

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

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Abstract

Background.

The increasing human population and global intensification of agriculture have had a major impact on the world's natural ecosystems and caused devastating effects on populations of mega-herbivores such as the African savanna 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~~ African savanna elephants, and focus the direction of future research. Peer reviewed literature available was generally geographically specific and on isolated populations of individual species. African savanna elephants have the capacity to extensively alter the landscape and have been more ~~extensively-greatly~~ studied than other ~~mega~~-herbivores, making them a good ~~predominant~~ example species to use for this review. Alongside this, their movement choices, potentially caused by nutritional drivers could be applicable to a range of other species. Relevant case study 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.

57 A review of peer reviewed literature was undertaken to examine nutritional drivers for
58 African elephant movement, exploring documented examples from free-rang~~ing~~ living African
59 savanna elephants and, where relevant, other herbivore species. ~~This could help inform~~
60 ~~intention of this was to aid in~~ prediction or mitigation of human-elephant conflict, potentially
61 when animals move according to nutritional needs, and related drivers for this movement. In
62 addition, appropriate grey literature was included to capture current research.

63 Introduction

64 ~~The~~ African savanna elephants (*Loxodonta africana*) ~~is~~^{are} categorised ~~as v~~^{as} vulnerable on the
65 IUCN Red List and free living populations have declined rapidly across Africa since 1970,
66 predominantly as a result of increased poaching and competition for resources with an
67 increasing human population (Blanc, 2008). This competition arises due to the intersection of
68 human activities with elephants' home ranges, and much research is devoted to investigating
69 the reasons why the animals move repeatedly through areas which lead them into conflict
70 with humans (Eltringham, 1990; Hoare & du Toit, 1999; Hoare, 2000). The aim of this
71 review is to consolidate the current understanding of nutritional drivers for animal movement,
72 ~~especially that of mega herbivores~~^{using the African savanna elephants as an example that}
73 ~~could be applied to other species~~, and focus the direction of future research. African savanna
74 elephants have the capacity to extensively alter the landscape and have been more extensively
75 studied than other ~~mega~~-herbivores, making them a good ~~predominant~~ example species to use
76 within this review. ~~Where r~~^{Where r} Relevant, examples ~~are included~~ of other herbivore movement
77 ~~(including other elephant species)~~ based on nutritional needs are included. No significant
78 reviews exist so far exploring the relationship between applied geochemistry and
79 physiological drivers for African savanna elephant movement.

80
81 Due to their vast food consumption and behaviour, elephants can cause significant damage to
82 crops and vegetation (Eltringham, 1990; Hoare, 2000) and pose a risk to human life and
83 infrastructure. Continued increase in the global human population, to 9.7 billion by 2050, and
84 the associated intensification of agriculture will have a major impact on the world's natural
85 ecosystems^s (Nyhus, 2016). This, coupled with a predicted reduction of 200-300 million
86 hectares of wildlife habitat worldwide ~~(Nyhus, 2016)~~, will ~~cause an increase~~ aggravate
87 human-animal conflict. Habitat encroachment and fragmentation poses a substantial threat to
88 elephant populations, forcing them to condense into ever-smaller geographical areas or
89 fenced reserves, whilst putting increased pressure on these areas to meet the animals'

resource needs (Nyhus, 2016). This can present a nutritional challenge and might cause animals to adapt their movement patterns to meet their dietary needs, including for specific minerals, presenting wildlife managers with new management issues.

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

1. Examine the relationship between the geochemistry and the associated soil of an area, and how this can alter the minerals available in plants to elephants as consumers (herbivores). ~~Use this information to examine in plants, and thus~~ how geochemistry may affect herbivore and specifically elephant movement. Only minerals are being considered within this review and ~~not~~ no 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 knowledge of mineral distribution in the landscape could be used to predict ~~or reduce~~ and mitigate human-elephant conflict in the future.

These objectives are achieved ~~examining~~ by examining documented nutritional requirements of elephants, including the ~~including the~~ differences between nutritional needs of cows and bulls, activity budget of the species to include time spent feeding, -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 identify possible mitigation measures to address~~ mitigate ~~associated human-elephant conflict.~~

This review is intended to benefit ~~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 and ~~or managed in situ in~~ fenced reserves. ~~No significant reviews exist so far exploring~~ There are no significant reviews already conducted to explore the relationship between applied geochemistry and elephant physiological drivers for elephant movement.

Survey MethodsMethodology

The following method was used to ensure comprehensive and unbiased coverage of the literature ~~was comprehensive and unbiased~~. Published studies were identified from ~~a number of three~~ databases, using a range of search terms relating to elephant movement choices, as described in Table 1. Search terms were selected based on a scan of the literature to give broad covering of subject of interest.

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Times New Roman, 12 Pt.

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 as full text.~~
- ~~3.2.~~ Was in a published peer-reviewed journal.
- ~~4.3.~~ Was in English.
- ~~5.4.~~ Was relevant to the subject matter (e.g. excluded irrelevant terms such as elephant grass *Pennisetum purpureum*).

Grey literature reviewed

Additional~~ly~~ a less detailed review of grey literature, which did not meet the inclusion criteria but was deemed relevant by the authors was also conducted. ~~relevant literature was identified using a number of different approaches.~~ ThisThis was identified as follows:
~~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). Keywords were selected based on scan of literature to give broad covering of subject of interest.

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. After applying the inclusion/ exclusion criteria, thirty- five papers were fully reviewed, detailed in appendix 1. Current work was generally geographically specific and on

isolated populations of individual species with dates ranging from 1969- 2018. Further details of the breakdown of the literature search can be seen in table 2. All reviewed papers were on wildfree-ranging African savannah elephants or other herbivore species.

From the review of grey literature, and additional peer-reviewed literature which did not meet the inclusion criteria, yielded eight further records-references were identified, which consisted of five books, one thesis and one short report. Dates of references ranged from 1977-2012, detailed in appendix 1.

African savanna elephant Ffeeding behaviour

African savanna elephants (*Loxodonta africana* and *L. cyclotis*) consume a variety of plant material including grasses, leaves, twigs, fruits, barks, herbaceous material and soil (Kabigumila, 1993; Dierenfeld, 2008). Although described as generalist herbivores consuming over 400 species of plants, populations-diet composition may vary regionally and seasonally in their plant choice (Kabigumila, 1993). African savanna elephants 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 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 savanna 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). Therefore it is thought that savanna elephant adopt both feeding strategies, and switch depending on environment and season.

Several studies indicate that savanna elephants spend over half of their daily time budget feeding.; eElephants 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, savanna 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 respond ~~ed to nutritional needs~~ and adapt their feeding strategy accordingly, with ~~available~~ varying availability of 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 (Laws, 1970; Beekman & Prins, 1989; Shannon et al., 2008). 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) to 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~~ intensified browse consumption during the ~~dry~~ 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 (Joy et al., 2015) (Table 32 provides specific examples). Due to the ~~generalist~~ generalist feeding nature of ~~both~~ African savanna elephants ~~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 (Codron et al., 2006). 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 [\(Codron et al., 2006\)](#). 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). This is in accordance of the observed trend of increased, ~~agreeing with an overall trend of increased~~ grass consumption during the wet season (Beekman and Prins, 1989). ~~Although e~~Elephants consume a vast number of different plant species, 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 [\(percentage of body weight on a dry matter, dry matter is feed excluding moisture content\)](#) whereas pregnant females consumed 1.2-1.5% BW DM. On an as-fed basis (feed including moisture content) elephants consumed about 4% of their body weight per day [\(Laws 1970\)](#).

Evidence shows differences between elephant bulls and reproductively active cows in their nutritional needs and associated diet choices, with cows [possibly](#) requiring higher levels of minerals and protein to support growing calves (Dierenfeld, 2008). 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 [savanna](#) elephants, with leaves containing more calcium and phosphorus than twigs. It is therefore suggested that cows and bulls [s](#) meet their differing nutritional needs primarily through plant part selection. ~~f~~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 and additional twigs (Greyling, 2004). This agreed with the previous work of Stokke and DuToit (2002), who

254 found bulls consumed more twigs than cows, and cows engaged in more leaf stripping than
255 bulls.

256 Greyling (2004) also documented bulls to consume more plant species with higher calcium
257 content than adult cows at maintenance (without calves) throughout the year. Greyling
258 suggested that such mineral selectivity may be due to a higher calcium requirement for tusk
259 growth in males compared to females at maintenance. This observation supports previous
260 work conducted by McCullagh (1969) who suggested a calcium requirement for male
261 elephants of 8-9g per day. Additionally, lactating females were found to have significantly
262 higher calcium needs than adult females at maintenance as summarised in Table 43.

263 During the dry season, Greyling (2004) found bull faeces contained significantly lower
264 phosphorus levels than faeces of cows in family groups. On average, ~~cow~~ faecal samples
265 contained ~~on average~~ 18% more phosphorus than bulls. Faecal phosphorus levels have been
266 used in agriculture to estimate dietary phosphorus in livestock, and they are a more reliable
267 index to diet quality than faecal nitrogen as they are not influenced by tannins (Holechek et
268 al., 1985; Wu, Satter & Sojo, 2000). Lower faecal phosphorus in bulls suggests that less
269 phosphorus was consumed in the diet, which might indicate ~~ing~~ that the requirement for bulls
270 was lower than that of cows (Grant, Meissner & Schultheiss, 1995; Wrench, Meissner &
271 Grant, 1997). Feeding time budgets of populations of both ~~bulls and cows~~ sexes, studied in
272 three reserves in South Africa, were found to be similar ~~by~~ (Shannon et al. 2008). This
273 suggests that cows obtained the required increased dietary energy for pregnancy or lactation,
274 by altering plant selection to preferentially select more energy dense plants, rather than by
275 increasing time spent feeding (Shannon et al., 2008). This finding contradicts that of Guy
276 (1975) who concluded that bulls consumed more 'trunk fulls' of plant material per minute
277 than cows, especially in the dry season, and bulls stayed for longer at feeding sites than
278 family groups do (Stokke & Du Toit, 2002). Stomach fill post mortem of non-pregnant or
279 lactating females and males was smaller than that of pregnant and lactating females,
280 suggesting that females increased overall food consumption to meet their nutritional demands
281 of pregnancy and lactation (Laws, 1975). These pieces of mixed evidence suggest that several
282 feeding strategies may be adopted by elephant cows and bulls to meet their specific
283 individual nutritional needs, depending upon the unique environments in which they live, and
284 seasonal resources available to them.

Documented literature on specific mineral needs in elephants is very limited and requirements *per se* have not been experimentally determined (Das et al., 2015). Table 43 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 ~~wildfree--ranging~~), ~~methods-parameters~~ 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 equids.

Human-elephant conflict (HEC)

Human- elephant conflict is caused when elephants make forays into human settlement resulting in some form of damage. Humans retaliate to injure, kill or displace the elephant (Hoare, 2000). The African Elephant Specialist Group (AfESG) conducted an inventory of sites across Africa where HEC occurs. It was concluded that the issue is widespread and HEC occurs where interactions happen between the home range of elephants and human activity. Approximately twenty percent of elephant home range is within legally protected areas however, conflict was documented to occur in both protected and non-protected areas (Said et al., 1995). Crop losses attributed to elephants across Africa was low (5-10%), and elephants were considered to be low on the list of agricultural pests (Hoare, 2000; Naughton-Treves, 2008). However, wide spread low level damage from non-dangerous crop pests were better tolerated by communities than rare, localised catastrophic damage caused by elephants (Said et al., 1995; Hoare, 2000; Naughton-Treves, 2008). There is limited evidence to support the relationship between problems caused by elephants and the level of elephant density or nutritional food limitation (Barnes, Asika & Asamoah-Boateng, 1995; Hoare, 1999). The optimum foraging theory has been suggested to explain the unpredictable nature of crop raiding across the savanna (Hoare, 1999). This theory predicts that animals will maximise quality of nutrient intake where possible and thus when crops of higher nutritional value than wild food plants are available, animals will prioritise consumption over their normal food crops (Begon, Harper & Townsend, 1986).

~~Elephant nutrition requirements and the domestic horse model~~Challenges of estimating elephant nutritional requirements

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 (Clauss, Kienzle & Wiesner, 2003). Therefore, when assessing published nutritional recommendations, the benefits and limitations of using this model must be considered. 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 considered~~ a suitable model for some aspects of elephant digestion. ~~These are~~ 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 ~~are lower~~achieved for all nutrients ~~are lower~~ (Bax & Sheldrick, 1963; Clauss et al., 2003). This must be factored into any comparisons with equid recommendations and extrapolation be used with caution.

Reported mineral deficiencies in captive and free-living elephants

As the evidence for specific mineral needs for elephants (of either species) is very limited, documented values for requirements of both African and Asian elephants (*Elephas maximus*) are included for these four key minerals; calcium, iodine, iron and zinc. Because Asian elephants are held in greater numbers in captivity, ~~for some minerals,~~ there has been more research on the mineral needs of the species.

Calcium

As previously discussed, it was suggested that elephants have highest calcium ~~(Ca)~~ demands when lactating (females) followed by during periods of intensive tusk growth (Dierenfeld, 2008). Calcium 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~~and excess excreted in the urine (Ullrey, Crissey & Hintz, 1997). 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 Calcium provision from grass or browse forages was not included in the calculations). Nonetheless, even the minimum concentrations ~~exceeded the~~ exceeded ~~the~~ captive adult elephant maintenance recommendation of 0.3% dietary DM (Ullrey, Crissey & Hintz, 1997). Similarly, diets fed to zoo elephants in the seven elephant-holding Brazilian zoos contained on average 0.7% Ca DM, ~~showing that~~ showing that minimum recommended levels were being ~~met~~ met (Carneiro et al., 2015). ~~and d~~ Diets of semi-captive Asian elephants in India contained 0.46-0.58% DM calcium (Das et al., 2015) 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 Calcium deficiency is higher in cows during partition and lactation, when calcium demand is increased (van der Kolk et al., 2008). Sub-clinical hypocalcaemia was reported in Asian elephants immediately prior to parturition 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).

Kommentar [C1]: This citation is missing in the reference list.

Iodine

The thyroid mass of an elephant relative to its body mass is double the predicted size, compared to other mammals (Milewski, 2000). This may indicate that the iodine ~~+~~ 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 iodine deficiency (Milewski, 2000). Due to the lack of essentiality of iodine 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 iodine levels of foliage in some situations (Watts et al., 2015). As an alternative iodine source, elephants may seek iodine supplementation from Iodine rich water or soil (via geophagy). Humans in Malawi were able to obtain as much as 70% of daily iodine requirements from drinking 2 litres of borehole water per day (Watts et al., 2015). Iodine is required for reproduction, and the high reproductive success of elephants in conservation areas such as Addo Elephant Park, which

383 contained several boreholes, was hypothesised to be linked with an increased supply of iodine
384 (Milewski, 2000; Milewski & Dierenfeld, 2012).

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

395 **Iron**

396 Iron ~~(Fe)~~ deficiency anaemia has rarely been reported in captive or free-~~rang~~ living elephants,
397 although several cases of anaemia caused by liver fluke infection, retained placenta,
398 tuberculosis, tuberculosis treatment and malabsorption syndrome have been documented
399 (Dierenfeld, 2008). Only a single reported Fi ~~rone~~ deficiency anaemia related to low dietary
400 iron intake, ~~affecting~~ affecting three newly imported Asian elephants, was documented. In
401 ~~this ;clinical case clinical~~ signs resolved upon dietary supplementation (Kuntze & Hunsdorff,
402 1978). Diets of semi-captive Asian elephants contained 105-126 mg/kg (Das et al., 2015),
403 significantly in excess of the Nutrition Advisory group recommendation of 50 mg/kg (Ullrey,
404 Crissey & Hintz, 1997; Das et al., 2015).

405 **Zinc**

406 The dietary recommendation for zinc ~~(Zn)~~ in captive elephants is 40 mg/kg DM diet, based
407 on determined requirements of equids (Olson, 2004; Ullrey et al. 1997). Partington (2012)
408 reported zinc levels of between 22 and 52 mg/kg DM in zoo elephant diets offered in 14 UK
409 facilities. However, this figure does not account for zincZn provision from grass and/or
410 browse forages, which comprise the majority of the diets, hence these data are limiteding.
411 Nonetheless the lower end values, suggest that some animals may have been consuming
412 inadequate levels of dietary zincZn. Semi-captive Asian elephants in India were reported to
413 consume diets containing 38.4 to 45.9 mg/kg Zzincn (Das et al., 2015). Again animals at the
414 lower end of this range may have been susceptible to zincZn deficiency, however, no clinical
415 signs of ~~deficiency were~~ deficiency were seen and serum concentrations were within the

416 ranges reported for healthy elephants (Ullrey, Crissey & Hintz, 1997; Das et al., 2015).
 417 Excess dietary calcium was documented to cause ~~zinc~~^{Zn} deficiency resulting in skin
 418 abnormalities in zoo elephants (Schmidt, 1989; Dierenfeld, 2008). Schmidt (1989) reported a
 419 case of zinc deficiency in a captive Asian elephant, resulting in ~~a~~-secondary immune
 420 deficiency and skin lesions. Dietary ~~Zzinc~~ level in that individual was increased from 22 to
 421 54 mg/kg ~~of feed~~-DM; ~~significant~~^{and significant} clinical improvement was seen within ~~2~~^{two}
 422 weeks, with lesions resolved after eight weeks.

423 **Environmental geochemistry as a driver for elephant dietary intake**~~Effect of~~
 424 ~~geochemistry on elephant dietary intake~~

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

440 Soil factors which affect a minerals' ~~bioavailability~~ soil-to-plant transfer include the
 441 composition of the parent material, quantity and composition of organic matter and the soil
 442 pH (Hurst et al., 2013). The relationship between mineral status of the soil and parent rock
 443 was strongest where there was minimal chemical weathering (Bowell & Ansah, 1994).
 444 Organic matter also affects bioavailability, especially that of iodine (Shetaya et al., 2012;
 445 Humphrey et al., 2018). Soil pH greatly influences the metal availability (Maskall &
 446 Thornton, 1996); in alkali soils, generally the bioavailability of molybdenum and selenium
 447 increases, whilst that of copper, cobalt and nickel decreases (Sutton, Maskall & Thornton,

2002). 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 the 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, it is believed to be a reliable index to be used to assess the general ability of forages to meet animals' mineral needs (McNaughton, 1988). However, the mineral profile of the soil can be depleted by -soil, plant, topography and weather factors ~~can influence plants, causing depletion in the mineral profile of the soil~~. In the Sabi Sands Reserve, South Africa, ~~ten~~ 10 species of grasses ~~were analysed; and,~~ 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 thought to be due to sampled species attributes, and the effect of the local micro-climate on the plants.

Geochemistry influence on herbivoreing animal movement and land use decisions of herbivores

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 km², 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 (Maskall & Thornton, 1996). 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-Copper~~ in ruminant animals, further exacerbating the deficiency of ~~cCopperu~~ (Underwood, 1977). A geochemical survey was conducted and results of this related to observed clinical ~~copperCu~~ deficiencies in animals (Maskall & Thornton, 1996). Following this investigation, recommendations were made to the Kenya Department of Wildlife Conservation and Management that mineral salts containing ~~cobaltCot~~, ~~copperCu~~ 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, elephants as non-ruminants,~~ are not as sensitive to this deficiency as ruminant species, ~~thus the~~ and a similar problem has not been ~~extensively~~ documented in elephants (Maskall & Thornton, 1996).

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

Land-useMovement decisions-choices 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, ~~fromeovering~~ smaller scale decisions around which plant part to select for consumption, through to decisions around seasonal movement patterns (Fryxell, 2008). De Knegt et al. (2011) concluded that forage availability, both in terms of quantity and nutritional quality, varies between seasons and years. Consequently those 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 ~~high and low~~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 (McNaughton, 1990). Grasses, as is common in many tropical soils, were not sufficient in magnesium and ~~phosphorus to~~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 (McNaughton, 1990). ~~A~~ animals have evolved with parturition periods being governed by the nutritional requirements of

545 reproducing females and growing young, seasonal rainfall and distance from forage of
546 sufficient quality being prioritised (McNaughton, 1990).

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

558 ~~Land-use decisions~~**Movement choices** of elephants

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

571 The significance of the impact of human activity on the natural movements of elephants is
572 rapidly increasing (Nyhus, 2016). ~~From data across 57 species,~~ Tucker et al. (2018)
573 concluded that in areas with a high level of human presence, mammal movement decreased
574 by 35-50% ~~across 57 species~~, compared with areas of low human presence. Over the last 150
575 years, expansion of human settlement into elephant habitat, and an increase in elephant
576 killing (~~from via~~ poaching and hunting) has significantly altered elephants' home ranges

Kommentar [C2]: Would you wish to cite here: Wall et al. (2006) Elephants avoid costly mountaineering? Why didn't you consider the publication: Wall et al. (2013) Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali?

577 across continental Africa (Eltringham, 1990; Hoare, 2000; Osborn, 2004; Nyhus, 2016).

578 Initially it was thought that there ~~was a~~would exist a simple linear relationship between rising

579 human and declining elephant densities at a national or subcontinental scale (Hoare & du

580 Toit, 1999). However, Hoare and du Toit (1999) found that in an area of 15,000 km² in

581 northwest Zimbabwe, the relationship ~~was~~turned out to be more complex. Using data from

582 human populations, and observed elephant densities in the region, the authors determined that

583 there was a threshold beyond which elephant and human coexistence could no longer occur,

584 and elephant populations rapidly declined. ~~The~~is threshold was related to agricultural

585 development, and was reached when land was spatially dominated by agricultural use, and

586 the ~~natural-original~~ woodland (that constituted the elephants' habitat) became sub-dominant.

587 When analysing elephant movement, water ~~Water~~-availability must be taken into account.

588 Water availability- is considered to ~~also~~-affects elephant movement, both on a daily and

589 seasonal basis and may be a greater driver for elephant movement than mineral availability. -

590 Three studies conducted in South Africa and Kenya, indicated that elephant movement

591 increased throughout the wet season when water availability was greatest, and then rapidly

592 decreased throughout the dry season, with elephants, especially lactating females, confining

593 themselves to areas within 1-2 days' travel from water to enable them to conserve energy

594 (Western & Lindsay, 1984; Codron et al., 2006; Thomas, Holland & Minot, 2008; Birkett et

595 al., 2012). Mineral composition of water is discussed as a driver for movement in the next

596 section.

597 ~~Elephant populations which have moved due to suspected mineral drivers~~

598 Pretorius et al. (2011) concluded that elephants made movement choices based on nutritional

599 provision in a specific area. Fertiliser was applied to mopane trees (*Colophospermum*

600 *mopane*) ~~in the~~ in the APNR, South Africa, in various patches, resulting in an increase in the

601 phosphorus and nitrogen levels in ~~the~~ mopane leaves. Elephants consumed more mopane

602 leaves per patch in fertilised patches compared to unfertilised patches, regardless of patch

603 size. Furthermore at a 100-m² patch size scale, elephants stripped leaves more in fertilised

604 ~~patches~~ than unfertilised patches, but were more likely to tree kill (through uprooting or

605 breaking main trunks) in unfertilised patches ~~than fertilised patches~~. Therefore, it it was

606 suggested that elephants caused more impact to trees of lower value (through tree killing)

607 whilst preserving trees of higher value (fertilised mopane) through coppicing (Pretorius et al.

608 2011).

Secondly Pretorius et al. (2012) ~~concluded-suggested~~ 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. ~~During the wet season, when food availability was greatest, nitrogen provision was prioritised, possibly to meet the elephants' needs for growth and reproduction. 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.~~ During the dry season, when food was potentially limited~~ing~~, E~~n~~ergy was prioritised by the ~~elephants~~. This could be because ~~during the dry season, possibly when this was potentially limited due to reduced food availability.~~ E~~n~~ergy 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 (Pretorius et al., 2012).

Nutritional factors affecting elephant movement

Minerals can be provided to elephants from multiple sources, ~~namely :-from plants~~from plants, ~~from~~ water or ~~from~~ soil (through geophagy). ~~E~~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-reported~~ by Rode et al. (2006) to be crop raiding to meet their sodium need. It was ~~suggested~~~~reported in the literature~~ 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 ~~might~~~~ean~~ 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~~~~compounds~~.

642 | ~~Especially the elephants avoided~~~~avoiding plants- plants with~~ high ~~phenol and in total phenols~~
643 | ~~and~~ steroidal saponin levels. Additionally in Kibale National Park, seasonal availability of
644 | wild food was not correlated to the timing of crop-raiding events (Chiyo et al., 2005). This
645 | suggests that elephants may be selecting specific food crops due to their nutritional provision,
646 | rather than just being attracted to the presence of food crops and increased overall availability
647 | of food (Chiyo et al., 2005).

648 |
649 | Finally, savanna elephants within the Mount Elgon region, Kenya, consumed salt deposits
650 | within the Kitum caves, which are rich in a variety of minerals including calcium, sodium,
651 | magnesium and phosphorus (Bowell, Warren & Redmond, 1996). Cases of uneven tusk wear
652 | were noted and presumed to result from ; ~~this was presumed to have resulted from~~ the use of
653 | tusks to scrape salts from the ceiling and walls (Bowell, Warren & Redmond, 1996). The
654 | environment within the cave can be warmer at 13.5°C than surrounding areas where night
655 | temperature can drop to 8°C, and although this could be encouraging the elephants to remain
656 | in the area overnight, it was suggested that there exists~~was~~ a nutritional drive causing them to
657 | seek out and consume the salt deposits on the rocks (Bowell, Warren & Redmond, 1996).

658 |
659 | Minerals can also be provided to elephants through ~~the drinking of water~~drinking water.
660 | Sienne, Buckwal and Wittemyer (2014) investigated elephant use of bais (natural forest
661 | clearings which often have seasonal or year round sources of water present as surface waters)
662 | in the central African rainforest and concluded that mineral provision from water is likely to
663 | be attracting elephants to specific bais. Mineral concentrations in water from elephant-
664 | evacuated pits were higher than in surface water, and thought to be a causative factor behind
665 | bai visitation choice. In particular iodine, sodium, sulphur and zinc were elevated, while;
666 | calcium, magnesium, manganese, iron and tin concentrations were at least ten times higher in
667 | elephant-evacuated water ~~than in~~compared to surface waters. Blake (2002) observed that
668 | elephants congregated around bais during the dry season, correlating with a seasonal peak in
669 | mineral levels in pit water, which may be due to the seasonal ebbing of spring water flow.
670 | Likewise, savanna elephants in the Hwange National Park, Zimbabwe were recorded by Weir
671 | (1972) in greater numbers surrounding water sources with higher sodium content~~;~~ Pans of
672 | high sodium water were reported to have three times as many elephants when censured,
673 | compared to the lowest sodium areas, indicating elephants ~~are making~~might make movement
674 | choices based upon sodium need.

Kommentar [C3]: Please provide reference here.

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

691 A further example of geophagy by elephants was reported by Mwangi, Milewski & Wahungu
692 (2004) in the Aberdares National Park, central Kenya, where elephants rely on browse and
693 unripe fruits to make up the majority of their diet due to limited availability of grasses.
694 Browse, unripe fruits and seeds generally contain more tannins and alkaloids than grasses,
695 suggesting that the elephants in this national park consume more potentially ~~are consuming~~
696 ~~more plant species that contain~~ harmful substances compared to ~~some~~ elephants that consume
697 higher levels of grasses ~~in their diets~~. As ~~elephants are~~ hindgut fermenters, neutralisation of
698 these harmful substances is not possible in the same way as it is for ruminants (where ~~they use~~
699 foregut fermentation is used to neutralise these harmful substances). As the geophagic soils
700 also contained higher levels of sodium and iodine than surrounding soils, it is not possible to
701 identify if minerals or clays are the driving force behind this geophagic behaviour, however it
702 was considered that both factors were important (Mwangi, Milewski & Wahungu, 2004).

703 In the Kalahari-sand region of Hwange National Park, elephants consumed high-sodium lick
704 soils during the dry season possibly in response to an unmet requirement for sodium (Holdø,
705 Dudley & McDowell, 2002). Lactating and pregnant females consumed more soil per visit to
706 a high sodium lick than males (Holdø, Dudley & McDowell, 2002). The latter might be; ~~this~~
707 ~~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 a nutritional need. Female elephants will increase geophagy to meet their additional nutritional needs during pregnancy and lactation. Table 3.2 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 (Holdø, Dudley & McDowell, 2002).

As well as the increased clay in the soil in the Aberdares National Park, Mwangi, Milewski and Wahungu (2004) found 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 Additionally, there was 250% more phosphorus and 50% more magnesium in the consumed soil than surrounding control soil (Mwangi, Milewski & Wahungu, 2004). This suggests that elephants in this area of this population 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 (Holdø & McDowell, 2004; Muvengwi, Mbiba & Nyenda, 2013; Muvengwi et al., 2014). 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, net 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 (Muvengwi et al., 2014).

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 (Muvengwi et al., 2014). ~~This is suspected to be due to~~ ~~it is suspected that this is due~~ to the increased soil and foliar mineral levels. ~~Concentrations of~~ ~~nitrogen, potassium, phosphorus, calcium and sodium were~~ ~~found to be~~ 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. ~~E~~ ~~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 probably 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 (Kalumanga, Mpanduji & Cousins, 2017). ~~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 mounds.~~ ~~Geophagic termite mounds are a resource used by elephants independent of distance from water~~ (Kalumanga, Mpanduji & Cousins, 2017).

Conclusions

This ~~work review collates evidence to provides some evidence suggest~~ that African savanna elephants (and other herbivores) consider nutritional drivers as a factor in their movement choices. ~~make movement choices based on nutritional needs.~~ The reasons dictating an

animals' daily, seasonal and annual movement are considered to be 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-undetermined mineral needs. There is a relationship between geochemistry and herbivore movement, and between the as well as the effect that geochemistry and has upon respectively mineral provision to the consumer, through consumption of plants, water and soil (through geophagy). This relationship ~~could~~ needs to 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~~ might force animals to make movement choices ~~to enable them~~ to obtain these minerals. In African savanna elephants this behaviour demonstrate this behaviour has been reported, although there is a need for further research. The latter might reveal correlation patterns which, ~~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 from 2014 to by 2050 for human population growth and agriculture ~~(to support the population)~~ will lead to a further ~~the~~ reduction in land available for ~~mega~~ herbivores such as savanna elephants, and ~~the increased habitat fragmentation~~, human-elephant conflict is predicted to increase (Nyhus, 2016). 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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