

# Step by Step: Using Step Selection Functions to Simulate Dispersal and Assess Landscape Connectivity

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May 14, 2021

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**Running Title:** Release the Dogs! Simulating Wild Dog Dispersal to Assess Landscape  
Connectivity

**Keywords:** dispersal, simulation, movement, integrated step selection, Kavango-Zambezi  
Transfrontier Conservation Area, landscape connectivity, *Lycaon pictus*

## Abstract

Dispersal is an important process that allows species to avoid inbreeding, to colonize new habitats and to reinforce non-viable subpopulations. Successful dispersal thus represents a crucial pre-requisite for long-term species persistence in wild animal populations. However, the ability to disperse is contingent a sufficient degree of landscape connectivity, which is why the estimation of connectivity and identification of dispersal corridors has become a task of extraordinary importance for conservation authorities worldwide.

Over the past two decades, ecologists have primarily relied on analytical tools such as least-cost analysis and circuit theory to model and investigate landscape connectivity. Despite their usefulness for a diverse suite of ecological applications, both methods make several restricting assumptions that limit their suitability in reality. To address these shortcomings, dispersal simulations from individual-based movement models have been proposed and applied. Yet, due to the almost infinite amount of non-trivial decisions a modeler faces when parametrizing such models, a unified and objective framework is missing.

Recent innovations in movement ecology have brought forward novel opportunities to study animal dispersal and estimate landscape connectivity. In particular, the rich suite of resource selection functions, namely point-, step-, and path-selection functions, have undergone substantial improvements over the past years. Most notably, step-selection functions have been generalized to *integrated* step selection functions, which essentially represent fully mechanistic movement models based on which an individual's movement could be simulated. While such models have been applied to study *steady-state* utilization distribution resident animals, a similar approach may be useful for investigating *transient* movement behavior and study landscape connectivity.

Here, we showcase the use of integrated step selection functions to simulate dispersal of the endangered African wild dog across the world's largest transboundary conservation area, the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). For this, we utilize data collected on 16 dispersing wild dog coalitions in combination with relevant habitat covariates. We analyse the data using integrated step selection functions and parametrize a fully mechanistic movement model rendering wild dog dispersal. Based on this model, we simulate 80'000 dispersers, originating from protected areas and moving across the extent of the KAZA-TFCA. We then generate a heatmap indicating regions frequently visited by dispersers, use network theory to reveal dispersal hotspots and crucial bottlenecks across the study area. Finally, we discuss the benefits and pitfalls of such dispersal simulations and highlight potential improvements to be made in the future.

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# **1 Introduction**

## **1.1 Importance of Dispersal & Connectivity (90%)**

Dispersal is defined as the movement of individuals away from their natal location to the site of first reproduction Howard (1960). It is a vital process governing the dynamics wild animal populations that are distributed in space (Hanski, 1998; Clobert et al., 2012) and may strongly affect population dynamics at different spatial and social scales (Hanski, 1999a; Clobert et al., 2012). Dispersal allows species to avoid inbreeding and maintain genetic diversity (Perrin and Mazalov, 1999, 2000; Frankham et al., 2002; Leigh et al., 2012; Baguette et al., 2013), to rescue small and non-viable populations (Brown and Kodric-Brown, 1977), and to promote the colonization of unoccupied habitats (Hanski, 1999b; MacArthur and Wilson, 2001). However, successful dispersal requires a sufficient degree of functional connectivity (Fahrig, 2003; Clobert et al., 2012), which is why the identification and protection of major dispersal corridors has become an important task in conservation science (Doerr et al., 2011; Rudnick et al., 2012). In order to pinpoint relevant dispersal hotspots, reliable information on movement behavior during dispersal and knowledge about factors that limit dispersal and connectivity is paramount (Baguette et al., 2013; Vasudev et al., 2015).

## **1.2 Advancements in GPS Technology & Movement Ecology (90%)**

Thanks to novel technologies developed over the past decades, particularly of GPS/Satellite radio-collars, the use of GPS data to study animal dispersal and connectivity has accelerated (Elliot et al., 2014; Jönsson et al., 2016; Williams et al., 2019). Additionally, the advent of publicly accessible satellite imagery and sophisticated remote sensing techniques to represent the physical landscape through which individuals disperse have heralded a “golden age of animal tracking” (Kays et al., 2015). Concurrently, the availability of large amounts of empirical data and an increased computational power have led to the development of numerous techniques to study dispersal movements and highlight critical corridors between subpopulations (Boyce et al., 2002; Fortin et al., 2005; Cushman and Lewis, 2010; Zeller et al., 2012; Diniz et al., 2020).

## **1.3 Resource Selection & Connectivity (90%)**

*Resource selection functions* (Boyce et al., 2002) and derived methods such as *step selection functions* (Fortin et al., 2005) and *path selection functions* (Cushman and Lewis, 2010) have proven particularly useful for studying animal movement (Fieberg et al., 2020) and modelling

32 connectivity (Diniz et al., 2020). These methods allow estimating habitat preferences of the  
33 focal species by comparing covariates at locations visited by the animal to the same covariates  
34 at locations available to, but not visited by the animal (Boyce et al., 2002; Fortin et al.,  
35 2005; Cushman and Lewis, 2010; Thurfjell et al., 2014). The so estimated preferences can  
36 then be used to predict a permeability surface, indicating the expected ease at which an  
37 animal can traverse a given area (Spear et al., 2010; Zeller et al., 2012; Etherington, 2016).  
38 Ultimately, the permeability surface serves as input to a connectivity model that is used to  
39 reveal movement corridors (Diniz et al., 2020). In this regard, two of the most prominent  
40 connectivity models are least-cost path analysis (LCP analysis; Adriaensen et al., 2003)  
41 and circuit theory (CT McRae, 2006; McRae et al., 2008), both graph-based methods that  
42 estimate conductance of the landscape. Despite their intuitive nature and ease of use, both  
43 methods make rigorous assumptions about animal movement that are often not fulfilled in  
44 reality (Diniz et al., 2020).

#### 45 **1.4 Issues with Least-Cost Paths & Circuit Theory (90%)**

46 In LCP analysis, for instance, a least costly path always exists, even if associated movement  
47 costs are unreasonably high and will never be incurred by a dispersing individual. The  
48 method also presumes that animals have an infinite perceptual range, a preconceived end-  
49 point in mind, and choose a cost-minimizing route accordingly. These assumptions may be  
50 reasonable for migrating animals, yet they are unlikely to hold for dispersers, which typically  
51 move over long distances into unknown territory (Koen et al., 2014; Abrahms et al., 2017;  
52 Cozzi et al., 2020). Finally, LCPs are only one pixel wide, meaning that their absolute size  
53 depends on the resolution of chosen covariate layers (Diniz et al., 2020). Although some  
54 of these deficiencies can be addressed using less stringent versions of the LCP algorithm  
55 (e.g. least-cost *corridors* (Pinto and Keitt, 2009), *thresholded* least-cost paths (Landguth  
56 et al., 2012), and *randomized* least-cost paths (Panzacchi et al., 2016; Van Moorter et al.,  
57 2021)), a certain degree of arbitrariness in the assumptions remains. CT entails similarly  
58 unreasonable restrictions. Because CT only considers movements from the source cell to its  
59 4 or 8 adjacent cells, it implicitly posits a perceptual range of a single pixel. As such, the  
60 perceptual range cannot be defined based on biological observations, but is imposed by the  
61 resolution of the reference grid. CT is also built on the assumption of a complete random  
62 walk (Diniz et al., 2020), implying that directional biases cannot be rendered, albeit being  
63 very common in dispersal movements (Cozzi et al., 2020; Hofmann et al., 2021). Ultimately,  
64 neither LCP analysis nor CT are capable of rendering the temporal dimension of dispersal.

65 Statements about the expected duration required to traverse a certain corridor are therefore  
66 impossible, albeit being important factors. Likewise, because movement is not modelled  
67 explicitly, neither of the methods allows to render interactions between movement and  
68 habitat preferences of the focal species. This implies that connectivity mainly arises as a  
69 result of the landscape structure and is referred to as structural connectivity. Structural  
70 connectivity stands in contrast to functional connectivity, which also renders the behavioral  
71 response of the animal with respect to prevailing habitat conditions (Tischendorf and Fahrig,  
72 2000). Even though functional connectivity is more difficult to estimate, a functional view  
73 is the ultimate goal in conservation science because it has direct consequences for gene flow  
74 (Baguette et al., 2013).

## 75 **1.5 What about IBMMs? (90%)**

76 To address the issues inherent to LCPs and CT, individual-based movement models (IBMMs)  
77 have been proposed and applied (Diniz et al., 2020). In these models, dispersal is simulated  
78 explicitly, based on movement rules that determine how individuals move over and interact  
79 with the prevailing landscape (Kanagaraj et al., 2013; Clark et al., 2015; Allen et al., 2016;  
80 Hauenstein et al., 2019; Zeller et al., 2020; Vasudev et al., 2021). Using the simulated  
81 trajectories, one can calculate a set of connectivity metrics, such as interpatch-connectivity  
82 and traversal frequency across the landscape to reveal major dispersal hotspots (Kanagaraj  
83 et al., 2013; Bastille-Rousseau et al., 2018; Hauenstein et al., 2019; Zeller et al., 2020). Even  
84 though IBMMS can be employed to overcome any of the shortcomings intrinsic to LCPs and  
85 CT, as well as to provide a more functional view on connectivity, they can be challenging  
86 to fit and require vast amounts of data collected during dispersal (Diniz et al., 2020).

## 87 **1.6 Step Selection Analysis (90%)**

88 Here, we investigate the usefulness of integrated step selection functions (ISSFs, Avgar et al.,  
89 2016), as a relatively simple but powerful IBMM based on which dispersal can be simulated.  
90 While regular SSFs were intended to learn about relative habitat preferences of the focal  
91 species (Fortin et al., 2005; Thurfjell et al., 2014; Avgar et al., 2017), the method has been  
92 generalized and now enables to jointly study habitat and movement preferences, as well as  
93 potential interactions between movement and habitat preferences (Avgar et al., 2016; Signer  
94 et al., 2017; Fieberg et al., 2020). ISSFs therefore provide a relatively simple method to  
95 model complex movement behavior where movement results from two intertwined behavioral  
96 kernels (e.g. Prokopenko et al., 2017; Munden et al., 2020). Importantly, a parametrized

97 ISSF model can be viewed as a fully mechanistic movement model based on which individual  
98 movement trajectories can be simulated (Avgar et al., 2016; Signer et al., 2017). In fact,  
99 Signer et al. (2017) used ISSF to simulate steady state utilization distributions of resident  
100 animals. However, the degree to which such simulations are helpful in detecting movement  
101 corridors and modeling landscape connectivity is unknown.

## 102 **1.7 Study Species & Study Area (90%)**

103 One of the species for which long-term viability relies on sufficient landscape connectivity is  
104 the endangered African wild dog *Lycon pictus*. While once present across entire sub-Saharan  
105 Africa, wild dogs have disappeared from a vast majority of their historic range due to perse-  
106 cution by humans, habitat fragmentation and destruction, and deadly diseases (Woodroffe  
107 and Sillero-Zubiri, 2012; ?). As of today, only 6'000 free-ranging individuals remain in small  
108 and spatially scattered subpopulations (Woodroffe and Sillero-Zubiri, 2012). Within those  
109 subpopulations, wild dogs form cohesive packs comprising 8 to 12 adults and their offspring  
110 McNutt (1995). After reaching sexual maturity, male and female offspring form same-sex  
111 coalitions and disperse from their natal pack (McNutt, 1996; Behr et al., 2020). New packs  
112 are formed when dispersing coalitions join unrelated opposite-sex dispersing coalitions (Mc-  
113 Nutt, 1996). Dispersing wild dogs can cover several hundred kilometers across a variety of  
114 landscapes (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020; Hofmann  
115 et al., 2021). One of the few strongholds for this species lies near the Moremi Game Reserve  
116 in northern Botswana, which is part of the world's largest transboundary protected area,  
117 namely the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). This area  
118 has originally been intended to facilitate migration of elephants, but is expected to benefit  
119 a multitude of other species (Elliot et al., 2014; Brennan et al., 2020; Hofmann et al., 2021).

## 120 **1.8 Previous Paper (90%)**

121 In a previous study, we assessed landscape connectivity for dispersing African wild dogs  
122 within the KAZA-TFCA using a least-cost corridor approach (Hofmann et al., 2021). For  
123 this, we fitted a basic habitat selection model based on which we predicted landscape per-  
124 meability. We now expand on this knowledge and use ISSF to develop a more detailed  
125 movement model of dispersing wild dogs (Figure 1). We then use this model to simulate  
126 dispersers moving across the KAZA-TFCA. Based on simulations, we compute heatmaps  
127 and identify potential dispersal hotspots. We also showcase how network metrics relevant  
128 to landscape connectivity can be computed. Our results show that a simulation-based ap-

129 proach yields several major benefits over traditional connectivity modeling techniques. Most  
130 importantly, simulations provide a more generic view on how connectivity emerges and to  
131 which degree connectivity depends on the dispersal duration. In addtion, by generating  
132 proper dispersal trajectories, network theory can be applied to calculate network metrics  
133 that are pertinent to connectivity analysis.

## 134 **2 Methods**

### 135 **2.1 Study Area (90%)**

136 The study area was defined by a bounding box centered at -17°13'9"S, 23°56'4"E (Figure 2a)  
137 stretching over 1.3 Mio. km<sup>2</sup> and ecompassing the entire KAZA-TFCA (Figure 2b). The  
138 KAZA-TFCA represents the world's largest transboundary conservation area and comprises  
139 parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia. It covers a total of 520'000  
140 km<sup>2</sup> and hosts a diverse landscape, ranging from savanna to grassland and from dry to moist  
141 woodland habitats. In its center lies the Okavango Delta, a dominant hydrogeographical  
142 feature and the world's largest flood-pulsing inland delta. The wet season within the KAZA-  
143 TFCA lasts from November to March and is out of phase with the flood in the Okavango  
144 Delta, which peaks between July and August (McNutt, 1996; Wolski et al., 2017). Although  
145 large portions within the KAZA-TFCA are designated national parks or other protected  
146 areas, considerable human influence remains due to roads, agricultural sites and settlements  
147 and villages that are distributed across the KAZA-TFCA's landscape.

### 148 **2.2 GPS Relocation Data (90%)**

149 Between 2011 and 2019, we collected GPS relocation data on dispersing wild dogs from a  
150 free-ranging wild dog population inhabiting the Moremi National Park in northern Botswana  
151 (Cozzi et al., 2020; Hofmann et al., 2021). We selected potential dispersers based on age,  
152 pack size, number of same-sex siblings within the pack, and presence of unrelated opposite-  
153 sex individuals in the pack (McNutt, 1996; Behr et al., 2020). We immobilized selected  
154 individuals using a cocktail of Ketamine/Xylazine/Atropine (Osofsky et al., 1996; Cozzi  
155 et al., 2020) that was injected by dart, fired from a CO<sub>2</sub>-pressurized gun (*DAN-Inject,*  
156 *Denmark*). Immobilized individuals were fitted with GPS/Satellite radio collars (*Vertex*  
157 *Lite*; *Vectronic Aerospace GmbH, Berlin*) that guaranteed automated drop-off through a  
158 decomposable piece of cotton. Handling and collaring of all individuals was supervised by  
159 a Botswana-registered wildlife veterinarian and all individuals quickly rejoined their pack

160 after immobilization.

161 16 collared individuals eventually dispersed, each in a separate same-sex dispersal coalition (162 7 female and 9 male coalitions). During dispersal, collars were programmed to record 163 a GPS fix every 4 hours. Collected relocations were regularly transmitted over the Iridium 164 satellite system, which allowed remote tracking of individuals, even if they left the main 165 study area and crossed international borders. Because behavior during dispersal is more 166 pertinent for assessing landscape connectivity (Elliot et al., 2014; Abrahms et al., 2017), we 167 discarded all data that was collected during residency and only retained GPS data recorded 168 during dispersal. In some instances, exact dispersal dates were known from field obser-169 vations. Where this was not the case, determined dispersal phases using the net-squared 170 displacement metric. Net squared displacement measures the squared Euclidean distance of 171 a GPS relocation to a reference point (Börger and Fryxell, 2012), which in our case was set 172 to the center of each individual's natal home range. As such, dispersal was deemed to have 173 started when an individual left its natal home range and ended once individuals became 174 sedentary again. As previous research revealed similar behavior of females and males during 175 dispersal (Woodroffe et al., 2019; Cozzi et al., 2020), we did not distinguish between sexes. 176 After collection, we converted collected GPS coordinates ( $n = 4'169$ ) to steps, where each 177 step represented the straight-line distance traveled by and individual between two consec-178 utive GPS relocations (Turchin, 1998). To ensure a regular sampling interval, we removed 179 fixes that were not successfully collected on the 4-hourly schedule ( $\pm 15$  minutes).

### 180 2.3 Covariates (90%)

181 We represented the physical landscape across the study area using a set of habitat covariates 182 that included water-cover, distance to water, woodland-cover, and shrub/grassland-cover. 183 Because water cover greatly changes within and between years in the Okavango Delta, we 184 applied a remote sensing algorithm and generated frequently updated water cover layers 185 and corresponding distance to water layers (see Wolski et al., 2017 and Appendix A3 in 186 Hofmann et al., 2021). Resulting water layers thus temporally aligned with our dispersal 187 events. We furthermore computed a proxy for human influence, rendering anthropogenic 188 pressures stemming from human-density, agricultural sites, and roads. All spatial layers 189 were coarsened or interpolated to a target resolution of 250 m by 250 m. Further details on 190 the sources and preparation of each habitat covariate are given in Hofmann et al. (2021).

191 Besides habitat covariates, we computed movement metrics that we used as movement 192 covariates in our models. Movement metrics were calculated for each step and included the

193 step length (`sl`), its natural logarithm (`log(sl)`), and the cosine of the relative turning angle  
 194 (`cos(ta)`) (for details see (Avgar et al., 2016; Fieberg et al., 2020)). Because wild dogs follow  
 195 a diurnal activity pattern, we also coded a binary variable (`LowActivity`) indicating whether  
 196 a step was realized during periods of low wild dog activity (17:00 to 09:00 local time) or  
 197 high wild dog activity (09:00 to 17:00 local time). Handling and manipulation of all data, as  
 198 well as all models and simulations were implemented with the statistical software R, version  
 199 3.6.6 (R Core Team, 2019). Several helper functions were written in C++ and imported into  
 200 R using the `Rcpp` package (Eddelbuettel and François, 2011; Eddelbuettel, 2013)

## 201 2.4 Movement Model (80%)

202 We used ISSFs to parametrize a mechanistic movement model for dispersing wild dogs  
 203 (Avgar et al., 2016). To conduct ISSF analysis, we paired each realized step with 24 ran-  
 204 dom steps. An observed and its 24 random steps formed a stratum and received a unique  
 205 identifier. We generated random steps by sampling random turning angles from a uniform  
 206 distribution  $(-\pi, +\pi)$  and step lengths from a gamma distribution that was fitted to re-  
 207 alized steps (scale = 6'308, shape = 0.37). Along each step, we extracted and averaged  
 208 spatial covariates using the `velox` package (?). We also calculated the movement metrics `sl`,  
 209 `log(sl)`, and `cos(ta)` for each observed and random step. To facilitate model convergence, we  
 210 standardized all continuous covariates to a mean of zero and a standard deviation of one.  
 211 Since correlation among covariates was low ( $|r| > 0.6$ ; Latham et al., 2011), we retained all  
 212 of them for modeling.

213 To contrast realized steps (scored 1) and random steps (scored 0), we assumed that ani-  
 214 mals assigned a selection score  $w(x)$  of the exponential form to each step (Fortin et al., 2005).  
 215 The selection score  $w(x)$  of each step depended on its associated covariates  $(x_1, x_2, \dots, x_n)$   
 216 and on the animal's preferences (i.e. relative selection strengths; Avgar et al., 2017) towards  
 217 these covariates  $(\beta_1, \beta_2, \dots, \beta_n)$ :

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n) \quad (\text{Equation 1})$$

218 The probability of a step being realized was then contingent on the step's selection score,  
 219 as well as on the selection scores of all other step in the same stratum:

$$P(Y_i = 1 | Y_1 + Y_2 + \dots + Y_i = 1) = \frac{w(x_i)}{w(x_1) + w(x_2) + \dots + w(x_i)} \quad (\text{Equation 2})$$

220 To estimate the preferences of interest, we ran conditional logistic regression analysis  
221 in the r-package `glmmTMB`. To handle multiple individuals, we applied the mixed effects  
222 technique developed by (Muff et al., 2020), which allows to effectively model random slopes.  
223 Thus, we treated animal IDs as random effect and modeled random slopes for each covariate.  
224 We fixed the random intercept variance at an arbitrary high value of  $10^6$  to make use of the  
225 “poission”-trick (Muff et al., 2020).

226 The formula for the movement model was based on the habitat selection model for dis-  
227 persing wild dogs presented in Hofmann et al. (2021). In the original model, no interactions  
228 between habitat covariates (`Water`, `DistanceToWater0.5`, `Woodland`, `Shrubs/Grazing`, `Human`  
229 `Influence`) and movement covariates (`sl`, `log(sl)`, `cos(ta)`) were considered. Here, we slightly  
230 expanded this base model and proposed interactions between all movement and habitat  
231 covariates. More specifically, we started with the base model and incrementally increased  
232 model complexity by adding all possible two-way interactions between habitat covariates and  
233 movement covariates. For instance, for the covariate `Water`, we proposed the interactions `Wa-`  
234 `ter:log(sl)`, `Water:log(sl)`, and `Water:cos(ta)`. Besides those combinations, we also proposed  
235 the interactions `sl:cos(ta)` and `log(sl):cos(ta)` to account for a correlation between turning  
236 angles and step lengths, as well as the interactions `sl:LowActivity` and `log(sl):LowActivity` to  
237 account for the fact that step lengths may differ due to wild dogs’ diurnal activity pattern.  
238 To compare competing models and assess the most parsimonious movement model, we ran  
239 stepwise forward model selection based on Akaike’s Information Criterion (AIC, Burnham  
240 and Anderson, 2002).

241 We validated the predictive power of the most parsimonious movement model using k-  
242 fold cross-validation for case-control studies as suggested by Fortin et al. (2009). For this,  
243 we randomly assigned 80% of the strata to a training set and the remaining 20% to a  
244 testing set. Using the training data we parametrized a movement model based on which  
245 we predicted selection scores  $w(x)$  for all steps in the test data. Within each stratum, we  
246 then assigned ranks 1-25 to each step based on predicted selection scores, where rank 1 was  
247 given to the step with the highest score  $w(x)$ . Across all strata we determined the realized  
248 step’s rank and we calculated rank frequencies of realized steps across all strata. Finally, we  
249 computed Spearman’s rank correlation between ranks and associated frequencies  $r_{s,realized}$ .  
250 We replicated the entire procedure 100 times and computed the mean correlation coefficient  
251 ( $\bar{r}_{s,realized}$ ), as well as its 95% confidence interval across all replicates. For comparison, we  
252 repeated the same procedure 100 times assuming random preferences, which we implemented  
253 by discarding the realized step from all strata and identifying the rank of a random step

254 in each stratum. Again, we calculated Spearman’s rank correlation coefficient ( $r_{s,random}$ ),  
255 its mean across repetitions ( $\bar{r}_{s,random}$ ), and its 95% confidence interval. This validation  
256 ultimately proofs a significant prediction in case the confidence intervals of  $\bar{r}_{s,realized}$  and  
257  $\bar{r}_{s,random}$  do not overlap.

## 258 **2.5 Dispersal Simulation (80%)**

259 We used the most parsimonious movement model to simulate 80’000 virtual dispersers mov-  
260 ing across the KAZA-TFCA. The simulation resembled an inverted ISSF and was set up as  
261 follows. (1) We defined a random source point and assumed a random initial orientation of  
262 the animal. (2) Departing from the source point, we generated 25 random steps by sam-  
263 pling turning angles from a uniform distribution  $(-\pi, +\pi)$  and step lengths from our fitted  
264 gamma distribution. Similar to the input data, each random step represented the straight  
265 line movement within 4 hours. To prevent unreasonably large steps, we capped sampled step  
266 lengths to a maximum of 35 km, which corresponded to the farthest distance ever traveled  
267 within 4 hours by one of our dispersers. (3) Along each random step, we extracted and  
268 averaged habitat covariates and we calculated movement covariates. To ensure compatible  
269 scales, we standardized extracted values using the same parameters applied to our input  
270 data. (4) We applied the parameterized movement model to predict the selection score  
271  $w(x)$ , which we translated into probabilities using Equation (Equation 2). (5) We sampled  
272 one of the random steps based on predicted probabilities and determined the animal’s new  
273 position. We repeated steps (2) to (5) until 2’000 steps were realized, implying a total 160  
274 Mio. simulated steps.

275 To minimize the influence of edge effects and to deal with random steps leaving the  
276 study area, we followed (Koen et al., 2010) and artificially expanded all covariate layers by  
277 adding a 100 km wide buffer zone. Within the buffer zone, we randomized covariate values  
278 by resampling values from the original covariate layers. Through this buffer zone, simulated  
279 dispersers were able to leave and re-enter the main study area. In cases where proposed  
280 random steps transgressed the border of this buffer zone, we resampled transgressing steps  
281 until they fully lied within the buffer, thereby forcing simulated individuals to “bounce off”  
282 from such invisible borders.

## 283 **2.6 Source Points (90%)**

284 We initiated virtual dispersers at 50’000 randomly selected source points within contiguous  
285 protected areas larger  $> 700 \text{ km}^2$  (Figure 3a). This conforms to the average home range

286 requirement of resident wild dogs (Pomilia et al., 2015) and allowed us to remove areas  
287 too small to host viable wild dog populations. By distributing source points randomly, the  
288 number of source points per km<sup>2</sup> within protected areas was approximately equal across the  
289 study area. To render potential immigrants into the study system, we placed additional  
290 30'000 source points inside the buffer zone around the main study area (Figure 3b). This  
291 resulted in a total of 80'000 source points, each representing the start point of an individual  
292 disperser.

## 293 **2.7 Heatmap (100%)**

294 To identify dispersal hotspots across our study area, we created a heatmap indicating the  
295 absolute frequency at which each raster-cell in the study area was visited by virtual dis-  
296 persers. For this, we rasterized all simulated trajectories and tallied them into a single map.  
297 If the same trajectory crossed a raster-cell twice, it was only counted once. This way, we  
298 did not consider revisits and mitigated biases arising from trapped individuals that were  
299 moving in circles. To achieve high performance rasterization, we used the R-package **terra**  
300 (Hijmans, 2020).

## 301 **2.8 Betweenness (80%)**

302 To pinpoint areas of exceptional relevance for connecting remote regions in our study area,  
303 we converted simulated trajectories into a network and calculated betweenness scores. For  
304 this, we overlaid the study area (including the buffer) with a regular raster resolved at 5  
305 x 5 km. We then used the simulated trajectories to determine all transitions occurring  
306 from one raster-cell to another, as well as the frequency at which those transitions occurred.  
307 This resulted in an edge-list that we translated into a weighted network using the r-package  
308 **igraph** (Csardi and Nepusz, 2006). Because **igraph** handles edge weights ( $\omega$ ) as costs,  
309 we inverted the traversal frequency in each cell by applying  $\omega = \frac{\sum_i^n TraversalFrequency_i}{TraversalFrequency_i}/n$ .  
310 Finally, we used the weighted network to calculate betweenness scores for each raster-cell  
311 in the overlaid raster. The betweenness metric indicates how often a specific raster-cell lies  
312 on a shortest path between two other raster-cells and is therefore a useful metric to detect  
313 movement corridors (Bastille-Rousseau et al., 2018).

## 314 **2.9 Interpatch-Connectivity (80%)**

315 We also assessed inter-patch connectivity between national parks in our study area. The  
316 decision to focus on national parks was purely out of simplicity and the same logic could

317 easily be expanded to include other protected areas as well. To quantify inter-patch connec-  
318 tivity, we computed the relative frequency at which dispersers originating from one national  
319 park successfully moved into another national park. This allowed us to determine *if* and  
320 *how often* dispersers moved between certain national parks. Moreover, because time was  
321 explicit in our IBMM, we were able to estimate *how long* dispersers had to move to realize  
322 those connections.

### 323 3 Results

#### 324 3.1 Movement Model (60%)

325 Compared to the base model reported in (Hofmann et al., 2021), our most parsimonious  
326 movement model included several additional interactions between habitat covariates and  
327 movement covariates (Figure 4 and Table 1). Although multiple models received an AIC  
328 weight above zero (Table 1 in Appendix S1), we only considered results from the most  
329 parsimonious model. Since all models with positive AIC weight contained similar covariates,  
330 this decision only marginally influenced subsequent analyses. Results from the selected  
331 model are given in Table 1 and illustrated in Figure 4 (a). Additional plots that facilitate  
332 the interpretation of the model are provided in Appendix S2.

333 When looking at the habitat kernel and holding constant the movement kernel, we find  
334 that dispersing wild dogs avoid water but prefer its proximity. Dispersers also avoid densely  
335 forested woodlands, yet prefer open shrublands or grasslands. Finally, dispersers avoid  
336 moving through landscapes that are influenced by humans. These results align with our  
337 previous findings reported in Hofmann et al. (2021).

338 When looking at the movement kernel, we observe several significant estimates. How-  
339 ever, except for the interaction `sl:LowActivity`, effect sizes are relatively small, suggesting  
340 that our proposal distributions for step lengths and turning angles were only marginally  
341 biased. For instance, the positive and significant effect for `cos(ta)` indicates that realized  
342 turning angles were slightly more directional than the turning angles proposed by our uni-  
343 form distribution, implying that realized steps in fact followed a von Mises Distribution with  
344 positive concentration parameter. On the other hand, the significant and negative interac-  
345 tion for `sl:LowActivity` reveals that wild dogs moved over shorter distances during low wild  
346 dog activity compared to the steps suggested by our gamma distribution.

347 Finally, we turn to the interactions between the two kernels. Here, we observe that  
348 movement behavior significantly differs depending on habitat covariates. In general, steps

349 tend to be shorter in areas with high water cover and high woodland cover, yet larger in  
350 areas with open shrubs and grasslands. Similarly, dispersers realized shorter steps in the  
351 vicinity to water, even though the size of this effect is negligible. Finally, it appears that  
352 dispersers move more tortuous in areas influenced by humans, and more directional when  
353 far from water.

354 As can be seen in Figure 4b, the k-fold cross-validation procedure reveals that our  
355 model substantially outperforms a random guess. The confidence intervals of  $\bar{r}_{s,realized}$   
356 and  $\bar{r}_{s,random}$  do not overlap and therefore proof a reliable prediction. Furthermore, the  
357 significant correlation between ranks and corresponding frequencies for realized steps indi-  
358 cates a good fit between predictions and observations (Figure 4b). In comparison to the  
359 base model ( $\bar{r}_{s,realized} = -0.55$ ; Hofmann et al., 2021), inclusion of interactions between  
360 movement and habitat covariates slightly improved model performance.

### 361 3.2 Dispersal Simulation (80%)

362 On a machine with an octacore AMD Ryzen 7 2700X processor (8 x 3.6 GHz) and 64 GB  
363 of RAM, a single batch of 1'000 simulated dispersers took roughly 90 minutes to compute  
364 ( $\mu = 88.90$ ,  $\sigma = 1.87$ ) and the simulation of all 80'000 dispersers terminated after 120  
365 hours, i.e. five days. Comparable computations will be substantially faster for smaller  
366 study areas or lower resolution covariates, as the covariate extraction from large rasters was  
367 computationally the most expensive task.

368 On average, step lengths realized by the simulated dispersers ( $\mu_{sl} = 2'093$  m,  $\sigma_{sl} = 3'067$ )  
369 were slightly shorter than those by observed dispersers ( $\mu_{sl} = 2'326$  m,  $\sigma_{sl} = 3'323$ ) and  
370 simulated dispersers moved marginally less directional ( $\mu_{cos(ta)} = 0.057$ ,  $\sigma_{cos(ta)} = 0.071$ )  
371 compared to observed dispersers ( $\mu_{cos(ta)} = 0.078$ ,  $\sigma_{cos(ta)} = 0.072$ ). These differences  
372 in step lengths and turning angles can be attributed to minor disparities between habitat  
373 conditions at the area within which we collected training data and habitat conditions within  
374 the entire study area. Out of the 50'000 dispersers initiated in protected areas, only 4.5%  
375 eventually hit a map boundary, suggesting that biases due to boundary effects should be  
376 limited. In contrast, 78% of the 30'000 dispersers originating from the buffer zone eventually  
377 hit a map boundary.

### 378 3.3 Heatmap (80%)

379 Figure 5 depicts the heatmap of all 80'000 simulated trajectories rendered after 2'000 steps.  
380 The map highlights that large portions of land beyond the borders of the KAZA-TFCA

381 are only infrequently visited by dispersers (dark blue areas), whereas within the KAZA-  
382 TFCA several extensive regions are regularly visited (bright yellow and red areas). Most  
383 notably, the region in northern Botswana south of the Linyanti swamp stands out as highly  
384 frequented dispersal hub. Still, the presence of several massive water bodies, such as the  
385 Okavango Delta, the Makgadikgadi Pan, and the Linyanti swamp, results in considerable  
386 dispersal barriers that limit realized connectivity within the KAZA-TFCA. Similarly, dis-  
387 persal appears to be very limited in Zambia's and Zimbabwe's part of the KAZA-TFCA,  
388 where only few areas are regularly traversed by dispersers. This which can largely be at-  
389 tributed to the strong high human influences in these regions. Outside the KAZA-TFCA,  
390 the most heavily trafficked regions include the areas of the Central Kalahari National Park  
391 in Botswana, the area south-west of the Khaudum National Park in Namibia, and the area  
392 around the Liuwa Plains National Park in Zambia.

### 393 **3.4 Betweenness (80%)**

394 Betweenness scores of each raster-cell the study area are presented in Figure 6 and reveals  
395 a set of discrete dispersal corridors. As can be seen, the dispersal hotspot in northern  
396 Botswana reported above is crossed by a corridor that receives a relativley high betweenness  
397 score. This implies that the region is particularly crucial for connecting other regions in  
398 the study system and hence represents a proper hub in the “network” . Towards east, the  
399 corridor runs through the Chobe National Park into the Hwange national park, where it  
400 branches out and further extends into the distant Matusadona National Park in Zimbabwe.  
401 Northwest of the Linyanty ecosystem, the same corridor expands into Angola, where it splits  
402 and finally traverses over a long stretch of unprotected area into the Kafue National Park  
403 in Zambia. Several additional corridors with slightly lower betweenness scores exist, yet  
404 most of them run within the boundaries of the KAZA-TFCA. In general, only few corridors  
405 directly link the peripheral regions of the KAZA-TFCA. For instance, there are only few  
406 corridors between the Matusadona National Park in Zimbabwe and the Kafue National Park  
407 in Zimbabwe. Similarly, there are no direct links between the Zimbabwean and Angolan  
408 “spikes” of the KAZA-TFCA.

### 409 **3.5 Interpatch Connectivity (50%)**

410 Results from the analysis of interpatch connectivity are given in Figure 7. It is worth  
411 pointing out that the figure is only intended as an example; for clarity we limited the  
412 network on national parks, albeit plenty of links to other protected areas exist. The map

413 shows all realized links by simulated dispersers between national parks and indicates the  
414 average duration a disperser had to move to realize those links. For instance, 6.8 % of  
415 the simulated dispersers originating from the Moremi National Park successfully reached  
416 the Chobe National Park and 4.2 % the Hwange National Park in Zimbabwe. On average,  
417 dispersers moved for 623 steps before arriving at Chobe ( $SD = 520$ ) and for 1'413 steps  
418 before arriving at Hwange ( $SD = 371$ ). While the map only depicts connections between  
419 national parks, this does not imply that no connections to other protected areas exist and is  
420 the result of our simplifying assumptions above. Interestingly, while we identified a potential  
421 dispersal corridor between Angola's NPs and the Kafue NP in Zambia, Figure 7 suggests  
422 that this link is only rarely realized and requires very long dispersal events. In contrast,  
423 we find that dispersal between the Moremi NP and Chobe NP are relatively frequent and  
424 require fewer steps, which can be expected given that the areas are located close to each  
425 other.

## 426 **4 Discussion**

### 427 **4.1 Short Summary (90%)**

428 To this end, we used integrated step selection functions to analyse data of dispersing wild  
429 dogs and parametrize a fully mechanistic movement model describing how dispersers move  
430 through the available landscape. We employed the parametrized model to simulate 80'000  
431 dispersing wild dogs, moving across the extent of the KAZA-TFCA, the world's largest  
432 transboundary conservation area. Based on simulated dispersal trajectories, we prepared  
433 a set of complementary maps, all geared towards a better understanding of dispersal and  
434 landscape connectivity. The set of maps included a heatmap, revealing frequently traversed  
435 areas, a betweenness-map, delineating critical dispersal corridors connecting different re-  
436 gions, and a map of inter-patch connectivity, indicating presence or absence of functional  
437 links between national parks, as well as the average dispersal duration required realize those  
438 links. With this, we showcase that integrated step selection analysis holds the potential to  
439 serve as simple, yet powerful mechanistic movement model to simulate animal movement and  
440 assess landscape connectivity. Importantly, such an individual-based approach overcomes  
441 several shortcomings of traditional connectivity models, such as least-cost analyses and cir-  
442 cuit theory. Nevertheless, we support the idea that simulations only serve as a complement,  
443 and not as substitute to more traditional connectivity modeling techniques.

444 **4.2 Movement Model (50 %)**

445 Our most parsimonious movement model comprised of a habitat kernel and a movement ker-  
446 nel that describe in detail how dispersers move through the available landscape. Parameter  
447 estimates revealed that dispersing wild dogs avoid water, prefer proximity to water, avoid  
448 woodland, prefer shrubs/grassland, and avoid areas dominated by humans. This is in line  
449 with an earlier dispersal model, where we primarily investigated the habitat kernel Hofmann  
450 et al. (2021), and suggests that the introduction of additional covariates only marginally  
451 impacted qualitative results. Even though corresponding effect sizes were moderate, the  
452 model suggested that movement behavior of dispersers differs depending on habitat charac-  
453 teristics. For instance, step lengths appear to be shorter (i.e. animals move slower) in areas  
454 covered by water in comparison to steps realized on dryland. We found similar interactions  
455 between movement covariates and other habitat covariates, highlighting how a simple ISSF  
456 can be employed to model relatively complex dispersal patterns. Correspondingly, the ISSF  
457 framework allowed us to generically model resting behavior by including a binary variable,  
458 signalling that dispersers moved were substantially slower between 17:00 and 09:00 o'clock  
459 compared to the rest of the day.

460 While this (shorter steps on water) could be caused by a bias in our data, where the  
461 straight line distance between two GPS relocations erroneously suggests movement through  
462 water, where in reality the animal circumvented water-bodies, we hypothesize that this  
463 slow-down is caused by dispersers that move through the KAZA-TFCA's floodlands and  
464 get trapped by the flood. In fact, we repeatedly observed individuals venturing across  
465 the Okavango Delta, suddenly getting surrounded by the advancing flood. Until the flood  
466 retracts, these individuals often remain on distinct "islands" on which movement is restricted  
467 to rather small steps. This also aligns with the finding that turning angles tend to be larger  
468 when individuals are close to water (or conversely, steps are larger when far from water). It  
469 seems that trapped individuals wander around, searching for a passage to escape through the  
470 inundated floodlands, unable to move in a straight-line manner. Quite similarly, our model  
471 revealed that steps are marginally shorter on woodland, but larger on shrubs/grassland,  
472 suggesting that wild dogs slow down when moving through areas densely covered by trees,  
473 but speed up when moving over shrubs/grassland. This can probably be attributed to resting  
474 periods, during which dispersing individuals seek protection in the shade. To effectively  
475 model this behavior, however, one would need to include a three-way interaction between the  
476 movement kernel, habitat kernel and a temporal measure. Instead, we generically modeled  
477 resting behavior using a binary variable, which, signaled that steps were substantially shorter

478 between 17:00 and 07:00 o'clock compared to the rest of the day. This result is rather  
479 unsurprising as it is well known that wild dogs' follow a diurnal activity pattern.

#### 480 4.3 Simulation (10%)

481 By treating the parametrized ISSF model as a fully mechanistic movement model, we were  
482 able to simulate 80'000 dispersers originating from large protected areas. Each individual  
483 was simulated over 2'000 steps, which resulted in a total of 160 Mio. simulated steps.  
484 Although the simulation only terminated after 6 days, this was largely owed to the massive  
485 extent considered (ca. 1.4 Mio. km<sup>2</sup>). Moreover, a smaller number simulated dispersers will  
486 often suffice, as the relative traversal frequency across the study area in our case converged  
487 rather quickly (Appendices).

#### 488 4.4 Maps (10%)

489 Our heatmap suggests that a large number of dispersers traverses the regions of the Moremi  
490 NP and the Chobe NP. from the Okavango Delta more likely disperse towards east than  
491 west. Indeed, only x out of our y observed dispersers ever reached the western part of the  
492 delta. Only when the flood retracts a small pathway between the city of Maun and the  
493 floodwaters of the delta emerges and enables dispersers to move towards the delta's western  
494 part.

495 While the segment running into Kafue receives a high betweenness score, it was actually  
496 only rarely traversed by our simulated dispersers, as can be seen from the dark colors in  
497 this region in Figure 5. It is therefore worth noting that the betweenness metric highlights  
498 crucial bottlenecks that are relevant for connecting remote regions, it does not directly yield  
499 information about the frequency at which these bottlenecks are used.

#### 500 4.5 General (20%)

501 A major benefit of the simulation-based approach is that the domain of endpoints does  
502 not need to be determined *a priori*. Instead, each endpoint emerges naturally as the result  
503 of a simulated dispersal trajectory. This is particularly important when modeling dispersers,  
504 mainly because dispersing individuals venture into unknown territory and do not necessarily  
505 move towards a predetermined endpoint. Nevertheless, in cases where individuals do exhibit  
506 such preferences, the incorporation of attraction points in the corresponding ISSF movement  
507 model allows to render them.

508 While endpoints emerge naturally from the dispersal process, startpoints still need to

509 be specified *a priori* by the modeler. Here, we placed source points within protected areas  
510 large enough to sustain viable wild dog populations. This was done under the simplifying  
511 assumption that wild dogs only survive in formally protected areas, which is in line with sci-  
512 entific findings (Woodroffe and Ginsberg, 1999; Woodroffe and Sillero-Zubiri, 2012; Van der  
513 Meer et al., 2014; ?). In some cases, exact locations of source populations are known and  
514 source points can easily be placed accordingly (Kanagaraj et al., 2013). In other cases,  
515 comparable knowledge may be lacking and it may be more appropriate to delineate likely  
516 source patches using habitat suitability models (Squires et al., 2013). Because we did not  
517 investigate the sensitivity of our results with respect to the exact location of source points,  
518 this is something that needs further investigation in the future.

519 Another advantage of simulation-based approaches is that they render time explicitly.  
520 This enables to answer questions such as: “*How long will it take a disperser to move from A to B?*” or *Is it possible for a disperser to move from A to B within X days?*. These are  
521 interesting questions and they shift the focus from a structural to a more functional point  
522 of view. However, an explicit representation of time requires that speed (step length) and  
523 directionality during motion is approapriately modeled (Kanagaraj et al., 2013). Because  
524 ISSFs enable to model these two components adequately, the method offers a powerful  
525 framework for simulations. Besides this, one also needs to decide on a meaningful dispersal  
526 duration when simulating movement. We decided to simulate individuals for 2'000 steps,  
527 which is at the upper end of observed dispersal durations and likely resulted in overestimated  
528 landscape connectivity. Nevertheless, it requires little tweaking to subset from the generated  
529 simulations to any dispersal duration desired. In fact, one could randomly sample dispersal  
530 durations based on observed dispersal events. In most cases, however, it will be more  
531 convenient and insightful to simulate relatively extensive dispersal events and only subsample  
532 afterwards.

534 While we have assumed a set of static covariates when simulating dispersal, an explicit  
535 representation theoretically allows to render seasonality in covariate layers. This is an im-  
536 portant aspect in ecosystems where seasonality substantially influences landscape connec-  
537 tivity. With least-cost analysis and circuit theory, seasonality can merely be incorporated  
538 by producing a multitude of permeability surfaces, each depicting landscape permeability  
539 in a different season, and then applying the connectivity models to those surfaces (Benz  
540 et al., 2016; Osipova et al., 2019). With individual-based simulations, on the other hand,  
541 seasonal covariates can be updated as the simulated dispersers move. As such, seasonality  
542 would directly influence movement, i.e. the process that ultimately leads to connectivity.

543 For instance, in our simulation we represented the Okavango Delta statically and assumed  
544 a relatively extended flood. In this regard, the maps presented in the results section may be  
545 most representative of the period shortly after the wet-season, when floodlevels in the Delta  
546 are at their maximum. During the dry season, however, the flood considerably retracts  
547 and potentially clears the way for wild dogs dispersing from the Moremi-Game reserve into  
548 the south-western section of the Delta. Consequently, instead of using a static floodmap,  
549 one could render the flood dynamically. Hence, the floodlevels would be updated as the  
550 dispersers move, which would allow studying how connectivity evolves as the flood climaxes  
551 and retracts again.

552 We simulated dispersal using point estimates from our most parsimonious movement  
553 model, yet the degree to which our results depend on those estimates is unknown. Given  
554 that data from dispersal studies on endangered species is scarce, point estimates may be  
555 quite inaccurate, therefore leading to erroneous inference (Wiegand et al., 2003; Kramer-  
556 Schadt et al., 2007). Rather than using point estimates, an alternative may be to simulate  
557 dispersers using a set of randomized preferences imposed by the uncertainty reported in the  
558 model output. We urge future studies to further investigate investigate the sensitivity of  
559 ISSF simulations with respect to estimated habitat preferences.

560 We have previously attributed the weak significance of distance to water to the fact that  
561 we did not control for the presence or absence of conspecifics. We stick to this reasoning  
562 as our expanded model still shows a rather large uncertainty around the respective beta  
563 coefficients. To better gauge the importance and influence of this covariate, future studies  
564 will need to control for inter- and intra-specific interactions that may explain why and when  
565 dispersers are attracted to or afraid of waterbodies.

566 Comparable simulations that are based on empirical data are also a fundamental compo-  
567 nent for spatially realistic population models in which dispersal is rendered more realistically  
568 and does not merely depend on the distance between habitat patches.

569 An important benefit of ISSF simulations is that the framework always considers avail-  
570 ability. That is, the propensity of a simulated disperser to realize a certain step is always  
571 contingent on the set of alternative steps. As such, a disperser surrounded by relatively  
572 unsuitable habitat will still move and disperse instead of getting stuck.

573 Even though connectivity is generally believed to promote population viability, it has  
574 also been pointed out that improved connectivity may cause ecological traps, especially when  
575 connectivity into or through human-dominated landscapes is promoted. In such instances,  
576 connectivity increases the risk of encountering humans and facilitates persecution by humans.

577 By overlapping simulated trajectories with a map of human influence, such ecological traps  
578 could be pinpointed.

579 We did not model mortality during dispersal in our simulations. This was a simplifying  
580 assumption that only inaccurately reflects true dispersal. It is well known that wild dogs  
581 often die during dispersal in result of deadly encounters with competing predators, but also  
582 due to road kills or human persecution (Woodroffe and Sillero-Zubiri, 2012; ?). In result,  
583 mortality during dispersal may limit realized connectivity, especially in areas that wild dogs  
584 are unfamiliar with and in areas with a high potential for human-wildlife conflict (Cozzi  
585 et al., 2020).

586 Due to a lack of information on wild dog densities across the extent of the KAZA-TFCA,  
587 we assumed and simulated an almost uniform distribution of dispersers across protected  
588 areas. In some cases, prior knowledge about the density of potential dispersers is available  
589 and can be used to adjust the number of simulated individuals accordingly. Instead of  
590 tweaking the number of simulated individuals, one could also weight each trajectory relative  
591 to the density of potential dispersers in the corresponding source areas, such that trajectories  
592 from areas with high density would enter the heatmap with a higher weight.

593 One of the major benefits of individual-based simulations is the ability to make the tem-  
594 poral dimension of movement explicit. This allows to investigate how connectivity depends  
595 on the dispersal duration, something that is not possible with traditional least-cost or circuit  
596 theory methods.

597 Optimally, one should simulate additional dispersers until the amount of newly gained  
598 information lies beyond a certain threshold, i.e. until some sort of convergence is achieved.  
599 However, due to the myriad of outcomes in movement behavior, this would often imply  
600 countless repetitions for each source points at each location where dispersal is possibly  
601 initiated. This is computationally infeasible.

602 In some European countries, the comeback of large predators, such as bears, lynx, and  
603 the wolf, has triggered emotional discussions and raised public concern (Behr et al., 2017),  
604 particularly in areas with free-roaming livestock that may be preyed upon by the returned  
605 species. In cases where recent locations of such predators are known, an early warning system  
606 based on simulations could serve to forewarn about potential encounters and thereby  
607 increase public acceptance of large predators.

608 We do not dismiss the application of least-cost analysis or circuit theory in any way.  
609 Rather, we propose to use simulations from IBMMs complementary to least-cost analysis and  
610 circuit theory in order to provide a more comprehensive analysis of landscape connectivity.

611 In fact, simulations from IBMMs could be employed to identify likely connections between  
612 habitat patches in a first place and only afterwards least-cost paths and corridors can be  
613 drawn between such likely connections. Thus far, dispersal kernels or thresholded least cost  
614 paths have been used for this.

615 Each map that we produced from simulated trajectories accentuates a different aspect  
616 of connectivity. The heatmap, for example, puts emphasis on areas that are frequently tra-  
617 versed, even if such areas represent “dead ends” where dispersers get trapped and bounce  
618 off from obstacles. Hence, the map is useful to determine locations where a disperser is  
619 likely to show up, yet not necessarily to determine corridors that are worthwhile to be pro-  
620 tected. The betweenness map, on the other hand, brings out those areas that are relevant  
621 in connecting different regions in the landscape. In this regard, the betweenness map is  
622 most pertinent to the delineation of dispersal corridors and may serve as an alternative to  
623 least-cost algorithms. Finally, the inter-patch connectivity map illustrates the frequency at  
624 which dispersal between distinct habitat patches occurs, as well as the average dispersal  
625 duration that passes when individuals move between those patches. This knowledge serves  
626 to gauge the amount of gene flow between habitat patches and can be employed to determine  
627 whether two habitats are connected or not.

## 628 **5 Authors' Contributions**

629 D.D.H., D.M.B., A.O. and G.C. conceived the study and designed methodology; D.M.B.,  
630 G.C., and J.W.M. collected the data; D.D.H. and D.M.B. analysed the data; G.C. and A.O.  
631 assisted with modeling; D.D.H., D.M.B., and G.C. wrote the first draft of the manuscript and  
632 all authors contributed to the drafts at several stages and gave final approval for publication.

## 633 **6 Data Availability**

634 GPS movement data of dispersing coalitions will be made available on dryad at the time of  
635 publication. Access to all R-scripts for our analyses is provided through Github.

## 636 **7 Acknowledgements**

637 We thank the Ministry of Environment and Tourism of Botswana for granting permission to  
638 conduct this research. We thank C. Botes, I. Clavadetscher, and G. Camenisch for assisting  
639 with wild dog immobilizations. We also thank B. Abrahms for sharing her data of three

640 dispersing wild dogs. Furthermore, we are indebted to Johannes Signer for assisting with the  
641 simulation algorithm. This study was funded by Basler Stiftung für Biologische Forschung,  
642 Claraz Foundation, Idea Wild, Jacot Foundation, National Geographic Society, Parrotia  
643 Stiftung, Stiftung Temperatio, Wilderness Wildlife Trust Foundation, Forschungskredit der  
644 Universität Zürich, and a Swiss National Science Foundation Grant (31003A\_182286) to A.  
645 Ozgul.

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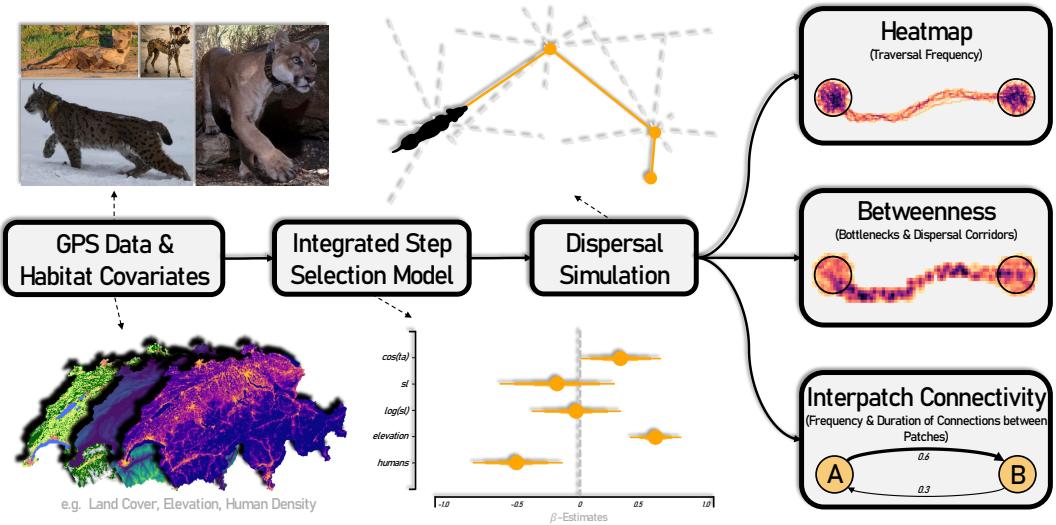
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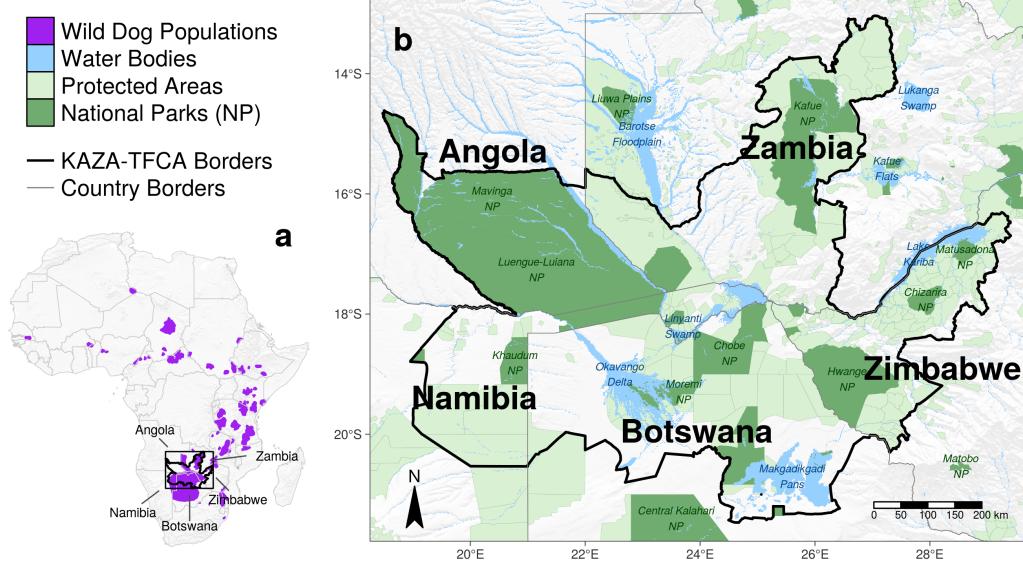
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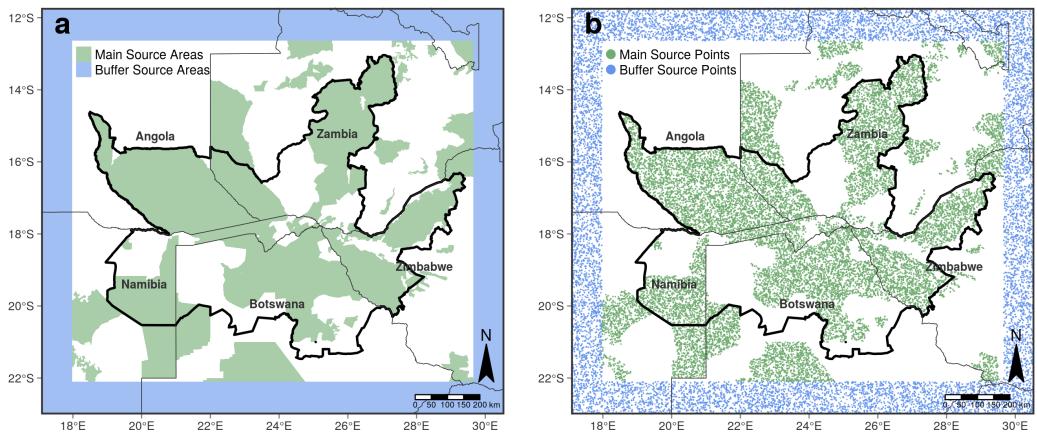
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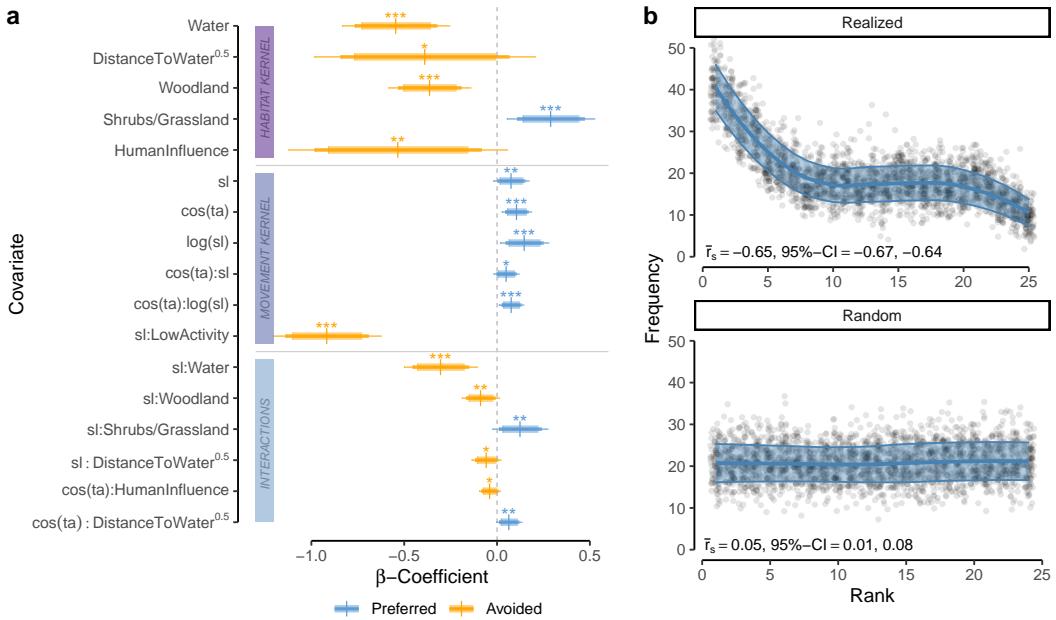
**Figure 1:** Flowchart of the simulation-based connectivity analysis. First, GPS data and habitat covariates have to be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement kernels. The parametrized model is then treated as an individual-based movement model and used to simulate dispersal trajectories. Ultimately, simulated trajectories serve to produce a set of maps that are pertinent to landscape connectivity. This includes a heatmap, indicating the relative traversal frequency across the study area, a betweenness map, highlighting movement corridors and bottlenecks, and, finally, an inter-patch connectivity map, where the frequency of connections and their average duration can be depicted. Photos: Whom to cite? Vectronics or Photographers?



**Figure 2:** Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA and encompassing parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA represents the world's largest terrestrial conservation area and covers a total of 520'000 km<sup>2</sup>. Its purpose is to re-establish connectivity between already-existing national parks (dark green) and other protected areas (light green). The dispersal data used in this study was collected on a free-ranging African wild dog population inhabiting the Moremi National Park in northern Botswana.

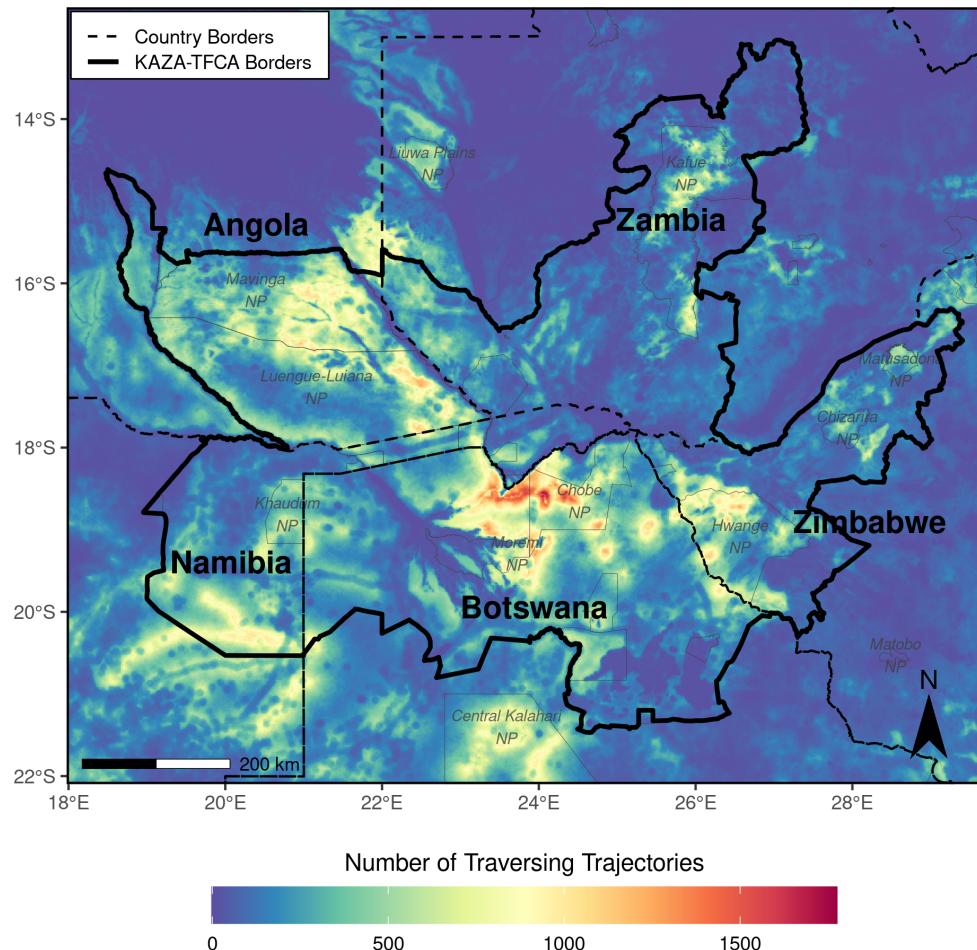


**Figure 3:** (a) Different source areas from which we released virtual dispersers. We only considered contiguous protected areas (national parks, game reserves, and forest reserves) that were larger than  $700 \text{ km}^2$  (green). This area corresponds to the average home range requirement for viable wild dog populations (Pomilia et al., 2015). To render potential immigrants into the study system, we also initiated dispersers within a buffer zone (blue) surrounding the main study area. (b) Source points from which dispersers were released. 50'000 dispersers were released from the main study area (green dots) and another 30'000 dispersers within the virtual buffer (blue dots).

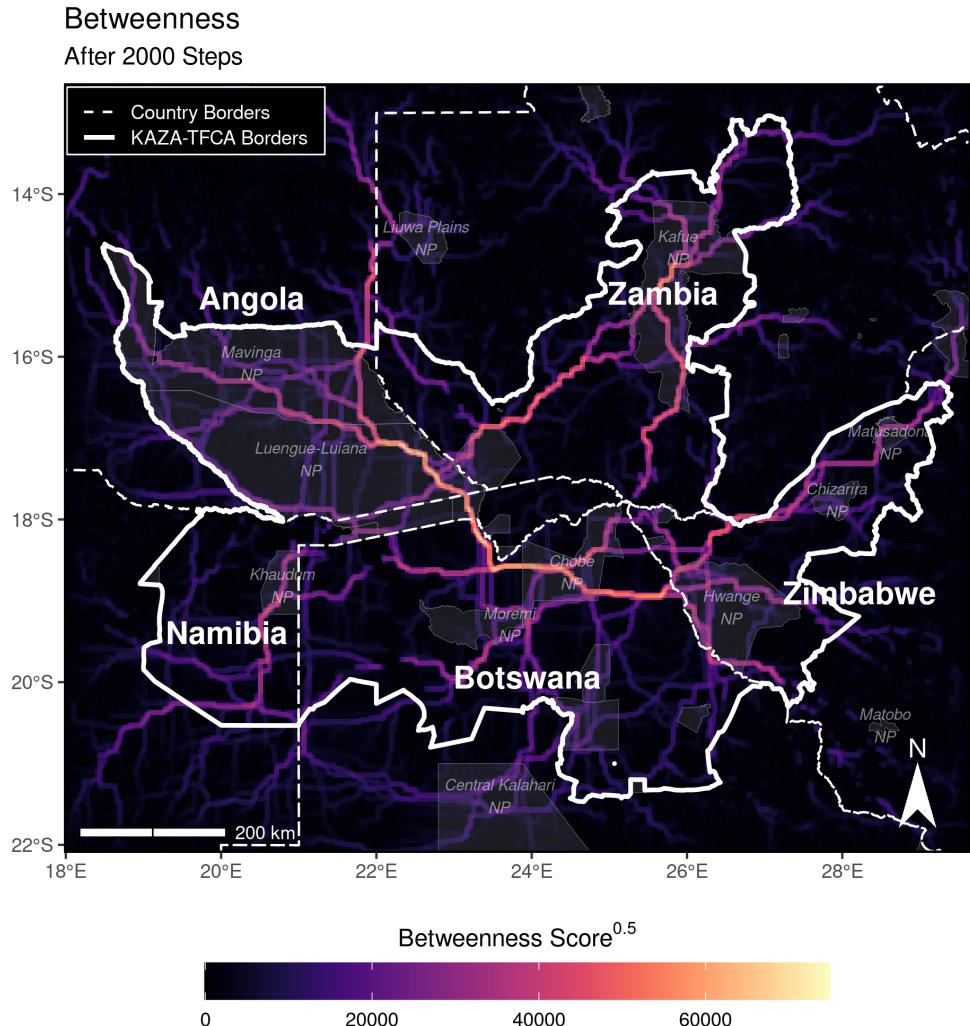


**Figure 4:** (a) Most parsimonious movement model for dispersing wild dogs. The model includes a habitat kernel, a movement kernel, as well as their interactions. The orange and blue line segments delineate the 90%, 95%, and 99% Confidence-Intervals around the respective  $\beta$  coefficients. Significance codes: \*  $p < 0.10$ , \*\*  $p < 0.05$ , \*\*\*  $p < 0.01$ . (b) Results from the k-fold cross validation procedure. The upper plot shows rank frequencies of predicted realized scores according to model predictions with known preferences, whereas the lower plot shows rank frequencies when assuming random preferences. The blue ribbon shows the prediction interval around a loess smoothing regression that we fitted to ease the interpretation of the plots.

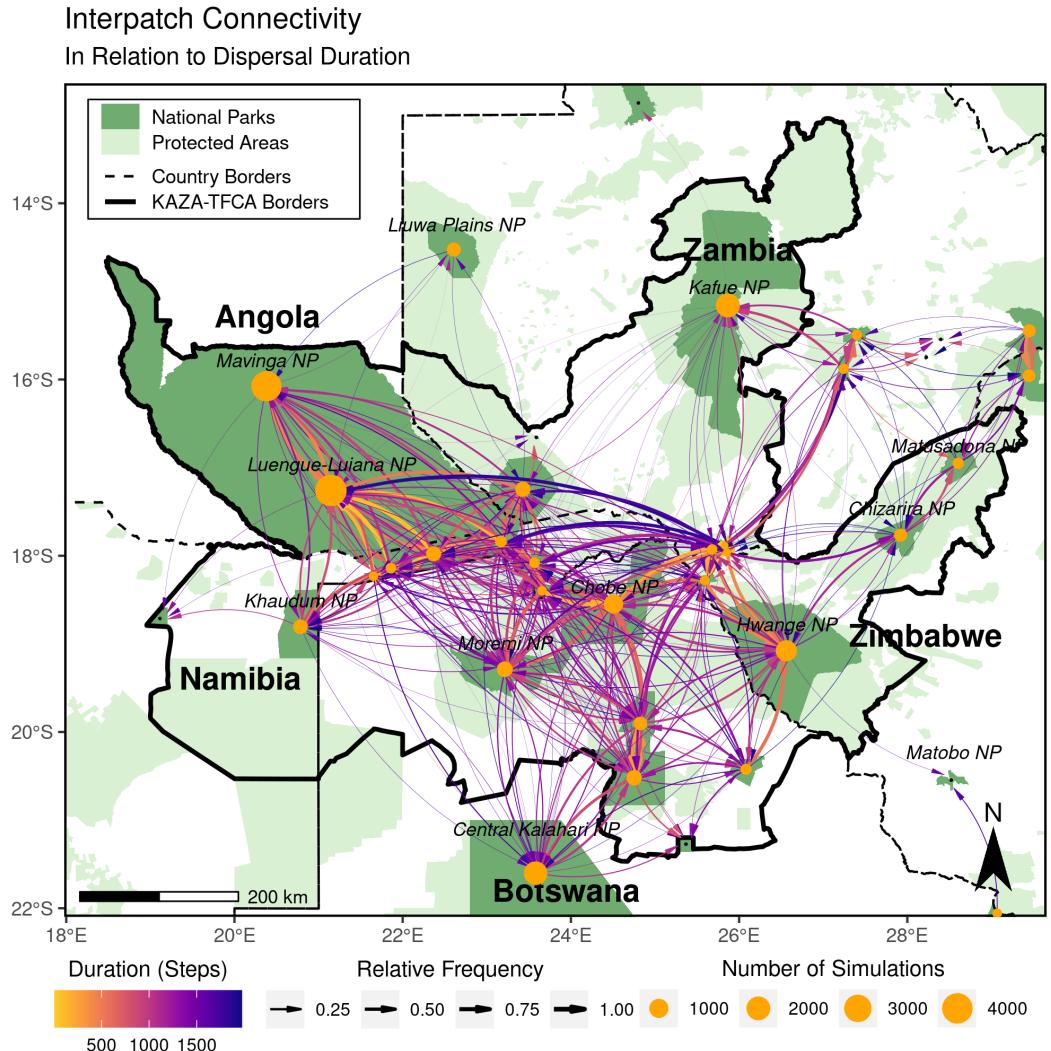
Heatmap  
After 2000 Steps



**Figure 5:** Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step selection model that we fit to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied all simulated trajectories. Consequently, the map highlights areas that are frequently traversed by virtual dispersers. Further heatmaps showing the traversal frequency after different numbers of steps are provided in Appendix S3.



**Figure 6:** Betweenness scores of each raster cell in a raster with  $5 \times 5$  km resolution. Betweenness scores were determined based on simulated dispersal events. A high betweenness score highlights cells that are exceptionally relevant in connecting different regions in the study area. That is, the higher the betweenness score, the more often a pixel lies on a shortest path between adjacent areas. In this sense the metric can be used to pinpoint discrete movement corridors. Note that we square-rooted betweenness scores to improve visibility of corridors with low scores.



**Figure 7:** Network on simulated dispersal trajectories highlighting connections between national parks (dark green). Yellow bubbles represent the center of the different national parks and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent national parks that were smaller than  $700 \text{ km}^2$  and therefore did not serve as source areas. Arrows between national parks illustrate between which national parks the simulated dispersers successfully moved and the color of each arrow shows the average number of steps (4-hourly movements) that were necessary to realize those connections. Additionally, the line thickness indicates the relative number of dispersers originating from a national park that realized those connections. Note that a similar network view could be adopted to investigate connectivity between other protected areas need not to be restricted to national parks.

**Table 1:** Most parsimonious movement model for dispersing wild dogs. The model consists of a movement kernel, a habitat kernel, and their interactions. The movement kernel describes preferences with regards to movement behavior, whereas the habitat kernel describes preferences with respect to habitat conditions. Interactions between the two kernels indicate that movement preferences are contingent on habitat conditions. Note that all covariates were standardized to a mean of zero and standard deviation of 1. Plots to aid with the interpretation of this model are given in Appendix S2.

Kernel	Covariate	Coefficient	SE	p-value	Sign.
Habitat Kernel	Water	-0.546	0.112	< 0.001	***
	DistanceToWater <sup>0.5</sup>	-0.390	0.231	0.092	*
	Woodland	-0.364	0.086	< 0.001	***
	Shrubs/Grassland	0.288	0.092	0.002	***
	HumanInfluence	-0.535	0.229	0.019	**
Movement Kernel	sl	0.075	0.037	0.042	**
	cos(ta)	0.105	0.031	0.001	***
	log(sl)	0.146	0.051	0.004	***
	cos(ta) : sl	0.049	0.026	0.064	*
	cos(ta) : log(sl)	0.076	0.026	0.003	***
Interaction	sl : LowActivity	-0.917	0.113	< 0.001	***
	sl : Water	-0.305	0.076	< 0.001	***
	sl : Woodland	-0.089	0.039	0.023	**
	sl : Shrubs/Grassland	0.124	0.058	0.032	**
	sl : DistanceToWater <sup>0.5</sup>	-0.058	0.031	0.056	*
		cos(ta) : HumanInfluence	-0.040	0.022	0.070
		cos(ta) : DistanceToWater <sup>0.5</sup>	0.063	0.026	0.017

Significance codes: \*  $p < 0.10$    \*\*  $p < 0.05$    \*\*\*  $p < 0.01$