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How do differences in species and part consumption affect diet nutrient concentrations? A test with red colobus monkeys in Kibale National Park, Uganda

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Abstract

Within a primate species, diet can be highly variable in composition, even at small spatial scales within the same forest, or temporally, suggesting that primates use different plant species and parts to meet similar nutritional needs. To test whether such differences in the plant species and parts that primates eat affects the nutrient concentrations that they obtain, we observed feeding of seven groups of red colobus monkeys (*Procolobus rufomitratus*) residing in Kibale National Park, Uganda. The different groups consumed mostly young leaves from many of the same plant species, but spent different amounts of time feeding on them. As protein and fibre are suggested to be important determinants of colobine food choice and abundance, we analysed multiple samples of 47 food species for protein and fibre. Despite the differences in the plant species and parts eaten, the protein and fibre concentrations for the seven red colobus groups were similar. Our results suggest that colobus monkeys eating diets with differing amounts of species and parts may ultimately receive similar concentrations of nutrients.

Key words: colobus, dietary variability, Kibale, nutritional ecology, plant chemistry, protein

Résumé

Au sein d'une même espèce de primate, la composition du régime alimentaire peut être très variable, même à petite échelle spatiale, dans la même forêt, ou temporelle, ce qui laisse entendre que les primates utilisent des espèces et des parties de plantes différentes pour satisfaire des besoins nutritionnels semblables. Pour vérifier si de telles différences d'espèces végétales et de parties de plantes consommées par les primates affectent les concentrations de nutriments obtenues, nous avons observé l'alimentation de sept groupes de colobes roux (*Procolobus rufomitratus*) résidant dans le Parc National de Kibale, en Ouganda. Les différents groupes consommaient principalement de jeunes feuilles de nombreuses plantes des mêmes espèces, mais ils passaient une durée différente à s'en nourrir. Comme les protéines et les fibres sont censées être des déterminants importants dans le choix et l'abondance de la nourriture des colobes, nous avons analysé le contenu en protéines et en fibres de multiples échantillons de 47 espèces consommées. Malgré les différences d'espèces et de parties de plantes consommées, les concentrations de protéines et de fibres étaient semblables pour les sept groupes de colobes rouges. Nos résultats suggèrent que les régimes alimentaires des colobes, qui diffèrent quant au nombre d'espèces et aux parties de plantes qui les composent, pourraient tout compte fait contenir des concentrations de nutriments semblables.

Introduction

There has been a developing awareness of the great diversity in primate diets on various spatial and temporal scales (Davies, Bennett & Waterman, 1988; Wrangham, Conklin-Brittain & Hunt, 1998; Chapman & Chapman, 1999; Yamashita, 2002; Ganas *et al.*, 2004; Russo *et al.*, 2005; Wieczkowski & Kinnaird, 2008). Previous studies have demonstrated sympatric species that are largely

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considered to have similar diets in terms of broad feeding categories (i.e., frugivory, folivory) in fact consume differing amounts of shared plant species along with using different species and parts that other primates do not eat (Davies, Bennett & Waterman, 1988; Wrangham, Conklin-Brittain & Hunt, 1998; Davies, Oates & Dasilva, 1999; Dierenfeld & McCann, 1999; Yamashita, 2002; Zhou *et al.*, 2009). Differences in diet composition as defined by plant species and parts consumed have also been found in populations of the same species (Codron *et al.*, 2006; Twinomugisha *et al.*, 2006; Rothman *et al.*, 2007; Zhou *et al.*, 2009) including populations that reside in the same geographic area or even have neighbouring or overlapping home ranges (Chapman & Chapman, 1999, 2002; Chapman, Chapman & Gillespie, 2002; Ganas *et al.*, 2004; Grassi, 2006; Harris & Chapman, 2007; Potts, Watts & Wrangham, 2011). However, differences in the quality and distribution of plants may have a dramatic effect on group size and population abundance; for example, Fimbel *et al.* (2001) suggest that large group sizes in black-and-white colobus (*Colobus angolensis*) in Rwanda compared with other *Colobus* spp. are a result of the high quality of mature leaves in comparison with other African forests because food competition in Rwanda is relaxed.

Nutritional analyses have revealed sympatric species with dissimilar use of plant species and parts can ultimately have diets with similar nutritional concentrations (Davies, Bennett & Waterman, 1988; Conklin-Brittain, Wrangham & Hunt, 1998; Dierenfeld & McCann, 1999). For example, after a previous conclusion that groups of chimpanzees and three cercopithecine species in Kibale had differing diet compositions, it was also found that the groups actually consumed similar diets in terms of fibre content (Conklin-Brittain, Wrangham & Hunt, 1998). Comparisons between groups of the same species suggest conspecifics in different groups use combinations of different plant species and parts to acquire similar nutrient concentrations in their diets. The diets of the golden monkey (*Cercopithecus mitis kandti*) and blue monkey (*Cercopithecus mitis stuhlmanni*) subspecies residing in two parks were compared and shown to be compositionally very different over time, between groups and between subspecies. However, the overall nutritional components of the diets were similar in terms of crude protein (CP), acid detergent fibre (ADF), lipids and sugars (Twinomugisha *et al.*, 2006). Similar results were obtained in a study of mountain gorillas (*Gorilla beringei*) living in different habitats, for two groups that consumed different plant species had diets with similar nutritional concentrations of CP, neutral detergent fibre (NDF) and nonstructural carbohydrates (Rothman *et al.*, 2007). Conversely, general environmental conditions may lead to differences in plant quality, which impacts available nutrients and potentially physiological parameters (Fimbel *et al.*, 2001).

While these previous studies analysed diet nutritional content for groups of the same species that reside in different locations, there is little information on how compositional diversity relates to nutritional intake for conspecifics that share the same forest. We address this question by using long-term dietary data from seven groups of red colobus monkeys (*Procolobus rufomitratus*) that reside in Kibale National Park, Uganda. Red colobus monkeys are folivores that subsist on a leaf diet of varying quality in terms of protein-to-fibre ratios and prefer foods with high protein and low ADF content (Chapman & Chapman, 2002). The red colobus groups in Kibale are well-studied, and plant species and parts fed on by groups across short distances or even within the same area are quite varied (Chapman & Chapman, 1999, 2002; Chapman, Chapman & Gillespie, 2002; Chapman & Pavelka, 2005).

To assess the nutrients in plants eaten by different groups of red colobus, we analysed plant species and parts consumed for protein and fibre content. The concentrations of these two nutritional components have been shown to reliability generate meaningful patterns for primate feeding behaviour and population density (Milton, 1979; Davies, Bennett & Waterman, 1988; Barton & Whiten, 1994; Davies, Oates & Dasilva, 1999; Dierenfeld & McCann, 1999; Chapman & Chapman, 2002) including for some of the same groups of red colobus in Kibale that are included in this investigation (Chapman & Chapman, 2002). We therefore hypothesized that the variation in diet composition observed in sympatric red colobus groups will ultimately translate to a similar nutritional profile across groups in terms of fibre and protein concentrations from the different combinations of plant species and parts consumed.

Methods

Study site

Kibale National Park (795 km²) (Fig. 1) is located east of the foothills of the Ruwenzori Mountains in western Uganda (0°13′–0°41′N and 30°19′–30°32′E). The mean daily minimum temperature is 15.5°C, and the mean maximum daily temperature is 23.7°C with little

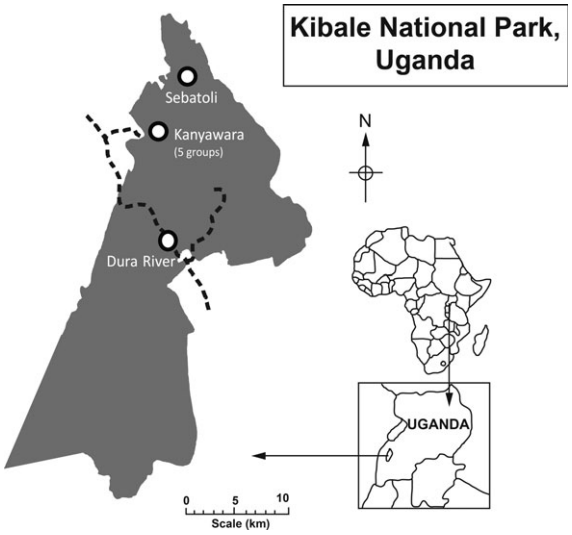

Fig 1 The locations of Uganda, Kibale National Park, and the Kanyawara, Sebatoli and Dura park sections where the red colobus groups in this study reside

seasonal variation. The mean annual rainfall around the park is 1701 mm (1990–2009), and rainfall is typically bimodal with two rainy seasons from March to May and September to November (Chapman *et al.*, 2012).

The red colobus groups studied live in different parts of Kibale, which are all composed of different tree species and degrees of human modification. Five of the seven red colobus groups live in the Kanyawara section, which is in the northern end of the park and has a range of heavily logged forest to mostly undisturbed forest (Chapman *et al.*, 2010). Two red colobus groups are further specified to live in the forestry components of K30 and K15 within Kanyawara. The K15 section is considered to be heavily logged, for it is estimated that this section had 50% of canopy trees destroyed from incidental damage and logging, whereas the K30 forestry compartment has not been commercially logged and the forest has experienced only very low levels of extraction by pit sawing (Chapman, Chapman & Gillespie, 2002) (Fig. 1).

Two additional red colobus groups live in sections that are close to Kanyawara. The northernmost section of the park and thus north of Kanyawara is Sebatoli, which has a canopy that mainly consists of timber trees such as *Parinari excelsa*, *Carapa grandiflora*, *Olea capensis subspecies welwitschii*, *Pouteria altissima*, *Strombosia scheffleri* and *Newtonia bucchananiii* (Chapman, Chapman & Gillespie, 2002). The Sebatoli section was commercially logged in the late 1960s and it is surmised that the section was logged in a similar fashion as the K15 section, which was harvested on average by 21 m^3 ha^{-1} or about 7.4 stems ha^{-1} (Chapman, Chapman & Gillespie, 2002). The final red colobus group lives in the Dura section of Kibale, which is south of Kanyawara. Unlike Kanyawara and Sebatoli, Dura is not considered a *Parinari* forest because the timber species such as *P. excelsa* observed in the northern half of Kibale are rare in Dura. Instead, Dura is mostly composed of *Pterygota mildbraedii*, *Cola gigantea*, *Piptadeniastrum africanum* and *Chrysophyllum albidum* in the canopy, and furthermore, the section has not been greatly impacted by logging or extraction (Chapman, Chapman & Gillespie, 2002).

Behavioural observations and plant collection

CAC and field assistants observed seven habituated groups of red colobus monkeys using the observation techniques described in Chapman, Chapman & Gillespie (2002). Briefly summarized, during each half-hour while observing a particular group, observers point-sampled the first five individuals observed. If the animal was feeding, then the observers recorded the plant species and part consumed. The categories for possible plant parts were; ripe fruit, unripe fruit, flower, young leaf, mature leaf, leaf petiole, leaf bud, bark, dead wood, pine needles, seeds, seed pods, fruit (unknown ripeness), pith and soil. Feeding was noted as discrete behavioural bouts; however, feeding rates within these bouts were not determined. For the purposes of analysing the potential differences in diet between the seven groups, it was assumed that there were equivalent feeding rates among individuals within and across the seven groups.

The seven groups were observed at different times with a varying amount of observations. The Sebatoli group (N = 18 individuals) was observed from August 1996 through April 1997 for 104 h with 387 feeding records, and the Dura group (N = 20) was observed from August 1995 through April 1997 for 88 h with 192 feeding records. For the five groups in Kanyawara, observations of the group residing in the K30 section of the forest, named 'Kanyawara 1' (K.1) (N = 40) in this report, were made from July 1994 through April 1997 for 1110 h with 3775 feeding records and the group residing in the K15 section of forest, named 'Kanyawara 2' (K.2) (N = 30), were made from August 1996 through May 1997 for 114 h with 337 feeding records. The Kanyawara 3 (K.3) (N = 48) and

Kanyawara 4 (K.4) (N = 24) groups were observed from August 1998 through June 1999 for 343 and 369 h, respectively, with 3264 feeding records. Finally, observations of the Kanyawara 5 (K.5) group (N = 80) were made from July 2006 through June 2007 for 528 h with 2400 feeding records.

We collected samples of plant species and parts consumed by the red colobus, and we made every effort to collect from the same tree and part that at least one group of the monkeys fed on. Plants were collected from 1999 through 2009 when the colobus monkeys were observed feeding on them. To account for intraspecific variability, we sampled 1–10 individuals, depending on the sample availability (Chapman *et al.*, 2003). Most samples were acquired by cutting branches with a tree pruner with about 0.5–1 kg of each part gathered (Rode *et al.*, 2003; Rothman *et al.*, 2007). We then dried the samples in a Nesco Plant dehydrator at 40°C, milled the samples with a Wiley mill with a 1-mm stainless steel screen and then stored them in a plastic bag until we transported the samples to Hunter College for nutritional analysis. On the basis of the factors such as plant species and part availability, we did not necessarily collect all the plant samples at the same time as we conducted behavioural observations; however, each species was sampled from more than one individual plant when possible, in different seasons and environments, which should provide a good representation of its nutrients.

Nutritional and statistical analyses

We determined the monthly percentages of foraging time spent consuming plant species/part combinations by each of the seven red colobus groups. The monthly percentages for each plant species/part combination were then used to assess annual mean percentage of foraging time for each species/part and red colobus group. To compare the diet compositions of the seven groups, we modified the standard approach typically used for interspecies dietary overlap. We began by measuring intergroup dietary overlap using the following formula:

$$D = \sum S_i$$

where D is dietary overlap and S_i is the percentage of diet shard between two groups, which is measured using common plant species/parts combinations. The interspecific dietary variability formula was originally used by Holmes & Pitelka (1968) and has been since used to determine dietary overlap in primate diets (Struhsaker, 1975; Chapman, Chapman & Gillespie, 2002; Chapman & Pavelka, 2005). We used this formula for all possible pair combinations between the seven groups and then determined the average dietary overlap. The diet compositions are presented in Table 1.

We analysed the CP, NDF, ADF and acid detergent lignin (ADL) content of up to ten samples per species, of the 47 different species and plant parts that contributed to the total diet for each of the seven groups (Table 2) to account for known intraspecific variability (Chapman *et al.*, 2003). Protein and fibre concentrations were determined on a 105°C dry matter (DM) basis (Rothman, Chapman, & Van Soest, 2012).

We analysed the samples for fibre content by measuring NDF (with α-amylase) and ADF (Van Soest, Robertson & Lewis, 1991) using filter bags in an A200 fibre analyzer (ANKOM, Macedon, NY, U.S.A.), and we then analysed the samples for ADL (Goering & Van Soest, 1970). We also analysed the samples using a Leco TruSpec (Leco, St. Joseph, MI, U.S.A.) via combustion (AOAC, 1990) to determine total nitrogen (N). We calculated CP by multiplying N by the standard of 6.25 (Maynard & Loosli, 1969). A subset of samples (n = 29) was analysed via near infrared reflectance spectroscopy using a Foss XDS spectrometer (Laurel, MD, U.S.A.) (Rothman *et al.*, 2009).

Once we measured the fibre and protein concentrations of the various plant species, we calculated the percentages of fibre and protein in the diet for each month that each group was observed. The percentage of each plant part combination included in each group's diet was multipled by the plant's protein or fibre concentration to determine its content in the group's diet. The data were determined to not be normal with unequal variance. Thus, an independent-samples Kruskal–Wallis test was used with $\alpha = 0.05$ (SPSS v.19; IBM, Armonk, NY, USA) to test whether the differences observed between groups in terms of diet protein (CP) and fibre content (NDF, ADF and ADL) were significant.

Results

Diet composition

The average percentage of intergroup dietary overlap was 52.7 ± 15.6%. Across the seven groups, roughly half of

Table 1 Mean percentage of foraging time spent consuming plant species/parts combinations by each of the seven red colobus groups. The species/parts are arranged from the overall most frequently consumed plants through the least consumed plants

Species (part)	Sebatoli	Dura	K1	K2	K3	K4	K5
Celtis durandii (YL)	3.03 ± 7.4	13.85 ± 16.4	7.44 ± 8.3	0 ± 0	17.02 ± 9.4	5.85 ± 7.1	3.89 ± 5.2
Celtis africana (YL)	4.80 ± 8.6	2.29 ± 5.4	8.26 ± 6.3	15.46 ± 17.7	7.24 ± 2.4	6.67 ± 5.6	6.88 ± 7.9
Albizzia grandbracteata (YL)	1.23 ± 2.8	5.08 ± 11.7	7.57 ± 7.2	8.43 ± 12.8	0.97 ± 2.6	2.76 ± 4.3	7.83 ± 8.6
Funtumia africana (YL)	2.78 ± 3.1	6.58 ± 9.5	3.47 ± 3.9	6.24 ± 8.1	3.21 ± 2.2	4.81 ± 4.5	3.07 ± 1.6
Trilepsium madagascariense (YL)	4.36 ± 14.5	3.13 ± 7.9	1.32 ± 2.9	0 ± 0	7.82 ± 3.0	4.25 ± 4.6	7.71 ± 4.7
Pouteria altissima (YL)	7.62 ± 11.8	9.15 ± 24.1	0.54 ± 1.4	7.46 ± 5.4	0.59 ± 1.0	0 ± 0	0.12 ± 0.3
Prunus africana (YL)	4.04 ± 6.8	0 ± 0	5.13 ± 5.0	0.29 ± 0.9	1.70 ± 4.0	4.31 ± 6.8	8.39 ± 8.0
Parinari excelsa (YL)	3.21 ± 7.5	0 ± 0	2.80 ± 4.1	0 ± 0	6.20 ± 4.2	8.00 ± 9.5	2.96 ± 2.9
C. durandii (*UF*)	1.26 ± 3.2	3.72 ± 5.6	4.44 ± 6.1	9.10 ± 10.9	2.04 ± 3.6	1.02 ± 2.8	1.06 ± 2.5
Strombosia scheffleri (YL)	5.17 ± 7.0	0 ± 0	4.28 ± 6.7	0.29 ± 0.9	5.25 ± 4.6	4.64 ± 6.1	1.95 ± 2.4
Dombeya kirkii (YL)	0 ± 0	0 ± 0	4.55 ± 7.3	2.70 ± 7.1	8.68 ± 7.7	2.51 ± 3.8	2.50 ± 2.4
Markhamia lutea (LP)	4.58 ± 11.1	0 ± 0	5.40 ± 4.1	3.75 ± 4.6	4.95 ± 4.8	1.23 ± 1.9	0.78 ± 0.7
S. scheffleri (LP)	3.78 ± 6.2	3.75 ± 6.3	4.63 ± 4.1	0.29 ± 0.9	2.77 ± 2.5	1.42 ± 1.9	3.62 ± 4.6
Newtonia bucchananii (YL)	7.12 ± 8.9	0 ± 0	0 ± 0	0 ± 0	0.44 ± 0.6	0.79 ± 1.2	8.77 ± 8.1
M. lutea (YL)	0 ± 0	1.67 ± 5.3	2.41 ± 2.7	3.60 ± 4.2	3.82 ± 2.3	2.14 ± 3.3	0.80 ± 1.5
P. africana (ML)	0 ± 0	0 ± 0	2.52 ± 5.0	0 ± 0	2.27 ± 5.9	7.32 ± 10.0	1.71 ± 2.1
Chrysophyllum sp. (YL)	1.90 ± 4.6	3.50 ± 8.2	1.25 ± 3.5	2.60 ± 5.2	1.21 ± 2.3	1.94 ± 2.0	0.57 ± 0.6
Millettia dura (YL)	2.53 ± 8.4	0 ± 0	3.30 ± 5.8	1.82 ± 3.7	1.09 ± 1.1	0.62 ± 0.8	1.76 ± 3.0
F. africana (RF)	0 ± 0	3.29 ± 6.7	0.09 ± 0.5	0.24 ± 0.7	4.05 ± 5.6	2.59 ± 5.6	0.30 ± 0.9
Ficus sansibarica (YL)	5.05 ± 13.1	0 ± 0	1.83 ± 5.2	0 ± 0	0.34 ± 0.9	1.16 ± 2.7	1.30 ± 1.4
Eucalyptus grandis (*bark*)	0 ± 0	0 ± 0	1.93 ± 4.0	0 ± 0	0 ± 0	3.43 ± 9.0	2.15 ± 2.2
N. bucchananii (ML)	6.70 ± 21.5	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.2	0 ± 0
Zanthoxylum gilletii (YL)	0 ± 0	0 ± 0	03 ± 0.2	6.06 ± 18.2	0 ± 0	0.25 ± 0.8	0.22 ± 0.6
Olea capensis subspecies *welwitschii* (YL)	0 ± 0	0 ± 0	0.25 ± 0.9	3.05 ± 6.0	1.82 ± 3.3	0.92 ± 1.6	0.22 ± 0.4
Macaranga schweinfurthii (YL)	0 ± 0	0 ± 0	1.02 ± 2.8	0 ± 0	0.46 ± 1.0	2.07 ± 3.1	1.85 ± 4.2
Ficus exasperata (YL)	2.61 ± 4.8	0 ± 0	0.10 ± 0.5	0 ± 0	1.93 ± 1.5	0.55 ± 1.4	0.04 ± 0.1
Mimusops bagshawei (YL)	0.65 ± 2.2	0 ± 0	0.85 ± 2.8	0 ± 0	0.24 ± 0.4	1.75 ± 3.8	0.83 ± 1.2
Cola gigantea (YL)	0 ± 0	3.63 ± 9.0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Trema orientalis (YL)	0 ± 0	2.11 ± 6.7	0 ± 0	0 ± 0	0.14 ± 03	0 ± 0	1.10 ± 1.6
Bridelia micrantha (YL)	0 ± 0	0 ± 0	1.70 ± 4.1	0 ± 0	0 ± 0	0.81 ± 1.7	0.71 ± 2.5
Diospyros abyssinica (YL)	0.33 ± 1.1	0 ± 0	0.08 ± 0.5	2.70 ± 6.6	0 ± 0	0.10 ± 0.3	0 ± 0
Croton sp. (YL)	3.11 ± 5.5	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Blighia unijugata (YL)	0.33 ± 1.1	0 ± 0	0 ± 0	2.42 ± 5.0	0.06 ± 0.2	0.09 ± 0.3	0.08 ± 0.2
A. grandbracteata (ML)	0 ± 0	2.00 ± 6.3	0.31 ± 0.6	0 ± 0	0 ± 0	0.12 ± 0.3	0.14 ± 0.5
O. capensis subspecies *welwitschii* (LP)	0 ± 0	0 ± 0	0.17 ± 0.6	0 ± 0	0 ± 0	1.05 ± 1.6	1.28 ± 2.8
Teclea nobilis (YL)	0 ± 0	0 ± 0	0.57 ± 2.0	0.95 ± 28	0.73 ± 1.6	0.07 ± 0.2	0.16 ± 0.3
C. durandii (ML)	0 ± 0	0 ± 0	1.43 ± 4.4	0 ± 0	0 ± 0	0.75 ± 1.9	0.04 ± 01
Sapium ellipticum (YL)	0.81 ± 1.9	0 ± 0	0.17 ± 0.9	0 ± 0	0 ± 0	0.96 ± 1.8	0.23 ± 0.8
Pancovia sp. (YL)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.50 ± 4.7	0.36 ± 1.1	0.30 ± 0.8
Ficus natalensis (YL)	1.23 ± 4.1	0 ± 0	0.29 ± 0.9	0 ± 0	0.20 ± 0.5	0 ± 0	0.40 ± 0.9
Urera sp. (YL)	1.23 ± 4.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.43 ± 1.0	0.17 ± 0.4
C. gigantea (ML)	0 ± 0	1.67 ± 5.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0

Table 1 *(continued)*

Species (part)	Sebatoli	Dura	K1	K2	K3	K4	K5
P. excelsa (ML)	1.14 ± 2.6	0 ± 0	0.32 ± 0.7	0 ± 0	0.06 ± 0.2	0.10 ± 0.3	0 ± 0
Celtis mildbraedii (YL)	1.40 ± 2.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Balanites wilsoniana (YL)	0 ± 0	0 ± 0	0.10 ± 0.6	0 ± 0	0 ± 0	1.21 ± 3.0	0 ± 0
M. lutea (ML)	0 ± 0	0 ± 0	0.83 ± 1.4	0 ± 0	0 ± 0	0.24 ± 0.8	0 ± 0
C. durandii (FL)	0 ± 0	0.31 ± 1.0	0.10 ± 0.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Percentage of diet represented	81.99	65.72	81.47	84.03	88.83	79.34	75.87

YL, young leaves, UF, unripe fruit, LP, leaf petiole, ML, mature leaf, RF, ripe fruit, FL, flower.

the plant species/parts combinations consumed were the same depending on the groups being compared. For the seven red colobus groups, young leaves comprised the vast majority of the diets for each group (Table 1). Across groups, *Celtis durandii* and *Celtis africana* species were more frequently consumed than any other species (Table 1). *Celtis durandii* and *C. africana* were in the top five species consumed for the seven groups with the exception of the Sebatoli group. In most cases, it was the young leaves being consumed although *C. durandii* ripe fruit was more frequently consumed than *C. durandii* young leaves in the K.2 and K.5 groups (Table 1).

Aside from these shared species and parts, the percentage of shared foods and the combination of species and plant parts consumed by each group was otherwise different. For example, the second most frequent plant part consumed was not consistent across the seven groups, for it was mature leaves for four of the groups but the other groups consumed bark, unripe and ripe fruit more than mature leaves (Table 1). Some of the groups also ate plant parts that other groups did not consume at all, such as ripe fruit, unripe fruit and bark. It is also evident that there is overall variation in the species each group consumed, as well as the amount of each species consumed. There are many examples of species such as *Dombeya kirkii*, *Albizia grandibracteata, Pouteria altissima, Trilepsium madagascariense* and *Newtonia bucchananii* in which some groups devoted much of their foraging time to consuming these species yet other groups were rarely if ever observed foraging on them.

Diet nutritional content

Although the plant species composition between groups noticeably differed, the fibre (NDF, ADF and ADL) and protein content (CP) of the diets were similar across groups (Table 3). Concentrations of dietary CP, NDF, ADF and ADL were similar (Kruskal–Wallis test; df = 6, $P = 0.186$ – NDF; $P = 0.338$ – ADF; $P = 0.499$ – ADL; $P = 0.060$ – CP). While the diet nutritional content was overall similar among groups, the between-group differences were greater for protein concentrations than fibre.

Discussion

Red colobus groups residing in Kibale consumed diets that consisted of differing combinations of plant species and parts, yet they ultimately received similar concentrations of nutrients. Nutrition has a direct influence on important components for reproductive success such as age when a female becomes sexually mature, birth rates and infant survival, so monkeys should strive to acquire sufficient nutrition through the selection of specific food items, even if these food items or the overall combination of food items differ among individuals and groups (Altmann, 1998). The protein-to-fibre ratio of mature leaves consumed has been demonstrated to predict colobine biomass in Kibale more effectively than measurements of energy availability (Chapman & Chapman, 2002; Wasserman & Chapman, 2003). The similar nutritional content found in this study provides further support for the suggestion that red colobus are selective for certain food items such as those with a high protein-to-fibre ratio (Snaith & Chapman, 2005; Harris, 2006). The sympatric red colobus groups studied seemed to be able to maintain similar concentrations of protein and fibre in their diet despite the differences in the forest and plant availability (Chapman, Chapman & Gillespie, 2002). Thus, the hypothesis that a similar nutritional profile would be observed across the red colobus groups was supported, which may support a physiological requirement whereby macronutrients are prioritized in relation to less digestible fibre.

Table 2 Mean fibre (as measured by NDF, ADF and ADL) and protein (CP) percentages present in plant species/parts consumed by at least one red colobus group. Concentrations were determined on a dry matter basis

Species (part) (number of samples analysed)	NDF	ADF	ADL	CP
Celtis durandii (YL) (n = 10)	44.71 ± 7.6	27.25 ± 4.9	11.58 ± 2.5	34.26 ± 5.3
Celtis africana (YL) (n = 10)	30.39 ± 5.5	22.21 ± 3.7	13.72 ± 2.7	27.64 ± 4.6
Albizia grandibracteata (YL) (n = 10)	50.59 ± 10.8	35.55 ± 12.4	21.72 ± 9.7	39.41 ± 4.4
Funtumia africana (YL) (n = 10)	46.83 ± 8.7	38.07 ± 9.4	24.02 ± 7.1	20.17 ± 3.9
Trilepsium madagascariense (YL) (n = 10)	47.99 ± 4.0	35.77 ± 5.0	20.86 ± 4.9	19.75 ± 1.6
Pouteria altissima (YL) (n = 5)	46.35 ± 6.1	37.19 ± 5.5	23.66 ± 5.8	21.36 ± 2.9
Prunus africana (YL) (n = 10)	34.71 ± 5.4	29.31 ± 6.0	19.08 ± 5.6	29.42 ± 2.7
Parinari excelsa (YL) (n = 10)	70.30 ± 5.5	59.96 ± 6.5	31.35 ± 4.3	16.11 ± 2.6
C. durandii (UF) (n = 4)	43.94 ± 11.9	31.60 ± 9.2	13.28 ± 3.3	23.95 ± 1.4
Strombosia scheffleri (YL) (n = 10)	47.09 ± 7.8	38.02 ± 7.9	21.84 ± 7.9	26.81 ± 6.0
Dombeya kirkii (YL) (n = 10)	42.86 ± 5.2	27.68 ± 2.5	15.91 ± 3.2	28.30 ± 3.6
Markhamia lutea (LP) (n = 7)	63.71 ± 9.9	45.94 ± 8.3	16.46 ± 2.2	15.32 ± 9.5
S. scheffleri (LP) (n = 8)	49.89 ± 6.2	40.07 ± 5.9	19.38 ± 5.9	16.54 ± 3.6
Newtonia bucchananii (YL) (n = 10)	51.27 ± 11.7	39.37 ± 14.8	24.52 ± 12.5	25.38 ± 4.4
M. lutea (YL) (n = 10)	57.67 ± 10.2	36.66 ± 9.4	18.73 ± 7.7	27.66 ± 5.1
P. africana (ML) (n = 4)	39.63 ± 2.5	29.70 ± 1.7	18.73 ± 1.7	15.96 ± 0.5
Chrysophyllum sp. (YL) (n = 10)	52.86 ± 12.4	41.06 ± 13.0	24.80 ± 10.0	26.37 ± 4.1
Millettia dura (YL) (n = 10)	49.82 ± 9.9	34.62 ± 8.4	16.08 ± 5.0	33.86 ± 5.4
F. africana (RF) (n = 1)	37.56 ± 0	28.00 ± 0	12.92 ± 0	13.33 ± 0
Ficus sansibarica (YL) (n = 10)	38.42 ± 10.3	27.33 ± 8.9	11.94 ± 7.2	19.63 ± 4.0
Eucalyptus grandis (bark) (n = 10)	58.64 ± 5.2	44.96 ± 5.1	10.01 ± 1.4	3.38 ± 0.5
N. bucchananii (ML) (n = 10)	56.88 ± 4.4	42.00 ± 5.9	26.73 ± 5.2	22.66 ± 6.2
Zanthoxylum gilletii (YL) (n = 1)	47.85 ± 0	31.96 ± 0	20.07 ± 0	25.17 ± 0
Olea capensis subspecies *welwitschii* (YL) (n = 10)	48.44 ± 6.6	36.79 ± 5.4	23.60 ± 3.3	16.59 ± 2.7
Macaranga schweinfurthii (YL) (n = 10)	33.88 ± 5.0	26.04 ± 3.9	9.13 ± 3.5	17.53 ± 3.0
Ficus exasperata (YL) (n = 10)	35.98 ± 6.2	23.30 ± 3.2	6.82 ± 1.7	27.38 ± 4.5
Mimusops bagshawei (YL) (n = 10)	62.24 ± 4.7	58.80 ± 5.3	41.52 ± 5.9	16.78 ± 2.4
Cola gigantea (YL) (n = 2)	43.46 ± 2.4	36.84 ± 3.5	30.45 ± 2.0	20.63 ± 2.7
Trema orientalis (YL) (n = 10)	41.32 ± 9.1	36.36 ± 8.6	24.40 ± 6.7	23.41 ± 2.0
Bridelia micrantha (YL) (n = 10)	55.45 ± 8.3	47.85 ± 6.2	25.78 ± 3.6	21.94 ± 3.5
Diospyros abyssinica (YL) (n = 10)	35.06 ± 7.6	24.15 ± 5.6	13.92 ± 3.7	26.70 ± 5.6
Croton sp. (YL) (n = 5)	42.51 ± 6.3	31.45 ± 5.4	16.33 ± 3.9	30.06 ± 7.1
Blighia unijugata (YL) (n = 4)	28.54 ± 5.7	16.84 ± 10.4	10.91 ± 7.4	25.70 ± 1.0
A. grandibracteata (ML) (n = 4)	56.02 ± 3.1	42.51 ± 4.1	25.25 ± 4.9	29.79 ± 7.8
O. capensis subspecies *welwitschii* (LP) (n = 4)	39.23 ± 6.1	27.40 ± 3.2	11.95 ± 2.3	6.91 ± 1.1
Teclea nobilis (YL) (n = 10)	39.58 ± 7.7	24.39 ± 5.8	9.66 ± 3.2	28.79 ± 2.9
C. durandii (ML) (n = 10)	44.98 ± 3.0	27.16 ± 1.6	9.94 ± 1.4	25.68 ± 3.5
Sapium ellipticum (YL) (n = 8)	35.78 ± 7.3	24.20 ± 4.7	11.70 ± 2.8	23.11 ± 3.1
Pancovia sp. (YL) (n = 7)	53.40 ± 18.0	39.27 ± 14.7	17.81 ± 8.0	21.30 ± 3.5
Ficus natalensis (YL) (n = 6)	51.17 ± 7.0	42.20 ± 9.3	27.82 ± 9.6	22.36 ± 4.2
Urera sp. (YL) (n = 5)	45.81 ± 7.5	40.03 ± 9.4	28.70 ± 6.2	28.48 ± 12.7
C. gigantea (ML) (n = 3)	52.97 ± 2.6	38.52 ± 2.6	22.84 ± 0.66	14.15 ± 1.9
P. excelsa (ML) (n = 5)	62.07 ± 6.9	52.48 ± 4.6	27.42 ± 2.7	13.36 ± 1.0
Celtis mildbraedii (YL) (n = 1)	54.24 ± 0	37.49 ± 0	20.21 ± 0	32.82 ± 0
Balanites wilsoniana (YL) (n = 10)	52.33 ± 4.9	33.34 ± 5.8	18.79 ± 3.8	28.20 ± 6.1
M. lutea (ML) (n = 8)	65.03 ± 5.6	48.50 ± 4.6	23.80 ± 2.2	21.03 ± 1.5
C. durandii (FL) (n = 1)	33.38 ± 0	22.55 ± 0	12.33 ± 0	42.52 ± 0

NDF, neutral detergent fibre; ADF, acid detergent fibre; ADL, acid detergent lignin; CP, crude protein n, number of samples analysed.

Table 3 Mean protein (CP) and fibre (as measured by NDF, ADF, and ADL) percentages contributed by consumed plant species/parts to each group's diet. Concentrations were determined on a dry matter basis

	Group						
	Sebatoli (n = 28)	Dura (n = 16)	K.1 (n = 20)	K.2 (n = 17)	K.3 (n = 20)	K.4 (n = 21)	K.5 (n = 17)
NDF	39.3 ± 8.1	30.7 ± 16.0	38.3 ± 5.1	37.1 ± 7.7	42.2 ± 2.8	37.8 ± 8.3	35.2 ± 5.4
ADF	29.9 ± 6.0	22.8 ± 11.3	28.3 ± 3.8	26.5 ± 5.8	30.7 ± 2.7	28.8 ± 6.6	26.7 ± 4.2
ADL	16.6 ± 4.1	13.1 ± 6.8	14.6 ± 2.2	14.7 ± 4.0	16.0 ± 1.9	15.5 ± 3.8	14.9 ± 2.5
CP	19.7 ± 4.1	16.8 ± 10.0	20.7 ± 3.4	22.4 ± 4.3	22.2 ± 2.3	17.7 ± 4.1	18.9 ± 2.5

NDF, neutral detergent fibre; ADF, acid detergent fibre; ADL, acid detergent lignin; CP, crude protein; n, number of plant species and parts analysed.

While the concentrations of protein and fibre across the seven groups are overall similar, a closer inspection reveals interesting points of differences and similarities between groups. First, protein and fibre concentrations were analogous across different home range locations. The Sebatoli and Dura groups had protein and fibre concentrations that were close to the means for all seven groups even though their home ranges did not overlap the other red colobus groups observed in Kanyawara and they tended to have the least percentage of dietary overlap when the seven groups were compared. The similarity in nutrition is especially notable considering that the forest composition in the Dura section of Kibale is quite different when compared to those encountered by red colobus in Sebatoli and Kanyawara (Chapman *et al.*, 2003). However, the red colobus ranging in Dura still achieved comparable concentrations of protein and fibre in their diet through their unique combination of plant species and parts consumed.

In terms of intergroup differences in nutrition, the variance in concentrations across groups was larger for protein than any of the fibre concentrations. Our results suggest that the seven red colobus groups observed encountered a more equivalent level of indigestible fibre in their diets than protein. Primates, even with digestive specializations seen in the red colobus, cannot fully digest fibrous components of plant cell walls. Hemicellulose recovered through detergent analyses can be estimated by subtracting ADF from NDF concentrations, while cellulose can be estimated by subtracting ADF from ADL. Red colobus are probably able to digest a large portion of dietary hemicellulose and cellulose. Although red colobus have not been subjects of digestibility studies, in a study of other five other species of colobines, NDF digestibility was 77% and ADF digestibility was 75%, on a 30% ADF diet (Edwards & Ullrey, 1999). Lignin is indigestible. The ADL values were the most similar across groups and suggest that the indigestible fibre is a factor that all the red colobus groups encounter.

We address two caveats to our results in terms of the determined concentrations of protein and fibre in the red colobus groups' diets. First, we did not measure the feeding rates; thus, we are assuming that the feeding rates between individuals and groups were similar. However, it is possible that individuals and groups were consuming the same foods at different rates. Secondly, we used the conventional techniques for determining protein content in primate diets, which includes measuring CP of plant samples and applying the nitrogen conversion factor of 6.25. Crude protein estimates the total N concentration in a plant (Maynard & Loosli, 1969). These protein measures do not account for the actual digestibility of the nitrogen present in the plant, for nitrogen may be bound to fibre in plant cell walls, secondary plant compounds such as tannins, and present in nonprotein compounds such as nucleic acids (DeGabriel *et al.*, 2008; Rothman, Chapman & Pell, 2008). A more complete assessment of protein should be undertaken in order to determine the amount of available protein versus the amount of N in a food source (DeGabriel *et al.*, 2008; Rothman, Chapman & Pell, 2008). Additionally, we used the standard conversion factor of 6.25 to extrapolate the amount of protein from the measured N concentration in the plant because using the conventional factor permits comparison with earlier primate nutrition studies. The factor of 6.25 was not originally developed for wild plants. It has since been demonstrated that wild plants, especially younger leaves that folivores favour, have more secondary compounds than this factor anticipates and thus 6.25 overestimates protein content (Rothman, Chapman & Pell, 2008; Rothman, Chapman, & Van Soest, 2012). More

appropriate conversion factors to use would be 4.4 (Milton & Dintzis, 1981) or 4.3 (Conklin-Brittain *et al.*, 1999). The factor of 6.25 also may not be appropriate for use in all plant parts such as fruit and flowers with differing amounts of secondary compounds (Conklin-Brittain *et al.*, 1999).

An understanding of both diet composition and nutritional content are needed to accurately capture the dynamics of primate feeding ecology (Harris & Chapman, 2007). The results of the present study add to the growing literature that demonstrates assumptions about the nutritional quality of diets cannot be made based on information about the plant species and parts eaten alone (Davies, Bennett & Waterman, 1988; Conklin-Brittain, Wrangham & Hunt, 1998; Davies, Oates & Dasilva, 1999; Dierenfeld & McCann, 1999; Twinomugisha *et al.*, 2006; Rothman *et al.*, 2007). Our results support the conclusion that groups may use different combinations and concentrations of plant species and parts in their diet but are still selecting food items that help them obtain similar nutrient concentrations.

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