

A peer-reviewed version of this preprint was published in PeerJ on 16 May 2017.

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Venter JA, Prins HHT, Mashanova A, Slotow R. 2017. Ungulates rely less on visual cues, but more on adapting movement behaviour, when searching for forage. PeerJ 5:e3178 <https://doi.org/10.7717/peerj.3178>

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

Jan A Venter^{Corresp., 1}, Herbert H. T. Prins^{2,3}, Alla Mashanova⁴, Rob Slotow³

¹ School of Natural Resource Management, Nelson Mandela Metropolitan University, George, Western Cape Province, South Africa

² Resource Ecology Group, Wageningen University, Wageningen, The Netherlands

³ School of Life Sciences, University of Kwazulu-Natal, Durban, South Africa

⁴ Department of Biological and Environmental Sciences, University of Hertfordshire, Hatfield, United Kingdom

Corresponding Author: Jan A Venter

Email address: Jan.Venter@nmmu.ac.za

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**

3 Jan A. Venter¹, Herbert H.T. Prins^{2;3}, Alla Mashanova⁴ and Rob Slotow²

4 ¹School of Natural Resource Management, George Campus, Nelson Mandela Metropolitan
5 University, Private Bag X6531, George, 6530, South Africa.

6 ²School of Life Sciences, University of Kwazulu-Natal, Westville Campus, Private Bag X54001,
7 Durban, 4000, South Africa.

8 ³Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6705PB Wageningen,
9 The Netherlands

10 ⁴Department of Biological and Environmental Sciences, University of Hertfordshire, Hatfield,
11 AL10 9AB, United Kingdom.

12

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.

29

30

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% C₄ 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% C₃ 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% C₄ 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 km² 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 Hawth's 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

323 **ACKNOWLEDGEMENTS**

324 Mkambati Nature Reserve staff, students from the University of Kwazulu-Natal and students
325 from Pennsylvania State University, Parks and People program for providing field assistance.

326

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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.

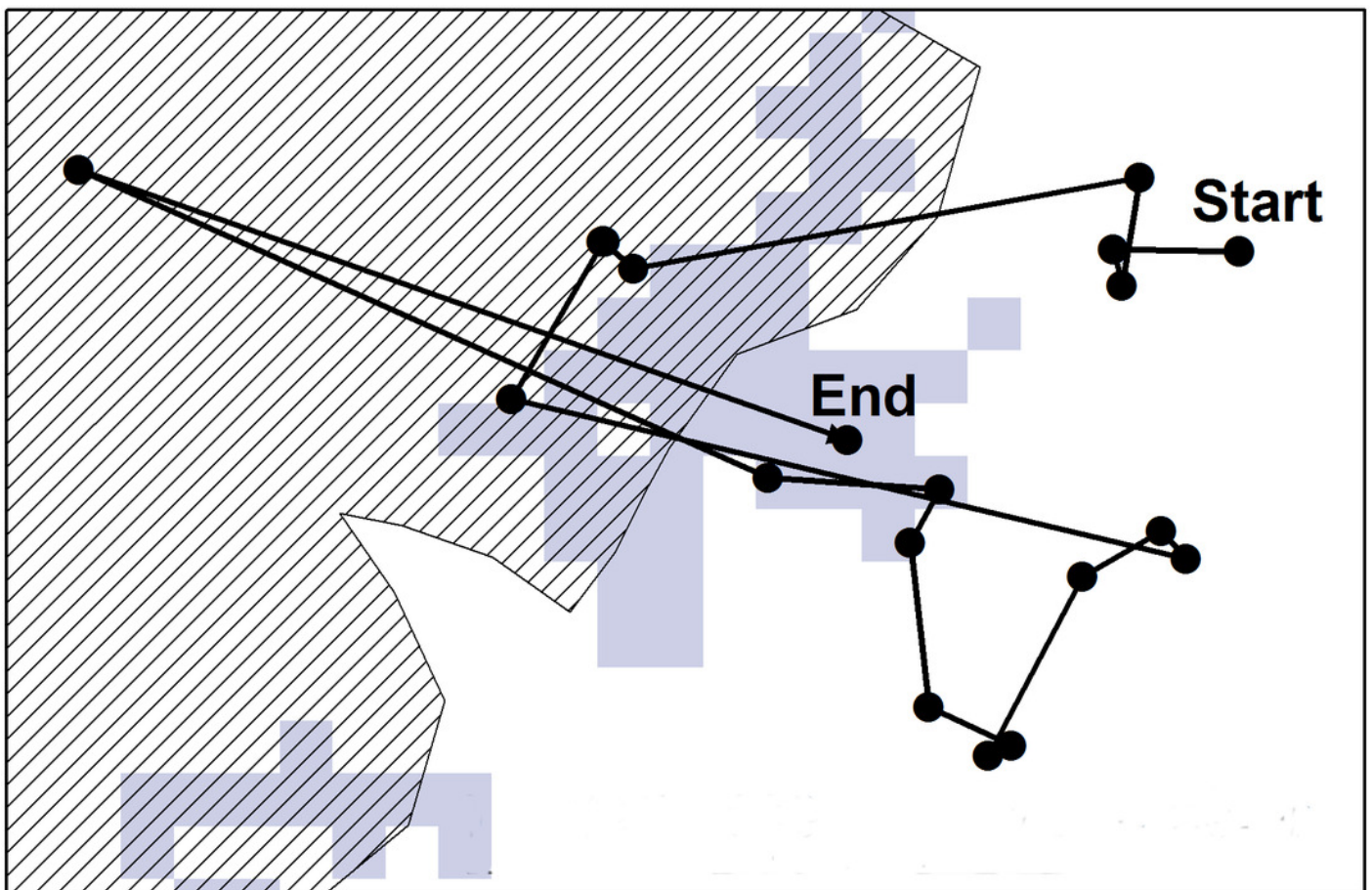


Figure 2

Mean \pm 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

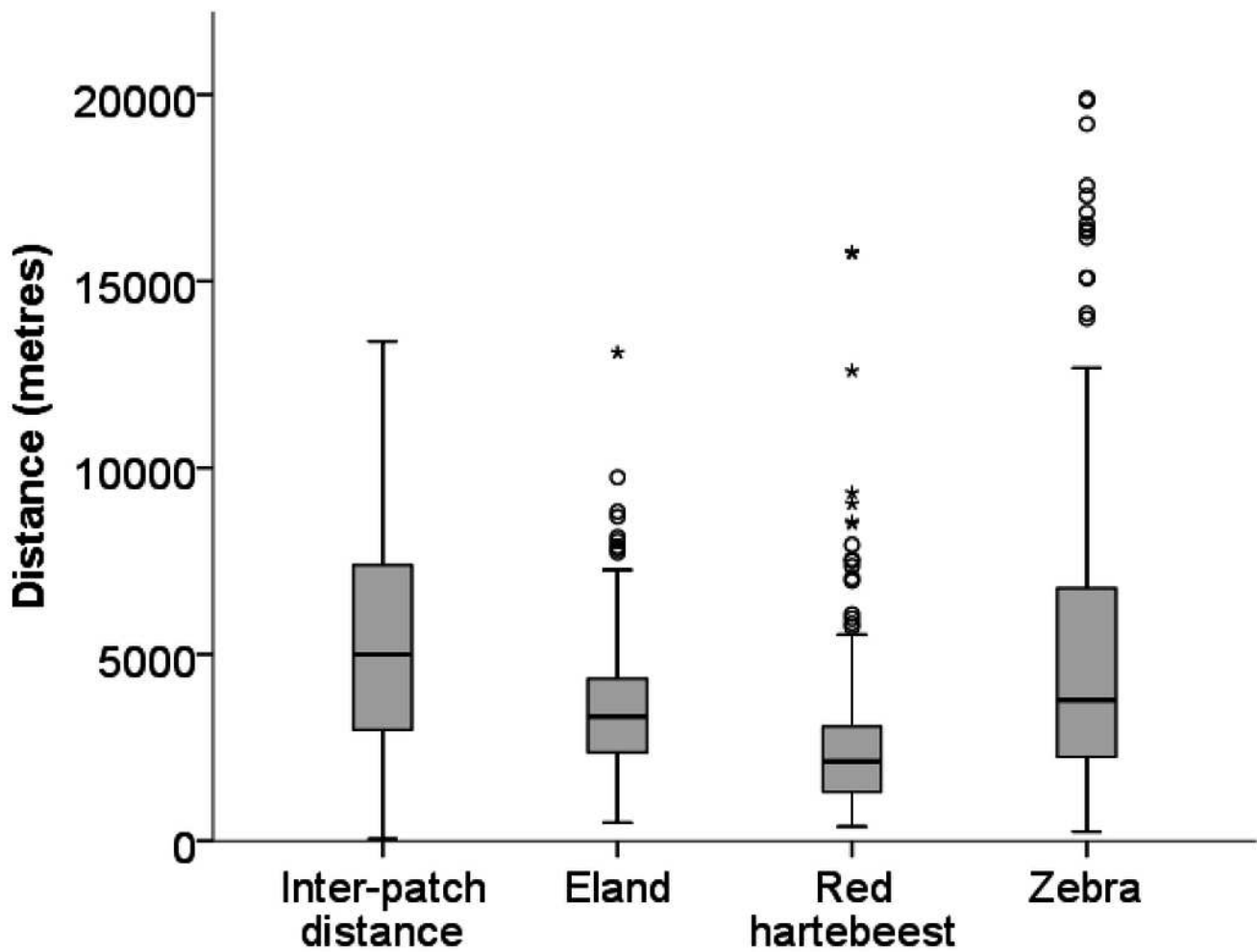
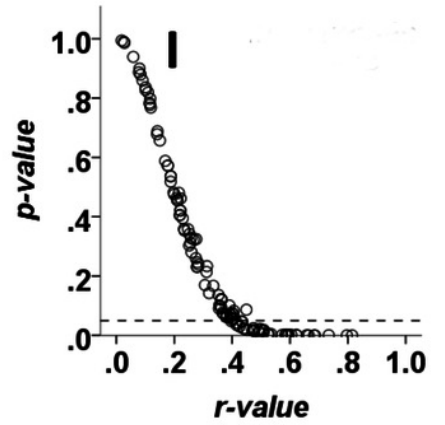
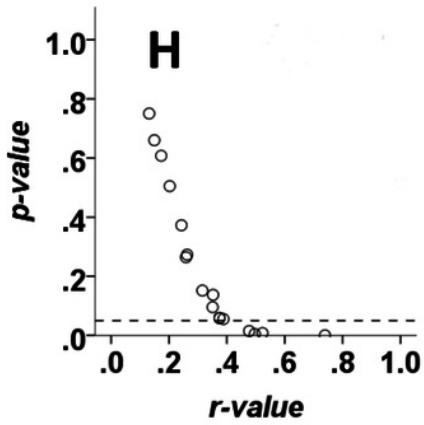
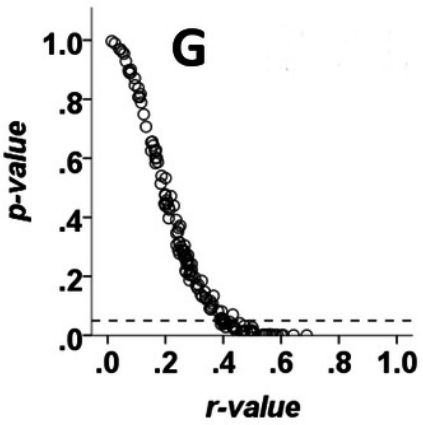
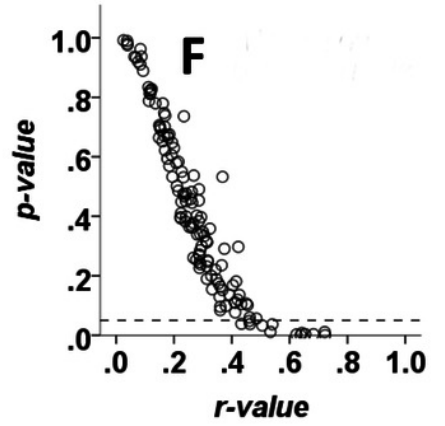
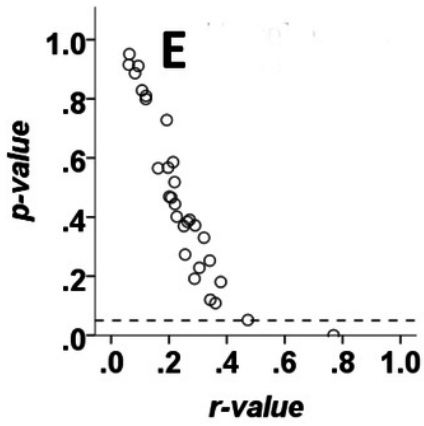
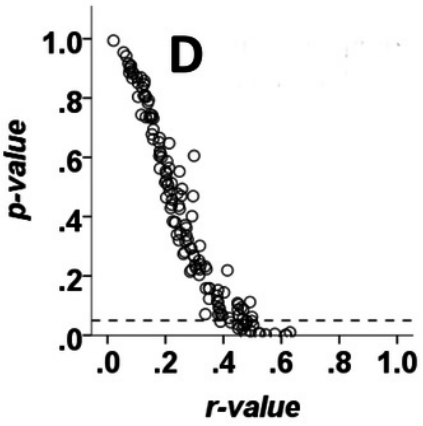
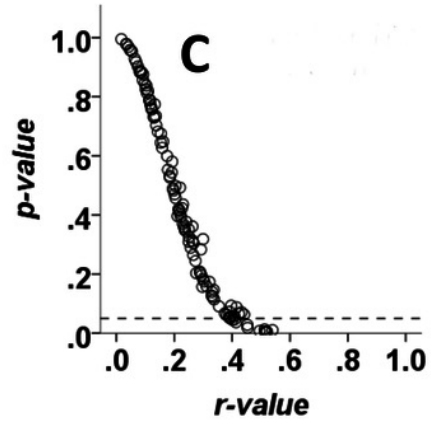
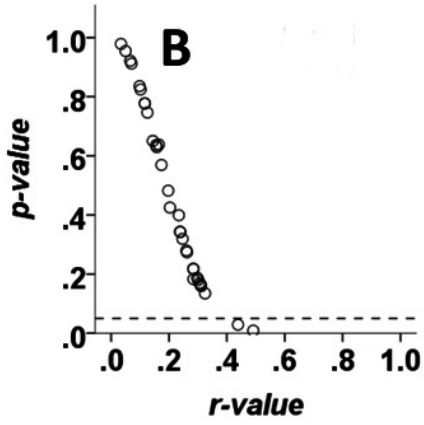
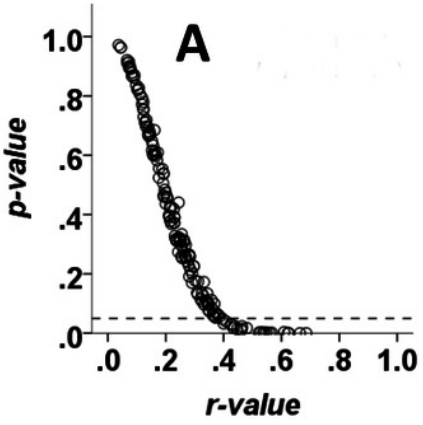


Figure 3

Directionality of movement of red hartebeest, eland and zebra in relation to visibility of the final location in 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.

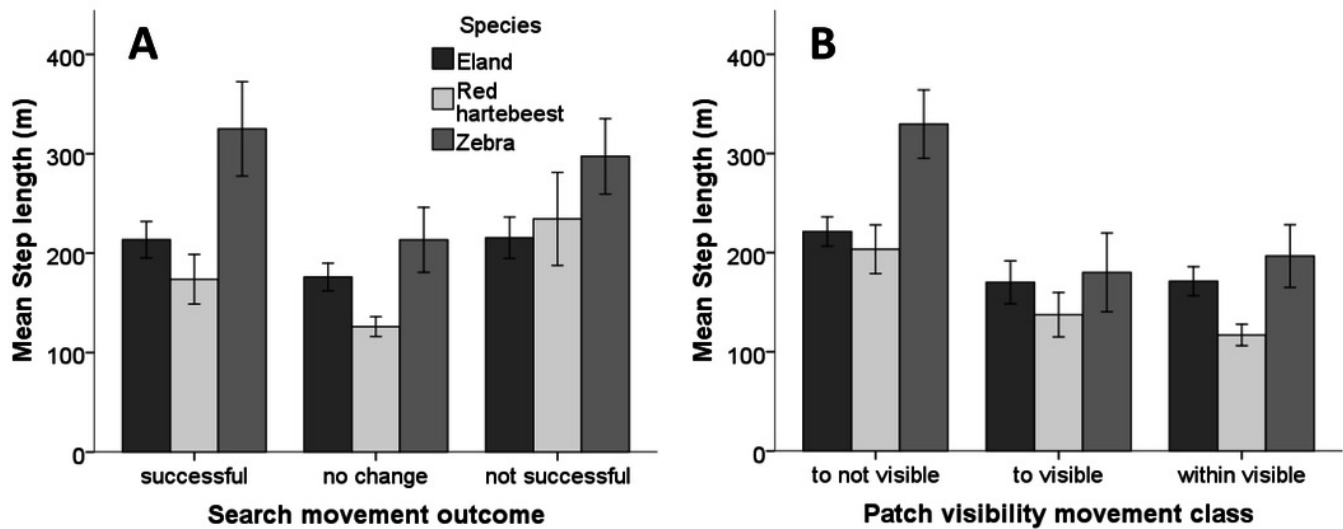


Table 1 (on next page)

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

Factor	Mean difference	Std. Error	df	Sig.
<i>Species</i>				
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**
<i>Search movement outcome</i>				
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
<i>Visibility movement class</i>				
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***