

1 **What you see is where you go: visibility influences movement decisions of a forest bird navigating**
2 **a 3D structured matrix**

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32 **Keywords**

33 Animal movement behaviour; viewshed analysis; perceptual range; step selection function; habitat

34 selection; LiDAR

35 **Abstract**

36 Animal spatial behaviour is often presumed to reflect responses to visual cues. However, inference of
37 behaviour in relation to the environment is challenged by the lack of objective methods to identify the
38 information that effectively is available to an animal from a given location. In general, animals are
39 assumed to have unconstrained information on the environment within a detection circle of a certain
40 radius (the perceptual range; PR). However, visual cues are only available up to the first physical
41 obstruction within an animal's PR, making information availability a function of an animal's location
42 within the physical environment (the effective visual perceptual range; EVPR). By using LiDAR data and
43 viewshed analysis, we model forest birds' EVPRs at each step along a movement path. We found that
44 the EVPR was on average 0.063% that of an unconstrained PR and, by applying a step-selection
45 analysis, that individuals are 1.55 times more likely to move to a tree within their EVPR than to an
46 equivalent tree outside it. This demonstrates that behavioural choices can be substantially impacted
47 by the characteristics of an individual's EVPR and highlights that inferences made from movement
48 data may be improved by accounting for the EVPR.

49

50 **Introduction**

51 Understanding the relationships between an animal's behaviour and the environment it
52 occupies is central to a broad range of ecological and evolutionary questions of both fundamental and
53 applied significance[1, 2]. Gaining insight into these relationships is frequently achieved either by using
54 a behavioural response to identify influential environmental cues or by using a cue that is known to
55 influence behaviour to quantify the response. For example, spatial characteristics of movement
56 trajectories are used to statistically identify factors that influence movement decisions[3, 4], or to
57 determine from what distance animals start moving towards a known attractor[5]. However, correct
58 inference of behaviour in relation to the environment is challenged by the lack of objective methods
59 to identify what information effectively is available to an animal at a given location[6].

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61 The information available to an individual from a specific location is determined by multiple
62 factors. First of all, the range over which information can be acquired is constrained by the
63 physiological properties of an animal's sensory system (i.e., its perceptual range [PR]; table 1). For
64 example, the distance over which an animal can discriminate a visual cue against background noise is
65 determined by the photoreceptor density of its eyes[7]. These data are lacking for most species
66 making objective quantification of a PR generally impossible. The response distance of an animal to a
67 known attractor (i.e., the functional perceptual range, FPR, table 1) is therefore often used as a proxy
68 in ecological research[8, 9]. However, even within an animal's FPR, visual information can be

69 inaccessible due to the physical structure of the environment (the effective visual perceptual range
70 [EVPR]; table 1). Hence, when the structure of the environment is spatially variable, an animal's EVPR
71 will be a dynamic property of its location. For example, an animal's EVPR will change drastically when
72 it moves from a valley up a mountain, or from a forest patch into a meadow.

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74 Not accounting for the EVPR carries the risk of making biased inferences. For instance, an
75 animal's behavioural decision may appear maladaptive, while in reality it acted optimally given the
76 information that it could effectively perceive from that location. For example, a dispersing individual
77 may have selected a habitat patch that is of modest quality compared to other similarly close patches.
78 However, that patch was perhaps the best quality of those visible to the individual. Recent analysis is
79 indicative of this effect influencing the patterns of patch occupancy observed in neotropical
80 primates[10]

81 Given its potential importance, it is surprising that, in the context of animal movement, few attempts
82 have been made to explicitly account for the effect of the environment on visual information
83 availability, neither in empirical research, nor in modelling (but see[10, 11]). A possible explanation
84 may be the limited availability of appropriate data and tools[12]. Light transmission through air is
85 unconstrained over distances usually considered in ecological research[7] making visual cues available
86 to an animal in every viewing direction up to the first physical obstruction. An animal's EVPR, hence,
87 can be modelled in function of a 3D model of the physical environment (a so called 'viewshed')[12,
88 13].

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90 While the use of viewsheds is beginning to gain some traction in ecological research[e.g.,14, 15], they
91 have not yet been used to determine the degree to which behavioural choices are constrained to
92 those options present within an EVPR. Here we use a unique set of movement steps of the placid
93 greenbul *Phyllastrephus placidus*, an Afrotropical forest bird, to test our hypothesis that individuals
94 navigating an agricultural matrix are constrained in selecting trees that, from our viewshed analyses,
95 we infer that they can see (i.e., are within their EVPR).

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103 **Table 1.**

104 Definitions of key terms and their abbreviations

| | Definition |
|---|--|
| Perceptual range (PR) | The range over which an animal is physiologically capable to perceive a visual cue |
| Effective visual perceptual range (EVPR) | The visual perceptual space available to an animal given the 3D structure of the environment |
| Functional perceptual range (FPR) | The range over which an animal tends to behaviourally respond to a visual cue |

105

106 **Methods**

107 Greenbul behaviour

108 Behavioural data were represented by visually confirmed discrete movement steps of 27 adult
109 greenbuls (e.g., a greenbul flying from one tree to the next) navigating an unfamiliar matrix. Individuals
110 were captured in forest fragments, radio-tagged and released in an agricultural matrix within homing
111 distance to their territories. Experiments were conducted in 2009-2010 (for details see[3]). Because
112 animals outside their home range and native habitat are likely to be deprived of social information
113 and memory-based spatial reference, we assume behavioural decisions to primarily reflect the
114 response to visual cues.

115

116 The matrix

117 Greenbul movement behaviour was documented in an agricultural matrix in the Taita Hills (SE Kenya).
118 This is a small-holder agricultural landscape characterised by plots of crops and scattered trees [16]
119 and a pronounced topography (figure 1).

120 The 3D structure of the matrix was modelled at 1m resolution (digital surface model [DSM] and canopy
121 height model [CHM]) using airborne LiDAR obtained in 2013 (for details see[17] and appendix A1).
122 Trees in the matrix were uniquely identified and crowns delineated based on the CHM using the
123 itcLiDAR function in the itcSegment package [18] (for details see appendix A2).

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126 **Figure 1.** The agricultural matrix greenbuls had to navigate while returning to their territories in forest
127 fragments (Photo: J. Aben, 2009).

128

129 Selection of steps

130 The package amt[19] was used to transform the movement data into a track object, where consecutive
131 locations are represented in consecutive steps. Only steps that were of length >10m and ended in a
132 tree were retained and paired with 300 random steps to form a stratum. Random steps were
133 generated using the function random_steps, with turning angles and step lengths sampled from a von
134 Mises distribution (centred on the direction of the preceding step) and Gamma distribution,
135 respectively. Both distributions were parameterized by fitting the corresponding distribution to the
136 observed data (appendix A3). Finally, only those strata with at least 15 random steps that ended in a
137 unique tree were retained, yielding 369 steps for 27 individuals (range 4 – 38 steps). If more than 15
138 random steps were available, 15 steps were selected randomly.

139

140 Viewsheds

141 For each location, viewsheds were modelled as a function of the DSM using the r.viewshed command
142 in GRASS-GIS[20] considering all possible viewing directions. A z-coordinate (observer_height
143 parameter) was derived from the CHM (represented either by the mean of the CHM within a 2m buffer
144 or calculated relative to the height of a tree). Search radius (i.e., viewshed radius) was set to 200m
145 just over the maximum step length in the data. To prevent a bird's visibility being blocked by the tree
146 it is in, unconstrained visibility was assumed within a radius of 5m. This was modelled by detracting

147 values from the CHM from those in the DSM raster within that 5m radius prior to modelling the
148 viewshed.

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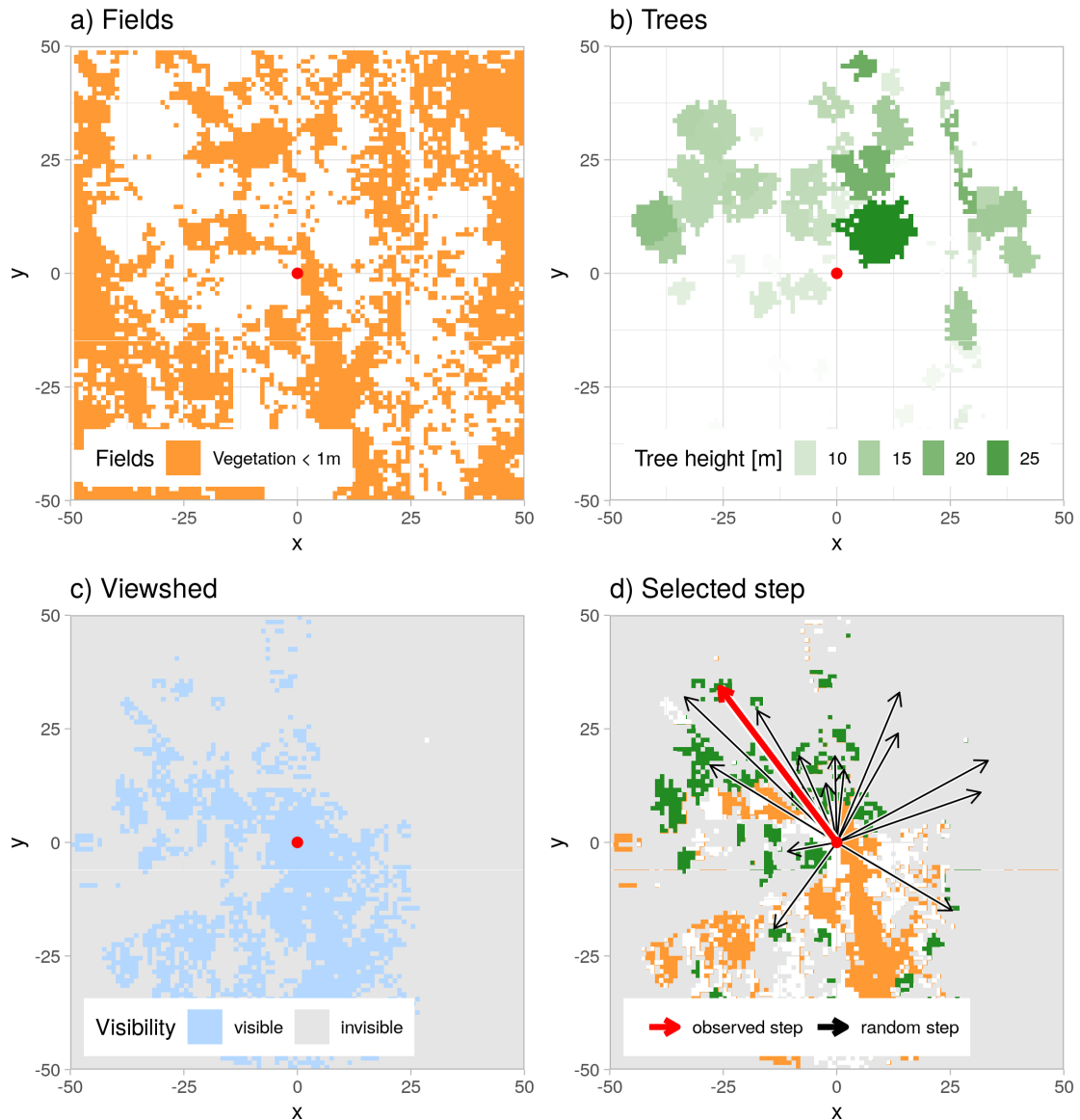
150 Step selection model

151 To infer the effect of visibility on tree selection by moving greenbuls, we modelled selection – the
152 response being whether a step was observed or simulated – while controlling for observed movement
153 patterns (i.e., directional autocorrelation and step lengths) and the potentially confounding effects of
154 percentage of field (defined as CHM < 1m) between the bird and a tree and tree height, using
155 integrated step selection functions (iSSF[21]) (figure 2, appendix A4).

156 Tree visibility was determined by intersecting the tree crowns with the corresponding viewshed raster
157 resulting in the binary indicator variable `in_viewshed`. We included log of the step length and the
158 cosine of turning angles, as these were sampled from a statistical distribution[21, 22]. The variables
159 percentage of field and tree height were standardised to have a mean of zero and an SD of 1 at the
160 stratum level (i.e., an observed step paired with 15 random steps). We used a Poisson regression with
161 random effects on individual strata with a fixed variance of 1e4 to be able to account for variation in
162 selection among individuals [23]. A Poisson regression specified in such a way, is likelihood equivalent
163 to a conditional logistic regression used in standard SSF [23]. We included a random coefficient for
164 percentage of field and tree height, but not for `in_viewshed` because individuals belonging to the same
165 species are likely to have similar visual acuity. We fitted the model using the package `glmmTMB`[24].
166 All analyses were carried out using programme R[25].

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170 **Figure 2.**

171 Graphical overview of the analytical approach. A greenbul selects one tree to move to next from its
 172 current position (red dot; all panels). The decision on which tree to move to may be influenced by the
 173 percentage of field to cross (panel a), on tree height (panel b), and if a tree is visible (panel c; viewshed
 174 was truncated at 65 m for illustration). To test our hypothesis, a step selection function is fitted to
 175 compare the covariates between the observed step and the alternative steps (panel d).

176

177 **Results**

178 The EVPR (area of viewshed) of greenbuls tracked in the matrix was on average 0.063% that of an
 179 unconstrained PR (range 7.166e-05 – 0.297%).

180 While controlling for the effects of tree height, percentage of field and movement, we find that visible
181 trees are substantially more likely to be selected by a moving greenbul (relative selection strength =
182 1.55) (table 2). In addition, greenbuls prefer tall trees over lower ones to move to.

183

184 **Table 2.** Estimated coefficients of the integrated step selection model. Effects with a p-value <0.05
185 were considered as significant.

| Variable | Estimate | SE | p-value |
|------------------|----------|-------|---------|
| tree height | 0.275 | 0.055 | < 0.001 |
| percent field | -0.100 | 0.066 | 0.130 |
| in_viewshed | 0.440 | 0.178 | 0.013 |
| log(step length) | -0.417 | 0.119 | < 0.001 |
| cos(turn angle) | 0.625 | 0.103 | < 0.001 |

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188 Discussion

189 Greenbuls returning to their territories after translocation had to navigate a heterogeneous matrix in
190 a topographically complex terrain. Their movement typically consisted of short flights interspersed
191 with pauses in vegetation[3]. Visual observations indicated that flights were generally straight,
192 suggesting that greenbuls typically decided where to go from one location and did not update their
193 decision while in flight. By modelling viewsheds from these locations and quantifying visibility of
194 potential target trees, we were able to demonstrate that, indeed, greenbul movement reflected
195 behavioural responses to information within their effective visual perceptual ranges; trees that were
196 within a greenbul's EVPR had a substantially higher probability to be chosen. Notably, while it is most
197 often the trees within the EVPR that are selected by individuals, there are still movement steps where
198 individuals move to a tree that is not. We suggest at least four potential reasons for this. Firstly,
199 because the LiDAR data we used is not fully 3D, modelled visibility is likely conservative compared to
200 what a greenbul could perceive in reality, which may result in a tree being wrongly classified as being
201 outside an individual's EVPR. Secondly, greenbul movement data was collected in 2009-2010, while
202 LiDAR data was obtained in 2013. While in this period there were virtually no changes in the trees
203 present in the landscape (only 1 tree visited by a bird in 2009-10 was no longer present in the LiDAR
204 data in 2013), changes in the matrix over that period of time may result in some viewsheds not
205 perfectly reflecting visibility as experienced by tracked greenbuls. Thirdly, in some cases birds may
206 update their choice on destination while in flight and new trees come into view. Finally, some decisions

207 may have been driven by information acquired through other sensory modalities (e.g., a bird avoiding
208 a road because of hearing vehicles).

209

210 Our finding that greenbuls selected relatively tall trees could reflect a positive association with
211 protection or food availability[26]. It could, however, also represent an adaptive behavioural strategy
212 in order to increase their EVPR. Field observations may support this hypothesis as, on multiple
213 occasions, greenbuls were found to move to the top of a tree prior to their next move. Vertical
214 movements influence an animal's EVPR and hence its ability to collect information[27]. By selecting
215 high viewing points in the matrix, greenbuls may increase navigation efficiency and reduce predation
216 risk due to more effective vigilance. Our results, hence, suggest that spatial behaviour may not only
217 be driven by a response to external information, but also by the need to collect it. Future studies that
218 seek to elucidate how the environment shapes spatial behaviour are encouraged to also consider the
219 role of visual information acquisition as a potential driver[28].

220

221 Animal movement is often presumed to reflect the behavioural response to environmental cues and
222 characteristics of movement trajectories are frequently used to quantify this relationship. Movement
223 steps considered in our study consisted of discrete flights from one location to the next and viewsheds
224 modelled from intermittent locations were found to correspond well to the operational scale of
225 decision-making. Movement steps typically considered in habitat selection analysis, however, reflect
226 the effective displacement of an individual over a given period of time [29] and locations may
227 therefore not correspond to the operational scale of decision-making limiting opportunities for
228 progress to be made by accounting for EVPR. Hence, the identification of the relevant scale of decision-
229 making should be a research priority. In concordance with our results, behavioural decisions are often
230 made by animals during pauses in the actual movement process[30]. The development and increased
231 availability of dedicated biologgers[31] may allow to statistically identify these pauses in movement
232 data allowing to develop more refined models of movement that account for sequentially updated
233 viewsheds along a movement trajectory.

234

235 Conclusion

236 Our key message, that individuals are more likely to move to desirable locations within a landscape
237 that they can see than to similarly desirable locations that they cannot see should probably not be
238 surprising! What is more surprising is that as far as we are aware it has not previously been
239 demonstrated. Furthermore, across the broad range of modelling approaches that are applied to
240 understand animal movement by analysing movement trajectories, we have found none that account

241 for an animal's EVPR. Not accounting for EVPR within movement modelling risks reducing our ability
242 to correctly infer behaviours and for some species and in some landscapes, this impact may be
243 substantial. Here we have introduced the effective visual perceptual range to movement modelling.
244 By gaining the necessary movement and environmental data to expand its use into habitat selection
245 analysis and predictive modelling we can improve predictions and make better management
246 recommendations.

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248 **Data accessibility**

249 The data and R code used for the statistical analysis is available at [32]

250

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