

Ungulates rely less on visual cues, but more on adapting movement behaviour, when searching for forage (#13615)

1

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3



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The English language should be improved to ensure that your international audience can clearly understand your text. I suggest that you have a native English speaking colleague review your manuscript. Some examples where the language could be improved include lines 23, 77, 121, 128 - the current phrasing makes comprehension difficult.

Organize by importance of the issues, and number your points

1. Your most important issue
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Line 56: Note that experimental data on sprawling animals needs to be updated. Line 66: Please consider exchanging "modern" with "cursorial".

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I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC

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I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.

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 if 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 but all movements showed little directionality. These large grazing herbivores did not use visual cues when foraging at a habitat patch scale, but rather adapted their movement behaviour 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 Human and Environmental Sciences, University of Hertfordshire, Hatfield, AL10
11 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  if they were using visual cues to find suitable forage

22 patches at a habitat patch scale. Step lengths were significantly longer for all species when
 23 moving to non-visible patches  but all movements showed little directionality.  These large
 24 grazing herbivores did not use visual cues when foraging at a habitat patch scale, but rather
 25 adapted their movement behaviour to the heterogeneity of the specific landscape.
















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28 INTRODUCTION

29 African ecosystems are well known for their exceptional diversity of large mammalian
 30 herbivores, of which a large proportion are ruminant bovids with a few non-ruminant equids
 31 (Grange et al. 2004). The feeding type, body size and mouth morphology of large herbivores are
 32 intrinsic constraints on the habitat that they can effectively use, and provide an understanding as
 33 to how one species may be more or less constrained than another in a particular set of
 34 environmental conditions. Different species of large herbivores may use a range of different
 35 behaviours to enhance their foraging efficiency (Bailey et al. 1996; Beekman & Prins 1989).

36 Finding a forage patch in a heterogeneous landscape where patches differ in suitability poses a
 37 challenge, especially if individuals have no a priori knowledge of the location of the most
 38 suitable patches (Bailey et al. 1996; Prins 1996; Senft et al. 1987). Large herbivores may gain a
 39 priori knowledge using memory (from a previous visit to the patch) (Brooks & Harris 2008;
 40 Dumont & Petit 1998; Edwards et al. 1996; Fortin 2003) or through visual cues (Edwards et al.
 41 1997; Howery et al. 2000; Renken et al. 2008). If the forage resource is complex (e.g., when
 42 forage patches are not well defined), or the distribution of the forage patches are likely to change
 43 continuously (e.g., when a patch is grazed or the grass sward becomes unpalatable due to
 44 ageing), then recalling the location of forage patches may be of limited value (Edwards et al.
 45 1997). In such situations, heterogeneous in both space and time, the ability to recognise and
 46 assess different forage patches at a distance through visual cues, would promote foraging success
 47 (Edwards et al. 1997). An alternative behaviour to the use of visual cues would be adaptive
 48 search/movement behaviour (Benhamou & Collet 2015; Martin et al. 2015). In heterogeneous
 49 environments, adaptive movement, at different scales of step lengths and directionality, e.g., a
 50 small-scale area-restricted search (within patches) mixed with a set of large more directional

51 movements (between patches), can be a **more optimal** search approach (Benhamou 2007) 
 52 especially when the forage resource is complex and in constant fluctuation.
 53 
 54  A number of studies have linked movement patterns to the use of memory (Brooks & Harris
 55 2008; Ramos-Fernandez et al. 2003),  or use of visual cues at a finer scale (e.g. bite, feeding
 56 station and food patch scale) (Howery et al. 2000; Laca 1998) by large herbivores to locate or
 57 revisit suitable forage patches. **But** it is not clear whether large herbivores use visual cues to find
 58 forage patches at a broader habitat patch scale.  We tested whether three grazing herbivore
 59 species,  **with a variety of traits (body size,** feeding type, digestive strategies and muzzle width) 
 60 use visual cues when foraging at the habitat patch scale. **By habitat patch scale we mean** a daily
 61 range at a 10  hour temporal scale while feeding, walking, drinking,  resting  with movement 
 62 within and between habitats, **a scale adapted from Owen-Smith (2010) and Bailey et al., (1996).**
 63 We did this by developing and testing predictions based on directionality and **step length**  under
 64 three patch visibility classes (Table 1). In particular, we expected  directional movements with
 65 longer step lengths when animals moved to visible patches and less directional movements with
 66 shorter step lengths to non-visible patches. Demonstrating a difference  **between** movement
 67 behaviour  **in response to visible versus invisible** habitat patches, would enable an understanding
 68 of the importance of visual cues to different large herbivore species when moving between
 69 patches at a habitat patch scale.

70

71 METHODS

72 *Study area*

Mkambati Nature Reserve is a 77 km² provincial nature reserve situated on the east coast of the Eastern Cape Province, South Africa (31°13'-31°20'S and 29°55'-30°04'E). The climate is mild sub-tropical with a relatively high humidity (de Villiers & Costello 2013). The coastal location, adjacent to the warm Agulhas Current, causes minimal variation in mean daily temperatures (18 °C winter and 22 °C summer) (de Villiers & Costello 2013). The average rainfall is 1 200 mm, with most precipitation in spring and summer (September -February) (Shackleton 1990). The high rainfall, mild temperatures, and presence of abundant streams and wetlands provide a landscape that is not water limited in any season. Forests occur in small patches (mostly in fire refuge areas), and wetland habitats are abundant. More than 80% of Mkambati consists of Pondoland–Natal Sandstone Coastal Sourveld grassland (Mucina et al. 2006). Mkambati contains a range of large herbivore species, but no large predators (Venter et al. 2014b).

The grassland is considered to be nutrient poor (Shackleton et al. 1991; Shackleton & Mentis 1992). Grassland fire stimulates temporary regrowth high in crude protein (8.6% compared to 4.6%, in older grassland), phosphorus concentrations (0.1% compared to 0.05%, in older grassland) and dry matter digestibility (38.6% compared to 27.1%, in older grassland) (Shackleton 1989). Nutrient concentrations remain elevated for up to 6 months post-burn, after which they are comparable to surrounding, unburnt grassland (Shackleton & Mentis 1992). Frequent fires cause a landscape mosaic of nutrient-rich burnt patches within a matrix of older, moribund grassland. This landscape is thus continuously changing due to new fires that are set and the maturing process of the grassland. Recalling the location of grazing forage patches (using memory) would in this case be of limited value which enabled us to test predictions of movement behaviour relative to visibility of forage patches.

96

97 **Data collection**



98 Five plains zebra (*Equus burchelli*)(4 female and 1 male), six red hartebeest (*Alcelaphus*
 99 *buselaphus* subspecies *camaa*)(5 females and 1 male) and five eland (*Tragelaphus oryx*)(3
 100 females and 2 males) were fitted with GPS-UHF collars (Africa Wildlife Tracking CC., Pretoria,
 101 RSA) between September 2008 and July 2012. These species represented a range of intrinsic
 102 constraints which could potentially influence their foraging strategies and subsequent search
 103 movement behaviour (Venter & Kalule-Sabiti 2016; Venter et al. 2014a; Venter et al. 2015). All
 104 animals were darted by an experienced wildlife veterinarian from a Robinson 44 helicopter. The
 105 work was approved by, and conducted in strict accordance with the recommendations in the
 106 approved standard protocols of the Animal Ethics Sub-committee of the University of KwaZulu-
 107 Natal (Approval number 012/09/Animal). All field work was conducted by, or under the
 108 supervision of the first author, while he was a staff member of the Eastern Cape Parks and
 109 Tourism Agency, as part of the operational activities of the appointed management authority of
 110 Mkambati (Eastern Cape Parks and Tourism Agency Act no. 2 of 2010, Eastern Cape Province,
 111 South Africa). The zebra and red hartebeest were in separate harems or herds when they were
 112 collared, but some eland (2 females) were in the same herd. The collars were set to take a GPS
 113 reading every 30 min, and data were downloaded via UHF radio signal. The collars remained
 114 functional between 4 and 16 months depending on various factors, including loss of animals to
 115 poaching, natural mortality, or malfunctioning. Data downloaded from the collars were
 116 converted to geographical information system (GIS) format and sections of the data sets with
 117 missing values were removed and not used in the analysis.

118

119 Step lengths were calculated for each “walk” using the Hawth's Analysis Tools extension (Beyer
 120 2007) to ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research
 121 Institute). “Walks” were extracted per species (Eland $n = 312$; Red hartebeest $n = 309$; Plains
 122 zebra $n = 279$). A “walk” consisted of 20 consecutive steps which constituted 10 hours of
 123 movement behaviour during daylight hours (6:00AM to 6:00PM) (Figure 1). Ten hours of
 124 movement represented movement between patches at a landscape scale as adapted from (Bailey
 125 et al. 1996) and (Owen-Smith et al. 2010). To confirm whether ten hours of movement were
 126 indeed within a realistic distance range for the landscape scale in **ours** situation, we **calculated**
 127 **and** compared the mean distance between patches **as well as** mean animal “walk” distances **per**
 128 species. Starting points were randomly selected, with the visibility from the starting point of each
 129 walk being determined using the “viewshed analysis tool” in the Spatial Analyst extension of
 130 ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research
 131 Institute). This resulted in a grid map (raster) layer that indicated all areas that were visible and
 132 not visible to the animal from that specific point at its shoulder height (female shoulder height:
 133 eland $\bar{x} = 1500$ mm (Posselt 1963); red hartebeest $\bar{x} = 1250$ mm (Stuart & Stuart 2007); plains
 134 zebra $\bar{x} = 1338$ mm (Skinner & Chimimba 2005)) (Figure 1). The end point was **classified** as the
 135 patch where the animal spent the majority ($\geq 50\%$) of the final 3 h (6 locations) of the “walk”
 136 (Figure 1). All patches in the landscape were allocated a unique number, and classified as either
 137 burnt grassland (fire patches) or unburnt grassland (unburnt patches) (Figure 1). When an
 138 animal, at the end of a “walk”, ended up in, a) a better forage patch we considered the movement
 139 as successful; b) the same we considered it as no change; and c) worse patch we considered it as
 140 unsuccessful. Forage quality was better in recently burnt (< 6 months post fire) grassland, see
 141 Shackleton & Mentis (1992), compared to older grassland.

142

143 The location of the fire patches were recorded by field rangers between January 2007 and July
 144 2012, and later digitally defined on maps using ArcGIS. Each GPS locality along a “walk” was
 145 linked to a patch classification using the Spatial Analyst extension of ArcGIS (ArcGIS Desktop:
 146 Release 10. Redlands, CA: Environmental Systems Research Institute). All unburnt areas (areas
 147 that were never noted as burnt between January 2007 and July 2012) were considered as one
 148 unburnt patch, and was given the same unique identification number. The “walks” were then
 149 classified into three different visibility classes, a movement: (a) to within the same patch where
 150 the departure point is located; (b) to a new patch that was visible from the departure point; and
 151 (c) to a new patch not visible from the departure point. All step lengths < 6 m were excluded
 152 during analysis in order to remove non-movements, as well as false movements due to GPS-
 153 error.

154

155 **Data analysis**

156 We tested whether there was excessive variability amongst individual animal step lengths, which
 157 could potentially influence the step length models, by comparing mean walk distance for
 158 different species and visibility classes using separate ANOVA's. This test was done using IBM
 159 Corp. Released 2014. IBM SPSS Statistics for Windows, Version 23.0. Armonk, NY.

160 We used the Rayleigh test of circular uniformity from CircStats package in R (R-Development-
 161 Core-Team 2011) to calculate the mean resultant length r for each individual “walk”. This
 162 parameter r provided a measure of concentration of turning angles that falls in the interval $[0, 1]$
 163 (Duffy et al. 2011). When r is close to 1, data are highly concentrated in one direction, and when

164 it is close to 0 data are widely dispersed (Duffy et al. 2011). Rayleigh test provides p-values
 165 associated with r to test whether it was reasonable to reject angle uniformity. When $r \geq 0.5$ and
 166 the p -value indicated significance ($p < 0.05$), walks were considered to be concentrated in one
 167 direction (directional).

168 We used a linear mixed model (LMM) to assess the effect of a number of factors on mean step
 169 length per “walk”. The fixed effects were species, visibility class and search outcome (success).
 170 The random effect was individual animal. Pairwise comparisons was done using a Bonferroni
 171 test. This test was done using IBM Corp. Released 2014. IBM SPSS Statistics for Windows,
 172 Version 23.0. Armonk, NY.

173

















174 RESULTS

175 A visual comparison of an error bar plot confirmed that the mean distance between patches \bar{x}
 176 = $5276 \pm 2846 SD$ as well as mean animal “walk” distances for the different species (Eland \bar{x}
 177 = $3529 \pm 1711 SD$; Red hartebeest $\bar{x} = 2664 \pm 2242 SD$; Zebra $\bar{x} = 5020 \pm 3866 SD$) was within a
 178 realistic distance range, reflecting movements at a landscape scale, as adapted from (Bailey et al.
 179 1996; Owen-Smith et al. 2010) (Figure 2).

180




181 A low proportion of walks for eland (7% to not visible; 0% to visible; and 5% within visible) and
 182 hartebeest (6% to not visible; 3% to visible; and 8% within visible) in each visibility class were
 183 directional ($P < 0.05$) (Figure 3). Zebra had a higher proportion of directional walks (12% to not
 184 visible; 17% to visible; and 17% within visible) compared to eland and hartebeest (Figure 3).

185


186  Linear mixed model  with success, visibility class and species as fixed effects and animal ID as a
187 random effect suggests that all fixed effects are significant
188 (p -values 0.045, < 0.0005  and 0.005  respectively). The Wald test suggests that there is a
189 significant variation in step length between individuals ($P = 0.026$)  and therefore  animal ID was
190 kept in the model as a random factor. For all three species, step lengths in the “within visible” 
191 and “to visible” classes were fairly similar, but the step lengths for both these categories were
192 significantly shorter than step lengths to “not visible” classes (Table 2  and Figure 4). Zebra had 
193 significantly longer step lengths  compared to red hartebeest , and the difference between eland 
194 and hartebeest  were not significant (Table 2  and Figure 4). With search movement outcome  the
195 difference in step length was not significant (Table 2  and Figure 4).



196

197 DISCUSSION










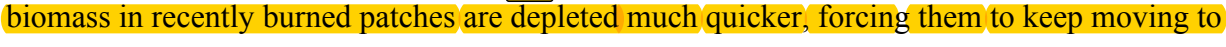
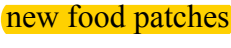



198 In our study we observed little directional movement when animals moved to visible patches 
199 which supports a view that large herbivores  don't exclusively rely on visual cues when moving
200 to search for patches at a habitat patch scale. Our results support  the simulations by Benhamou
201 (2007) which showed that, in patchy environments adaptive movements combining small-scale
202 area-restricted searches (within patches) and large movements between patches, were used as an
203 optimal strategy to search for habitat patches.



204





205 During fine scale search modes at the bite, feeding station and food patch scale (Owen-Smith et
206 al. 2010)  animals would make use of visual and olfactory cues to find suitable forage items


207 (Edwards et al. 1997; Laca 1998). At  courser scales (e.g. habitat patch scale), herbivores would
 208 randomly move, with an increased intensity (larger step lengths) until they are able to detect
 209 more suitable forage (at the finer scale). The search patterns displayed by our study animals thus
 210 indicate an adaption of their movement to the patchiness of the environment rather than long and
 211 directional step lengths, as expected if visual cues (or the lack thereof) had played a major role
 212 (Benhamou 2007; Benhamou & Collet 2015). Adaptations of animal movement behaviour to
 213 patchiness at the habitat scale,  was observed elsewhere (de Knegt et al. 2007; Duffy et al. 2011;
 214 Viswanathan et al. 1999), and is confirmed by this study.







215

216  Zebra used larger step lengths,  had more directional walks (although still a small proportion of
 217  their walks), compared to the eland and hartebeest. These variations could be linked to
 218 differences in the species intrinsic traits, such as digestive system, muzzle width and body weight
 219 (Prins & Van Langevelde 2008; Senft et al. 1987). Zebra, a non-ruminant,  are less efficient at
 220  digesting food,  and  have to maintain a higher intake-rate to maintain  their energy requirements
 221 (Bell 1971; Demment & Soest 1985; Illius & Gordon 1992). This should cause them to move
 222 more frequently from one food patch to another as food patches are depleted due to grazing (Bell
 223 1971). In addition, they have a wider muzzle than the two ruminant species which makes them
 224 capable of using very short grass swards (which are common in recently burned grass patches).
 225 Zebra have been shown to prefer newly burned grassland (Sensenig et al. 2010), but  the lower
 226  biomass in recently burned patches are depleted much quicker, forcing them to keep moving to
 227  new food patches (Venter et al. 2014a). In addition, higher directionality of zebra movement
 228  could indicate that they  may be more efficient in finding new forage patches. Both these factors
 229  would cause higher movement intensity and complexity, as we observed with this species. Red

 230 hartebeest **compared to zebra and eland** had the shortest step lengths. Red hartebeest is an
 231 example of a concentrate selector; its skull morphology is specially adapted to be very selective
 232 at times when good forage is scarce (Schuette et al. 1998). In areas with much moribund
 233 vegetation, grazing ruminants such as the red hartebeest face particular constraints because
 234 nearly all vegetation biomass has a low quality, which reduces food intake rates (Drescher et al.
 235 2006a; Drescher et al. 2006b; van Langevelde et al. 2008). By being more selective, hartebeest
 236 would probably need to have more spatially complex movement scales. Red hartebeest, being the
 237 smaller ruminant (compared to eland), needing less, but better quality, forage to meet their
 238 nutritional and energy requirements (Demment & Soest 1985; Illius & Gordon 1992), used a
 239 strategy where they foraged using smaller and less directional steps  whether they were moving
 240 within patches or to unseen patches. They thus make use of less suitable patches **as well as more**
 241 **nutritious patches** in a similar way.  This behaviour relates to previous observations in the study
 242 area where red hartebeest moved  **slower, and spend** more time in less nutritious patches
 243  **compared to** zebra (Venter et al. 2014a)

244


 245 Eland are one of the larger African ruminant species and are considered to be selective feeders
 246 (which includes browse) that requires  a diet of high nutritive value, low fibre and high protein
 247 content (Arman & Hopcraft 1975). In Mkambati they primarily use browse and make little use of
 248 grass as forage (Venter & Kalule-Sabiti 2016). They also have a relatively small rumen in
 249 relation to their body size and retain food in the rumen for a shorter time  (**comparable** to cattle),
 250  **which allows** for a greater  **appetite** (compared to hartebeest) (Arman & Hopcraft 1975). It is,
 251 therefore, surprising that they showed shorter step lengths compared to zebra which is
 252  **comparable to eland even though they** are non-ruminants and smaller  **on** body size, see Demment

253 & Soest (1985). This behaviour could possibly be linked to their diet, as being able to browse
 254 they can overcome the challenge of dealing with a landscape of nutrient poor moribund grassland
 255 by eating forbs and trees (when available). Forbs are common, especially in newly burned
 256 patches in Mkambati (Shackleton 1989). In the case with trees, which is a resource that does not
 257 change as continuously burnt grassland, eland should be able to return to browsing patches by
 258 using memory. This could possibly explain the less complex movement behaviour. However one
 259 would have expected more directional movements if that were the case.

260

261 Our study provides evidence that large grazers do not exclusively rely on visual cues when
 262 foraging at a habitat patch scale, but rather adapt their search mode according to habitat or forage
 263 heterogeneity and quality. The animals used this adaptive approach to foraging to cope with
 264 continuously changing forage conditions. In addition it shows that species traits such as body
 265 size, feeding type, digestive strategy and muzzle width do play a role in how these animals
 266 search for forage.

267

268 ACKNOWLEDGEMENTS

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 270 from Pennsylvania State University, Parks and People program for providing field assistance.

271

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390

Figure 1

An 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 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.

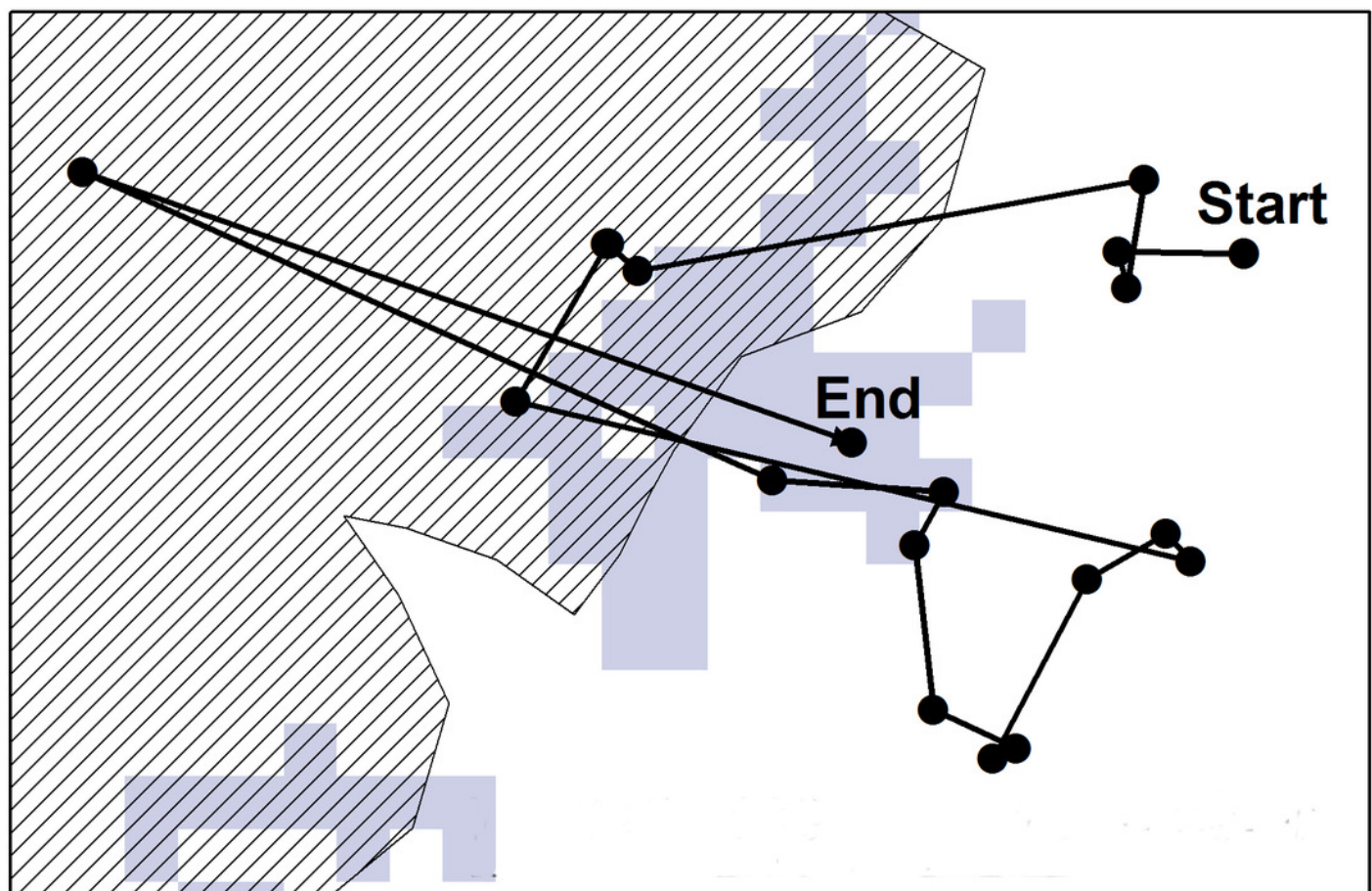


Figure 2

The mean distance between patches as well as mean animal “walk” distances per species.

The mean distance between patches as well as mean animal “walk” distances per species indicates that ten hours of movement are within a realistic distance range. Error bars indicate \pm SD.

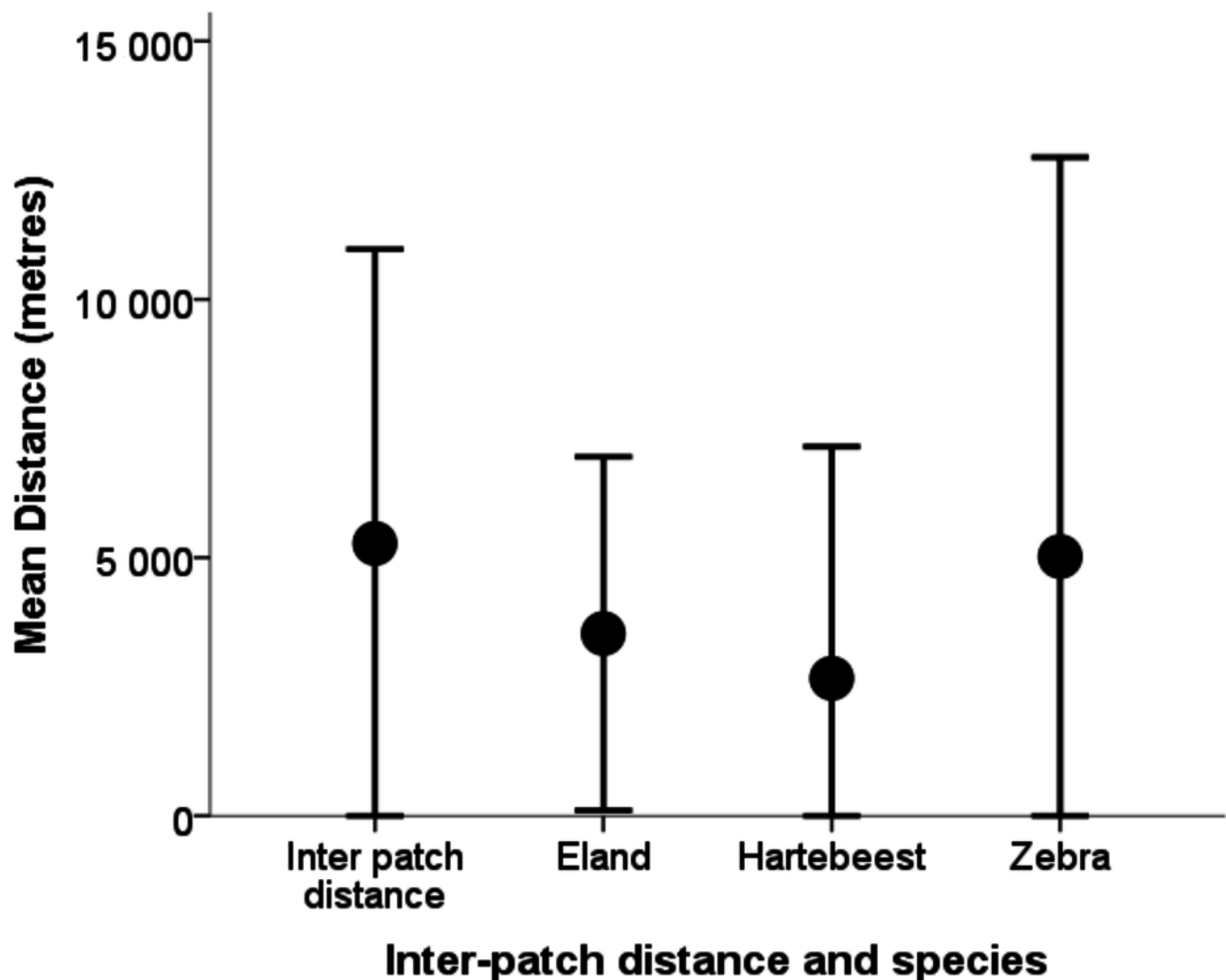


Figure 3

The effect of visibility classes on the directionality of “walks” of the zebra, red hartebeest and eland studied in Mkambati Nature Reserve.

Visibility classes were A) Eland to not visible; B) Eland to visible; C) Eland within visible; D) Hartebeest to not visible; E) Hartebeest to visible; F) Hartebeest within visible; G) Zebra to not visible; H) Zebra to visible; and I) Zebra within visible. When r and the value indicated significance (as indicated by the reference line), walks were considered as concentrated in one direction (directional) (Duffy et al. 2011).



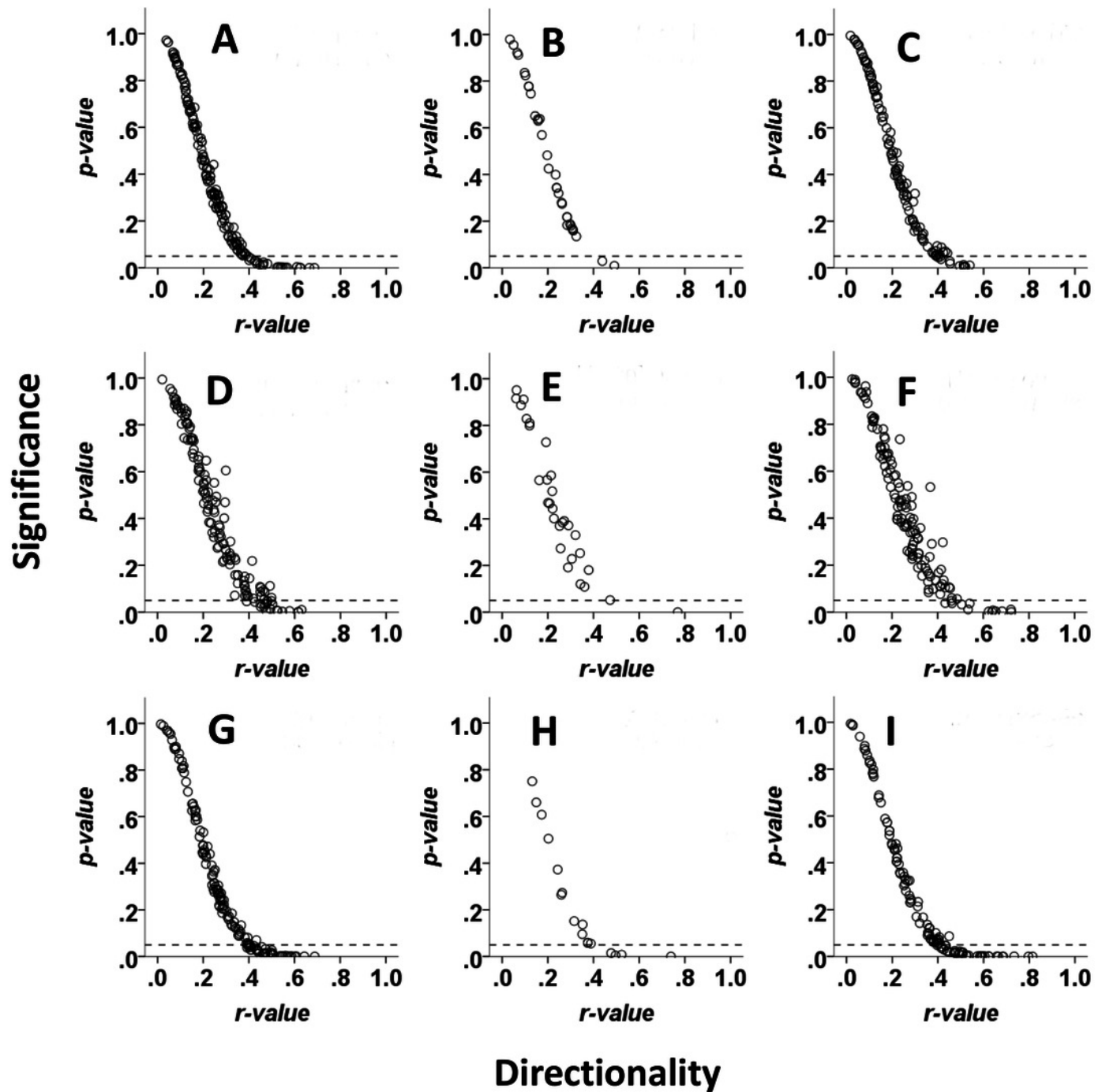


Figure 4

Step mean length of search movement outcomes and patch visibility classes

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

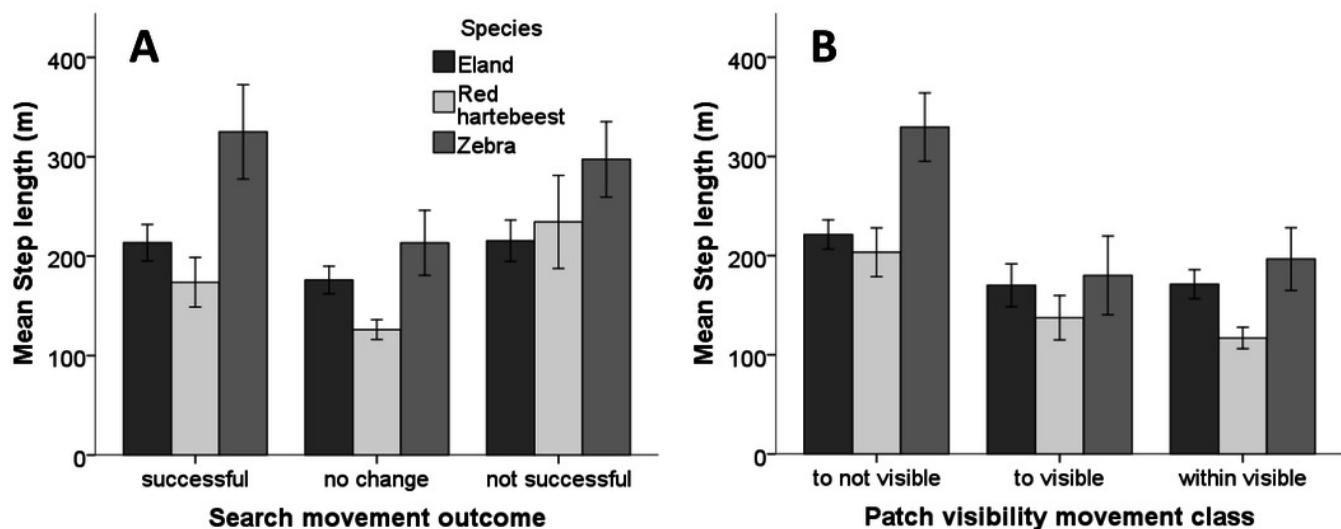



Table 1(on next page)

Predictions and observations in assessing whether visual cues are used in habitat scale movement/search strategies of zebra, red hartebeest and eland across three different patch visibility classes

Visibility class	Directionality		Step length	
	Predicted	Observed	Predicted	Observed
Movement within a visible patch	Less directional	Not directional	Short, variable length	Short, variable length
Movement to visible patch	Very directional	Not directional	Long, constant length	Short, variable length
Movement to a non-visible patch	Very non-directional	Not directional	Variable length	Long, variable length

Table 2 (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 vs Zebra	-94.835	25.068	16.497	0.005**
<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
<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

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