Chemical composition of mineral licks used by elephants in Aberdares National Park, Kenya

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Abstract

Physical and chemical properties of mineral licks and their use by the African elephant (*Loxodonta africana*) in a forest ecosystem in Aberdares National Park, Kenya, were investigated. Samples of lick earths and of control earths not ingested in the immediate vicinity were compared for nutrient composition and particle size. Mean concentrations of several macronutrients were greater in the lick earths than in the controls while there was no observable difference in the mean concentrations of micronutrients except iodine. Eaten earths differed from the uneaten earths primarily in their significantly higher sodium and iodine concentrations. The mineral lick samples had higher clay content than the control samples. This work therefore isolated sodium, iodine and clay content as the possible stimuli for geophagy among elephants in Aberdares National Park. Sodium preference could be attributed to palatability; clay has a possible medicinal function and also retards leaching of sodium and iodine. This study provides evidence that elephants supplement not only sodium but also the associated element iodine from inorganic sources.

Additional key words: geophagy, clay, sodium, iodine, nutrients, supplementation

Résumé

Les propriétés physiques et chimiques des *salt-licks* et leur utilisation par l'éléphant africain (*Loxodonta africana*) dans l'écosystème forestier du parc National des Aberdares, au Kenya, ont été étudiées. On a comparé la composition chimique et la taille des particules d'échantillons du sol qui est léché et du sol-contrôle voisin non consommé. Les concentrations moyennes des plusiers macro-éléments étaient plus fortes dans les sols léchés que dans les sols-contrôles, alors qu'il n'y avait pas de différence observable de la concentration moyenne des micro-éléments, excepté l'iode. Les sols léchés étaient différentes des sols non-léchés dans leur concentrations significativement supérieur en sodium et en iode. Les échantillons de minéraux léchés avaient un contenu en argile à celui des échantillons contrôles. Ce travail met en évidence le sodium, l'iode et le contenu en argile comme les stimuli possibles de la géophagie chez les éléphants du Parc National des Aberdares. La préférence pour le sodium pourrait peut-être être attribuée au goût ; l'argile a peut-être une fonction médicinale et retient peut-être le sodium et l'iode avec un effet retard. Cette étude apporte des preuves du fait que les éléphants ne suppléent pas seulement le sodium, mais aussi l'élément iode qui lui est associé, à partir de sources inorganiques.

Mots clés supplémentaires : géophagie, argile, sodium, iode

Introduction

Ingestion of earth (geophagy) has been observed in various animal species throughout the world. Elephants often seek out natural mineral licks, located where nutrients are concentrated for various reasons. Geophagy appears to be normal behaviour of all species of elephants in most of their habitats (Hanks 1979; Spinage 1994). The most spectacular evidence is the excavation of caves on the volcanic slopes of Mt Elgon in Kenya (Bowell et al. 1996). It is believed that lick earths may offer nutritional benefits or have medicinal properties (Henshaw and Ayeni 1971; Mahaney et al. 1996; Huffman 1997), as they do for humans.

Geophagy has important implications for conservation (Milewski 2000). Elephants are increasingly confined by human interests to mere fragments of their original range. Elephants were naturally nomadic over large distances, partly owing to movements to and from scattered mineral licks. This means that many conservation areas may not, in the long term, be viable for elephants unless appropriate provision is made for nutrient supplementation. In turn, many ecosystems may collapse without the pivotal role that elephants play.

This paper documents the location and chemical composition of mineral licks and their use by the African elephant (*Loxodonta africana*) in Aberdares National Park in central Kenya. The study area is part of the same montane forest ecosystem as Mt Elgon National Park but is located on the eastern side of the Rift Valley. Twelve nutrient elements were analysed: the macronutrients sodium, potassium, calcium, magnesium and phosphorus, and the micronutrients zinc, copper, manganese, iron, iodine, cobalt and chromium. Molybdenum, selenium and sulphur, although nutritionally important, were not analysed for practical reasons. Nutrient requirements vary with age, sex, season and reproductive status (Robbins 1993).

Study area

Aberdares National Park covers approximately 767 km^2 (fig. 1). The park lies between longitude 36º31′ and 36º57′ E and latitudes 0º08′ and 0º42′S within the Aberdare mountain range, which contains many valleys draining a series of peaks as high as 4000 m.

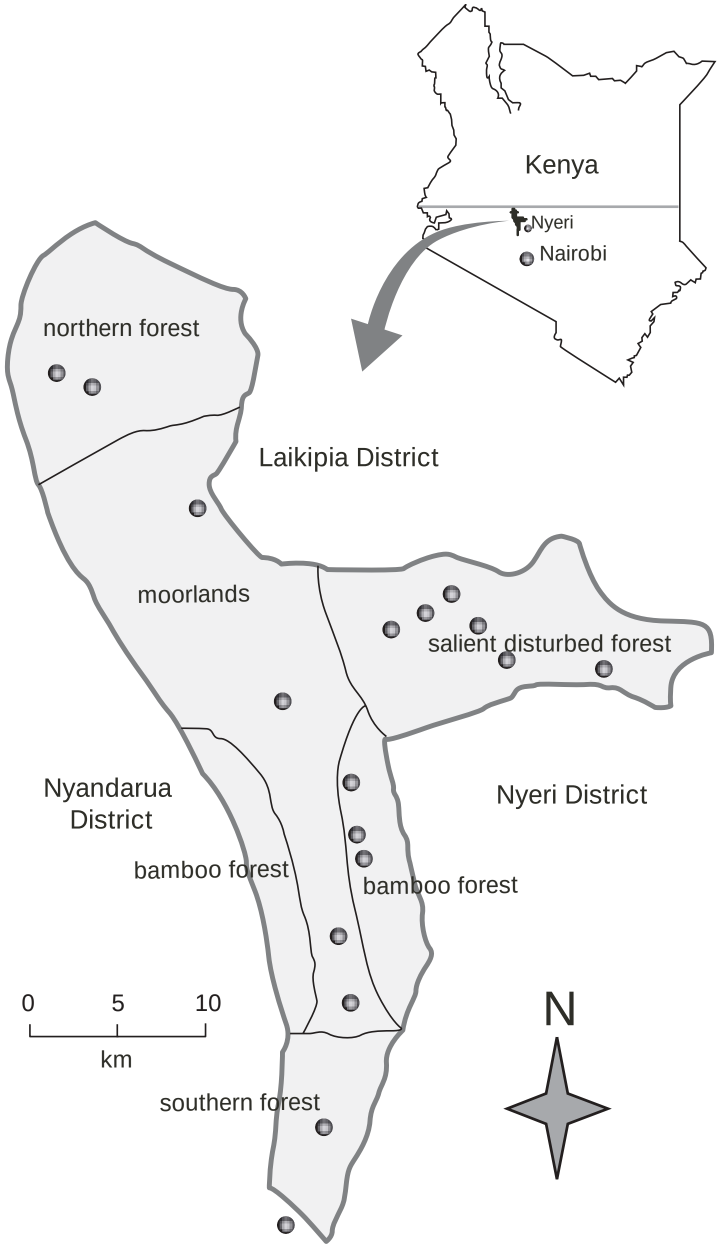

Figure 1. Aberdares National Park, showing the distribution of mineral licks (●).

The earth is mainly alkaline, derived from volcanic rocks such as basalts and rhyolites. Over much of the study area, deep clays predominate at lower altitudes, giving way to relatively coarse materials at higher altitudes. The earth desiccates and disintegrates in dry seasons, and become soggy and waterlogged during heavy rains.

Methods

Sampling approach

Active mineral licks were initially surveyed in July–August 2002, using the Gamins 12XL global positioning system (GPS). Fourteen licks were selected for chemical sampling based on altitude, habitat and status of use. Three of these had been artificially supplemented, occurring in open glades containing two tourist lodges (Treetops and The Ark) and one tented camp in Aberdares National Park. The lodges regularly replenished the salt at these three licks, which were far richer in sodium and calcium, and somewhat richer in magnesium and potassium than the natural licks. Because of this deliberate supplementation, these licks were omitted from statistical analysis.

At each lick site, earth samples were taken with a soil auger for subsequent analysis. The samples totalled 56 lick earths and 52 control earths. Lick earth samples were randomly collected in four replicates at a depth of 0.3–0.5 m. Control samples of uneaten earths were collected at a depth of 0.5 m, at a minimum distance of 200 m from the licks, in surrounding forest. All 108 earth samples were air dried in the field.

At the selected licks, dung, footprints, trampling and recent excavations were recorded to indicate how often elephants used the site for geophagy (table 1).

Laboratory analysis

Laboratory analysis was undertaken at the national agricultural research centre in Muguga, near Nairobi. Soil pH was measured on a 2.5:1 water to soil suspension using a pH meter. Exchangeable Na, K, Ca, Mg and P were extracted by leaching 10 g of earth with 100 ml of 1 M-ammonium acetate at pH 7. Cu, Mo, Zn, Co, Cr, Mn and I were extracted by leaching in 1% EDTA (ethylenediaminetetraacetic acid). EDTA is a chelating agent and 1% suspension with earth forms metal chelate ionic complexes (Okalebo et al. 2002). Flame photometry was used to determine concentrations of Na and K, and concentrations of Ca, Mg, P, Cu, Zn, Mn, Cr, Co, I and Fe were measured using an atomic absorption spectrophotometer (McKeague 1976). All nutrient concentrations were recorded in parts per million.

The hydrometer method (Bouyoucos 1962) was used to determine the particle sizes of composite samples from 10 lick earths and 10 control earths. A Calgon solution was used to disperse earth into its individual particles, categorized as sand, silt and clay, using standard procedures (Okalebo et al. 2002).

Frequency of lick use

The frequency with which elephants visited licks was observed at two of the artificial licks. Preliminary observations indicated that elephants do not visit licks

Table 1. Classification of mineral licks according to levels of use by elephants

Lick use status	Indicators
Heavy	Deep holes and cavities inside the lick with fresh tusk markings Presence of more than five fresh dung piles Visible footprints, trampling and tracks around the lick
Moderate	Relatively shallow holes and cavities inside the lick, with few tusk markings Presence of 2–5 fresh dung piles Moderate trampling around lick
Light	No holes and very few cavities inside the lick Few tusk marks One dung pile at most No trampling around the lick
Abandoned	Old holes and cavities with algal growth Decayed, scattered dung No recent sign of elephants

during the hours of bright daylight. Therefore, the number of individual elephants visiting the licks over a standard period was recorded, from 1500 to 0900 the following morning, for 15 days at each lick. Age and sex composition of the elephants was noted where possible. It was assumed that elephants visiting the artificial licks do visit the natural licks with similar frequency and similar group composition.

Statistical analysis

Lick earth was compared with uneaten (control) earths for differences in mineral concentration using one-way analysis of variance. The Kruskal-Wallis test was used to compare mineral concentration of three samples of each of the lick-use categories of heavily, moderately or lightly used. The Statistical Package for Social Scientists (SPSS) computer package was used for all the analyses.

Results

Chemical composition of the licks

Earths eaten at the natural licks (not replenished with salt) and uneaten control earths in the surrounding forest did not differ in pH (table 2). When the mean concentrations of elements in lick samples were compared with those in control samples, the results showed that the lick earths were relatively enriched in some macronutrients. Among the micronutrients, only iodine showed a trend of being more concentrated in lick than in control earths (table 2). One-way analysis of variance showed that sodium was highly significantly different ($p < 0.01$), and phosphorus and magnesium significantly different ($p < 0.05$) between lick earths and control earths. Zinc, manganese and iron were also significantly ($p < 0.05$) different, but more concentrated in control than in lick earths.

Table 2. Chemical compositions of lick and control earth samples (means ±SE) and their mean differences in concentration (ppm) by ANOVA

Element	Lick earth (eaten)	Control earth (uneaten)	Mean difference (df = 1.87)
pH	4.96 ± 0.1	4.95 ± 0.1	0.0
P	39.3 ± 12.2	11.2 ± 2.6	26.9*
K	275 ± 53.4	291.7 ± 68.2	109.4
Na	464 ± 49.5	226.6 ± 29.4	272.3**
Ca	524.5 ± 101.3	585 ± 130.9	84.5
Mg	313.0 ± 68.2	206.0 ± 34.5	146.8*
Fe	170.2 ± 30.3	353.0 ± 49.2	–115.4*
Cu	2.0 ± 0.4	2.2 ± 0.5	–1.2
Zn	4.5 ± 0.4	13.7 ± 3.1	–5.74**
Mn	292.3 ± 69.8	851 ± 199.9	–235.81*
Co	0.11 ± 0.004	0.2 ± 0.004	–0.0052
Cr	9.7 ± 0.6	10.2 ± 0.5	0.02
I	89.0 ± 17.1	65.0 ± 9.1	20.5

*$p \leq 0.05$ – significant, **$p \leq 0.01$ – very significant

Earth texture

Student's *t*-test performed on the data displayed no significant differences ($p = 0.05$). However, eaten earths were overall richer in clay than the uneaten earths sampled in the surrounding forest. The lick samples contained 16–64% clay (mean 37.7%), whereas the control samples contained 3–37% (mean 23.4%) (table 3).

Nutrient preference

Kruskal-Wallis rank analysis showed that at licks of different levels of use (see table 1) sodium concentration was significantly different at $p < 0.05$ and iodine at $p < 0.01$ between heavily and lightly used licks (table 4).

Two of the five heavily used licks showed concentrations of sodium lower than those found in the moderately or lightly used licks. It was, however, noted that these heavily used licks were located on major elephant paths or near watering points, which may have been the reason that they were well frequented.

Age and sex of elephants using licks

The ages and sex of elephants visiting and using the artificial licks at Treetops and The Ark over a 15-day period are given in table 5.

All adults and subadults were distinguishable as female or male. At Treetops 65% of the elephants that visited the licks were females and 35% males. At The Ark 59% were females and 41% males.

Discussion

Is sodium a proximate or an ultimate factor?

Scientists have long hypothesized that animals use 'salt' licks to supplement an insufficient dietary

Table 3. Particle size composition of lick and control earth samples (percentages)

Sample pair	Clay Eaten	Clay Uneaten	Sand Eaten	Sand Uneaten	Silt Eaten	Silt Uneaten
1	16	3	36	17	48	80
2	16	3	49	20	35	77
3	18	5	54	40	28	55
4	24	23	50	74	26	3
5	35	29	36	70	29	1
6	39	29	40	62	21	9
7	54	37	30	48	16	15
8	55	35	30	64	15	1
9	56	37	24	61	20	2
10	64	33	19	58	17	9
Mean	37.7	23.4	36.8	51.4	25.5	25.2

Table 4. Kruskal-Wallis analysis and significance testing for concentration difference between heavily, moderately and lightly used lick samples ($n = 36$)

Element	Mean conc. (ppm)	Kruskal-Wallis mean rank Heavy	Kruskal-Wallis mean rank Moderate	Kruskal-Wallis mean rank Light	*P* value df, 2
P	33.56	19.67	13.96	21.88	164.0
K	308.26	17.42	23.71	14.38	0.086
Na	470.36	24.33	18.17	13.00	0.03*
Ca	570.47	19.71	16.96	18.83	0.808
Mg	296.50	16.83	19.42	19.25	0.218
Fe	205.08	21.58	20.33	13.58	0.135
Cu	1.12	14.92	20.83	19.75	0.218
Zn	4.25	13.63	22.75	19.13	0.102
Mn	294.10	18.67	19.58	17.25	0.861
Co	0.12	20.71	19.75	15.04	0.356
Cr	9.56	24.23	15.67	15.58	0.068
I	81.13	24.92	24.08	6.5	0.001**

* significant at $p \leq 0.05$, ** significant at $p \leq 0.01$
n = 36 because tests involved only 9 natural licks—3 heavily used, 3 moderately used and 3 lightly used

Table 5. Artificial salt lick visitation by elephants for 15 days

Age and sex	Treetops lick visits no.	Treetops lick visits %	The Ark lick visits no.	The Ark lick visits %	Total visits no.	Total visits %
Juveniles	20	15	29	15	49	15
Subadult males	16	12	18	9	34	11
Subadult females	18	14	19	10	37	11
Adult males	25	19	51	26	76	23
Adult females	53	40	79	40	132	40
Total	132	100	196	100	328	100

intake of sodium (Weir 1973; Fraser and Reardon 1980; Redmond 1982). Several authors have confirmed that sodium is the major macronutrient that elephants seek at mineral licks. Holds et al. (2002) in Hwange National Park in Zimbabwe observed that elephants with sodium-poor faeces ingested more earth than did individuals with relatively sodium-rich faeces, suggesting that geophagy was stimulated by sodium deficiency in the body of the herbivore.

The present study provides further evidence for the importance of sodium but suggests that other nutrients may also be important. All the lick earths that elephants in Aberdares National Park ate had significantly higher concentrations of sodium than found in adjacent earths that were not eaten. However, the elephants preferred licks with relatively great concentrations of not only sodium, but also iodine.

Sodium is unlike other macronutrients in that most woody plants do not concentrate this element in their tissues to the degree that herbivorous mammals do (Michell 1994). This would explain behaviour resulting in nutritional supplementation. Most of the sodium in earths is either in solution or weakly held as exchangeable ions on the surface of clay particles (Phillips and Chicy 1995). Sodium is thus more susceptible to leaching than are divalent cations. This explains the finding in the present study that sodium was more concentrated at depth than near the earth's surface, and at lower than at higher altitudes in Aberdares National Park.

Although there is consensus on the importance of sodium in geophagy by elephants, an appetite for salt does not prove a deficiency of this element (Phillips 1993). Studies of domestic herbivores have shown that ungulates consistently prefer sodium-rich foods over sodium-poor foods, implying that the animals may be indulging in luxury consumption (Reid and Horvath 1980; Michell 1994).

The nutritional wisdom of herbivores can apparently be overridden. Experimentally increasing the sodium content of food beyond requirements results in an increased intake (Phillips and Chicy 1995). Animals may choose a palatable but nutrient-poor diet over a nutritious but unpalatable diet (McDowell 1995). Excess sodium is readily excreted in urine and faeces. For these reasons, sodium deficiency in elephants will remain inconclusive until requirements have been quantified at a physiological level. The salt provided at artificial licks should be analysed for iodine.

Sodium and iodine have similar cycling properties and are linked in the geochemical cycle. Both elements are soluble, easily leached, and required in minimal amounts by plants, and this means that both are naturally concentrated only in certain situations. It is possible that elephants use a salty taste as an indicator of a likely concentration of iodine. Therefore, neglect of iodine in the many published analyses of mineral licks may help to explain the emphasis on sodium, and the otherwise generally inconsistent reported composition of mineral licks.

Earth is known to be a significant source of iodine. However, the analysis of iodine is often ignored because land plants have never been recorded as deficient in iodine, and analyses of this ultra-trace element are difficult and expensive. Iodine has the most categorical separation of any nutrient between animals and land plants. This is because it is required in animals for thyroid hormone synthesis at concentrations far greater than those required by land plants (Milewski 2000). Elephants are likely to be limited by the supply of iodine, inasmuch as their plant foods are deficient in this element relative to their hormonal requirements. The main supply of iodine in terrestrial ecosystems is atmospheric from marine sources, so that concentrations decrease with remoteness from the sea. Poverty of iodine can be expected not only at high altitudes far from a coast but also in areas subjected to glaciation in the Pleistocene (Underwood 1981), such as Aberdares National Park.

The present finding, that iodine is the only micronutrient with mean concentration higher in preferred than in less-preferred mineral licks, has implications for management. Inasmuch as cultivated crop species have higher iodine concentrations than wild plants, this might partly explain seasonal raiding of crops by elephants. Milewski (2000) has suggested variation of iodine concentration as a possible approach to elephant population control. The supply of iodine may particularly affect reproductive rate, since age of sexual maturation and frequency of oestrus depend on hormonal sufficiency, and the thyroid gland is an integral part of the endocrine system. Thyroxine is required in relatively large quantities for the rapid metabolism and growth of mammalian offspring, which depend on the mother for iodine until weaned. Milewski (2000) pointed out that in wild ungulates the mother takes priority in providing for her own thyroid, partly by delaying her reproductive attempts until she has sufficient iodine to support offspring. This implies that environmental poverty of iodine is likely to limit the reproductive rates of elephant populations.

Nutritional value of clay

Elephants are unable to lick earth surfaces directly. They differ from other ungulates in that they consume earths by gross excavation, usually by gouging clods with their tusks, and then transferring them to the mouth with their trunks. Even at artificial licks, where salt was placed on the surface, elephants did not merely consume surface deposits. While this may be partly owing to the relatively great appetite for mineral nutrients, it is also consistent with indirect benefits of inert mineral matter such as clays.

The present analyses showed that mineral licks were relatively rich in clay. This is consistent with previous studies of geophagy, in humans and other animals. Klaus et al. (1998) observed that natural mineral licks in the Hokou area of Dzanga National Park, Central African Republic, were located at dolerite intrusions that had weathered to clay-rich earths. Geophagy is also common at the mounds of termites, which are clay rich relative to their surrounds (Ayeni 1977; Davies and Baillie 1988; Ruggiero and Fay 1994; Mahaney et al. 1997, 1999). Termites transport clay particles from depth, enriching their mounds with nutrients as well as clay, even where topsoils are sandy.

Clay obtained from mineral licks is thought to aid in the neutralization of secondary plant compounds that animals ingest, such as tannins and alkaloids (Kreulin 1985; Knight et al. 1988). Clay components have been shown to bind and absorb plant toxins (Mahaney et al. 1999). The clay mineral metahalloysite is one of the principal ingredients in the pharmaceutical kaopectate, used to treat minor gastric ailments in humans (Vermeer and Ferrell 1985). Chimpanzees in Tanzania and colobus monkeys in Uganda, which eat mainly leaves, bark and pith, have been reported to consume clay-rich earth, believed to absorb secondary plant compounds (Oates 1978; Mahaney et al. 1999).

Elephants in Aberdares National Park probably eat several plant species that contain harmful substances because they rely on browse more than grass, and on the ripe and unripe fruits of various species (pers. obs.). The diet of large herbivores such as elephants is composed of many plant species, because it is more economical to include suboptimal species than to take the time to discriminate (Crawley 1983). Leaves, green fruits and seeds are generally heavily defended chemically, compared with grasses (Mattson 1980; Wink 1993). For example, condensed tannins have detrimental effects in many mammals by reducing protein digestibility (Mole and Waterman 1987). Although the foregut fermentation of ruminants neutralizes most of these substances, elephants rely on hindgut fermentation alone.

Management implications of lick location

Most of the natural mineral licks in Aberdares National Park are in road banks. Road construction has exposed nutrient- and clay-rich subsurface earth, on which elephants have capitalized for geophagy. It appears to be easier for elephants to excavate with their tusks on banks than to dig on a flat surface. At artificial licks, elephants were observed to dig by using their forelegs, sometimes kneeling on them to lower their tusks to ground level in an awkward posture. It was also observed that open glades are often flooded during the rainy season and their mineral licks were located at the edges of the glades, forming small banks. In Aberdares National Park, elephants appear to use mineral licks more in the wet than in the dry season. These patterns are possibly partly due to mineral licks in the open being exposed to volatilization and leaching (Underwood 1977).

Elephants appear to have degraded the artificial lick site at Treetops but not that at The Ark. Treetops is situated on what used to be a major migration route of elephants between the Aberdares and Mt Kenya, through Nyeri Forest. The vegetation around the lick at Treetops has only scattered trees left from the original woodland cover (pers. obs.).

Social patterns of geophagy

It has been shown in ungulates that geophagy is driven by nutritional requirements that tend to be greatest in females due to the demands of growing offspring (Holds et al. 2002). The present study provides inconclusive evidence for this pattern.

Although data on elephants visiting artificial licks at The Ark and Treetops indicate a preponderance of females, the population structure is unfortunately not known. It was observed that visits of males involved not only geophagy but also playing, wallowing and socializing. Adult females appeared to be purposeful, ingesting more mouthfuls of earth than did adult males. Male elephants visited the artificial licks alone or in groups of two to four, whereas females visited as part of family groups consisting of the matriarch, several related daughters and their juveniles. The time spent by the family group at the lick appeared to be greatly influenced by the matriarch's appetite for salt, because of her role as leader.

Conclusions and recommendations

- Where the traditional range of elephants has been reduced, as in Aberdares National Park, the possibility must be borne in mind that elephants can no longer supplement their diet by visiting scattered, naturally enriched sites.
- Road banks appear to be attractive to elephants for geophagy, but it is unclear whether these are a sufficient substitute for resources lost by confinement to limited ranges. Further analyses should be done in other national parks.
- The reasons for geophagy by elephants remain inconclusive. Direct physiological work should be done to confirm deficiencies of sodium and iodine.
- Permission to provide salt to attract wildlife should not be given without considering its ecological effect. The sites for mineral supplementation should be judiciously selected and the chemical composition monitored and, if necessary, managed.
- The natural diet of elephants and supplements artificially provided to them should be analysed for iodine as well as sodium and other elements.
- Further comparative analyses of geophagy by elephants among different ecosystems in Africa and Asia should be carried out.

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References

Ayeni, J.S.O. 1977. Waterholes in Tsavo National Park, Kenya. *Journal of Applied Ecology* 14:369–378.

Bouyoucos, G.J. 1962. Hydrometer method improved for making particle size analysis. *Agronomy Journal* 5(3):464–465.

Bowell, R.J., and Ansah, R.K. 1994. Mineral status of soil and forage in the Mole National Park, Ghana, and implications for wildlife nutrition. *Environmental Geochemistry and Health* 16:41–58.

Bowell, R.J., Warren, A., and Redmond, I. 1996. Formations of cave salts and utilization by elephants in the Mt Elgon Region, Kenya. In: J.D. Appleton, R. Fuge and G.J.H. McCall, eds., *Environmental geochemistry and health with special reference to developing countries.* Special Publication 113. Geological Society of London, p. 63–80.

Crawley, M.J. 1983. *Herbivory: the dynamics of animal plant interactions.* Blackwell Scientific Publications. London.

Davies, A.G., and Baillie, I.C. 1988. Soil eating by red leaf monkeys *(Presbytis rubicunda)* in Sabah, northern Borneo. *Biotropica* 20:252–258.

Fraser, D., and Reardon, E. 1980. Sampling problems and interpretation of chemical analysis of mineral springs used by wildlife. *Journal of Wildlife Management* 44:623–731.

Hanks, J. 1979. *A struggle for survival: the elephant problem.* Struik, Cape Town.

Henshaw, J., and Ayeni, I. 1971. Some aspects of big game utilization of mineral licks in Yankari Game Reserve, Nigeria. *East African Wildlife Journal* 9:73–82.

Holds, R.M., Dudley, J.P., and McDowell, L.R. 2002. Geophagy in the African elephant in relation to availability of dietary sodium. *Journal of Mammalogy* 83(3):652–664.

Huffman, M.A. 1997. Current evidence for self-medication in primates: a multidisciplinary perspective. *Yearbook of Physical Anthropology* 40:171–200.

Klaus, G., Klaus, H.C., and Schimid, B. 1998. Geophagy by large mammals at natural licks in the rain forest of Dzanga National Park, Central African Republic. *Journal of Tropical Ecology* 14:829–839.

Knight, M.H., Eloff, A.K., and Bornman, J.J. 1988.The importance of borehole water and lick sites to Kalahari ungulates. *Journal of Arid Environments* 15:269–281.

Kreulin, D.A. 1985. Lick use by large herbivores: review of benefits and banes of soil consumption. *Mammal Review* 15:107–123.

Mahaney, W.C., Hancock, R.G.V., Aufreiter, S., Huffman, M.A. 1996. Geochemistry and clay minerology of termite mound soil and the role of geophagy in chimpanzees of the Mahale Mountains, Tanzania. *Primates* 37:121–134.

Mahaney, W.C., Hancock, R.G.V., Aufreiter, S., Huffman, M.A., and Zippin, J. 1999. Chemistry, mineralogy and microbiology of termite mound soil eaten by the chimpanzees of the Mahale Mountains, western Tanzania. *Journal of Tropical Ecology* 15:565–588.

Mahaney, W.C., Milner, M.W., Sanmugadas, K., Hancock, R..G.V., Aufreiter, S., Wrangham, R., and Pier, H.W. 1997. Analysis of geophagy soils in Kibale forest, Uganda. *Primates* 38:323–333.

Mattson, J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119–161.

McDowell, L.R. 1995. Effect of low calcium or low phosphorus diets on free choice consumption of dietary phosphate by lactating dairy cows. *Journal of Dairy Science* 59:571–579.

McKeague, J.A. 1976. *Manual on soil sampling and methods of analysis.* Soil Survey Commission, Soil Research Institute, Ottawa.

Michell, A.R. 1994. Physiological roles of sodium in mammals. In: C.J.C. Phillips and P.C. Chicy, eds., *Effects of sodium on farm animal behavior*. Chalcombe Publications, UK.

Milewski, A. 2000. Iodine as a possible controlling nutrient for elephant populations. *Pachyderm* 28:78–90.

Mole, S., and Waterman, P.G. 1987. A critical analysis of techniques for measuring tannins in ecological studies: techniques for chemically defining tannins. *Oecologia* 72:137–147.

Oates, J.F. 1978. Water-plant and soil consumption by guereza monkeys *(Colobus guereza)*: a relationship with minerals and toxins in the diet. *Biotropica* 10:241–253.

Okalebo, J.R., Gathua, K.W., and Woomer, P.L. 2002. *Laboratory methods of soil and plant analysis: a working manual*, 2nd ed. Tropical Soil Biology and Fertility Programme, Nairobi.

Phillips, C.J.C. 1993. Sodium application to pasture: rumen dynamics. *Grass and Forage Science* 46:325–331.

Phillips, C.J.C., and Chicy, P.C. 1995. *Effects of sodium on farm animal behavior.* Chalcombe Publications, UK.

Redmond, I. 1982. Salt mining elephants of Mount Elgon. *Swara* 5:28–31.

Reid, P., and Horvath, J. 1980. Nutrient assessment environment. In: *Assessing nutrient status of herbivores.* Academic Press, New York.

Robbins, C.T. 1993. *Wildlife feeding and nutrition.* Academic Press, New York.

Ruggiero, R.G., and Fay, J.M. 1994. Utilization of termitarium soils by elephants and its ecological implications. *African Journal of Ecology* 32:222–232.

Spinage, C.A.1994. *Elephants*. A.D. Poyser, London.

Underwood, E.J. 1977. *Trace elements in animal and human nutrition.* Academic Press, New York.

Underwood, E.J. 1981. *The mineral nutritional of livestock*, 2nd ed. Academic Press, New York.

Vermeer, D.E., and Ferrell, R.E. 1985. Nigerian geophagical clay: a traditional anti-diarrhea pharmaceutical. *Science* 227:634–636.

Weir, J.S. 1973. Exploitation of soluble soil by elephants in Murchison Falls National Park, Uganda. *East African Wildlife Journal* 11:1–7.

Wink, M. 1993. Quinolizidine alkaloids. In: P.G. Waterman, ed., *Methods in plant biochemistry*. Academic Press, New York.