What drives the seasonal movements of African elephants (*Loxodonta africana*) in Ithala Game Reserve?

by

Kayleigh Muller

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Pietermaritzburg

Supervisors:

Prof. David M. Ward and Dr. Adrian M. Shrader

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COLLEGE OF AGRICULTURE, ENGINEERING AND

SCIENCE

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November 2013

Preface

The work described in this thesis was carried out at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa, from January 2012 to November 2013, under the supervision on Professor David Mercer Ward and Dr. Adrian M. Shrader.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the authors and has not been submitted in any form to another university. Where use of other work was made, it has been acknowledge in the document.

K.Muller

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Kayleigh Muller

DMWard

………………………………….

Professor David Mercer Ward

Supervisor

Ch. M. Sh

…………………………………..

Dr. Adrian M. Shrader

Co-supervisor

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SUCCESS is not final, FAILURE is not fatal; it is the COURAGE to continue that counts. – Winston Churchill

1

2 **Summary**

3 The changes in plant quality and availability in space and time present a substantial problem

4 to mammalian herbivores. As a result, these herbivores need to alter their foraging behaviour

5 to maximize their energy gain at both small (plant level) and large (landscape level) scales. A

6 megaherbivore, the African elephant (*Loxodonta africana*), has been shown to be selective in

7 its foraging choices at both of these scales. Furthermore, the ratio of palatability:defences

8 (e.g. fibre and total polyphenols) has been highlighted as an important determinant of habitat

9 selection in elephants. The elephants in Ithala Game Reserve (IGR) frequently leave IGR

10 during the wet season and forage outside the reserve. However, they predominantly feed on

11 the low-nutrient granite soils of the reserve and return to a high-nutrient area with dolerite

12 soils during the dry season. In an attempt to understand these seasonal movements, I focused

13 on how the small-scale foraging decisions of the elephants lead to large-scale seasonal

14 movements in IGR, KwaZulu-Natal. Plant availability was determined seasonally for seven

15 target species across four areas in the reserve. Crude protein, fibre, energy and total

16 polyphenols as well as the ratios of palatability:digestion-reducing substances were analysed

17 in the wet and dry seasons. All factors and their interactions were significant in a MANOVA.

18 Consequently, I employed a dimension-reducing Principal Components Analysis (PCA) to

19 better understand the factors of greatest importance. The PCA highlighted four of the six

20 most important factors to be the ratios of palatability:digestion-reducing substances. The

21 other two important variables were total polyphenols (negative effect) and crude protein

22 (positive effect). At small spatial scales, I found that the elephants were selective in their

23 decisions, especially during the dry season. For example, the increased inclusion of the

24 principal tree species *Acacia nilotica* from 2.9% in the wet season to 39.3% during the dry

25 season appears to be a result of a decline in total polyphenols and fibre during the dry season.

26 At large spatial scales, the elephants moved back into IGR from the low-nutrient granite soils

27   in the east in response to an increase in forage quality in the west as the quality declined in

28   the east at the same time. However, it is unclear as to why the elephants are leaving the

29   reserve during the wet season. Some possible explanations for this are discussed.

30

31   **Key-words:** acid detergent fibre, crude protein, *Loxodonta africana,* neutral detergent fibre,

32   total polyphenols, plant part quality.

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45

Fig. 8. The seasonal values of the $\log_{10}$ reciprocal of ADF:TP ratios for a) principal and b) avoided species. TP= total polyphenol concentrations. High values indicate high quality vegetation. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.

46

Fig. 9. The seasonal values of the $\log_{10}$ CP:NDF ratios for a) principal and b) avoided species. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.

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71 **List of Appendices**

72 **Appendix 1**

73 **Appendix 1a:** Global positioning system points (determined by satellite observations) of the

74 elephants' distributions from 2008 in Ithala Game Reserve between seasons wet (black

75 triangles) and dry seasons (grey stars).

76 **Appendix 1b:** Global positioning system points (determined by satellite observations) of the

77 elephants' distributions from 2009 in Ithala Game Reserve between seasons wet (black

78 triangles) and dry seasons (grey stars).

79 **Appendix 1c:** Global positioning system points (determined by satellite observations) of the

80 elephants' distributions from 2010 in Ithala Game Reserve between seasons wet (black

81 triangles) and dry seasons (grey stars).

82 **Appendix 2:** MANOVA statistics between the nutritional factors (season, area, species and

83 second- and third-order interactions) and plant quality data. Error degrees of freedom = 1005.

84

85

86

Thesis outline

88 Herbivores forage in an environment that exhibits variation in food quality and availability
89 (Senft *et al.* 1987; Shipley 2007). This is particularly evident in the seasonal fluctuations
90 between wet and dry periods (van Aarde *et al.* 2008). In addition, spatial heterogeneity in
91 quality differs from individual plants up to the landscape scale (Pickett & Cadenasso 1995;
92 Skarpe *et al.* 2000; Shipley 2007). Consequently, as a result of changes in plant availability
93 and quality herbivores need to alter their foraging behaviours in a way to maximize their
94 energy gain, especially during forage-limited periods (Stephens & Krebs 1986; Owen-Smith
95 2002). At small scales, herbivores can alter diet breadths, intake rates and foraging durations
96 while at larger scales, herbivores can increase their range use and the habitats they utilise
97 (Senft *et al.* 1987; Ward & Saltz 1994; Searle *et al.* 2005).

98 The African elephant (*Loxodonta africana,* (Blumenbach, 1797)) is the largest
99 terrestrial megaherbivore (>1000 kg). They have been shown to be selective in their feeding
100 habits at both small (Pretorius *et al.* 2011; Pretorius *et al.* 2012) and large scales (Loarie, van
101 Aarde & Pimm 2009b; Young, Ferreira & van Aarde 2009; Shrader *et al.* 2012).

102

103 **Elephants in Ithala Game Reserve in northern KwaZulu-Natal**

104 The elephants in Ithala Game Reserve alter their habitat use seasonally (Shrader *et al.* 2012).
105 They forage in a relatively low-nutrient area with granite soils and occasionally venture
106 outside the reserve during the wet season and move back to a higher nutrient area with
107 dolerite soils during the dry season. This movement back into the reserve is also away from
108 their largest source of water in the dry season (Shrader *et al.* 2012). As water is not limiting

109   within the reserve (van Rooyen & van Rooyen 2008), it is likely that food quality and/or

110   availability influence these seasonal movement patterns.

111   To explore this possibility, I recorded the seasonal changes in food quality and

112   availability across the IGR. I did this by dividing the reserve area into four sections, based on

113   previously recorded feeding areas of preferences and avoidances (Shrader *et al.* 2012).

114   Ultimately, I wanted to determine how changes in plant quality and availability influenced

115   the elephants' seasonal habitat use and movement patterns. I did this by determining the

116   nutritive quality of three principal tree species and four avoided tree species in the elephants'

117   diet across the reserve, as determined by Shrader *et al.* (2012). I also wanted to see how the

118   nutritive quality changed seasonally, so I recorded data in both the wet and dry seasons.

119   The thesis is formatted so that Chapter 1 comprises an introduction and literature

120   review where I discuss factors that influence foraging and habitat selection in more detail and

121   set up what is already known about elephant movement and forage quality. The subsequent

122   chapters comprise the *Materials and Methods*, *Results* and *Discussion,* respectively.

123   Formatting for this thesis follows the ***Journal of Animal Ecology***.

124

125 # Chapter 1: Literature review

126

127

128 **FORAGING**

129 Foraging forms a central part of a herbivore's daily activities. Food items are not uniformly

130 distributed across the environment, but instead both food quality and availability exhibit

131 spatial and temporal variation (Senft *et al.* 1987; Pickett & Cadenasso 1995; Shipley 2007).

132 Optimal foraging theory is one of the most commonly used theories to explain the decisions

133 that animals employ (Stephens & Krebs 1986). Factors influencing foraging decisions include

134 time spent travelling to a patch, the type and quality of food in a patch and the density of food

135 found in the patch (Charnov 1976; Stephens & Krebs 1986; Brown 1999).

136   At a most fundamental level, plant quality is influenced by soil quality (Bardgett &

137 Wardle 2010). Low concentrations of nutrients in the soil generally result in low

138 concentrations of nutrients in plant organs (Coley, Bryant & Chapin 1985; Owen-Smith &

139 Cooper 1987; Holdo 2003). Furthermore, plant species growing in nutrient-poor areas have

140 been shown to have higher levels of secondary metabolites, which are compounds not

141 involved in primary cell functions. Plants typically use these secondary metabolites to defend

142 the parts that they have (Coley *et al.* 1985; Owen-Smith & Cooper 1987). As a result of

143 heterogeneous plant quality and availability, a herbivore's diet varies both spatially and

144 temporally across the environment. Spatially, differences occur between plant species as well

145 as between the parts of the plant eaten, and on larger scales, between feeding patches and

146 habitats (Senft *et al.* 1987; Bailey *et al.* 1996). Food resources fluctuate naturally as

147 vegetation grows and decays (Owen-Smith 2002). Furthermore, not all available food is

148 accessible to herbivores. Accessibility may be temporary, such as results from the loss of

149 leaves of deciduous plants (Shorrocks 2007). Additionally, leaves at the tops of trees are not

150 available to shorter herbivores, while woody matter is not edible for many smaller herbivores

151 as their digestive systems are not equipped to handle high fibre diets (Lundberg & Astrom

152 1990; Owen-Smith 2002). Within feeding patches and habitats, the key determinant of food

153 intake is how long it takes the herbivore to handle the food type (Emlen 1966). Food intake is

154 limited by bite size and bite rate. Intake rate ultimately determines whether the herbivore will

155 need to include other sources of less preferred species in their diets (Owen-Smith 2002).

156 Temporally, a herbivore's diet is heterogeneous across seasons. This is particularly

157 evident in systems where there are seasonal fluctuations between wet and dry periods

158 (Shorrocks 2007; van Aarde *et al.* 2008). In southern African savannas, there are two distinct

159 seasons, wet and dry (Scholes & Walker 1993; du Toit, Rogers & Biggs 2003). The wet

160 season is associated with increased resource availability with a higher nutritive quality

161 (Owen-Smith 1988). Conversely, the dry season is known to have limited water availability

162 with a reduction in plant quality and availability (Chamaille-Jammes, Valeix & Fritz 2007).

163 These seasonal changes result in range shifts in herbivores (Owen-Smith 1988; Holdo, Holt

164 & Fryxell 2009). For example, the African buffaloes (*Syncerus caffer*) in Kruger National

165 Park changed their grass species selection and habitat utilisations between seasons in

166 responses to changes in quality and quantity of grass (Macandza, Owen-Smith & Cross

167 2004). Similarly, wildebeest (*Connochaetes gnou*) is the Serengeti National Park are known

168 to shift their foraging in relation to plant quality (Holdo *et al.* 2009)

169 Another factor that influences food quality and thus potentially movement patterns,

170 are digestion-reducing substances. Physical defences and plant secondary metabolites

171 increase the difficulty of digestion and intake rates respectively (Freeland & Janzen 1974).

172 These physical defences include spines, thorns and cell structure, e.g. cell wall thickness

173 (Shipley 1999). Physical defences can be effective for smaller-bodied mammalian herbivores,

174 the so-called "mesoherbivores" (35-180 kg) (Cooper & Owen-Smith 1986), but less effective

175 against the larger mouths of large-bodied herbivores, the so-called "megaherbivores" such as

176 elephants, giraffes and rhinoceroses (Owen-Smith 1988; Sukumar 1992; Rafferty, Byron &

177 Hanley 2005). Physical defences also interact with leaf size so that smaller leaves are hidden

178 among long thorns (e.g. Cooper & Owen-Smith 1986; Rohner & Ward 1997).

179   A second, and more prevalent, form of plant defence is plant secondary metabolites.

180 Secondary metabolites are chemicals found in plant cells that are not important for primary

181 cell functions (Iason 2005). Phenolics are an abundant group of structurally diverse chemicals

182 commonly used by plants. The most well-known phenolic compounds are tannins (Waterman

183 & Mole 1994). There are two main types of tannins: hydrolysable tannins and condensed

184 tannins (Cooper & Owen-Smith 1985; Bryant *et al.* 1991; Bryant, Reichardt & Clausen

185 1992). Hydrolysable tannins inhibit digestive enzymes by hindering the digestion of plant

186 material (Waterman & Mole 1994). Condensed tannins bind to protein and reduce the

187 digestibility of the plant (Robbins *et al.* 1987; Freeland 1991). Tannins have an dose-

188 dependent effect, such that the more the herbivore ingests the less protein they are able to

189 digest (Cooper & Owen-Smith 1985; Waterman & Mole 1994). As a result, herbivores have

190 had to develop ways to maximise their forage intake while limiting the intake of secondary

191 metabolites (Provenza *et al.* 2003).

192   To counteract these dietary limitations, herbivores have been found to avoid plants

193 containing high concentrations of secondary compounds (e.g.Owen-Smith 1994; Frye *et al.*

194 2013). For example, kudus (*Tragelaphus strepsiceros*) avoided plants containing high

195 concentrations of tannins (Cooper & Owen-Smith 1985). Similarly, giraffes avoided

196 hydrocyanic acid (Zinn, Ward & Kirkman 2007). Interestingly, the ratio of digestion-

197 enhancing:digestion-reducing ratio was the most important factor influencing elephant

198 foraging decisions (Shrader *et al.* 2012). Elephants utilised tree species with lower tannins

199 and higher crude proteins rather than trees based on crude protein alone. This highlights the

200   fact that the ratio of digestion-enhancing substances (such as crude protein) relative to the

201   digestion-reducing substances (such as structural fibre and defensive compounds) of the plant

202   are important for determining herbivore foraging decisions (Wallis *et al.* 2012). Similar

203   results have been obtained for vertebrates dispersing fruits (e.g. Cipollini & Levey 1997).

204   Furthermore, Wallis *et al.* (2012) highlights the importance of the use of available nitrogen,

205   dry matter digestibility and tannins as better indicators of the nutritional quality of leaves for

206   mammalian herbivores.

207   A key way that herbivores cope with plant defences is to have varied diets (Westoby

208   1978). A varied diet allows an animal to limit the intake of potentially lethal chemicals while

209   complementary chemicals partially neutralise the effects of other lethal chemicals if eaten

210   together (Westoby 1974; Westoby 1978; Provenza *et al.* 2003). This varied diet allows a

211   limitation on the chemical intake of unpalatable substances while still maintaining their

212   nutritional requirements (Freeland & Janzen 1974; Lundberg & Astrom 1990; Belovsky &

213   Schmitz 1994). For example, lambs that had the choice between diets containing three plant

214   secondary metabolites (i.e. tannins, terpenes or oxalates) ate more than lambs encountering

215   only one secondary metabolite (Villalba, Provenza & Han 2004). The lambs were able to eat

216   more when three plant secondary metabolites were presented to them because mixing

217   complementary chemicals reduces the toxicity of the chemical on its own. It is clear that

218   experience and availability of toxins alters perception of food quality for herbivores

219   (Provenza *et al.* 2003). Additionally, diet switching allows an individual to maintain high

220   quality diets (Freeland & Janzen 1974; Wiggins *et al.* 2006). For example, the common

221   brushtail possum (*Trichosurus vulpecula*) was found to have an increased intake when they

222   were given the opportunity to switch between food types rather than the no-choice diet. This

223   highlights the importance of diet switching when plants are heterogeneously distributed in

224   space and time (Wiggins, McArthur & Davies 2006). An increase in diet breadth also helps to

225   maximize nutritional gain when resources are limited, e.g. introduction of more plant species

226   during resource-limiting periods (Emlen 1966).

227   Diet breadth is another way in which herbivores can compensate for changes in plant

228   quality. An increased diet breadth, during forage-limited periods, allows an individual to

229   maintain its metabolic requirements (Owen-Smith 1994; Macandza *et al.* 2004). In a study

230   that assessed the seasonal foraging decisions and diet breadth of kudus (*Tragelaphus*

231   *strepsiceros*) in response to changes in quality, these animals were found to increase their diet

232   breadth substantially from 19 woody species in the wet season to 31 species during the dry

233   season (Owen-Smith 1994). A similar pattern of increased diet breadth was seen in another

234   experiment on kudus by Owen-Smith and Cooper (1989). These authors also found that there

235   was inclusion of small amounts of unpalatable species, i.e. high in secondary plant

236   metabolites, in late August (the end of the dry season).

237   Small-scale changes in diet quality have the ability to lead to large-scale patterns

238   (Shipley 2007). Herbivores tend to select high-quality vegetation. Therefore, if an individual

239   experiences numerous consecutive poor-quality foraging bouts they will be forced to search

240   further for better quality food (Senft *et al.* 1987; Shipley 2007). These poor quality feeding

241   bouts results in herbivores moving to adjacent patches and eventually adjacent habitats (Senft

242   *et al.* 1987). Consequently, these movement changes may result in the seasonal movements of

243   animals. As a result, small-scale decisions regarding bite quality have the ability to influence

244   large-scale foraging patterns (Owen-Smith 2002; Shipley 2007).

245   The study of animal movement patterns allows ecologists to understand the factors

246   influencing animal distributions in space and time. Changes in abiotic factors, including

247   rainfall and temperature, have been found to be some of the determinants of herbivore

248   migratory patterns (e.g. Saino *et al.* 2007). Changes in rainfall and temperature patterns alter

249   the quality and availability of food resources. This change in forage quality is the trigger that

250   initiates the movement of herbivores (Holdo *et al.* 2009) because herbivores try to balance

251   their metabolic requirements by means of seasonal changes in forage quality and abundance.

252   A classic example is the migration of wildebeest (*Connochaetes gnou*) in the Serengeti

253   National Park. The onset of seasonal movement patterns in this species was based on the

254   quality of available forage (Holdo *et al.* 2009). The intake rate of green grass coupled with

255   high nitrogen content were the best predictors of both the short- and long-distance

256   movements of the wildebeest (Holdo *et al.* 2009). As grass declined in quality and

257   availability the wildebeest moved on to adjacent habitats where availability and quality of

258   grass remained higher. The migration of the wildebeest shows that small-scale foraging

259   decisions and plant quality can lead to large-scale foraging patterns, and possibly migration

260   (Holdo *et al.* 2009). Similarly, elk (*Cervus canadensis*) foraging could be explained by fine-

261   scale foraging choices they made based on how much effort they invested in digging to find

262   grass and forbs in the snow (Fortin, Morales & Boyce 2005). Elk foraging decisions were

263   linked to habitat structure whereby they adjusted their foraging based on the spatial

264   distribution of forage and snow.

265

PHYSIOLOGICAL FORAGING CONSTRAINTS

267   Several physiological factors influence herbivore forage selectivity, including metabolic rate

268   (Owen-Smith 1988), body size (Bell 1971; Jarman 1974), gut size (Demment & van Soest

269   1985) and digestive morphology (Janis 1976; Owen-Smith 1988). The metabolic

270   requirements of an animal are the maintenance energy requirements to fulfil all the basic

271   needs of the animal (Owen-Smith 1988). These requirements vary in relation to body mass

272   (White, Blackburn & Seymour 2009).

273   Body size is a key factor affecting foraging decisions (Jarman 1974). Larger animals

274 have higher absolute food demands and require more total energy than their smaller

275 counterparts (Demment & van Soest 1985). However, large animals have a lower energy cost

276 per gram than smaller animals (Demment & van Soest 1985; White *et al.* 2009). Furthermore,

277 gastro-intestinal tract (GIT) size increases in length with an increase in body size because

278 there is increased gut volume space (Uden & van Soest 1982; Demment & van Soest 1985;

279 Robbins 1993). Therefore, small-bodied herbivores need to be more selective than large-

280 bodied herbivores because of their higher mass-specific metabolic requirements and smaller

281 GIT (Jarman 1974). However, the influence of secondary compounds is not taken into

282 account in these body-size:energetic-demand calculations, which will change with the

283 relative nutritional quality of food (Cipollini & Levey 1997). Gut physiology will also

284 influence energetic demands of an animal, such as those affecting ruminants and non-

285 ruminants (Demment & van Soest 1985; Robbins 1993).

286   Non-ruminants, or hind-gut fermenters such as horses, rhinos and elephants, are able

287 to have higher passage rates than ruminants because they do not need a separate fermentation

288 chamber to digest fibre (Demment & van Soest 1985; Robbins 1993; Clauss *et al.* 2003).

289 Hind-gut fermenters make use of an enlarged section of the colon. The increased passage rate

290 in the hind-gut fermenter (Robbins 1993) allows an individual to process more food per unit

291 time than a ruminant (Clauss *et al.* 2003). This also allows hind-gut fermenters to consume

292 lower quality plant material (Demment & van Soest 1985; Robbins 1993). Furthermore, this

293 faster passage rate and ability to process lower quality plant material becomes more

294 beneficial during the dry season when hind-gut fermenters are able to survive on poorer

295 quality forage than ruminants, while still maintaining their body condition (Demment & van

296 Soest 1985; Robbins 1993).

297

298   **ELEPHANTS**

299   The African elephant (*Loxodonta africana*) is the largest terrestrial non-ruminant herbivore.

300   Male elephants are 5500 - 6000 kg in mass while the average female is 2500 - 2800 kg

301   (Owen-Smith 1988). This large size, however, results in high absolute food demands with

302   high absolute energy requirements (Demment & van Soest 1985). Elephants also have shorter

303   GITs in relation to their body sizes, but the widths of their GIT are larger than expected

304   (Clauss *et al.* 2003; Clauss *et al.* 2005). This means that elephants have lower absorbance-

305   surfaces:ingesta ratios, resulting in faster passage rates with lower nutritional gains (Clauss *et*

306   *al.* 2003; Clauss *et al.* 2005).

307   Elephants typically have a mixed diet (Cerling, Harris & Leakey 1999). However,

308   elephants have been shown to eat a large portion of woody plants throughout the year,

309   especially during the dry season (Codron *et al.* 2006). Elephant selectivity at different spatial

310   scales in Chobe National Park was studied by Owen-Smith and Chafota (2012). These

311   authors found that 40-70% of the elephant's diets were comprised of 1 or 2 prominent woody

312   species in each season. Similarly, Shrader *et al.* (2012) found elephants, in Ithala Game

313   Reserve (IGR), to select three principal (tree) species in both wet and dry seasons.

314   A number of studies have examined varying aspects of elephant movement patterns

315   including daily movement (Dai *et al.* 2007; Fernando *et al.* 2010), seasonal movement

316   (Wittemyer *et al.* 2007; Loarie, van Aarde & Pimm 2009a), and seasonal home ranges

317   (Leggett 2005; Shannon *et al.* 2006; Thomas, Holland & Minot 2011). These studies

318   highlight different uses of space during the wet and dry seasons. De Villiers and Kok (1997)

319   found that elephants increased their range use during the wet season in the Mpumalanga

320   lowveld. Similarly, Thomas *et al.* (2011) also found that elephants in the Kruger National

321   Park and adjacent private Sabi Sand Reserve (Mpumalanga) increased their home ranges in

322   wet seasons and concentrated their activities in certain habitats close to water in dry seasons.

323   Conversely, elephants increased their range use during the dry season in Pongola Private

324   Game Reserve (Shannon *et al.* 2006). The authors attributed this increase in range use in the

325   dry season to either the reduced availability of food and therefore the greater need to increase

326   their ranges to maintain their metabolic requirements or because the higher quality habitats

327   were more sparsely distributed throughout the area (Shannon *et al.* 2006). Leggett (2005),

328   studying elephants in the arid regions of Namibia, demonstrated variability in home ranges of

329   elephants between seasons, but attributed these differences to rainfall and water availability

330   as water stress is more prominent in arid areas. As Shannon *et al.* (2006) pointed out, space

331   use is usually a determinant of another more essential limiting resource, for example, surface-

332   water availability.

333   Elephants are known to be a water-dependent species (Western 1975), requiring water

334   every 2-4 days and daily when calves are present. Thus, surface-water availability tends to

335   limit dry season distributions (Owen-Smith 1988; Chamaille-Jammes *et al.* 2007; van Aarde

336   *et al.* 2008). In the wet season, there is a higher availability of surface water in temporary

337   shallow water bodies, streams and rivers than in the corresponding dry season (Shorrocks

338   2007; van Aarde *et al.* 2008). In contrast, as the dry season progresses the availability of

339   surface-water declines. In response to this reduction in water availability, elephants move to

340   areas with permanent surface water (Chamaille-Jammes *et al.* 2007). For example, Loarie *et*

341   *al.* (2009a) found that water availability drives elephant seasonal movements, concentrating

342   their activities around larger water sources in the dry season. As a result, habitat selection and

343   utilization of vegetation is influenced by water availability, especially during the dry season.

344   Conversely, Shannon *et al.* (2006) found no movement away from water in the wet season or

345   towards water in the dry season at Pongola Private Game Reserve. They suggest that the

346   small size of the reserve, about 73 km^2, and the high availability of permanent water across

347   the reserve allowed easy year-round access to water.

348   Despite their reliance on surface-water, diet selection is another important factor in

349   determining elephant movement decisions. Although elephants have the ability to digest

350   lower quality forage, they may still be selective in their foraging habits (e.g. Owen-Smith &

351   Chafota 2012; Shrader *et al.* 2012). Furthermore, elephants do not utilise vegetation

352   homogeneously (Boundja & Midgley 2009), but rather show selectivity and clear preferences

353   (Boundja & Midgley 2009; Chira & Kinyamario 2009; Shrader *et al.* 2012). For example,

354   elephants damaged tree species with higher nutritional composition than tree species that

355   were less nutritious (Holdo 2003).

356   Within habitats, elephants show preferences for specific tree species (Shrader *et al.* 2012).

357   For example, Boundja and Midgley (2009) found that elephants completely avoided *Acacia*

358   *karroo* and *Dichrostachys cinerea* tree species in Hluhluwe-iMfolozi Park in KwaZulu-Natal,

359   South Africa. This was contrary to what Shrader *et al.* (2012) found where the elephants

360   heavily utilised both these species. Chira and Kinyamario (2009) found elephants selected

361   five woody species; *Acacia ataxacantha, A. brevispica*, *Grewia bicolor*, *G. tembensis* and *G.*

362   *virosa*, as a result of their high coppice rates after utilization in Mwea National Reserve,

363   Kenya. Elephants may show preferences for previously utilised trees because heavy browsing

364   may promote shoot production and improve foliage quality (du Toit, Bryant & Frisby 1990;

365   Chira & Kinyamario 2009).

366   At broader scales, elephants selecting areas of higher nutrition (Osborn 2004; Loarie *et al.*

367   2009b) could be a driver of seasonal movements. In Senwa Wildlife Research Area,

368   Zimbabwe, elephants have been found to make large-scale movements in response to plant

369   quality. When the quality of wild grasses declined below the quality of the adjacent crop

370   species, elephants switched their diets from wild grasses to the crops (Osborn 2004). At a

371   large scale, Loarie at al. (2009b) found that elephants selected habitats that were "greener"

372   than expected in the dry season. Greenness may be a good indicator of plant nitrogen

373   concentrations and therefore crude protein (Loarie *et al.* 2009b). These elephants were found

374   to follow the flush of green across the seven countries studied despite the constraint of

375   surface-water availability, indicating that elephants change their habitat use seasonally

376   (Loarie *et al.* 2009b).

377   The main conclusions of these studies are that despite their large body size, and thus

378   ability to tolerate lower quality food, elephants are selective individuals when they forage

379   (Boundja & Midgley 2009; Chira & Kinyamario 2009). They alter their home ranges between

380   wet and dry seasons and thus utilise different habitats seasonally (Osborn 2004; Loarie *et al.*

381   2009b). Furthermore, they may show preferences for either the crude protein in their diets

382   (see e.g. Loarie *et al.* 2009b) or the ratio of crude protein:digestibility inhibitors such as

383   tannins (Shrader *et al.* 2012). This suggests that small-scale foraging changes in food quality

384   may influence the large-scale movements of this large-bodied mixed-feeder.

385

386   **RATIONALE FOR THIS STUDY: ELEPHANTS OF THE ITHALA GAME**

387   **RESERVE**

388   Ithala Game Reserve was proclaimed in 1972. Prior to that the area was used for crop lands

389   and communal livestock farming (Gordijn, Rice & Ward 2012). Translocation of large

390   mammalian herbivores predominantly occurred from 1973-1987 (Gordijn *et al.* 2012). From

391   1990-1994, about 50 elephants were released into the Ngubhu basin in the southwestern

392   corner of IGR (Wiseman, Page & O'Connor 2004). In 2000, there were about 56 elephants

393   (Wiseman *et al.* 2004). However, by 2007 there were about 130 elephants in the reserve (van

394   Rooyen & van Rooyen 2008), indicating a very high population growth rate.

395   A 2009 study by Shrader *et al.* (2012) was done on the spatial scale of IGR elephant

396   diets and distributions. Shrader *et al.* (2012) found that the elephants move away from their

397   largest source of water, the Pongola River, during the dry season. Furthermore, they found

398   that during the wet season, the elephants in IGR utilised the northeastern (NE) portion of the

399   reserve. The eastern section has granitic nutrient-poor soils while the west has doleritic

400   nutrient-rich soils (van Rooyen & van Rooyen 2008). The elephants congregated in this

401   relatively small area in the NE around the Pongola River that forms the northern border of the

402   reserve (Shrader *et al.* 2012). Often during this time, the elephants also wandered out of the

403   reserve and foraged in the areas surrounding IGR, despite the fact that nutrient availability

404   was considered to be non-limiting during this wet season (Shrader *et al.* 2012).

405   More recently, there has been an increase in utilisation of areas outside of the reserve

406   during the wet season (Fig. 1) and measures have had to be implemented by Ezemvelo

407   KwaZulu-Natal Wildlife to chase the elephants back into the reserve with the use of

408   helicopters (pers. comm. C. Barichievy). However, during the dry season, when nutrients are

409   limited, the elephants of IGR move back into the reserve, dispersing into a larger area in the

410   southwest (SW) (see supplementary material in Appendix 1). In 2011, the elephants utilised

411   the East in the wet season and West in the dry season (Fig. 1). This is contrary to predictions

412   that IGR has insufficient forage, because if IGR was not able to sustain the forage

413   requirements of the elephants then we might expect the elephants to search for extra sources

414   of forage during forage-limited periods in the dry season and not during the wet season as

415   they currently do (e.g. Osborn 2004). Furthermore, Gordijn *et al.* (2012) recorded an increase

416   in woody plant density from 2783.3 ± 251.35 indiv ha^{-1} in 2000 to 9939.6 ± 1522.52 indiv

417   ha^{-1} in 2009. Reserve managers have expressed concern about the elephants foraging outside

418   the reserve, where soil type and vegetation type are the same as the reserve, and approached

419   me to find out why they were doing so.

420   Therefore, the aim of this study was to determine how the plant availability and/or plant

421   quality of the seven target species influences elephant seasonal distributions in IGR. More

422   specifically, I wanted to determine the quality of three principal tree species and four avoided

423 species in the elephants' diet across the reserve. Principal species are determined as a

424 function of preference and the abundance of those species (Shrader et al. 2012). I also wanted

425 to determine how the quality changed seasonally. Ultimately, I did this because I expected the

426 elephants to utilize areas with a higher nutritional quality and lower defence seasonally,

427 which presumably influenced their movement patterns.

428 More specifically, I wanted to determine:

429 　　1) the seasonal quality of the seven target tree species (crude protein, neutral detergent

430 　　fibre (NDF), acid detergent fibre (ADF) and the most common defensive compounds,

431 　　total polyphenols),

432 　　2) how the ratio of digestion-reducing substances and digestion-enhancing substances

433 　　explains elephant seasonal movement, and

434 　　3) how branch and leaf quality of the different tree species differ because it is often

435 　　assumed that branches only add fibre to the diet and are less chemically defended.

436

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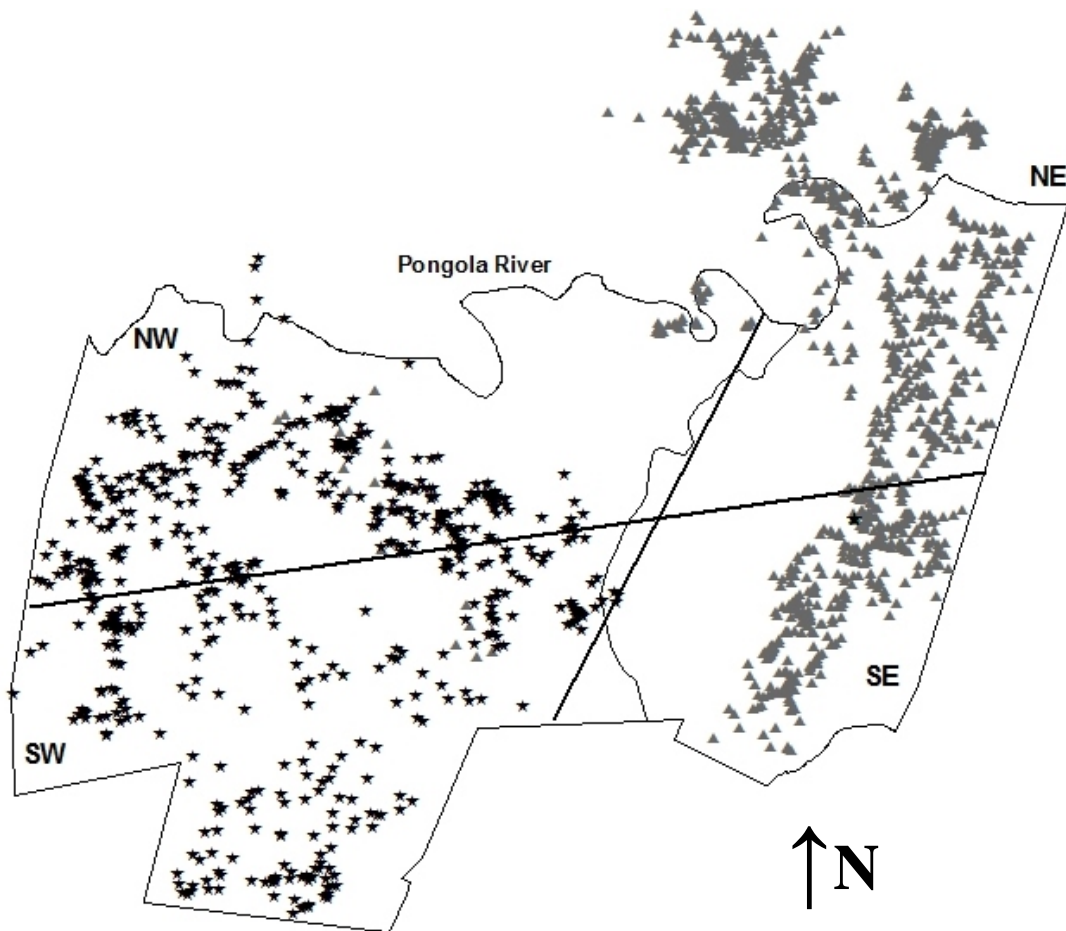
438

439   **Fig. 1.** Global positioning system points (determined by satellite observations) of the

440   elephants' distributions from 2011 in Ithala Game Reserve between wet (grey triangles) and

441   dry seasons (black stars). Most elephants were found in the eastern side of IGR in the wet

442   season while the west was most heavily used in the dry season. There was virtually no

443   overlap in section use between wet and dry seasons in the elephant observations. The four

444   sections sampled were: northwest (NW), northeast (NE), southwest (SW), and southeast

445   (SE). The northern border is the Pongola River.

446

447 # Chapter 2: Materials and methods

448

449 **STUDY AREA**

450 Ithala Game Reserve (IGR) is situated in northern KwaZulu-Natal near Louwsburg, South

451 Africa (27^o30'S, 31^o25'E). The 29,653 ha reserve is highly variable with regard to elevation,

452 vegetation, geology and soils. The Pongola River is the northern border of the reserve,

453 flowing from west to east, with the confluence of the Bivane and Pongola Rivers lying in the

454 northwestern corner of the reserve (van Rooyen & van Rooyen 2008). In addition, surface

455 water is readily available year-round in smaller rivers, streams and dams spread across IGR

456 (Fig. 2).

457 The landscape of the area is variable with cliffs, scarps, plateaux and valleys.

458 Elevation ranges from 320 m a.s.l. at the Pongola River to 1446 m a.s.l. on the escarpment

459 plateau (van Rooyen & van Rooyen 2008). The underlying geology is often directly related to

460 soil types, especially as a result of *in situ* formation of soils in IGR (van Rooyen & van

461 Rooyen 2008). The most common soil types occurring at Ithala are granites, dolerites and

462 diabases. Granite soils are coarser-grained and are often associated with nutrient-poor soils

463 (see e.g. Laffan, Grant & Hill 1998). Conversely, dolerites and diabases have more fertile

464 soils, but usually have poorer drainage (Hillel 1998). The eastern section of IGR is dominated

465 by granite soils whereas the western section is dominated by dolerites (van Rooyen & van

466 Rooyen 2008). There are a number of vegetation types present in IGR: these are the northern

467 Zululand mistbelt grassland, Ithala quartzite sourveld, KaNgwane montane grassland,

468 Swaziland sour bushveld and northern Zululand sourveld (Mucina *et al.* 2006). The IGR

469 essentially has two seasons, viz. a wet (November-February) and a dry (May-August) season

470 with brief transitional periods in-between. The mean annual rainfall for the area is 791 mm

471   (van Rooyen & van Rooyen 2008). The mean rainfall for Kwasambane during 2012 was

472   1137 mm.
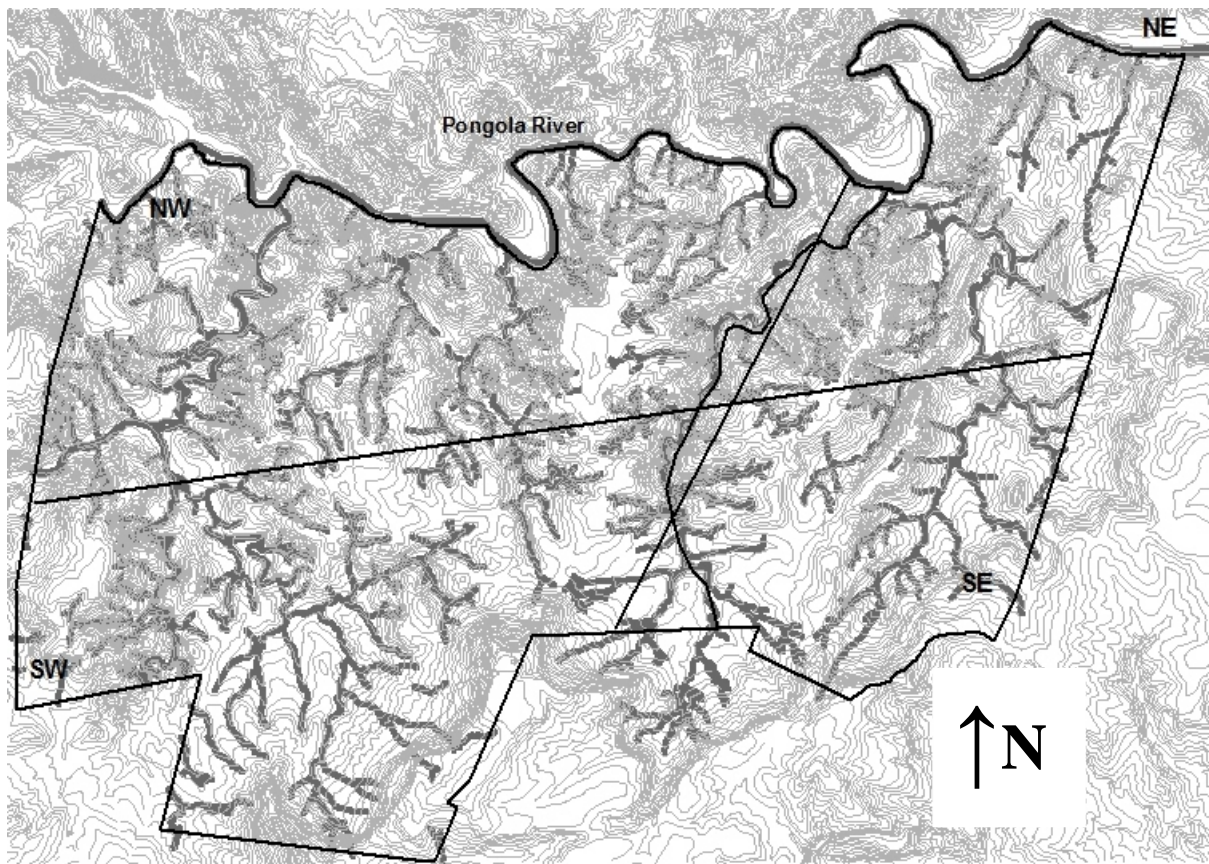
473

474   **Fig. 2.** Topography ranging from 320 m a.s.l to 1446 m a.s.l (light grey lines) and rivers

475   (darker grey lines) of Ithala Game Reserve. The Pongola River forms the northern border of

476   the reserve. Thick black northern line is the Pongola River.

477

478   **DATA COLLECTION**

479   To determine the seasonal changes in food quality and availability, two sampling trips were

480   undertaken, each 14 days long, one in the peak of the dry season (10-24 July 2012) and one in

481   the peak of the wet season (30 November – 14 December 2012). Sampling intensity increased

482   from that described by Shrader *et al.* (2012) into four sections of IGR, viz. northeast (NE),

483   southwest (SW), northwest (NW) and southeast (NE) (Fig. 1) to obtain a more complete

484   representation of elephant diets. Division of IGR into four sections occurred prior to any

485   sampling. In each of these sections, two 4 km strip transects were set up. The strip transects

486   were 8 m wide, which is approximately the width of an elephant's foraging area (Owen-

487   Smith 1988). In each of these strip transects, I counted the total number of trees available to

488   elephants and the total number of target tree species available. The target species consisted of

489   three principal species (i.e. plant species that make up most of the diet, which is a function of

490   availability and preference) as determined by Shrader *et al.* (2012), viz. *Dichrostachys*

491   *cinerea*, *Acacia karroo*, and *A. nilotica* (Table 1). In addition, I also focused on four species

492   avoided by elephants in Ithala in both seasons, viz. *Searsia pentheri* (formerly known as *Rhus*

493   *pentheri*), *Euclea natalensis*, *Gymnosporia buxifolia*, and *Peltophorum africanum* (Shrader *et*

494   *al.* 2012). I note that physical defences appear not to be related to the choices that elephants

495   make because the three principal species (*A. karroo*, *A. nilotica* and *D. cinerea*) are thorny

496   while three of the four avoided species (*E. natalensis*, *P. africanum* and *S. pentheri*) have no

497   physical defences. For each of the 7 target species (3 principal and 4 avoided), availability

498   was determined in each of the four sections of IGR. Finally, to determine nutritive and

499   secondary compound concentrations I collected approximately 10 g of leaves and branches

500   from 10 individual trees of the seven target species in each of the 4 regions in the wet and dry

501   seasons (N= 1120). Leaf and branch samples were taken from adult trees, during the

502   sampling period mentioned above. Each sample was placed in its own brown paper bag with

503   the species, area and season clearly marked. They were dried in an oven at 60 °C for 48 h and

504   milled using a standard 1 mm sieve.

505

506

507

508

509   **Table 1.** Percentage of principal species making up the wet and dry season diets. Data taken

510   from Shrader *et al.* (2012).

	Wet	Dry	Deciduous
Dichrostachys cinerea	48.4	40.9	Yes
Acacia nilotica	2.9	39.3	Semi
Acacia karroo	3.2	7.8	Yes

511

512   To determine the protein concentrations, secondary metabolites, and percentage fibre

513   of both the preferred and avoided species, I used the protocol from the Association of Official

514   Analytical Chemists (AOAC) (1970). Protein was determined by Kjeldahl nitrogen analysis

515   and multiplied by 6.25 to obtain values in %. Fibre determination were done by neutral

516   detergent fibre (NDF) and acid detergent fibre (ADF) analysis (van Soest 1994). NDF

517   represents the fibre and cell wall content of forage (van Soest 1994) and includes cellulose,

518   hemicellulose, and lignin. ADF measures the least digestible portion of the forage and

519   includes lignin, cellulose, ash and silica but does not include hemicellulose. In addition, I ran

520   a modified Prussian blue test for total polyphenol analysis (TP) (Hagerman 2011). Total

521   polyphenols are represented as gallic acid equivalents (GAE) because there is no unique

522   value for total polyphenols (Waterman & Mole 1994).

523   Elephant movement data were collected from a satellite-based Global Positioning

524   System (GPS). Currently three cow elephants and two bull elephants are collared. Generally,

525   they remain in herds. However, the bulls tend to wander between herds and on their own. The

526   GPS positions are recorded on a computer where they are downloaded and utilized. These

527   point data I then utilized to determine which areas of the reserve the elephants utilized during

528   the different seasons by mapping the points (Appendix 1).

529 **DATA ANALYSIS**

530 To determine seasonal differences in plant abundance in each area between the seven target

531 species, I ran an Analysis of Variance (ANOVA). Note that I use the term SE to indicate the

532 southeast while I use S.E. to indicate standard error.

533 To determine the differences between each of the plant nutrient contents (crude

534 protein, ADF, NDF, total polyphenol concentrations, and the ratios of crude

535 protein:digestion-reducing substances), I ran a Multiple Analysis of Variance (MANOVA) to

536 control for type I statistical error. I created the ratio of crude protein:total polyphenols, the

537 ratio of crude protein:ADF and the ratio of crude protein:NDF as well as the ratio of the

538 reciprocal of ADF and NDF relative to total polyphenols, with large values indicating high

539 quality. I generated the reciprocal because a higher ratio will mean that there is less fibre,

540 indicating a better quality. Calculating the reciprocal ratio is similar to (but not the same as)

541 estimations of digestible dry matter (DDM) or dry matter digestibility (DMD) (van Soest

542 1994). Furthermore, the reciprocal of ADF and NDF may represent DDM, but this is only

543 probably true for species with low concentrations of phenolic compounds, which reduce

544 digestibility. I limited these analyses to leaf data. Prior to analysis, I $\log_{10}$ transformed the

545 data to meet assumptions of normality and homogeneity of variance. Significance was found

546 among all parameters in the MANOVA. Therefore, I ran a principal components analysis

547 (PCA) as a dimension-reduction technique. All tests were run using SPSS version 21.

548 To determine differences in quality and elephant habitat-selection, I used contingency

549 tables in Excel 2010. I counted the number of elephants based on the proportion of satellite-

550 determined observations in the wet and dry seasons in each of the four quadrants of the

551 reserve in 2011. These served as the expected values of preference for the contingency tables.

552 That is, I sought to determine whether the elephant preferences matched the dietary values for

553   the four sections of the reserve, based on the observations that elephants were most common

554   in the west during the dry season and most common in the east during the wet season.

555   To determine the difference between plant parts (leaves and branches) I ran a ranked

556   MANOVA between season, area and species (Seaman *et al.* 1994). A ranked MANOVA was

557   used as a result of the data violating the assumptions of normality and equality of variances.

558   Conventional transformations were tried, including $\log_{10}$, square root and power

559   transformations. I then employed a Box-Cox transformation and assumptions were still

560   violated. Ranked transformations are widely accepted and are robust when testing main

561   effects. However, they are less effective with interactions (Seaman *et al.* 1994; Conover

562   2012).

563

564 # Chapter 3: Results

565

566 **AVAILABILITY OF PLANTS**

567 The seven target species' abundances did not differ significantly between areas (p=0.61) or

568 seasons (p=0.259). However, abundance differed between species (p=0.0001). A Bonferroni

569 *post hoc* test revealed that *D. cinerea* had the highest abundance (22.98 ± 5.1% abundance

570 across the reserve) of all seven target species. *A. karroo* (2.64 ± 0.7 % abundance across the

571 reserve) was less abundant than *D. cinerea*. *A. nilotica* was the least abundant species of all

572 the target species (0.82 ± 0.4 % abundance across the reserve) (Fig. 3).

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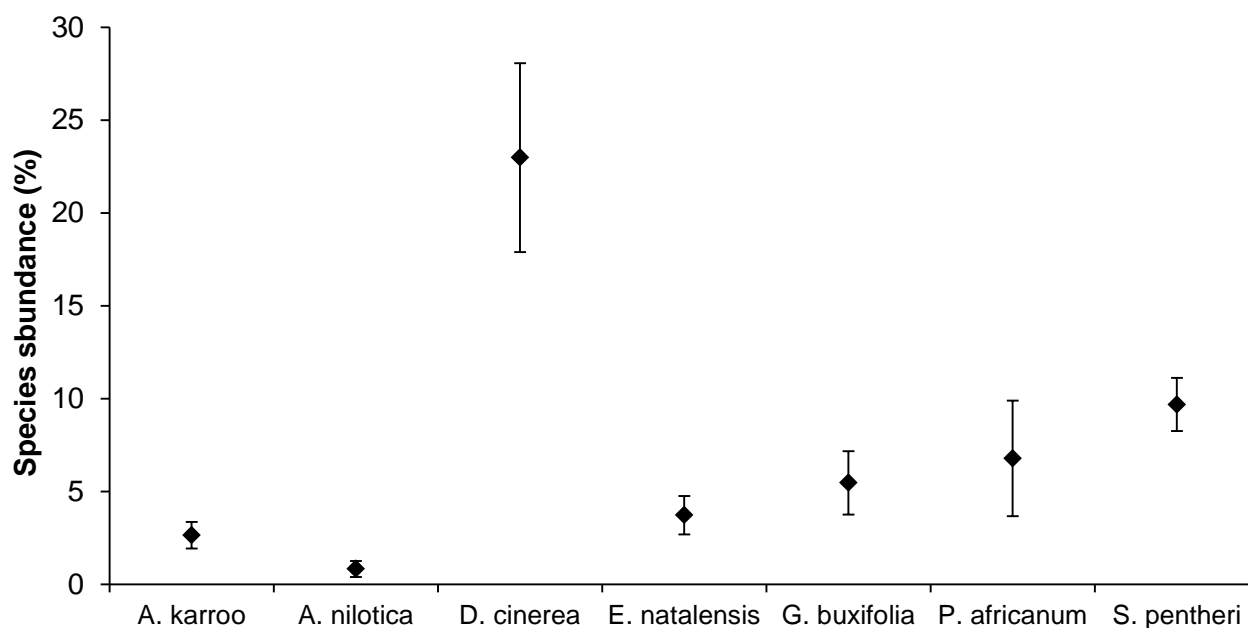
Fig. 3. Percentage abundance of each of the seven target species. Bars represent 1±S.E. *A.*

karroo= *Acacia karroo*, *A. nilotica*= *Acacia nilotica* and *D. cinerea*= *Dichrostachys cinerea*

(the three principal species). *S. pentheri*= *Searsia pentheri* (formerly known as *Rhus*

pentheri), *E. natalensis*= *Euclea natalensis, P. africanum*= *Peltophorum africanum* and *G.*

buxifolia= *Gymnosporia buxifolia* (the four avoided species).

QUALITY OF PLANTS

Overall, the MANOVA was significant for all main effects and all interaction effects (Table

2). All individual nutritional parameters were significant (see supplementary material in

Appendix 2). Therefore, I ran a principal component analysis (PCA) as a dimension-

reduction technique. I found the first PC axis eigenvalue was 3.658 and explained 40.6% of

the variance. The second PC axis eigenvalue was 2.801 and explained 31.1 % of the variance.

The cumulative variance explained by the first two axes of the PCA was 71.8%. Thus, I

focused on these two axes. Most of the variance in PC1 was explained by total polyphenols

(TP) (component= -0.891), the CP:TP ratio (component= 0.775), and the reciprocal of

590   ADF:TP ratio (component=0.739) (Table 3). Note that there is a negative relationship with

591   total polyphenols and a positive relationship with the ratios. The CP:TP result is consistent

592   with what Shrader *et al.* (2012) found. Most of the variance on PC2 was explained by

593   CP:ADF ratio (component = 0.841), followed by crude protein (component = 0.803), and

594   CP:NDF ratio (component = 0.756). Therefore, I focused on these six factors on the first two

595   axes highlighted by the PCA, noting that the first axis (by definition) explains most of the

596   variance (Flury & Riedwyl 1988). Furthermore, I focused on the principal species only as

597   they are the species used by the elephants.

598

599 **Table 2.** MANOVA statistics of the effects of season, area, species and their interactions on

600 the seven target species to determine forage quality. Forage quality was measured for: crude

601 protein, acid detergent fibre (ADF), neutral detergent fibre (NDF) and total polyphenols (TP).

602 Additionally, ratios of some of these parameters were also considered.

Factor	Wilks Lambda	DF	P-Value
Season	0.397	218	0.0001
Area	0.649	617.1	0.0001
Species	0.069	960.1	0.0001
Season*Area	0.669	617.1	0.0001
Season*Species	0.220	960.1	0.0001
Area*Species	0.271	1256.5	0.0001
Season*Area*Species	0.290	1256.5	0.0001

603

604

605 **Table 3.** Component weightings for the principal components analysis (PCA) for $\log_{10}$ crude

606 protein (CP), $\log_{10}$ total polyphenols (TP), acid detergent fibre (ADF), neutral detergent fibre

607 (NDF), the $\log_{10}$ ratio of crude protein:total polyphenols (CP:TP), $\log_{10}$ crude protein:ADF

608 ratio (CP:ADF), $\log_{10}$ crude protein:NDF ratio (CP:NDF), $\log_{10}$ reciprocal of acid detergent

609 fibre: total polyphenol concentrations (ADF:TP) and $\log_{10}$ reciprocal of neutral detergent

610 fibre:total polyphenol concentrations (NDF:TP). Note that it is the absolute value that

611 determines importance.

	Principal Component		612
Factors	1	2	
$\log_{10}$ CP	-0.251	0.803*	
$\log_{10}$ TP	-0.891*	-0.43	
ADF	0.475	-0.219	
NDF	0.592	-0.081	
$\log_{10}$ CP:TP	0.775*	0.038	
$\log_{10}$ CP:ADF	-0.482	0.841*	
$\log_{10}$ CP:NDF	-0.607	0.756*	
$\log_{10}$ ADF:TP	0.739*	0.562	
$\log_{10}$ NDF:TP	0.691	0.565	

613 ***most important**

614

615

616   The season X area X species interaction showed that during the wet season two out of

617   three principal species (*A. karroo* and *D. cinerea)* had lower total polyphenol concentrations

618   in the SE of IGR (Fig. 4). The eastern section of IGR is a common wet-season foraging area.

619   *A. karroo* had increased CP:TP ratio, CP:ADF ratio and crude protein during the wet season

620   in the SE of IGR (Figs. 5, 6 and 7). *D. cinerea* was the only species with increased reciprocal

621   of ADF:TP in the SE during the wet season (Fig. 8). All three principal species showed no

622   significant differences between areas during the wet season for CP:NDF ratio (Fig. 9).

623   During the dry season, elephants preferred to forage in the west (Fig. 1). *A. karroo*

624   was the only species with lower total polyphenols during this time in the SW. All three

625   principal species had increased levels of CP:TP ratio, CP:ADF ratio and crude protein in the

626   SW during the dry season (Figs. 5, 6 and 7). *D. cinerea* and *A. nilotica* had a higher

627   reciprocal of ADF:TP ratio during the dry season in the NW (and SW for *A. nilotica* only)

628   (Fig.8). Only *A. karroo* had higher CP:NDF during the dry season in the SW relative to the

629   other two principal species (Fig. 9).

630   There was a decline in mean total polyphenol concentrations in *A. nilotica* between

631   the wet season and dry season, which is consistent with the change in preference for this

632   species between wet and dry seasons (2.9% in the wet season and 39.3% in the dry season -

633   Shrader *et al.* 2012). Similarly, the CP:TP ratio, the reciprocal of ADF:TP ratio and CP:ADF

634   ratio all had higher values for *A. nilotica* in the dry season than in the wet season (Figs. 5, 6,

635   8).

636   Overall, total polyphenol concentrations were higher in principal species (mean $\pm$ S.E.

637   ratio ($\log_{10}$) -0.64 $\pm$ 0.07) than avoided species (mean $\pm$ S.E. ratio ($\log_{10}$) -0.91$\pm$ 0.06) (Fig.

638   4). However, principal species had higher ratios of CP:ADF (principal (mean $\pm$ S.E. ratio

639   ($\log_{10}$)): -1.00 $\pm$ 0.06; avoided: -0.80 $\pm$ 0.05) and CP:NDF (principal (mean $\pm$ S.E. ratio

640   ($\log_{10}$)): -0.91 $\pm$ 0.09; avoided (mean $\pm$ S.E. ratio ($\log_{10}$)): -0.77 $\pm$ 0.07) (Figs. 7, 9).

641   Elephant numbers were determined from Global Positioning System (GPS) satellite

642 data. I counted elephant numbers in each area for both wet and dry seasons from the mapped

643 GPS data. The contingency table analyses indicated that the CP:TP ratio was the only

644 significant parameter within both the wet (χ^2= 12.40; p= 0.0001) and dry seasons (χ^2 = 10.88;

645 p= 0.0001). A significant result indicates that the elephants utilized that section more

646 frequently than by chance alone. The SW had the highest CP:TP ratio in the dry season which

647 is consistent with the highest elephant numbers in that quadrant (391 sightings from June-

648 August). However, the NW had similarly high elephant numbers (314 sightings from June-

649 August). The SE section had the highest CP:TP ratio during the wet season with lower

650 elephant numbers (307 sightings from December- February) than the NE (368 sightings from

651 December- February) (Table 4).

652
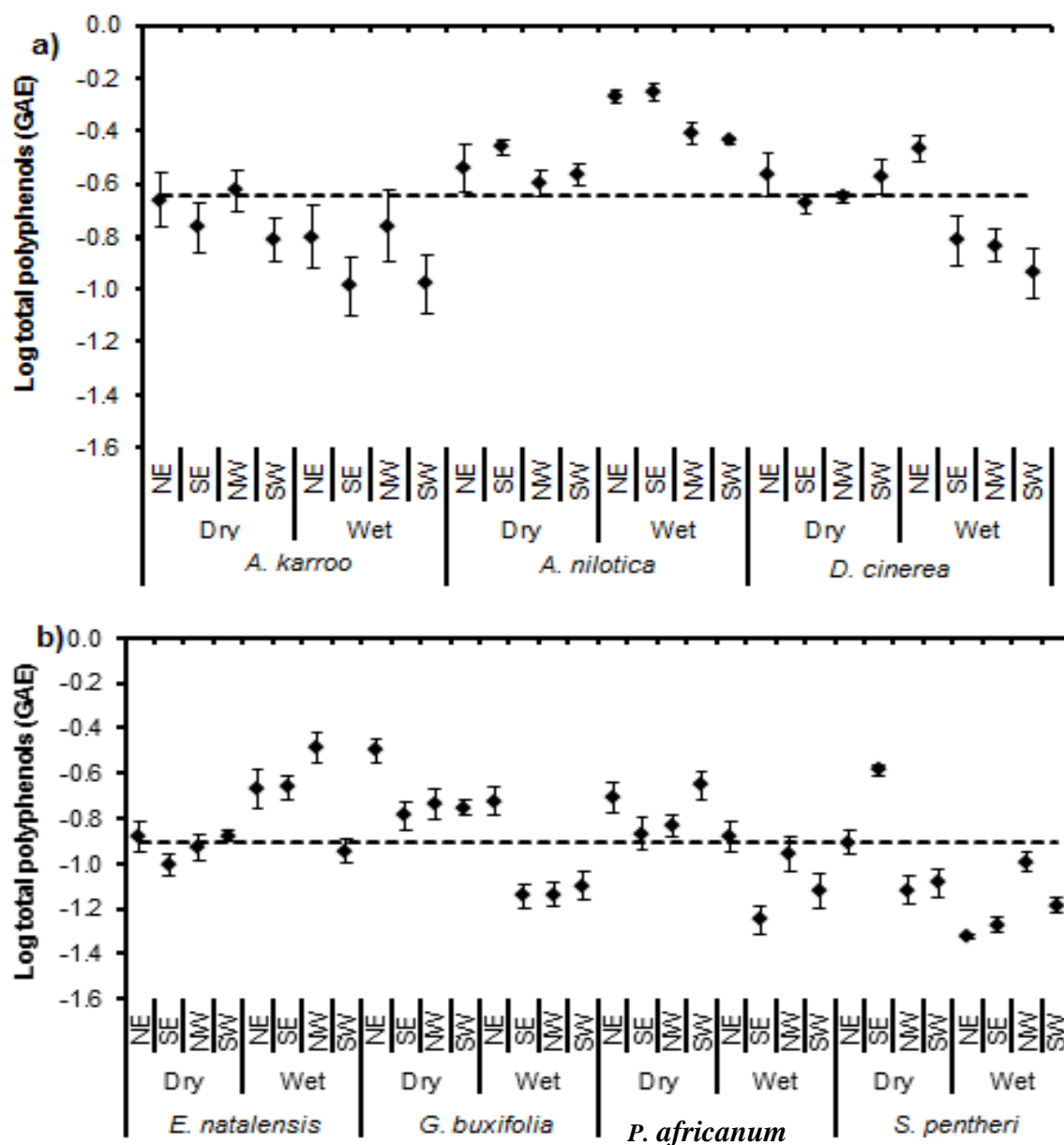
Fig. 4. The seasonal values of $\log_{10}$ total polyphenol concentrations for a) principal and b) avoided species. Bars represent 1±S.E. Dashed line is the overall mean. GAE = gallic acid equivalents. Full names as for Fig. 3.
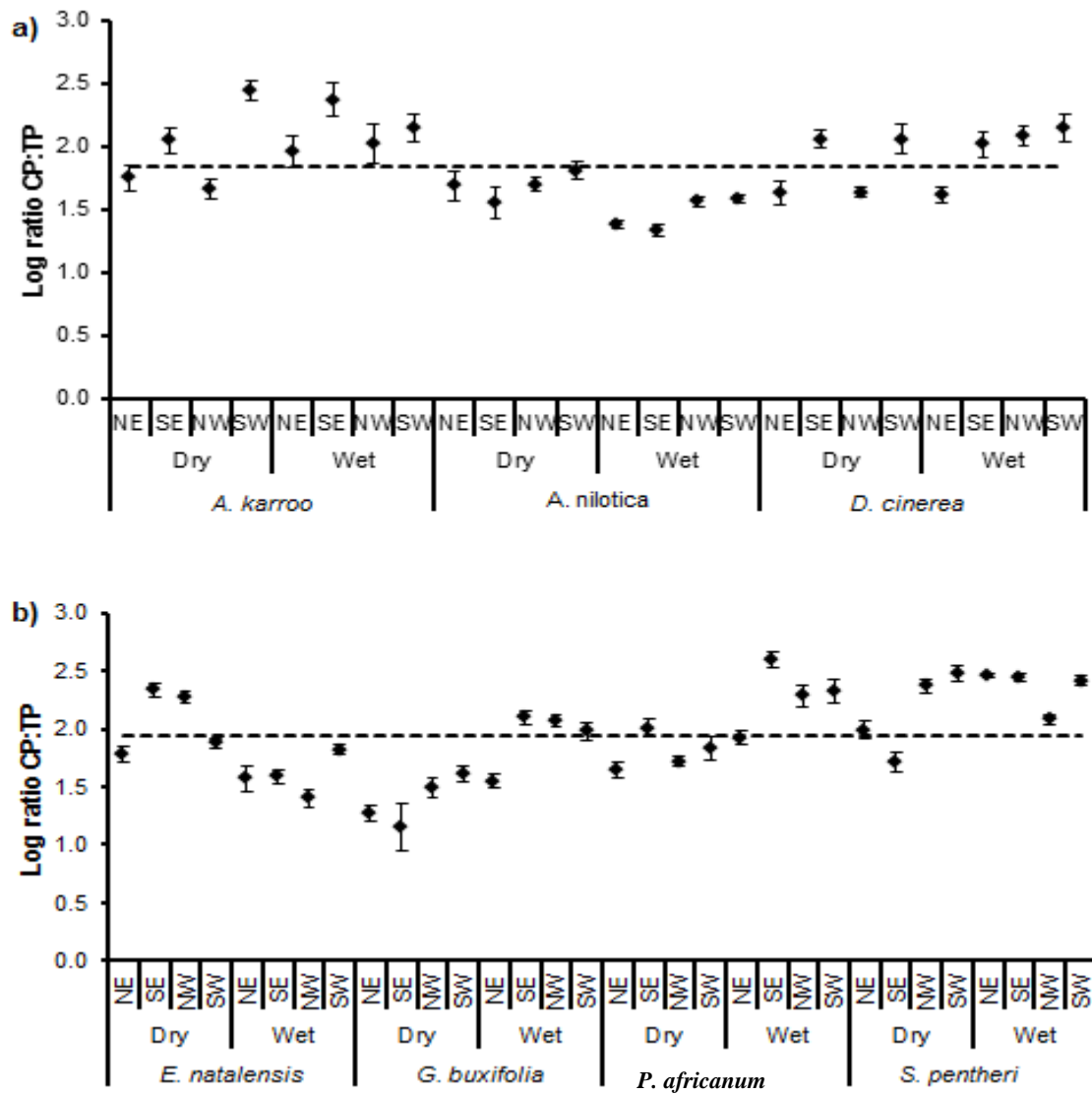
Fig. 5. The seasonal values of the $\log_{10}$ crude protein:total polyphenol (CP:TP) ratios for a) principal and b) avoided species. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.

662
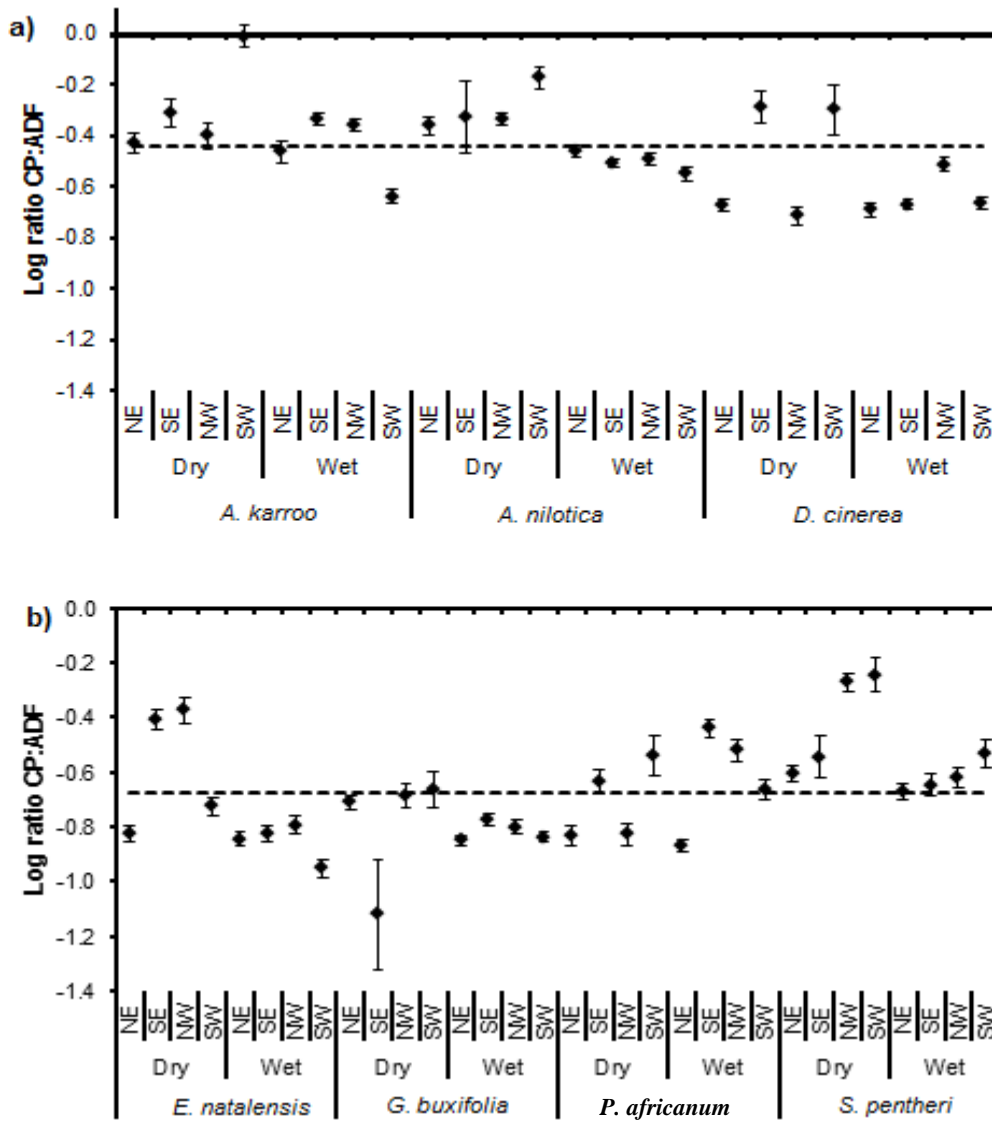
Fig. 6. The seasonal values of the $\log_{10}$ CP:ADF ratios for a) principal and b) avoided species.

CP = crude protein; ADF = acid detergent fibre. Bars represent 1±S.E. Dashed line is the

overall mean. Full names as for Fig. 3.

666

Fig. 7. The seasonal values of the $\log_{10}$ crude protein values for a) principal and b) avoided species. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.

Fig. 8. The seasonal values of the $\log_{10}$ reciprocal of ADF:TP ratios for a) principal and b) avoided species. TP= total polyphenol concentrations. High values indicate high quality vegetation. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.

Fig. 9. The seasonal values of the $\log_{10}$ CP: NDF ratios for a) principal and b) avoided

species. CP = crude protein; TP = total polyphenol concentrations. Bars represent 1±SE.

Dashed line is the overall mean. Full names as for Fig. 3.

684   **Table 4:** Contingency table analyses of total polyphenols (TP), the ratio of crude protein to

685   total polyphenols (CP:TP), reciprocal of Acid Detergent Fibre:total polyphenol ratio

686   (ADF:TP), crude protein:ADF ratio (CP:ADF), crude protein (CP), crude protein:Neutral

687   Detergent Fibre ratio (CP:NDF) and elephant numbers between the four sections in the wet

688   and dry seasons. Predictions are based on elephant numbers found in each quadrant in each

689   season. Elephant numbers were based on satellite observations in 2011.

	NW		NE	
	WET	**DRY**	**WET**	**DRY**
Elephant no.	42	314	368	0
TP	0.28	0.25	0.37	0.30
CP:TP	110.01	50.60	63.82	64.56
ADF:TP	0.12	0.14	0.10	0.13
CP:ADF	0.36	0.36	0.30	0.35
CP (%)	16.69	11.07	13.76	12.67
CP:NDF	0.49	0.36	0.45	0.39
	SW		SE	
Elephant no.	5	391	307	1
TP	0.219	0.25	0.30	0.26
CP:TP	132.14	177.48*	152.86*	108.93
ADF:TP	0.13	0.13	0.13	0.13
CP:ADF	0.25	0.77	0.33	0.65
CP (%)	15.00	32.14	17.36	22.15
CP:NDF	0.42	0.54	0.45	0.82

690   *significant difference

691

692   **PLANT PARTS**

693   It is often assumed that branches only add fibre to the diet and are less chemically defended

694   (Owen-Smith & Chafota 2012). The ranked MANOVA between leaves and branches was

695   significant (Wilks' lambda = 0.284; df= 546; p<0.01). Crude protein (mean ± S.E. ratio

696   ($\log_{10}$)) leaf: 1.10 ± 0.02; branch: 0.77 ± 0.02) and the CP:TP ratio (mean ± S.E. ratio ($\log_{10}$))

697   leaf: 1.90 ± 0.04; branch: 1.53 ± 0.04) were significantly higher in leaves than branches. ADF

698   (mean ± S.E. ratio) leaf: 50.48 ± 1.53; branch: 61.99 ± 0.87) and NDF (mean ± S.E. ratio)

699   leaf: 44.71 ± 3.13; branch: 66.30 ± 1.63) were significantly higher in branches than leaves.

700   Similarly, the reciprocal of ADF:TP (mean ± S.E. ratio ($\log_{10}$)) leaf: -0.88 ± 0.03; branch: -

701   1.02 ± 0.03) and the reciprocal of NDF:TP ratios (mean ± S.E. ratio ($\log_{10}$)) leaf: -0.83 ±

702   0.05; branch:-1.06 ± 0.05) were significantly higher in branches than in leaves. In contrast,

703   there was no significant difference in total polyphenol concentration between leaves and

704   branches (mean ± S.E. ratio ($\log_{10}$)) leaf: -0.80 ± 0.03; branch: -0.76 ± 0.03) (Table 5).

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707   **Table 5.** MANOVA statistics from the ranked comparisons of leaf and branch for the

708   different plant quality parameters. CP = crude protein; TP = total polyphenol concentrations;

709   ADF = acid detergent fibre; NDF = neutral detergent fibre.

Parameter		F	P-value
Plant Part	CP	484.365	0.0001
	TP	0.580	0.446
	ADF	124.262	0.0001
	CP:TP	113.097	0.0001
	CP:ADF	719.450	0.0001
	NDF	420.894	0.0001
	CP:NDF	909.516	0.0001
	ADF:TP	99.515	0.0001
	NDF:TP	345.040	0.0001

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Chapter 4: Discussion

The distribution of forage in an environment is heterogeneous in time and space (Senft *et al.* 1987; Shipley 2007; Holdo *et al.* 2009). As a result, herbivores alter their foraging behaviour to compensate for these changes, e.g. by changing diet breadth, or habitat usage (Senft *et al.* 1987; Bailey *et al.* 1996). Numerous studies have shown that elephants do not homogenously consume vegetation but are selective at both small and large scales (Boundja & Midgley 2009; Loarie *et al.* 2009b; Pretorius *et al.* 2012; Shrader *et al.* 2012). Therefore, I predicted that elephants would alter their seasonal movement patterns in response to either 1) changes in the availability of principal species, and/or 2) changes in forage quality.

In contrast to my prediction that principal species will determine seasonal use of elephants in IGR, I found no difference in the seasonal percentage abundance and spatial distribution of principal tree species across the reserve. The high proportion of *D. cinerea* in both wet and dry season diets may be as a result of the higher abundance of this principal species across the reserve as compared with the other two principal species sampled. This choice is as a result of foraging preferences being based on both the abundance and quality of the most preferred food type (Senft, Rittenhouse & Woodmansee 1985).

Plant quality has been shown to be an important determinant of herbivore foraging decisions (Cooper & Owen-Smith 1985; Jia *et al.* 1997; Frye *et al.* 2013). Holdo (2003) showed that elephant damage was more prominent in species with higher levels of protein, calcium, magnesium and potassium. Furthermore, secondary metabolites have also been shown to alter foraging choices (Cooper & Owen-Smith 1985; Cipollini & Levey 1997; Frye *et al.* 2013). Consistent with my predictions, I found plant quality to differ seasonally and across the reserve. In line with previous studies (Pretorius *et al.* 2011; Pretorius *et al.* 2012; Shrader *et al.* 2012), I found that the inclusion of plant species into their diets (i.e. at small

741 spatial-scales), the elephants in IGR are selective. Specifically, the increased inclusion of *A.*

742 *nilotica* in the dry season (2.9% in the wet season and 39.3% in the dry season - Shrader *et al.*

743 2012) can be explained by the seasonal decline in total polyphenols from the wet to the dry

744 season and an increase of the digestion-enhancing: digestion-reducing ratios during the dry

745 season.

746   Elephants in IGR avoided species with higher digestion-reducing substances,

747 including fibre and total polyphenols. However, total polyphenol concentrations were higher

748 in principal species than in avoided species. Nevertheless, the avoided species are known to

749 contain high levels of plant toxins. For example, *Euclea* spp. contain naphthaquinones and

750 triterpenoids (Gordijn *et al.* 2012; Shrader *et al.* 2012). *Searsia* spp. contain inositol, malic

751 and nonanoic acids (Gordijn *et al.* 2012). I measured total polyphenol concentrations, which

752 include tannins, because these are the most common digestion-reducing compounds (Cooper

753 & Owen-Smith 1985; Freeland 1991; Waterman & Mole 1994) and did not focus on specific

754 compounds. Similar to the results of Shrader *et al.* (2012), I found that the digestion-

755 enhancing: digestion-reducing ratio was the most important factor influencing foraging

756 decisions. The PCA ranked four of the six most important factors to be digestion-enhancing:

757 digestion-reducing ratios, explaining 71.8% of the variability. The remaining two factors

758 were total polyphenols and crude protein. Thus, elephants in IGR are selective in their small-

759 scale foraging decisions. The elephants may be selecting plant species, and areas, with lower

760 secondary metabolites (see negative value for total polyphenols - Table 3) and higher crude

761 protein concentrations (note positive value for crude protein - Table 3). Similarly, elephants

762 in Timbavati Private Reserve (Mpumalanga) utilised patches that had higher leaf-nitrogen

763 contents on nutrient-enriched soils (Pretorius *et al.* 2011). However, on soils that were not

764 enriched by fertilizers, elephants pushed over trees to get to the higher quality roots (Pretorius

765   *et al.* 2011). This indicates that elephants are selecting food based on their quality and will

766   even utilise specific plant parts with higher nutrients.

767   Little is known about how woody matter adds to the diet of elephants. It is often

768   assumed that branches only add fibre to the diet and are less chemically defended (Owen-

769   Smith & Chafota 2012). As expected, leaves had an overall higher quality than branches with

770   increased crude protein and fewer digestion-reducing substances. I found that there was no

771   significant difference in total polyphenols between leaves and branches. Owen-Smith and

772   Chafota (2012) found that the part of the plant that elephants forage on is more important

773   than species *per se*. These authors attributed this to lower chemical defences. However, these

774   authors never tested these hypotheses directly. Moose (*Alces alces*) are known to also forage

775   on branches (Bergstrom & Danell 1987; Bergström & Danell 1995; Jia *et al.* 1997). Jia *et al.*

776   (1997) studied moose feeding behaviour with different quality of birch (*Betula pendula*)

777   clones to test the effects of quality on foraging and found differences in total polyphenol

778   concentration between birch clones. Contrary to common assumptions, they found moose

779   were more likely to reduce fibre intake than total polyphenol intake by feeding on younger

780   shoots (Jia *et al.* 1997). This is not inconsistent with my results, which show that leaves had

781   higher levels of crude protein than their branches. Elephants also preferred leaves which had

782   lower levels of fibre.

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784   **ELEPHANT MOVEMENT IN IGR**

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786   Small-scale foraging decisions, i.e. changes in plant quality, have also been linked with

787   changes in large-scale foraging patterns, such as migrations. However, the small-scale

788   changes in foraging by the elephants in IGR do not seem to explain all of their broader-scale

789   foraging choices. During the wet season the elephants used the east, mainly the NE (Fig. 1).

790   However, the section with the highest nutritional quality, at least for *A. karroo*, was the SE

791   where there was increased CP:TP ratio, CP:ADF ratio and crude protein. Total polyphenols

792   were also lower in the SE for *A. karroo* and *D. cinerea*. Nonetheless, elephants clearly

793   preferred the eastern section of the reserve over the west during the wet season, which is

794   consistent with my results.

795   Where my results do help to explain elephant movement in IGR is during the dry

796   season when the elephants move into and forage in the west (Fig. 1). During this time, the

797   SW had higher CP:TP ratios, CP:ADF ratios and crude protein for all three principal species.

798   *A. nilotica* and *D. cinerea* had higher reciprocal of ADF:TP ratio in the NW (and SW for *A.*

799   *nilotica*) while *A. karroo* had higher CP:NDF ratios in the SW. *A. karroo* also had lower total

800   polyphenols in the SW during the dry season. Similarly, the contingency table analysis

801   showed the SW had higher CP:TP ratios than the other sections (Table 4). Therefore, this

802   increase in plant quality in the west, compared with a reduction in the east at this same time,

803   appears to influence these seasonal movements of the elephants back into IGR.

804   It is clear that plant quality is an important factor in the movement patterns of IGR

805   elephants. The elephants are moving back into IGR and are utilizing the west when the best

806   forage quality is found there. However, it is not clear why the elephants are utilizing the east

807   during the wet season. It is possible that I found this pattern of movement because of

808   behavioural learning. That is, when animals are released into a new environment they have no

809   knowledge of the environment (Owen-Smith 2003). They need to learn where the best quality

810   forage is distributed seasonally. Other factors influencing re-introduced individuals are the

811   distribution of water and areas of predation risk. For an individual to learn the optimal

812   distribution of an environment takes time (Owen-Smith 2003). For example, the Arabian oryx

813   (*Oryx leucoryx*) were released in two groups into the central desert region of the Oman

814   during the 1980s (Owen-Smith 2003). The animals were housed in an enclosure for

815 acclimation to occur prior to release. Animals in the first release found an area where there

816 were no conspecifics and had larger home ranges. After the rains they temporarily utilised

817 more areas. However, when drought followed, the oryx returned to their release site where

818 supplementary fodder was provided (Owen-Smith 2003). These oryx had smaller home

819 ranges, as a result of the presence of conspecifics. About 6-8 years after the release of the

820 oryx they had established where they could find needed resources and consequently utilised

821 less space (Owen-Smith 2003). Similar patterns were found for Asiatic wild asses (*Equus*

822 *hemionus*) (Saltz & Rubinstein 1995).

823 The elephants at IGR were released into the southwestern section of IGR. Over time,

824 they may have utilised more areas of the reserve and learned that the western section has a

825 higher nutritional quality during the dry season. In translocation studies on elephants it has

826 been shown that elephants do not utilise vegetation uniformly once released but will

827 congregate in areas of refuge as they slowly learn about their environments (Dublin &

828 Niskanen 2003). Furthermore, the elephants at IGR may have slowly explored the reserve

829 (Appendix 1). Thus, when resources declined at the onset of the dry season, the elephants

830 returned to the west where forage quality was known to be better.

831 A second, and perhaps less important, factor influencing elephant movement back

832 into the reserve during the dry season may be related to increased human interactions.

833 Elephants are known to avoid unnecessary human interaction (Dublin & Niskanen 2003). To

834 the north of the Pongola River there are communal areas with large numbers of people and

835 cattle. During the dry season, when water availability is reduced, the people may more

836 frequently come to the river to collect water, resulting in increased potential contact and

837 interference with the elephants. As a result, they may move to avoid this increased human

838 presence along the Pongola River.

MANAGEMENT AND FUTURE STUDIES

839

840   There were about 56 elephants in 2000 (Wiseman *et al.* 2004) and about 130 individuals in

841   2008 (van Rooyen & van Rooyen 2008; Shrader *et al.* 2012). I expect that these increasing

842   numbers are the reason for increased utilization of the reserve during the dry season.

843   Primarily, the elephants use the SW section with the best quality during the dry season.

844   However, they are also utilizing the NW section, where quality is not as high. This may be as

845   a result of these increasing elephant numbers and possible intraspecific competition.

846   Wiseman *et al.* (2004) noted that an increase in elephant numbers is a potential

847   problem in IGR. They calculated the "carrying capacity" of elephants in IGR to be about 50

848   elephants. Furthermore, they found that elephants did not utilise 50% of the space due to

849   topography (Wiseman *et al.* 2004). Elephants are known to avoid costly "mountaineering"

850   (Wall, Douglas-Hamilton & Vollrath 2006). In this study, elephants used the roads to access

851   forage in the steeper areas (pers. obs.). More than 20% of the reserve had gradients greater

852   than 40°, reducing access for large mammals, such as elephants (Wiseman *et al.* 2004). Thus,

853   the total area available to elephants is considerably less than expected based on total reserve

854   size.

855   The density of elephants that Wiseman *et al.* (2004) calculated in 2000 in IGR was

856   0.19 elephants/km^2, which was lower than the stocking density for elephants in valley

857   bushveld (0.4 elephants/km^2 (Penzhorn, Robbertse & Olivier 1974)). This stocking density is

858   also below the optimal stocking density for dry savannas of 0.5 elephants/km^2 (Fowler &

859   Smith 1973), which is considered to be the threshold where elephants can cause serious plant

860   damage (Fowler & Smith 1973; Wiseman *et al.* 2004). Currently, the density of elephants in

861   IGR is 0.43 elephants/km^2, exceeding the recommended stocking density for elephants in

862   valley bushveld and approaching the recommended stocking density for elephants in dry

863   savanna. This original stocking density for IGR may have been calculated on the basis of a

864 standard model for grazers (Meissner 1982). This calculation would then be exaggerated

865 elephants are largely browsers and because neither nutritional yield (Hobbs & Swift 1985)

866 nor secondary plant compounds (Windels & Hewitt 2011) were incorporated into the

867 calculations. Furthermore, the densities of elephants in IGR includes areas that the elephants

868 cannot use because they are too steep to access (see above). Additionally, even if there is

869 sufficient vegetation to allow for increased elephant numbers it is important to allow the

870 vegetation time to recover (e.g. Horsley, Stout & DeCalesta 2003; Holdo *et al.* 2011).

871   There is no clear reason for the elephants to leave the reserve as there is sufficient

872 food available to them. Although the density of elephants is increasing in IGR, this is not the

873 primary reason for the movement patterns we are seeing. If density was the main determinant

874 we would expect to see elephants searching for extra sources of forage during the forage-

875 limited dry season. However, elephants are leaving during the *wet* season. Additionally, food

876 selection would change. We would expect to see elephants feeding less selectively, using a

877 range of habitat types and species. There are 26 possible habitat types in IGR; during the wet

878 season, elephants utilized 9 habitat types while they only utilised 8 habitat types during the

879 dry season (Shrader *et al.* 2012). Furthermore, two or three principal species made up ca.

880 80 % of the diet in each season (Table 1). Nevertheless, we can see that they are slowly

881 exploring further and further out of the reserve each wet season (Appendix 1). The reasons

882 for this pattern are somewhat unclear. They may be accessing a greater spatial distribution of

883 resources (Owen-Smith 2003) because of increased population densities. There may also be

884 another food-related reason that I did not test that is influencing their movement. For

885 example, elephants have shown that selection of plant parts was more important rather than

886 species *per se* (Owen-Smith & Chafota 2012). This may be as a result of different growth

887 forms, i.e. shoots vs. leaves vs. branches, and/or having varied physical and chemical

888 defences (Rehill *et al.* 2006). Further research at IGR may reveal the interactions of species

889   selection and plant-part selection. The digestion-enhancing: digestion-reducing ratios may

890   explain more about why the elephants are utilizing the eastern section during the wet season.

891   However, this extremely fine-scale decision making by elephants is not realistic for managers

892   to monitor.

893   Further findings from this study include the fact that the digestion-enhancing:

894   digestion-reducing ratio was of importance. This finding is important as the quality of a plant

895   is not only determined by the crude protein but also the defences that the plant invests in,

896   including chemical or physical defences. These findings were analogous with those of

897   Shrader *et al.* (2012). Interestingly, physical defences appear not to be related to the choices

898   that elephants make because the three principal species (*A. karroo*, *A. nilotica* and *D. cinerea*)

899   are thorny while three of the four avoided species (*E. natalensis*, *P. africanum* and *S.*

900   *pentheri*) have no physical defences. Therefore, future research on elephants must include

901   both measures of the palatability as well as the digestion-reducing substances the plant uses

902   when determining forage quality.

903   Of potential concern is that the high utilization of *A. nilotica* in the dry season may

904   ulitmately negatively affect the survival of this species in the reserve. Although we did not

905   explicitly test this, Wiseman *et al.* (2004) found *A. nilotica* to be markedly reduced during an

906   eight-year period in IGR. The largest size class of *A. nilotica* declined due to high browsing

907   pressure by megaherbivores and low recruitment rates (Wiseman *et al.* 2004). This may

908   explain the very low abundance of *A. nilotica* in IGR, which will further be influenced by the

909   high utilization by elephants. Similarly, Bond and Loffell (2001) found that *Acacia davyi* had

910   been extirpated in IGR, although they ascribed this to the introduction of giraffes (*Giraffa*

911   *camelopardalis*). Furthermore, Gordijn *et al.* (2012) highlighted the change in species in IGR

912   toward an increase in more unpalatable species, including *Searsia spp*. and *Euclea spp*., as a

913   result of avoidance by megaherbivores. These authors also found that there was an overall

914   decline in more palatable species as a result of heavy utilization by megaherbivores (Gordijn

915   *et al.* 2012).

916   Ultimately, I wanted to know if the elephants are making small-scale decisions and if

917   these decisions explain the elephant's large-scale movement patterns. At small spatial scales

918   the elephants select for more nutrient-rich and less defended species. At large spatial scales

919   the elephants are moving into the reserve during the dry season as a result of increased

920   nutrients in their principal species. However, it is unclear why the elephants are moving out

921   of the reserve during the wet season.

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1179   **Appendix 1.**

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1181   **Appendix 1a**. Global positioning system points (determined by satellite observations) of the

1182   elephants' distributions from 2008 in Ithala Game Reserve between seasons wet (black

1183   triangles) and dry seasons (grey stars). Straight lines indicate the quadrants (NW, SW, SE,

1184   NE) where I measured tree abundances and nutrient quality.

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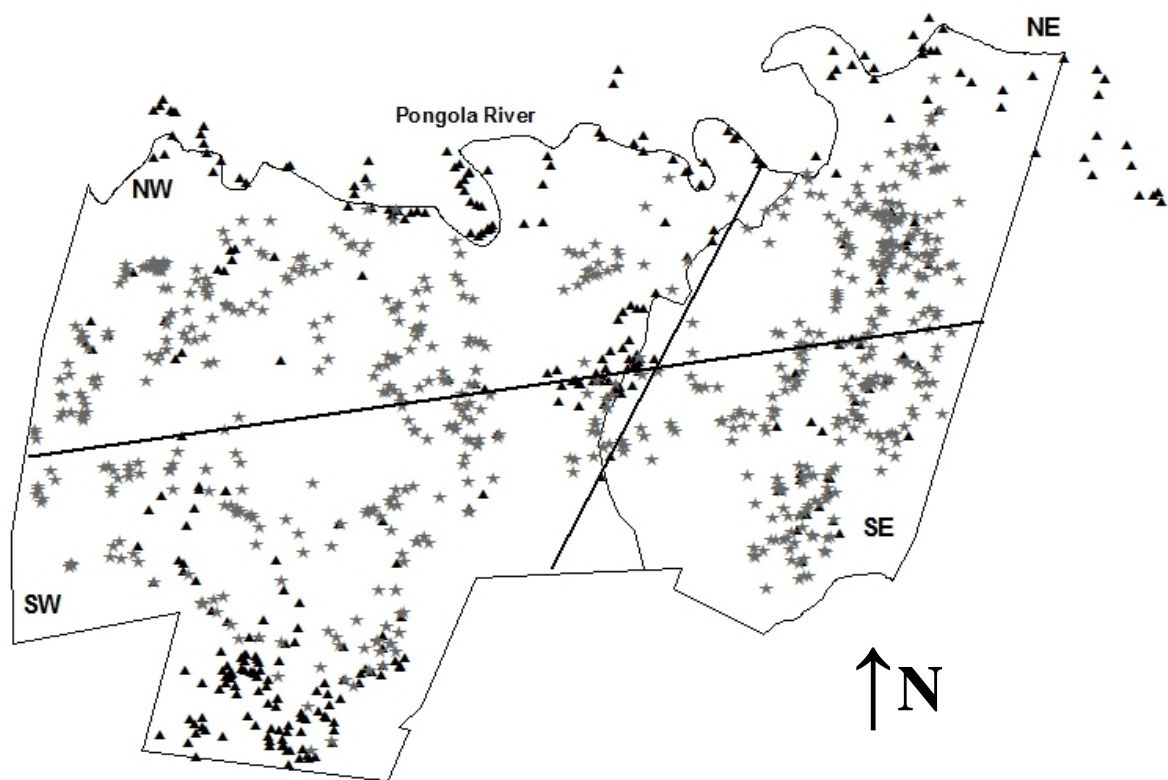
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1192 **Appendix 1b**. Global positioning system points (determined by satellite observations) of the

1193 elephants' distributions from 2009 in Ithala Game Reserve between seasons wet (black

1194 triangles) and dry seasons (grey stars). Straight lines indicate the quadrants (NW, SW, SE,

1195 NE) where I measured tree abundances and nutrient quality.

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1203   **Appendix 1c**. Global positioning system points (determined by satellite observations) of the

1204   elephants' distributions from 2010 in Ithala Game Reserve between seasons wet (black

1205   triangles) and dry seasons (grey stars). Straight lines indicate the quadrants (NW, SW, SE,

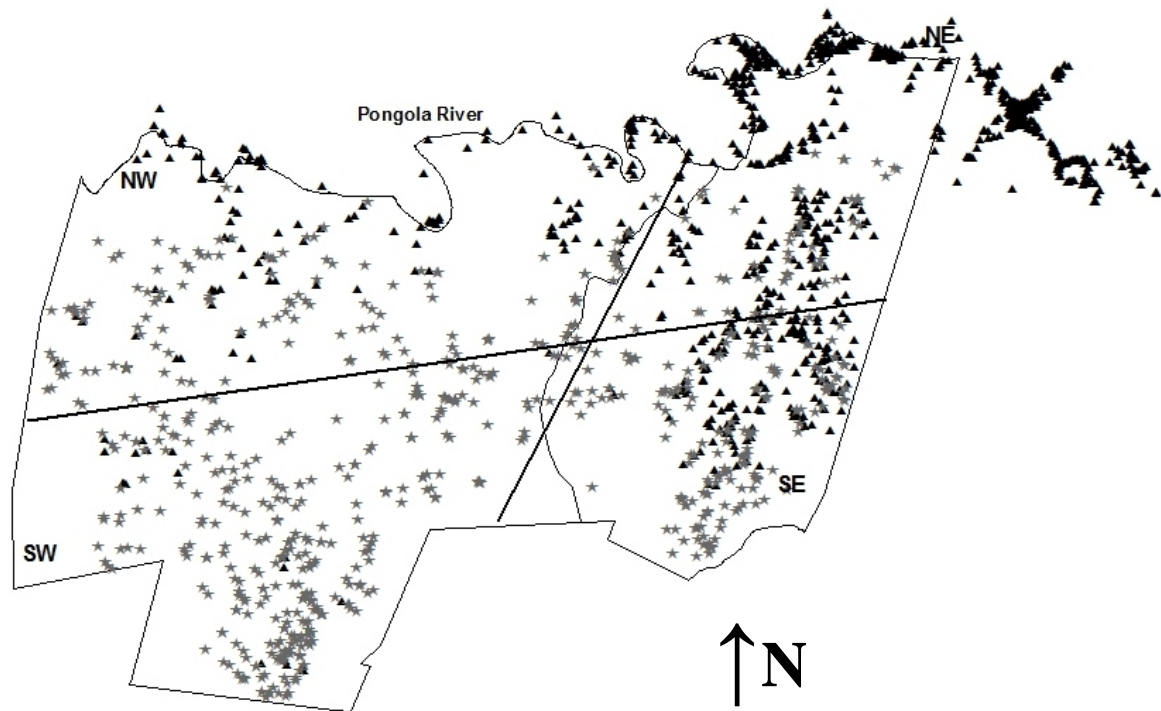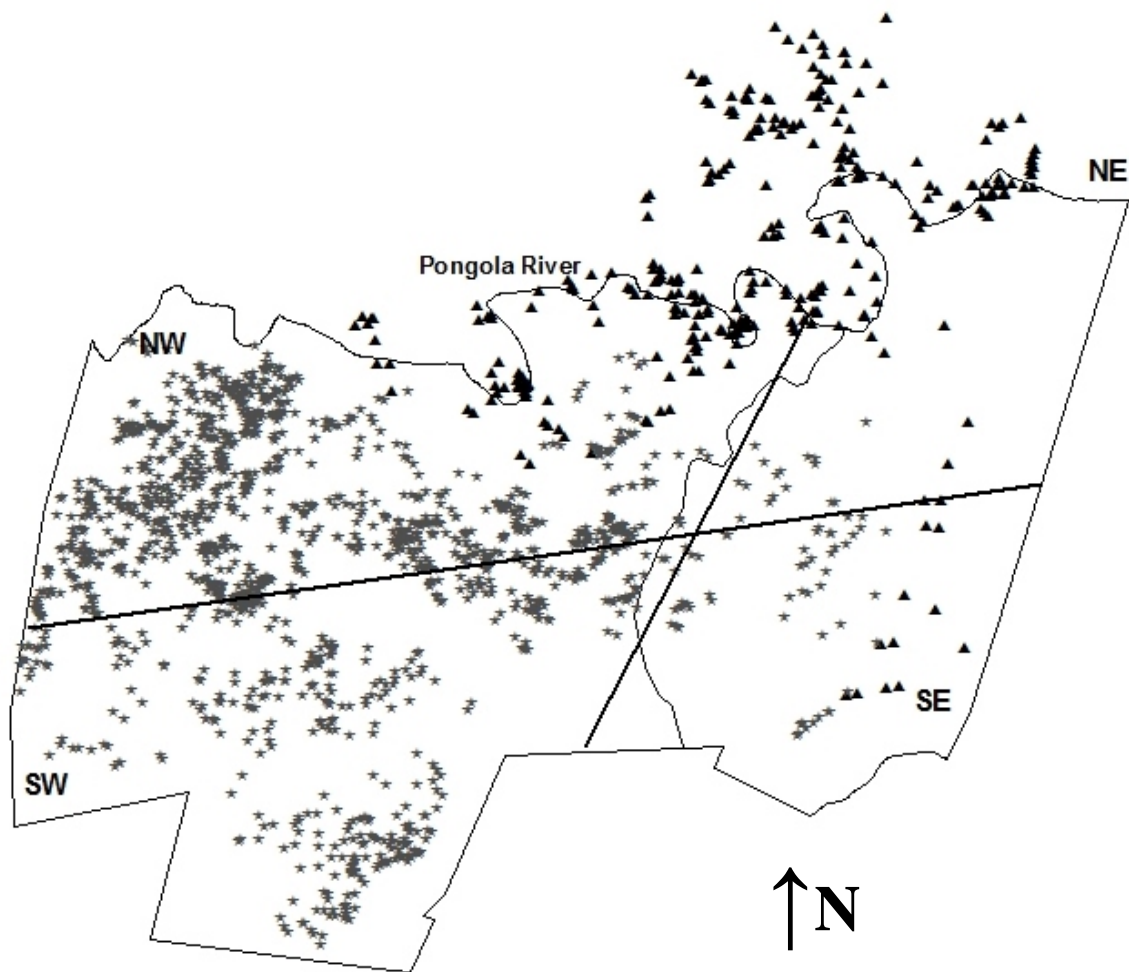1206   NE) where I measured tree abundances and nutrient quality.

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1211 **Appendix 2.**

1212 MANOVA statistics between plant quality data and the factors (season, area, species and

1213 higher-order interactions). Error degrees of freedom = 1005. CP = crude protein; TP = total

1214 polyphenol concentrations, ADF = acid detergent fibre; NDF = neutral detergent fibre.

Parameter		F	P-value
Season	CP	0.023	0.88
	TP	19.999	0.0001
	ADF	290.09	0.0001
	CP:TP	12.217	0.001
	CP:ADF	37.809	0.0001
	NDF	51.576	0.0001
	CP:NDF	12.001	0.001
	ADF:TP	0.758	0.385
	NDF:TP	2.122	0.147
Area	CP	9.368	0.0001
	TP	8.172	0.0001
	ADF	13.244	0.0001
	CP:TP	13.703	0.0001
	CP:ADF	6.846	0.0001
	NDF	7.89	0.0001
	CP:NDF	6.555	0.0001
	ADF:TP	7.084	0.0001
	NDF:TP	7.538	0.0001

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Parameter		F	P-value
Species	CP	31.547	0.0001
	TP	30.024	0.0001
	ADF	71.564	0.0001
	CP:TP	24.384	0.0001
	CP:ADF	28.84	0.0001
	NDF	22.085	0.0001
	CP:NDF	36.012	0.0001
	ADF:TP	27.031	0.0001
	NDF:TP	19.181	0.0001
Season* Area	CP	4.260	0.006
	TP	5.333	0.001
	ADF	2.910	0.035
	CP:TP	0.435	0.728
	CP:ADF	4.087	0.008
	NDF	1.697	0.169
	CP:NDF	2.289	0.079
	ADF:TP	5.164	0.002
	NDF:TP	8.598	0.0001
Season* Species	CP	7.884	0.0001
	TP	13.918	0.0001
	ADF	5.958	0.0001
	CP:TP	17.296	0.0001
	CP:ADF	4.945	0.018
	NDF	9.931	0.0001
	CP:NDF	4.684	0.0001
	ADF:TP	11.997	0.001
	NDF:TP	7.400	0.0001

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Parameter		F	P-value
Area* Species	CP	2.358	0.002
	TP	2.597	0.001
	ADF	4.218	0.0001
	CP:TP	2.512	0.001
	CP:ADF	2.164	0.005
	NDF	2.696	0.0001
	CP:NDF	2.129	0.006
	ADF:TP	2.229	0.004
	NDF:TP	2.842	0.0001
Season* Area*Species	CP	3.625	0.0001
	TP	2.337	0.002
	ADF	3.064	0.0001
	CP:TP	3.948	0.0001
	CP:ADF	3.01	0.0001
	NDF	1.923	0.015
	CP:NDF	2.045	0.009
	ADF:TP	2.622	0.001
	NDF:TP	1.943	0.014

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