Colobus satanas*, *Piliocolobus badius*, and *Trachypithecus vetulus*, eat alkaloid-rich food items that sympatric primates avoid (Hladik, 1978; McKey, 1978). Further, at sites where researchers have systematically studied food choice relative to alkaloid content in vegetation, there is little evidence that colobines avoid consuming alkaloids (Burgess and Chapman, 2005; Chapman and Chapman, 2002; Oates *et al.*, 1980). Unfortunately, we were unable to determine whether guerezas at Kakamega fit this pattern because none of the food or nonfood items we assayed contained alkaloids. This absence of alkaloids from our samples is not surprising because we sampled primarily from woody species, which, unlike herbaceous species, often produce tannins rather than alkaloids (Bate-Smith and Metcalfe, 1957; Levin, 1976). Still, there are East African forests such as Kibale where alkaloids occur in up to 40% of woody species including some of the same species from which alkaloids were absent at Kakamega (Burgess and Chapman, 2005; Gartlan *et al.*, 1980). Explaining this wide interforest variation in alkaloid prevalence will require more detailed data on soil quality, forest composition, and plant chemistry both across species and among individuals of the same species (Chapman *et al.*, 2003; Gartlan *et al.*, 1980).

Tannins influence food choice in some colobine populations, e.g., *Procolobus verus* (Oates, 1988) and *Trachypithecus johnii* (Oates *et al.*,

1980), but not in others, e.g., *Colobus angolensis* (Bocian, 1997), *Ptilocolobus rufomitatus* (Mowry *et al.*, 1996), and *P. tephrosceles* (Chapman and Chapman, 2002). Even within a single species, *Colobus guereza*, Oates *et al.* (1977) described a population at Kibale as avoiding tannins while Bocian (1997) reported another at Ituri to be undeterred by them. We provide a third site to examine the influence of tannins on guereza food choice. As at Kibale, we found that tannin concentrations at Kakamega are significantly lower in the leaves guerezas consumed than in the leaves they ignored. However, several other pieces of evidence suggest that tannins may not have a particularly strong influence on Kakamega guereza food choice. First, as with Ituri guerezas (Bocian, 1997), there is no relationship between food item selection ratio and tannin concentration for Kakamega guerezas. In fact, the leaf item dominating foliage intake at Kakamega, mature leaves of *Prunus africana*, featured some of the highest condensed tannin concentrations (58% QTE) of any leaves in the diet (Appendix I.A). Second, Kakamega guerezas consumed large quantities of unripe fruit (Fashing, 2001b), which, based on nutritional studies in other locations, tends to be higher in tannins than the ripe fruit most other primates prefer (Waterman and Kool, 1994; Wrangham and Waterman, 1983). Kakamega guerezas also periodically ate the bark of *Callistemon* sp., which was extremely high in condensed tannins (154% QTE). Thus, while guerezas avoid most high-tannin plant items at Kakamega, they make exceptions for some species and experience few apparent deleterious effects. Considering the wide interpopulational variability in degrees of tannin avoidance that researchers have now documented both within and among colobine species, further research aimed at explaining this variability is needed.

Can the Nutritional Properties of Soil and Myrtaceae Bark Explain Why Guerezas Travel Such Long Distances to Access Them?

Colobines often supplement their relatively leafy diets with the periodic exploitation of unusual foods, including soil, swamp plants, tree bark, charcoal, or even concrete (Davies and Baillie, 1988; Fashing, 2001b; Harris, 2005; Oates, 1978; Struhsaker *et al.*, 1997). In some cases, these foods can be accessed within a group's normal home range, though in others, they must travel long distances to reach them. For colobines, many of which rank among the least active primates (Fashing, 2006), extensive trips to access rare resources represent substantial expenditures of energy and imply that these resources must be highly prized (Pages *et al.*, 2005). Members of 1 particularly sedentary species, *Colobus guereza*, travel periodically distances of

up to nearly twice their usual daily path length to reach rare food items outside their normal home range in 2 different forests, Kibale and Kakamega (Fashing, 2001a; Harris, 2005; Oates, 1978). The rare, unusual food items that guerezas travel long distances to reach at Kibale are the leaves of several herbaceous swamp plant species, the bark and leaves of the exotic tree species *Eucalyptus grandis* (Myrtaceae), and clay soil from inside a cave along a stream bank (Harris, 2005; Oates, 1978). At Kakamega, guerezas travel long distances to access bark from 2 exotic tree species of Myrtaceae (*Callistemon* sp. and *Eucalyptus* sp.) and soil from under a rest house on the edge of the forest (Fashing, 2001a,b).

Chemical analyses of samples from both Kibale and Kakamega suggest that the guerezas at these sites may be using swamp plants and trees in the Myrtaceae family to remedy mineral deficiencies in their normal diets. For example, the foliage available to guerezas in their usual ranging areas at both sites is well below NRC-recommended (2500 mg/kg) Na levels (Kibale: Oates, 1978; Rode *et al.*, 2003; Kakamega: Appendix I.B), suggesting that the foods normally available to guerezas at these sites are Na deficient. Swamp plants at Kibale and Myrtaceae bark at both sites consistently contained extremely high Na levels relative to that of the foliage in the normal ranges of the study groups at each site. It thus seems likely that the long journeys guerezas embark upon to reach these rare plants are largely Na-driven, which may help to explain why daily path length and home range size do not correlate tightly with group size in the species (Fashing, 2001a; Harris, 2005). Isolated Na sources also attract large concentrations of ungulates in grassland environments (Klaus and Schmid, 1998), and Na availability may even regulate population density in at least 1 moose population (Botkin *et al.*, 1973).

The benefits of geophagy to guerezas appear to differ somewhat across sites. At Kibale, the clay-rich soils that guerezas consume are not unusually high in Na or other minerals (except perhaps Cu) in which guerezas may be deficient (Oates, 1978). Therefore, instead of regarding geophagy as a means of increasing mineral intake, Oates (1978) suggested that clay ingestion neutralizes the deleterious effects of secondary compounds in foliage Kibale guerezas consume. While geophagy may also play a role in detoxifying secondary compounds for Kakamega guerezas, we found that the soil they consumed is much higher than foliage in concentrations of Na and Zn, 2 minerals much sought after by guerezas (Harris, 2005; Oates, 1978; Rode *et al.*, 2003; this study). An additional potential benefit of geophagy for colobines that we did not evaluate is its possible role in the alleviation of forestomach acidosis, a potentially fatal condition afflicting colobines that consume fruits (Davies and Baillie, 1988) like the Kakamega guerezas.

Do Data from Kakamega Fit the Pattern of Protein-to-Fiber Ratio Predicting Colobine Biomass?

Primate biomass varies widely among sites, with folivorous taxa exhibiting particularly marked intersite variability, e.g., lemurs (Ganzhorn, 1992), howlers (Chapman and Balcomb, 1998), and colobines (Fashing and Cords, 2000). While researchers have proposed numerous biotic and abiotic factors as possible influences on primate biomass, the strongest predictor of folivorous primate biomass appears to be the mean protein-to-fiber ratio of mature leaves in a forest (Chapman *et al.*, 2004; Ganzhorn, 1992; Oates *et al.*, 1990). Several researchers (Davies, 1994; Waterman *et al.*, 1988) have suggested that the link between mature leaf protein-to-fiber ratio and the biomass of colobines can be explained by the fact that mature leaves act as fallback foods for many colobines when preferred foods are scarce (Dasilva, 1994; Marsh, 1981; Oates, 1977a; Stanford, 1991; Struhsaker, 1975).

Though our study population of guerezas at Kakamega were foli-frugivores that tended to select whole fruits over leaves when both were available (Fashing, 2001b), they fed heavily on mature leaves during extended periods when fruits were scarce (Fashing, 2001b, 2004). This reliance on mature leaves as a fallback resource by the only colobine species living at Kakamega led us to expect that data on mature leaf protein-to-fiber ratio and colobine biomass for Kakamega would be consistent with the pattern established for other rain forests containing colobines (Waterman and Kool, 1994). Indeed, among the 8 rain forests from which data on mature leaf protein-to-fiber ratio and colobine biomass are now available, Kakamega ranks second in both categories (Fig. 3). With up to 81% of the variance in colobine biomass across 8 widely scattered Paleotropical rain forests explained by mature leaf protein-to-fiber ratio, there appears to be little question that leaf quality is the primary variable influencing colobine abundance in tropical rain forests. Recent evidence from Kibale suggests that this link between foliage quality and colobine biomass may exist even among sites within the same rain forest (Chapman *et al.*, 2002). Nevertheless, there are almost certainly additional factors that play roles in directly or indirectly influencing colobine abundance, including soil quality; habitat disturbance; tree-species composition; climatic, historic, and zoogeographic forces; competition; predation; and disease (Oates *et al.*, 1990, pp. 339–340). While evidence from rain forests suggests a clear link between mature leaf quality and colobine biomass, it remains to be determined whether these variables correlate as tightly in other habitats such as dry, coastal, and montane forests where colobines also occur but have been studied less intensively.

Appendix I.A. Macronutrient and condensed tannin concentrations of samples from Isecheno study site, Kakamega Forest, Kenya

Plant species or item	Family	Plant part	Eaten?	CP (% DM)	ADF (% DM)	CP/ADF	NDF (% DM)	Lignin (% DM)	HC (% DM)	CEL (% DM)	Ash (% DM)	CT (% QTE)
<i>Alangium chinense</i>	Alangiaceae	YL	Y	25.0	16.4	1.52	25.1	4.8	8.7	11.7	8.8	0.7
<i>Bequartiodendron oblancoellatum</i>	Sapotaceae	YL	N	10.8	55.8	.19	70.9	28.8	15.1	27.0	5.7	61.4
<i>Celtis africana</i>	Ulmaceae	YL	Y	28.9	28.2	1.03	38.8	18.4	10.7	9.7	11.2	2.2
<i>Celtis gomphophylla</i>	Ulmaceae	YL	Y	30.5	22.7	1.34	34.8	8.9	12.1	13.8	9.0	5.8
<i>Croton megalocarpus</i>	Euphorbiaceae	YL	N	26.1	28.1	.93	40.7	13.2	12.6	14.9	6.5	64.7
<i>Funtumia africana</i>	Apocynaceae	YL	N	14.4	35.1	.41	44.6	23.2	9.5	11.9	4.6	70.2
<i>Markhamia lutea</i>	Bignoniaceae	YL	Y	34.5	32.9	1.05	50.1	19.3	17.2	13.6	7.5	2.7
<i>Olea capensis</i>	Oleaceae	YL	N	14.6	30.3	.48	43.7	21.5	13.4	8.7	2.9	0.8
<i>Piper guineense</i>	Piperaceae	YL	Y	28.7	33.4	.86	43.8	20.3	10.4	13.1	14.4	0.8
<i>Prunus africana</i> ^a	Rosaceae	YL	Y	21.4	29.3	.73	38.2	21.2	8.9	8.1	4.5	78.1
<i>Strombosia scheffleri</i>	Oleaceae	YL	N	29.1	37.7	.77	43.2	26.2	5.5	11.4	6.0	2.7
<i>Teclea nobilis</i>	Rutaceae	YL	Y	23.0	23.4	.98	38.4	15.8	15.0	7.6	7.9	1.0
<i>Zanthoxylum gillettii</i>	Rutaceae	YL	Y	27.5	26.1	1.05	43.4	22.9	17.3	3.2	6.6	8.0
<i>Alangium chinense</i>	Alangiaceae	ML	Y	19.3	25.8	.75	35.1	10.4	9.3	15.4	9.7	1.1
<i>Albizia gummifera</i>	Mimosaceae	ML	Y	20.0	57.0	.35	68.5	35.3	11.4	21.7	4.4	7.7
<i>Anigeria altissima</i>	Sapotaceae	ML	N	15.0	45.8	.33	57.9	29.0	12.2	16.8	7.8	123.4
<i>Antiaris toxicaria</i>	Moraceae	ML	N	11.9	41.4	.29	53.9	28.8	12.5	12.6	26.0	143.8
<i>Bequartiodendron oblancoellatum</i>	Sapotaceae	ML	N	11.2	50.9	.22	63.7	27.6	12.7	23.3	8.1	0.9
<i>Celtis africana</i>	Ulmaceae	ML	Y	25.5	33.1	.77	42.7	22.6	9.6	10.5	12.4	1.7
<i>Celtis gomphophylla</i>	Ulmaceae	ML	Y	22.4	33.2	.67	45.5	14.5	12.3	18.7	14.1	0.4

Appendix I.A. Continued

	CP	ADF	CP/	NDF	Lignin	HC	CEL	Ash	CT
<i>Croton megalocarpus</i>	23.0	33.7	.68	45.8	19.4	12.1	14.3	8.5	139.5
<i>Ficus exasperata</i>	17.7	34.1	.52	45.8	12.9	11.8	21.2	15.6	2.4
<i>Funtumia africana</i>	13.0	29.6	.44	39.4	22.8	9.9	6.8	6.0	58.0
<i>Markhamia lutea</i>	23.4	58.8	.40	73.6	26.5	14.8	32.3	6.5	0.7
<i>Morus mesozygia</i>	16.7	30.6	.55	52.3	18.8	21.7	11.7	14.1	79.2
<i>Olea capensis</i>	13.5	33.4	.40	46.6	21.6	13.2	11.8	5.5	1.0
<i>Piper guineense</i>	22.3	39.8	.56	56.6	22.7	16.8	17.1	14.3	0.6
<i>Prunus africana</i> ^d	15.1	32.0	.47	51.1	20.0	19.1	12.0	7.5	53.1
<i>Strombosia scheffleri</i>	19.8	41.2	.48	55.7	27.5	14.5	13.7	6.0	1.9
<i>Strychnos usambarensis</i>	11.9	36.5	.33	53.8	20.1	17.3	16.4	11.9	0.6
<i>Teclea nobilis</i>	16.9	26.3	.64	43.2	10.9	16.9	15.4	12.7	0.5
<i>Triplepisium madagascariense</i>	13.6	40.6	.33	68.2	23.9	27.6	16.7	10.4	199.1
<i>Zanthoxylum gillettii</i>	17.3	43.4	.40	56.5	22.5	13.1	21.0	7.3	6.3
<i>Callistemon</i> sp. ^a	2.7	48.6	.06	73.8	38.9	25.2	9.7	10.5	153.9
<i>Eucalyptus</i> sp. ^b	1.9	51.8	.04	76.5	22.3	24.7	29.6	y8.3	12.0
Soil	0.5	- ^c	- ^c	- ^c	- ³	- ³	- ³	92.0	0.1
NRC-recommended values ^d	8.0	15.0	-	30.0	-	-	-	-	-

^aWe analyzed samples from 2 individuals of the species; mean values are given here.

^bWe analyzed samples from 3 individuals of the species; mean values are given here.

^cFiber values for soil are not reported owing to logistical difficulties inherent in accurately assaying soil fiber content.

^dEstimated ADF and NDF requirements are for colobines; estimated CP requirements are for macaques because no CP recommendations exist for colobines (NRC, 2003).

Appendix I.B. Mineral concentrations of samples from Isecheno study site, Kakamega Forest, Kenya

Plant Species or Item	Family	Plant Part	Eaten?	Na (mg/kg)	Mg (mg/kg)	P (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mn (mg/kg)	Fe (mg/kg)	Co (mg/kg)	Cu (mg/kg)	Zn (mg/kg)
<i>Alangium chinense</i>	Alangiaceae	YL	Y	11.2	989	2270	15,500	4750	10	50	.04	7.1	16
<i>Bequaertiodendron oblancoelatum</i>	Sapotaceae	YL	N	37.5	2954	1480	14,695	4648	202	99	.06	5.2	8
<i>Celtis africana</i>	Ulmaceae	YL	Y	15.4	5595	5980	21,009	26,782	86	230	.08	17.7	42
<i>Celtis gompophylla</i>	Ulmaceae	YL	Y	20.8	1750	3710	19,400	3280	234	68	.06	20.3	42
<i>Croton megalocarpus</i>	Euphorbiaceae	YL	N	12.6	2502	4595	25,338	4705	130	68	.24	12.0	19
<i>Funtumia africana</i>	Apocynaceae	YL	N	11.9	2467	1790	13,243	3442	191	86	.53	6.3	11
<i>Markhamia lutea</i>	Bignoniaceae	YL	Y	12.4	2760	5410	27,500	1890	37	88	.34	29.9	59
<i>Olea capensis</i>	Oleaceae	YL	N	25.0	2530	5400	34,421	8359	28	70	.04	16.7	15
<i>Piper guineense</i>	Piperaceae	YL	Y	18.6	2070	2970	24,300	4640	37	134	.11	24.9	60
<i>Prunus africana</i> ^a	Rosaceae	YL	Y	21.1	2423	4276	30,558	8923	67	146	.09	19.2	34
<i>Strombosia scheffleri</i>	Oleaceae	YL	N	27.7	5290	4270	60,100	7120	82	108	.05	22.7	32
<i>Teclea nobilis</i>	Rutaceae	YL	Y	20.7	3245	3855	19,650	3560	24	106	.34	8.6	38
<i>Zanthoxylum gillettii</i>	Rutaceae	YL	Y	17.9	2340	4770	26,700	3910	81	82	.24	16.7	46
<i>Alangium chinense</i>	Alangiaceae	ML	Y	16.6	2541	2957	23,096	7512	44	96	.50	22.3	34
<i>Albizia gummifera</i>	Mimosaceae	ML	Y	44.3	2916	1370	6411	9156	331	139	.26	5.8	9
<i>Aningeria altissima</i>	Sapotaceae	ML	N	29.3	2636	1240	7422	22,971	162	203	.56	4.9	13
<i>Avitarius toxicaria</i>	Moraceae	ML	N	9.6	1701	905	14,157	12,884	1418	83	.15	9.2	17
<i>Bequaertiodendron oblancoelatum</i>	Sapotaceae	ML	N	32.6	4129	919	15,160	9109	354	141	.14	4.7	10
<i>Celtis africana</i>	Ulmaceae	ML	Y	23.5	3128	2980	28,600	18,333	54	136	.09	9.7	14
<i>Celtis gompophylla</i>	Ulmaceae	ML	Y	18.2	2727	2307	14,341	12,048	609	159	.09	8.9	15

Appendix I.B. Continued

		Na	Mg	P	K	Ca	Mn	Fe	Co	Cu	Zn		
<i>Croton megalocarpus</i>	Euphorbiaceae	ML	N	9.8	4213	2065	20,201	15,698	542	113	.08	6.8	9
<i>Ficus exasperata</i>	Moraceae	ML	Y	9.8	1803	1570	8586	11,980	22	82	.05	5.8	10
<i>Funtumia africana</i>	Apocynaceae	ML	N	20.5	2513	1393	13,093	9784	624	193	.98	4.5	15
<i>Markhamia lutea</i>	Bignoniaceae	ML	Y	15.2	4021	1360	15,546	11,496	331	115	.06	8.2	12
<i>Morus mesozygia</i>	Moraceae	ML	N	34.6	4539	1440	16,230	41,435	515	207	.09	5.3	11
<i>Olea capensis</i>	Oleaceae	ML	Y	21.2	5113	1299	9643	26,640	40	157	.24	5.8	11
<i>Piper guineense</i>	Piperaceae	ML	Y	22.8	6340	2647	41,481	14,612	126	130	.07	14.7	16
<i>Prunus africana</i> ^d	Rosaceae	ML	Y	27.1	3504	2038	17,438	14,236	37	109	.36	5.0	34
<i>Strombosia scheffleri</i>	Oleaceae	ML	Y	22.5	3484	2286	20,120	24,780	130	180	.05	8.6	14
<i>Strychnos usambarensis</i>	Loganiaceae	ML	N	20.0	5082	978	12,276	34,917	129	177	.18	9.9	13
<i>Teclea nobilis</i>	Rutaceae	ML	N	15.5	2460	1400	14,686	31,139	116	213	.08	6.1	20
<i>Trielipsisium madagascariense</i>	Moraceae	ML	Y	10.5	2256	2072	12,078	12,499	265	101	.68	12.5	19
<i>Zanthoxylum gillettii</i>	Rutaceae	ML	Y	12.8	5805	3468	14,277	34,758	127	162	.07	19.3	32
<i>Callistemon</i> sp. ^a	Myrtaceae	Bark	Y	1368.5	1917	150	4259	30,009	86	494	.39	1.7	24
<i>Eucalyptus</i> sp. ^b	Myrtaceae	Bark	Y	409.7	2661	264	5140	25,909	1264	137	.55	3.3	4
Soil	-	Soil	Y	505.0	466	218	812	12,307	1109	96961	11.40	60.5	78
NRC-recommended values ^c	-	-	-	2500.0	400	3300	2400	5500	44	100	-	15.0	13

^aWe analyzed samples from 2 individuals of the species; mean values are given here.

^bWe analyzed samples from 3 individuals of the species; mean values are given here.

^cBecause no estimated mineral requirements are available for colobines, estimated mineral requirements provided here are for macaques and baboons (NRC, 2003).

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