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Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour

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Abstract: This study investigated the nutritional ecology of forest elephants in Kibale National Park, Uganda relative to crop-raiding behaviour, and examined nutritional differences between crops and food consumed by wild elephants. An index of dietary nutrient concentration was determined by quantifying the species and parts of plants consumed along feeding trails, collecting food items, and analysing foods for energy, fibre, protein, minerals and secondary compounds. Frequency of crop raiding was quantified over 13 mo. Energy and protein concentration was within suggested levels, but concentrations of several minerals, particularly sodium, were low relative to requirements based on captive elephants and values reported for other wild populations. The very low sodium concentrations of Kibale elephant diets and low availability of alternative sodium sources, such as soil or water, suggest that sodium drive is very likely in this population. Crops consumed by Kibale elephants had higher Na concentrations and lower concentrations of fibre and secondary compounds than wild diets. The known attraction of elephants to mineral sources throughout their range and the low mineral concentration of leaves, fruits, bark, and stems consumed by forest elephant in this study suggest that mineral nutrition is likely to be an important factor driving elephant behaviour and patterns of habitat use.

Key Words: Africa, energy, fibre, forest elephants, *Loxodonta africana*, minerals, nutrition, requirements, sodium

INTRODUCTION

Despite tremendous effort to manage and conserve both Asian (*Elephas maximus* Linnaeus) and African elephant populations (*Loxodonta a. africana* Blumenbach; *Loxodonta a. cyclotis* Mataschie) little is known about the environmental factors affecting survival and growth. Rainfall and frequency of droughts is thought to influence population dynamics of savanna elephants (Armbruster & Lande 1993, Lindsay 1994), but other than poaching and habitat availability (Blake & Hedges 2004), factors important in affecting the health of forest elephants are largely unknown. There is extensive evidence that elephants congregate and travel great distances both in savanna and forested habitats to utilize mineral sources, such as bais (clearings in West and Central African forests with mineral-rich water-holes) (Klaus *et al.* 1998, Magliocca & Gautier-Hion 2002), termite mounds (Holdo & McDowell 2004, Ruggiero & Fay 1994), and mineral licks (Holdo *et al.* 2002, Vanleeuwe *et al.* 1997). Several studies have suggested that nutrition, and mineral consumption in particular, may be important in affecting elephant population densities (McNaughton *et al.* 1997, Milewski 2000, Vanleeuwe *et al.* 1997). However, a comprehensive look at the nutritional content of elephant diets and the identification of potentially limiting nutrients is largely lacking.

Most studies of elephant diets use forage quality indices which determine the relative contribution of different food types (e.g. browse, grasses, fruits) rather than analysing the nutrient composition of specific food items (Chiyo *et al.* 2005, Kabigumila 1993, Ruggiero 1992). Studies that have examined the nutritional content of food items have collected and analysed only a small fraction of the large variety of food items elephants consume (Jachmann 1989). However, several

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studies have suggested and documented, via either information on nutrient availability, blood parameters or dietary measures, deficiencies in calcium, phosphorus, sodium, potassium, iodine and essential fatty acids (Dierenfeld 1994, Holdo *et al.* 2002, Zhang & Wang 2003). Deficiencies of iodine and sodium in plant foods consumed by elephants have been associated with a drive to seek alternative sources, such as soil and well-water (Holdo *et al.* 2002, Milewski 2000). Additionally, though deficiencies have not been documented in forest elephants, congregations of elephants at mineral licks (Vanleeuwe *et al.* 1997) suggest that mineral availability is an attraction and affects habitat use and elephant behaviour. The potential for deficiencies and the attraction of elephants to sources of specific nutrients leads to the question of whether nutrition could play a role in crop-raiding behaviour.

Crop raiding is a common management concern throughout the range of Asian and African elephants and is a serious threat to both conservation efforts and local economies (Chiyo *et al.* 2005, Sukumar 1989, Tchamba 1996, Zhang & Wang 2003). Though crop raiding has a number of potential causes, including proximity, density and seasonal availability of crops (Naughton-Treves 1998, Sitati *et al.* 2003), seasonal differences in nutrient concentration of wild and cultivated plants has been suggested as a factor contributing to crop raiding in several studies (Chiyo 2000, Dudley *et al.* 1992, Nyhus *et al.* 2000, Sukumar 1989). Food crops are selected to be highly digestible, high in energy and low in secondary compounds. Some or all of these factors may make them particularly attractive to elephants. Several studies have documented selection by elephants of foods low in secondary compounds and high in energy, protein and minerals (Jachmann 1989, Omondi 1995, Sukumar 1989) and foods of wild elephants have been found to be lower in protein and minerals than crops (Osborn 1998, Sukumar 1989). Thus crop consumption could be used to supplement deficient diets. The total area under cultivation of a crop does not appear to be related to the frequency of elephant raids (Sukumar 1990), thus elephants may be selecting for specific crops. In Kibale National Park, Uganda, seasonal availability of wild foods was not correlated with the timing of crop-raiding events, indicating that factors other than total food availability may be involved (Chiyo *et al.* 2005).

In order to better understand the nutritional ecology of forest elephants, identify potential limiting nutrients and examine relationships between nutrition and crop-raiding, this study (1) quantified seasonal nutrient concentration of diets consumed by Kibale elephants to identify potential deficiencies via comparisons with suggested requirements and nutrition of other elephant populations; (2) examined relationships between nutrient concentration of wild diets and frequency of crop raiding by Kibale elephants; and (3) compared nutrient concentration of frequently consumed crops and wild diets.

METHODS

Study site

Moist semi-deciduous and evergreen forest make up 57% of Kibale National Park, with grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%) and exotic tree plantations (1%) making up the remainder. Mean annual rainfall totals 1734 mm (1990–2000) and is bimodal in distribution with peak rainfall occurring from March–May and September–November. Mean maximum temperature is 23.7 °C and mean minimum temperature is 15.5 °C (1990–2000; Chapman & Chapman 1997).

The Kibale elephant population is estimated at 300 individuals (Chiyo 2000). Prior to 1980, approximately 600 individuals existed in this area migrating south into Queen Elizabeth National Park during the December to February dry season. Migrations south ceased between 1950–1980. The Queen Elizabeth game corridor still exists to the south of Kibale with the rest of the area surrounding the park being dominated by subsistence agriculture and pockets of tea plantations in the north (Chiyo *et al.* 2005). The park boundary is clearly defined by the conversion of forest to agricultural land at its edge.

The two most abundant crops surrounding Kibale are banana (perennial: *Musa paradisiaca*) and maize (annual: *Zea mays*) which cover an estimated 58.0% and 23.7%, respectively (Chiyo 2000) (authorities for crop species can be found in Mabberley 1997). Some commonly cultivated crops such as beans (*Phaseolus vulgaris*), sweet potatoes (*Ipomoea batatas*), cassava (*Manihot esculenta*), sorghum (*Sorghum vulgare*), potatoes (*Solanum tuberosum*) and others combined covered 12.5%, 2.8%, 3.6%, 7.6%, 1.4% and 5.7% of land, respectively (Chiyo *et al.* 2005). Bananas are available all year with no seasonal fluctuations in availability, whereas maize and other annual crops show marked seasonal fluctuations in availability. Ripening and harvesting of maize coincide with dry seasons.

Nutrient concentrations of elephant diets and food items

Food items consumed by Kibale elephants were quantified along fresh feeding trails < 3 d old, a method commonly used to determine species composition and nutritional quality of forest elephant diets (Short 1981, Tchamba & Seme 1993, White *et al.* 1993). Multiple feeding trails from a single group of elephants were randomly chosen and followed for a minimum distance of 5 km each month. Thus, diets reflect foods eaten by elephant groups rather

Table 1. Nutrient concentrations (per dry matter basis) of Kibale elephant diets estimated from feeding trails, averages across all food items and compared with suggested requirements.

	Kibale diets	Kibale food items	Elephant requirements[1]	Horse requirements[2]
Copper (ppm)	10.5 ± 1.1	10.7 ± 5.3		10
Manganese (ppm)	148.2 ± 71.5	149.7 ± 193.8		40
Zinc (ppm)	27.9 ± 5.2	27.5 ± 18.7		40
Iron (ppm)	133.3 ± 20.9	135.6 ± 93.7	157.0	50
Sodium (ppm)	130.4 ± 10.7	139.0 ±79.3	2000	1000
Magnesium (%)	0.3 ± 0.1	0.25 ± 0.15	0.1	0.3–0.4
Potassium (%)	1.6 ± 0.2	1.5 ± 0.7	0.6	0.3–0.6
Calcium (%)	0.9 ± 0.18	1.0 ± 0.8	1.5	
Phosphorus (%)	0.24 ± 0.06	0.2 ± 0.07		
Crude protein (%)	22.2 ± 2.2	20.0 ± 7.2	10–12	8.0
ADF[3] (%)	32.4 ± 3.0	34.7 ± 10.3		
Energy (kJ g^{-1})	19.3 ± 0.8	18.6 ± 1.4	16.7	

[1] Dierenfeld 1994.
[2] NRC 1989.
[3] Acid detergent fibre.

than individuals. The number of plants consumed was recorded, including plant species and parts eaten (e.g. stems, young leaves, mature leaves, lianas, bark, roots or fruits). Counts of each food item consumed were made for similar sizes of food items (e.g. dbh of stem), except for fruits. Since elephants sometimes feed on fallen fruit, we recorded fruit as eaten if elephant feeding trails passed through a fruiting tree with fallen ripe fruit. Stems that were broken off and discarded were not included as eaten stems. Although liana diversity in Kibale is poor, consumption of lianas was detectable since elephants rarely consumed the entire plant. Feeding trails provide a reasonable estimate of elephant diet since elephants in Kibale ate mostly browse and for all browse species, variation in the size of stems was small (3.45 ± 0.06 cm dbh). Determination of elephant diets and forage quality are commonly determined from signs of elephant feeding rather than direct observations, particularly in forested habitats (Chiyo *et al.* 2005, Kabigumila 1993, Short 1981, Tchamba & Seme 1993, Theuerkauf *et al.* 2000, White *et al.* 1993). However, determination of diet from feeding trails may be biased towards stems and leaves and biased against foraging of food items that leave little evidence, such as fruit fall consumption. Additionally, because the size of food items consumed could not be determined and included in calculations of dietary nutrient concentration, caution should be used in comparing food items and nutritional content of elephant diets in this study with data collected using alternative methods.

Elephant food items, including bark, fruits, leaves and stems, and crops were sampled between January 2001 and February 2002, once elephant diets had been determined. A sample of 100 g dry weight of each food item was collected twice during the sampling period from multiple locations. Collected samples were separated into parts (e.g. leaves, stems and fruit) for both wild forages and crops and dried using either a dehydrator or light-bulb-heated oven to prevent volatilization of secondary compounds. Samples were ground in a stainless steel Wiley mill with a 1-mm screen and were run in duplicate for all analyses. Analyses of energy, crude protein (CP), minerals, alkaloids, cyanogenic glycosides, saponins and acid detergent fibre (ADF) followed methods used by Chapman *et al.* (2003) and Rode *et al.* (2003). Minerals analysed included copper (Cu), zinc (Zn), iron (Fe), sodium (Na), manganese (Mn), magnesium (Mg), potassium (K), calcium (Ca) and phosphorus (P).

Monthly indices of dietary concentrations of energy, crude protein, ADF, and minerals in Kibale elephant diets were determined by the following equation:

$$\sum P_i N_i$$

where P_i is the proportion of a food item i based on feeding trails and N_i is the proportion of nutrient per g of dry matter of the food item. This equation was also used to quantify consumption of saponins, cyanogenic glycosides and alkaloids. However, chemical analyses provided indices for these compounds rather than quantities per dry matter, thus these values were considered relative scores. Because feeding rates and dry matter of individual food items could not be quantified, total nutrient intake could not be determined. Although nutrient analyses provide precise estimates of nutrient concentration in food items, food items are likely to vary seasonally (Chapman *et al.* 2003). In addition to reporting nutrient concentration of diets based on feeding trails, means and standard deviations of nutrient concentrations for all food items are reported (Table 1).

Nutrient concentrations of Kibale elephant diets were compared with suggested requirements for elephants reported by Dierenfeld (1994), suggested requirements for horses and reported values for other wild elephant populations. Requirements for horses were used for comparison since they are the largest hind-gut fermenter in which requirement levels have been determined (NRC

1989) and because, unlike captive elephants, extensive feeding trials have been conducted more accurately quantifying true requirements. Values for horses were treated as minimum suggested requirements for elephants since larger animals, such as elephants, consume less total food (g dry matter) per body weight yet their bodies contain the same proportions of minerals (McDowell 2003). There is currently conflicting evidence regarding the relationship between mineral requirements and body weight across species (Hellgren & Pitts 1997, McDowell 2003, Robbins 1993). Requirements for captive elephants are likely to be maximums, even for wild elephants, since they are established to prevent any possible nutrient deficiency in captive animals. Thus, we expect adequate levels for wild elephants to fall between the range suggested for horses and elephants.

Crop-raiding patterns of Kibale elephants

Frequency and timing of crop damage at Kibale was monitored from November 1996 through November 1997 in four administrative areas where crop-raiding activity was most common. Crop-raiding incidents were defined as discrete events where elephants left the park to raid crops and subsequently returned to the park (Naughton-Treves 1998). For feeding trails that led through agricultural areas, the number and species of crop stems consumed was recorded. Correlations and step-wise regressions were used to identify relationships between monthly frequency of crop raiding and nutrient concentrations of wild food items.

Comparisons between nutrient concentrations of crops and wild foods

Nutrient concentrations of consumed crops, non-consumed crops, and wild foods of Kibale elephants were compared. Non-consumed crops were defined as those within the same proximity to elephant habitats with similar availability as other crops, but that were rarely raided or consumed. Kruskal–Wallis tests were used for comparing three or more samples. If significant differences were illustrated in the initial analysis, Mann–Whitney U-tests were conducted with a Bonferroni correction.

RESULTS

Nutrient concentration of Kibale elephant diets

The majority (70.2 ± 2.9%) of food items in monthly elephant diets were analysed including major and minor wild food items. Gross energy and crude protein concentration of foods consumed by Kibale elephants were higher than suggested requirements based on captive elephants (Table 1). ADF (32.4 ± 3.0% of dry matter) was similar to levels reported by Jachmann (1989) for a wild population (35–37.4%). Relative to suggested requirements (Dierenfeld 1994, NRC 1989) and available values reported for wild elephant populations, foods consumed were seasonally low in Fe, Na, Zn, and Cu, and adequate in P, K, Mg, and Mn (Table 1). While Ca concentrations of wild foods were below suggested requirements, values were similar to those reported by McCullagh (1969: 0.4–0.6% Ca) and Jachmann (1989: 0.9%). Na concentration of Kibale elephant foods were well below suggested requirements for all mammals (McDowell 2003, Robbins 1993).

No forest foods tested met the suggested Na requirement for elephants or the lower estimate for horses (0.1%). Energy concentrations in fruits were significantly higher than leaves, stems and bark (Energy: $H = 10.5$, $df = 2$, $N = 33$, $P = 0.005$) and calcium concentrations in bark were 3.5 times higher than leaves and stems ($H = 8.84$, $N = 38$, $df = 2$, $P = 0.012$). Crude protein concentration was significantly higher in leaves than fruits and bark ($H = 16.9$, $df = 2$, $P = 0.001$). Relative concentrations of alkaloids and saponins were higher in bark than other food items (Alk: $H = 11.6$, $N = 51$, $P = 0.009$, Sap: $H = 9.41$, $N = 51$, $P = 0.024$). Only one food consumed by elephants contained cyanogenic glycosides: both the mature leaves and fruits of *Prunus africana* Hook. f. *Prunus africana* constitutes 0.58% of stems consumed along feeding trails by Kibale elephants annually.

Relationships between crop raiding and dietary nutrient concentration

Nutrient concentration of elephant diets during months that crop raiding occurred and during months prior to raiding did not predict the frequency of raiding ($P > 0.05$ for all correlations). A comparison of months categorized as high crop raiding (> 5 events) and low crop raiding (< 5 events) resulted in a significantly lower dietary ADF concentration during months of low crop raiding ($U = 64.0$, $N = 13$, $P = 0.04$). There was no difference in concentrations of any other nutrients between high and low crop-raiding periods ($P > 0.05$ for all tests).

Comparison of nutrients in crops and wild foods

Crops consumed by Kibale elephants had higher Na concentrations and lower concentrations of ADF, P, crude protein, energy, Cu, Zn, Ca and saponins than wild diets ($N = 47$, $P < 0.05$ for all tests) (Tables 2 and 3). Consumed crops had higher Na concentrations than non-consumed

Table 2. Acid detergent fibre (ADF) and sodium (Na) concentrations of wild foods consumed by elephants in Kibale National Park, Uganda.

Species	Part	ADF (%)	Na (ppm)
Acalypha sp.	Leaves and stems	25	119
Aframomum sp.	Leaves	43	210
Alangium chinense Lour.	Bark	57	28
Alangium chinense	Leaves	22	115
Albizia grandibracteata Taub.	Bark	55	72
Albizia grandibracteata	Leaves	42	160
Aningeria altissima A. Chev.	Leaves	37	236
Antiaris toxicara Leschenault	Leaves	38	28
Blighia unijugata Bak.	Leaves	48	162
Brillantaisia sp.	Leaves	23	82
Dasylepis sp.	Fruit	14	184
Dichrostachys cinerea L.	Leaves	32	152
Diospyros abyssinica Hiern.	Leaves	29	80
Dombeya mukole Mast.	Bark	44	188
Dovyalis abyssinica A. Rich.	Fruit	29	52
Dracaena laxissima Engl.	Leaves	42	122
Erythrophleum sp.	Leaves	24	192
Ficus asperifolia Miq.	Leaves and stems	30	114
Funtumia latifolia Preuss	Ripe fruits	23	211
Kigelia moosa Sprague	Ripe fruits	33	164
Leea guineensis G. Don.	Leaves	41	107
Lovoa sp.	Young leaves	22	313
Maesa lanceolata Forssk.	Young leaves	29	122
Maesa lanceolata	Fruits	44	496
Marantochloa leucantha K. Schum	Leaves and stems	32	136
Millettia dura Dunn	Fruits	57	119
Mimusops bagshawei S. Moore	Leaves	48	164
Myrianthus holstii Engl.	Fruit	57	98
Oncoba routledgei Sprague	Leaves	37	271
Oxyanthus sp.	Fruit	28	33
Pancovia turbinata Radlk.	Leaves	32	148
Pennisetum purpureum Schum.	Leaves	41	168
Phoenix reclinata Jacq.	Leaves	59	470
Pseudospondias microcarpa A. Rich.	Leaves	31	63
Pterygota mildbraedii Engl.	Leaves	28	147
Rothmannia urcelliformis Hiern	Fruit	26	178
Setaria sp.	Leaves	36	86
Teclea nobilis A. R. Delile	Fruit	42	131
Trema orientalis L.	Fruit	23	51
Trichilia sp.	Leaves	46	125
Trilepisium madagascariense DC.	Leaves	37	8
Urera trinervis Hochst.	Leaves	38	83
Uvariopsis congensis Robyns & Ghesquiere	Leaves	40	56
Uvariopsis congensis	Fruit	26	600
Vernonia sp.	Leaves	23	131

Table 3. Acid detergent fibre (ADF) and sodium (Na) concentrations of crops and parts available to elephants around Kibale National Park, Uganda (bold items are parts and species most commonly consumed).

Species[1]	Part	ADF (%)	Na (ppm)
Ipomoea batatas	**Tuber**	**4**	**145**
Solanum tuberosum	Tuber	3	87
Musa paradisiaca	**Stems**	**25**	**164**
Musa paradisiaca	Mature leaves	32	116
Musa paradisiaca	**Young leaves**	**29**	**169**
Zea mays	**Cob**	**16**	**300**
Zea mays	Leaves	25	40
Manihot esculenta	Tuber	4	120

[1] Mabberley (1997).

crops (Mann–Whitney test: U = 22.0, df = 1, P = 0.05), whereas ADF concentrations were similar (U = 10.0, N = 7, P = 0.60). Alhough cassava has been reported to contain cyanogenic glycosides (Vetter 2000), no crops analysed in this study contained cyanogenic glycosides or alkaloids.

DISCUSSION

Nutrient concentrations of foods consumed by elephants in this study suggest that minerals, rather than energy and protein, may be limited in availability. Low mineral availability in tropical environments is well documented in the management of domestic herbivores frequently requiring supplementation to maintain adequate productivity (McDowell 1997). Copper and sodium, which exhibited low concentrations in elephant foods, are considered to be two of the three most limiting nutrients (along with phosphorus) for herbivores and deficiencies of these minerals are particularly common in tropical environments (McDowell 1997, McNaughton 1988).

Crops consumed by Kibale elephants contained lower concentrations of fibre and secondary compounds, and higher concentrations of sodium than wild foods. Additionally, sodium concentrations of wild diets were low and fibre content was higher during months with high frequencies of crop raiding than during months of low frequency. Contrary to previous studies (Osborn 2004, Sukumar 1990), protein concentrations were not higher in crops than wild foods nor did protein appear to be deficient in wild foods. Lower fibre concentration of crops is likely to have significant effects on diet digestibility. Regressing data from multiple feeding trials reported by Clauss *et al.* (2003), fibre concentrations of wild food diets and crops would result in 61.7% and 80% digestibility, respectively ($y = -1.6x + 113$, $R^2 = 0.48$, $F = 5.6$, $P = 0.056$). Frequent reporting of the role of secondary compounds in affecting elephant food preferences (Milewski 2002, Omondi 1995, Seydack *et al.* 2000), and the importance of sodium in elephant behaviour (Holdo *et al.* 2002, Jachmann & Bell 1985) suggest that these factors along with the increased digestibility associated with crops could contribute to crop-raiding behaviour.

Higher sodium concentrations and lower concentrations of secondary compounds in crops may allow elephants to solve the complexities of meeting sodium requirements from wild foods. Plants that accumulate sodium typically contain low concentrations of protein and high concentrations of secondary compounds (Masters *et al.* 2001). For example, sodium concentration of wild foods available to Kibale elephants were associated with high saponin concentration and the food item with the highest sodium, *Uvariopsis congensis* unripe fruits (600 ppm), had a high alkaloid score. Additionally, consumption of secondary compounds can increase Na excretion and thus, exacerbate low Na intake (Robbins 1993). Optimizing diets for high sodium concentration and low concentrations of fibre and secondary compounds appears to be common across several elephant populations (Jachmann 1989, Nakamura 1996, Omondi 1995).

Though geophagy has been associated with acquisition of minerals (Holdo *et al.* 2002, Krishnamani & Mahaney 2000, Weir 1972), there is no evidence that Kibale elephants consume soil (P. Chiyo, K. Rode & C. Chapman, pers. obs.). Forest clearings and licks are unknown in Kibale despite decades of on-going research and human activity throughout the park. Soils analysed from Kibale were found to contain concentrations of sodium (400–500 ppm, Mahaney *et al.* 1997) higher than most plant foods. Thus, either elephant use of soils has somehow gone undetected or some other component of soils, such as high iron levels (soil levels: 32000–85000 ppm, Oates 1973; max. tolerable iron concentration: 3000 ppm, NRC 1980), prevents Kibale elephants from using this source of sodium. Some swamp plants in Kibale are significant sources of sodium (700–6400 ppm, Oates 1973), including *Hydrocotyle ranunculoides* L.f., *Oenanthe procumbens* H. Wolff. Though feeding trails passing through swamps did not show any evidence of feeding on these plant species, elephants do use swamp habitats and may be consuming these plants without leaving significant evidence. A study of colobus monkeys in Kibale found that they consumed both soil and swamp plants, but still were unable to consume sodium at levels close to suggested requirements (Oates 1973).

Though concentrations of minerals other than sodium were marginal in the portion of elephant diets examined in this study, alternative wild food sources exist for some of these nutrients. Bark contained high levels of calcium (1.8–5.7%) similar to several other studies (Holdo *et al.* 2002, Sukumar 1990), and two fruit species, *Celtis durandii* Engl. (a very common tree) and *Prunus africana*, contained iron levels exceeding 250 ppm. Calcium, phosphorus and copper were within or above at least some of the suggested requirement levels for domestic herbivores (NRC 1989) and concentrations found in food items consumed by other elephant populations, thus alternative sources may not be necessary.

Several authors suggest that the sodium budget of elephants may be very precarious and in general, sodium concentrations of elephant browses throughout their ranges in Asia and Africa are extremely low (Holdo *et al.* 2002, Jachmann 1989, Sukumar 1989, Weir 1972). However, interpretation of appropriate concentrations is dependent on requirement estimates. For example, though sodium concentrations in Kibale elephant diets increase with the addition of bananas, is a 30 ppm increase beneficial if requirements are 1000 or 2000 ppm? Sodium requirements for elephants have been suggested at 45 g d^{-1} based on extrapolations of estimates made for other species (Holdo *et al.* 2002, Robbins 1993). However, a study of white-tailed deer (*Odocoileus virginianus*) by Hellgren & Pitts (1997) documented considerably lower sodium requirements than values estimated from the same extrapolative measure used by Holdo *et al.* (2002). Using the Hellgren & Pitts (1997) sodium requirement for deer of 3.3 mg kg^{-1} d^{-1}, a 5000-kg elephant would require only 16.5 g d^{-1} of sodium. This value would be even less if, as Hellgren & Pitts (1997) suggest, sodium requirements scale exponentially with body weight to 0.75 rather than 1.0. Assuming 62 kg dry matter d^{-1} of forage intake (Kozaki *et al.* 1991) and multiplying by dietary sodium concentration, Kibale elephants consumed only 8.06 ± 0.66 g d^{-1} of sodium. The low concentration of sodium in most foods consumed by Kibale elephants and the lack of apparent alternative sodium sources suggests that sodium concentrations required to maintain individual condition and survival may be lower than previously suggested. However, sodium drive has occurred in elephants consuming sodium concentrations higher than that consumed by Kibale elephants in this study. Thus, at this level of dietary sodium, the drive for sodium could cause elephants to pursue foods that only incrementally improve their total intake.

Preference for food items with high sodium concentration has been documented in several studies (Jachmann 1989, Nakamura 1996, Omondi 1995) and use of barks, soils, salt licks and bais by elephants has often been attributed to a craving for sodium (Holdo *et al.* 2002, Turkalo & Fay 1995). Holdo *et al.* (2002) documented low levels of sodium in Kalahari elephant diets (0.019%) and attributed sodium craving to use of salt licks, movements, and habitat use patterns. In Taman Negara National Park, Malaysia, elephants repeatedly raided outhouses consuming urine-soaked wood at tourist observation towers (K. Rode, pers. obs.), a behaviour also observed in sodium-deprived mountain goats (*Oreamnos americanus* Rafinesque) (Robbins 1993) and domestic cattle (*Bos* spp.) (McDowell 2003). Thus, despite the lack of precise sodium requirements in elephants, documented behaviours suggest that many elephant populations both in savanna and forest habitats experience salt craving, which is the earliest and most obvious sign of a sodium deficiency (McDowell 2003). The importance of sodium in driving herbivore behaviour, migration patterns, food selection and population densities is well-documented (Bazely 1989, Holdo *et al.* 2002, McDowell 2003, Robbins 1993, Weir 1972) and may be an important consideration in managing elephant populations.

Though crop raiding is likely driven by a variety of factors, including proximity of elephant habitats to crops, timing of crop ripening, and dense spatial distribution of crops relative to wild foods that reduce time-constraints on foraging, considering the role secondary compounds, sodium, and fibre play in elephant food choice may aid in identifying management solutions. Utilizing the nutritional needs of elephants, two low-cost strategies could be used to reduce crop-raiding behaviour. (1) Planting of buffer crops that are high in fibre and secondary compounds and low in sodium. Though further investigation is needed to determine the required width of buffers, this method is often suggested as a possible deterrent (Ebregt & Greve 2000). This strategy would require a community-based effort such that landowners near forests or elephant habitat borders plant crops non-preferred or less preferred such as tea (*Camellia sinensis*), cowpea (*Vigna unguiculata*) and coffee (*Coffea* sp.). Cotton (*Gossypium* spp.) may also be effective buffer crops in some areas. Though *Eucalyptus* has been suggested as a buffer crop due to high secondary compounds (IUCN 1999), all parts of this species are very high in sodium and elephants do consume the bark (Milewski 2002). Crops such as sorghum, some fruits, and cocoa, have higher tannin concentrations (Gu *et al.* 2004) and may aid in reducing the total amount of crops consumed. Crop genotypes with high tannin concentrations, such as cotton and sorghum, are currently being created via genetic selection (Lege *et al.* 1993). (2) Use of salt blocks to manage elephant movements and encourage use of natural habitats away from forest or habitat edges. Proximity of elephants to villages and agricultural lands has been documented as an important factor predicting frequency of crop raids (Chiyo 2000, de Boer & Ntumi 2001, Nyhus *et al.* 2000). Salt supplementation is an effective strategy for attracting and managing livestock and wildlife throughout the world, including altering habitat use and movement patterns (Faber *et al.* 1993, Mason *et al.* 1993, McDowell 2003, Miller *et al.* 2000). In Simao, China, human-made salt pools were used successfully to attract elephants and prevent travel to nearby villages where elephant–human conflicts had previously occurred (Zhang & Wang 2003). Salt provisioning sites may need to be moved frequently to prevent forage depletion in surrounding areas and implications for other wildlife which may be attracted to salts, would need to be considered. Additionally, salt supplementation has resulted in population growth in rodents (Batzli 1986, Woolfenden & Millar 1997); this potential effect would need to be considered in management objectives.

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