Ungulates rely less on visual cues, but more on adapting movement behaviour, when searching for forage

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Finding suitable forage patches in a heterogeneous landscape, where patches change dynamically both spatially and temporally could be challenging to large herbivores, especially if they have no a priori knowledge of the location of the patches. We tested whether three large grazing herbivores with a variety of different traits, improve their efficiency when foraging at a heterogeneous habitat patch scale, by using visual cues to gain a priori knowledge about potential higher value foraging patches. For each species (zebra (*Equus burchelli*), red hartebeest (*Alcelaphus buselaphus* subspecies *camaa*) and eland (*Tragelaphus oryx*)), we used step lengths and directionality of movement to infer whether they were using visual cues to find suitable forage patches at a habitat patch scale. Step lengths were significantly longer for all species when moving to non-visible patches than to visible patches, but all movements showed little directionality. Of the three species, zebra movements were the most directional. Red hartebeest had the shortest step lengths and zebra the longest. We conclude that these large grazing herbivores may not exclusively use visual cues when foraging at a habitat patch scale, but would rather adapt their movement behaviour, mainly step length, to the heterogeneity of the specific landscape.

1   **Ungulates rely less on visual cues, but more on adaptive movement behaviour, when**

2   **searching for forage**

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13   **ABSTRACT**

14   Finding suitable forage patches in a heterogeneous landscape, where patches change dynamically

15   both spatially and temporally could be challenging to large herbivores, especially if they have no

16   a priori knowledge of the location of the patches. We tested whether three large grazing

17   herbivores with a variety of different traits, improve their efficiency when foraging at a

18   heterogeneous habitat patch scale, by using visual cues to gain a priori knowledge about

19   potential higher value foraging patches. For each species (zebra (*Equus burchelli*), red hartebeest

20   (*Alcelaphus buselaphus* subspecies *camaa*) and eland (*Tragelaphus oryx*)), we used step lengths

21   and directionality of movement to infer whether they were using visual cues to find suitable

22   forage patches at a habitat patch scale. Step lengths were significantly longer for all species when

23   moving to non-visible patches than to visible patches, but all movements showed little

24   directionality. Of the three species, zebra movements were the most directional. Red hartebeest

25   had the shortest step lengths and zebra the longest. We conclude that these large grazing

26   herbivores may not exclusively use visual cues when foraging at a habitat patch scale, but would

27   rather adapt their movement behaviour, mainly step length, to the heterogeneity of the specific

28   landscape.

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31   **INTRODUCTION**

32   African ecosystems are well known for their exceptional diversity of large mammalian

33   herbivores, of which a large proportion are ruminant bovids with a few non-ruminant equids

34   (Grange et al. 2004). The feeding type, body size and mouth morphology of large herbivores are

35   intrinsic constraints on the habitat that they can effectively use, and provide an understanding as

36   to how one species may be more or less constrained than another in a particular set of

37   environmental conditions. Different species of large herbivores may use a range of different

38   behaviours to enhance their foraging efficiency (Bailey et al. 1996; Beekman & Prins 1989).

39   Finding a forage patch in a heterogeneous landscape where patches differ in suitability poses a

40   challenge, especially if individuals have no a priori knowledge of the location of the most

41   suitable patches (Bailey et al. 1996; Prins 1996; Senft et al. 1987). Large herbivores may gain a

42   priori knowledge using memory (from a previous visit to the patch) (Brooks & Harris 2008;

43   Dumont & Petit 1998; Edwards et al. 1996; Fortin 2003) or through visual cues (Edwards et al.

44   1997; Howery et al. 2000; Renken et al. 2008). If the forage resource is complex (e.g., when

45   forage patches are not well defined), or the distribution of the forage patches are likely to change

46   continuously (e.g., when a patch is grazed or the grass sward becomes unpalatable due to

47   ageing), then recalling the location of forage patches may be of limited value (Edwards et al.

48   1997). In such situations, heterogeneous in both space and time, the ability to recognise and

49   assess different forage patches at a distance through visual cues, would promote foraging success

50   (Edwards et al. 1997). An alternative behaviour to the use of visual cues would be adaptive

51   search/movement behaviour (Benhamou 2007; Benhamou & Collet 2015; Martin et al. 2015). In

52   heterogeneous environments, adaptive movement, at different scales of step lengths and

53   directionality, e.g., a small-scale area-restricted search (within patches) mixed with a set of large

54   more directional movements (between patches), can be a better search approach than an

55   approach of using visual cues, especially when the forage resource is complex and in constant

56   fluctuation.

57

58   A number of studies of forage patch location or re-visitation in large herbivores have linked

59   movement patterns to the use of memory (Brooks & Harris 2008; Ramos-Fernandez et al. 2003)

60   or visual cues at finer scales (e.g., bite, feeding station, and food-patch scales) (Howery et al.

61   2000; Laca 1998). However it is not clear whether large herbivores use visual cues to find forage

62   patches at a broader habitat patch scale. Our definition of habitat patch scale, adapted from

63   Owen-Smith (2010) and Bailey et al., (1996), refers to a daily range at a 10-hour temporal scale

64   while feeding, walking, drinking and resting, with movement within and between habitats. . We

65   tested whether three grazing herbivore species use visual cues when foraging at the habitat patch

66   scale. The selection of species represented differences in intrinsic traits (differences in body size,

67   feeding type, digestive system and muzzle width) which presumably would influence their

68   interaction with forage resources, e.g. search behaviour.

69   Red hartebeest are considered to be predominantly selective grazers that will make use of browse

70   under limited resource conditions (Kilian, 1993; Murrey, 1993). They are medium-sized (150 kg,

71   average of both sexes) ruminants with a preference for grass. In Mkambati Nature Reserve, South

72   Africa (our study area, hereafter referred to as Mkambati) they use 87% C_4 grasses (Venter &

73   Kalule-Sabiti 2016). In areas with much moribund vegetation, grazing ruminants such as the red

74   hartebeest face particular constraints because nearly all vegetation biomass has a low quality,

75   which reduces food intake rates (Drescher et al. 2006a; Drescher et al. 2006b; van Langevelde et

76   al. 2008). The hartebeest is an example of a concentrate selector; its muzzle width and length is

77   specially adapted (long and narrow) to be very selective at times when good forage is scarce

78   (Schuette et al. 1998). Eland are considered to be mixed feeders preferring browse (Hofmann &

79   Stewart 1972; Watson & Owen-Smith 2000) and in Mkambati their diet consist of 79% C_3 forage

80   (Venter & Kalule-Sabiti 2016). They are ruminants with a large body size (511 kg, average of both

81   sexes)(Venter et al. 2014b). Zebra are non-ruminants and they are much more tolerant to poor

82   quality forage but must maintain a high rate of intake to be able to survive on this type of food

83   (Bell 1971; Okello et al. 2002; van Soest 1982). They are mainly grazers with their diet consisting

84   of 89% C_4 grasses in Mkambati (Venter & Kalule-Sabiti 2016). They are medium sized (235 kg,

85   average male and female) equids (Venter et al. 2014b) with a wide muzzle classifying them as

86   bulk grazers (Bell 1971).

87

88   We developed and tested predictions based on directionality (an indication if a number of turning

89   angles, i.e. the absolute angle between movement i and movement $i+1$, from a series of

90   movements are uniform, i.e. highly concentrated in one direction, or not), step length (distance

91   between two consecutive fixes from GPS telemetry data), and success (outcome of the search

92   movement, whether animals landed up in better forage or not) under three patch visibility

93   classes. In particular, we expected more directional movements with longer step lengths when

94   animals moved to visible patches and less directional movements with shorter step lengths to

95   non-visible patches. We expected, if animals used visual cues, that there would be longer step

96   lengths which are more directional when they move to better forage, because they could

97   anticipate success. No difference in step length or directionality when comparing the outcome of

98   movements (successful and not successful) would indicate that visual cues are not used at this

99   particular scale because then the animal did not adapt the movement (walking straight towards a

100 observed patch) to anticipated success to find better forage. Due to the different intrinsic

101 constraints different species of ungulates have to deal with, we expected that each species would

102 approach its forage search strategy in different ways regardless of the use of visual cues or not or

103 because one species could be using visual cues more than another. Demonstrating a difference in

104 movement behaviour between visible and invisible habitat patches, and successful or not

105 successful movements would enable an understanding of the importance of visual cues to

106 different large herbivore species when moving between patches at a habitat patch scale.

107

108 **METHODS**

109 ***Study area***

110 Mkambati is a 77 km^2 provincial nature reserve situated on the east coast of the Eastern Cape

111 Province, South Africa (31°13'-31°20'S and 29°55'-30°04'E). The climate is mild sub-tropical

112 with a relatively high humidity (de Villiers & Costello 2013). The coastal location, adjacent to

113 the warm Agulhas Current, causes minimal variation in mean daily temperatures (18 °C winter

114 and 22 °C summer) (de Villiers & Costello 2013). The average rainfall is 1 200 mm, with most

115 precipitation in spring and summer (September -February) (Shackleton 1990). The high rainfall,

116 mild temperatures, and presence of abundant streams and wetlands provide a landscape that is

117 not water-limited in any season. More than 80% of Mkambati consists of Pondoland–Natal

118 Sandstone Coastal Sourveld grassland (Mucina et al. 2006). Forests occur in small patches

119 (mostly in fire refuge areas)(Mucina et al. 2006). Mkambati contains a range of large herbivore

120 species, but no large predators (Venter et al. 2014b).

121

122   The grassland is considered to be nutrient poor (Shackleton et al. 1991; Shackleton & Mentis

123   1992). Grassland fire stimulates temporary regrowth high in crude protein (8.6% compared to

124   4.6%, in older grassland), phosphorus concentrations (0.1% compared to 0.05%, in older

125   grassland) and dry matter digestibility (38.6% compared to 27.1%, in older grassland)

126   (Shackleton 1989). Nutrient concentrations remain elevated for up to 6 months post-burn, after

127   which they are comparable to surrounding, unburnt grassland (Shackleton & Mentis 1992).

128   Frequent fires cause a landscape mosaic of nutrient-rich burnt patches within a matrix of older,

129   moribund grassland. This landscape is thus continuously changing due to new fires that are set

130   and the maturing process of the grassland. Recalling the location of grazing forage patches

131   (using memory) would in this case be of limited value which enabled us to test predictions of

132   movement behaviour relative to visibility of forage patches.

133

134   ***Data collection***

135   Five plains zebra (*Equus burchelli*) (4 female and 1 male), six red hartebeest (*Alcelaphus*

136   *buselaphus* subspecies *camaa*) (5 females and 1 male) and five eland (*Tragelaphus oryx*) (3

137   females and 2 males) were fitted with GPS-UHF collars (Africa Wildlife Tracking CC., Pretoria,

138   RSA) between September 2008 and July 2012. These species represented a range of intrinsic

139   constraints which could potentially influence their foraging strategies and subsequent search

140   movement behaviour (Venter & Kalule-Sabiti 2016; Venter et al. 2014a; Venter et al. 2015). All

141   animals were darted by an experienced wildlife veterinarian from a Robinson 44 helicopter. The

142   work was approved by, and conducted in strict accordance with the recommendations in the

143   approved standard protocols of the Animal Ethics Sub-committee of the University of KwaZulu-

144   Natal (Approval number 012/09/Animal). All field work was conducted by, or under the

145   supervision of the first author, while he was a staff member of the Eastern Cape Parks and

146   Tourism Agency, as part of the operational activities of the appointed management authority of

147   Mkambati (Eastern Cape Parks and Tourism Agency Act no. 2 of 2010, Eastern Cape Province,

148   South Africa). The zebra and red hartebeest were in separate harems or herds when they were

149   collared, but some eland (2 females) were in the same herd. The collars were set to take a GPS

150   reading every 30 min, and data were downloaded via UHF radio signal. The collars remained

151   functional between 4 and 16 months depending on various factors, including loss of animals to

152   poaching, natural mortality, or malfunctioning. Data downloaded from the collars were

153   converted to geographical information system (GIS) format and sections of the data sets with

154   missing values were removed and not used in the analysis.

155

156   Step lengths (the distance travelled between each 30 min GPS fix) were calculated for each

157   "walk" using the Hawths Analysis Tools extension (Beyer 2007) to ArcGIS (ArcGIS Desktop:

158   Release 10. Redlands, CA: Environmental Systems Research Institute). Walks were extracted per

159   species (Eland $n = 312$; Red hartebeest $n = 309$; Plains zebra $n = 279$). A walk consisted of 20

160   consecutive steps lengths which constituted 10 hours of movement behaviour during daylight

161   hours (6:00AM to 6:00PM) (Figure 1). Ten hours of movement represented movement between

162   patches at a habitat patch scale. To confirm whether ten hours of movement were indeed within a

163   realistic distance range for the habitat patch scale in our situation, we compared the mean

164   distance between patches to the mean animal walk distances per species. Starting points for each

165   walk were randomly selected (by day), with the visibility from the starting point of each walk

166   being determined using the "viewshed analysis tool" in the Spatial Analyst extension of ArcGIS

167   (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). This

168   resulted in a grid map (raster) layer that indicated all areas that were visible and not visible to

169   the animal from that specific starting point at its shoulder height (female shoulder height: eland

170    $\bar{x}$ = 1500 mm (Posselt 1963); red hartebeest $\bar{x}$ = 1250 mm (Stuart & Stuart 2007); plains zebra $\bar{x}$

171   = 1338 mm (Skinner & Chimimba 2005)) (Figure 1). The end point was defined by the patch

172   where the animal spent the majority ($\geq$50%) of the final 3 h (7 locations) of the "walk" (Figure

173   1). All patches in the landscape were allocated a unique number, and classified as either burnt

174   grassland (fire patches) or unburnt grassland (unburnt patches) (Figure 1). The location of the

175   fire patches were recorded by field rangers between January 2007 and July 2012, and later

176   digitally defined on maps using ArcGIS. Each GPS locality along a "walk" was linked to a patch

177   classification using the Spatial Analyst extension of ArcGIS (ArcGIS Desktop: Release 10.

178   Redlands, CA: Environmental Systems Research Institute). All unburnt areas (areas that were

179   never noted as burnt between January 2007 and July 2012) were considered as one unburnt

180   patch, and was given the same unique identification number. The "walks" were then classified

181   into three different visibility classes which could be a movement: (a) to within the same patch

182   where the starting point was located; (b) to a new patch that was visible from the starting point;

183   and (c) to a new patch not visible from the starting point.

184   When an animal, at the end of a walk, ended up in, a) a better forage patch we considered the

185   movement as successful; b) the same we considered it as no change; and c) worse patch we

186   considered it as unsuccessful. Forage quality was better in recently burnt (<6 months post fire)

187   grassland, see Shackleton & Mentis (1992), compared to older grassland. All step lengths < 6 m

188   were excluded during analysis in order to remove non-movements, as well as false movements

189   due to GPS-error.

190

191   ***Data analysis***

192   We tested whether there was excessive variability amongst individual animal walk distances,

193   which could potentially influence the models, by comparing mean walk distance for different

194   species to inter-patch distances using visual inspection of box plots. This was done using IBM

195   Corp. Released 2014. IBM SPSS Statistics for Windows, Version 23.0. Armonk, NY.

196   We used the Rayleigh test of circular uniformity from CircSTats package in R (R-Development-

197   Core-Team 2011) to calculate the mean resultant length r for each individual "walk". This

198   parameter r provided a measure of the concentration of turning angles ranging between 0 and 1

199   (Duffy et al. 2011). When r is close to 1, data are highly concentrated in one direction, and when

200   it is close to 0, data are widely dispersed (Duffy et al. 2011). The Rayleigh test provides p-values

201   associated with r to test whether it is reasonable to reject angle uniformity. When $r \geq 0.5$ and the

202   p-value indicated significance ($p < 0.05$), walks were considered to be concentrated in one

203   direction (directional).

204   We used a linear mixed model (LMM) to assess the effect of a number of factors on mean step

205   length per "walk". The fixed effects were species, visibility class and search outcome (success).

206   The random effect was individual animal. Wald test was used to determine whether variation in

207   step length between individuals was significant and should be included as a random effect. We

208   did not include interactions between the fixed effects as they were not significant when included

209   in the model. Therefore, we used post-hoc pairwise comparisons with a Bonferroni correction to

210   determine differences in the main effects (IBM SPSS Statistics for Windows, Version 23.0.).

211

212   **RESULTS**

213   Median walk distances for red hartebeest 2120 m (1305-3068 m), eland 3328 m (2374-4341 m)

214   and zebra 3771 m 3771 m (2255-6755 m) were similar to distances between patches 4994 m

215   (2978-7371 m)(values in brackets give the first and the third quartiles), indicating that walks

216   represented movements at a landscape scale as defined by (Bailey et al. (1996)and Owen-Smith et

217   al. (2010) (Figure 2).

218   A low proportion of walks in each visibility class were directional for red hartebeest (6% to not

219   visible; 3% to visible; and 8% within visible) and eland (7% to not visible; 0% to visible; and 5%

220   within visible)(Figure 3). Zebra had a higher proportion of directional walks (12% to not visible;

221   17% to visible; and 17% within visible) than eland and red hartebeest (Figure 3).

222   A linear mixed model with step lengths as dependant variable, success, visibility class and

223   species as fixed effects, and animal ID as a random effect suggests that all fixed effects are

224   significant (p − values 0.045, < 0.0005 and 0.005, respectively). The Wald test suggests that there

225   is a significant variation in step length between individuals ($P = 0.026$). We therefore kept

226   animal ID in the model as a random factor. With search movement outcome, the difference

227   between "no change" versus both "successful" and "not successful" were marginally significant

228   (p=0.054 and p=0.074, respectively) (Table 1, Figure 4A). Zebra had significantly longer step

229   lengths than red hartebeest (p=0.005) and approached significance for eland (p=0.06) (Table 1,

230   Figure 4B). The difference between eland and hartebeest was not significant (p=0.69) (Table 1,

231 Figure 4B). For visibility classes, step lengths in the "within visible" and "to visible" classes

232 were not different (p=0.37), but the step lengths for both these categories were significantly

233 shorter than step lengths to "not visible" classes (p=0.002 and p<0.0005 respectively) (Table 1,

234 Figure 4B).

235

236 **DISCUSSION**

237 In our study we observed little directional movement when animals (from all species) moved to

238 visible patches, which supports a view that large herbivores do not rely exclusively on visual

239 cues when moving to search for patches at a habitat patch scale. Our results support the

240 simulations by Benhamou (2007) which showed that, in patchy environments adaptive

241 movements combining small-scale area-restricted searches (within good forage patches) and

242 large directional movements between patches (in our case, movement to forage patches which

243 were not visible), were used as an optimal strategy to search for habitat patches. However we did

244 not observe a clear pattern in the directionality of the movements (more directional movements

245 between patches) which could indicate that our study animal's strategy could potentially not be

246 as optimal a search strategy compared to the Benhamou (2007) simulations.

247 During fine scale search modes at the bite, feeding station and food patch scale, as defined by

248 Owen-Smith et al. (2010), animals would make use of visual and olfactory cues to find suitable

249 forage items (Edwards et al. 1997; Laca 1998). At coarser scales (e.g. habitat patch scale),

250 herbivores would randomly move, with larger step lengths until they are able to detect more

251 suitable forage (at the finer scale). The search patterns displayed by our study animals thus

252 indicate an adaption of their movement to the patchiness of the environment rather than long and

253   directional step lengths, as expected if visual cues (or the lack thereof) had played a major role

254   (Benhamou 2007; Benhamou & Collet 2015). Adaptations of animal movement behaviour to

255   patchiness at the habitat scale, has been observed elsewhere (de Knegt et al. 2007; Duffy et al.

256   2011), and is confirmed by this study.

257   Red hartebeest had the shortest step lengths of the three study species. Red hartebeest is an

258   example of a concentrate selector; its skull morphology is specially adapted to be very selective

259   at times when good forage is scarce (Schuette et al. 1998). In areas with much moribund

260   vegetation, grazing ruminants such as the red hartebeest face particular constraints because

261   nearly all vegetation biomass has a low quality, which reduces food intake rates (Drescher et al.

262   2006a; Drescher et al. 2006b; van Langevelde et al. 2008). By being more selective, hartebeest

263   would probably need to have more spatially complex movement scales. Red hartebeest, being the

264   smaller ruminant (compared to eland), needing less, but better quality, forage to meet their

265   nutritional and energy requirements (Demment & Soest 1985; Illius & Gordon 1992), used a

266   strategy where they foraged using smaller and less directional steps (compared to zebra), whether

267   they were moving within patches or to visible patches, but increased their step lengths when

268   moving to invisible patches, just like zebra and eland. The smaller step lengths could be

269   explained by their tendency to move slower and spend more time in less nutritious patches which

270   was observed by Venter et al. (2014a). They could thus be more effective in extracting more

271   nutritious material from older moribund grass tufts (due to their adapted muzzle) and therefore

272   be moving in shorter more concentrated steps. In addition, because they are ruminants, they

273   probably spend a significant amount of time ruminating, and moving less, compared to a non-

274   ruminant such as zebra.

275

276 Eland had shorter step lengths than zebra but slightly larger step lengths than red hartebeest.

277 Eland is one of the larger African ruminant species and is considered to be a selective feeder

278 (which includes browse) that require a diet of high nutritive value, low fibre and high protein

279 content (Arman & Hopcraft 1975). In Mkambati they primarily use browse and make little use of

280 grass as forage (Venter & Kalule-Sabiti 2016). They also have a relatively small rumen in

281 relation to their body size and retain food in the rumen for a shorter time (shorter compared to

282 cattle), which allowing for a greater consumption rate (compared to hartebeest) (Arman &

283 Hopcraft 1975). Zebra (non-ruminant) and eland (ruminant) have different body sizes but have

284 similar digestive capacity due to differences in their digestive system (Demment & Soest 1985).

285 It is, therefore, surprising that eland has shorter step lengths than zebra. . This behaviour could

286 possibly be linked to their diet, as being able to browse they can overcome the challenge of

287 dealing with a landscape of nutrient poor, moribund grassland by eating forbs and trees (when

288 available). Forbs are common, especially in newly burned patches in Mkambati (Shackleton

289 1989). Because trees a resource that does not change as rapidly as continuously burnt grassland,

290 eland should be able to return to browsing patches using memory. This could possibly explain

291 their movement behaviour, although one would have expected more directional movements if

292 memory were being used.

293 Zebra used larger step lengths and had more directional walks (although still a small proportion

294 of their walks), compared to the eland and hartebeest. These variations could be linked to

295 differences in the species intrinsic traits, such as digestive system, muzzle width and body weight

296 (Prins & Van Langevelde 2008; Senft et al. 1987). Zebra, a non-ruminant, is less efficient at

297 digesting food and has to maintain a higher intake-rate to maintain its energy requirements (Bell

298 1971; Demment & Soest 1985; Illius & Gordon 1992). This should cause them to move more

299 frequently from one food patch to another as food patches are depleted due to grazing (Bell

300 1971). In addition, they have a wider muzzle than the two ruminant species which makes them

301 capable of using very short grass swards (which are common in recently burned grass patches).

302 Zebra have been shown to prefer newly burned grassland (Sensenig et al. 2010), but they are

303 forced to keep moving to new food patches because the lower biomass in a given patch is

304 depleted much more quickly (Venter et al. 2014a). In addition, the overall higher directionality

305 of zebra movement could indicate that they are more efficient in finding new forage patches.

306 Both these factors would cause movements with larger step lengths and more directionality, as

307 we observed with this species.

308 There is a certain degree of uncertainty whether walk directionality was affected by the step

309 length. Hurford (2009) showed that GPS measurement errors might lead to reporting overly

310 tortuous movement when the distances between locations were smaller than 20 m. Although we

311 removed all distances smaller than 6 m from the analysis there is a chance that part of our turning

312 angle measurements were affected by GPS error. For example, larger proportion of short steps in

313 hartebeest might explain why directionality in hartebeest movements was smaller than we

314 expected.

315 Our study provides some evidence indicating that large grazers might not exclusively rely on

316 visual cues when foraging at a habitat patch scale, but rather adapt their search mode, mainly

317 longer step lengths, when they move to invisible patches. The animals used this adaptive

318 approach to foraging to cope with continuously changing forage conditions. In addition, it shows

319 that different species search for forage in different ways, which could indicate that search

320 strategies are linked to intrinsic traits such as body size, feeding type, digestive strategy and

321 muzzle width.

322

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326

327   **REFERENCES**

328   Arman P, and Hopcraft D. 1975. Nutritional studies on East African herbivores. *British*
329   *Journal of Nutrition* 33:255-264.
330   Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, and Sims
331   PL. 1996. Mechanisms that result in large herbivore grazing distribution patterns.
332   *Journal of Range Management* 49:386-400.
333   Beekman JH, and Prins HHT. 1989. Feeding strategies of sedentary large herbivores in
334   East Africa, with emphasis on the African buffalo, *Syncerus caffer*. *African*
335   *Journal of Ecology* 27:129-147.
336   Bell RHV. 1971. A grazing ecosystem in the Serengeti. *Scientific American* 225:86-93.
337   Benhamou S. 2007. How many animals really do the Lévy walk? *Ecology* 88:1962-
338   1969.
339   Benhamou S, and Collet J. 2015. Ultimate failure of the Lévy Foraging Hypothesis:
340   Two-scale searching strategies outperform scale-free ones even when prey are
341   scarce and cryptic. *Journal of Theoretical Biology* 387:221-227.
342   Beyer HL. 2007. Haw's Analysis Tools for ArcGIS. 3.27 ed.
343   Brooks CJ, and Harris S. 2008. Directed movement and orientation across a large
344   natural landscape by zebras, *Equus burchelli antiquorum*. *Animal Behaviour*
345   76:277-285.
346   de Knegt HJ, Hengeveld GM, van Langevelde F, de Boer WF, and Kirkman KP. 2007.
347   Patch density determines movement patterns and foraging efficiency of large
348   herbivores. *Behavioral Ecology* 18:1065-1072.
349   de Villiers D, and Costello J. 2013. *Mkambati and the Wild Coast, Second edition*. Port
350   St Johns, South Africa: Div deVilliers and John Costello
351   Demment MW, and Soest PJV. 1985. A nutritional explanation for body-size patterns of
352   ruminant and nonruminant herbivores. *The American Naturalist* 125:641-672.
353   Drescher M, HeitkÖnig IMA, Van Den Brink PJ, and Prins HHT. 2006a. Effects of
354   sward structure on herbivore foraging behaviour in a South African savanna: An
355   investigation of the forage maturation hypothesis. *Austral Ecology* 31:76-87.
356   Drescher M, Heitkönig IMA, Raats JG, and Prins HHT. 2006b. The role of grass stems
357   as structural foraging deterrents and their effects on the foraging behaviour of
358   cattle. *Applied Animal Behaviour Science* 101:10-26.
359   Duffy KJ, Dai X, Shannon G, Slotow R, and Page B. 2011. Movement patterns of
360   African elephants (*Loxodonta africana*) in different habitat types. *South African*
361   *Journal of Wildlife Research* 41:21-28.
362   Dumont B, and Petit M. 1998. Spatial memory of sheep at pasture. *Applied Animal*
363   *Behavior Science* 60:43-53.
364   Edwards GR, Newman JA, Parsons AJ, and Krebs JR. 1996. The use of spatial
365   memory by grazing animals to locate food patches in spatially heterogeneous
366   environments: an example with sheep. *Applied Animal Behaviour Science*
367   50:147-160.
368   Edwards GR, Newman JA, Parsons AJ, and Krebs JR. 1997. Use of cues by grazing
369   animals to locate food patches: an example with sheep. *Applied Animal*
370   *Behaviour Science* 51:59-68.

371   Fortin D. 2003. Searching behavior and use of sampling information by free-ranging
372   bison (*Bos bison*). *Behavioral Ecology and Sociobiology* 54:194-203.
373   Grange S, Duncan P, Gaillard J-M, Sinclair ARE, Gogan PJP, Packer C, Hofer H, and
374   Marion E. 2004. What limits the Serengeti zebra population? *Oecologia* 140:523-
375   532.
376   Hofmann RR, and Stewart DRM. 1972. Grazer or browser: a classification based on the
377   stomach-structure and feeding habitats of East African ruminants. *Mammalia*
378   36:226-240.
379   Howery LD, Bailey DW, Ruyle GB, and Renken WJ. 2000. Cattle use visual cues to
380   track food locations. *Applied Animal Behaviour Science* 67:1-14.
381   Illius AW, and Gordon IJ. 1992. Modeling the nutritional ecology of ungulate herbivores:
382   Evolution of body size and competitive interactions. *Oecologia* 89:426-434.
383   Laca EA. 1998. Spatial memory and food searching mechanisms of cattle. *Journal of
384   Range Management* 51:370-378.
385   Martin J, Benhamou S, Yoganand K, and Owen-Smith N. 2015. Coping with spatial
386   heterogeneity and temporal variability in resources and risks: Adaptive
387   movement behaviour by a large grazing herbivore. *PLoS ONE* 10:e0118461.
388   Mucina L, Scott-Shaw CR, Rutherford MC, Camp KGT, Matthews WS, Powrie LW, and
389   Hoare DB. 2006. Indian Ocean Coastal Belt. In: Mucina L, and Rutherford MC,
390   eds. *The Vegetation of South Africa, Lesotho and Swaziland*. Pretoria: South
391   African Biodiversity Institute.
392   Okello MM, Wishitemi REL, and Muhoro F. 2002. Forage intake rates and foraging
393   efficiency of free-ranging zebra and impala. *South African Journal of Wildlife
394   Research* 32:93-100.
395   Owen-Smith N, Fryxell JM, and Merrill EH. 2010. Foraging theory upscaled: the
396   behavioural ecology of herbivore movement. *Philosophical Transactions of the
397   Royal Society* 365:2267-2278.
398   Posselt J. 1963. Domestication of the eland. *Rhodesian Journal of Agricultural
399   Research* 1:81-87.
400   Prins HHT. 1996. *Behavior and Ecology of the African Buffalo: Social Inequality and
401   Decision Making*. London: Chapman & Hall.
402   Prins HHT, and Van Langevelde F. 2008. *Resource Ecology*. New York: Springer.
403   R-Development-Core-Team. 2011. R: A language and environment for statistical
404   computing. Vienna: R Foundation for Statistical Computing.
405   Ramos-Fernandez G, Mateos JL, Miramobtes O, Cocho G, Larralde H, and Ayala-
406   Orozco B. 2003. Levy walk patterns in the foraging movements of spider
407   monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology* 55:223-230.
408   Renken WJ, Howery LD, Ruyle GB, and Enns RM. 2008. Cattle generalise visual cues
409   from the pen to the field to select initial feeding patches. *Applied Animal
410   Behaviour Science* 109:128-140.
411   Schuette JR, Leslie DM, Lochmiller RLJ, and Jenks JA. 1998. Diets of hartebeest and
412   roan antelope in Burkina Faso: Support of the long-faced hypothesis. *Journal of
413   Mammalogy* 79:426-436.
414   Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, and Swift DM. 1987.
415   Large herbivore foraging and ecological hierarchies. *BioScience* 37:789-799.

416 Sensenig RL, Demment MW, and Laca EA. 2010. Allometric scaling predicts
417   preferences for burned patches in a guild of East African grazers. *Ecology*
418   91:2898-2907.
419 Shackleton CM. 1989. An ecological survey of a selected area of Pondoland Sourveld
420   with emphasis on its response to the management practices of burning and
421   grazing Masters Degree Thesis. University of Transkei.
422 Shackleton CM. 1990. Seasonal changes in biomass concentration in three coastal
423   grassland communities in Transkei. *Journal of the Grassland Society of South*
424   *Africa* 7:265-269.
425 Shackleton CM, Granger JE, Mcenzie B, and Mentis MT. 1991. Multivariate analysis of
426   coastal grasslands at Mkambati Game Reserve, north-eastern Pondoland,
427   Transkei. *Bothalia* 21:91-107.
428 Shackleton CM, and Mentis MT. 1992. Seasonal changes in nutrient content under
429   three defoliation treatments in two coastal grassland communities of Transkei.
430   *Tydskrif van die Weidingsvereniging van Suid Afrika* 9:30-37.
431 Skinner JD, and Chimimba CT. 2005. *The Mammals of the Southern African Subregion*.
432   New York: Cambridge University Press.
433 Stuart C, and Stuart T. 2007. *Field guide to Mammals of southern Africa*. Cape Town:
434   Struik Publishers.
435 van Langevelde F, Drescher M, Heitkönig IMA, and Prins HHT. 2008. Instantaneous
436   intake rate of herbivores as function of forage quality and mass: Effects on
437   facilitative and competitive interactions. *Ecological Modelling* 213:273-284.
438 van Soest PJ. 1982. *Nutritional ecology of the ruminant*. Corvallis: OB Booksa.
439 Venter JA, and Kalule-Sabiti MJ. 2016. Diet composition of the large herbivores in
440   Mkambati Nature Reserve, Eastern Cape, South Africa. *African Journal of*
441   *Wildlife Research* 46:49-56.
442 Venter JA, Nabe-Nielsen J, Prins HT, and Slotow R. 2014a. Forage patch use by
443   grazing herbivores in a South African grazing ecosystem. *Acta Theriologica*
444   59:457-466.
445 Venter JA, Prins HHT, Balfour DA, and Slotow R. 2014b. Reconstructing grazer
446   assemblages for protected area restoration. *PLoS ONE* 9:e90900.
447 Venter JA, Prins HHT, Mashanova A, de Boer WF, and Slotow R. 2015. Intrinsic and
448   extrinsic factors influencing large African herbivore movements. *Ecological*
449   *Informatics* 30:257-262.
450 Watson LH, and Owen-Smith N. 2000. Diet composition and habitat selection of eland
451   in semi-arid shrubland. *African Journal of Ecology* 38:130-137.

452

Figure 1

A hypothetical example of a "walk" extracted for the study

Walks were extracted from the data which included the departure point (indicated by "Start") to where the animal ended (indicated by "End"). Here the animal hypothetically spent the majority of the last three hours of its "walk" in an area which was not visible from the starting point (indicated by grey). The striped area indicates a recent fire patch.

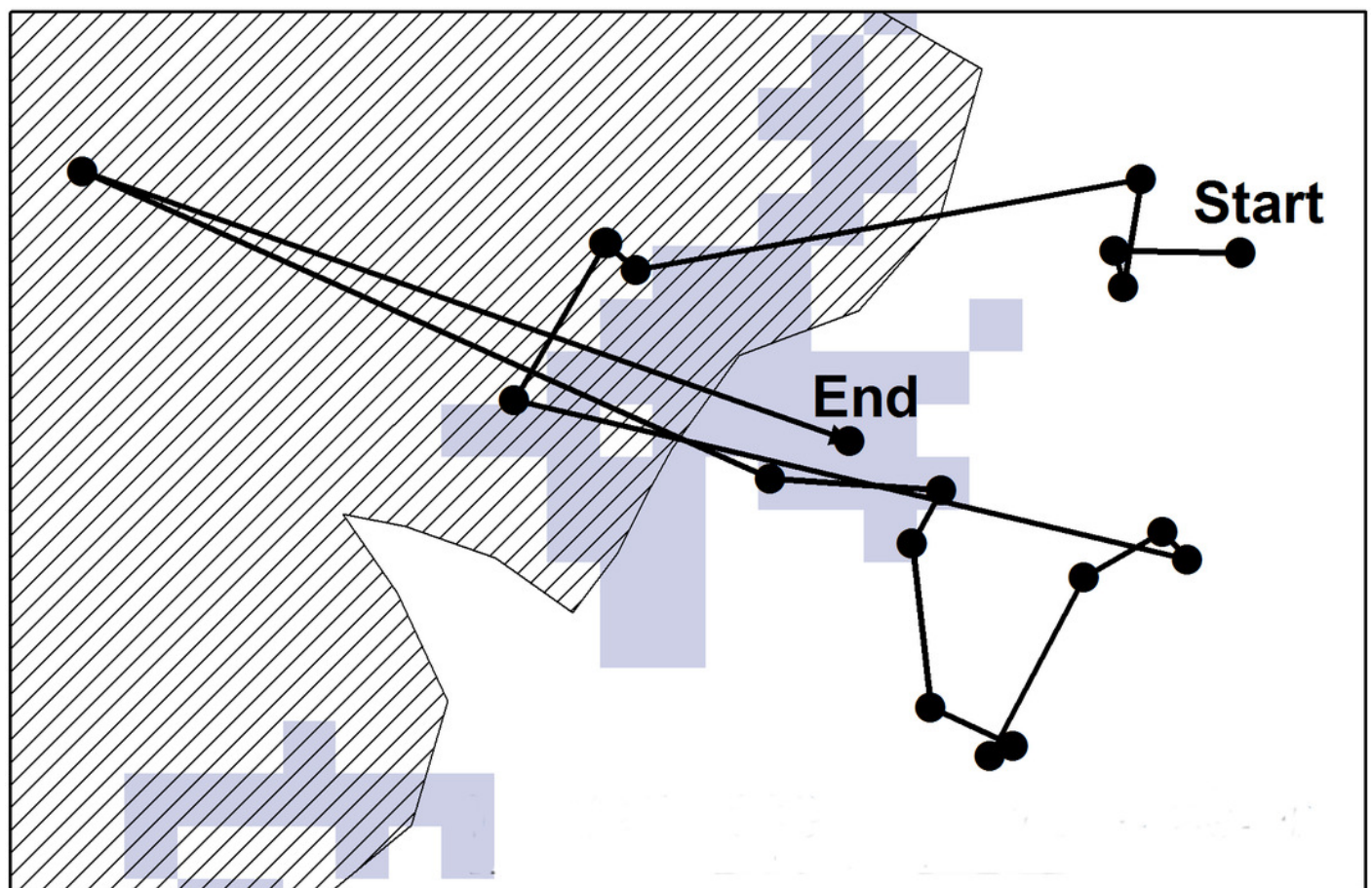



Figure 2

Mean +/- 1 S.D. (m) of inter-patch distances and distances moved in a 10-h walk by red hartebeest, eland and zebra in Mkambati Nature Reserve

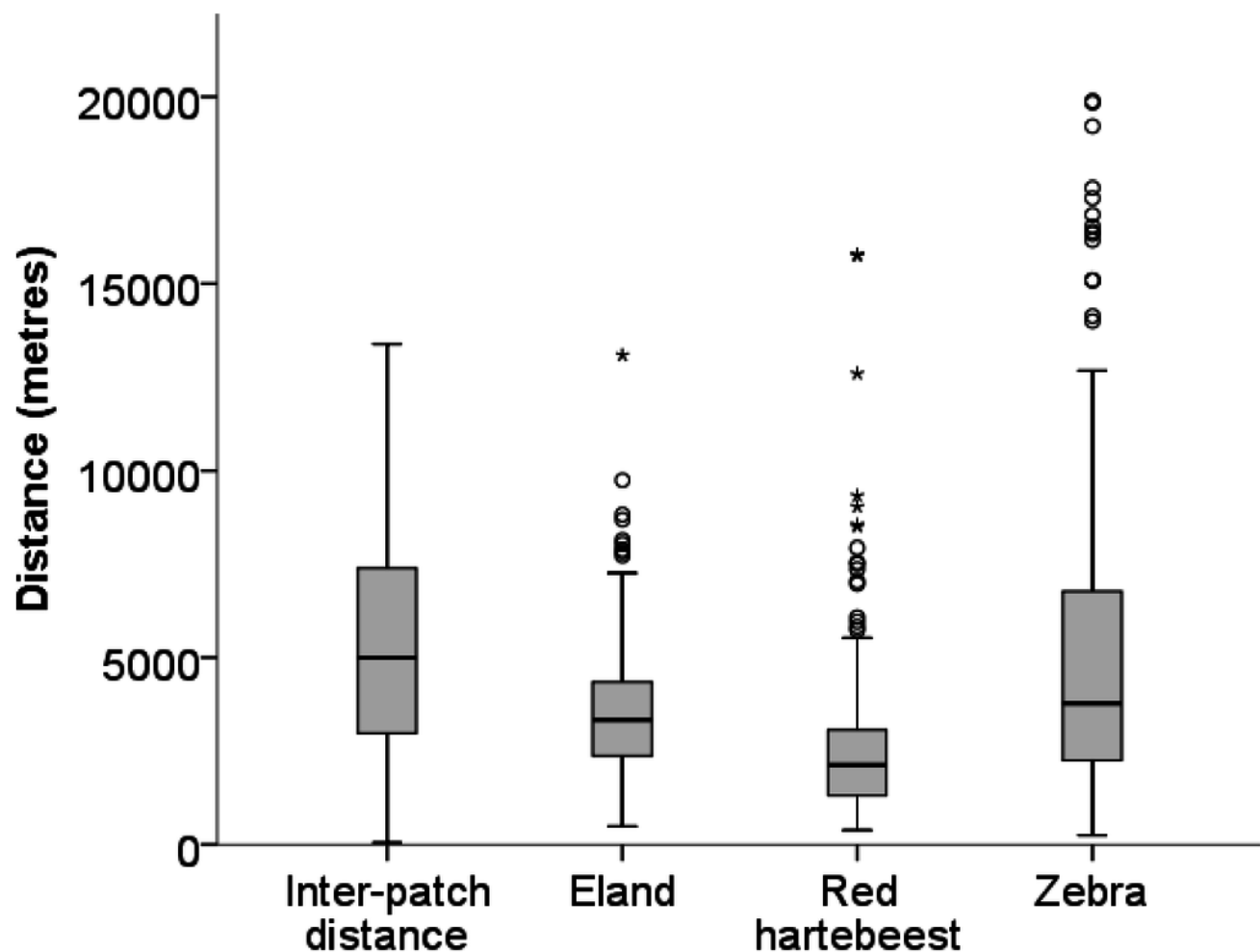



Figure 3

Directionality of movement of red hartebeest, eland and zebra in relation to visibility of the final locationin Mkambati Nature Reserve

Each point represents the r and associated p-value from a Rayleigh test for a single 10-h walk to locations in different patches that were not visible from the start (left column), to locations in the same patch that were visible from the start (middle column), and to locations in different patches that were not visible from the start (right column). Data are shown for eland (A,B,C), hartebeest (D,E,F) and zebra (G,H,I).

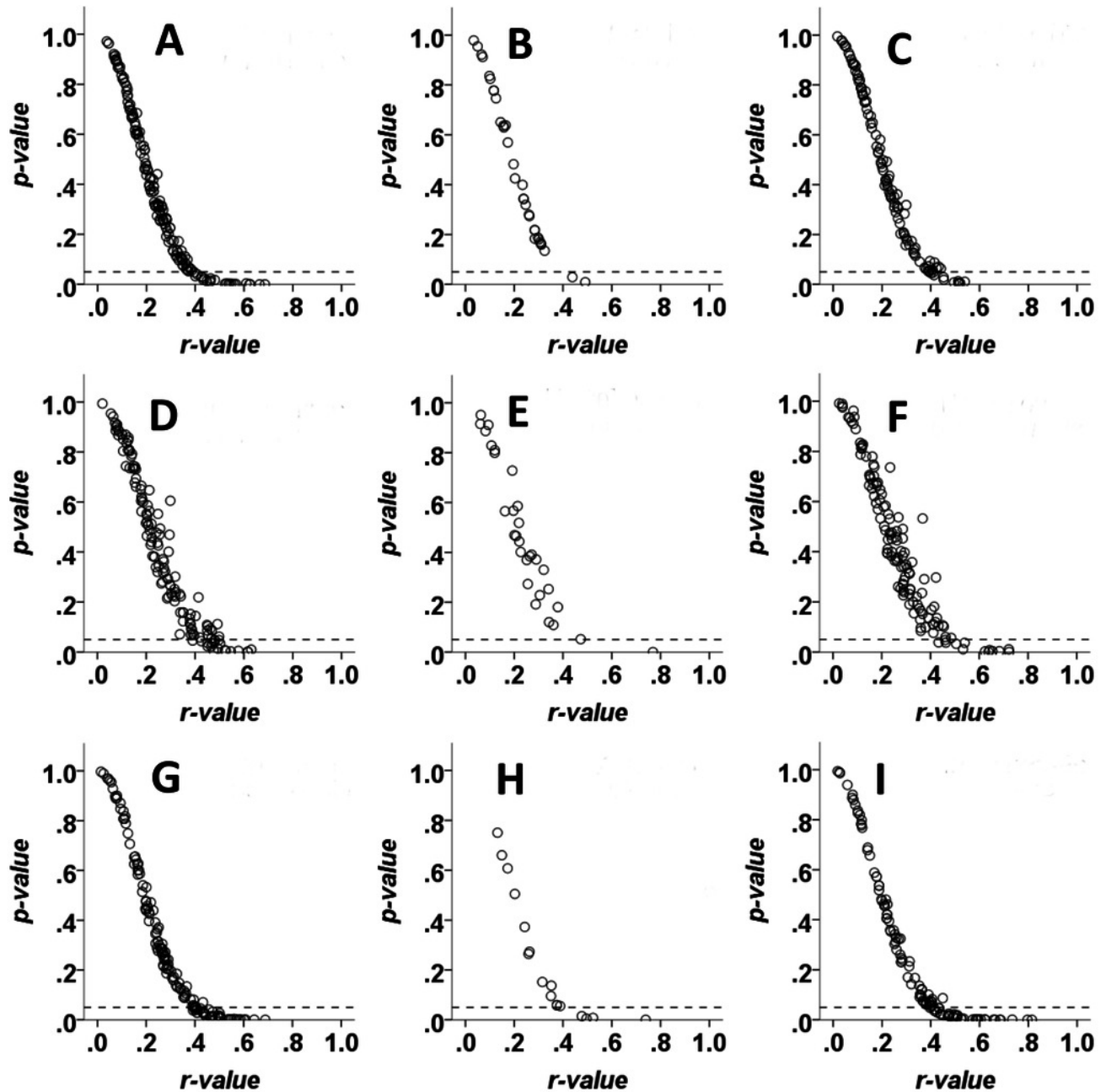
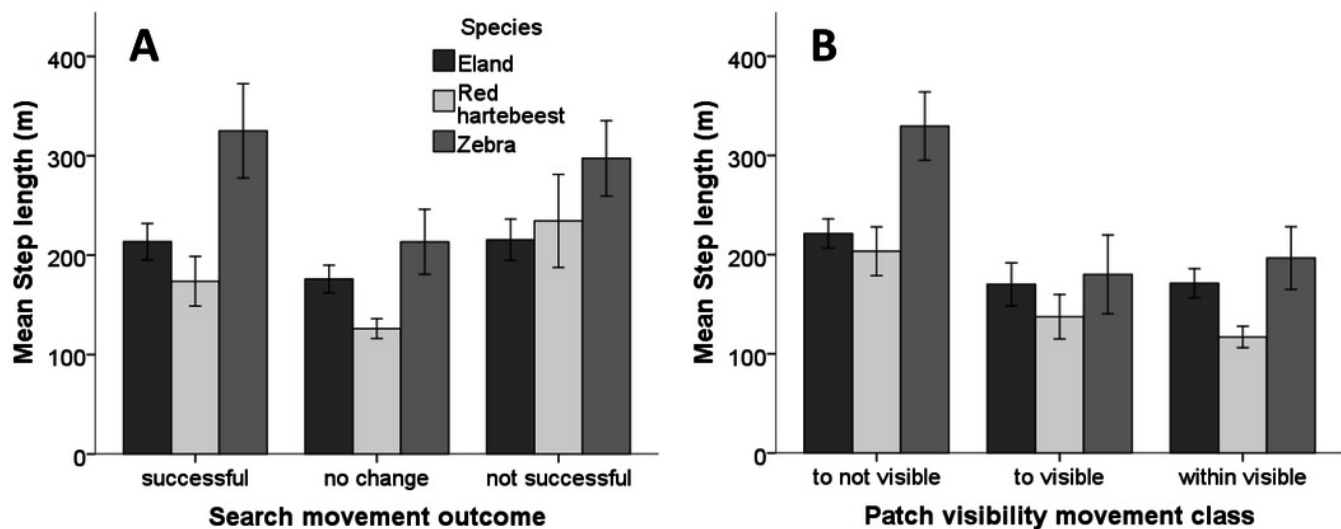
Significance

Directionality

Figure 4

Mean step length of search movement outcomes and patch visibility classes for three herbivore species in Mkambati Nature Reserve

The relationship of A) search movement outcome (success) and B) patch visibility movement classes with mean step length of zebra, red hartebeest and eland studied in Mkambati Nature Reserve. Error bars indicate 95%CI.

The results of the pairwise comparisons between species, visibility movement class and search movement outcome

Factor	Mean difference	Std. Error	df	Sig.
Species				
Eland vs Red hartebeest	30.505	24.531	17.737	0.69
Eland vs Zebra	-64.331	25.029	16.69	0.06
Red hartebeest * Zebra	-94.835	25.068	16.497	**0.005****
Search movement outcome				
Successful vs no change	40.801	17.202	880.753	0.054
Successful vs not successful	2.367	12.681	874.701	1
no change vs not successful	-38.434	17.094	879.703	0.074
Visibility movement class				
to not visible vs to visible	89.509	16.214	873.165	**<0.0005*****
to not visible vs within visible	54.408	15.837	877.081	**0.002****
to visible vs within visible	-35.102	22.758	881.966	0.37

Significance: <0.05*; <0.005**; 0.0005***