African savanna elephants (*Loxodonta africana*) as an example of a 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 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 African savanna elephants, and focus the direction of future research. Peer reviewed literature available was generally geographically specific and studies conducted on isolated populations of individual species. African savanna elephants have the capacity to extensively alter the landscape and have been more greatly studied than other herbivores, making them a good example species to use for this review. Alongside this, their movement choices, potentially linked with nutritional drivers could be applicable to a range of other species. Relevant case study examples of other herbivores moving based on nutritional needs are 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-ranging African savanna elephants and, where relevant, other herbivore species. This could help inform 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.

1   **African savanna elephants (*Loxodonta africana*) as an example of a herbivore making**

2   **movement choices based on nutritional needs**

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24 **Abstract**

25 **Background.**

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27 impacts on the world's natural ecosystems and caused devastating effects on populations of

28 mega-herbivores such as the African savanna elephants, through habitat reduction and

29 fragmentation and increased human-animal conflict. Animals with vast home ranges are forced

30 into increasingly smaller geographical areas, often restricted by fencing or encroaching

31 anthropogenic activities, resulting in huge pressures on these areas to meet the animals' resource

32 needs. This can present a nutritional challenge and cause animals to adapt their movement

33 patterns to meet their dietary needs for specific minerals, potentially causing human-animal

34 conflict.

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36 movement, especially that of African savanna elephants, and focus the direction of future

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40 herbivores, making them a good example species to use for this review. Alongside this, their

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42 other species. Relevant case study examples of other herbivores moving based on nutritional

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53 **Discussion.** A review of peer-reviewed literature was undertaken to examine nutritional drivers

54 for African elephant movement, exploring documented examples from free-ranging African

55   savanna elephants and, where relevant, other herbivore species. This could help inform

56   prediction or mitigation of human-elephant conflict, potentially when animals move according to

57   nutritional needs, and related drivers for this movement. In addition, appropriate grey literature

58   was included to capture current research.

59   1. **Introduction**

60   The African savanna elephant (*Loxodonta africana*) is categorised as vulnerable on the IUCN

61   Red List and free-ranging populations have declined rapidly across Africa since 1970,

62   predominantly as a result of increased poaching and competition for resources with an increasing

63   human population (Blanc, 2008). This competition arises due to the intersection of human

64   activities with elephants' home ranges, and much research is devoted to investigating the reasons

65   why the animals move repeatedly through areas which lead them into conflict with humans

66   (Eltringham, 1990; Hoare & du Toit, 1999; Hoare, 2000). The aims of this review are to examine

67   the current knowledge on the mineral requirements of the African savanna elephant, to

68   consolidate the current understanding of nutritional drivers for African savanna elephant

69   movement, to examine how geochemistry may affect herbivore movement and to consider how

70   this knowledge could be applied to predict and mitigate human-elephant conflict in the future.

71   African savanna elephants have the capacity to extensively alter the landscape and have been

72   more extensively studied than other herbivores, making them a good example species to use

73   within this review. Where relevant, examples of other herbivore movement (including other

74   elephant species) based on nutritional needs are included.

75

76   Due to their vast food consumption and behaviour, African savanna elephants can cause

77   significant damage to crops and vegetation (Eltringham, 1990; Hoare, 2000) and pose a risk to

78   human life and infrastructure. Continued increase in the global human population, to 9.7 billion

79   by 2050, and the associated intensification of agriculture will have major impacts on the world's

80   natural ecosystems (Nyhus, 2016). This, coupled with a predicted reduction of 200-300 million

81   hectares of wildlife habitat worldwide, will aggravate human-animal conflict. Wide ranging

82   landscape-level herbivores are increasingly threatened globally (Wall et al., 2013). Habitat

83   encroachment and fragmentation poses a substantial threat to elephant populations, forcing them

84   to condense into ever-smaller geographical areas or fenced reserves, whilst putting increased

85   pressure on these areas to meet the animals' resource needs (Nyhus, 2016). This can present a

86 nutritional challenge and might cause animals to adapt their movement patterns to meet their

87 dietary needs, including for specific minerals, presenting wildlife managers with new

88 management issues.

89

90 It is the aim of this review to consolidate understanding of nutritional drivers for animal

91 movement especially those of the African savanna elephant, and focus the direction of future

92 research. This will be achieved with the following objectives:

93 1. Examine current knowledge on mineral requirements in elephants, including the

94   differences between the nutritional needs of cows and bulls and the activity budget of the

95   species, including time spent feeding,

96 2. Examine the relationship between the geochemistry and the associated soil of an area,

97   and how this can alter the minerals available in plants to elephants as consumers

98   (herbivores). Use this information to examine how geochemistry may act as a driver for

99   African savanna elephant movement. Only minerals are being considered within this

100   review.

101 3. Consider how knowledge of mineral distribution in the landscape could be used to predict

102   and mitigate human-elephant conflict in the future.

103 This review is intended to benefit conservation managers, ecologists, conservation biologists,

104 national park management authorities, and potentially managers of animals under human care

105 both within zoos and fenced reserves.

106 **2. Methods**

107 The following method was used to ensure comprehensive and unbiased coverage of the

108 literature. Published studies were identified from three databases, using a range of search terms

109 relating to elephant movement choices.

110 **Search terms:**

111 List 1: 'elephant', 'Elephantidae', 'Loxodonta', 'mega herbivore'

112 List 2: 'soil', 'mineral', 'minerals', 'nutrition' 'geochemistry' 'movement'

113 The clause 'and' was included between each word in list 1 and list 2. Each search contained 1

114 word from list 1 and one from list 2. Each word from each list was searched together.

115   Search terms were selected based on a scan of the literature to give broad covering of subject of

116   interest.

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

118   2018).

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

120   **Inclusion/exclusion criteria:**

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

122   1. Contained at least one of the search terms from each list in the abstract, title or keywords.

123   2. Was in a published peer-reviewed journal.

124   3. Was in English.

125   4. Was relevant to the subject matter (e.g. excluded irrelevant terms such as elephant grass

126   *Pennisetum purpureum*).

127   **Grey literature reviewed**

128   Additionally, relevant grey literature which did not meet the inclusion criteria was reviewed.

129   This was identified as follows:

130   1. Theses, books, and conference proceedings

131   2. Using internet searches of key terms and snowballing by searching the reference lists of

132   relevant literature (Sayers, 2007). Keywords were selected based on a scan of the literature, to

133   give a broad coverage of the subject of interest.

134   **3. Results**

135   Initial searches yielded 1,870 records. After applying the inclusion/exclusion criteria, 35 papers

136   were fully reviewed, detailed in Appendix 1. Current work was generally geographically specific

137   and conducted on isolated populations of individual species with dates ranging from 1969 to

138   2018. Further details of the breakdown of the literature search can be seen in Figure 1. All

139   reviewed papers were on free-ranging African savanna elephants or other herbivore species

140   including wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), roe deer (*Capreolus*

141   *capreolus*) and black rhino (*Diceros bicornis*). Seventy percent of reviewed papers focused

142   specifically on African savanna elephants, 30% of reviewed papers focused more broadly on

143   herbivores.

144

145   From the review of the grey literature, and additional peer-reviewed literature that did not meet

146   the inclusion criteria, 8 further references were identified, which consisted of five books, one

147   thesis and one short report, as detailed in Figure 1. Dates of references ranged from 1977-2012,

148   detailed in Appendix 1.

149   **4. Elephant Nutritional Needs**

150   **Challenges of estimating elephant nutritional requirements**

151   Due to the lack of knowledge on the digestive physiology of many wild animals, animal

152   nutritionists use domestic species as physiologic models when designing diets for captive exotic

153   animals. For large hindgut fermenters like elephants and rhinos, the recommendations given for

154   the domestic horse (National Research Council, 1989) have been suggested as the appropriate

155   model for most nutrients, due to the similarities in gastrointestinal tract anatomy (Clauss, Kienzle

156   & Wiesner, 2003). Therefore, when assessing published nutritional recommendations, the

157   benefits and limitations of using this model must be considered. This approach of using the

158   domestic horse model was validated for white rhinos (*Ceratotherium simum*) and Indian rhinos

159   (*Rhinoceros unicornis*) but not for black rhinos (*Diceros bicornis*) or any elephant species

160   (Clauss, Kienzle & Wiesner, 2003). Clauss et al. (2007) demonstrated that black rhinos absorb

161   micronutrients in the same manner as horses, and suggested the same may apply in elephant

162   species. Despite the lack of validation, the horse has been extensively used as a model for captive

163   elephant nutritional physiology (Olson, 2004; Clauss et al., 2007; Walter, 2010) and overall, it is

164   considered a suitable model for many aspects of elephant digestion including the mechanisms by

165   which dietary supplements and dietary crude fibre content influence digestibility, calcium

166   absorption, and faecal volatile fatty acid composition. However, elephants have a faster ingesta

167   passage rate than horses, with a total gut transit time of 11-46 hours, compared to an average of

168   48 hours in horses, and thus digestibility coefficients are lower for all nutrients (Bax &

169   Sheldrick, 1963; Clauss et al., 2003). This must be factored into any comparison with domestic

170   horse recommendations and extrapolation be used with caution.

171   **Reported mineral deficiencies in captive and free-ranging elephants**

172   As the evidence for specific mineral needs for elephants (of either species) is very limited,

173   documented values for requirements of both African and Asian elephants (*Elephas maximus*) are

174   included for four key minerals; calcium, iodine, iron and zinc. Recommendations are often made

175   on a dry matter basis (DM; feed excluding moisture content). Because Asian elephants are held

176 in greater numbers in captivity, there has been more research on the mineral needs of this

177 species.

178 **Calcium**

179 It has been suggested that elephants have their highest calcium demands when lactating

180 (females) followed by during periods of intensive tusk growth (Dierenfeld, 2008). Calcium

181 metabolism in elephants appears to be similar to that of domestic horses, with approximately

182 60% absorbed from the diet directly in the intestines, independent of total consumption or

183 requirement, with excess excreted in the urine (Ullrey, Crissey & Hintz, 1997). As with other

184 mammals, elephants maintain serum calcium within a narrow range through intestinal

185 absorption, renal excretion and mobilisation of bone (Ullrey, Crissey & Hintz, 1997; Clauss et

186 al., 2003).

187 Partington (2012), while assessing calcium intake in elephants at 14 UK zoos, determined that a

188 minimum of 0.33-0.77% DM calcium was provided in the offered diets (values represented

189 minimums as calcium provision from grass or browse forages was not included in the

190 calculations). Nonetheless, even the minimum calculated concentrations exceeded the captive

191 adult elephant maintenance recommendation of 0.3% DM calcium (Ullrey, Crissey & Hintz,

192 1997). Similarly, diets fed to zoo elephants in 7 elephant-holding Brazilian zoos contained on

193 average 0.7% DM calcium, showing that minimum recommended levels were being met

194 (Carneiro et al., 2015). Diets of semi-captive Asian elephants in India contained 0.46-0.58% DM

195 calcium (Das et al., 2015) further supporting the conclusion that calcium deficiencies have rarely

196 been documented in healthy adult captive elephants on maintenance diets. There is, however,

197 evidence that incidence of calcium deficiency is higher in cows during partition and lactation,

198 when calcium demand is increased (van der Kolk et al., 2008). Sub-clinical hypocalcaemia was

199 reported in Asian elephants immediately prior to partition at Rotterdam Zoo when calcium

200 demand was not met through dietary provision (van der Kolk et al., 2008).

201 Metabolic bone disease (rickets) was reported in captive hand-reared Asian elephant calves. This

202 disease results from an imbalance in the calcium to phosphorus ratio or from intestinal

203 malabsorption, and unbalanced milk formulation may have played a role in this case (Ensley et

204 al., 1994).

Iodine

205
206 The thyroid mass of an elephant relative to its body mass is double its predicted size, compared
207 to other mammals (Milewski, 2000). This may indicate that the iodine requirements of elephants
208 are proportionally higher than those of other herbivores, and that due to the exclusively
209 herbivorous diet of elephants, they may be susceptible to iodine deficiency (Milewski, 2000).
210 Due to the lack of essentiality of iodine to plant metabolism, land plants have little reason to
211 translocate iodine from soil to foliage, therefore plants consumed by elephants may be low to
212 deficient in iodine (Shetaya et al., 2012; Humphrey et al., 2018). Soil dust deposition has been
213 documented to increase iodine levels of foliage in some situations (Watts et al., 2015). As an
214 alternative iodine source, elephants may seek iodine supplementation from iodine rich water or
215 soil (via geophagy). Humans in Malawi were able to obtain as much as 70% of daily iodine
216 requirements from drinking two litres of borehole water per day (Watts et al., 2015). Iodine is
217 required for reproduction, and the high reproductive success of elephants in conservation areas
218 such as Addo Elephant Park, which contained several boreholes, was hypothesised to be linked
219 with an increased supply of iodine (Milewski, 2000; Milewski & Dierenfeld, 2012).

220 In the Kitum caves, Mount Elgon, Kenya, elephants consume the cave salts that correlate with
221 high levels of calcium, sodium, magnesium and phosphorus (Bowell, Warren & Redmond,
222 1996). Iodine was measured in the salt crusts at 1,149 mg/kg, which was >100 times higher than
223 iodine concentrations in the most iodine-rich soils in the vicinity. Reproductive outputs of
224 elephant populations consuming these minerals were also high (Bowell, Warren & Redmond,
225 1996). Given these various lines of inferential evidence, supply or restriction of iodine-rich bore
226 holes could be further investigated as an effective method of population control *in situ*, without
227 affecting reproductive success of smaller herbivores that may have a proportionally lower
228 requirements for iodine, which could be realised by diet, water or geophagy (Milewski, 2000;
229 Milewski & Dierenfeld, 2012).

Iron

230
231 Iron deficiency anaemia has rarely been reported in captive or free-ranging elephants, although
232 several cases of anaemia linked with liver fluke infection, retained placenta, tuberculosis,
233 tuberculosis treatment and malabsorption syndrome have been documented (Dierenfeld, 2008).
234 Only a single reported iron deficiency anaemia related to low dietary iron intake, affecting three
235 newly imported Asian elephants, was documented. In this case, clinical signs resolved upon

236 dietary supplementation (Kuntze & Hunsdorff, 1978). Diets of semi-captive Asian elephants

237 contained 105-126 mg iron/kg DM (Das et al., 2015), considerably in excess of the Nutrition

238 Advisory group recommendation of 50 mg iron/kg DM (Ullrey, Crissey & Hintz, 1997; Das et

239 al., 2015).

240 **Zinc**

241 The dietary recommendation for zinc in captive elephants is 40 mg/kg DM diet, based on

242 determined requirements of domestic horses (Olson, 2004; Ullrey et al. 1997). Partington (2012)

243 reported zinc levels of between 22 and 52 mg/kg DM in zoo elephant diets offered in 14 UK

244 facilities. However, this figure does not account for zinc provision from grass and/or browse

245 forages, which comprise the majority of the diets, hence these data are limited. Nonetheless the

246 lower end values suggest that some animals may have been consuming inadequate levels of

247 dietary zinc. Semi-captive Asian elephants in India were reported to consume diets containing

248 levels of zinc between 38.4 to 45.9 mg/kg DM (Das et al., 2015); no clinical signs of deficiency

249 were seen and serum concentrations were within the ranges reported for healthy elephants

250 (Ullrey, Crissey & Hintz, 1997; Das et al., 2015). Excess dietary calcium was observed to

251 interfere with zinc bioavailability resulting in skin abnormalities in a zoo elephant (Schmidt,

252 1989; Dierenfeld, 2008). Schmidt (1989) reported a case of zinc deficiency in a captive Asian

253 elephant, resulting in secondary immune deficiency and skin lesions. The dietary zinc level in

254 that individual was increased from 22 to 54 mg/kg DM and significant clinical improvement was

255 seen within two weeks, with lesions resolved after 8 weeks.

256 Together, these observations confirm that the domestic horse may indeed provide a suitable

257 physiologic model for mineral nutrition of elephants.

258

259 **5. African savanna elephant feeding behaviour**

260 African savanna elephants (*Loxodonta africana*) consume a variety of plant material including

261 grasses, leaves, twigs, fruits, barks, herbaceous material and soil (Kabigumila, 1993; Dierenfeld,

262 2008). Although described as generalist herbivores consuming over 400 species of plants, diet

263 composition may vary regionally and seasonally (Kabigumila, 1993). African savanna elephants

264 are predominantly seasonal grazers and browsers with fruit, barks and soil being consumed as

265 secondary food choices (Kabigumila, 1993). There is debate as to whether savanna elephants are

266 predominantly grazers or browsers, with evidence supporting both feeding strategies:

267 Williamson (1975) reported elephant diets in Hwange National Park, Zimbabwe to consist

268 almost entirely of woody plants whereas Wing and Buss (1970) reported that elephants in

269 Uganda relied primarily on grasses (approximately 90% of bulk) and therefore labelled the

270 species as grazers. Such geographical variations in diet have prompted some authors to classify

271 elephants as browsers (Jachmann & Bell, 1985), whereas others maintain they are primarily

272 grazers (Beekman & Prins, 1989; Tangley, 1997). Therefore it is thought that savanna elephants

273 adopt both feeding strategies, and switch depending on environment and season.

274

275 Several studies indicate that savanna elephants spend over half of their daily time budget

276 feeding. Elephants in Tsavo National Park, Kenya were observed to feed for 48-63% of daylight

277 hours (Dougall & Sheldrick, 1964) and elephants in Lake Manyara National Park, Tanzania were

278 observed to spend on average 76% of daylight hours feeding (Beekman & Prins, 1989). Where

279 feeding conditions improved and food availability increased, Guy (1975) observed elephants in

280 Zimbabwe to reduce the total amount of time spent feeding to 50-60% of overall time budget,

281 from a greater proportion of their time budget when food resources were limited. Likewise,

282 savanna elephants in areas of food scarcity in Uganda were reported by Beekman and Prins

283 (1989) to spend as much as 74% of their total time budget feeding. Flexibility in food items

284 consumed and time spent feeding, indicated that elephants respond and adapt their feeding

285 strategy according to varying availability of food resources.

286 Savanna elephants have been documented to feed throughout the day, with decreased feeding

287 and increased resting during the middle part of the day; 12:00-14:00 hrs (Laws, 1970; Beekman

288 & Prins, 1989; Shannon et al., 2008). This pattern was observed in both sexes. Seasonally, the

289 total amount of time spent feeding per day has not been documented to change, although

290 elephants were observed by Shannon et al. (2008) to adjust the time of day spent feeding in the

291 hotter summer months. Evidence suggests that plant selection and feeding strategy changes

292 depending upon availability. During the wet season elephants were observed by Beekman and

293 Prins (1989) to spend 67% of time grazing with 8% browsing, whilst during the dry season

294 proportions shifted to 23% of time grazing and 60% browsing. During the dry season, the protein

295 content of the grasses decreased. When the protein content of the grasses dropped to <2.5%,

296 elephants in Tanzania were seen by Barnes (1982) to increase their browse consumption. Browse

297   typically contains higher levels of secondary compounds such as tannins than grass (Ellis, 1990)

298   and thus, as a by-product of this intensified browse consumption during the dry season, tannin

299   and associated levels of toxin accumulation were seen to increase (Barnes, 1982).

300   Mineral levels in plants vary seasonally, geographically and between different parts of the plant

301   (Joy et al., 2015) (Table 1 provides specific examples). Due to the generalist feeding nature of

302   African savanna elephants, it is thought that they are able to adapt their food selection as

303   required to meet their target levels of (as yet undetermined) mineral requirements (Bax &

304   Sheldrick, 1963). This was demonstrated in elephants within the Kruger National Park (KNP),

305   South Africa, where there is substantial geographical and seasonal variation in plant types

306   consumed by elephants (Codron et al., 2006). Stable carbon isotope analysis of faecal material

307   indicated that during the dry season, elephants in northern KNP consumed significantly more

308   grass than their southern counterparts; 40% of their diet was grass in the northern part of the park

309   during the dry season, compared to just 10% in southern KNP (Codron et al., 2006). In contrast,

310   this difference in grass consumption between elephants in the northern and southern parts of this

311   national park was not apparent during the wet season, when elephants throughout the park

312   consumed grass at approximately 50% of their overall diet (Codron et al., 2006). This is in

313   accordance of the observed trend of increased grass consumption during the wet season

314   (Beekman and Prins, 1989). Although elephants consume a vast number of different plant

315   species, they generally receive the bulk of their diet from a few selected species which vary

316   seasonally and geographically (Meissner et al., 1990; Kabigumila, 1993). Bax and Sheldrick

317   (1963) observed elephants in the Tsavo National Park, Kenya, to select specific plant parts,

318   notably bark rich in calcium.

319   Free-ranging African savannah elephant daily food intake is estimated from either the weight of

320   the stomach contents (post mortem) or from extrapolation of data on feeding rates and time spent

321   feeding. Both methods have produced similar estimates of daily dry matter intake for adults of

322   about 1.0-1.5% of body weight (Meissner et al., 1990; de Villiers et al., 1991; Ullrey, Crissey &

323   Hintz, 1997). Dry matter intake relative to body weight is influenced by a number of factors: dry

324   matter digestibility, environmental stressors, activity levels and life stage of the animal (adult

325   maintenance, growth, pregnancy or lactation) (Meissner et al., 1990). Laws (1970) concluded

326   that non-pregnant females and males consumed 1.0-1.2% BW DM (percentage of body weight

327   on a dry matter basis whereas pregnant females consumed 1.2-1.5% BW DM. On an as-fed basis

328   (feed including moisture content) elephants consumed about 4% of their body weight per day

329   (Laws 1970).

330   Evidence shows differences between elephant bulls and reproductively active cows in their

331   nutritional needs and associated diet choices, with cows possibly requiring higher levels of

332   minerals and protein to support growing calves (Dierenfeld, 2008). Greyling (2004) documented

333   that in the Associated Private Nature Reserves (APNR), South Africa, there was a nutritional

334   difference between various parts of the plants consumed by savanna elephants, with leaves

335   containing more calcium and phosphorus than twigs. It is therefore suggested that cows and bulls

336   meet their differing nutritional needs primarily through plant part selection. Family groups with

337   pregnant and lactating females consumed proportionally more leaves and bark in their diet

338   compared to bulls. In the dry season, females consumed 3% leaves and 14% bark, whereas males

339   consumed 1% leaves and 6% bark and additional twigs (Greyling, 2004). This agreed with the

340   previous work of Stokke and DuToit (2002), who found that bulls consumed more twigs than

341   cows, and cows engaged in more leaf stripping than bulls.

342   Greyling (2004) also documented bulls to consume more plant species with a higher calcium

343   content than adult cows at maintenance (without calves) throughout the year. Greyling suggested

344   that such mineral selectivity may be due to a higher calcium requirement for tusk growth in

345   males compared to females at maintenance. This observation supports previous work conducted

346   by McCullagh (1969) who suggested a calcium requirement for male elephants of 8-9 g/day.

347   Additionally, lactating females were found to have significantly higher calcium needs than adult

348   females at maintenance, as summarised in Table 2.

349   During the dry season, Greyling (2004) found bull faeces contained significantly lower

350   phosphorus levels than faeces of cows in family groups. On average, cow faecal samples

351   contained 18% more phosphorus than bulls. Faecal phosphorus levels have been used in

352   agriculture to estimate dietary phosphorus in livestock, and they are a more reliable index to diet

353   quality than faecal nitrogen as they are not influenced by tannins (Holechek et al., 1985; Wu,

354   Satter & Sojo, 2000). Lower faecal phosphorus in bulls suggests that less phosphorus was

355   consumed in the diet, which might indicate that the requirement for bulls was lower than that of

356   cows (Grant, Meissner & Schultheiss, 1995; Wrench, Meissner & Grant, 1997).

357 Feeding time budgets of populations of both sexes, studied in three reserves in South Africa,

358 were found to be similar (Shannon et al. 2008). This suggests that cows obtained the required

359 increased dietary energy for pregnancy or lactation, by altering plant selection to preferentially

360 select more energy dense plants, rather than by increasing time spent feeding (Shannon et al.,

361 2008). This finding contradicts that of Guy (1975), who concluded that bulls consumed more

362 'trunk fulls' of plant material per minute than cows, especially during the dry season, and bulls

363 stayed for longer at feeding sites than family groups (Stokke & Du Toit, 2002). Stomach fill post

364 mortem of non-pregnant or lactating females and males was smaller than that of pregnant and

365 lactating females, suggesting that females increased their overall food consumption to meet the

366 nutritional demands of pregnancy and lactation (Laws, 1975). These pieces of mixed evidence

367 suggest that several feeding strategies may be adopted by elephant cows and bulls to meet their

368 specific individual nutritional needs, depending upon the unique environments in which they

369 live, and seasonal resources available to them.

370 Documented literature on specific mineral needs in elephants is very limited and requirements

371 *per se* have not been experimentally determined (Das et al., 2015). Table 2 documents minerals

372 for which estimates have been recorded for African elephants directly. As these values were

373 reached from various different studies, on different populations (captive and free-ranging),

374 parameters of measurement were different e.g. grams required per day compared to mg required

375 per kg dry matter intake or body weight of the animal. This table does not include requirements

376 extrapolated from domestic horses.

377   **6. Elephant movement patters, as related to geochemistry/nutritional factors**

378 The availability of minerals to the plant from the soil underpins the relationship between

379 herbivores and their food supply. The distribution of vegetation was suggested to be strongly

380 associated with the geomorphology of the soil (Lawson, Jenik & Armstrong Mensah, 1968; Bell,

381 1982). Generally plants will reflect the soil profile and those growing in mineral deficient areas

382 will lack key minerals, thus potentially resulting in deficiencies in the consumer. In contrast,

383 those growing in mineral abundant areas will reflect this, and pass the mineral abundance on to

384 the consumer organism (Hurst et al., 2013; Joy et al., 2015). The ability of an area to supply

385 minerals to an animal does not solely depend on the mineral status of the soil and geochemical

386 parameters (such as organic matter and soil pH), but also on the ability of the plant to incorporate

387   the minerals (Bowell & Ansah, 1994). Additional factors affect the mineral levels within a plant:

388   the pathway of nutrients from the soil to the plant depends upon the amount of element present,

389   the various soil factors that affect the minerals' bioavailability and the plant factors which

390   determine the rate of uptake of the mineral (Maskall & Thornton, 1996).

391   Soil factors which affect a mineral's soil-to-plant transfer include the composition of the parent

392   material, quantity and composition of organic matter and the soil pH (Hurst et al., 2013). The

393   relationship between mineral status of the soil and parent rock was strongest where there was

394   minimal chemical weathering (Bowell & Ansah, 1994). Organic matter also affects

395   bioavailability, especially that of iodine (Shetaya et al., 2012; Humphrey et al., 2018). Soil pH

396   greatly influences the metal availability (Maskall & Thornton, 1996); in alkali soils, generally

397   the bioavailability of molybdenum and selenium increases, whilst that of copper, cobalt and

398   nickel decreases (Sutton, Maskall & Thornton, 2002). Further, increased availability of

399   phosphorus in alkaline soil contributes to its enhanced uptake into the plant (Maskall &

400   Thornton, 1996; Sutton, Maskall & Thornton, 2002).

401   Plant factors affecting rate of uptake of a mineral include: age of the plant (with levels of trace

402   elements decreasing in older plants), rate of plant growth (with rapidly growing plants displaying

403   reduced levels of trace elements), and plant species (with differences seen between levels of

404   trace elements in different plant species grown in the same soil (Maskall & Thornton, 1996). The

405   greatest differences in mineral content were reported between grasses and browses (Gomide et

406   al., 1969; Ben-Shahar & Coe, 1992). Seasonally, trace element levels were reported to be higher

407   in plants in the wet season: in the grazing pastures in the Kenyan highlands (Howard & Burder,

408   1962), in grasses by Lake Nakuru in the Rift Valley (Maskall & Thornton, 1991) and in the Mole

409   National Park, Ghana (Bowell & Ansah, 1994). Finally grazing status of the plant was seen to

410   influence plant mineral levels, with increased mineral concentrations of up to 300% in grazed

411   areas, notably sodium, phosphorus and calcium, compared to ungrazed areas supporting low

412   animal densities (McNaughton, 1988).

413   Forage mineral analysis data is routinely used to assess mineral levels in agriculture, and despite

414   its limitations, it is believed to be a reliable index to be used to assess the general ability of

415   forages to meet animals' mineral needs (McNaughton, 1988; Nellemann, Moe & Rutina, 2002).

416   However, the mineral profile of the soil can be depleted by soil, plant, topography and weather

417 factors. In the Sabi Sands Reserve, South Africa, 10 species of grass were analysed and grasses

418 from soils of higher mineral levels accumulated lower mineral concentrations, compared to

419 grasses from soils where the minerals were found in lower levels (Ben-Shahar & Coe, 1992). In

420 this case, this was thought to be due to sampled species attributes, and the effect of the local

421 micro-climate on the plants.

422 **Movement choices of elephants**

423 Several studies concluded that elephant habitat use is not random, but that elephants have

424 specific preferences for various habitats and move to fulfill their resource needs (Whitehouse &

425 Schoeman, 2003; Osborn, 2004; Douglas-Hamilton, Krink & Vollrath, 2005; Dolmia et al.,

426 2007; Thomas, Holland & Minot, 2008; Leggett, 2015). There are a myriad of factors that

427 contribute towards elephants' movement choices including availability of food and water,

428 opportunity for social interaction, human presence and associated activities. Hydrology and

429 topography may also influence animal movement (Bowell & Ansah, 1994; Wall, Douglas-

430 Hamilton &Vollrath, 2006). Elephants tend to avoid steep slopes due to the increased energy

431 expenditure required to climb them; even minor hills can be considerable energy barriers to an

432 elephant (Wall, Douglas-Hamilton &Vollrath, 2006). De Knegt et al. (2011) suggested that daily

433 movement of elephants related predominantly to food availability, and movements become

434 extended by the distance traversed to water sources. Elephants in that study area of the KNP,

435 South Africa concentrated their foraging within areas of high forage availability that were closest

436 to water, whilst still being large enough areas to optimise efficiency of movement and foraging.

437 The significance of the impact of human activity on the natural movements of elephants is

438 rapidly increasing (Nyhus, 2016). Tucker et al. (2018) concluded that in areas with a high level

439 of human presence, mammal movement decreased by 35-50% across 57 species, compared with

440 areas of low human presence. Over the last 150 years, expansion of human settlement into

441 elephant habitat, and an increase in elephant killing (from poaching and hunting) has

442 significantly altered elephants' home ranges across continental Africa (Eltringham, 1990; Hoare,

443 2000; Osborn, 2004; Nyhus, 2016). Initially it was thought that a simple linear relationship

444 would exist between rising human and declining elephant densities at a national or

445 subcontinental scale (Hoare & du Toit, 1999). However, Hoare and du Toit (1999) found that in

446 an area of 15,000 km^2 in northwest Zimbabwe, the relationship turned out to be more complex.

447   Using data from human populations, and observed elephant densities in the region, the authors

448   determined that there was a threshold beyond which elephant and human coexistence could no

449   longer occur, and elephant populations rapidly declined. This threshold was related to

450   agricultural development, and was reached when land was spatially dominated by agricultural

451   use, and the original woodland (that constituted the elephants' habitat) became sub-dominant.

452   When analysing elephant movement, water availability must be taken into account; elephants are

453   obligate drinkers (Wall et al., 2013). Water availability is considered to affect elephant

454   movement, both on a daily and seasonal basis and may be a greater driver for elephant

455   movement than mineral availability. Three studies conducted in South Africa and Kenya

456   indicated that elephant movement increased throughout the wet season when water availability

457   was greatest, and then rapidly decreased throughout the dry season, with elephants, especially

458   lactating females, confining themselves to areas within 1-2 days' travel from water to enable

459   them to conserve energy (Western & Lindsay, 1984; Codron et al., 2006; Thomas, Holland &

460   Minot, 2008; Birkett et al., 2012).

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

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

463   the APNR, South Africa, in various patches, resulting in an increase in the phosphorus and

464   nitrogen levels in mopane leaves. Elephants consumed more mopane leaves per patch in

465   fertilised patches compared to unfertilised patches, regardless of patch size. Furthermore at a 100

466   m^2 patch size scale, elephants stripped leaves more in fertilised than unfertilised patches, but

467   were more likely to tree kill (through uprooting or breaking main trunks) in unfertilised patches.

468   Therefore, it was suggested that elephants caused more impact to trees of lower value (through

469   tree killing) whilst preserving trees of higher value (fertilised mopane) through coppicing

470   (Pretorius et al. 2011).

471   Secondly Pretorius et al. (2012) suggested that phosphorus may be a key driver for elephant

472   movement, with elephants moving throughout the year to maximise intake of this mineral. In this

473   study area in the APNR, there was a suspected local deficiency in phosphorus, potentially

474   explaining why the elephants prioritised obtaining this mineral. During the wet season, when

475   food availability was greatest, nitrogen provision was prioritised, possibly to meet the elephants'

476   needs for growth and reproduction. During the dry season, when food was potentially limited,

477 energy was prioritised by the elephants. This could be because energy costs to obtain food and

478 water during the dry season were often higher as elephants had to travel further, due to a reduced

479 abundance of forage and availability of water (Pretorius et al., 2012).

480 **Nutritional factors affecting elephant movement**

481 Minerals can be provided to elephants from multiple sources, including plants, water or soil

482 (through geophagy). Examples of mineral provision from plants include sodium, calcium,

483 magnesium and phosphorus. Forest elephants (*Loxodonta cyclotis*) in the Kibale National Park,

484 Uganda, were reported by Rode et al. (2006) to be crop raiding to meet their sodium need. It was

485 reported in the literature that minerals such as copper and sodium, rather than energy and/or

486 protein, were limited in the elephants' wild food plants, and were found in higher concentrations

487 in crops. Often, wild elephant food plants which are high in sodium are also high in secondary

488 compounds (Rode et al., 2006), which might inhibit the uptake of essential minerals and increase

489 sodium excretion, and thus may further exacerbate low sodium intake (Jachmann, 1989). Crops

490 contained lower levels of secondary compounds compared to wild plants, which allowed the

491 elephants to resolve the complexities of meeting sodium needs without interference from

492 secondary compounds. For example, the highest sodium-concentration wild plant in this study,

493 *Uvariopsis congensis* also contained high levels of secondary compounds, saponin and had a

494 high alkaloid score (Jachmann, 1989). Jachmann (1989) has also reported examples of elephant

495 populations in the Miombo biome, Africa, making plant choices to create diets that contained

496 high sodium and digestible sugar concentrations, and low concentrations of indigestible fibre and

497 secondary compounds. The elephants especially avoided plants with high phenol and steroidal

498 saponin levels. Additionally in Kibale National Park, seasonal availability of wild food was not

499 correlated to the timing of crop-raiding events (Chiyo et al., 2005). This suggests that elephants

500 may be selecting specific food crops due to their nutritional provision, rather than just being

501 attracted to the presence of food crops and increased overall availability of food (Chiyo et al.,

502 2005).

503

504 Finally, savanna elephants within the Mount Elgon region, Kenya, consumed salt deposits within

505 the Kitum caves, which are rich in a variety of minerals including calcium, sodium, magnesium

506 and phosphorus (Bowell, Warren & Redmond, 1996). Cases of uneven tusk wear were noted and

507 presumed to result from the use of tusks to scrape salts from the ceiling and walls (Bowell,

508   Warren & Redmond, 1996). The environment within the cave can be warmer at 13.5°C than

509   surrounding areas where night temperature can drop to 8°C, and although this could be

510   encouraging the elephants to remain in the area overnight, it was suggested that there exists a

511   nutritional drive causing them to seek out and consume the salt deposits on the rocks (Bowell,

512   Warren & Redmond, 1996).

513

514   Minerals can also be provided to elephants through drinking water. Sienne, Buckwal and

515   Wittemyer (2014) investigated elephant use of bais (natural forest clearings which often have

516   seasonal or year round sources of water present as surface waters) in the central African

517   rainforest and concluded that mineral provision from water is likely to be attracting elephants to

518   specific bais. Mineral concentrations in water from elephant-evacuated pits were higher than in

519   surface water, and thought to be a causative factor behind bai visitation choice. In particular

520   iodine, sodium, sulphur and zinc were elevated, while calcium, magnesium, manganese, iron and

521   tin concentrations were at least ten times higher in elephant-evacuated water compared to surface

522   waters. Blake (2002) observed that elephants congregated around bais during the dry season,

523   correlating with a seasonal peak in mineral levels in pit water, which may be due to the seasonal

524   ebbing of spring water flow. Likewise, savanna elephants in the Hwange National Park,

525   Zimbabwe were recorded by Weir (1972) in greater numbers surrounding water sources with

526   higher sodium content. Pans of high sodium water were reported to have three times as many

527   elephants when censured, compared to the lowest sodium areas, indicating that elephants might

528   make movement choices based upon sodium need (Weir 1972).

529   Finally geophagy appears to be a normal behaviour of all elephant species in the majority of

530   habitats and is thought to aid elephants in meeting their nutritional (mineral) needs (Holdø,

531   Dudley and McDowell, 2002). There is some evidence that elephants also conduct geophagy to

532   support detoxification of unpalatable secondary compounds in their diet (Mwangi, Milewski &

533   Wahungu, 2004; Chandrajith et al., 2009). In other ungulate species, clay may decrease the

534   harmful effects of secondary plant compounds and intestinal infections (Klaus & Schmidg, 1998;

535   Ayotte et al., 2006). Soil is never consumed randomly within an elephants' home range, but

536   instead it is consumed from specific spatially circumscribed sites (Klaus & Schmidg, 1998). It is

537   thought that elephants principally consume soil(s) at specialised licks to supplement sodium

538   intake, although calcium, magnesium and potassium are also often higher in lick soils compared

539 to the surrounding soils (Holdø, Dudley & McDowell, 2002). Additionally elephants are known

540 to consume soil on termite mounds, although it remains unclear as to the driving mineral(s)

541 behind this behaviour. In contrast to the situation at lick sites, sodium levels do not seem to be

542 persistently higher in termite mounds than surrounding soils (Holdø & McDowell, 2004).

543 A further example of geophagy by elephants was reported by Mwangi, Milewski & Wahungu

544 (2004) in the Aberdares National Park, central Kenya, where elephants rely on browse and

545 unripe fruits to make up the majority of their diet due to a limited availability of grasses. Browse,

546 unripe fruits and seeds generally contain more tannins and alkaloids than grasses, suggesting that

547 the elephants in this national park consume more potentially harmful substances compared to

548 elephants that consume higher levels of grasses. As hindgut fermenters, neutralisation of these

549 harmful substances is not possible in the same way as it is for ruminants (where foregut

550 fermentation is used to neutralise these harmful substances). Since the soils consumed also

551 contained higher levels of sodium and iodine than surrounding soils, it is not possible to identify

552 if minerals or clays are the driving force behind this geophagic behaviour, however it was

553 considered that both factors were important (Mwangi, Milewski & Wahungu, 2004).

554 In the Kalahari-sand region of Hwange National Park, elephants consumed high-sodium lick

555 soils during the dry season possibly in response to an unmet requirement for sodium (Holdø,

556 Dudley & McDowell, 2002). Lactating and pregnant females consumed more soil per visit to a

557 high sodium lick than males (Holdø, Dudley & McDowell, 2002). The latter might be due to

558 their increased requirement for sodium during pregnancy and lactation (Michell, 1995). This

559 suggests that there is a physiological cause for this geophagy and that in these cases, lick use is

560 driven by a nutritional need. Female elephants will increase geophagy to meet their additional

561 nutritional needs during pregnancy and lactation (Michell, 1995). Table 1 documents sodium

562 levels in browse species during the dry season that are lower than during the wet season, and

563 were suggested by Holdø Dudley & McDowell (2002) to be insufficient. The soil in the mineral

564 lick areas also contained elevated levels of magnesium and calcium, however, these minerals

565 were also available in adequate amounts from other sources such as termite mounds or dietary

566 browse. Interestingly, consumptions of termite mound soils was not observed. Therefore the

567 authors concluded that these elephants were conducting geophagy based on sodium need (Holdø,

568 Dudley & McDowell, 2002).

569

570 As well as the increased clay in the soil in the Aberdares National Park, Mwangi, Milewski and

571 Wahungu (2004) found that the soil consumed by the elephants also contained higher levels of

572 sodium and iodine than the surrounding areas, but was significantly lower in zinc, manganese

573 and iron levels. Additionally, there was 250% more phosphorus and 50% more magnesium in the

574 consumed soil than the surrounding control soil (Mwangi, Milewski & Wahungu, 2004). This

575 suggests that elephants of this population chose to consume soil in certain areas based on

576 nutrition provision, and that specific minerals were prioritised.

577

578 There is debate as to whether elephants alter their movements to seek out and consume either the

579 soil from termite mounds, or plant material growing on the termite mounds, to meet their mineral

580 needs (Holdø & McDowell, 2004; Muvengwi, Mbiba & Nyenda, 2013; Muvengwi et al., 2014).

581 Soil from termite mounds includes both surface soil and deeper subsoil, raised to the surface by

582 termites. Previous studies generally focused on one geographical area and thus results may be

583 geographically specific depending upon surrounding mineral availability. It appears to be

584 universally acknowledged that soils from termite mounds contain more minerals than

585 surrounding areas as the termites mine deeply into the substrate (Holdø & McDowell, 2004;

586 Muvengwi, Mbiba & Nyenda, 2013; Muvengwi et al., 2014). However, the evidence as to

587 whether elephants move to seek and consume specific soils (and plants) for targeted minerals is

588 variable. Muvengwi, Mbiba & Nyenda (2013) showed that tree diversity did not vary

589 significantly on termite mounds or control plots, in Chewore North, Zimbabwe, yet net biomass

590 removal by mega-herbivores was up to five times higher on control plots than termite mounds.

591 Specifically when measuring consumption of *Colophospermum mopane*, there was no difference

592 in biomass removal between termite mounds and control plots (Muvengwi et al., 2014).

593 In contrast, black rhino in Chipinge Safari, Zimbabwe, were observed to browse on foliage

594 growing on termite mounds more than off termite mounds, seen by increased bite intensity on the

595 plants from the termite mounds (Muvengwi et al., 2014). This is suspected to be due to the

596 increased soil and foliar mineral levels. Concentrations of nitrogen, potassium, phosphorus,

597 calcium and sodium were found to be approximately double in the soil and leaves on termite

598 mounds, compared to those off the termite mounds (Muvengwi et al., 2014). In the Kalahari

599   Sand Hwange National Park, Zimbabwe elephants consumed soil from the high sodium, sparsely

600   grassed areas on top of the termite mounds if the surrounding soil had a low concentration of

601   sodium, but not if the surrounding soil areas had comparably higher sodium content (Weir,

602   1969). In western Zimbabwe, 12 paired sample sites were compared. Each site consisted of an

603   area with a termite mound and a corresponding area within woodland, containing no termite

604   mound. Holdø and McDowell (2004) concluded that although the soils within the termite

605   mounds contained more of all tested minerals, the plants on the termite mounds contained less

606   sodium than the plants in woodland plots. Elephants fed more intensively from the plants on the

607   termite mounds than within the woodlands indicating that in this situation, the animals were

608   probably seeking other minerals in addition to sodium from the termite mounds (Holdø &

609   McDowell, 2004).

610   Finally, termite mounds which are consumed by elephants within the Mimbo ecosystem of the

611   Ugalla Game reserve, Tanzania, contained more minerals than termite mounds which are not

612   used for geophagy (Kalumanga, Mpanduji & Cousins, 2017). Amounts of each mineral

613   correlated with each other, making it impossible to distinguish a single versus multiple specific

614   driver(s) underlying geophagy. However, it is clear that mineral-rich termite mounds are being

615   selected for consumption over less mineral-rich termite mounds (Kalumanga, Mpanduji &

616   Cousins, 2017).

617

618   **7.   Applications to ameliorating Human-Elephant Conflict (HEC)**

619   Human-elephant conflict is caused when elephants make forays into human settlement resulting

620   in some form of damage. Humans retaliate to injure, kill or displace the elephant (Hoare, 2000).

621   The African Elephant Specialist Group (AfESG) conducted an inventory of sites across Africa

622   where HEC occurs. It was concluded that the issue is widespread and HEC occurs where

623   interactions happen between the home range of elephants and human activity. Approximately

624   20% of elephant home range is within legally protected areas however, conflict was documented

625   to occur in both protected and non-protected areas (Said et al., 1995). Crop losses attributed to

626   elephants across Africa was low (5-10%), and elephants were considered to be low on the list of

627   agricultural pests (Hoare, 2000; Naughton-Treves, 2008). However, wide spread low level

628   damage from non-dangerous crop pests were better tolerated by communities than rare, localised

629   catastrophic damage caused by elephants (Said et al., 1995; Hoare, 2000; Naughton-Treves,

630   2008). There is limited evidence to support the relationship between problems caused by

631   elephants and the level of elephant density or nutritional food limitation (Barnes, Asika &

632   Asamoah-Boateng, 1995; Hoare, 1999). The optimum foraging theory has been suggested to

633   explain the unpredictable nature of crop raiding across the savanna (Hoare, 1999). This theory

634   predicts that animals will maximise the quality of nutrient intake where possible and thus when

635   crops of higher nutritional value than wild food plants are available, animals will prioritise

636   consumption over their normal food crops (Begon, Harper & Townsend, 1986).

637   **8. Applications to other herbivore species in comparable environments**

638   Consideration of geochemistry is required for maintenance of healthy animal populations,

639   especially within fenced reserves where animal migration is impossible. For example, in Lake

640   Nakuru National Park, Kenya which is a fenced area of 160 km^2, the soil is derived from

641   volcanic ash, pumice and lake sediment, with low levels of extractable cobalt, copper and acetic

642   acid with a high alkaline soil pH (Maskall & Thornton, 1996). In this region of the Rift Valley,

643   mineral deficiencies including copper and cobalt were seen in domestic cattle, as well as in

644   impala (*Aepyceros melampus*) and waterbuck (*Kobus defass*) (Maskall & Thornton, 1996). The

645   increased soil pH caused increased uptake of molybdenum by the plants, which in turn inhibited

646   the utilisation of copper in ruminant animals, further exacerbating the deficiency of copper

647   (Underwood, 1977). A geochemical survey was conducted and results of this related to observed

648   clinical copper deficiencies in animals (Maskall & Thornton, 1996). Following this investigation,

649   recommendations were made to the Kenya Department of Wildlife Conservation and

650   Management that mineral salts containing cobalt, copper and selenium should be made available

651   to wildlife in the park to mitigate these mineral deficiencies (Thornton, 2002). Due to the

652   physiological differences in mechanisms of copper absorption in ruminants and non-ruminants,

653   elephants are not as sensitive to this deficiency as ruminant species and a similar problem has not

654   been documented in elephants (Maskall & Thornton, 1996).

655   Clinically observed copper deficiencies caused by an increased uptake of molybdenum by the

656   plant and thus interference in the utilisation of copper by the animal were seen in Grant's gazelle

657   (*Gazelle granti*) from another area of the Kenyan Rift valley (Maskall & Thornton, 1996).

658   Additionally this was seen in moose (*Alces gigas*) in Alaska (Kubota, Rieger & Lazar, 1970) and

659   several herbivores at the San Diego Wild Animal Park (USA) where hypocuprosis was

660   diagnosed, caused by feeding alfalfa with a high molybdenum (and sulphur) concentration

661   (Kubota, Rieger & Lazar, 1970; Nelson, 1981; Maskall & Thornton, 1996). In northeast

662   Zimbabwe, it was suggested that high concentrations of iron in the soil and forage inhibited the

663   availability of phosphorus to the plants, and thus to the cattle consuming the plants. The high

664   iron concentration in the soil also reduced the absorption of copper and zinc in cattle (Fordyce,

665   Masara & Appleton, 1996).

666   Due to the ever-changing environment in which herbivores live, they are forced to make a series

667   of prioritised decisions to ensure survival. These decisions range from spatial to temporal and

668   vary in scale, from smaller scale decisions around which plant part to select for consumption,

669   through to decisions around seasonal movement patterns (Fryxell, 2008). De Knegt et al. (2011)

670   concluded that forage availability, both in terms of quantity and nutritional quality, varies

671   between seasons and years. Consequently those individual herbivores adapt their ranging

672   behaviour to meet their nutritional needs and ensure survival. This is especially important in

673   times of resource scarcity, where poor decision making may result in a reduced reproductive

674   output or death (Shannon et al., 2010). Appropriate discrimination between food items of high or

675   low quality can thus produce a selective advantage for long term survival (Fryxell, 2008).

676   From tracking data on 803 individuals of 57 species, Tucker et al. (2018) concluded that animal

677   movements are on average shorter in resource rich environments. For example red deer *(Cervus*

678   *elaphus)* in Slovenia were found to have reduced home ranges due to the enhancement of

679   resources, via supplementary feeding (Jerina, 2012), further agreeing with the work conducted

680   by Morellet et al. (2013) and Teitelbaum et al. (2015). Morellet et al. (2013) showed that the

681   home range of roe deer *(Capreolus capreolus)* at higher altitudes, was significantly larger than

682   roe deer at lower altitudes, despite forage availability at higher altitudes being more abundant

683   and of higher quality, although the growing season was shorter than at lower altitudes. This

684   suggested that home range, on an individual basis, is linked to a balance between metabolic

685   requirements and ability to acquire food, accounting for seasonal variation. Teitelbaum et al.

686   (2015) concluded from a review of 94 land migrations of 25 large herbivore species that there

687   was a ten-fold increase in the migration distance between resource high and low areas. These

688   studies indicated that animals living in resource poor areas will have larger home ranges and
689   longer migration distances than those living in resource abundant areas.

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

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

Conclusions

Evidence-based values for mineral requirements of elephants remain undetermined. Suspected deficiencies in local key minerals might force animals to make movement choices to obtain these minerals. In African savanna elephants this behaviour has been reported, although there is a need for further research. The latter might reveal correlation patterns which could aid conservation managers in making informed decisions surrounding elephant movement, and the mitigation of human-elephant conflict.

This review collates evidence to suggest that African savanna elephants (and other herbivores) consider nutritional drivers as a factor in their movement choices. 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 plants, water and soil, and all contribute to meeting their, as yet, undetermined mineral needs. There is a relationship between geochemistry and herbivore movement, respectively mineral provision to the consumer, through consumption of plants, water and soil (through geophagy). This relationship needs to be further explored to aid in predicting animal movement.

National Parks and fenced reserves may occupy marginalised land of poorer quality, which has not been assigned to agriculture. The vast increase in land required from 2014 to 2050 for human population growth and agriculture will lead to a further reduction in land available for herbivores such as savanna elephants, and human-elephant conflict is predicted to increase (Nyhus, 2016). Wide ranging, landscape-level movements made by terrestrial herbivores are increasingly threatened globally (Wall et al., 2013). From a practical conservation perspective, there is limited research on the impact 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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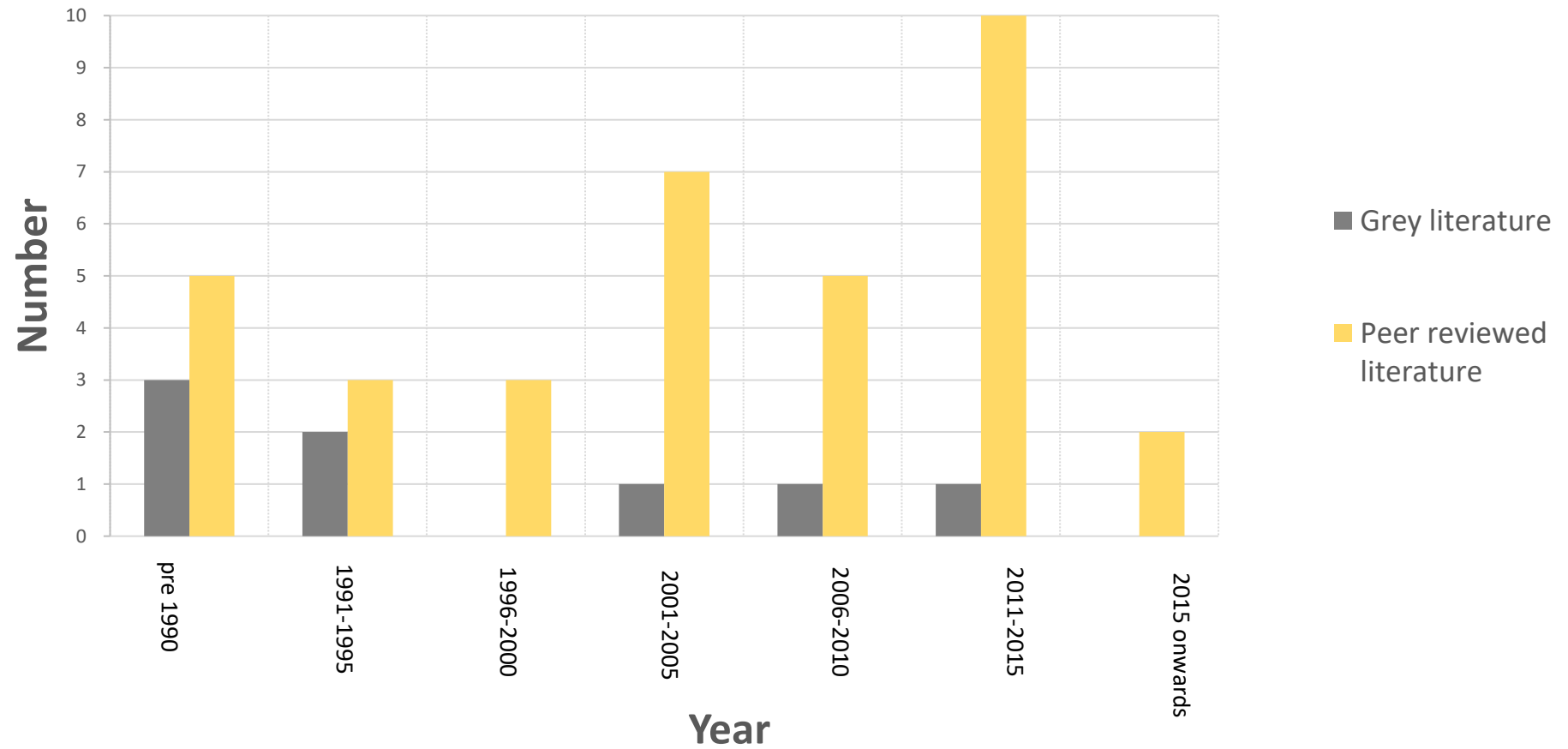
Breakdown of the literature by date after the application of the inclusion/exclusion criteria

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

Mineral levels in various southern and eastern african plant parts

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				

Reported dietary mineral recommendations for African elephants (Loxodonta africana)

Estimated mineral requirements for African elephants

Mineral	Species	Detail	Daily Estimated Mineral Requirements	Source
Calcium	*L. africana*	Lactating females Intensive tusk growth	60 g 8-9 g	(McCullagh, 1969; Dierenfeld, 2008)
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)