



Mineral Resource Availability and Consumption by Colobus in Kibale National Park, Uganda

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Very little information exists on mineral nutrition of tropical, forest-dwelling species, yet minerals are critical to growth, reproduction, and survival. We examined the mineral resources available to and consumed by colobus in Kibale National Park, Uganda. We combined behavioral data on black-and-white (Colobus guereza) and red colobus (Piliocolobus tephrosceles) in a section of unlogged forest, a heavily logged area, and a forest fragment with mineral analysis of their foods to estimate the proportion of the diet containing specific minerals (mineral content). We compared mineral content of colobus foods (natural and crops) across plant parts and among plant species. Additionally, we estimated mineral intake of frugivorous primates in Kibale from published dietary data and our estimates of mineral content of foods. Dietary mineral content for all colobus groups and frugivorous species is similar despite significant differences in the mineral content of foods. Ripe and unripe fruits are lower in mineral content than most foods. Foods rarely consumed, such as bark, petioles, and caterpillars have high levels of some minerals. The mineral content of crops is low in comparison to that of natural foods. For all colobus groups of both species, sodium content of foods was extremely low and iron content was generally low, suggesting that intake is below suggested requirements, though current suggested iron requirements may overestimate physiological needs. Copper content was marginal and deficient seasonally for most colobus groups. Despite a sodium-limiting environment, only one of 8 colobus groups appeared to select sodium; however, this may be due to a lack

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of variation in sodium content among plant species and a positive correlation between high plant sodium content and secondary compounds. Despite the lack of selection for sodium by colobines, some behaviors point to a potential sodium deficiency, including urine drinking, consumption of high-sodium swamp plants, and use of mud-puddles.

KEY WORDS: colobines; minerals; nutrition; herbivory; crop raiding; foraging; sodium; population regulation.

INTRODUCTION

Mineral resources are critical for physiological function, growth, and reproduction in animals (McDowell, 1992; Robbins, 1993). Because plants and animals differ in their mineral requirements, herbivores face a difficult task of identifying and consuming plant species and parts to meet their mineral requirements. For example, sodium (Na) makes up 90% of total blood cations and is necessary for muscle contraction, nerve impulse transmission, acid-base balance, and metabolism in animals (Robbins, 1993); however, it is not required by plants, resulting in very low concentrations of sodium in most plants (Smith, 1976). Due to such discrepancies, mineral deficiencies are common in herbivores (Bell, 1995; Faber *et al.*, 1993; Fox *et al.*, 2000; Krishnamani and Mahaney, 2000; McDowell, 1992). This is particularly true in the tropics, since tropical plants are generally lower in nutrients than temperate plants are (Chiy and Phillips, 1995; McDowell, 1985, 1997).

Very little is known about the availability and use of minerals by tropical herbivores that feed on canopy trees. In many tropical forests, primates are the predominant canopy-dwelling herbivore with several species, including colobines (*Colobus* spp., *Nasalis larvatus*), some lemurs (*Lemur* spp., *Haplemur* spp.), and howlers (*Alouatta* spp.), consuming ca. 100% of their diet as plant parts (Chapman and Chapman, 1999; Silver *et al.*, 2000; Yeager, *et al.*, 1997). They likely face the same challenges of meeting mineral requirements as other more commonly studied herbivores, such as rodents (Weeks and Kirkpatrick, 1978), elephants (*Loxodonta africana*; Holdo *et al.* 2002, 1999; Weir, 1972), moose (*Alces alces*; Belovsky 1981), and other ungulates, e.g., Bison (*Bison bison*, Delgiudice *et al.*, 1994) and white-tailed deer (*Odocoileus virginianus*; Hellgren and Pitts, 1997; Ramirez *et al.*, 1996).

Although a few researchers have examined the mineral content of some primate foods (Oates, 1978; Silver *et al.*, 2000; Yeager *et al.*, 1997), information on the mineral intake of wild, native primate populations is limited.

This information is important for several reasons. Minerals affect dietary choices (Laska *et al.*, 2000; Oates, 1978; Power *et al.*, 1999; Yeager *et al.*, 1997), health (Robbins, 1993), home range patterns (McNaughton, 1988), and population densities (McNaughton, 1988; Milewski, 2000; Weeks and Kirkpatrick, 1976). Janson and Chapman (2000) list mineral availability as one of 3 factors possibly determining primate population densities, and numerous studies suggest that primates select specific plant foods or soils to meet mineral requirements (Hladik, 1978; Nagy and Milton, 1979; Oates, 1978; Yeager *et al.*, 1997). Minerals, particularly calcium (Ca) and Na, are important for lactating females, and limitations of them can result in slower growth and higher infant mortality (Buss and Cooper, 1970; Power *et al.*, 1999). Literature on humans and domestic animals suggest that mineral deficiencies are widespread and lead to disease and reduced growth, immunity, and reproduction (Cunningham-Rundles and Lin, 1998; Hambidge, 2000; Hotz and Brown, 2001; Jackson *et al.*, 2000; Minatel and Carfagnini, 2000; Ruel and Bouis, 1998; Sandstead and Lofgren, 2000). Thus, mineral nutrition in primates probably has direct impacts on population health and viability both via increased susceptibility to disease (Milton, 1996; 1999; 2000) and via direct effects on condition and reproduction.

Information on nutrient requirements of nonhuman primates is scarce (Kaumanns *et al.*, 2000; Oftedal, 1991), resulting in mineral deficiencies and toxicities in captive primates (Dorrestein *et al.*, 2000; Spelman *et al.*, 1989) and difficulties in accessing habitat quality of wild primates. Existing estimates of nutrient requirements for nonhuman primates are based on the National Research Council (1978) and Nicolosi and Hunt (1979), but both require updating (Crissey and Pribyl, 1997). National Research Council (1978) mineral requirements are based on a few species with simple stomachs (Kaumanns *et al.*, 2000) and therefore, are unlikely to reflect the mineral requirements of all primates, especially those with differing digestive morphology, such as colobines. Nicolosi and Hunt (1979) included a wide safety margin when suggesting mineral requirements for nonhuman primates, thus the values are likely to be higher than actual requirements (Altmann, 1998).

We examined mineral resources available to and consumed by colobus in Kibale National Park, Uganda. Specifically, our objectives were: 1) to estimate mineral consumption by red (*Ptilocolobus tephosceles*) and black-and-white colobus (*Colobus guereza*) in or near Kibale National Park, Uganda, based on observations in an unlogged forest, a logged area, and a forest fragment, 2) to compare mineral consumption to suggested mineral requirements for nonhuman primates to evaluate if mineral intake may be limiting, 3) to determine if colobines select for specific minerals, and 4) to

compare mineral resource availability and food content for folivorous (as determined by our study) and frugivorous primates (based on literature) in Kibale National Park.

METHODS

Study Areas

Kibale National Park (766 km²) is located in western Uganda, east of the Ruwenzori Mountains. Moist semideciduous and evergreen forest makes up 57% of the park, with grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and exotic tree plantations (1%) making up the remainder of the park (Chapman and Lambert, 2000). Mean annual rainfall is 1749 mm (1990–2001, or 1547 mm from 1903–2001) and is bimodal in distribution, with peak rainfall occurring from March–May and September–November. September to November rains tend to be heavier than March-to-May rains. Mean maximum temperature is 23.8°C, and mean minimum temperature is 15.5°C (1990–2001; Chapman and Chapman, 1997).

We observed colobus in three areas: the unlogged K-30 forestry compartment; Mikana, a heavily logged section of forest; and, Nkuruba, a forest fragment outside the park. K-30 is a 282-ha area that has not been commercially harvested. However, before 1970, a few large stems (0.03–0.04 trees/ha) were removed by pit-sawyers. The tree removal has had little impact on forest structure and composition (Skorupa, 1988; Struhsaker, 1997).

Mikana lies in the K-14 forestry compartment. K-14 contains a gradient of light to heavy logging with Mikana located in the heaviest logged portion of the compartment. The extraction in the area used by the study groups is thought to have averaged *ca.* 21 m³/ha or *ca.* 7.4 stems/ha. Incidental damage was high, and it is estimated that *ca.* 50 % of all trees were destroyed by logging and incidental damage (Chapman and Chapman, 1997). Finally, Crater Lake Nkuruba (0° 32' N and 30° 19' E; 9.2-ha forest, 3-ha lake) is an explosion crater (lake depth mean = 16 m, maximum = 38 m; Chapman *et al.*, 1998), at the northern end of the Kasenda cluster of *ca.* 40 crater lakes (Melack, 1978). Being too steep to encourage agriculture, forest remains on the rim of the crater. In 1991, we initiated a conservation project at the lake to protect the system. However, with improved transport in the region, clearing for timber, gin brewing, charcoal, brick making, and agriculture have become more profitable; consequently, some neighboring fragments have been cleared (Chapman *et al.*, 2002). As a result, the black-and-white colobus populations have increased by 320% since 1995, likely due to immigration from cleared fragments.

Behavioral Observations

We followed 2 groups of both red and black-and-white colobus in the unlogged forest and a single group of each species in the heavily logged area, and in the forest fragment. The 2 groups in the unlogged area differed in size (red colobus $n = 48$ and 24 individuals, black-and-white colobus $n = 9$ and 6 individuals). We made behavioral observations from dawn to dusk for 4 days each month from July 1998–June 1999 for all groups in the unlogged forest (*ca.* 600 h for both species) and from July 1999 to May 2000 for the groups in the heavily logged area (*ca.* 374 h), and from August 1999 to April 2000 for forest fragment groups (*ca.* 306 h). Groups from each study area were clearly identifiable due to unique characteristics of individuals within the group. All colobus groups were well habituated, and observers following the groups did not appear to disturb them. Differences in the rate with which observations were made (observation hours) resulted largely from the fact that the groups in the heavily logged areas and in the forest fragment could get into areas where the observers could not see them, i.e., areas on the steep sides of the crater lake or in dense vegetation in the heavily logged area.

During each half-hour the observer was with the group, 5-point samples were made of different individuals. If it was feeding, we recorded the species and plant part, e.g., fruit, young leaf, leaf petiole. Part categories include petiole, leaf bud, flowers, young leaves, mature leaves, ripe fruit, unripe fruit, seeds, and bark. We tried to record activities of both conspicuous and hidden group members.

Habitat Data and Selection

To examine food selection by colobus, we measured tree density in all 4 habitats. We established 12 vegetation transects (200×10 m) in the unlogged forest compartment, and established 4 transects in heavily logged area (200×10 m). In the forest fragment, we established 10 (10×60 m) transects around the crater rim from the top of the crater to the bottom. We individually marked each tree >10 cm DBH (diameter at breast height) ≤ 5 m of each side of the trail with a numbered aluminum tag and measured its DBH. This produced a sample of 1189 trees in the unlogged forest, 270 trees in the logged area, and 267 in the forest fragment.

We calculated selection as the percentage of point samples a group fed on a food item divided by the tree density (# of trees/ha). We observed some tree species to be consumed, but they were not encountered on transects within a given habitat. For these species, we assumed there was one tree present in the habitat, and calculated tree density as 1 divided by the sampled area.

Nutritional Analyses

We collected food items as part of ongoing studies of both colobine species and red-tailed monkeys (*Cercopithecus ascanius*). We present some non-colobine food items for comparative purposes. We collected all items within one week of the time a primate group consumed them, but they are not necessarily from the tree in which the monkeys fed. We collected most items by cutting branches with a tree pruner. We collected a few fruits once they fell to the ground if the canopy was too high to reach branches with a tree pruner. We collected caterpillars when red-tailed monkeys were feeding on them and some fell to the forest floor. We also collected crop foods since primates are common crop raiders (Naughton-Treves, 1998) and motivation for crop raiding in other species has been attributed to higher mineral content of crops versus available wild foods (Sukumar, 1990; Sukumar and Gadgil, 1988).

We processed food items in a fashion to mimic the feeding behavior of the subjects, and we collected only those parts selected by the animals. For example, if the monkeys ate leaf petioles, we collected the length of petiole typically consumed. We dried samples in the field either by sun-drying, via a dehydrator that circulated warm air past the samples, or via a light-bulb heated box with a series of racks. We stored dried samples in sealed plastic bags until they could be transported to the University of Florida for analysis. Samples were dried thoroughly to avoid mold. While drying temperature will not influence mineral analyses, it will influence other analyses. As a result, we assured that the samples were dried $<50\text{ C}^\circ$ by placing Max/Min thermometers with drying samples. When samples were dried in the drying oven, the oven was set at its lowest heat setting (37 C°).

We ground all samples in a stainless steel Wiley mill with a 1-mm stainless steel screen. Preparation for mineral analysis and protocol for analysis with an atomic absorption spectrophotometer follow procedures outlined by Miles *et al.* (2001). We determined sample concentrations of each element by comparing absorbancy to a standard linear regression via 3 standard points for each element. We corrected concentrations based on 2 blanks run per set of 60 samples. Additionally, we ran a sample of known mineral concentration (Certified National Bureau of Standards Citrus leaves SRM-1572) with each set of samples to ensure that values obtained from the atomic absorption spectrophotometer were accurate (NBS, 1982; NIST, 1982). We tested 8 minerals for each sample: iron (Fe), copper (Cu), manganese (Mn), zinc (Zn), sodium (Na), potassium (K), magnesium (Mg), and calcium (Ca). We ran multiple samples for most colobus foods and averaged the results to get a single mineral value for each food item (Appendix 1). However, due to the difficulty of collecting more seasonally and spatially

available foods, such as fruits, only a single analysis could be done on some of them.

It seems valid to combine multiple samples from Mikana and K-30 since they are adjacent sites along the same gentle slope. However, the forest fragment at Crater Lake Nkuruba is 10–12 km from them. Examination of the soils at the sites (soil pits and cores - Zanne and Chapman unpublished data), suggested that there was little variation in soil type over the spatial scale in the region. However, to evaluate if it is valid to use the mineral content of foods collected in Kibale to represent Nkuruba and vice versa, we collected 17 food items in both areas and contrasted their mineral content (Cu, Mn, Zn, Fe, Na, Mg, K, Ca) via a paired t-test (paired by species). There is no significant difference for any mineral among the two sites.

Determination of Annual and Seasonal Dietary Mineral Content

We assumed the percent of feeding spent—the number of point samples on that item/all feeding point samples—on a food item to be equal to the percent contribution of the item to total dry matter intake. This assumption is probably valid since colobines consume primarily leaves and variation in intake rates and dry matter content between leaf species is relatively low (Rode and Chapman, unpubl. data).

We calculated the mineral content of colobus diets via the average mineral content for all samples of a single species and plant part collected between August 1998 and July 2001. We used the following formula to determine seasonal and annual average mineral food content—the proportion of the diet containing each mineral—for all primate groups:

$$D \text{ min} = \Sigma[(\% \text{ of obs.} * \text{ min. in food})/100] \quad (1)$$

where in $D \text{ min}$ is dietary mineral content, Σ is the sum for all food items, $\% \text{ of obs.}$ is the percent of time observed feeding on an item, and min. in food is the parts per million (mg/kg) of a mineral in each food item.

We calculated for each colobus group, the contribution of each item to their total annual mineral consumption via the following formula:

$$\% \text{ contribution} = [(\% \text{ of obs.} * \text{ min. in food})/100] / \text{ann. min. content} * 100\% \quad (2)$$

where in ann. min. content is the annual mineral content. We used this value to determine the primary sources of minerals in colobus diets.

We compared total mineral content of all colobus groups between species and between disturbed (Mikana and Nkuruba) and undisturbed

habitats (K30). In addition, we compared mineral content to primate requirements (National Research Council, 1978; Nicolosi and Hunt, 1979), to requirements for birds, cattle, and other mammals (National Research Council, 1984; Robbins, 1983), and to total mineral consumption of captive and semifree-ranging primate groups (Dierenfeld and McCann, 1999; Nagy and Milton, 1979; Oates, 1978; Schwitzer and Kaumanns, 2000). Because current estimates of primate mineral requirements (National Research Council, 1978; Nicolosi and Hunt, 1979) are based on trials of animals with simple stomachs, it is important to compare colobines with other foregut fermenting mammals that may have more similar requirements. An updated version of the National Research Council's estimates of primate mineral requirements is soon to be published. We examined seasonal mineral content in the unlogged areas only, since observations there cover 11 mo, while the other groups were only observed for 9 mo. Our evaluation of whether they have diets that meet requirements should be viewed as tentative given that we do not have estimates of g dry matter of food eaten per time unit for each species and part. However, if our estimates of the mineral content of foods are consistently less than mineral requirements, their diet is probably deficient in that mineral. Stated another way, if the monkeys spend the majority of time eating foods low in a particular mineral, intake of that mineral is likely below requirements.

Comparison of Mineral Content by Folivorous and Frugivorous/Omnivorous Primates

We used existing data on food parts consumed by frugivorous/omnivorous primates in Kibale to calculate dietary mineral content and to compare the values to dietary mineral content of colobus groups. We averaged mineral content for all species within a food item category, e.g., young leaves or fruit, and included foods that were consumed by ≥ 1 of 4 frugivorous primates (not exclusively the colobus foods listed in Appendix A; $N = 57$ for ripe fruits, 7 for unripe fruits, 15 for seeds, 10 for flowers, 64 for young leaves, 5 for pith/stem, and 5 for bark). We used the percentage of each plant part consumed by chimpanzees (*Pan troglodytes*), blue monkeys (*Cercopithecus mitis*), mangabeys (*Lophocebus albigena*), and red-tailed monkeys (*Cercopithecus ascanius*) from Wrangham *et al.* (1998) in Equation 1 to estimate dietary mineral content of the frugivorous species. We excluded roots and wood from the diets analyzed because they were not collected. Additionally, Wrangham *et al.* (1998) did not include insect consumption in dietary analyses of the primates; nor did they collect sufficient insect samples to determine their mineral content. Because all diets of frugivorous primate groups

Table I. Foraging effort (% of foraging scans) devoted to different plant parts by red colobus (RC) and black-and-white colobus (BWC) groups in unlogged forest (large group = LG & small group = SG), heavily logged forest (Mikana = Mk), and a Crater Lake forest fragment (Nkuruba = Nk) in or near Kibale National Park, Uganda

Food Item	RC				BWC			
	LG	SG	Mik	Nk	LG	SG	Mik	Nk
Ripe fruit	5.0	6.4	2.3	0	0	2.5	0	0.8
Unripe fruit	1.6	2.5	0.7	1.9	7.4	6.3	14.3	1.0
Flowers	3.5	0.8	2.2	2.3	2.3	0.1	4.1	6.1
Young leaves	75.3	62.8	87.0	67.3	86.8	81.0	67.1	71.7
Mature leaves	5.6	13.3	2.0	18.4	1.9	4.7	3.6	17.9
Petioles	7.9	6.4	4.2	2.8	0.8	0.4	5.9	1.8
Leaf buds	0.3	1.3	0.4	0.3	0.6	1.1	4.9	0
Bark	0.3	6.4	0	6.4	0	4.0	0.1	0.8
Other	0	0	0	0	0.2	0	0	0

had been determined in unlogged and lightly logged habitats, we compared them with the diets of the 4 red colobus and black-and-white colobus groups (1 large and 1 small group of each species) that range in similar areas.

Statistical Analyses

We categorized samples into one of 10 food item categories: bark, crops, flowers, ripe fruit, unripe fruit, seeds, petioles, mature leaves, young leaves, and caterpillars. We compared mineral content across categories via a one-way ANOVA with a Scheffe's post hoc test after testing for normality and homogeneity of variance. We square-root transformed percentages to obtain homogeneity of variances. Although we collected >1000 caterpillars for analysis, the combined dry weight was sufficient only for 2 mineral analyses. Thus, we omitted caterpillars from statistical comparisons. We compared mineral content of mature and young leaves from 28 species via a paired t-test (paired by species). We conducted comparisons of the mineral content among species of young leaves from 20 species via a one-way ANOVA.

We conducted partial correlation analysis for all colobus groups to determine if food selection is based on any of the 8 minerals when the linear effects of availability of that food (tree density) are statistically removed. The data are log-transformed.

We used a one-way ANOVA to test whether dietary mineral content differed among red and black-and-white colobus groups, among groups in different habitats—unlogged, logged, fragment—and among frugivorous/omnivorous primates and folivorous primates. When necessary, We square-root transformed data to meet the homogeneity of variance assumption.

RESULTS

Food Items Consumed by Colobus Groups

For all colobus groups of both species, young leaves were the most common plant part consumed (Table I). For both colobus species, young leaves of *Celtis durandii* and *C. africana* ranked in the top 5 foods consumed by all groups except those in the forest fragment. *Celtis durandii* was not available in the forest fragment. For black-and-white colobus groups in unlogged and logged areas, the 2 tree species were the top 2 species consumed, accounting for 37–45% of all feeding observations. Red colobus relied less heavily on them alone and included a variety of other species in their diets, such as *Dombeya mukole*, *Parinari excelsa*, *Prunus africana*, and *Millettia dura*.

Mineral Content of Food Items

Food parts differ significantly in Cu, Mn, Zn, Mg, and Ca ($p < 0.001$ for all tests, here and below), but not Fe, Na, and K (all non-significant tests $p > 0.11$, here and below; Fig. 1). Crops are significantly lower in most minerals, except K. Cu content is significantly higher in young leaves than mature leaves and higher in flowers than bark and mature leaves. Mature leaves contained significantly higher levels of Mn than those of flowers, petioles, and young leaves. In contrast, ripe fruit contains significantly less Mn than those of flowers, petioles, and young leaves. Petioles and flowers contain significantly higher levels of Zn than those of bark, ripe fruit, and mature leaves. Petioles also contain considerable amounts of Mg (significantly higher than ripe fruit) and Ca (significantly higher than flowers, ripe fruit, unripe fruit, and seeds, and young leaves). Bark contains the highest levels of Ca, significantly higher than in all other foods tested, except petioles. Although caterpillars are not included in statistical tests, they are exceptional sources of Cu, Zn, and Fe (Fig. 1).

Paired tests of young leaves and mature leaves from the same tree species illustrate that young leaves have less ash, and more Cu and Zn than those of mature leaves (Table II). A comparison of the mineral content of 20 species of young leaves show significant differences among species across all minerals ($p < 0.01$ for all tests). However, differences between species are most common for K, Zn, and Cu (Appendix 1).

Less than 50% of all the primate foods are deficient in Mn, Zn, Mg, K, and Ca relative to primate nutritional requirements suggested by the National Research Council (1978; Appendix 1). However, 60% of the foods are deficient in Cu, 82% are deficient in Fe, and 100% are deficient in Na.

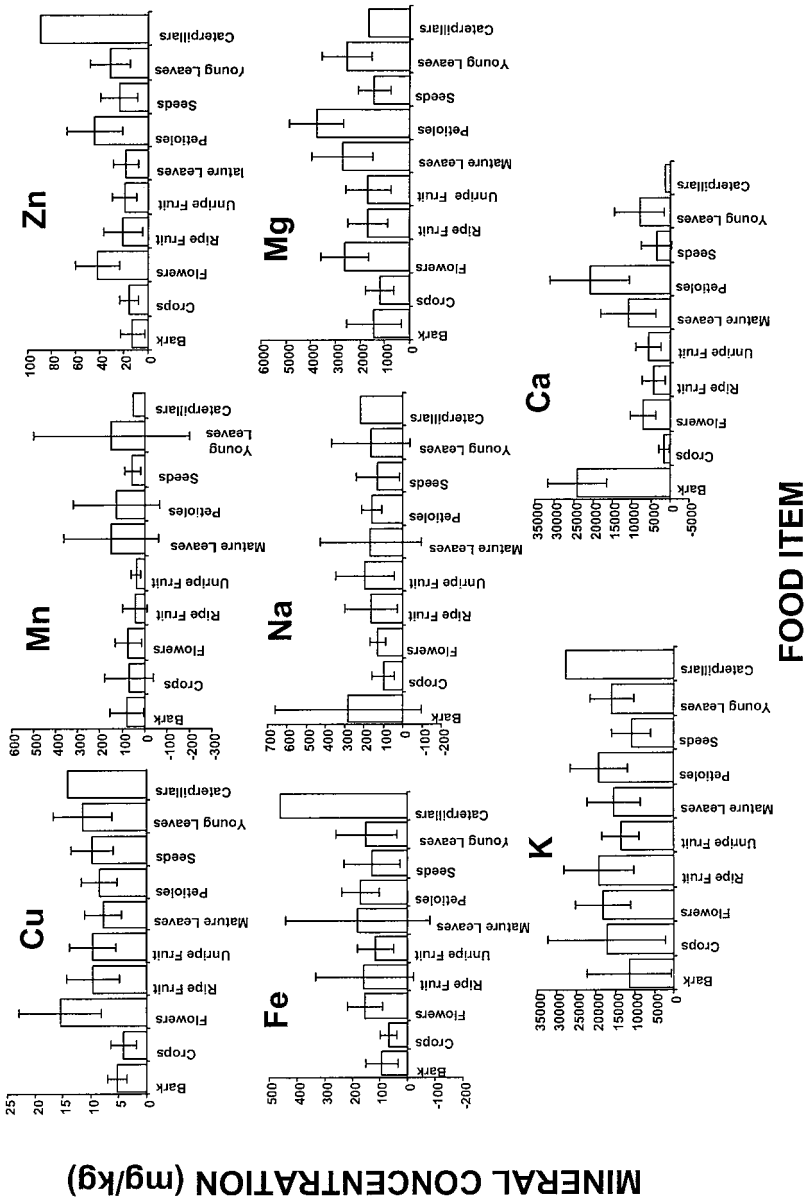


Fig. 1. Comparison of mean mineral concentrations (mg/kg) of food items consumed by primates in Kibale National Park, Uganda (N = 5 (bark), 6 (crops), 10 (flowers), 58 (ripe fruit), 7 (unripe fruit), 42 (mature leaves), 9 (petioles), 15 (seeds), and 64 (young leaves); dry matter basis).

Table II. Results of paired t tests of mineral content (mg/kg) in mature and young leaves (N = 28 for all minerals, dry matter basis) consumed by colobines in Kibale National Park, Uganda and comparison with leaves consumed by black howlers (*Alouatta pigra*) at two sites in Belize (Silver *et al.*, 2000)

	Mature Leaves		Young Leaves		ML & YL this study	
	This study (Mean (\pm SD))	Silver <i>et al.</i> (2000)	This study (Mean (\pm SD))	Silver <i>et al.</i> (2000)	t value	p value
% Ash	10.1 (\pm 3.5)		8.4 (\pm 2.8)		-3.71	0.001
Cu	7.2 (\pm 2.9)	11.1	10.2 (\pm 4.2)	12.7	4.16	0.0003
Mn	119.0 (\pm 100.9)	120.2	154.1 (\pm 337.8)	160.3	0.53	0.6
Zn	17.4 (\pm 11.5)	20.3	26.8 (\pm 11.6)	34.3	5.2	<0.0001
Fe	137.5 (\pm 133.6)	123.3	117.1 (\pm 60.9)	155.4	-0.82	0.42
Na	180.4 (\pm 318.6)	500	149.6 (\pm 73.0)	1100	-0.5	0.62
Mg	2962.7 (\pm 1236.1)	4200	2676.9 (\pm 807.7)	3900	-1.25	0.22
K	16583.2 (\pm 6429.4)	—	16307.3 (\pm 5501.3)	—	-0.19	0.85
Ca	10496.6 (\pm 6086.1)	10700	9990.9 (\pm 6854.0)	6200	-0.31	0.76

As one might expect, food item contribution to annual mineral content is highest from food items that were consumed the most frequently (Appendix B). *Celtis durandii*, *Celtis africana*, *Millettia dura*, *Markhamia platycalyx*, and *Bosqueia phoberos* are some of the most frequently consumed foods and are also within the top 5 food items contributing to annual mineral content for most minerals. Na is a marked exception, with *Eucalyptus* commonly contributing a large portion of total Na intake for groups with it in their home range.

Seasonal and Annual Content of Minerals

Annual mineral content does not differ between species (Table III, combining groups from all habitats for both species: n = 4 per species, p > 0.111 for all minerals except for Zn, p = 0.041) or between disturbed and undisturbed habitats (both species combined compared between disturbed and undisturbed areas; p > 0.30 for all minerals). This analysis should be viewed with caution given that we sampled only 4 groups of each colobine species.

It is likely that intake of Mn, Zn, Mg, K, and Ca exceeded requirements for nonhuman primates suggested by both the National Research Council (1978) and Nicolosi and Hunt (1979; Table III). Fe and Na intakes are likely deficient for all groups relative to nonhuman primate requirements and Cu is deficient for 5 of the 8 groups based on National Research Council (1978) suggestions, but both Cu and Fe are above requirements suggested by Nicolosi and Hunt (1979). Additionally, Na requirements for

Table III. Annual mineral content by colobines in 4 habitats in and around Kibale National Park, Uganda (all values are in mg/kg (dry matter basis); number in parentheses is % of requirement met in the diet; bold items are below nonhuman primate requirements suggested by the NRC (1978))

	% of diet	Cu mg/kg	Mn mg/kg	Zn mg/kg	Fe mg/kg	Na mg/kg	Mg mg/kg	K mg/kg	Ca mg/kg
<i>Red Colobus</i>									
Nkuruba	68.06	8.2 (82)	63.3 (158)	29.6 (296)	152.3 (85)	247.2 (12)	2803.4 (107)	17163.3 (215)	11129.4 (223)
Mikana	95.33	9.5 (95)	65.8 (165)	29.7 (297)	141.4 (79)	155.3 (8)	2480.2 (165)	16526.5 (207)	9714.8 (194)
K30 small	79.13	9.2 (92)	70.3 (176)	26.3 (263)	143.0 (79)	197.6 (10)	2690.2 (179)	15830.0 (198)	10573.4 (211)
K30 big	90.5	10.1(101)	73.5 (184)	30.6 (306)	160.9 (89)	173.3 (9)	2752.3 (183)	18826.6 (235)	10553.6 (211)
Average		9.2 (92)	68.2 (171)	29.1 (290)	149.4 (83)	193.3 (10)	2681.5 (179)	17086.6 (214)	10492.8 (210)
<i>Black-&-white colobus</i>									
Nkuruba	89.11	8.8 (88)	94.9 (237)	34.4 (344)	139.4 (77)	197.9 (10)	2598.4 (173)	17105.5 (214)	10574.6 (211)
Mikana	96.53	10.5(105)	57.5 (144)	36.4 (364)	171.7 (95)	158.8 (8)	2561.3 (171)	16970.4 (212)	9970.1 (199)
K30 small group	93.13	9.4 (94)	75.3 (188)	29.7 (297)	164.0 (91)	233.0 (12)	2533.9 (169)	16304.6 (204)	9964.7 (199)
K30 large group	94.02	10.1 (101)	63.5 (159)	33.3 (333)	160.7 (89)	170.0 (8)	2456.9 (164)	17757.0 (222)	9914.3 (198)
Average		9.7 (97)	72.8 (182)	33.5 (335)	158.9 (88)	189.9 (9)	2537.6 (164)	17034.4 (213)	10105.9 (202)
<i>Requirements</i>									
Nonhuman primates (NRC, 1978)		10	30	11	196	2000	1600	8000	5400
Nonhuman primates (Nicolosi and Hunt, 1979)		2	20	20	100	2200	1000	2400	6000
Cattle (NRC, 1984)		8	40	30	50	800	1000	6500	2000-4000
Mean in commercial primate diets (Ofstedal, 1991)		17.6	89	196	492	4000	1800	10500	12900
Req for birds and mammals ^a (Robbins, 1993)		1.6-6	3.7-50	9.2-30	25-180	500-2000	300-1500	2000-8000	4000-25000
<i>Other Studies</i>									
<i>Macaca silenus</i> (Dierenfeld and McCann, 1999)		8.09	106.45	28.41	85.52	500	2800		3800
<i>Lemur catta</i>		13.59	48.6	35.42	65.03	800	3500		6300
<i>Colobus guerezda</i> ^b (Oates, 1978)		21	42	42	252	406	2604		15106
<i>Alouatta palliata</i> —leaf diet (Nagy and Milton, 1979)		6.8	50		99.7	956.9	3200	10307.4	12300

^aBirds and mammals include pheasants, quail, ducks, geese, turkeys, guinea pigs, hamsters, laboratory mice, nonhuman primates (except for Cu) and domestic rabbits.

^bConsidered a maximum mineral intake based on 100% consumption of a common, relatively high nutrient food item, *Celtis durandii*.

Note. % of diet is the % of the food items consumed that were analyzed for mineral content.

cattle are above Na content of colobine foods (National Research Council, 1984).

The small and large group of red colobus and black-and-white colobus in the unlogged area of Kibale experienced seasonal variation in mineral content (Fig. 2). This resulted from changes in the plant foods eaten at different times of the year. Only the large black-and-white colobus group and the large red colobus group maintained stable intakes of Na throughout the year. Seasonal highs in Na intake are similar for the small group of both red colobus and black-and-white colobus peaking in October which corresponds to the peak in seasonal rainfall. Ca, Mn, Cu, Zn, and Fe content are highest for most groups in October and November, during and immediately after the most intense rainy season in Kibale.

Selection of Minerals by Colobines

Both multiple regression analysis between mineral content and selection and partial correlation analyses between mineral content and feeding time when tree density is held constant, revealed little evidence of selection based on mineral content. However, partial correlation analysis suggests that the black-and-white colobus group in the heavily logged forest selected plant parts high in Zn and Na more than expected based on availability, but they avoided plants with high Cu, Mn, and Fe content (Table IV). The large black-and-white colobus group in the unlogged forest also selected plants with high Zn levels, but avoided plant parts with high levels of Mn and K.

Comparison of Frugivorous/Omnivorous and Folivorous Primates

Estimated mineral content of frugivorous/omnivorous primates in Kibale that consume 50–75% of their diet as fruit is similar across species (Table V). In comparison to foods eaten by the colobus, the content of foods eaten by the frugivorous/omnivorous species of Kibale National Park is significantly lower in Zn, Mg, and Ca and marginally lower in Fe ($p < 0.02$ for all tests; Table VI).

DISCUSSION

Our study suggests that Na content is low in the foods available to and consumed by colobus in Kibale National Park. Additionally, Fe and Cu content is marginal relative to suggested requirements for nonhuman primates.

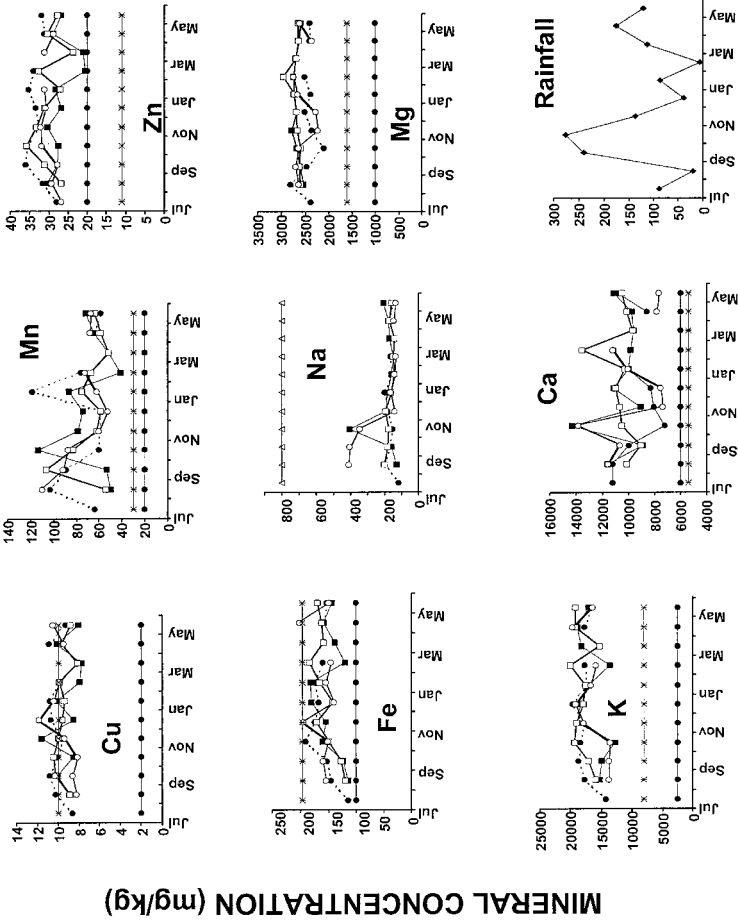


Fig. 2. Comparison of monthly rainfall patterns, suggested mineral requirements, and mineral content of 4 groups of colobus in Kibale National Park, Uganda (open circles = black-and-white colobus-K30 small group, closed circles on dashed line = BWC-K30 large group, open squares = red colobus-K30 large group, closed squares = RC-K30 small group, open triangles = cattle requirements (NRC 1984), closed circles on solid line = primate requirements suggested by Nicolosi and Hunt (1979), asterisks = primate requirements suggested by the National Research Council (1978)).

Table IV. Partial correlation analysis between feeding time on specific plant parts and mineral content when the linear effects of tree species density providing the part (density = individuals/ha) is statistically removed. Values presented are probability values and those in parentheses are correlaton coefficients.

Sample size Partial Probability (partial <i>r</i>)	RC				BWC			
	LG	SG	Mik	Nk	LG	SG	Mik	Nk
	41	53	58	56	30	28	40	49
Copper	0.253 (-0.202)	0.259 (-0.170)	0.318 (-0.143)	0.489 (-0.101)	0.071 (-0.383)	0.249 (-0.263)	0.021* (-0.400)	0.546 (0.096)
Manganese	0.439 (-0.137)	0.174 (-0.204)	0.235 (-0.169)	0.027* (0.316)	0.054 (-0.406)	0.825 (-0.051)	0.017* (-0.413)	0.613 (0.080)
Zinc	0.016 (0.409)	0.031* (0.319)	0.001* (0.462)	0.926 (0.014)	0.014* (0.506)	0.582 (0.127)	0.000* (0.579)	0.891 (-0.022)
Iron	0.935 (0.014)	0.564 (0.087)	0.110 (0.227)	0.902 (0.018)	0.582 (-0.121)	0.777 (-0.066)	0.050* (-0.344)	0.999 (0.000)
Sodium	0.654 (-0.080)	0.420 (0.122)	0.786 (-0.039)	0.791 (-0.039)	0.260 (0.245)	0.409 (0.19)	0.022* (0.397)	0.621 (0.079)
Magnesium	0.724 (-0.063)	0.878 (0.023)	0.818 (0.033)	0.270 (0.161)	0.911 (0.025)	0.167 (0.313)	0.135 (-0.266)	0.810 (0.038)
Potassium	0.758 (-0.055)	0.038* (-0.307)	0.115 (-0.224)	0.358 (-0.134)	0.009* (-0.529)	0.612 (-0.117)	0.067 (-0.322)	0.722 (-0.056)
Calcium	0.813 (0.042)	0.537 (0.093)	0.744 (0.047)	0.064 (-0.266)	0.400 (-0.184)	0.552 (-0.137)	0.534 (0.112)	0.736 (0.054)

Note. Sample size = # of food items in each groups diet that were considered, RC = red colobus, BWC = black-and-white colobus, LG = large group (K30), SG = small group (K30), Mik = heavily logged forest at Mikana, Nk = Crater Lake Nkuruba forest fragment.
* p < 0.05.

Table V. Estimated average mineral intake (mg/kg) of frugivorous/omnivorous primates in Kibale National Park, Uganda (calculated from average mineral content of food item categories, e.g., ripe fruits, unripe fruits, leaves, bark, and percentage intake of food item categories as reported by Wrangham *et al.* (1998))

	Cu	Mn	Zn	Fe	Na	Mg	K	Ca
Chimpanzee (<i>Pan troglodytes</i>)	9.63	61.87	24.08	154.87	162.93	1989.77	18693.8	6641.2
Blue monkeys (<i>Cercopithecus mitis</i>)	10.61	87.86	25.75	142.26	168.04	2059.41	16158.66	6252.5
Mangabeys (<i>Lophocebus albigena</i>)	10.3	83.28	24.89	169.66	169.66	1976.37	15592.9	6655.3
Red-tailed monkey (<i>Cercopithecus ascanius</i>)	10.44	83.72	25.03	170.52	170.52	2010.92	15776.6	6272.6

Note. Food item mineral contents are based on average from foods known to be eaten by ≥ 1 of the 4 species.

Table VI. Results of a one-way ANOVA comparing mineral contents (mg/kg) of frugivorous/omnivorous primates to folivorous colobines in unlogged and lightly logged areas of Kibale National Park, Uganda (n = 4 for all tests)

	Cu	Mn	Zn	Fe	Na	Mg	K	Ca
Mean – colobines ^a	9.7	70.65	29.98	157.2	193.4	2608.33	17179.6	10251.5
Mean – frugivores/ omnivores	10.25	79.2	24.94	143.9	167.8	2009.12	16555.5	6455.4
F value	2.94	1.77	11.52	4.79	3.21	79.64	0.39	342.46
p value	0.14	0.23	0.015	0.071	0.123	<0.001	0.554	<0.001

^aValues for 2 groups of each colobus species, black and white colobus and red colobus.

These results are strikingly similar to those of Nagy and Milton (1979), Dierenfeld and McCann (1999), and Schwitzer and Kaumanns (2000). Although Dierenfeld and McCann (1999) did not describe total mineral intake, they also found Na content of naturally occurring foods to be exceedingly low for a semifree-ranging group of lion-tailed macaques (*Macaca silenus*) and ring-tailed lemurs (*Lemur catta*) on St. Catherine's Island, Georgia, U.S.A. Schwitzer and Kaumanns (2000) documented low intakes of Fe, Na, and Mn in 2 groups of captive black-and-white ruffed lemurs (*Varecia variegata variegata*) relative to suggested requirements. Na and Cu intake were also low in wild-caught howlers that ate natural fruits and leaves (Nagy and Milton, 1979; Table IV).

Evaluating whether Fe intake is insufficient is difficult because estimates of intake values fall between the values suggested by Nicolosi and Hunt (1979) and the National Research Council (1978). Several researchers have suggested that current estimates of Fe requirements for nonhuman primates are too high (Dierenfeld and McCann, 1999; Dorrestein *et al.*, 2000), which is supported by evidence of hemosiderosis or Fe overload in some captive primates (Dorrestein *et al.*, 2000; Spelman *et al.*, 1989). Thus, it seems likely that current recommended Fe requirements are above the true physiological needs of some primate groups. Further, primates are almost always at the high end for mineral requirements in comparison to other mammalian taxa (Robbins, 1993). Suggested requirements for Na, K, Mg, and Fe are higher than for any other species, including humans (Ofstedal, 1991; Robbins, 1993). However, although the suggested Na requirement may also be high, intake levels fall far below listed requirements of most taxonomic groups. Thus, it is possible that they experience Na deficiency and Na resources are limited.

Based on the low availability of Na to colobines, it is surprising that only one of the 8 groups selected foods that were high in Na. There are

several possible explanations for this. First, Na content does not appear to be highly variable among food items or species. This is evident from the lack of differences in Na content among young leaf species and food items. Na appears to be present at high concentrations only in plant parts of *Eucalyptus* and at low concentrations in most other tree species. Without sufficient variation in Na concentration, correlations between selectivity and plant Na content are unlikely. Second, Na accumulation in plants is typically associated with reduced concentrations of protein and other minerals and high concentrations of secondary compounds (Masters *et al.*, 2001). Protein is important in colobine dietary selection (Chapman and Chapman, 2002), and it influences population size (along with fiber – Chapman *et al.*, 2002; Oates *et al.*, 1990). Thus, overall, colobines may choose to consume only the minimum amount necessary to meet their Na requirements since overall, Na containing plants are low in other important nutrients.

Although there is only one correlation between selectivity and Na content, there is evidence that colobines and other primates in Kibale occasionally seek out resources high in Na. Oates (1978) found that black-and-white colobus in Kibale come to the ground and even wade through water to forage swamp plants with high Na concentrations. Other Na-limited herbivores use swamp plants as sources of Na (Fraser, 1979; Fraser *et al.*, 1984; MacCracken *et al.*, 1993; Pletscher, 1987; Sun *et al.*, 1997). Oates (1978) suggested that the presence of swamp areas containing Na-rich plants partly explains the relatively high density of black-and-white colobus in the logged areas of Kibale (Oates, 1978). Kibale primates commonly drink from mud puddles (Chapman and Rode, unpubl. data), which may be driven by the need to meet Na requirements. Most primates appear to meet their hydric needs from water in foods (Nagy and Milton, 1979), suggesting that use of free water may be driven by an alternative dietary requirement. Since mud-puddling behavior of tropical butterflies has been attributed primarily to Na consumption (Beck *et al.*, 1999), consumption of water from mud puddles by primates could serve the same purpose. Finally, urine consumption, a common symptom of Na deficiency, occurs in Kibale primates (Chapman unpubl. data, Lambert, 2000). Mountain goats, porcupines, and domestic cattle seek out urine soaked wood in response to Na deficiency (Blair-West *et al.*, 1968, McDowell, 1992; Robbins, 1993). In addition, for 2 colobine groups, the dietary selection analysis shows a negative correlation with K, which could be a mechanism for Na conservation since lower K intake reduces Na excretion (Bell, 1995; Chiy and Phillips, 1995; Faber *et al.*, 1993).

With the exception of Na and Fe, foods consumed by colobines in Kibale are relatively well-balanced in terms of mineral nutrition. Although variation in mineral content is high among young leaves of different species

consumed by colobines, values are typically above suggested requirements. The presence of several key mineral resources appears to be important to maintain high levels of mineral intake both seasonally and across groups of both colobus species. All colobine groups obtained a majority of minerals from major foods in their diet, such as *Celtis durandii* and *C. africana*. The high protein and low fiber content of *Celtis durandii* and *C. africana* combined with their adequate mineral contents makes them important nutritional resources for Kibale Colobinae (Chapman and Chapman in press). Despite a majority of minerals being derived from these major foods, young leaves of most tree species provide adequate mineral levels, which explains why mineral content among groups and seasons is relatively constant.

Seasonal variation in the dietary mineral content of colobines is much less pronounced than seasonal variation in the leaves of individual trees (Baranga, 1983) in Kibale, which suggests that colobines may experience pronounced seasonality in mineral availability, but buffer it with appropriate food choices. The significance of seasonal variation is only important for minerals that drop below suggested requirements: Fe, Cu, and Na.

Frugivorous/omnivorous primates face more complex decisions relative to maintaining adequate mineral intake since typical fruit-based diets are lower in zinc, magnesium, calcium, and iron in comparison to colobus diets dominated by leaves. However, estimates for frugivorous/omnivorous primates in this study were still adequate in all minerals except iron and sodium. Because redtails and blue monkeys consume a relatively large proportion of their diet as invertebrates (>20%; Chapman *et al.*, 2003), estimates may change significantly when insects are included in mineral intake calculations. Iron content of caterpillars is exceedingly high compared to plant resources and compared to invertebrates analyzed from previous studies (e.g., earthworms, mealworms, crickets, and fruit flies; Barker *et al.*, 1998), suggesting the importance of insects for frugivorous primates.

Future research on primate mineral nutrition will be important for identifying the significance of iron and sodium deficiencies in primate diets. Because sodium appears to be limiting, artificial resources of sodium, such as sodium blocks, may be useful in managing primate habitat use, particularly relative to crop raiding activities. Sodium resources have been an effective management tool for controlling movement patterns in some species (Conover, 1998; Hailey and Coulson, 1996) and are known to effect wildlife habitat use (Faber *et al.*, 1993; Hailey and Coulson, 1996; Mattfield *et al.*, 1972; Miller and Litvaitis, 1992).

APPENDIX A. Mineral composition (mg/kg) of plant samples from Kibale National Park, Uganda.

	N	% Ash	Cu	Mn	Zn	Fe	Na	Mg	K	Ca
Barks										
<i>Alangium chinense</i>	1	16.05	3.16	46.15	3.18	46.42	28.12	440.31	9416.25	35118.62
<i>Albizia grandibracteata</i>	1	7.81	3.82	29.44	7.13	81.8	71.89	384.93	2575.63	20152.16
<i>Dombeya mukole</i>	1	10.94	5.47	19.58	5.93	35.08	187.63	1218.24	8538.55	19687.61
<i>Eucalyptus sp.</i>	3	11.99	7.25	205.64	23.43	167.50	949.95	2808.60	6484.87	28547.31
<i>Prunus africana</i>	1	6.50	6.69	91.38	23.81	131.50	167.05	2348.24	30351.30	16404.73
Crops										
Sweet potato tubers	1	2.43	3.79	18.53	5.67	35.03	144.85	676.9	9217.9	1324.7
Irish potato tubers	1	3.52	4.59	6.90	16.23	38.96	87.21	807.6	14243.3	43.9
Banana pith	1	10.40	2.07	93.48	24.72	84.21	163.87	1403.5	45518.9	2030.7
Banana leaves	1	9.05	7.08	303.74	14.50	92.03	141.67	2084.9	29354.3	2852.3
Maize cob	1	1.71	3.34	11.00	25.69	67.67	8.23	666.4	2727.2	
Maize leaves	1	11.58	7.15	40.79	13.93	116.78	40.10	1758.5	13276.5	3449.2
Cassava tuber	1	1.97	1.15	5.68	7.33	41.20	119.66	978.8	6140.3	957.8
Flowers										
<i>Celtis durandii</i>	1	8.67	14.73	63.54	57.99	192.47	171.15	2855.26	25312.39	8050.67
<i>Cordia abyssinica</i>	1	9.32	9.38	21.78	27.22	194.59	158.68	1897.59	20626.78	5113.20
<i>Erythrina abyssinica</i>	2	9.24	13.96	95.91	47.27	134.38	125.77	3154.36	21713.30	6867.49
<i>Jacaranda mimosifolia</i>	4	3.31	14.36	51.61	31.94	161.73	155.76	1775.10	15110.70	6381.00
<i>Mar-khamia platycalyx</i>	1	2.47	19.06	48.64	82.69	214.46	93.74	1335.39	16758.64	2414.31
<i>Monodora myristica</i>	1	10.56	33.84	30.93	36.65	123.46	88.07	3984.31	17274.1	4671.08
<i>Symphonia globulifera</i>	1	3.47	7.51	104.53	21.18	77.70	78.69	2214.78	11311.47	8888.24
<i>Tragia sp.</i>	1	13.99	18.01	57.67	48.6	263.97	131.07	3795.66	15885.17	13415.89
Ripe Fruit										
<i>Albizia grandibracteata</i>	2	4.43	3.53	25.01	25.59	100.11	146.67	797.94	13375.17	3719.21
<i>Aningeria altissima</i>	1	4.39	6.32	8.83	14.37	130.22	148.98	430.39	12387.44	2742.34

APPENDIX A. (Continued.)

	N	% Ash	Cu	Mn	Zn	Fe	Na	Mg	K	Ca
<i>Bridelia micrantha</i>	2	4.41	7.23	47.85	25.63	133.15	359.11	2433.63	11936.79	10327.32
<i>Celtis durandii</i>	1	7.87	16.41	46.89	25.46	329.35	115.85	2118.46	6923.6	13350.69
<i>Chaetacme aristata</i>	1	8.45	8.90	20.99	17.25	162.04	78.92	973.94	9613.45	906.77
<i>Cordia millenii</i>	1	7.65	11.56	7.23	9.22	41.99	139.2	981.84	30940.75	645.94
<i>Cordia abyssinica</i>	1	8.87	4.47	56.6	46.31	1235.74	184.09	883.43	20816.14	5660.3
<i>Dasyalepis eggelingii</i>	1	7.18	6.56	51.59	7.88	182.24	183.36	1861.61	22457.10	3706.40
<i>Diospyros abyssinica</i>	2	4.69	4	23.1	12.24	56.46	85.48	725.92	15901.18	2938.26
<i>Dovyalis sp.</i>	1	5.55	6.57	10.91	11.75	100.9	179.99	1058.12	19607.95	1554.46
<i>Ehretia cymosa</i>	1	8	6.44	25.88	24.22	167.08	96.19	1935.15	21011	2750.84
<i>Euadenia emimens</i>	1	8.98	5.01	24.43	17.61	97.54	207.99	2475.6	30263.82	2304.45
<i>Eucalyptus sp.</i>	1	4.67	5.00	317.69	10.89	96.24	967.96	2318.21	11032.77	10386.76
<i>Ficus brachylepis</i>	2	5.41	9.17	6.13	11.51	67.64	73.48	1978.95	14218.72	5104.932
<i>Ficus capensis</i>	3	8.40	14.44	34.79	64.13	195.65	115.89	2650.29	26568.69	4153.82
<i>Ficus exasperata</i>	2	10.81	8.17	26.53	13.88	107.49	132.34	2264.87	21898.71	9047.37
<i>Ficus exasperata</i>	1	5.69	7.61	37.06	14.52	65.27	176.99	1438.05	13965.71	6012.17
<i>Ficus stipulifera</i>	1	9.51	11.04	9.34	9.24	87.73	200.64	2841.23	32770.37	8829.32
<i>Ficus urceolaris</i>	1	11.1	7.86	40.27	17.05	203.48	217.19	3588.4	21993.42	10174.24
<i>Funtumia latifolia</i>	3	6.93	10.20	15.08	37.35	66.44	141.93	1470.84	15702.41	763.95
<i>Kigelia moosa</i>	1	3.43	6.35	6.02	2.89	47.53	163.94	529.41	12874.19	360.96
<i>Lindackeria sp.</i>	1	8.01	10.34	89.4	21.42	116.82	122.31	1914.17	19114.32	4278.1
<i>Linociera johnsonii</i>	1	4.21	11.92	13.05	15.98	75.48	143.01	822.89	13081.13	3223.46
<i>Lychnodiscus cerospermus</i>	1	5.74	10.66	151.99	13.79	225.24	86.46	1723.68	12693.57	5363.79
<i>Maesa lanceolata</i>	1	8.65	8.79	67.11	21.2	489.01	358.22	1721.85	26115.82	5361.84
<i>Markhamia platycalyx</i>	1	5.04	11.32	35.78	14.22	90.47	109.12	874.02	15538.11	4395.65
<i>Milletia dura</i>	1	2.42	8.05	23.81	12.32	49.82	109.87	1255.37	11681.73	4720.78
<i>Mimusops bagshawei</i>	2	3.97	1.65	29.02	3.82	255.08	121.12	759.11	9181.94	2935.99
<i>Monodora myrsinitica</i>	1	5.35	10.72	8.64	13.78	75.9	61.58	1134.42	5942.22	1993.34
<i>Myrianthus holstii</i>	1	9.58	26.54	93.45	22.96	165.78	97.66	3255.42	32280.66	3392.2
<i>Neoboutonia macrocalyx</i>	4	8.51	13.08	48.17	37.23	212.60	183.61	3231.59	27605.01	11256.43
<i>Olea welwitschii</i>	1	6.82	8.46	19.72	18.43	239.91	233.33	1456.96	14323.12	8177.6
<i>Piper guineensis</i>	1	9.99	15.45	20.75	10.4	149.16	223.73	2439.22	32270.55	1968.19
<i>Psidium guajava</i>	1	4.41	6.24	19.85	10.84	201.2	184.43	747.63	15887.15	1264.38
<i>Prunus africana</i>	3	4.31	7.88	13.68	19.23	122.05	85.69	1821.72	12024.77	2786.58

<i>Rothmannia urcelliformis</i>	2	5.45	16.04	22.36	11.69	69.76	178.32	1317.02	15191.42	1238.79
<i>Spathodea campanulata</i>	2	6.80	10.56	28.00	23.68	51.63	125.95	2169.94	22244.72	6950.19
<i>Strychnos mitis</i>	1	6.43	1.47	5.53	4.12	13.83	51.47	282.23	11538.21	807.95
<i>Tabernaemontana sp.</i>	1	6.51	16.43	140.51	30.48	159.74	71.59	2008.76	20915.7	1998.08
<i>Trema orientalis</i>	1	14.93	9.52	228.18	51.95	310.475	53.815	3055.12	10182.13	9211.54
<i>Uvarioopsis congensis</i>	7	8.93	14.29	20.03	19.65	79.78	71.15	1781.95	32965.52	3263.11
<i>Vangueria apiculata</i>	1	7.47	7.56	84.62	9.83	97.87	125.65	564.14	13932.58	1051.35
Unripe fruit										
<i>Bridelia sp.</i>	1	4.21	16.81	25.92	38.54	247.33	132.08	1476.1	16733.5	5493.2
<i>Celtis durandii</i>	3	10.51	10.11	55.12	23.76	139.88	90.24	3566.1	11455.1	12249.9
<i>Eucalyptus sp.</i>	1	4.77	5.79	17.49	14.07	109.52	537.87	1768.8	7284.7	6279.3
<i>Ficus natalensis</i>	4	6.16	11.48	30.32	22.67	81.40	184.02	1664.7	22443.7	5117.5
<i>Strychnos mitis husks</i>	3	4.23	11.17	65.50	17.03	34.67	149.15	770.5	11750.7	1667.7
Mixed leaves										
<i>Acalypha sp.</i> leaves, twigs	1	12.07	21.75	23.08	45.15	64.05	118.87	1863.9	21899.0	2562.1
<i>Alangium chinense</i>	1	8.59	4.31	33.35	10.76	88.54	115.22	2207.4	6094.6	9211.6
<i>Albizia grandibracteata</i>	1	5.02	10.22	64.77	19.82	92.11	160.45	2608.8	21006.7	11255.1
<i>Anitarsis toxicaria</i>	1	11.47	11.96	945.28	24.74	33.44	27.77	3473.4	15386.3	9486.8
<i>Blighia unijugata</i>	1	6.35	7.64	26.26	20.34	51.36	161.65	4400.2	10883.8	9500.7
<i>Bosquetia phoberos</i>	1	10.19	17.95	29.06	45.27	66.67	7.98	1589.9	8747.0	1407.5
<i>Diospyros abyssinica</i>	1	7.04	8.65	363.64	26.86	421.15	79.96	2218.0	11856.8	12776.8
<i>Dracena sp.</i>	1	9.65	16.54	16.80	24.90	49.74	121.45	3856.8	9012.1	4147.5
<i>Erythrophleum sp.</i>	1	10.96	14.85	904.66	26.08	229.57	191.82	7840.0	18841.9	14244.3
<i>Ficus asperifolia</i> leaf/twig	1	12.00	9.70	51.72	27.11	155.74	114.48	4858.1	12058.1	15916.7
<i>Leea guineensis</i>	1	9.11	12.91	1.74	16.26	116.91	107.02	2059.0	17187.4	3774.8
<i>Mimusops bagshawei</i>	1	6.48	6.90	8.56	21.54	146.05	164.30	1477.6	25643.5	1437.6
<i>Newtonia buchanani</i>	1	3.90	11.97	88.39	24.17	99.71	113.19	1520.0	6710.4	3918.5
<i>Phytolacca sp.</i>	1	19.36	6.80	588.68	37.76	269.17	123.20	10828.2	40816.8	32139.2
<i>Rothmannia urcelliformis</i>	1	6.16	12.10	63.16	22.46	538.96	157.62	3459.3	14197.2	6115.7
<i>Trichilia splendida</i>	1	8.31	7.83	22.05	28.14	163.14	124.56	2386.5	13916.5	4304.5
<i>Uvarioopsis congensis</i>	1	10.32	6.39	234.37	10.53	88.68	55.95	2576.0	13328.5	12869.2

APPENDIX A. (Continued.)

	N	% Ash	Cu	Mn	Zn	Fe	Na	Mg	K	Ca
Mature leaves										
<i>Acanthus pubescens</i>	2	8.70	7.77	73.81	34.69	132.10	111.17	5544.9	12530.4	11277.4
<i>Albizia grandibracteata</i>	2	5.09	5.10	46.26	15.12	92.28	194.40	1674.9	15751.0	7244.2
<i>Bosquetia phoberos</i>	1	8.51	7.70	142.36	8.23	74.24	75.35	2427.3	14458.3	4526.6
<i>Cassipourea ruwensorenensis</i>	1	8.23	3.58	159.09	9.48	93.40	115.57	2979.4	25720.1	13109.5
<i>Celtis africana</i>	2	17.96	5.68	32.53	13.24	68.77	76.76	1720.6	32528.3	5644.0
<i>Celtis durandii</i>	3	12.37	9.50	87.80	24.12	152.49	213.97	2432.1	17366.2	5875.5
<i>Chaetame aristata</i>	1	14.94	10.39	76.75	7.13	41.94	100.59	2255.8	11786.3	5482.0
<i>Clausena anisata</i>	1	12.38	10.43	36.43	55.48	127.27	120.50	1961.8	19469.5	1516.4
<i>Diospyros abyssinica</i>	1	9.49	8.32	57.28	12.47	63.98	58.09	1555.2	13866.0	2430.6
<i>Dombeya mukole</i>	3	11.45	4.92	52.16	18.23	116.52	110.81	2720.6	13711.3	7987.5
<i>Ficus exasperata</i>	1	16.53	4.75	114.72	11.04	59.82	88.04	1438.7	16809.8	1490.8
<i>Ficus natalensis</i>	2	10.91	5.99	36.46	25.37	158.44	315.25	2226.7	23374.1	16788.3
<i>Funtumia latifolia</i>	2	6.64	7.69	253.01	21.13	565.60	1781.99	3271.1	16258.6	8234.1
<i>Ilex mitis</i>	1	14.50	4.96	313.78	12.36	77.23	108.66	2322.2	13927.7	13944.0
<i>Leptonychia mildbraedii</i>	1	11.09	11.69	33.64	37.92	90.88	153.27	5965.3	19151.9	11670.2
<i>Markhamia platycalyx</i> leaflets	3	5.76	16.54	31.82	15.75	70.50	178.58	2405.8	9491.3	11960.2
<i>Markhamia platycalyx</i> leaflets and petioles	2	7.70	12.07	43.22	18.52	180.93	106.73	3104.2	9278.9	18147.9
<i>Milletia dura</i>	2	5.92	9.00	103.20	15.33	143.99	101.87	1852.2	16639.0	5074.7
<i>Mimosaops bagshawei</i>	2	7.85	2.59	60.06	8.64	161.97	76.04	3714.6	4672.9	15798.9
<i>Neoboutonia macrocalyx</i>	1	10.93	9.56	316.41	25.41	158.48	129.82	4699.4	21388.3	15897.9
<i>Olea welwitschii</i>	1	5.73	5.36	236.10	8.57	82.20	123.71	1959.4	14877.4	10392.6
<i>Pancovia turbinata</i>	1	6.86	4.54	244.84	8.71	34.55	70.46	2908.2	10011.3	31666.2
<i>Parinari excelsa</i>	1	5.61	4.63	33.21	4.07	64.02	82.77	3741.9	10017.8	14383.8
<i>Prunus africana</i>	4	7.38	5.34	18.73	11.16	99.81	163.18	2836.0	11757.0	11265.2
<i>Strombosia scheffleri</i>	2	10.05	6.58	371.74	12.88	594.38	144.15	3677.3	10339.7	15798.4
<i>Strychnos mitis</i>	1	11.84	5.96	163.48	6.89	94.83	87.35	3363.1	24949.3	10503.3
<i>Tealea nobilis</i>	1	13.88	9.96	41.07	25.81	76.87	48.01	2744.7	30305.1	10035.1
<i>Uvariopsis congensis</i>	1	11.71	6.46	91.61	10.36	90.25	96.79	5684.7	20066.7	12105.5
<i>Vernonia</i> sp.	2	11.60	6.67	103.92	28.85	263.73	126.14	2872.9	13104.6	11802.3

APPENDIX A. (Continued.)

	N	% Ash	Cu	Mn	Zn	Fe	Na	Mg	K	Ca
Young leaves										
<i>Acacia vine</i>	2	7.03	5.18	39.79	46.12	116.04	141.79	1367.8	10383.7	15280.0
<i>Acalypha</i> sp.	1	9.21	11.01	48.26	28.17	177.59	138.28	4357.1	25052.6	9497.8
<i>Acanthus pubescens</i>	1	8.60	15.84	49.94	42.03	104.02	153.40	5095.6	17398.9	8995.1
<i>Albizia grandibracteata</i>	11	6.44	11.99	51.98	41.64	140.51	170.46	2562.8	20126.0	5915.0
<i>Blighia unijugata</i>	12	6.59	8.97	29.24	27.40	119.96	138.21	2954.0	15282.8	3632.5
<i>Bosqueia ploberos</i>	5	7.91	9.18	91.15	20.70	133.09	132.77	2699.7	16896.1	10034.7
<i>Cassipourea ruwensorensis</i>	1	8.11	7.19	1634.11	5.56	55.36	75.15	1773.2	9628.1	7140.9
<i>Celtis africana</i>	21	12.83	7.63	71.33	31.83	133.94	122.93	3067.7	13615.2	22887.5
<i>Celtis durandii</i>	27	8.81	9.52	64.05	35.14	207.54	146.94	2176.1	18121.1	7165.7
<i>Chaetama aristata</i>	2	9.55	5.67	69.66	5.53	20.73	95.93	3010.5	10670.8	8232.5
<i>Clausena anisata</i>	1	7.61	13.68	26.07	44.75	85.59	171.18	2675.0	25703.5	4993.1
<i>Cordia abyssinica</i>	1	10.73	12.06	34.05	13.60	70.88	35.44	1984.9	10851.9	2379.2
<i>Diospyros abyssinica</i>	7	5.59	6.35	135.01	25.65	106.41	66.04	2231.5	14777.9	7673.3
<i>Dombeya mukole</i>	14	9.65	10.23	65.48	36.26	151.05	448.44	3399.9	22727.4	11999.1
<i>Ehretia cymosa</i>	1	9.14	4.16	58.33	32.89	94.84	56.52	1765.9	18444.8	6688.7
<i>Erythrina abyssinica</i>	1	7.06	19.49	60.29	58.93	152.41	224.92	2079.2	25129.2	2953.3
<i>Erythrina abyssinica (no petiole)</i>	1	7.80	18.32	118.66	38.59	192.95	37.28	2669.8	20266.3	3383.8
<i>Eucalyptus</i> sp.	4	5.39	7.22	237.20	24.39	106.32	1646.81	2986.4	11814.8	5531.0
<i>Ficus asperifolia</i>	1	11.81	8.42	62.68	32.06	121.18	128.90	3731.2	21519.1	14719.8
<i>Ficus capensis</i>	1	8.15	9.53	11.52	20.31	281.77	77.53	1090.7	8142.0	1422.8
<i>Ficus exasperata</i>	5	14.19	9.09	46.03	22.83	144.20	111.13	2561.4	16524.0	7300.7
<i>Ficus natalensis</i>	4	15.38	7.34	36.00	24.14	122.08	190.59	2254.2	23047.9	15605.8
<i>Ficus vallis</i>	2	10.30	3.12	32.05	29.17	175.39	129.27	6339.0	10223.9	14495.0
<i>Funtumia latifolia</i>	2	5.30	10.75	70.26	22.84	158.39	133.87	2665.5	15364.3	4254.3
<i>Ilex mitis</i>	1	12.00	16.55	143.91	28.78	92.47	249.87	4123.3	9443.9	32547.8
<i>Leptonychia miltbraedii</i>	1	9.70	14.01	102.03	50.26	71.53	169.24	3128.4	18354.6	5328.2
<i>Macaranga</i> sp.	1	5.49	9.36	152.91	22.49	8.98	129.51	2184.9	11808.6	4160.2
<i>Maesa lanceolata</i>	4	8.44	9.29	37.45	30.92	154.05	172.71	1710.1	16199.6	6552.5
<i>Markhamia platycalyx</i>	6	7.37	17.11	29.40	38.32	109.06	218.53	1940.7	25124.3	4408.0
<i>Millettia dura</i>	7	5.81	10.32	103.21	29.48	144.84	145.95	1936.5	14383.8	2896.2
<i>Mimusops bagshawei</i>	4	4.54	5.62	31.11	22.03	115.80	141.68	2016.7	11167.2	6914.9
<i>Neoboutonia macrocalyx</i>	1	10.30	21.01	165.21	33.11	105.51	85.51	3488.1	12132.5	14978.5

<i>Olea welwitschii</i>	8	8.34	6.18	24.82	16.83	72.97	122.63	1208.5	12181.1	5447.0
<i>Panconvia turbinata</i>	2	5.88	5.87	43.13	9.45	28.12	100.74	1455.1	6988.7	4613.7
<i>Parinari excelsa</i>	5	4.40	10.27	38.65	21.91	110.83	113.96	3142.8	11580.5	10735.4
<i>Polyscias fulva</i> (no petiole)	1	5.02	13.92	100.85	37.96	227.71	75.27	2342.1	12725.8	4578.6
<i>Polyscias fulva</i>	3	5.59	8.67	36.53	33.01	128.77	183.28	3001.3	21720.0	4981.9
<i>Prunus africana</i>	14	5.08	8.01	61.84	33.52	269.66	132.36	2704.2	14954.9	7355.3
<i>Rothmannia urcelliformis</i>	1	6.03	10.10	61.83	17.69	120.90	73.42	2031.5	3726.3	2798.9
<i>Spathodea campanulata</i>	1	6.55	10.74	18.85	23.92	115.89	81.18	2362.9	17629.5	5898.4
<i>Strombosia scheffleri</i>	4	6.93	11.95	71.97	23.32	106.39	221.80	3093.2	22151.6	7044.0
<i>Strychnos mitis</i>	4	7.91	6.51	30.99	18.48	107.90	111.66	2595.2	18407.4	7584.2
<i>Teclea nobilis</i>	4	7.41	12.10	962.33	37.17	79.32	126.20	2670.3	20745.1	13382.0
<i>Uvariopsis congensis</i>	1	7.94	11.56	52.46	13.08	24.01	107.51	1939.6	26451.9	9184.3
<i>Vernonia</i> sp.	1	11.07	2.77	41.79	16.87	277.64	120.80	3337.3	7936.4	25127.5

Note. Bold species are consumed by colobines. Mineral values in bold are below requirements for nonhuman primates (National Research Council 1978).

APPENDIX B. Mineral sources of colobines in Kibale National Park, Uganda (percentages represent the % of total mineral content that is contributed by each food item)

	Black-and-white colobus (<i>Colobus guereza</i>)						Red colobus (<i>Ptilocolobus badius</i>)								
	K30 Large G		K30 Small G		Nkuruba		K30 Large G		K30 Small G		Mikana		Nkuruba		
	Food	%	Food	%	Food	%	Food	%	Food	%	Food	%	Food	%	
<i>Copper</i>															
C. d. YL	32.8	C. d. YL	29.3	C. d. YL	24.3	Alb. YL	41.5	C. d. YL	20.0	Par. YL	11.0	C. d. YL	15.4	Alb. YL	18.3
Mark. YL	18.0	C. a. YL	9.9	Alb. YL	12.8	C. a. YL	8.9	Domb. YL	8.3	Strom. YL	7.5	C. a. YL	11.1	Pru. YL	14.6
C. a. YL	10.6	Mark. YL	9.6	C d URF	12.7	Pru. YL	8.6	Mark. YL	8.0	C. a. YL	7.4	Mark. YL	10.1	Domb. YL	14.4
Domb. YL	7.8	Pru. YL	6.3	C. d. LB	12.5	Vines ML	4.0	Bos. YL	7.8	C. d. YL	7.0	Mil. YL	8.8	C. a. YL	8.2
C. d. YL	5.5	Alb. YL	5.5	C. a. YL	8.2	Stryc. YL	3.6	Par. YL	7.6	Funt. YL	6.8	Olea YL	8.3	Blig. YL	5.1
<i>Manganese</i>															
C. d. YL	35.0	C. d. YL	24.7	C. d. YL	30.0	Tec. YL	25.9	C. d. YL	18.4	Euc. Bark	12.7	C. a. YL	14.9	Euc. YL	17.5
C. a. YL	15.8	C. a. YL	11.6	C. a. YL	13.9	Alb. YL	16.6	Tec. YL	12.0	C. a. YL	9.0	C. d. YL	14.9	Pru. YL	14.6
Domb. YL	7.9	Euc. Bark	11.4	C.d. URF	12.6	Phyt. ML	14.1	Bos. YL	10.6	Bos. YL	6.3	Mil. YL	12.6	Domb. YL	11.9
Tec. YL	5.6	Euc. YL	7.5	Alb. YL	10.1	C. a. YL	7.7	C. a. YL	7.6	C. d. YL	6.2	Dios. YL	7.4	Alb. YL	10.3
Mark. YL	4.9	Euc. RF	6.5	Mil. YL	7.9	Euc. YL	6.4	Domb. YL	7.3	Strom. YL	5.9	Domb. YL	5.3	C. a. YL	10.0
<i>Zinc</i>															
C. d. YL	36.6	C. d. YL	34.3	C. d. YL	25.7	Alb. YL	36.8	C. d. YL	24.2	C. a. YL	10.8	C. d. YL	18.1	Alb. YL	17.6
C. a. YL	13.4	C. a. YL	13.1	Alb. YL	12.8	C. a. YL	9.5	Domb. YL	9.7	C. d. YL	9.0	C. a. YL	14.8	Pru. YL	17.0
Mark. YL	12.2	Pru. YL	8.3	C. d. LB	11.3	Vines ML	9.1	C. a. YL	8.2	Par. YL	8.1	Mil. YL	8.0	Domb. YL	14.1
Domb. YL	8.4	Mark. YL	6.8	C. a. YL	9.8	Pru. YL	9.1	Mark. Pet	7.6	Pru. YL	7.3	Mark. YL	7.2	C. a. YL	9.5
Alb. YL	4.8	Alb. YL	6.4	C.d. URF	8.6	Claus. YL	3.0	Mark. YL	5.9	Alb. YL	5.9	Olea YL	7.2	Vines YL	5.7
<i>Iron</i>															
C. d. YL	44.8	C.d. YL	36.7	C.d. YL	32.2	Alb. YL	30.7	C. d. YL	27.2	Pru. YL	10.7	C. d. YL	22.4	Pru. YL	26.5
C. a. YL	11.7	Pru. YL	12.1	C. d. LB	12.9	Pru. YL	18.1	Mark. Pet	10.3	C. d. YL	9.8	C. a. YL	13.0	Alb. YL	11.6
Domb. YL	7.2	C. a. YL	10.0	C.d. URF	10.7	C. a. YL	9.8	Domb. YL	7.7	C. a. YL	8.3	Mil. YL	8.2	Domb. YL	11.5
Mark. YL	7.2	Chry. YL	5.1	Alb. YL	9.2	Vines ML	5.7	Bos. YL	7.1	Par. YL	7.6	Olea YL	6.5	Mim. ML	8.1
C. d. URF	4.8	Funt. YL	4.4	C. a. YL	8.7	Phyt. ML	4.4	C. a. YL	6.5	Pru. ML	6.6	Pru. YL	6.4	C. a. YL	7.8
<i>Sodium</i>															
C. d. YL	30.0	C. d. YL	18.3	C. d. YL	24.7	Alb. YL	26.2	Domb. YL	21.1	Euc. Bark	20.9	Domb. YL	15.2	Euc. YL	31.1
Domb. YL	20.3	Euc. Bark	17.0	C. d. LB	13.7	Euc. YL	21.3	C. d. YL	17.9	Pru. ML	7.8	C. d. YL			

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