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A call for viewshed ecology : advancing our understanding of the ecology of information through viewshed analysis

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1 **A call for viewshed ecology: advancing our understanding of the ecology of information through**
2 **viewshed analysis**

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15

16 **Abstract**

17 1. There has been rapid increase of interest in the role that information acquisition plays in
18 ecological process and in shaping life histories and their evolution. Compared to auditory and
19 olfactory cues, the range at which visual cues are likely to be informative to animals is particularly
20 sensitive to the spatial structure of the environment. However, quantification of and accounting for
21 availability of visual information in fundamental and applied ecological research remains extremely
22 limited.

23

24 2. We argue that a comprehensive understanding of animal behaviour in a spatial context
25 would greatly benefit from objective quantification of the area an animal can potentially obtain
26 visual information from and therefore draw broad attention to viewshed analysis. This analysis
27 identifies all cells of a gridded surface that are connected by lines-of-sight to a viewpoint, hence,
28 providing information on how much of the environment surrounding a location can be seen given the
29 structure of the environment. Although heavily used in non-ecological disciplines including civil
30 planning and archaeology, viewshed analysis has seldom been applied in an ecological context.

31

32 3. Here, we highlight the opportunity to make use of viewshed approaches in conjunction with
33 three-dimensional remote sensing data and (3D) data from animal tracking to make major progress
34 in understanding how visual information influences animal spatial behaviour, ecology and evolution.

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38 Keywords: viewshed analysis; LiDAR; visual information; animal behaviour; visual ecology; distance
39 sampling; perceptual range; conservation planning

40

41 **Introduction**

42 The ecology of information (Schmidt *et al.* 2010) is a rapidly developing field that is producing
43 increased understanding of the role that information acquisition and use by individuals and groups
44 plays in a broad range of ecological processes. These include eavesdropping to avoiding predation
45 (Magrath *et al.* 2015), social foraging (Fernández-Juricic *et al.* 2004), location of and foraging on
46 resources in complex environments (Verdeny-Vilalta *et al.* 2015), individual movement decisions
47 (Strandburg-Peshkin *et al.* 2013), the use of social information in determining decisions related to
48 dispersal (Boulinier *et al.* 2008) and habitat choice (Forbes & Kaiser 1994, Doligez *et al.* 2002).
49 Information from the environment is acquired mainly through perception of visual, olfactory or
50 auditory cues. Vision is often of particular importance as it provides information of high precision (i.e.
51 ability to discriminate a signal from background noise) and accuracy (ability to locate a detected
52 signal in space) (Stevens 2013). For visual information to be transferred, sender and receiver need to
53 be directly linked in space which makes the range over which animals can obtain visual information
54 particularly sensitive to the spatial structure of the environment. However, accounting for the
55 availability of visual information in ecological research remains extremely limited, constraining our
56 ability to understand animal behaviour in a spatial context. For instance, an apparent suboptimal
57 movement decision of a forest bird may simply be attributable to the fact that a nearby forest
58 corridor was visually obscured by other land cover.

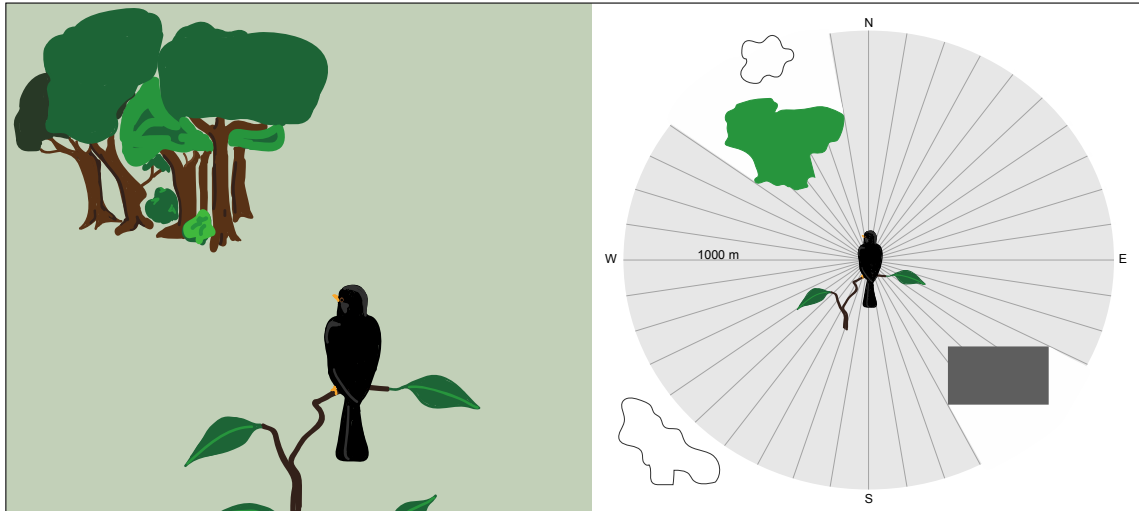
59 Here, we highlight the opportunity to make use of viewshed approaches in conjunction with three-
60 dimensional (x, y, z) remote sensing data (LiDAR) and data from animal tracking to advance
61 understanding of how visual information influences animal spatial behaviour, ecology and evolution.

62

63 *The dimension of an animal's visual space*

64 Regardless of the effects of the structural environment on the transmission of visual cues, availability
65 of visual information is determined by the range at which an animal can detect objects with sufficient
66 resolution to inform behavioural decisions. This distance is determined by the upper limit of an

67 animal's maximum spatial resolving power (visual acuity) which in turn is determined by eye-size
68 (Kiltie 2000) and the retinal ganglion cell density (Collin & Pettigrew 1989). Information on spatial
69 visual acuity and the size of a visual stimulus allows calculation of the threshold distance at which an
70 object can be resolved from the background. For instance, brown-headed cowbirds *Molothrus ater*
71 have an estimated spatial visual acuity of 5.1 cycles/degree which would allow them to resolve a 2m
72 high feature from a distance of 1012m (Blackwell *et al.* 2009). Hence, depending on the visual
73 stimulus of interest, information on an animal's visual acuity allows ecologists to estimate the
74 dimension of the visual space. In reality, this visual space is additionally structured by the
75 architecture of the animal's eye implying that its dimension at any one instance varies around an
76 animal's head (Martin 2007). Fig. 1 illustrates the potential visual space from a given location
77 considering all possible head angles of the animal (i.e. imagine an individual perched in a tree, taking
78 time to look in all directions prior to making a decision). In addition, external factors affecting visual
79 signal transmission or reception may modulate the relationship between spatial visual acuity and the
80 dimension of the visual space. For instance, an object that is barely detectable at a certain distance
81 at high light levels will only be detectable at a much shorter distance at lower light levels (Cronin
82 2014). This means that the dimension of an animal's visual space can vary in time (e.g. midday versus
83 dusk) and in space (e.g., open canopy versus closed canopy forest or shallow versus deeper water).
84 Despite these physical and external factors influencing the size of an animal's visual space, in many
85 situations, a visual threshold distance will surpass the scale of the structural environment making the
86 dimension of an animal's visual space primarily a function of its location in 3D space. For example,
87 imagine an individual of a bird species that has the ability to recognise suitable fruiting trees from up
88 to 1000m away. Perched on a tree, it will be able to acquire this visual information for up to 1000m if
89 it is looking over an open field of wheat. But, if there is a patch of woodland located within the field
90 at 500m, the visual information obtainable in that direction will be curtailed to 500m (Fig. 1).
91



92

93 **Figure 1.** Simplified graphical representation of the visual space, in this case of a blackbird *Turdus*
 94 *merula* perched atop of a tree with an assumed threshold distance of 1000m (grey circle). The
 95 blackbird's potential visual space is curtailed by a woodland patch to the NW (green), and a building
 96 (dark grey) to the SE. The white woodland patches outlined in grey are not visible to the blackbird -
 97 the one to the SW is located beyond the bird's threshold distance while visibility of the one to the
 98 NW is obstructed by a nearby patch in the same direction (see text for further explanation).

99

100 As information acquisition is key to individual fitness (McNamara & Dall 2010), an animal's spatial
 101 behaviour can be expected to be co-driven by the need to collect visual information from it's
 102 surroundings (i.e. optimizing the size of the visual space). Indeed, there are studies that provide
 103 evidence for this relationship. Animals may move vertically in order to collect visual information at
 104 larger distances (Dokter *et al.* 2013), choose territories offering good views such that they can be
 105 efficiently defended against rivals (Eason and Stamps 1992, 2001), or choose locations allowing good
 106 views of the surroundings to optimize anti-predatory vigilance (Krams 2001, Embar *et al.* 2011).

107 The other way around, an animal's spatial behaviour can also determine its visual exposure to
 108 potential viewers. In some cases, animals may select highly exposed locations allowing for visual
 109 signals to be optimally communicated to a targeted audience, for instance during behavioural

110 displays (Alonso *et al.* 2012), while in other cases, animals may prefer locations that offer high
111 degree of concealment to minimize predation risk (Kopp *et al.* 1998). Most likely, many of the
112 decisions an individual makes on location choice represent a trade-off between visibility and
113 concealment (Camp *et al.* 2012), with the balance between the two likely to be highly context
114 dependent. For example, we might anticipate that during the breeding season, when young require
115 high levels of resource provisioning, an adult bird may trade-off a degree of concealment in order to
116 increase access to visual information that results in a higher rate of resource acquisition.

117

118 Despite the potential strong influence of the interaction between location and visual information
119 acquisition on animal behaviour, few studies have addressed this. This may be explained by
120 challenges in quantifying what an animal can potential see or is visually exposed to in a structured
121 environment using traditional field methods – for instance, by visual estimation (Eason & Stamps
122 2001, van der Meer *et al.* 2013), photographing cover boards (Camp *et al.* 2012), or through
123 measurement of the distance and angle to obstruction of sightlines from the perspective of a prey
124 animal (Kopp *et al.* 1998). These approaches are limited in applicability by poor repeatability of
125 measurements and sampling inefficiency and also because the information they provide on a visual
126 space cannot straightforwardly be integrated with other spatially explicit data. However, a
127 confluence of technical advances in computational tools and remote sensing means that there are
128 now excellent opportunities to substantially advance beyond these field methods to provide high
129 resolution representations of an animal’s potential visual space and to thus begin to understand how
130 behavioural decisions and ecological and evolutionary processes and patterns relate to them.

131

132 *A call for ‘viewshed ecology’*

133 We argue that objective quantification of an animal’s potential visual space would strongly advance
134 our understanding of animal behaviour in a spatial context and draw attention to the opportunities
135 offered by “viewshed analysis”. A viewshed refers to the area in a spatial environment that is directly

136 visible from a particular location (Tandy 1967). This concept has been implemented in Geographic
137 Information System (GIS) software (ArcGIS, GRASS GIS) to calculate viewsheds across digital elevation
138 surfaces (hererafter “viewshed analysis”; see Chang 2006 for a useful introduction and Box 1 for
139 guidance). In a GIS, a viewshed is represented by all cells of a gridded surface that are connected by
140 lines-of-sight to the viewpoint. A viewshed, hence, provides information on how much of the
141 environment surrounding a location can be seen given the terrain. Further, viewshed analysis can be
142 used to quantify relative visibility of each cell in a landscape by determining how well it can be seen
143 from many viewpoint locations and generating what is termed, the cumulative viewshed (Fig. 2b)
144 (Wheatley 1995).

145

146 Viewshed analysis has been well developed for and heavily used in a range of disciplines, particularly
147 in civil planning and archaeology. In these disciplines, viewsheds have provided major gains in both
148 understanding and predictive capability. For example, viewshed analysis allowed archaeologists to
149 demonstrate that historical site-placement decisions were influenced by the degree to which a
150 location allowed man to control the surroundings visually (i.e. sites had significantly larger viewsheds
151 compared to random locations; Marsh & Schreiber 2015), or by the degree to which locations
152 allowed inter-visibility between sites (Wright *et al.* 2014). In the present, decisions on infrastructure
153 siting are also influenced by human visibility, and viewshed analysis, for instance, is used to either
154 minimize the visual impact of large infrastructure (Griffin *et al.* 2015), or to find building locations
155 that offer highly valued views to its future inhabitants (Alphan and Sonmez 2015). However, despite
156 the technical methods used to generate and analyse viewsheds maturing they have, to date, seen
157 very limited use in ecological research. Indeed, we have found just eight studies that applied
158 viewshed analysis in conjunction with ecological data (i.e. Camp *et al.* 1997, Aspbury & Gibson 2004,
159 Hopcraft *et al.* 2005, Alonso *et al.* 2012, Ransom *et al.* 2012, Loarie *et al.* 2013, Davies *et al.* 2016a,
160 Davies *et al.* 2016b), and a single methodological study (Olsoy *et al.* 2015).

161

162 Of these eight studies, however, only four applied viewshed analysis to explicitly consider visual
163 information acquisition: Camp *et al.* (1997) used viewsheds from golden eagle *Aquila chrysaetos*
164 nests to determine buffer zones where recreational use should be limited to minimize disturbance,
165 Ransom *et al.* (2012) used viewsheds from human observer locations to account for spatially
166 structured visibility and Aspbury & Gibson (2004) and Alonso *et al.* (2012) used viewsheds to explain
167 selection of lekking sites of ground-displaying birds in mountainous terrain. The latter two being the
168 only examples where animal visual acuity was taken into account for generating the viewsheds (i.e.
169 viewsheds were curtailed using threshold distances that were based on actual estimates of visual
170 acuity). The remaining studies, merely used viewshed analysis to derive a measure of structural
171 complexity of the environment (i.e. the size of the viewshed area was used as measure of vegetation
172 density) as an explanatory variable to analyse site selection and, as such, do not represent examples
173 of viewshed ecology.

174

175 Perhaps a major reason why viewshed approaches have not been more widely adopted by ecologists
176 is the challenge of obtaining appropriate high quality data on 3D landscape attributes. In comparison
177 to the questions civil planners and archaeologists address using viewshed analyses, ecologists will
178 often require substantially higher spatial and/or temporally resolved information to answer many of
179 the ecological questions that viewshed analysis can potentially inform. While an archaeologist asking
180 questions related to inter-visibility between archaeological sites can make good use of viewshed data
181 that is generated using a digital elevation model (DEM), an ecologist interested in the foraging
182 behaviour of a frugivorous bird across a landscape is likely to require 3D data on vegetation structure
183 in order to obtain relevant information on a location's viewshed.

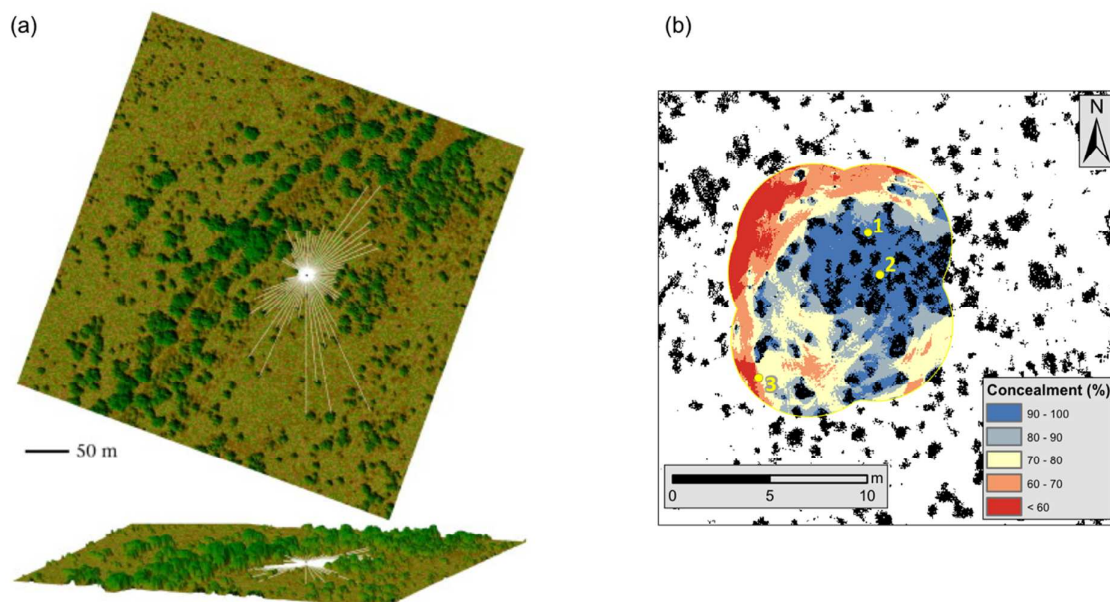
184

185 A model of 3D vegetation structure can be obtained by means of Light Detection and Ranging (LiDAR)
186 (Lefsky *et al.* 2002); an active remote sensing technique that measures the location of a structure
187 in 3D space based on return-times of laser pulses emitted from an airborne (i.e. airborne laser

188 scanning; ALS) or a ground-based platform (i.e. terrestrial laser scanning; TLS). Amongst the wide
 189 uptake of LiDAR in ecology (Davies & Asner 2014), four recent studies perfectly demonstrated the
 190 potential LiDAR offers for viewshed ecology: ALS was used by Loarie *et al.* (2013) to model lines-of-
 191 sight at a height of 1m above the ground (essentially a 2D viewshed) from lion *Panthera leo*
 192 relocation data (Fig. 2a), by Davies *et al.* (2016a) to model viewsheds from African wild dog *Lycaon*
 193 *pictus* den locations, and by Davies *et al.* (2016b) to model viewsheds both from lion kill sites and
 194 resting sites, while TLS was used by Olsoy *et al.* (2015) for mapping ‘fearscapes’ (i.e. spatial explicit
 195 representation of predation risk) thereby demonstrating the potential of the cumulative viewshed
 196 approach (Fig. 2b).

197

198



199

200 **Fig. 2.** Using (a) airborne LiDAR to model the size of the viewshed (here represented by lines-of-sight
 201 in white) for lion locations and (b) terrestrial LiDAR and the cumulative viewshed approach to
 202 quantify level of prey concealment. Hypothetical prey locations are indicated by the numbers 1, 2,
 203 and 3 and, in this example, individual 3 will be much more visible to predators than individuals 1 and
 204 2. Examples from Loarie *et al.* (2013) and Olsoy *et al.* (2015), respectively.

205

206 The nature of the LiDAR data will influence the type of ecological questions that can be addressed
207 using viewshed analysis. Typically, TLS has a much higher resolution than ALS, hence, it is better
208 suited for modelling realistic viewsheds in complex environments (e.g., within a woodland)
209 (Murgoitio *et al.* 2014). Also, by having the option to scan the environment horizontally, TLS provides
210 a method for modelling views from the opposing perspectives of both predator and prey (Olsoy *et al.*
211 2015). ALS, on the other hand, allows data collection over larger areas hence making it particularly
212 useful for integration with remotely collected animal movement data (see Strandburg-Peshkin *et al.*
213 2017 for an example) or for viewshed applications in landscape ecology (see below). When collected
214 at sufficiently high density (~ 170 pt/m²), ALS point clouds can also be used to model 3D structure of
215 individual vegetation strata which allows modeling viewsheds below forest canopies (Hamraz *et al.*
216 2017). ALS (both processed and as point clouds) is becoming freely available for a rapidly increasing
217 number of countries. However, usefulness of these data for viewshed ecology will depend on LiDAR
218 point density requirements and on the date of collection (i.e. vegetation structure may vary within
219 and between years). In this respect, the increased availability of unmanned aerial vehicles (UAVs)
220 offers ecologists an unprecedented opportunity to obtain LiDAR data at a user-defined scale and
221 point density (Anderson & Gaston 2013, Strandburg-Peshkin *et al.* 2017). In addition, technical
222 advances in animal tracking (Cagnacci *et al.* 2010, Kays *et al.* 2015, De Margerie *et al.* 2015) has
223 drastically increased the spatial resolution (also in 3D) of location data which means that the spatial
224 precision offered by LiDAR can increasingly be utilized to its full potential for viewshed ecology.

225

226 **Opportunities for viewshed ecology:**

227 The few recent applications of viewshed approaches in ecology begin to illustrate the potential of the
228 method in conjunction with emerging opportunities for data acquisition and modelling. We believe
229 that there is substantial potential for viewshed ecology to transform the quality of our understanding
230 regarding how individuals behave in order that they acquire visual information and also how they
231 may behave such as to increase or decrease the likelihood that they are seen (e.g., by a potential

232 mate, or a predator, respectively). There are also major opportunities for integrating these
233 approaches with methods used for modelling and predicting animal decisions and behaviours, (e.g.,
234 movement behaviours, foraging site selection) and for using the insights that these provide for
235 informing conservation and landscape management. We structure the next sections by first
236 considering how we can make progress by defining viewsheds from recorded animal locations and,
237 second, to make progress by applying viewshed analysis from multiple hypothetical locations to
238 define relative visibility of landscape features. Third, and finally, we consider how we can use
239 viewsheds to improve our interpretation of human visual sampling of ecological systems, recognizing
240 the fact that visual observations by humans will also be influenced by the environment.

241

242 *Viewsheds from actual viewpoints – defining the potential visual space*

243 This application lends itself to address questions that relate to (1) spatial behaviours that are
244 hypothesized to be related to the dimension of the visual space, or (2) to improve understanding of
245 variables (other than properties of the viewshed itself) driving spatial behaviours or selection of
246 habitat/resources or (3) that seek to model animal spatial behaviours realistically in function of a
247 landscape (e.g., spatially explicit individual-based models; IBMs). These applications broadly fall into
248 two categories: (a) where the size of the viewshed is taken as an explanatory variable (questions
249 under 1) and (b) where the viewshed is used in a GIS to identify landscape features that are potential
250 visible from a given location (2 and 3).

251

252 *Information acquisition and spatial behaviour*

253 Information results in better informed decisions and one could investigate if a relationship exists
254 between the size of a viewshed and movement behaviours of an individual. For instance, it could be
255 hypothesized that individuals having, on average, large viewsheds should travel more efficient routes
256 and have less tortuous movement paths compared to individuals that had, on average, smaller
257 viewsheds. The fact that previous studies found that path tortuosity was higher in structurally more

258 complex landscapes (where relatively small viewsheds can be assumed) (Prevedello *et al.* 2010) may
259 be indicative of such a relationship, although other factors could also provide explanations (e.g., path
260 tortuosity determined by physical obstruction of land cover). The viewshed approach can help
261 disentangle these likely interacting effects of the structural environment on spatial behaviours.

262 From this a second question naturally follows; if we assume that a better view of the landscape
263 increases navigation capacity, could it be that animals select locations that increase their ability to
264 obtain visual information? Contrasting the size of viewsheds from actual locations with those
265 calculated from a set of random locations could provide insight into how individuals exploit their
266 environments to optimise information acquisition.

267

268 *Information availability, spatial behaviour and habitat or resource selection*

269 At the core of several research fields, notably in movement and landscape ecology, an individuals'
270 decision routinely needs to be interpreted or set according to its perceptual range. In this context,
271 the perceptual range does not necessarily refer to the range at which an animal can perceive a
272 particular visual cue (the actual threshold distance) but rather to the range at which an animal is
273 likely to respond to it (i.e. the realized perceptual range, *sensu* Olden *et al.* 2004) which, in a
274 landscape ecology context, has been experimentally defined only for a small number of species (e.g.,
275 Zollner 2000, Schtickzelle *et al.* 2007, Turgeon *et al.* 2010, Prevedello *et al.* 2011). However,
276 whatever threshold distance is used to delimit the perceptual range, it is virtually always assumed
277 that the animal has unobstructed views across it (e.g., Fronhofer *et al.* 2013, Laforge *et al.* 2016). This
278 reduces our ability to use models to infer how individuals respond to different features of the
279 landscape because we are not properly controlling for the locations that are actually visible.
280 Systematic biases may occur where visual signals are more rapidly curtailed by particular habitat
281 features or where particular habitat features are routinely more (or less) visible than would be
282 expected by chance. For example, if we were fitting a movement model that incorporated
283 resistance/preference/cost values for different landscape elements and one high quality habitat

284 category was typically obscured from view by another (as an extreme example, imagine forest glades
285 hidden by trees), then by not accounting for relative visibilities we might incorrectly assign too high a
286 cost value to what is actually a preferred and high quality habitat type, that is simply hard to find.
287 Incorporating viewshed analysis in models that fit parameters describing animal spatial behaviours
288 can yield significant improvements, as it can allow sampling of alternatives from what is actually
289 visible within the hypothesized perceptual range, hence likely increasing the power of models to
290 detect relationships between the landscape and animal behaviour.

291

292 The concept of a spatially explicit perceptual range can be applied in individual-based movement
293 models. For instance, the Stochastic Movement Simulator (SMS; Palmer *et al.* 2011) simulates
294 movement across a gridded surface where transition probabilities are governed by cost values within
295 a predefined perceptual range. This modelling approach, and an extended version that can work in
296 3D, has already been applied to fundamental and applied research questions in both terrestrial and
297 marine environments (Chimienti *et al.* 2014; Coulon *et al.* 2015; Aben *et al.* 2016). In SMS's current
298 form, the perceptual range represents a predefined number of grid cells evenly distributed around
299 the location of the virtual animal. Adding a layer that gives information on the z value (height) of
300 each cell and calculating the viewshed would account for the effects of topography and vegetation
301 structure on movement behaviour which in turn is likely to increase realism in IBM predictions (Pe'er
302 and Kramer-Schadt 2008). For instance, Graf *et al.* (2007) demonstrated that estimates of patch
303 connectivity were closer to expert predictions when the perceptual range of simulated capercaillie
304 *Tetrao urogallus* individuals was constrained by mountain topography.

305 One potential application of these movement models is to utilise them in conjunction with inverse
306 fitting methods to make inference about ecological behaviours and processes for which direct
307 estimates are hard to obtain. For example, given 3D data on the landscape and on movement
308 trajectories, Approximate Bayesian Computation (van der Vaart *et al.* 2015) could be used together
309 with stochastic simulations to provide estimates for an animal's perceptual range threshold distance

310

311 *Viewsheds from hypothetical viewpoints – defining a location’s relative visibility using the cumulative*
312 *viewshed approach*

313 Viewshed analysis can be used to quantify relative visibility of a location of interest. This is done by
314 calculating viewsheds from multiple hypothetical viewpoints and adding them up to create a “heat
315 map” where each cell gives the number of overlapping viewsheds. Because this analysis can be
316 performed for all locations in the area of interest, it provides a superior alternative for the
317 conventional photograph-based visibility measures (Olsoy *et al.* 2015) that are routinely used in
318 behavioural ecology.

319

320 *Relative visibility to guide landscape scale conservation management*

321 Interestingly, by taking the cumulative viewshed approach we can begin to characterise the relative
322 visibility of different landscape elements, providing potentially useful applications. For example,
323 visibility of corridors and stepping-stones in a landscape can be hypothesized to influence the rate at
324 which these features are encountered by dispersing individuals (Vergara *et al.* 2013) which in turn
325 will affect their effectiveness in promoting functional connectivity. The cumulative viewshed
326 approach could be used to determine relative visibility of landscape features and use this
327 information to evaluate relative effectiveness of alternative scenarios of corridor placement. A
328 similar approach could be taken to evaluate to what extent patch functional connectivity is
329 influenced by variation in patch visibility. For example, it could be hypothesized that patches that are
330 relatively visible in a landscape have higher immigration rates compared to patches that are less
331 visible or that the degree of patch inter-visibility explains patterns of connectivity (e.g., are ‘visually
332 connected’ patches also functionally connected?).

333 We see great potential of the cumulative viewshed approach to inform landscape management. For
334 example, it would allow planners to constrain placement of stepping-stones, corridors and additional
335 patches of habitat to locations that render them relatively visible at relevant spatial scales and to

336 create 'visually connected' landscapes. As a large proportion of animals uses visual cues to navigate
337 through a landscape – accounting for visibility in landscape planning is likely to increase its
338 effectiveness.

339 Typically, the cumulative viewshed approach requires calculating multiple viewsheds on large
340 datasets which may prove computational challenging. However, viewshed modelling is central in a
341 range of non-ecological research fields and technical developments are yielding improvements which
342 will facilitate its application in landscape planning (Sang 2016). For example, a recently developed
343 software that uses raycasting algorithms adapted from computer gaming engines calculates
344 viewsheds up to 1500 times faster than standard GIS algorithms (Carver & Washtell 2012) allowing
345 real-time viewshed visualization and interactive planning with stakeholders.

346

347 *Viewsheds from researcher locations*

348 Visual census of animals is common in ecological research. In many cases, these data are used to
349 estimate the size or density of biological populations (i.e. distance sampling). A key assumption of
350 distance sampling is that all subjects occurring on the census area can be detected. If they are not,
351 densities will be underestimated (Smolensky & Fitzgerald 2010). Violation of the assumption can
352 occur from imperfect detection of subjects that are available in the sampling area (i.e. the perception
353 bias), or when subjects that are in the census area cannot be detected visually (i.e. the 'availability
354 bias'). Especially the latter represents a problem that is difficult to account for. A recent paper, for
355 example, showed that nearly 30 % of sampling area could not be censused visually due to the terrain
356 (Ransom *et al.* 2012). Ultimately, the authors chose not to account for this availability bias in their
357 density estimates but the study nicely illustrates the potential confounding effects of constrained
358 observers' viewsheds in distance sampling. The viewshed approach can be used to account for the
359 availability bias by quantifying for each census location the proportion of area that is actually visible
360 to the observer or to select census locations that allow maximum visual coverage of the census area.

361

362 Opportunities for new collaborations with visual ecologists

363 An animal's location determines what it potentially can see and how visible it is from its
364 surroundings. The properties of a suite of locations encountered by an organism can be seen as
365 exerting potentially strong selective pressures on the evolution of both visual ability (e.g., eye
366 physiology) and individual spatial behaviour that influences information acquisition (Spiegel &
367 Crofoot 2016). Recent work at the interface of animal ecology and sensory ecology, for example,
368 showed that the bog fritillary butterfly *Boloria eunomia*, a species inhabiting naturally fragmented
369 habitat, had larger facet sizes in the frontal and lateral region of the eye compared to the cranberry
370 fritillary butterfly *B. aquilonaris* that inhabits more continuous habitat, and that, within *B. eunomia*,
371 dispersers had larger facets in the frontal region of the eye than resident individuals (Turlure *et al.*
372 2016). As larger facets potentially offer increased spatial visual acuity, these findings lead to the
373 intriguing possibility, suggested by the authors, that better navigation abilities have evolved to aid
374 dispersal in the more fragmented landscapes. This study highlights the opportunities that can be
375 gained through ecological researchers collaborating with visual ecologists (see Cronin *et al.* 2014 for
376 an excellent introduction to this field), especially when the aim is to understand factors that affect
377 visual spatial information acquisition.

378 Viewshed analyses have traditionally been applied from the human perspective, a species for which
379 relatively much is known with respect to its visual sensory capabilities, its spatial vision and visual
380 information processing. Compared to other animals, the human eye is exceptional when it comes to
381 resolving spatial detail, surpassed only by the eyes of some large birds of prey. Hence, most animals
382 may only be able to resolve spatial details at shorter distances than humans can. Published estimates
383 of spatial visual acuity for an increasingly large number of species from different groups (e.g., insects
384 [Bergman & Rutowski 2015], crustacea [Caves *et al.* 2016], fish [Collin & Pettigrew 1989], birds
385 [Mitkus *et al.* 2014]) may help to generate estimates of the dimension of the visual space required in
386 viewshed ecology to appropriately delimit viewsheds. Given the fact that both spatial visual acuity as
387 the perceptual range (inferred from release experiments) has been found to be correlated with body

388 size (Kiltie 2000, Mech & Zollner), these estimates may also be approximated for species for which no
389 experimental data are yet available. Despite the many challenges that exist, careful application of the
390 standard implemented viewshed tool in a GIS is likely to greatly increase our ability to understand
391 the relationship between the availability of visual information and spatial behaviour of animals in
392 structured environments. For species that may see the world very differently from us or that inhabit
393 a different environment (e.g., aquatic), ecologists may need to modify existing tools to be able to
394 account for these factors such that viewsheds can appropriately capture an animal's visual space.

395

396 **Concluding remarks**

397 Information represents the basis of an individual's behaviour and as such strongly influences
398 biological processes at larger temporal and spatial scales (i.e. populations, communities and
399 ecosystem functioning). Understanding this complex network starts with objective quantification of
400 the information that potentially drives observed responses. However, we have exemplified that, at
401 least in the case of visual information, this objective is not currently at the core of much ecological
402 research. Secondly, integration of the ecology of information in landscape scale research and
403 conservation is hampered by limited connectivity between the different disciplines that investigate
404 information in biology (Lima & Zollner 1996, Schmidt *et al.* 2010, Greggor *et al.* 2014). In this respect,
405 viewshed ecology may represent the much needed link between these fields to facilitate
406 advancements in the ecology of information.

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Box 1: Performing viewshed analyses

Tools:

Viewshed analyses can be performed using ArcGIS Spatial Analyst (ESRI, Redlands, California) or, for an open source alternative, using the `r.viewshed` command in GRASS GIS (Neteler *et al.* 2012) which also can be controlled in R using the `rgrass7` package (Bivand 2016). Essentially, both methods are similar but the tool in ArcGIS provides more flexibility in setting parameters to control the calculation of a viewshed. In both tools, viewing height is automatically assigned to a location based on the corresponding elevation layer plus a default value that equals to approximately one meter in ArcGIS and to 1,75m in `r.viewshed`. The latter value can be adjusted to reflect the viewing height of any species relative to the DEM or DSM (see below).

Input data:

1. Digital elevation model (DEM): this data is useful when viewshed analysis is performed in three-dimensionally structured environments devoid of vegetation or seascapes. DEMs with global coverage are freely available through a number of online data portals.
2. Digital surface model (DSM): this data is needed when viewshed analyses are performed in areas that are (primarily) structured by vegetation. This data represents elevation including natural (trees, bush) and built features extruding from the earth obtained by means of light detection and ranging (LiDAR). These data are becoming freely available for a rapidly increasing number of countries through online data portals (e.g., <https://data.gov.uk/dataset/lidar-composite-dsm-1m1>).
3. Canopy-height model (CHM): These data represent the elevation of features extruding the earth and is obtained by subtracting a DEM from a DSM. High point density LiDAR allows to model vegetation structure of individual forest strata. These models are useful for modelling viewsheds from locations below a forest canopy.

Location data:

Viewshed analysis requires entering an *x*, *y*, *z* coordinate. For location data of ground-dwelling animals, the *z* coordinate should simply reflect viewing height of a species (e.g., for lions, a viewing height of 100cm was chosen [Loarie *et al.* 2013]). For animals that move in 3D space, viewing heights will vary between *xy* locations. In this case, *z* coordinates can be derived from 3D tracking data or from *xy* data in combination with an elevation surface model. Viewing heights relative to the elevation surface can be set using the `OFFSETA` parameter in ArcGIS or the `observer_elevation` parameter in GRASS GIS. Please note that it is not possible to set a viewing height below the value of the elevation surface. For example, a location for a bird in a tree will be assigned a viewing height corresponding to the value in the elevation surface. Absolute viewing height can also be set directly using the `SPOT` parameter in ArcGIS.

Viewsheds can be curtailed depending on the estimated visual distance threshold of a species by specifying the `Radius2` and `max_distance` parameter in ArcGIS and GRASS GIS, respectively (see Aspbury & Gibson 2004 for an example).

414

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419

420 **AUTHORS' CONTRIBUTIONS**

421 JA and JMJT conceived the idea for the paper. JA led the writing of the manuscript, supported by
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424 **DATA ACCESSIBILITY**

425 There is no data archived for this manuscript.

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