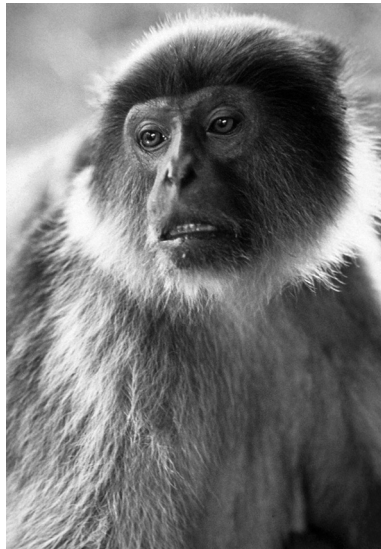


18 *The role of sugar in diet selection in redbtail and red colobus monkeys*

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Introduction

When considering the distribution of nutrients in tropical forests, the traditional view has been that fruits tend to be high quality, provide easily digested forms of carbohydrates but low levels of fiber, usually contain

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few secondary compounds, but also provide little protein. In contrast, leaves offer more protein but have higher levels of fiber, little energy, and are more likely to include undesirable secondary compounds (Waterman, 1984; Milton, 1993; Janson & Chapman, 1999). From an evolutionary perspective, there are two ways to cope with this distribution of nutrients (Ganzhorn, 1989; Milton, 1993). The first is to have a digestive tract that allows the structural polysaccharides of fiber to be metabolized via a fermentative digestion process involving the use of microbes. This is the foraging strategy used by folivorous primates, including *Alouatta* spp., colobines, and some lemurs (Milton, 1998). The second means of coping is the adoption of behavioral strategies that will obtain foods of the highest quality. The tendency for species to be large in size is associated with morphological changes that allow animals to survive on lower-quality plant parts. Larger animals can obtain adequate nourishment by taking in less energy per unit of body mass and thus can meet their energy requirements on lower-quality foods (Milton, 1993; Robbins, 1993; Cork, 1996; McNab, 2002; Remis, 2002). Thus, large-bodied primates tend to be folivorous, consuming a low-quality diet (high fiber/low energy), while many small-bodied primates typically consume a largely frugivorous diet, presumably due to the high energy provided by sugars (Ungar, 1995; Cork, 1996).

However, viewing diet selection in such a dichotomous fashion may curtail studies that examine the importance of particular nutrients (e.g., sugars) and may bias our initial perception of dietary preferences. For example, despite expectations based on body size differences, gorillas and chimpanzees exhibit similar food preferences (Remis, 2002; male gorillas are almost triple the weight of male chimpanzees, Rowe, 1996). Both species prefer foods high in non-starch sugars and low in fiber, and do not avoid foods containing tannins. Furthermore, the diets of different populations of species traditionally classed as frugivores or folivores can be highly variable with respect to the amount of fruit and leaves they consume (Chapman & Chapman, 1990; Norconk & Conklin-Brittain, 2004), suggesting that care must be taken in accepting any generalization with respect to fiber/sugar use and primate digestive strategies.

The objective of this study was to contrast the use of sugars by the redtail monkeys (*Cercopithecus ascanius*) and red colobus (*Piliocolobus tephroceles*) of Kibale National Park, Uganda. Red colobus are anatomically adapted for digesting leaves, while redtail monkeys are not. Therefore, we had three specific goals: to (1) provide a comparable description of the diet of these two species; (2) contrast the sugar content of plant foods each species eats; and (3) evaluate if either of these species is selecting for or against food items based on the food's sugar content.

Redtail monkeys (adult male 4.2 kg, female 3.3 kg) and other guenons are generally considered frugivorous (Conklin-Brittain *et al.*, 1998; Chapman *et al.*, 2002a). Fruit makes up an average of 47% of the diet of redtail monkeys, while leaves and insects each make up an average of 24%. However, there is a great deal of variation among redtail populations, particularly in the consumption of fruit and leaves. For example, the consumption of fruit has been documented as ranging from 13%–61% and the consumption of leaves ranges from 7%–74% across populations (Chapman *et al.*, 2002a). Redtail monkeys do not have specialized stomachs (Lambert, 2002), and as a result, cannot effectively metabolize the structural carbohydrates found in leaves.

Unlike guenons, the colobines, including the red colobus (adult male 10.5 kg, female 7.0 kg), are considered folivorous (Oates, 1994; Milton, 1998). For example, leaves make up an average of 62.4% of the diet of the red colobus (Oates, 1994). Fruit makes up an average of 27.9% of their diet, but the consumption of fruit can be as low as 5.7%. Colobine monkeys use forestomach fermentative digestion to metabolize the structural carbohydrates found in leaves (Bauchop, 1978; Chivers, 1994). It is believed that colobines avoid foods that are high in sugar since these foods can lower forestomach pH, which can result in a decrease in fermentation efficiency or cause acidosis, and in extreme cases can result in death (Kay & Davies, 1994; Milton, 1998). Thus, the ingestion of ripe fruit has been viewed as incompatible with a diet containing significant amounts of leaf material (Kay & Davies, 1994). Furthermore, given the long retention time in colobines (Lambert, 1998), they may not be able to obtain sufficient quantities of other nutrients (e.g., protein) on a diet with large amounts of fruit.

Based on anatomical adaptations, body size differences, and the fact that high levels of sugar can cause acidosis in folivores, the expectation is that redtail monkeys will frequently feed on foods that have high sugar contents, while red colobus monkeys will not. However, the large variation among populations of these species in the amount of time they spend eating fruit suggests that the consumption of simple sugars needs to be carefully evaluated.

Methods

Plant samples were gathered in Kibale National Park (795 km²) in western Uganda (0°13'–0°41'N and 30°19'–30°32'E) near the foothills of the Rwenzori Mountains (Chapman & Chapman, 2002; Chapman *et al.*, 2002b). Mean rainfall in the region is 1741 mm (1990–2003). Rainfall is bimodal with the

two rainy seasons generally occurring from March to May and September to November. The mean daily minimum temperature is 15.5 °C and the mean daily maximum temperature is 23.7 °C.

Information on the diets of red colobus and redbtail monkeys was derived from Chapman *et al.* (2002b) and Rode *et al.* (submitted). For redbtails, six groups were observed from May 2001–May 2002. A preliminary field season conducted from May–July 2000 identified six study groups: three in the unlogged area (Kanyawara K-30 Forestry Compartment) and three in logged areas (Mikana, K-15). Preceding the beginning of data collection in May 2001, the four less habituated groups were followed every month for 4 months to increase habituation. To examine seasonal variation in diet, a single redbtail group (primary group) was followed in each area for 6 days each month. The two other groups in each area (secondary groups) were followed 3 days every other month to determine if diets and behaviors observed in the primary group in each area were characteristic of both logged and unlogged habitats. An average of 418 hours of observation was collected on each of the two primary groups and 134 hours on each of the four secondary groups for a total of 1372 hours.

For red colobus, behavioral observations were made in the Kanyawara area of Kibale between July 1994 and June 1999 for a total of 2425 hours. This area (K-30, elevation = 1500 m) consists of 282 ha that have not been commercially harvested. However, prior to 1970, a few large stems (0.03 to 0.04 trees/ha) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Struhsaker, 1997). In both of these studies, during each half-hour the observer was with the group, five point samples were made of different adults. If the animal was feeding, the species and plant part (e.g., fruit, young leaf, and leaf petiole) were recorded. We made an effort to avoid repeatedly sampling particularly conspicuous animals by moving throughout the group when selecting subjects and by sampling animals that were both in clear view and those that were more hidden. Groups were followed from approximately 700–1700 hours, with scans being conducted every 15 minutes.

Interspecific dietary overlap between redbtail and red colobus monkeys was calculated using the following formula: $D = \sum S_i$ where D = dietary overlap and S_i = percentage of diet shared between two species, evaluated on a plant species and part basis. This formula was first used by Holmes & Pitelka (1968) and has become a standard means of expressing dietary overlap for primates (Struhsaker, 1975; Struhsaker & Oates, 1975; Chapman, 1987; Maisels *et al.*, 1994).

Plant samples were obtained using a tree-pruning pole to cut down a limb from individual trees that had reached mature size (Chapman & Chapman, 2002). Items were processed in the same manner as that used by the study animals, and only those parts selected by the study animals were collected. Samples were dried in the field by sun drying, using a dehydrator that circulated warm air past the samples, or using a light-bulb heated box containing a series of racks (Chapman *et al.*, 2003). Samples were dried thoroughly to avoid mold. We assured that all samples were dried below 50 °C by placing max/min thermometers with the drying samples. When samples were dried in the drying oven, the oven was set at its lowest heat setting (37 °C). Dried samples were stored in sealed plastic bags until they could be transported to the University of Florida for analysis. Dried samples were ground finely enough 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. Due to variations in nutritional parameters over time and between individual trees, four different samples were analyzed for each species, provided that there were a sufficient number of samples.

The primary components of plant carbohydrates that are easily digestible by mammalian enzymes were quantified using a phenol-sulfuric acid assay method that requires extraction (80% ethanol) and digestion with colorimetric analysis of filtrates (Dubois *et al.*, 1956; Hall *et al.*, 1999; Hall, 2001). Standards were made using sucrose and absorbance was read from a spectrometer at 490 nm. This procedure allows an assessment of all simple sugars lumped together monosaccharides- (glucose, fructose), disaccharides- (sucrose, lactose), and oligosaccharides. Oligosaccharides include α -galactosides (raffinose, stachyose) and short chain fructans (fructooligosaccharides). These oligosaccharides are not considered digestible; as a result, the level of sugar in primate diets may be overestimated (Asp, 1993). However, it is not known whether the foregut (ruminal) fermentation of the red colobus monkeys allows oligosaccharides to be digested. The concentration of these oligosaccharides in primate foods is also not known; α -galactosides are generally found in leguminous seeds, while fructans are found in several vegetables, including onions and artichokes. For ease of discussion we refer to all of these compounds as an evaluation of sugar content.

We present a standard description of foraging efforts (per cent of foraging scans devoted to particular items) for each species and contrast species and plant part using t-tests. To determine whether the monkeys select for foods based only on the sugar content we correlate foraging effort and sugar content using data presented in Tables 18.1a and b. We also conduct partial correlation analyses to statistically control for the effects of tree density and size (DBH).

Results

Red colobus spent an average of 2.7% (sd = 4.60) of their monthly foraging time eating fruit; however, this value ranged from 0–31.8% (Figure 18.1). In contrast, redtail monkeys fed on fruit much more often and spent an average of 34.1% (sd = 10.6) of their monthly foraging time eating fruit. Over the course of the observation months, the proportion of the foraging time they devoted to fruit ranged from 20.1%–52.4% (Figure 18.2).

In contrast, red colobus spent an average of 74.3% (mature 8.10, sd = 8.46 / young 66.2, sd = 14.28; also petioles 11.24, flowers 2.22) of their monthly foraging time eating leaves; however, young leaf consumption ranged from 47.8–100%. Redtail monkeys fed on leaves much less often and they spent an average of 14.9% (mature 0.23, sd = 0.74, young 10.66, sd 4.73, petioles 4.65, sd 4.41) of their monthly foraging time eating leaves. Over the course of the observation months, the proportion of their foraging time devoted to leaves ranged from 4.8%–26.9% (Figure 18.2).

The mean sugar content of fruits consumed by red colobus monkeys (13.65%) did not differ significantly from that of fruits consumed by redtail monkeys (16.10%, $t = 0.555$, $p = 0.584$). Fruits consumed by redtail monkeys were expected to be high in sugar; however, the folivorous red colobus monkeys also ate fruits with high levels of sugar (maximum for both species = 38.89%).

The mean sugar content of leaves consumed by red colobus monkeys (7.71%) was not significantly lower than that of leaves consumed by redtail

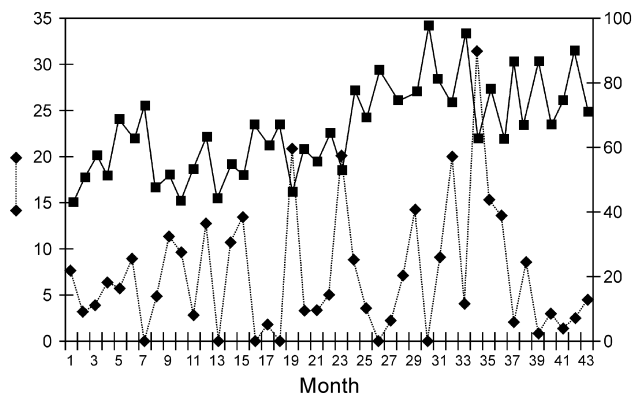


Figure 18.1. Monthly variation in red colobus foraging efforts (percent of feeding scans) devoted to eating young leaves (squares with solid line) and fruits (diamonds with dashed line) in Kibale National Park, Uganda.

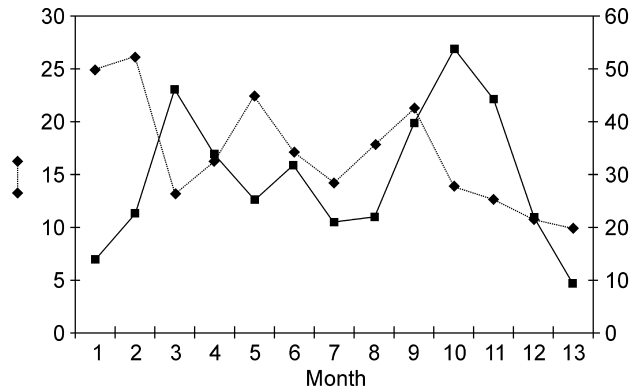


Figure 18.2. Monthly variation in redbtail monkeys foraging efforts (percent of feeding scans) devoted to eating leaves (young, old, and petioles: squares with solid line) and fruits (diamonds with dashed line) in Kibale National Park, Uganda.

monkeys (8.49%, $t = 0.456$, $p = 0.652$). Given the amount of time typically spent eating leaves in a single day, the red colobus ingest substantial amounts of sugars in their daily diet.

For both red colobus ($t = 2.146$, $p = 0.041$) and redbtails ($t = 2.363$, $p = 0.027$) the sugar content of fruits eaten was higher than that of leaves. However, a number of fruit species have sugar contents similar or even lower than the mean sugar level of the leaves that were eaten (Table 18.1). Thus, it is evident that leaves are a potentially significant source of sugars.

There was no evidence to suggest that either species was selecting food items based only on the sugar content (i.e., there was no correlation with foraging effort – percent of the feeding scans – and sugar content). This held true for both leaves and fruits, and regardless of whether we statistically controlled for the effects of tree density or size (the lowest probability in any of these relationships was 0.347).

While in this study we collected the data on foraging and nutritional content of red colobus and redbtail foods at different times, previously we have observed the association patterns and foraging behavior of these two species simultaneously (Chapman & Chapman, 1996; 2000), but did not in these cases collect items for nutritional analysis. The data collected in these previous studies indicates that these species were in association between 23.0 and 52.5% of the time, depending on the year of study, and that their diets overlapped by 25.1%. They were often observed feeding in the same tree on the same food item when in association.

Table 18.1. *The foraging effort (% of all feeding scans) and sugar content (mean and range, if multiple samples could be analyzed) of young leaves (1a) and fruits (1b) consumed by redbtail and red colobus monkeys*
 (a)

Leaves	% Sugar	Range	RC	RT All foods	RT Plant Foods
Apocynaceae					
<i>Funtumia latifolia</i> (YL)	8.98%	7.72–11.10	0.018	0.017	0.030
Bignoniaceae					
<i>Markhamia lutea</i> (YL)	4.83%	2.80–8.80	2.964	0.474	0.826
Ebenaceae					
<i>Diospyros abyssinica</i> (YL)	15.00%	11.50–16.70	0.054	0.090	0.157
Euphorbiaceae					
<i>Macaranga</i> sp. (YL)	6.24%	6.02–6.47	0.029	0	0
Leguminosae					
<i>Albizia grandibracteata</i> (YL)	7.81%	5.40–9.78	5.643	0.011	0.019
Moraceae					
<i>Trilepisium Madagascariense</i> (YL)	7.00%	5.85–9.04	3.036	7.490	13.059
<i>Ficus brachylepsis</i> (YL)	8.37%	8.37	0.643	0	0
<i>Ficus exasperata</i> (YL)	1.73%	0.84–2.93	0.768	0.022	0.038
Olacaceae					
<i>Strombosia scheffleri</i> (YL)	3.32%	1.77–4.79	4.143	0	0
Oleaceae					
<i>Olea welwitschii</i> (YL)	17.39%	15.48–20.67	0.643	0.33	0.575
Rosaceae					
<i>Parinari excelsa</i> (YL)	9.38%	7.60–11.11	4.429	0	0
<i>Prunus africana</i> (YL)	13.31%	10.75–17.36	4.750	0.022	0.038
<i>Prunus africana</i> (ML)	11.15%	9.37–13.13	2.786	0	0
Rubiaceae					
<i>Rothmannia urcelliformis</i> (YL)	3.43%	1.75–4.81	0	2.63	4.586
Sapotaceae					
<i>Pouteria altissima</i> (YL)	6.11%	6.11	0.768	0	0
<i>Chrysophyllum</i> sp. (YL)	5.06%	5.06	0.875	0	0
<i>Mimusops bagshawei</i> (YL)	3.22%	1.33–4.21	1.643	0	0
Sterculiaceae					
<i>Dombeya kirkii</i> (YL)	3.63%	2.51–5.10	4.429	0	0
Ulmaceae					
<i>Celtis africana</i> (YL)	4.03%	2.02–5.27	8.768	0.045	0.078
<i>Celtis durandii</i> (YL)	9.97%	6.89–13.97	10.696	0.338	0.589
Rubiaceae					
<i>Rothmannia urcelliformis</i> (YL)	3.43%	1.75–4.81	0	2.63	4.586

(b)

Fruit	% Sugar	Range	RC	RT All foods	RT Plant Foods
Annonaceae					
<i>Uvariopsis congensis</i> (RF)	5.47%	4.35–6.80	0	4.66	8.125
<i>Uvariopsis congensis</i> (UF)	7.80%	4.19–11.40	0	1.18	2.057

Table 18.1. (cont.)

Fruit	% Sugar	Range	RC	RT All foods	RT Plant Foods
Boraginaceae					
<i>Cordia millenii</i> (RF)	34.65%	34.65	0	0.32	0.558
Ebenaceae					
<i>Diospyros abyssinica</i> (RF)	26.55%	16.24–36.20	Obsv'd	0.520	0.907
<i>Diospyros abyssinica</i> (UF)	13.35%	9.19–19.20	Obsv'd	0.63	1.098
Euphorbiaceae					
<i>Bridelia micrantha</i> (RF)	17.17%	17.17	Obsv'd	0.090	0.157
Leguminosae					
<i>Millettia dura</i> (RF)	6.66%	6.66	Obsv'd	0	0
Moraceae					
<i>Ficus brachylepsis</i> (RF)	12.21%	11.31–13.10	0.089	1.55	2.703
<i>Ficus natalensis</i> (RF)	7.80%	6.20–9.40	Obsv'd	0	0
Oliniaceae					
<i>Psidium guajava</i> (RF)	3.37%	2.49–4.24	Obsv'd	Obsv'd	Obsv'd
Rosaceae					
<i>Prunus africana</i> (RF)	38.89%	38.89	0.036	0.650	1.133
Rubiaceae					
<i>Rothmannia urcelliformis</i> (RF)	33.81%	33.81	0	0.022	0.038
<i>Vangueria apiculata</i> (RF)	4.71%	4.71	0	0.135	0.235
Sapotaceae					
<i>Mimusops bagshawei</i> (RF)	20.85%	15.10–28.50	0	1.250	2.179
Ulmaceae					
<i>Celtis africana</i> (UF)	1.34%	1.30–1.38	0.018	1.420	2.476
<i>Celtis durandii</i> (RF)	10.00%	2.75–12.80	1.204	1.420	2.476
<i>Celtis durandii</i> (UF)	12.90%	4.95–22.60	3.125	1.860	3.243
<i>Chaetacme aristata</i> (RF)	22.72%	22.72	0	0.022	0.038

For redtail monkeys, foraging effort is presented with respect to all foods (i.e., including insects) and all plant foods (i.e., excluding insects). Obsv'd indicates that animals have been seen eating that species/part, but it was not recorded in the scan data; this includes instances when neighboring groups ate this species/part (abbreviations RC = red colobus, RT = redtails, UF = unripe fruit, RF = ripe fruit, ML = mature leaves, YL = young leaves).

Discussion

Although the sugar content of leaves is less than that of fruits, it is evident that leaves have the potential to be an important source of sugars. As a result, some leaves can be considered high-quality food since they are a source of protein (Chapman & Chapman, 2002), minerals (Rode *et al.*, 2003), and sugars (this study). Thus, since redtail monkeys are frugivorous and small-bodied, it is not surprising that their diet includes leaves whose high sugar

content helps meet their heavy metabolic demands. By consuming leaves, redbtail monkeys can obtain protein and minerals that they do not typically get from fruits, while still consuming a significant quantity of sugar. The high sugar content of leaves may make them a more valuable food source for frugivores than has typically been thought. Additionally, the availability of leaves with high sugar content may be important as fall-back foods for frugivorous primates during periods of fruit scarcity.

Interpreting the dietary strategy of the folivorous red colobus with respect to sugars is more difficult. Some of the leaves they feed on have considerable amounts of sugar and thus are likely a significant source of energy. There is evidence that this is also the case for other folivores. For example, Koenig *et al.* (1998) documented that two out of the three key resources for a population of Hanuman langurs (*Presbytis entellus*) contained significantly higher levels of sugar than other foods. Even the mature and young leaves of the most preferred food plant contained over 9.7% sugar on a dry matter basis. On average, the red colobus of Kibale did not feed on fruits to any great extent. However, during some months fruits did constitute a large proportion of their diet. For example, in one month the study group spent 21.2% of their foraging time eating fruit. During this month the most frequently eaten fruit was *Celtis durandii*, which has a relatively high sugar content (10%). Koenig *et al.* (1998) similarly documented that Hanuman langurs can feed extensively on fruits that contain high sugar levels (e.g., *Dillenia pentagyna*, 27.6% sugar on a dry matter basis). Other small-bodied animals with fermentative digestion systems have also been reported to consume foods high in sugars. For example, the fruits eaten by duiker (*Cephalophus* spp.) vary in their sugar content from 0.2%–15.7% (there are no data regarding the sugar content of the leaves consumed by duikers, nor comparable information on their efforts to forage for these fruits; Dierenfeld *et al.*, 2002).

Studies that have examined the effects of sugars on foregut fermentation and apparent nutrient supply in dairy cattle offer some insights into the use of sugars by colobines. Sudden introduction of sucrose and other sugars have been used to induce low ruminal pH (Krehbiel *et al.*, 1995); however, this detrimental effect was not seen in animals used to consuming sugars (Broderick *et al.*, 2002). Reduced microbial fermentation of fiber that is not related to low pH has been noted with sugar consumption by cattle when nitrogen degradable by microbes was limiting (Heldt *et al.*, 1999) or was apparently due to proteinaceous inhibitors produced by glucose utilizing microbes in vitro (Piwonka & Firkins, 1996). In contrast, improvement in fiber digestion has been reported with sugar consumption by cattle when microbially degradable protein was not limiting (Heldt *et al.*, 1999). In terms of the net effect of sugars on nutrient supply from fermentation, reduction in nutrient yield

from fiber digestion may be balanced by nutrients from fermented sugars, whereas an increase in fiber digestion could increase the overall supply. Additionally, some portion of the sugars may be stored as glycogen by microbes (Thomas, 1960), offering a source of digestible glucose if it passes to the small intestine.

In cattle used to consuming higher dietary concentrations of sugar (10%–13% of dry matter), sugars supported high levels of milk production relative to starch, suggesting that the nutrient supply was not compromised and may have been enhanced (Broderick *et al.*, 2002). However, in both studies, efficiency of nitrogen utilization was decreased for animals on the specially prepared sugar diets. That may be a function of the lower yield of microbial protein from sucrose than from starch (Hall & Herejk, 2001; Sannes *et al.*, 2002), but may also be related to decreases in ammonia and branch chain volatile fatty acid concentrations (Sannes *et al.*, 2002) – components that are essential to protein production by fiber digesting bacteria. Some studies have reported either decreased milk production in dairy cattle (Sannes *et al.*, 2002) or no change (McCormick *et al.*, 2001) with sugar supplementation. In the latter case, the ryegrass forage that formed the basal diet contained approximately 14%–17% nonfiber carbohydrates, of which more than half would likely have been classified as sugars. These studies suggest that the effect of adding a food item that is high in sugars to the diet will depend on the level of protein and sugar in the basal diet and the animal's previous exposure to the diet. Given the importance of protein to folivorous primates (Ganzhorn, 1992; Chapman & Chapman, 2002; Chapman *et al.*, 2004), it seems likely that colobus will only eat foods high in sugars when protein acquisition will not be compromised. In the month that the red colobus fed the most on fruit (21.2% of feeding scans), they also fed extensively on the young leaves of *Celtis durandii*, which has the highest protein to fiber ratio of any plant part eaten; in fact it is 35% higher than the protein/fiber content of the next species/part. Norconk & Conklin-Brittain (2004) found that lipids were as important in a similar fashion for white-faced saki (*Pithecia pithecia*) as proteins are for colobines: namely that the saki select foods high in lipids even when lipids are negatively correlated with sugars and positively correlated with lignin.

Several studies have shown that the composition of sugars can affect both food selection and fermentation processes. A study of frugivorous bats showed that even in a mammal with a non-fermenting digestive system, thresholds for sugar intake existed and differed with respect to the types of sugars ingested (Herrera *et al.*, 2000). Additionally, the composition of volatile fatty acids in the rumen of sheep differed depending on what type of sugar was added to the diet (Chamberlain *et al.*, 1993). Thus, it is possible

that red colobus and redbelt monkeys consume fruits and leaves that differ in specific types of sugars. For example, in sheep, sucrose had less of a negative effect on microbial fermentation than did fructose (Chamberlain *et al.*, 1993). Similar effects could occur in colobines, which would be an interesting area for future studies.

It is apparent that we do not yet fully understand the fermentative digestion system. This study presents data that contradict the historically accepted idea that high levels of sugar cannot be consumed by primates with fermentative digestion systems, and this challenge of the historical view is supported by investigations of other non-primates with similar digestive systems. As opposed to being harmful, sugars may simply alter the digestion efficiency of other nutrients, particularly protein and fiber. It is possible that this decrease in efficiency is a reasonable exchange for the benefit of consuming sugars, but only under certain conditions (e.g., when protein intake is high). Clearly, more research is needed to understand the physiological limitations of fermentative digestive systems. It seems reasonable to hypothesize that there is a threshold ratio of sugar to fiber for colobus at which diet digestibility declines, and that compared with colobus, redbelts could tolerate a much higher sugar to fiber ratio. Furthermore, the effect of sugar on digestibility may be dependent on sugar type. To address these questions, feeding trials are desperately needed and would be a fascinating direction for future research.

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