# African elephants (Loxodonta africana) as an example of a mega-herbivore making movement choices based on nutritional needs (#29144)

First submission

## Editor guidance

Please submit by **16 Jul 2018** for the benefit of the authors (and your $200 publishing discount).

**Literature Review article**
This is a Literature Review article, so the review criteria are slightly different.
Please write your review using the criteria outlined on the 'Structure and Criteria' page.

**Image check**
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

**Files**
Download and review all files from the materials page.

3 Table file(s)

# Structure and Criteria



## Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **STUDY DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

## Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

### BASIC REPORTING

- Clear, unambiguous, professional English language used throughout.
- Intro & background to show context. Literature well referenced & relevant.
- Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- Is the review of broad and cross-disciplinary interest and within the scope of the journal?
- Has the field been reviewed recently? If so, is there a good reason for this review (different point of view, accessible to a different audience, etc.)?
- Does the Introduction adequately introduce the subject and make it clear who the audience is/what the motivation is?

### STUDY DESIGN

- Article content is within the Aims and Scope of the journal.
- Rigorous investigation performed to a high technical & ethical standard.
- Methods described with sufficient detail & information to replicate.
- Is the Survey Methodology consistent with a comprehensive, unbiased coverage of the subject? If not, what is missing?
- Are sources adequately cited? Quoted or paraphrased as appropriate?
- Is the review organized logically into coherent paragraphs/subsections?

### VALIDITY OF THE FINDINGS

- Impact and novelty not assessed. Negative/inconclusive results accepted. Meaningful replication encouraged where rationale & benefit to literature is clearly stated.
- Conclusions are well stated, linked to original research question & limited to supporting results.
- Speculation is welcome, but should be identified as such.
- Is there a well developed and supported argument that meets the goals set out in the Introduction?
- Does the Conclusion identify unresolved questions / gaps / future directions?

# Standout reviewing tips



The best reviewers use these techniques

| Tip | *Example* |
| --- | --- |
| **Support criticisms with evidence from the text or from other sources** | *Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.* |
| **Give specific suggestions on how to improve the manuscript** | *Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).* |
| **Comment on language and grammar issues** | *The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.* |
| **Organize by importance of the issues, and number your points** | *1. Your most important issue*<br>*2. The next most important item*<br>*3. …*<br>*4. The least important points* |
| **Please provide constructive criticism, and avoid personal opinions** | *I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC* |
| **Comment on strengths (as well as weaknesses) of the manuscript** | *I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.* |

# African elephants (Loxodonta africana) as an example of a mega-herbivore making movement choices based on nutritional needs

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**Background.** The increasing human population and global intensification of agriculture have had a major impact on the world’s natural ecosystem and caused devastating effects on populations of mega herbivores such as elephants, through habitat reduction and fragmentation and increased human-animal conflict. Animals with vast home ranges are forced into increasingly smaller geographical areas, often restricted by fencing or encroaching anthropogenic activities, resulting in huge pressures on these areas to meet the animals’ resource needs. This can present a nutritional challenge and cause animals to adapt their movement patterns to meet their dietary needs for specific minerals, potentially causing human-animal conflict. The aim of this review is to consolidate understanding of nutritional drivers for animal movement, especially that of mega-herbivores and focus the direction of future research. Peer reviewed literature available was generally geographically specific and on isolated populations of individual species. African elephants have the capacity to extensively alter the landscape and have been more extensively studied than other mega-herbivores, making them a good predominant example species to use for this review. Relevant examples of other herbivores moving based on nutritional needs are also discussed.

**Methods.** Three databases were searched in this review: Scopus, Web of Science, and Google Scholar, using identified search terms. Inclusion and exclusion criteria were determined and applied as required. Additional grey literature was reviewed as appropriate.

**Results.** Initial searches yielded 1,870 records prior to application of inclusion and exclusion criteria. A less detailed review of grey literature, and additional peer-reviewed literature which did not meet the inclusion criteria but was deemed relevant by the authors was also conducted to ensure thorough coverage of the subject.

**Discussion.** A review of peer reviewed literature was undertaken to examine nutritional drivers for African elephant movement, exploring documented examples from free-living African elephants and, where relevant, other herbivore species. The intention of this was to aid in prediction or mitigation of human-elephant conflict, potentially when animals move according to nutritional needs, and related drivers for this movement. In addition, appropriate grey literature was included to capture current research.

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## Abstract

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The increasing human population and global intensification of agriculture have had a major impact on the world's natural ecosystem and caused devastating effects on populations of mega herbivores such as elephants, through habitat reduction and fragmentation and increased human-animal conflict. Animals with vast home ranges are forced into increasingly smaller geographical areas, often restricted by fencing or encroaching anthropogenic activities, resulting in huge pressures on these areas to meet the animals' resource needs. This can present a nutritional challenge and cause animals to adapt their movement patterns to meet their ~~dietary~~ needs for specific minerals, potentially causing human-animal conflict.

The aim of this review is to consolidate understanding of nutritional drivers for animal movement, especially that of mega-herbivores and focus the direction of future research. Peer reviewed literature available was generally geographically ~~specific~~ and on isolated populations of individual species. African elephants have the capacity to extensively alter the landscape and have been more extensively studied than other mega-herbivores, making them a good ~~predominant~~ example species ~~to use~~ for this review. Relevant examples of other herbivores moving based on nutritional needs are ~~also~~ discussed.

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## Introduction

African elephants (*Loxodonta africana*) are categorised ~~as~~ Vulnerable on the IUCN Red List and free living populations have declined rapidly across Africa since 1970, predominantly as a result of increased poaching and competition for resources with an increasing human population (Blanc, 2008). This competition arises due to the intersection of human activities with elephants' home ranges, and much research is devoted to investigating the reasons why the animals move through areas which lead them into conflict with humans. The aim of this review is to consolidate the current understanding of nutritional drivers for animal movement, especially that of mega-herbivores and focus the direction of future research. Current work was generally geographically specific and on isolated populations of individual species. African elephants have the capacity to extensively alter the landscape and have been more extensively studied than other mega-herbivores, making them a good ~~predominant~~ example species to use within this review. Relevant examples are included of other herbivore movement based on nutritional needs.

Due to their vast food consumption and behaviour, elephants can cause significant damage to crops and vegetation (Sukumar, 1990; Hoare, 2000) and pose a risk to human life and infrastructure. Continued increase in global human population, to 9.7 billion by 2050, and associated intensification of agriculture will have a major impact on the world's natural ecosystem. This, coupled with a predicted reduction of 200-300 million hectares of wildlife habitat worldwide (Nyhus, 2016), will ~~cause an increase in~~ human-animal conflict. Habitat encroachment and fragmentation poses a substantial threat to elephant populations, forcing them to condense into ever-smaller geographical areas or fenced reserves, whilst putting increased pressure on these areas to meet the animals' resource needs. This can present a nutritional challenge and cause animals to adapt their movement patterns to meet their dietary needs ~~for~~ specific minerals.

The aim of this review ~~is~~ to consolidate understanding of nutritional drivers for animal movement especially those of mega-herbivores, and focus the direction of future research. ~~The aim~~ will be achieved with the following objectives:

1. Examine the relationship between the geochemistry and associated soil of an area, and how this can alter the minerals available to consumers (herbivores) in plants, and thus how geochemistry may affect herbivore and specifically elephant movement. Only minerals are being considered within this review and not other nutrients for example vitamins, ~~because they do not contribute directly to the relationship between mineral status and environmental geochemistry of the soil.~~
2. Examine current knowledge on mineral requirements in elephants
3. Assess current evidence that minerals in the soil (and plants) can act as drivers for elephant movement.
4. Consider how mineral distribution in the landscape could be used to predict ~~or reduce~~ human-elephant conflict in the future.

This review is intended ~~for~~ conservation managers, ecologists, conservation biologists, national park management authorities, and potentially ~~to be of benefit to~~ managers of animals under human care both within zoos ~~or managed in situ in~~ fenced reserves. There ~~are no~~ significant reviews ~~already conducted to~~ explore the relationship between applied geochemistry and ~~elephant~~ physiological drivers for movement.

**Methods**

The following method was used to ensure coverage of the literature ~~was comprehensive and unbiased~~. Published studies were identified from ~~a number of~~ databases, using a range of search terms relating to elephant movement choices, as described in Table 1.

**Databases searched:** Scopus, Web of Science, and Google Scholar (searched up to 1st April 2018).

**Fields searched:** titles, keywords, abstracts

Only publications which met the following criteria were included in this review. The publication:

1. Contained at least one of the search terms from each box in Table 1 in the abstract, title or keywords.
2. Was available to the authors ~~in full.~~
3. Was in a peer-reviewed journal.
4. Was in English.
5. Was relevant to the subject matter (e.g. excluded irrelevant terms such as elephant grass *Pennisetum purpureum*).

**Grey literature reviewed**

Additional relevant literature was identified using a number of different approaches. This included literature identified:

1. In the repeatable database search, but which did not meet the inclusion criteria for the critical appraisal (such as reviews, books, and conference proceedings)
2. Using internet searches of key terms and snowballing by searching the reference lists of relevant literature (Sayers, 2007).

The literature identified included non-peer-reviewed papers in journal articles, books, as well as some specific literature on land use choices of wild elephants.

**Results**

A repeatable search and appraisal of peer-reviewed literature using repeatable search methods and detailed criteria of inclusion and appraisal was conducted, and initial searches yielded 1,870 records. A less detailed review of grey literature, and additional peer-reviewed literature which did not meet the inclusion criteria but was deemed relevant by the authors was also conducted ~~to ensure thorough coverage of the subject~~. Additionally, some key papers on wild elephants were also reviewed.

**Discussion**

A review of literature was undertaken to examine nutritional drivers for African elephant movement, exploring examples from free-living African elephants and, where relevant, other herbivorous species. The aims of the review was to explore documented nutritional requirements of elephants, ~~as well as~~ differences between nutritional needs of cows and bulls, how geochemistry affects the consumer (elephant) through consumption of food plants, water and soil, and finally to consider how this could be used to predict elephant movement and associated human-elephant conflict.

## **Introduction – Feeding behaviour**

African elephants (*Loxodonta africana* and *L. cyclotis*) consume a variety of plant material including grasses, leaves, twigs, fruits, barks, herbaceous material and soil. Although described as generalist herbivores consuming over 400 species of plants, populations may vary regionally and seasonally in their plant choice. African savanna elephants (*L. africana*) are predominantly seasonal grazers and browsers with fruit, barks and soil being consumed as secondary food choices (Kabigumila, 1993). African forest elephants (*L. cyclotis*) were documented to consume more fruit than savanna elephants; White, Tutin and Fernandez (1993) recorded consumption of 72 species of fruit by forest elephants in the Lopé reserve, Gabon, significantly more than the occasional opportunistic consumption, documented for the savanna elephant. There is debate as to whether savannah elephants are predominantly grazers or browsers, with evidence supporting both feeding strategies: Williamson (1975) reported elephant diets in Hwange National Park, Zimbabwe to consist almost entirely of woody plants whereas Wing and Buss (1970) reported that elephants in Uganda relied primarily on grasses (approximately 90% of bulk) and therefore labelled the species as grazers. Such geographical variations in diet have prompted some authors to classify elephants as browsers (Jachmann & Bell, 1985), whereas others maintain they are primarily grazers (Beekman & Prins, 1989; Tangley, 1997).

Several studies indicate that savanna elephants spend over half of their daily time budget feeding; elephants in Tsavo National Park, Kenya were observed to feed for 48-63% of daylight hours (Dougall & Sheldrick, 1964) and elephants in Lake Manyara National Park, Tanzania were observed to spend on average 76% of daylight hours feeding (Beekman & Prins, 1989). Where feeding conditions improved and food availability increased, Guy (1975) observed elephants in Zimbabwe to reduce the total amount of time spent feeding to 50-60% of overall time budget, from a greater proportion of their time budget when food resources were limited. Likewise, savannah elephants in areas of food scarcity in Uganda were reported by Beekman and Prins (1989) to spend as much as 74% of their total time budget feeding. Flexibility in food items consumed and time spent feeding, indicated that elephants responded to nutritional needs and adapt their feeding strategy accordingly, in line with available food resources.

Savanna elephants have been documented to feed throughout the day, with decreased feeding and increased resting during the middle part of the day; 12:00-14:00 hrs. This pattern was observed in both sexes (Laws, 1970; Beekman & Prins, 1989; Shannon et al., 2008). Seasonally, the total amount of time spent feeding per day has not been documented to change, although elephants were observed by Shannon et al. (2008) adjust the time of day spent feeding in the hotter summer months. Evidence suggests that plant selection and feeding strategy changes depending upon availability. During the wet season elephants were observed by Beekman and Prins (1989) to spend 67% of time grazing with 8% browsing, whilst during the dry season proportions shifted to 23% of time grazing and 60% browsing. During the dry season, the protein content of the grasses decreased; when the protein content of grasses dropped to <2.5%, elephants in Tanzania were seen by Barnes (1982) to increase their browse consumption to compensate. Browse typically contains higher levels of secondary compounds such as tannins than grass (Ellis, 1990) and thus, as a by-product of this increased browse consumption during the wet season, tannin and associated levels of toxin accumulation were seen to increase (Barnes, 1982).

Mineral levels in plants vary seasonally, geographically and between different parts of the plant; Table 2 provides specific examples. Due to the generalistic feeding nature of both African elephant species, and their feeding strategies adopted, it is thought they are able to adapt food selection as required to meet their target levels of (as yet undetermined) mineral requirements (Bax & Sheldrick, 1963). This was demonstrated in elephants within the Kruger National Park (KNP), South Africa, where there is substantial geographical and seasonal variation in plant type consumption by elephants. Stable carbon isotope analysis of faecal material indicated that during the dry season elephants in northern KNP consumed significantly more grass than their southern counterparts; 40% of their diet was grass in the northern part of the park during the dry season, compared to just 10% of elephants' diet in southern KNP. In contrast, this difference in grass consumption between elephants in the northern and southern parts of this national park was not apparent during the wet season, when elephants throughout the park consumed grass as approximately 50% of their overall diet (Codron et al., 2006), agreeing with an overall trend of increased grass consumption during the wet season (Beekman and Prins, 1989). Elephants consume a vast number of different plant species, however they generally receive the bulk of their diet from a few selected species which vary seasonally and geographically (Meissner et al., 1990; Kabigumila, 1993). Bax and Sheldrick (1963) observed elephants in the Tsavo National Park, Kenya, to select specific plant parts, notably bark rich in calcium.

Free living African elephant daily food intake is estimated from either the weight of the stomach contents (post mortem) or from extrapolation of data on feeding rates and time spent feeding. Both methods have produced similar estimates of daily dry matter intake by adults of about 1.0-1.5% of body weight (Meissner et al., 1990; de Villiers et al., 1991; Ullrey, Crissey & Hintz, 1997). Dry matter intake relative to body weight is influenced by a number of factors: dry matter digestibility, environmental stressors, activity levels and life stage of the animal (adult maintenance, growth, pregnancy or lactation) (Meissner et al., 1990). Laws (1970) concluded that non-pregnant females and males consumed 1.0-1.2% BW DM whereas pregnant females consumed 1.2-1.5% BW DM. On an as-fed basis, elephants consumed about 4% of their body weight per day.

Evidence shows differences between elephant bulls and reproductively active cows in their nutritional needs and associated diet choices, with cows requiring higher levels of minerals and protein to support growing calves. Greyling (2004) documented that in the Associated Private Nature Reserves (APNR), South Africa, there was a nutritional difference between various sampled parts of the plants consumed by elephants, with leaves containing more calcium and phosphorus than twigs. However, plant parts (e.g. leaves) consumed by cows and bulls contained similar concentrations of these two minerals. Leaves consumed by cows and bulls contained 0.14% DM and 0.15% DM phosphorus respectively, whereas twigs consumed by cows and bulls contained significantly lower levels of phosphorus; 0.06% DM and 0.057% DM respectively. It is therefore suggested that cows and bull meet their differing nutritional needs primarily through plant part selection; family groups with pregnant and lactating females consumed proportionally more leaves and bark in their diet compared to bulls. In the dry season, females consumed 3% leaves and 14% bark, whereas males consumed 1% leaves and 6% bark. Males consumed additional twigs to account for this difference. This agreed with the previous work of Stokke and DuToit (2000), who found bulls consumed more twigs than cows, and cows engaged in more leaf stripping than bulls.

Greyling (2004) also documented bulls to consume more plant species with higher calcium content than adult cows at maintenance (without calves) throughout the year. Greyling suggested that such mineral selectivity may be due to a higher calcium requirement for tusk growth in males compared to females at maintenance. This observation supports previous work conducted by McCullagh (1969a) who suggested a calcium requirement for male elephants of 8-9g per day. Additionally, lactating females were found to have significantly higher calcium needs than adult females at maintenance as summarised in Table 3.

During the dry season, Greyling (2004) found bull faeces contained significantly lower phosphorus levels than cows in family groups; cow faecal samples contained on average 18% more phosphorus than bulls. Faecal phosphorus levels have been used in agriculture to estimate dietary phosphorus in livestock, and they are a more reliable index to diet quality than faecal nitrogen as they are not influenced by tannins. Lower faecal phosphorus in bulls suggests that less phosphorus was consumed in the diet, indicating that the requirement for bulls was lower than that of cows (Holechek et al., 1985; Grant, Meissner & Schultheiss, 1995; Wrench, Meissner & Grant, 1997; Wu, Satter & Sojo, 2000). Feeding time budgets of populations of both bulls and cows, studied in three reserves in South Africa, were found by Shannon et al. (2008) ~~to be similar.~~ This suggests that cows obtained the required increased dietary energy for pregnancy or lactation, by altering plant selection to preferentially select more energy dense plants, rather than by increasing time spent feeding (Shannon et al., 2008). This finding contradicts that of Guy (1975) who concluded that bulls consumed more 'trunk fulls' of plant material per minute than cows, especially in the dry season, and bulls stayed for longer at feeding sites than family groups (du Toit, 2000). Stomach fill post mortem of non-pregnant or lactating females and males was smaller than that of pregnant and lactating females, suggesting that females increased overall food consumption to meet their nutritional demands of pregnancy and lactation (Laws, 1975). These pieces of mixed evidence suggest that several feeding strategies may be adopted by elephant cows and bulls to meet their specific individual nutritional needs, depending upon the unique environments in which they live, and resources available to them.

Documented literature on specific mineral mineral needs in elephants is very limited and requirements *per se* have not been experimentally determined (Das et al., 2015). Table 3 documents minerals for which estimates have been recorded for African and Asian elephants (Elephas maximus) directly. As these values were reached from various different studies, on different populations (captive and ~~wild~~), ~~methods~~ of measurement were different e.g. grams required per day compared to mg required per kg dry matter intake or body weight of the animal. This table does not include requirements extrapolated from ~~that of the~~ domestic equid.

### Comparison of elephant nutrition requirements with the domestic horse model

Due to the lack of knowledge on the digestive physiology of many wild animals, animal nutritionists use domestic species as physiologic models when designing diets for captive exotic animals. For large hindgut fermenters like elephants and rhinos, the horse (equid) has been suggested as the appropriate model for most nutrients due to the similarities in gastrointestinal tract. This approach was validated for white rhinos (*Ceratotherium simum*) and Indian rhinos (*Rhinoceros unicornis*) but not black rhinos (*Diceros bicornis*) or any elephant species (Clauss, Kienzle & Wiesner, 2003). Clauss et al. (2007) demonstrated that black rhinos absorb micronutrients in the same manner as equids, and suggested the same may apply in elephant species. Despite the lack of validation, the horse was extensively used as a model for captive elephant nutrition (Olson, 2004; Clauss et al., 2007; Walter, 2010) and overall, it is acknowledged that it is a suitable model for some aspects of elephant digestion: the mechanisms by which dietary supplements and dietary crude fibre content influence digestibility, and the mechanism of calcium absorption and faecal volatile fatty acid composition. However, elephants have a faster ingesta passage rate than equids, with a total gut transit time of 11-46 hours, compared to an average of 48 hours in equids, and thus digestibility coefficients achieved for all nutrients are lower (Bax & Sheldrick, 1963; Clauss et al., 2003). This must be factored into any comparisons with equid recommendations and used with caution.

## Reported mineral deficiencies in captive and free-living elephants

### Calcium

As previously discussed, it was suggested that elephants have highest calcium (Ca) demands when lactating (females) followed by tusk growth (males). Ca metabolism in elephants appears to be similar to that of equids, with approximately 60% being absorbed from the diet directly in the intestines, independent of total consumption or requirement, with excess excreted in the urine. As with other mammals, elephants maintain serum calcium within a narrow range through intestinal absorption, renal excretion and mobilisation of bone (Ullrey, Crissey & Hintz, 1997; Clauss et al., 2003).

Partington (2012), while assessing calcium intake in elephants at 14 UK zoos, determined that a minimum of 0.33-0.77% DM calcium was provided in the offered diets (values represented minimums as Ca provision from grass or browse forages was not included in the calculations).

Nonetheless, even the minimum concentrations exceeded the captive adult elephant maintenance recommendation of 0.3% dietary DM (Ullrey, Crissey & Hintz, 1997). Similarly, diets fed to zoo elephants in the 7 elephant-holding Brazilian zoos contained on average 0.7% Ca DM, showing that minimum recommended levels were being met (Carneiro et al., 2015) and diets of semi-captive Asian elephants in India contained 0.46-0.58% DM calcium further supporting the conclusion that calcium deficiencies have rarely been documented in healthy adult captive elephants on maintenance diets. There is, however, evidence that incidence of Ca deficiency is higher in cows during partition and lactation, when calcium demand is increased; sub-clinical hypocalcaemia was reported immediately prior to partition at Rotterdam Zoo when calcium demand was not met through dietary provision (van der Kolk et al., 2008).

Metabolic bone disease (rickets) was reported in captive hand-reared Asian elephant calves. This disease results from an imbalance in the calcium to phosphorus ratio or from intestinal malabsorption, and unbalanced milk formulation may have played a role in this (Ensley et al., 1994).

**Iodine**

The thyroid mass of an elephant relative to its body mass is double the predicted size, compared to other mammals. This may indicate that the iodine (I) requirements of elephants are proportionally higher than those of other herbivores, and that due to the exclusively herbivorous diet of elephants, they may be susceptible to I deficiency (Milewski, 2000). Due to the lack of essentiality of I to plant metabolism, land plants have little reason to translocate iodine from soil to foliage, therefore plants consumed by elephants may be low to deficient in iodine (Shetaya et al., 2012; Humphrey et al., 2018). Soil dust deposition has been documented to increase I levels of foliage in some situations (Watts et al., 2015). As an alternative I source, elephants may seek iodine supplementation from I rich water or soil (via geophagy). Humans in Malawi were able to obtain as much as 70% of daily I requirements from drinking 2 litres of borehole water per day (Watts et al., 2015). I is required for reproduction, and the high reproductive success of elephants in conservation areas such as Addo Elephant Park, which contained several boreholes, was hypothesised to be linked with an increased supply of iodine (Milewski, 2000; Milewski and Dierenfeld, 2012).

In the Kitum caves, Mount Elgon, Kenya, elephants consume the cave salts due to the high levels of calcium, sodium, magnesium and phosphorus provided (Bowell, Warren and Redmond, 1996). Iodine was measured in the salt crusts at 1,149 mg/kg, which was >100 times greater than iodine concentrations in the most I-rich soils in the vicinity. Reproductive output of elephant populations consuming these minerals are also high. Given these various lines of inferential evidence, supply or restriction of I-rich bore holes could be used as an effective method of population control *in situ*, without affecting reproductive success of smaller herbivores that may have a proportionally lower requirements for I, which could be realised by diet, water or geophagy (Milewski, 2000; Milewski & Dierenfeld, 2012).

**Iron**

Iron (Fe) deficiency anaemia has rarely been reported in captive or free living elephants, although several cases of anaemia caused by liver fluke infection, retained placenta, tuberculosis, tuberculosis treatment and malabsorption syndrome have been documented (Dierenfeld, 2008). Only a single reported Fe deficiency anaemia related to low dietary iron intake, affecting three newly imported Asian elephants, was documented; clinical signs resolved upon dietary supplementation (Kuntze & Hunsdorff, 1978). Diets of semi-captive Asian elephants contained 105-126 mg/kg, significantly in excess of the Nutrition Advisory group recommendation of 50 mg/kg (Ullrey, Crissey & Hintz, 1997; Das et al., 2015).

**Zinc**

The dietary recommendation for zinc (Zn) in captive elephants is 40 mg/kg DM (dry matter) diet, based on determined requirements of equids (Olson, 2004; Ullrey et al. 1997). Partington (2012) reported zinc levels of between 22 and 52 mg/kg DM in zoo elephant diets offered in 14 UK facilities. However, this figure does not account for Zn provision from grass and/or browse forages, which comprise the majority of the diets, hence these data are limiting. Nonetheless the lower end values, suggest that some animals may have been consuming inadequate levels of dietary Zn. Semi-captive Asian elephants in India were reported to consume diets containing 38.4 to 45.9 mg/kg Zn. Again animals at the lower end of this range may have been susceptible to Zn deficiency, however, no clinical signs of deficiency were seen and serum concentrations were within the ranges reported for healthy elephants (Ullrey, Crissey & Hintz, 1997; Das et al., 2015). Excess dietary calcium was documented to cause Zn deficiency resulting in skin abnormalities (Schmidt, 1989; Dierenfeld, 2008). Schmidt (1989) reported a case of zinc deficiency in a captive Asian elephant, resulting in ~~a~~ secondary immune deficiency and skin lesions. Dietary Zn level in that individual was increased from 22 to 54 mg/kg ~~of feed~~ DM; significant clinical improvement was seen within 2 weeks, with lesions resolved after eight weeks.

**Effect of geochemistry on elephant dietary intake**

The availability of minerals to the plant from the soil underpins the relationship between herbivores and their food supply. The distribution of vegetation was suggested to be strongly associated with the geomorphology of the soil (Lawson, Jenik & Armstrong Mensah, 1968; Bell, 1982). Generally plants will reflect the soil profile; those growing in mineral deficient areas will lack key minerals resulting in deficiencies in the consumer; those growing in mineral abundant areas will reflect this, and the mineral abundance passed onto the organism consuming ~~it~~ (Hurst et al., 2013; Joy et al., 2015). The ability of an area to supply minerals to an animal does not ultimately depend ~~exclusively~~ on the mineral status of the soil and geochemical parameters (such as organic matter and soil pH), but also ~~with~~ the ability of the plant to incorporate the minerals (Bowell & Ansah, 1994). Additional factors affect the mineral levels within a plant: the pathway of nutrients from the soil to the plant depends upon the amount of element present, the various soil factors that affect the minerals' bioavailability and the plant factors which determine the rate of uptake of the mineral (Maskall & Thornton, 1996).

Soil factors which affect a minerals' bioavailability include the composition of the parent material, quantity and composition of organic matter and the soil pH (Hurst et al., 2013). The relationship between mineral status of the soil and parent rock was strongest where there was minimal chemical weathering (Bowell & Ansah, 1994). Organic matter also affects bioavailability, especially that of iodine (Shetaya et al., 2012; Humphrey et al., 2018). Soil pH greatly influences the metal availability; in alkali soils, generally the bioavailability of molybdenum and selenium increases, whilst that of copper, cobalt and nickel decreases. Further, increased availability of phosphorus in alkali soil contributes to its enhanced uptake into the plant (Maskall & Thornton, 1996; Sutton, Maskall & Thornton, 2002).

Plant factors affecting rate of uptake of a mineral include: age of plant (with levels of trace elements decreasing in older plants), rate of plant growth (with rapidly growing plants displaying reduced levels of trace elements), and plant species (with differences seen between levels of trace elements in different plant species grown in the same soil (Maskall & Thornton, 1996). The greatest differences in mineral content were reported  between grasses and browses (Gomide et al., 1969; Ben-Shahar & Coe, 1992). Seasonally, trace element levels were reported to be higher in plants in the wet season: in the grazing pastures in the Kenyan highlands (Howard & Burder, 1962), in grasses by Lake Nakuru in the Rift Valley  (Maskall & Thornton, 1991) and in the Mole National Park, Ghana (Bowell & Ansah, 1994). Finally grazing status of the plant was seen to influence plant mineral levels, with increased mineral concentrations of up to 300% in grazed areas, notably sodium, phosphorus and calcium, compared to un-grazed areas supporting low animal densities (McNaughton, 1988).

Forage mineral analysis data is routinely used to assess mineral levels in agriculture, and despite limitations is a reliable index to be used to assess the general ability of forages to meet animals' mineral needs (McNaughton, 1988). However, soil, plant and weather factors can influence plants, causing depletion in the mineral profile of the soil. In the Sabi Sands Reserve, South Africa, 10 species of grasses were analysed; grasses from soils of higher mineral levels accumulated lower mineral concentrations in the grasses, compared to grasses from soils where the minerals were found in lower levels ~~in the soils, and higher levels in the grasses~~ (Ben-Shahar & Coe, 1992). ~~It was thought~~ in this case, this was due to sampled species attributes, and the effect of the local micro-climate on the plants.

**Geochemistry influencing animal movement**

Consideration of geochemistry is required for maintenance of healthy animal populations, especially within fenced reserves where animal migration is impossible. For example, in Lake Nakuru National Park, Kenya which is a fenced area of 160 km$^2$, the soil is derived from volcanic ash, pumice and lake sediment, with low levels of extractable cobalt (Co), copper (Cu) and acetic acid with a high alkaline soil pH. In this region of the Rift Valley, mineral deficiencies including copper and cobalt were seen in domestic cattle, as well as in impala (*Aepyceros melampus*) and waterbuck (*Kobus defass*) (Maskall & Thornton, 1996). The increased soil pH caused increased uptake of molybdenum by the plants, which in turn inhibited the utilisation of Cu in ruminant animals, further exacerbating the deficiency of Cu (Underwood, 1977). A geochemical survey was conducted and results related to observed clinical Cu deficiencies in animals. Following this investigation, recommendations were made to the Kenya Department of

Wildlife Conservation and Management that mineral salts containing Cot, Cu and selenium should be made available to wildlife in the park to mitigate these mineral deficiencies (Thornton, 2002). Due to the physiological differences between copper absorption in ruminants and non-ruminants, elephants as non-ruminants, are not as sensitive to this deficiency as ruminant species, thus the similar problem has not been extensively documented in elephants (Maskall & Thornton, 1996).

Further examples of clinically observed Cu deficiencies caused by an increased uptake of molybdenum by the plant and thus interference in the utilisation of Cu by the animal were seen in Grant's gazelle (*Gazelle granti*) from another area of the Kenyan Rift valley, moose (*Alces alces gigas*) in Alaska, and San Diego Wild Animal Park (USA) where hypocuprosis was diagnosed in several herbivores caused by feeding alfalfa with a high molybdenum (and sulphur) concentration (Kubota, Rieger & Lazar, 1970; Nelson, 1981; Maskall & Thornton, 1996). In northeast Zimbabwe, it was suggested that high concentrations of Fe in the soil and forage inhibit the availability of P to the plants, and thus to the cattle ~~consuming the plants~~. The high Fe concentration in the soil also reduced the absorption of Cu and Zn in cattle (Fordyce, Masara & Appleton, 1996).

**Land use decisions of herbivores**

Due to the ever-changing environment in which herbivores live, they are forced to make a series of prioritised decisions to ensure survival. These decisions range from spatial to temporal and vary in scale, ~~covering~~ smaller scale decisions around which plant part to select for consumption, through to decisions around seasonal movement patterns. De Knegt et al. (2011) concluded that forage availability, both in terms of quantity and nutritional quality, varies between seasons and years, meaning that individual herbivores adapt their ranging behaviour to meet ~~their~~ nutritional needs and ensure survival. This is especially important in times of resource scarcity, where poor decision making may result in a reduced reproductive output or death (Shannon et al., 2010). ~~A herbivore that is able~~ to discriminate between food items of high or low quality will have a selective advantage for long term survival (Fryxell, 2008).

From tracking data on 803 individuals of 57 species, Tucker et al. (2018) concluded that animal movements are on average shorter in resource rich environments. For example red deer *(Cervus elaphus)* in Slovenia were found to have reduced home ranges due to the enhancement of resources, via supplementary feeding (Jerina, 2012), further agreeing with the work conducted by Morellet et al. (2013) and Teitelbaum et al. (2015). Morellet et al. (2013) showed that the home range of roe deer *(Capreolus capreolus)* at higher altitudes, was significantly larger than ~~roe deer~~ at lower altitudes, despite forage availability at higher altitudes being more abundant and of higher quality, although the growing season was shorter than at lower altitudes. This suggested that home range, on an individual basis, is linked to a balance between metabolic requirements and ability to acquire food, accounting for seasonal variation. Teitelbaum et al. (2015) concluded from a review of 94 land migrations of 25 large herbivore species that there was a ten-fold increase in the migration distance between resource low and high areas. These studies indicated that animals living in resource poor areas will have larger home ranges and longer migration distances than those living in resource abundant areas.

African herbivores are not distributed heterogeneously. In the Serengeti National Park (SNP), areas of high herbivore concentration corresponded with areas providing forages of higher mineral content, implying that mineral content in foods was an important determinant of the spatial distribution of herbivores within this park (McNaughton, 1988). For example, magnesium, sodium and phosphorus had a particular influence on herbivore distribution, with high herbivore density areas having 300% more sodium, 50% more phosphorus and 10-23% more magnesium respectively than low herbivore density areas. Secondly, migratory grazing ungulate species in the SNP were reported to make seasonal movements based on grass mineral content[illegible]asses, as is common in many tropical soils, were not sufficient in magnesium and phosphorus to meet the mineral requirements for lactating and growing ruminants, and overall were lower in minerals than grasses growing in temperate soils (McDowell, 1985). The nutritional needs of lactating females and growing young were reported to be influential on movement choices, [illegible]mals have evolved with parturition periods being governed by the nutritional requirements of reproducing females and growing young, seasonal rainfall and distance from forage of sufficient quality being prioritised (McNaughton, 1990).

Herbivores have responded to plant evolutionary development through exhibiting seasonal habitat selection and a reported change in movement behaviour. This was shown by Shannon et al. (2010), from examining ranging behaviours and broad scale decision making of wildebeest (*Connochaetes taurinus*), Thomson's gazelle (*Gazella thomsoni thomsoni*), red deer (*Cervus* *elaphus*), reindeer (*Rangifer tarandus*) and elk (*Cervus Canadensis*). Zebra and wildebeest around the Sabi Sands Reserve, South Africa were seen to move seasonally to habitat types characterised by grass communities with a high proportion of nutritious species, and generally increased level of grass diversity, rather than selecting a particularly nutritious species within a broader habitat. Home range movement showed that diet composition and habitat use of these animals was influenced by the availability of nitrogen and phosphorus in grasses (Ben-Shahar & Coe, 1992)

**Land use decisions of elephants**

Several studies concluded that elephant habitat use is not random; elephants have specific preferences for various habitats and move to fulfill their various resource needs (Whitehouse & Schoeman, 2003; Osborn, 2004; Douglas-Hamilton, Krink & Vollrath, 2005; Dolmia et al., 2007; Thomas, Holland & Minot, 2008; Leggett, 2015). There are a myriad of factors that contribute towards an elephants' movement choices including availability of food and water, opportunity for social interaction, and human presence and associated activities. Hydrology and topography may also influence animal movement (Bowell & Ansah, 1994). De Knegt et al. (2011) suggested that daily movement of elephants related predominantly to food availability, and movements become extended by the distance traversed to water sources. Elephants in that study area of the KNP, South Africa concentrated foraging within areas of high forage availability that were closest to water, whilst still being large enough areas to optimise efficiency of movement and foraging.

The significance of the impact of human activity on the natural movements of elephants is rapidly increasing. From data across 57 species, Tucker et al. (2018) concluded that in areas with a high level of human presence, mammal movement decreased by 35-50%, compared with areas of low human presence. Over the last 150 years, expansion of human settlement into elephant habitat, and an increase in elephant killing (via poaching and hunting) has significantly altered elephants' home ranges across continental Africa (Osborn, 2004). Initially it was thought that there was a simple linear relationship between rising human and declining elephant densities at a national or subcontinental scale. However, Hoare and du Toit (1999) found that in an area of 15,000 km$^2$ in northwest Zimbabwe, the relationship was more complex. Using data from human populations, and observed elephant densities in the region, the authors determined that there was a threshold beyond which elephant and human coexistence could no longer occur, and elephant populations rapidly declined. The threshold was related to agricultural development, and was reached when land was spatially dominated by agricultural use, and the natural woodland (that constituted the elephants' habitat) became sub-dominant.

Water availability also affects elephant movement, both on a daily and seasonal basis. Three studies conducted in South Africa and Kenya, indicated that elephant movement increased throughout the wet season when water availability was greatest, and then rapidly decreased throughout the dry season, with elephants, especially lactating females, confining themselves to areas within 1-2 days' travel from water to enable them to conserve energy (Western & Lindsay, 1984; Codron et al., 2006; Thomas, Holland & Minot, 2008; Birkett et al., 2012).

**Elephant populations which have moved due to suspected mineral drivers**

Pretorius et al. (2011) concluded that elephants made movement choices based on nutritional provision in a specific area. Fertiliser was applied to mopane trees (*Colophospermum mopane*) in the in the APNR, South Africa, in various patches, resulting in an increase in the phosphorus and nitrogen levels in the mopane leaves. Elephants consumed more mopane leaves per patch in fertilised patches compared to unfertilised patches, regardless of patch size. Furthermore at a 100-$m^2$ patch size scale, elephants striped leaves more in fertilised patches than unfertilised patches, but were more likely to tree kill (through uprooting or breaking main trunks) in unfertilised patches than fertilised patches. It was suggested that elephants caused more impact to trees of lower value (through tree killing) whilst preserving trees of higher value (fertilised mopane) through coppicing.

Secondly Pretorius et al. (2012) concluded that phosphorus may be a key driver for elephant movement, with elephants moving throughout the year to maximise intake of this key mineral. In this study area in the APNR, there was a suspected local deficiency in phosphorus, potentially explaining why the elephants prioritised obtaining this mineral. Through the use of linear programming, it was determined that when phosphorus was excluded from the model, to account for the suspected deficiency, nitrogen provision was prioritised by the elephants during the wet season, when food availability was greatest, possibly for growth and reproduction. Energy was prioritised by the elephants during the dry season, possibly when this was potentially limited due to reduced food availability. Energy costs to obtain food and water during the dry season were often higher as elephants had to travel further, due to reduced abundance of forage and availability of water.

**Nutritional factors affecting elephant movement**

Minerals can be provided to elephants from multiple sources: from plants, from water or from soil (through geophagy). Firstly, examples of mineral provision from plants include sodium, calcium, magnesium and phosphorus. Forest elephants (*Loxodonta cyclotis*) in the Kibale National Park, Uganda, were suspected by Rode et al. (2006) to be crop raiding to meet their sodium need. It was suggested that minerals such as copper and sodium, rather than energy and/or protein, were limited in their availability, in the elephants' wild food plants, and were found in higher levels in crops. Often, wild elephant food plants which are high in sodium are also high in secondary compounds (Rode et al., 2006), which can inhibit the uptake of essential minerals and increase sodium excretion, and thus may further exacerbate low sodium intake (Jachmann, 1989). Crops contained lower levels of secondary compounds compared to wild plants, which allows the elephants to solve the complexities of meeting their sodium need, without interference from secondary compounds. For example, the highest sodium wild plant in this study, *Uvariopsis congensis* also contained high levels of secondary compound, saponin and had a high alkaloid score (Jachmann, 1989). Jachmann (1989) has also reported examples of elephant populations in the Miombo biome, Africa, making plant choices to create diets that contained high sodium and digestible sugar concentrations, and low concentrations of indigestible fibre and secondary compounds, especially avoiding plants high in total phenols and steroidal saponin. Additionally in Kibale National Park, seasonal availability of wild food was not correlated to the timing of crop-raiding events. This suggests that elephants may be selecting specific food crops due to their nutritional provision, rather than just being attracted to the presence of food crops and increased overall availability of food (Chiyo et al., 2005). Similarly, migrating Asian elephants in western Bengal were observed to preferentially consume nutritionally richer food crops opposed to natural fodder (Santra et al., 2008)

Finally, savannah elephants within the Mount Elgon region, Kenya, consumed salt deposits within the Kitum caves, which are rich in a variety of minerals including calcium, sodium, magnesium and phosphorus (Bowell, Warren & Redmond, 1996). Cases of uneven tusk wear were noted; this was presumed to have resulted from the use of tusks to scrape salts from the ceiling and walls. The environment within the cave can be warmer at 13.5°C than surrounding areas where night temperature can drop to 8°C, and although this could be encouraging the elephants to remain in the area overnight, it was suggested that there was a nutritional drive causing them to seek out and consume the salt deposits on the rocks.

Minerals can also be provided to elephants through the drinking of water. Sienne, Buckwal and Wittemyer (2014) investigated elephant use of bais (natural forest clearings which often have seasonal or year round sources of water present as surface waters) in the central African rainforest and concluded that mineral provision from water is likely to be attracting elephants to specific bais. Mineral concentrations in water from elephant-evacuated pits were higher than in surface water, and thought to be a causative factor behind bai visitation choice. In particular iodine, sodium, sulphur and zinc were elevated, calcium, magnesium, manganese, iron and tin concentrations were at least ten times higher in elephant-evacuated water than in surface waters. Blake (2002) observed that elephants congregated around bais during the dry season, correlating with a seasonal peak in mineral levels in pit water, which may be due to the seasonal ebbing of spring water flow. Likewise, savannah elephants in the Hwange National Park, Zimbabwe were recorded by Weir (1972) in greater numbers surrounding water sources with higher sodium content, pans of high sodium water were reported to have three times as many elephants when censured, compared to the lowest sodium areas, indicating elephants are making movement choices based upon sodium need.

Finally geophagy appears to be a normal behaviour of all elephant species in the majority of habitats and is thought to aid elephants in meeting their nutritional (mineral) needs (Holdø, Dudley and McDowell, 2002). There is some evidence that elephants also conduct geophagy to aid with detoxifying unpalatable secondary compounds in their diet (Mwangi, Milewski & Wahungu, 2004; Chandrajith et al., 2009). In other ungulate species, clay may decrease the harmful effects of secondary plant compounds and intestinal infections (Ayotte et al., 2006; Klaus and Schmidg, 1998). Soil is never consumed randomly within an elephants home range, but instead is consumed from specific spatially limiting sites (Klaus & Schmidg, 1998). Nutritionally, it is thought that elephants principally consume soil(s) at specialised licks to supplement sodium intake, although calcium, magnesium and potassium are also often higher in lick soils than in the surrounding soils. Elephants also consume soil on termite mounds although it remains unclear as ~~to the~~ driving mineral(s) behind this behaviour; sodium levels do not seem to be persistently higher in termite mounds than surrounding soils~~, as is seen at lick sites~~ (Holdø, Dudley and McDowell, 2002; Holdø and McDowell, 2004).

A further example of geophagy by elephants was reported by Mwangi, Milewski & Wahungu (2004) in the Aberdares National Park, central Kenya, where elephants rely on browse and unripe fruits to make up the majority of their diet due to limited availability of grasses. Browse, unripe fruits and seeds generally contain more tannins and alkaloids than grasses, suggesting that the elephants in this national park ~~are consuming more plant species that contain~~ harmful substances compared to ~~some~~ elephants that consume higher levels of grasses ~~in their diets~~. ~~As elephants are~~ hindgut fermenters, neutralisation of these harmful substances is not possible in the same way as it is for ruminants (~~which~~ use foregut fermentation ~~to neutralise these harmful substances~~). As the geophagic soils also contained higher levels of sodium and iodine than surrounding soils, it is not possible to identify if minerals or clays are the driving force behind this geophagic behaviour, however it was considered that both factors were important.

In the Kalahari-sand region of Hwange National Park, elephants consumed high-sodium lick soils during the dry season possibly in response to an unmet requirement for sodium. Lactating and pregnant females consumed more soil per visit to a high sodium lick than males (Holdø, Dudley & McDowell, 2002); ~~this~~ may be due to their increased requirement for sodium during pregnancy and lactation (Michell, 1995). This suggests that there is a physiological cause for this geophagy and that in these cases; lick use is driven by nutritional need. Female elephants will increase geophagy to meet their additional nutritional needs during pregnancy and lactation. Table 2 documents sodium levels in browse species during the dry season that are lower than during the wet season, and were suggested by Holdø Dudley & McDowell (2002) to be insufficient. The soil in the mineral lick areas also contained elevated levels of magnesium and calcium; however, these minerals were also available in adequate amounts from other sources such as termite mounds or dietary browse. Interestingly consumptions of termite mounds were not observed; therefore the authors concluded that these elephants were conducting geophagy based on sodium need.

As well as the increased clay in the soil in the Aberdares National Park, the soil consumed by the elephants also contained higher sodium and more concentrated levels of iodine than surrounding areas, but was significantly lower in zinc, manganese and iron levels. In addition to this, there was 250% more phosphorus and 50% magnesium in the consumed soil than surrounding control soil (Mwangi, Milewski & Wahungu, 2004). This suggests that elephants ~~in this area~~ chose to consume soil in certain areas based on nutrition provision, and that specific minerals were prioritised. ~~Sodium, iodine, phosphorus and magnesium.~~

There is debate as to whether elephants alter their movements to seek out and consume either the soil from termite mounds, or plant material growing on the termite mounds, to meet their mineral needs. Soil from termite mounds includes both surface soil and deeper sub soil, raised to the surface by termites. Previous studies generally focused on one geographical area and thus results may be geographically specific depending upon surrounding mineral availability. It appears to be universally acknowledged that soils from termite mounds contain more minerals than surrounding areas as the termites mine deeply into the substrate (Holdø & McDowell, 2004; Muvengwi, Mbiba & Nyenda, 2013; Muvengwi et al., 2014). However, the evidence as to whether elephants move to seek and consume specific soils (and plants) for targeted minerals is variable. Muvengwi, Mbiba & Nyenda (2013) showed that tree diversity did not vary significantly on termite mounds or control plots, in Chewore North, Zimbabwe, yet biomass removal by mega-herbivores was up to five times higher on control plots than termite mounds. Specifically when measuring consumption of *Colophospermum mopane*, there was no difference in biomass removal between termite mounds and control plots.

In contrast, black rhino in Chipinge Safari, Zimbabwe, were observed to browse on foliage growing on termite mounds more than off termite mounds, seen by increased bite intensity on the plants on the termite mounds. It is suspected ~~that this is~~ due to the increased soil and foliar mineral levels; concentrations of nitrogen, potassium, phosphorus, calcium and sodium were approximately double in the soil and leaves collected on ~~the termite mounds~~ compared to those off the termite mounds (Muvengwi et al., 2014). In the Kalahari Sand Hwange National Park, Zimbabwe elephants consumed soil from the high sodium, sparsely grassed areas on top of the termite mounds if the surrounding soil had a low concentration of sodium, but not if the surrounding soil areas had comparably higher sodium content (Weir, 1969). In western

Zimbabwe, 12 paired sample sites were compared, each site consisted of an area with a termite mound and a corresponding area within woodland, containing no termite mound. Holdø and McDowell (2004) concluded that although the soils within the termite mounds contained more of all tested minerals, the plants on the termite mounds contained less sodium than the plants in woodland plots. Elephants fed more intensively from the plants on the termite mounds than within the woodlands indicating that in this situation, the animals were seeking other minerals in addition to sodium from the termite mounds (Holdø & McDowell, 2004).

Finally, termite mounds which are consumed by elephants within the Mimbo ecosystem of the Ugalla Game reserve, Tanzania, contained more minerals than termite mounds which are not used for geophagy, with both compared to the surrounding soil. The amounts of each mineral correlated to each other, making it impossible to distinguish a single vs multiple specific driver(s) underlying geophagy; however, it is clear that mineral-rich termite mounds are being selected for consumption over less mineral-rich termite mounts. Geophagic termite mounds are a resource used by elephants independent of distance from water (Kalumanga, Mpanduji & Cousins, 2017).

## Conclusions

This work provides some evidence that African elephants (and other herbivores) make movement choices based on nutritional needs. Reasons dictating an animals' daily, seasonal and annual movement are multifactorial, with availability of water, human activity, social behaviour and topography all playing a role alongside nutrient availability, specifically mineral provision. Minerals are available to elephants from multiple sources: plants, water and soil, and all contribute to meeting their, as yet, unknown mineral needs. There is a relationship between geochemistry and herbivore movement as well as the effect that geochemistry has upon mineral provision through consumption of plants, water and soil (through geophagy). This relationship could be further explored to aid in predicting future animal movement.

Evidence-based values for mineral requirements of elephants remain undetermined. Suspected deficiencies in local key minerals cause animals to make movement choices to enable them to obtain these minerals. African elephants demonstrate this behaviour, although there is a need for further research, which could aid conservation managers in making informed decisions surrounding elephant movement, and the mitigation of human-elephant conflict.

National Parks and fenced reserves may occupy marginalised land of poorer quality, which has not been assigned to agriculture. With the vast increase in land required by 2050 for human population growth and agriculture (to support the population), the reduction in land available for mega herbivores such as elephants, and the increased habitat fragmentation, human-elephant conflict is predicted to increase. From a practical conservation perspective, there is limited research on the impact that mineral provision may have on prediction or mitigation of human-elephant conflict, and how this could be used as a tool for conflict resolution.

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## Table 1(on next page)

Search terms used for databases

| | |
|---|---|
| ‘elephant’, ‘Elephantidae’, ‘Loxodonta’, ‘mega herbivore’ | ‘soil’, ‘mineral’, ’minerals’, ’nutrition’ ‘geochemistry’ |

## Table 2 (on next page)

Macro-mineral concentrations (%dry matter) in native plants consumed by African elephants (Loxodonta *africana*) in southern Africa

| Location | Season | Plant part | Calcium | Phosphorus | Magnesium | Sodium | Source |
|---|---|---|---|---|---|---|---|
| **Hwange National Park, Zimbabwe** | unknown | Mature leaves | 0.02-3.12 | | 0.08-0.64 | 0.02-0.06 | (Holdø, Dudley & McDowell, 2002) |
| | | Young leaves | 0.01-1.32 | | 0.1-0.57 | 0.005-0.05 | |
| | | Stems, twigs | 0.11-1.85 | | 0.02-0.20 | 0.001-0.02 | |
| | | Bark | 0.13-3.93 | | 0.01-0.33 | <0.001-0.02 | |
| | End wet season | Browse | 0.35-2.47 | 0.11-0.33 | | | (Williamson, 1975) |
| | | Grass | 0.41-0.66 | 0.09-0.20 | | | |
| **Kasungu National Park, Malawi** | unknown | Tree leaves (12 sp.) | | | | 0.10-1.25 | (Jachmann & Bell, 1985) |
| **Tsavo National Park, Kenya** | unknown | Grass and browse (59 sp.) | 0.37-3.61 | 0.08-0.36 | | 0.01-1.67 | (Dougall & Sheldrick, 1964) |
| | Wet season | Mixed plant sp. | 0.13-0.38 | | | | (McCullagh, 1969a) |
| | Dry season | | 0.38 | | | | |
| | unknown | Grasses and herb type vegetation | 0.36-1.44 | | | | |
| | | shrub | 0.53-8.92 | | | | |

## Table 3(on next page)

Reported dietary mineral recommendations for African (*Loxodonta africana*) and Asian *(Elephas maximus)* elephants

BW= body weight, DM= dry matter (consumed)

| **Mineral** | **Species** | **Detail** | **Daily Estimated Mineral Requirements** | **Source** |
|---|---|---|---|---|
| Calcium | *L. africana* | Lactating females<br>Tusk growing males | 60g<br>8-9g | (McCullagh, 1969b; Sukumar, 1989) |
| Sodium | *L. africana* | | 9 mg Na $kg^{-1}$ BW | (Holdø, Dudley & McDowell, 2002) |
| Iodine | *L. africana* | | 0.03 mg I $kg^{-1}$ BW | (Milewski, 2000) |
| Zinc | *Elephas maximus* | Deficiency seen below this limit | >22 mg Zn $kg^{-1}$ DM | (Schmidt, 1989) |