1    **Do African savanna elephants (*Loxodonta africana*) eat crops because they crave**

2    **micronutrients?**

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24

**Abstract**

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26    1. Elephants can cause negative consequences for both themselves and for humans by

27    consuming agricultural crops. It is unclear whether savanna elephant crop

28    consumption is merely opportunistic behaviour or related to insufficient quality of

29    natural forage. We analysed the role of vegetation quality on elephant crop

30    consumption. We focused on the role of micronutrients, as natural elephant diets are

31    thought to be insufficient in elements such as sodium and phosporus, which can

32    influence their foraging decisions.

33    2. For 12 months across four seasons we collected elephant feeding trail data along

34    with tree, grass and crop samples. We investigated how the quality and availability of

35    these items influenced elephant dietary choices across months and seasons.

36    Subsequently, we compared levels of fibre, digestible energy, dry matter intake, and

37    micronutrients, together with secondary compounds (tannins) across the three

38    vegetation groups. As elephants do not make dietary choices based on one

39    component, we also analysed the nutrient balance of food items with right-angle

40    mixture models.

41    3. The levels of phosphorus, magnesium and dry matter intake corresponded to

42    foraging preference. Compared to trees and grasses, crops contained significantly

43    higher amounts of digestible energy content, dry matter intake, nitrogen, phosphorus,

44    calcium and magnesium. PCA results showed that crops differed in phosphorus and

45    magnesium levels. The right-angle mixture models indicated that except for one tree

46    species, all food items elephants consumed were relatively deficient in phosphorus.

47    4. The combined results of these analyses suggest a phosphorus deficiency in elephant

48    diet in northern Botswana. Crops, with their high absolute phosphorus levels and dry

49    matter intake, provide an alternative source of phosphorus to reduce the deficiency.

50    This may explain the high intensity of crop consumption in the wet season in our

51    study area. A potential mitigation measure against elephant crop consumption might

52    be to provide supplementary phosphorus sources.

53

54    **Keywords**

55    Human-wildlife coexistence, human-wildlife conflict, human-elephant conflict, crop

56    raiding, foraging preference, vegetation quality, micronutrient, nutritional geometry.

57

## 1. Introduction

58

59 The consumption and destruction of crops by wildlife, often described as 'crop

60 raiding', can impede co-existence of wildlife and people (Nyhus, 2016). Many rodent

61 and mammal species, such as ungulates and primates, are known to consume crops

62 (Naughton-Treves, 1998; Pérez & Pacheco, 2006; Arlet & Molleman, 2007; Anand &

63 Radhakrishna, 2017). Across Asia and Africa, elephants (respectively *Elephas* spp.

64 and *Loxodonta* spp.) are also well known for their crop consumption behaviours

65 (Sitati et al., 2003; Hoare, 2012). African elephants consume between 100 - 300 kg of

66 wet mass vegetation per day (Laws, 1970) and are generalist, mixed-feeders, being

67 both browsers and grazers (Codron et al., 2011). Cultivated crops are commonly

68 included in the diet of elephants that roam human inhabited areas (Sitati et al., 2003).

69 Crop consumption by elephants can threaten food security for people (Mackenzie &

70 Ahabyona, 2012). The sharing of limited resources, and the associated close

71 proximity of humans and elephants, can also result in conflicts causing deaths and

72 injuries to both species (Sitati et al., 2003; Galanti et al., 2006; Kioko et al., 2008; Le

73 Bel et al., 2010). Elephant crop consumption is prevalent in areas with high

74 concentrations of both elephants and subsistence farmers, as in northern Botswana

75 (Osborn, 2004; Pozo et al., 2017; Songhurst, 2017). Here, entire harvests can be

76 destroyed by elephants, posing a threat to the livelihoods, food security, and nutrition

77 of farmers (Gupta, 2013). As a response, the Government of Botswana and

78 nongovernmental organizations, such as Ecoexist, partner with farmers on

79 agricultural, policy, land use, and mitigation strategies, while also conducting

80 research projects, including this study. Mitigation efforts often address the symptoms

81 of crop consumption, by aiming to find ways to keep elephants out of fields.

82 However, it is imperative that management strategies also focus on the causes of the

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83    behaviour and thus the reasons why elephants include crops in their diet (Barnes,

84    2002; Jackson et al., 2008). Therefore, we aim to increase understanding in how

85    elephants make foraging decisions, and gain insights in the reasons behind crop

86    consumption.

87    Given their large size, elephants are expected to be flexible in their dietary decisions,

88    as according to the Jarman-Bell principle larger herbivores have higher digestive

89    efficiency and a high tolerance to low quality forage (Bell, 1971; Jarman, 1974;

90    Müller et al., 2013). Indeed, elephants do not show preferences for specific grass

91    species, as they consume them relative to their availability (De Boer et al., 2000).

92    However, elephants feed selectively on woody species available, neglecting or

93    rejecting abundant forage species, and this selectiveness varies across seasons (De

94    Boer et al., 2000; Kos et al., 2011; Owen-Smith & Chafota, 2012). Elephants also

95    show low tolerance of secondary chemicals such as tannins and tend to avoid

96    phenolic-rich leaves that smaller ruminants eat (Owen-Smith & Chafota, 2012).

97    Plants develop chemical defences as tannins and other secondary chemicals to deter

98    animals from consuming them (Molyneux & Ralphs, 1992; Kanallakan et al., 2005).

99    These chemical plant defences are particularly present in areas with nutrient-deficient

100   soils such as in northern Botswana (Owen-Smith & Chafota, 2012).

101   Seasonal patterns in crop consumption indicate that both crop and natural forage (i.e.

102   browse and grass) quality and quantity could play a role in driving crop consumption

103   patterns (Chiyo et al., 2005; Rode et al., 2006). During the dry season grass matures

104   and decreases in nutritional quality, while the quality of browse changes due the

105   availability of flowers, fruits and young leaves  (De Boer et al., 2000; Kos et al.,

106   2011; Pretorius et al., 2012; Shannon et al., 2013). During this time we expect

107  elephants to transition from grazing to browsing, or crop consumption, as this is an

108  attractive alternative to browsing (Osborn, 2004). Temporal variation in crop

109  consumption correlates with crop availability at certain phenological stages

110  (Sukumar, 1990; Tchamba, 1996; Chiyo et al., 2005; Sitati & Walpole, 2006).

111  Agricultural crops offer high intake rates, retain high micronutrient value and a low

112  fibre content at maturation, and contain few chemical or physical defences (Sukumar,

113  1990; Osborn, 2004). Therefore, elephant crop consumption is in line with predictions

114  derived from the optimal foraging theory, selecting the best available food items from

115  a set of foraging alternatives, based on the gain and costs of each choice (Krebs, 1977;

116  Stephens & Charnov, 1982; Lambert & Rothman, 2015). In particular, the high levels

117  of sodium and other micronutrients in crops, in combination with a high digestibility

118  due to low fibre content and deterrent chemicals, could lead to crop-consumption

119  behaviour (Rode et al., 2006).

120  It remains unclear to what extent elephants consume crops because of their high

121  digestibility (i.e. low levels of fibres and secondary compounds) or their micronutrient

122  content. Crops could simply be the best alternative, or a way to avoid dietary

123  deficiencies in micronutrients to which elephants may be prone (Chiyo et al., 2005;

124  Rode et al., 2006). Elephants show potential for micronutrient deficiencies (Weir,

125  1969; Sukumar, 1990; Holdø et al., 2002), as also illustrated by the occurrence of

126  diseases associated with micronutrient deficiencies (Wang et al., 2007). Nutrients in

127  which elephants are potentially deficient are sodium (Na), phosphorus (P), nitrogen

128  (N), potassium (K), magnesium (Mg) and calcium (Ca) (Pretorius et al., 2012).

129  Elephants can obtain their required nutrients through water sources, by geophagy –

130  the consumption of soil (Klaus et al., 1998; Holdø et al., 2002), e.g. from termite

131  mounds or salt deposits in caves (Weir, 1969; Bowell et al., 1996) or through optimal

132    foraging decisions (Pretorius et al., 2012). In Kibale National Park, Uganda, forest

133    elephants (*Loxodonta cyclotis*) are limited by minerals, rather than other factors such

134    as energy and protein (Rode et al., 2006). Agricultural crop availability appears the

135    main motivation for forest elephant crop consumption, while it is suggested that in

136    savanna habitats seasonal fluctuations in natural forage quality, and therefore the risk

137    of nutrient deficiency, may play a more important role (Chiyo et al., 2005).

138    To examine this hypothesis, we analysed year-round levels of micronutrients, tannins,

139    and fibre measures (i.e. digestible energy and dry matter intake) of browse, grass and

140    crop included in elephant diet. First, we analysed how they influenced elephant

141    foraging choices in browse over the year (De Boer et al., 2000; Kos et al., 2011;

142    Owen-Smith & Chafota, 2012). Secondly, we compared the levels of the vegetation

143    quality measures between the crops, trees and grasses in order to examine whether

144    crops are the optimal forage alternative. Finally, since animals do not make their

145    dietary choices based solely on individual nutrient levels, but need to maintain the

146    intake of multiple nutrients at the same time, we analysed elephant foraging options

147    with Right-Angle Mixture Triangles (RMTs; Simpson & Raubenheimer, 1993). The

148    use of RMTs has proven useful in understanding the dietary choices animals make

149    (Chambers et al., 1995; Hewson-Hughes et al., 2013; Raubenheimer et al., 2015;

150    Cabana et al., 2017). This method from nutritional geometry considers dietary choices

151    to be based on the levels of multiple elements (Raubenheimer & Simpson, 2003;

152    Simpson et al., 2004; Raubenheimer et al., 2014). We combined these methods to

153    understand to what extent crop consumption is influenced by nutrient deficiencies or

154    by opportunistic foraging behaviour.

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## 2. Methods

### 2.1 Study site

We studied the role of crop consumption in the diet of elephants in the eastern

panhandle of the Okavango Delta (Figure 1), an area of approximately 8,000 km$^2$ in

northern Botswana (Songhurst et al., 2015a). The soil in the area mainly consists of

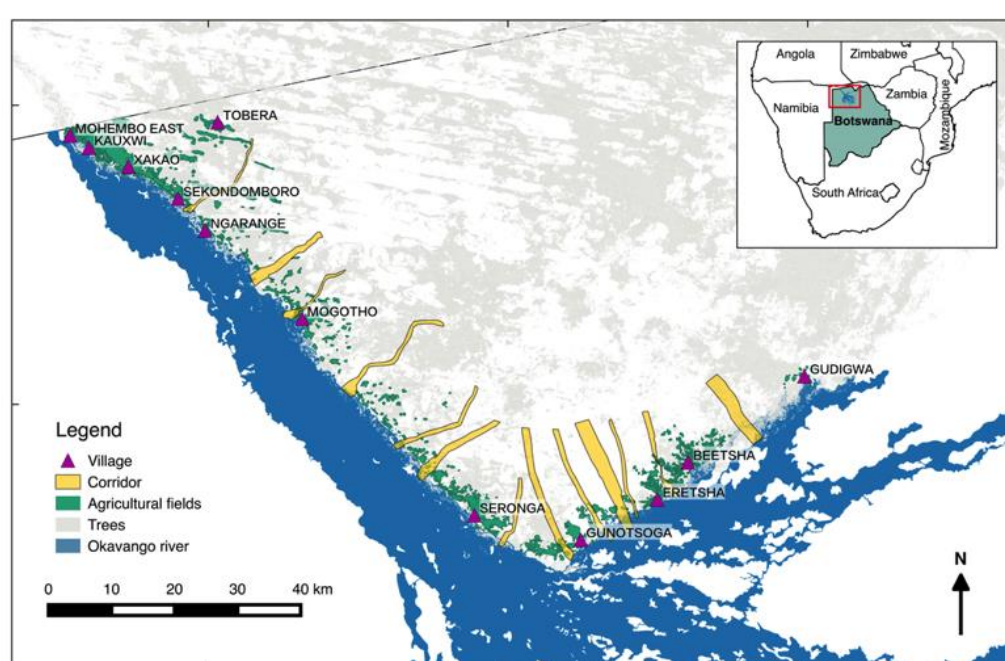nutrient-poor Kalahari sands (Dougill & Thomas, 2004).



*Figure 1. Study site in the eastern panhandle of the Okavango delta, Botswana*

*including habitat features used in this study. The green areas represent agricultural*

*fields, with the purple triangles representing the location of the villages, with highly*

*used elephant corridors in yellow markings running through them towards the*

*Okavango River in blue. White and grey areas represent savanna and tree groups,*

*respectively.*

Annually, there is one main wet season, which has on average 503 mm of rain divided

over the early wet season from November until January, and the late wet season from

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177    February until April (Statistics Botswana, 2016). The crop season starts with the

178    germination of crops in January and crop maturation continues until harvest in April-

179    May (Songhurst, 2012). From May until July the weather becomes dry, with the late

180    dry season from August until October. Mean maximum temperatures vary over these

181    seasons from 26ºC in July to 36ºC in October (2000-2015, Statistics Botswana, 2016).

182    Within this area live approximately 18,000 elephants (Songhurst et al., 2015a).

183    The area consists of floodplains, dry bush and agricultural fields, with seven

184    distinguishable tree vegetation categories (Ben-Shahar, 1993; Songhurst, 2012).

185    Around the river the floodplain vegetation type occurs, with floodplain grassland and

186    riverine woodland with large fruit-bearing trees and small shrubs. Parts of the dry

187    bush are dominated by mopane trees (*Colophospermum mopane*), heavily browsed by

188    elephants, sometimes combined with other species into mixed mopane woodland. The

189    dry bush also consists of acacia woodland with thorny browse species, areas with

190    mixed silver terminalia (*Terminalia sericea*) vegetation, and the false mopane

191    (*Guibourtia coleosperma*), Zambezi teak (*Baikiaea plurijuga*) and wild syringa

192    (*Burkea Africana*) woodland. During the wet season grasses occur throughout the dry-

193    bush area. In this area 106 pathways were identified that elephants use to walk from

194    the uninhabited area through human dominated areas towards the river (Songhurst et

195    al., 2015). In the same area along the river and Delta there are 13 villages with around

196    16,000 inhabitants (CSO, 2011). Around these villages there are (subsistence)

197    agricultural fields including cereals like millet, sorghum and maize (*Pennisetum*

198    *glaucum/ Eleusine coracana, Sorghum bicolour*, *Zea mays*, Songhurst, 2011; Heath &

199    Heath 2009).

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201    **2.2 Data collection**

202    Data were collected with permission of the Republic of Botswana Ministry of

203    Environment, Wildlife and Tourism, research permit EWT 8/36/4 XXXI (49). First,

204    we constructed a vegetation focal list including the mean browse and grass species

205    included in the local elephant diet. Secondly, we followed fresh elephant feeding

206    trails to record tree and shrub species available to, and consumed by, elephants and

207    collected tree, grass and crop samples for nutritional content analyses.

208    *2.2.1 Constructing vegetation focal list*

209    From August until September 2015 we constructed a vegetation focal list of species

210    including elephant forage species present in the area verified with foraging evidence

211    on one of seven elephant feeding trails (less than 24 h old) in each of the seven

212    vegetation categories (Stokke, 1999; De Boer et al., 2000; Greyling, 2004; Chiyo et

213    al., 2005; Rode et al., 2006; Kos et al., 2011; Owen-Smith & Chafota, 2012; Pretorius

214    et al., 2012). Grass identification was verified at Wageningen University, and browse

215    identifications were verified and included in a reference specimen collection at the

216    Okavango Research Institute (ORI) herbarium in Maun.

217    *2.2.2 Acceptance and availability plots*

218    From October 2015-September 2016 we followed 7-10 fresh (with spoor less than 24

219    h old) elephant feeding trails, during the first week of each month for 11 months

220    (excluding April due to logistical reasons), between 6.00 AM and 6.00 PM. We took a

221    stratified random selection of seven of the 106 pathways to focus our search effort for

222    fresh spoor, spread over the entire region, and incorporating all dominant vegetation

223    types in the area. We collected feeding trail information following acceptance and

224   availability methods developed and adapted by Owen-Smith and Cooper (1987),

225   Stokke (1999), and Greyling (2004). At the first tree with fresh elephant impact, we

226   created a 5 m radius circular 'food plot' in which we recorded all trees > 20cm high

227   that where available to the elephant, and those trees that were consumed by the

228   elephant. Of each tree we recorded species, height, DBH, type of elephant impact (no

229   damage, leaves removed, twigs and leaves removed, branch broken, debarked, main

230   stem broken, uprooted) and percentage of the tree impacted. We repeatedly continued

231   50 m along the feeding trail and collected another food plot until in every feeding trail

232   we collected six food plots. At every other food plot we created a 'control plot'

233   similar to the food plot but 50 m perpendicular to the feeding trail, randomly to the

234   left or right, in order to record available trees in close proximity to the feeding trail.

235   We followed a total of 103 feeding trails, 74 from females in breeding herds and 27

236   from male elephants. We aimed to collect equal amounts of samples from female and

237   male elephants but this was not feasible, as male elephant spoor was harder to find.

238   We collected information on 594 food plots and 293 control plots. Each of these plots

239   contained approximately 13 trees; as a result we measured 13,461 trees in total, of

240   which 9,017 were in food plots and 4,444 in control plots.

241   *2.2.3 Vegetation content analyses*

242   In the last month of each season (October, January, April, and July) we collected

243   vegetation samples of all tree species on the focal list. In each month of the crop

244   season (February, March, April) when crops and grasses were available, we also

245   collected samples of all grass species with signs of elephant impact and of crop

246   species. We included 27 tree species for year-round dietary choice analyses (108 trees

247   in total), during we compared 27 tree species (an additional 81 trees), 15 grass species

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248 (45 grass samples) and 7 crop types (21 crop samples) collected during the crop

249 season.

250 Vegetation samples were air-dried in a cabinet following collection, before being

251 dried for a further 24 h at 70°C in the laboratory. Dried samples were ground to fit

252 through a 1 mm mesh. We extracted condensed tannins using a butanol-HCl-iron

253 assay run with 50% aqueous acetone and measured using a spectrophotometer (Mole

254 & Waterman, 1987). We calculated the Dry Matter Intake (DMI) of the samples by

255 measuring the Neutral Detergent Fibre (NDF), and the Digestible Energy (DE) from

256 the concentration of Acid Detergent Fibre (ADF) in the samples. We measured the

257 NDF and ADF by measuring sample weight differences after subsequently applying

258 the ANKOM Fiber Analyzer vessel according to NDF and ADF guidelines (ANKOM

259 Technology). Finally, we measured the concentration of phosphorus (P), calcium

260 (Ca), magnesium (Mg), potassium (K), sodium (Na), and nitrogen (N) using a

261 continuous flow analyser after destruction of the samples with salicylic acid,

262 sulphuric acid-selenium and hydrogen peroxide (Novozamsky et al., 1983).

263 **2.3 Data analyses**

264 For our data analyses we used R (R Core Team, 2017). To construct our study site

265 map, we used QGIS (Quantum GIS Development Team, 2015), the Semi-Automatic

266 Classification plugin (Congedo, 2016) and Landsat 8 data, courtesy of the U.S.

267 Geological Survey.

268 *2.3.1 Control plots*

269 In order to test whether control plots and food plots consisted of similar vegetation,

270 we modelled the proportion of plots in which a browse species was present versus the

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271    proportion in which it was absent, using a generalized linear model with a binomial

272    error structure. Plot type (control or feeding trail) and month were fitted as

273    explanatory variables.

274    *2.3.2 Acceptance/availability indices*

275    We used the data from the food plots to calculate an index for the availability of each

276    browse species and an index for consumption -or acceptance- of each species, per

277    season and averaged over feeding trails. We calculated the availability index by

278    dividing the frequency at which a species was present with the number of food plots,

279    per season, and the acceptance index by dividing the frequency a species was

280    accepted by their availability to elephants, per season. Plotting these acceptance and

281    availability indices against each other for the four seasons (early dry, late dry, early

282    wet, late wet) reveals the feeding trail-based foraging preferences and avoidances

283    (Greyling, 2004; Owen-Smith & Chafota, 2012).

284    *2.3.3 Analysing browse choices*

285    To examine how elephants' dietary choices were influenced by vegetation

286    characteristics, we constructed a generalized linear model with a binomial error

287    structure with the seasonal proportion a species was accepted and those in which it

288    was present as the response variable. To remove pseudo-replication, we averaged the

289    acceptance ratio's and vegetation characteristics over the food plots per feeding trail.

290    As explanatory variables, we used the following vegetation characteristics: nutrient

291    concentrations (N, Na, P, K, Mg, Ca), tannin levels, digested energy and dry matter

292    intake percentages. The latter were based on respectively ADF and NDF percentages.

293    NDF is a measure of the fibre content of a plant, and a plant's NDF content

294    determines how much of the plant an elephant can consume (van Soest & McQueen,

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295    1973; van Soest, 1978). We use these NDF levels to calculate the daily Dry Matter

296    Intake (DMI) for elephants: $\% \; of \; DMI \; per \; kg \; body \; mass \; = \; 120/\% \; NDF$, for

297    each of the vegetation samples (Moore & Undersander, 2002). ADF can be used to

298    calculate proxies for the energy content of vegetation.  We used the ADF levels to

299    calculate digested energy for elephants, following the formulas used by Pretorius et

300    al. (2012): $digested \; Energy = 64.850 \; \times$

301     $digested \; ADF^{-0.205}, with \; digested \; ADF = 6.665e^{0.0246(ADF \; diet)}$. Models were

302    simplified using a backward selection procedure until variable removal significantly

303    reduced the variance explained by the model.

304    *2.3.4 Comparing vegetation characteristics between vegetation types*

305    We compared these same characteristics with one-way ANOVAs between trees,

306    grasses and crops during the early (February), mid (March) and late (April) crop

307    season, as crops and grasses are predominantly present in these months. If residuals

308    were not normally distributed or we observed evidence of heteroscedasticity, we used

309    non-parametric Kruskal-Wallis tests. Due to the high number of dimensions and

310    complexity of relationships, we combined this with Principal Component Analyses

311    (PCA) in order to visualise these differences.

312    *2.3.5 Right-angle mixture model*

313    When making dietary decisions, animals do not only aim to avoid nutrient

314    deficiencies, but also nutrient excess, resulting in a rule of compromise balancing the

315    under and over consumption of nutrients (Raubenheimer & Simpson, 1999; Simpson

316    et al., 2004). We can analyse this nutrient balance visually by plotting the different

317    relative nutrient levels in a multidimensional space in which we plot both required

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318     and available food items (Simpson & Raubenheimer, 1993). This results into a Right-

319     angle Mixture Triangle (RMT); a two-dimensional plot with three axes, each

320     representing a vegetation quality measure (e.g. sodium). These axes show the

321     percentages in which different components are present in a dietary composition

322     (Raubenheimer, 2011). If each of the elephant food items is considered to be a

323     composition of the elements of these three axes (e.g sodium, phosphorus,

324     magnesium), it is possible to calculate their relative percentage based on their

325     concentration in the vegetation samples. We calculated the ideal nutrient balance as a

326     nutrient space from estimated minimum and average elephant dietary requirements

327     (phosphorus: $\%P_{min}=0.15$, $\%P_{av}=0.2$, potassium: $\%K_{min}=0.5$, $\%K_{av}=0.7$, magnesium:

328     $\%Mg_{min}=0.1$, $\%Mg_{av}=0.3$, Pretorius et al., 2012). RMTs demonstrate how balanced

329     different food items are in their micronutrient composition, and how the elephant

330     could combine food items to achieve the balanced diet and reach minimum nutrient

331     requirements (Raubenheimer & Simpson, 1999; Simpson et al., 2004). Hence, we

332     selected those vegetation characteristics that appeared most important in the first two

333     analyses, and plotted these elements of the three types of vegetation against the

334     required compositions of elephant diets. Since we are mainly interested in

335     understanding the role and potential deficiency of micronutrients in elephant diet, we

336     focus on these instead of macronutrients as conventional in RMT analyses

337     (Raubenheimer & Simpson, 1999; Raubenheimer et al., 2015).

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339   **3. Results**

340   **3.1 Summary of results**

341   The analyses of browsing preference indicated that elephant foraging choices are

342   positively associated with magnesium, phosphorus, and dry matter intake. The

343   subsequent analyses comparing vegetation types revealed that crops have higher

344   concentrations of most nutrients, digestible energy and dry matter intake and a lower

345   tannin concentration than browse. Finally, right-angle mixture triangles showed that

346   elephant diet is unbalanced in phosphorus. We now explain how these findings

347   emerged from the statistical analyses we conducted.

348   **3.2 Dietary choices**

349   *3.2.1 Control plots*

350   Over all feeding trails and months, food plots had a 9% higher occurrence of most

351   common vegetation species compared to control plots (Linear model, $F_{1,532}=19.58$,

352   $p<0.0001$).

353   *3.2.2 Acceptance/availability plots*

354   The acceptance and availability plots reveal that changes in elephant selection of

355   browse species are related to vegetation quality changes, as these changes occurred

356   over the dry and wet seasons (Figure 2).
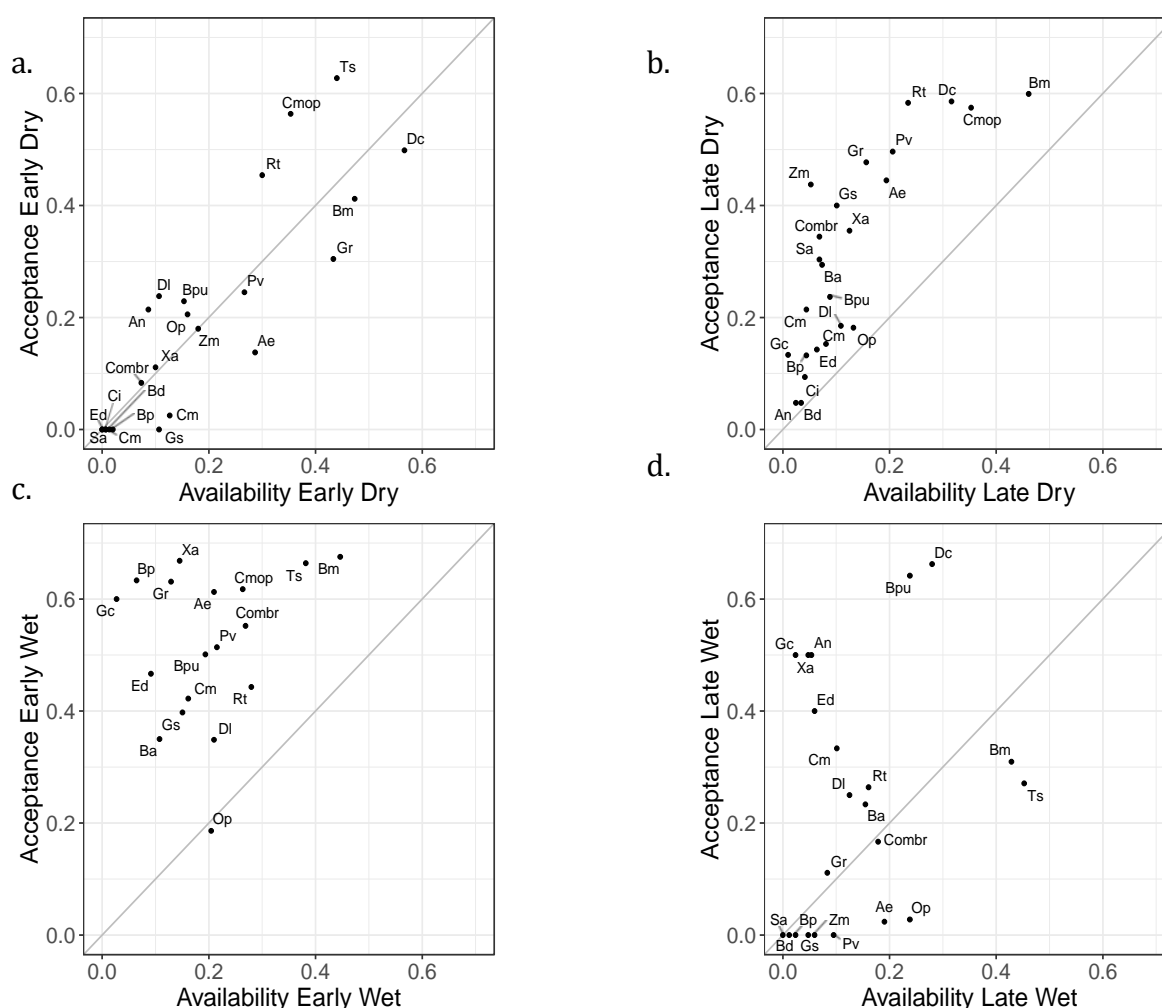
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*Figure 2. Acceptance versus availability plots divided in different seasons: a. early*

*dry, b. late dry, c. early wet and d. late wet. Species abbreviations: Bm= Baphia*

*mossaiensis, Ts=Terminalia sericea, Cm=Croton megalobotrys, Dl=Diospyros*

*lycioides, Rt= Rhus tenuinervis, Op= Ochna pulchra, Ba= Burkea africana, Gs=*

*Gymnosporia senegalensis, Gc= Guibourtia coleosperma, Cmop= Colophosperum*

*mopane, Combr= Combretum spp., Gre= Grewia spp., Xa= Ximenia*

*Americana/caffra, Ae= Acacia erioloba, Bpu= Bauhinia petersiana, Ed= Euclea*

*divinorum, An= Acacia nigrescens, Cm= Combretum mossambicense, Zm= Ziziphus*

*mucronata, Bd= Berchemia discolor, Ci= Combretum imberbe, Bp= Baikiaea*

*plurijuga, Pv= Philenoptera violacea, Sa= Senegalia ataxancantha.*

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369    Species above the 1:1 line irrespective of season, i.e. preferred species, were

370    *Terminalia sericea*, *Colophospermum mopane*, *Ximenia Americana/caffra*,

371    *Guibourtia coleosperma*, *Acacia nigrescens*, *Burkea africana* and *Rhus tenuinervis*.

372    Species for which elephants show a moderate to low preference were *Diospyros*

373    *lycioides*, *Euclea divinorum*. For species such as *Dichrostachys cinerea*, *Combretum*

374    *mossambicensis*, *Ziziphus mucronata*, *Baikiaea plurijuga* and *Grewia* spp. elephants

375    show preference in some seasons, while in other seasons elephants avoided them.

376    Elephants either avoided *Ochna pulchra*, or consumed it relative to the availability of

377    the species. Note that in some seasons, our feeding trails did not include sufficient

378    quantities of each species to include them into our analyses. Not only did the level of

379    selection by elephants change, so did the general patterns of species on the plots of

380    Figure 2. During the early dry season elephants had few preferred tree species, as

381    most species were grouped along the line or even below it, revealing aversion. In the

382    late dry season elephants start to show clear preference and avoidance for certain

383    species. This preference becomes more pronounced in the early wet season, but

384    during the late wet season elephant general tree preferences become less strong,

385    returning to the 1:1 ratio line.

386    *3.2.3 Explaining browse choices*

387    Elephant browse choices were influenced by season, the levels of phosphorus,

388    magnesium and potassium, and the dry matter intake. The number of plots in which a

389    species was eaten versus the number of plots in which it was not eaten per feeding

390    trail, differed significantly between seasons (GLM binomial logistic regression:

391    $\chi^2_3 = 154.83$, P<0.0001, parameter estimates: Early Dry $\mu$=-2.61, SE=0.42; Late Dry:

392    $\mu$=0.48, SE=0.18; Early Wet $\mu$=0.50, SE=0.19; Late Wet $\mu$=-0.50, SE=0.22). This

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393     corresponds to the acceptance/availability plots in Figure 2, where there is a clear

394     difference in pattern across the seasons in acceptance and availability. During the

395     early wet and late dry when elephants show strongest species preferences, these

396     parameter estimates are positive, while during the early dry and late wet parameter

397     estimates are negative, corresponding to elephants being more selective and avoiding

398     certain species. Of the nutrient levels we included in the initial model, only

399     phosphorus, potassium and magnesium remained in the final simplified model. Of

400     these, phosphorus and magnesium were significant in explaining the variance in the

401     data (GLM binomial logistic regression, phosphorus: $\chi^2_1$=131.09, P<0.0001,

402     parameter estimates $\mu$=5.53, SE=1.08; magnesium: $\chi^2_1$=124.52, P<0.05, parameter

403     estimate $\mu$=0.34, SE=0.16). In particular, phosphorus was important in determining

404     the ratio between numbers of plots where a tree is eaten compared to not eaten, with a

405     strongly significant positive parameter estimate. On the contrary, potassium had an

406     opposite effect with a negative parameter estimate, yet this effect was not significant

407     ($\chi^2_1$=128.37, P=0.10, parameter estimates $\mu$=-0.40, SE=0.16). Finally, dry matter

408     intake, which is the variable we calculated based on the NDF content of the

409     vegetation, had a positive influence on the eaten/not eaten ratio in this final model

410     ($\chi^2_1$=111.89, P<0.0001, parameter estimate $\mu$=0.56, SE=0.16).

411     **3.3 Comparing vegetation characteristics between vegetation types**

412     The three vegetation types of grasses, trees, and crops differed on each of the

413     vegetation characteristics when averaged across the crop-growing season, and crops

414     particularly distinguished themselves from the other vegetation types by their high

415     DMI, phosphorus and magnesium values. During the crop season, there was a steady

416     increase in both ADF and NDF for grasses, while crops and trees remained relatively

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417     stable in their levels (ANOVA: NDF: $\chi^2_2=109.60$, p<0.0001, ADF: $\chi^2_2=40.39$,

418     p<0.0001). Regardless of their phenological state throughout the season, crops scored

419     highest for digestible energy content, and dry matter intake (DE: ANOVA, $\chi^2_2=41.52$,

420     p<0.0001, DMI: Kruskal-Wallis test, $F_2=156.52$, p<0.0001, Figure 3).
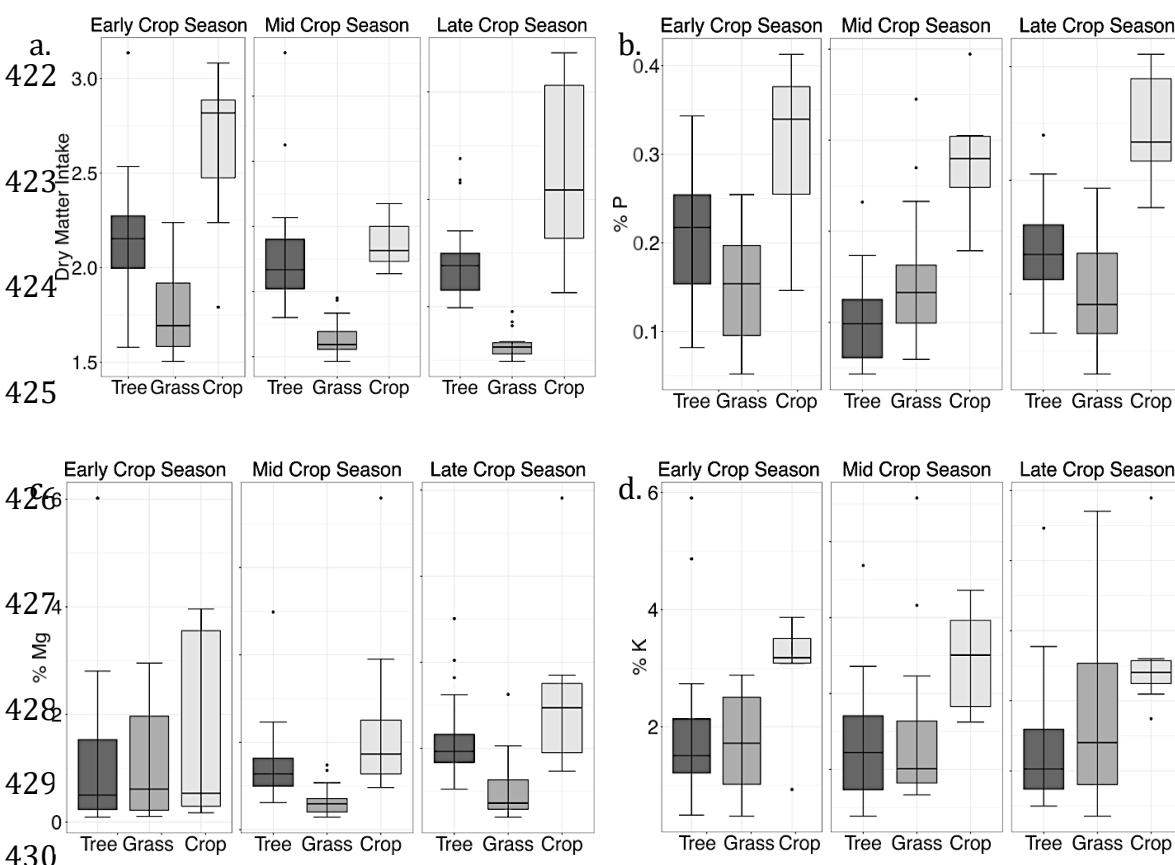
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431     *Figure 3. Boxplots comparing the differences in the vegetation characteristics a. Dry*

432     *Matter Intake, b. Phosphorus (P), c. Magnesium (Mg) and d. Potassium (K) between*

433     *trees, grasses and crops, and their changes over the crop season.*

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435     In the late crop season (April) just before crops are harvested, crops had higher

436     concentrations of nitrogen, phosphorus, calcium and magnesium compared to trees

437     and grasses (ANOVA: nitrogen: $\chi^2_2=72.98$, p<0.0001, phosphorus: $\chi^2_2=38.89$,

438     p<0.0001, Kruskal-Wallis test: potassium: $\chi^2_2=26.52$, p<0.0001, calcium: $\chi^2_2=42.51$,

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439    p<0.0001, magnesium: $\chi^2_2$=23.78, p<0.0001, sodium: $\chi^2_2$=1.85, p=0.4877). During the

440    different phenological crop stages, this difference between crops and the other

441    vegetation types increased for calcium, magnesium and phosphorus, while it remained

442    stable for nitrogen. The potassium levels in grasses were similar to crops, while

443    sodium levels were highest for grasses, and maturation reduced sodium levels in

444    crops. Tannin levels were over ten times higher for trees than for crops and grasses,

445    and the levels remained stable across seasons (Kruskal-Wallis test: tannin: $\chi^2_2$=96.29,

446    p<0.0001).

447    In the early crop season the first three components of the PCA explained 80% of the

448    total variation. The first component explained over half of the variance in the data,

449    and was loaded with each of the vegetation characteristics besides tannin. For this

450    first component, especially digestible energy appeared to have a positive correlation,

451    while % ADF had a similar negative influence. The second components appeared to

452    be dominated negatively by tannin and positively by phosphorus (Figure 4). During

453    the mid crop season, there was a small change in the percentages of variance

454    explained in the first and second component, while the construction of the

455    components remained the same as in the early season. During the late crop season

456    when crops were maturing, the first component of the PCA increased again in the

457    percentage of variance it explains, while the second reduced. The first component did

458    not change, except tannin was no longer loaded, yet the reloading on the second

459    component changed considerably. Nitrogen, which at first played only a role in the

460    first component, loaded most strongly, and phosphorus remained important in the first

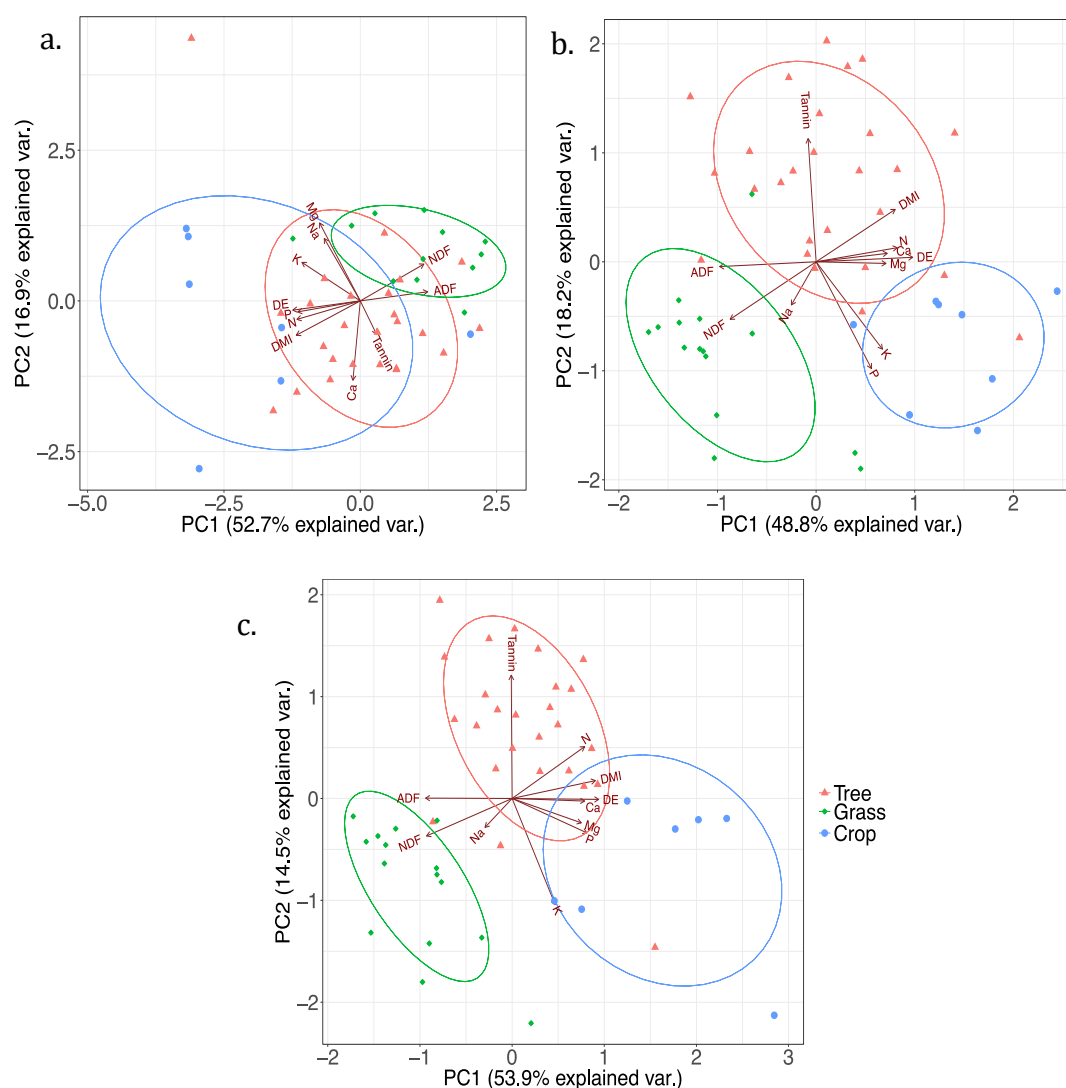461    component yet strongly reduced in its importance for the second component.

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*Figure 4. Biplots of PCAs for the a. early, b. mid and c. late crop season, revealing the clusters of groups of trees, grasses and crops.*

The PCA biplots (Figure 4) showed three distinctive groups; with the grasses data grouped around the fibre measurements ADF and NDF, whereas crops were grouped among most of the nutrient variables. Sodium (Na) was more associated with grasses than with crops. Finally, trees were centred in the middle, grouped around tannin. With progression of the crop season and rainfall stimulating crop and grass growth, the differences between trees, grasses and crops increased. Crops seemed to be

476  centred and especially distinguished from the other two vegetation types by their

477  higher levels of phosphorus and magnesium.

478  **3.4 Right-angle mixture models**

479  Since our final model on foraging preferences included phosphorus (P), magnesium

480  (Mg) and potassium (K), we used these three micronutrients as our RMT axes, with P

481  on the x-axis, Mg on the y-axis and K on the tertiary axis. Because P and Mg levels

482  were all below 60% and K levels above 40%, our axes start at these values, with the

483  tertiary axis of 40% at the base of the triangle, and reaching 100% in the origin of the

484  plot (Figure 5). Grey lines indicate the nutrient space between the minimal and

485  average required nutrient balances for elephants for each of the three micronutrients.

486  For example, food sources within the horizontal grey lines constitute the required

487  concentration of Mg, while those above the lines have a relative surplus of Mg and

488  those below a relative deficiency in Mg. The parallelogram created by these six grey

489  lines represents the nutrient space in which food items are optimally balanced in these

490  three micronutrients. If a food source lies within this nutrient space, elephants can

491  reach a diet balanced in these three micronutrients by only consuming that food item.

492  Nevertheless, it is also possible to reach this dietary balance by combining food

493  sources, and thus consuming food items with matching surpluses and deficiencies in

494  other to reach a balance on average (Raubenheimer et al., 2015). Our RMT plots

495  indicate that the ratio between P:Mg:K varies over the seasons, with in the early and

496  mid crop season excessive ratios of Mg and K, and in each of the seasons a relative

497  imbalance in phosphorus (Figure 5). Only one tree species *Ochna pulchra* reached the

498  required P level in the late crop season with 19%. In the late crop seasons when crops

499  are mature, the P:Mg:K ratios of trees, crops and grasses are clustered. We also

500    display these plots including the dry matter intake levels based on the NDF (Figure

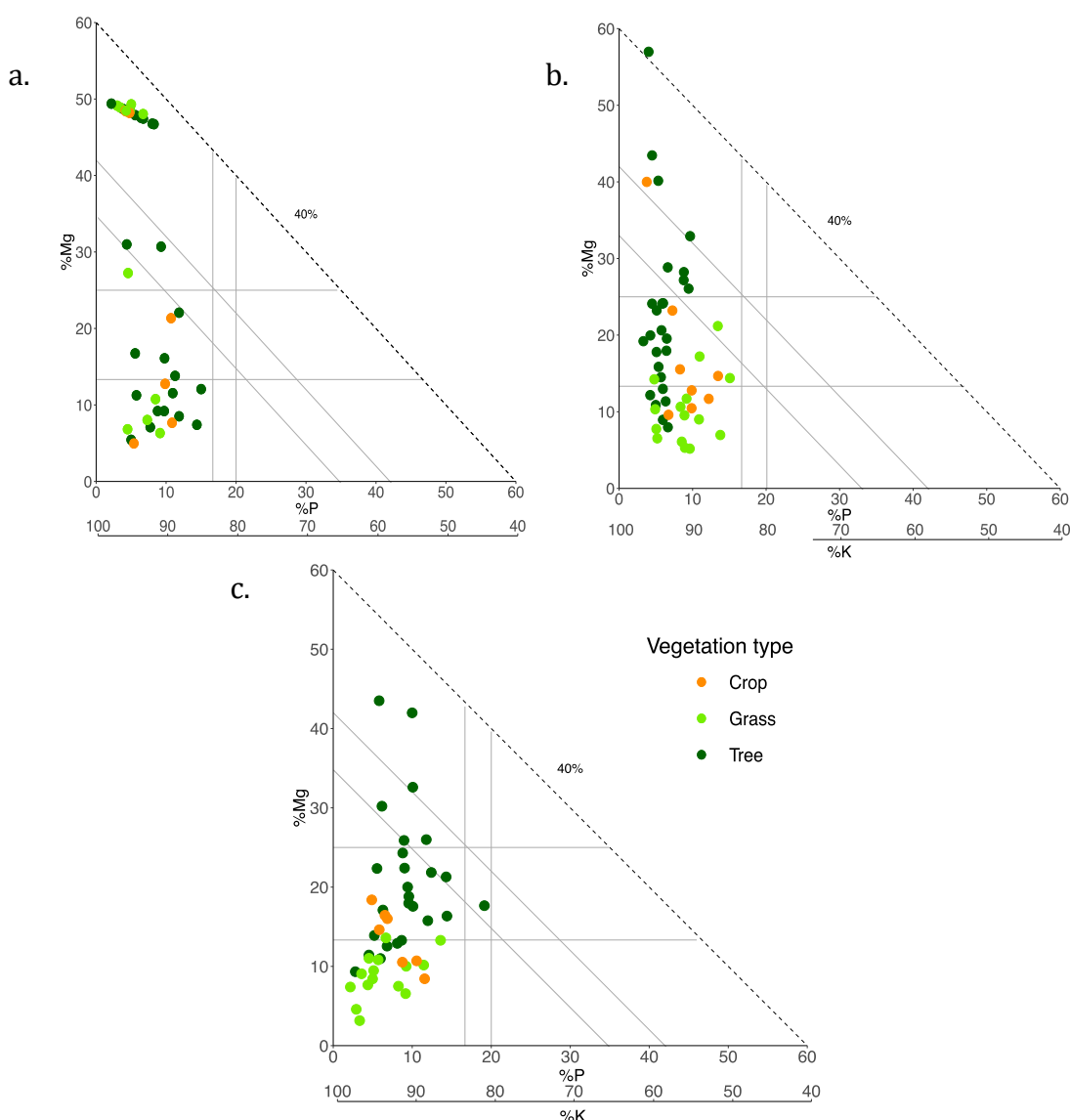501    6a) and relative condensed tannin (Figure 6b).



*Figure 5. Right-angle Mixture Triangles, plotted with phosphorus on the X-axis (P),*

*magnesium on the Y-axis (Mg) and potassium on the diagonal Z-axis (K). Plot a, b*

*and c show the P:Mg:K ratio for respectively the early, mid and late crop season, for*

*crops, grass and trees. The axes are scaled from 0-60% and 100-40%, none of the*

*points contained a percentage of Mg or P higher than 60%, and only one a*

*percentage of K lower than 40%.*

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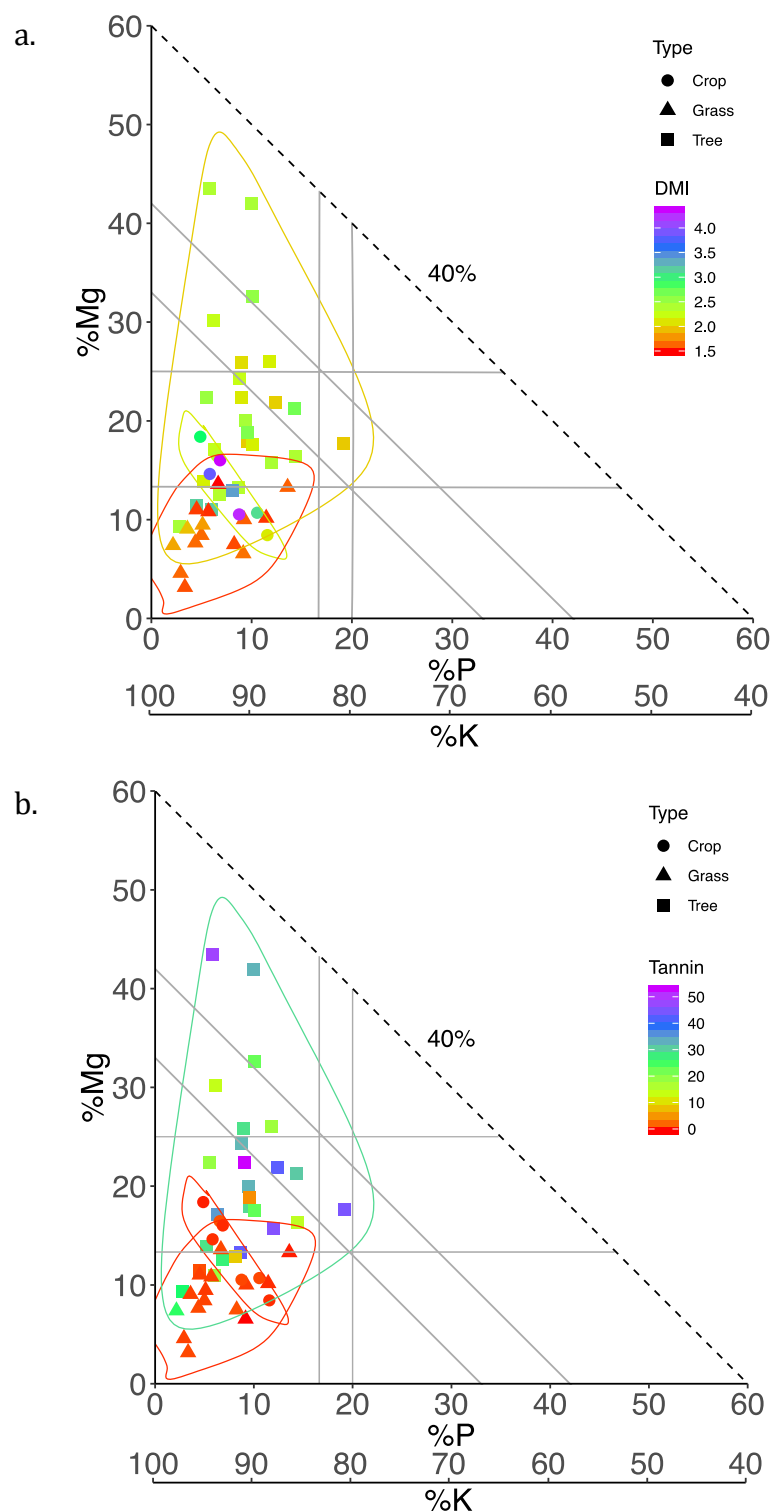528
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538   *Figure 6. Plots shows the same data as plot c in Figure 5, however the colour of the*

539   *food items indicates the dry matter intake levels (a) or condensed tannin (b). The axes*

540   *are scaled from 0-60% and 100-40%, none of the points contained a percentage of*

541   *Mg or P higher than 60%, and only one a percentage of K lower than 40%.*

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542 **4. Discussion**

543 Our results suggest that in our study site micronutrient concentrations are an

544 important determinant in elephant crop consumption, and that crop consumption

545 could be a strategy to avoid or minimize dietary deficiencies.

546 The acceptance/availability plots indicate that foraging preferences vary over the

547 season. Our analyses of foraging preference indicate that elephants select browse

548 species based on the dry matter intake value and concentrations of phosphorus and

549 magnesium, and potentially potassium. Phosphorus and magnesium had a positive

550 effect on browse preference. Dry matter intake appeared to also have a positive

551 influence on dietary preferences towards tree species. This appears contrary to

552 previous research that showed fibre measures were unrelated to elephant food intake

553 (Meyer et al., 2010).

554 Our comparison between crops, grasses, and trees on nutrient and fibre measurements

555 showed that grasses were highest in ADF and NDF fibre contents, and that these

556 levels increased towards maturation when the fresh green grass started to dry. By

557 contrast, the digestible energy and dry matter intake were highest in crops; thus

558 consuming crops increases energy levels faster than consuming grass or trees. This

559 concurs with previous research that showed that digestible energy is an important

560 factor in elephant dietary optimisation (Pretorius et al., 2012). Tannin levels were

561 significantly higher in trees than in crops and grasses, making them less desirable for

562 digestion (Owen-Smith & Chafota, 2012). However, in our analysis tannin levels did

563 not influence elephant dietary browse preferences, suggesting that unless there is a

564 threshold relationship above which tannins do not play a role, tannin levels are not an

565 important driver in forage choice by elephants. This could be related to the large

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566    salivary glands which may buffer against the effect of tannins (Schmitt, 2017). Even

567    if there is a threshold relationship, tannin cannot explain elephants consuming crops

568    over grasses, as there was no significant difference between the tannin levels of crops

569    and grasses.

570    During crop maturation, nutrient concentrations in crops became significantly higher

571    than those in browse and grass, except for sodium, which was more available in

572    grasses than crops. Therefore, we did not find support for sodium deficiency in

573    elephant diet in our study area or evidence that crop consumption is a response to

574    sodium cravings, in contrast to comparable studies in other areas (Sukumar, 1990;

575    Holdø et al., 2002; Rode et al., 2006).

576    The clustering of trees, grasses and crops in the PCA concentrated into separate

577    groups towards the end of the crop season. Nutrients played an important role in

578    explaining the variation within the data, with crops clustered around a correlated

579    group of dry matter intake, digestible energy, phosphorus, magnesium, calcium and

580    potassium. Browse species were mainly concentrated around tannin, nitrogen, and

581    grass around the fibre measures NDF and ADF and sodium levels.

582    Finally, the RMT graphs displayed how the ratios between the three nutrients were

583    distributed over trees, grasses and crops. Grasses appeared to result in the highest and

584    trees in the lowest relative potassium percentages, with crops in an intermediate

585    position. Regarding magnesium, crops contained intermediate percentages compared

586    to trees and grasses. At the same time, most trees achieved the required ratio in

587    magnesium, while most grasses had lower values. While there were multiple food

588    sources that fell within the nutrient space indicating balanced magnesium and

589    potassium values, neither natural forage nor crops reached a nutrient balance for

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590      elephants regarding phosphorus, revealing a potential deficiency in phosphorus in

591      elephant diet. An increase in the ratio between calcium and phosphorus could

592      furthermore accentuate a deficiency in available phosphorus (McNaughton, 1990).

593      The intermediate position of crops could also contribute to crops' attractiveness to

594      elephants. By selecting crops, elephants could balance out the excess of potassium

595      and possibly calcium and deficiencies in other nutrients, which in the RMT

596      framework is considered a 'rule of compromise' (Raubenheimer & Simpson, 1999).

597      Moreover, the RMT plot including the dry matter values (Figure 6.a), clearly

598      illustrates the significantly lower dry matter values of crops, meaning that elephants

599      can consume significantly more crops than trees and grasses, thus allowing a higher

600      possibility of consuming sufficient amounts of phosphorus. The RMT plot including

601      tannin levels (Figure 6.b) visualises the higher tannin levels of trees, however we

602      know from the vegetation content comparisons that there was no significant

603      difference between tannin levels of grasses and crops.

604      **5. Conclusion & management implications**

605      Together, our results provide insights into the importance of micronutrients in crop

606      consumption behaviour, and the potential effectiveness of mitigation measures such

607      as artificial salt licks (Zhang & Wang, 2003). Our study suggests that consuming

608      crops could be more than just a better alternative to browse and grass, and could even

609      be a necessity to cope with micronutrient deficiencies in natural forage. Crops are a

610      better option to browse and grass due to their higher dry matter intake, digestible

611      energy and micronutrient values. However, the importance of phosphorus levels in

612      increasing browsing preference, the extreme levels of phosphorus in crops, the

613      importance of phosphorus in clustering the vegetation types and furthermore the

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614   potential phosphorus deficiency indicated by the RMT models, suggest that crop

615   consuming behaviour in elephants could be explained by a phosphorus deficiency

616   when only feeding on grasses and trees. Phosphorus has more known functions than

617   any of the major minerals (McDonald et al., 2011) and plays an important role in the

618   development of cells and tissues (Ihwagi et al., 2011), energy metabolism and is in

619   close association with calcium in bone (McDonald et al., 2011). Deficiencies in

620   phosphorous are widespread, since most soils worldwide are deficient in this element,

621   especially in (sub-) tropical regions (McDonald et al., 2011, McDowell 2003,

622   O'Halloran et al., 2010). Deficiencies in phosphorus can have a direct impact on

623   fertility and reproduction (McDonald et al., 2011). Elephants can crave phosphorus,

624   suggested to be the main reason behind tree debarking, due to the high concentrations

625   of phosphorus in bark (Ihwagi et al., 2011). Elevated levels of phosphorus can also be

626   found in soil licks (Klaus et al., 1998) and in vegetation on termite mounds (Grant &

627   Scholes, 2006). Further research including absolute dietary input is needed to confirm

628   the role of phosphorus deficiency in stimulating elephant crop consumption, taking

629   into account not only the quality but also the quantity of forage elements. Our study

630   also reveals the importance of including information on feeding ecology into

631   addressing crop consuming behaviour, as these influences can be site specific.

632   Incorporating knowledge on crop consumption drivers into mitigation measures can

633   increase efficiency and effectiveness of them. For example, providing supplementary

634   licks rich in phosphorus away from crop fields warrants further investigation as a crop

635   consumption mitigation technique.

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**7. Data accessibility**

Data will be available from the Figshare data repository.

**8. Author contributions**

SMV conceived the idea for the study and SMV, WFB and MDH designed methodology; SMV, TC, ACS, GM and ALS adapted methods to study site; SMV and MM lead data collection; SMV and TC analysed the data; SMV and TC led the writing of the chapter. All authors contributed critically to the drafts and gave final approval for publication.

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