

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

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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 and preservation 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 number 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 as a simple individual-based and spatially explicit model 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 model describing how dispersing wild dogs move through the landscape. Based on this model, we simulate 80'000 dispersers moving across the extent of the KAZA-TFCA. We then generate a set of connectivity related maps in order to exemplify how simulated data helps detecting and interpreting likely movement corridors relevant to preserve connectivity. 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 1 Introduction

² 1.1 Importance of Dispersal & Connectivity (90%)

³ Dispersal is defined as the movement of individuals away from their natal location to the
⁴ site of first reproduction Howard (1960). It is a vital process governing the social structure
⁵ of wild animal populations that are distributed in space (Hanski, 1998; Clobert et al., 2012)
⁶ and may strongly affect population dynamics at different spatial and social scales (Hanski,
⁷ 1999a; Clobert et al., 2012). Dispersal allows species to avoid inbreeding and maintain ge-
⁸ netic diversity (Perrin and Mazalov, 1999, 2000; Frankham et al., 2002; Leigh et al., 2012;
⁹ Baguette et al., 2013), to rescue small, non-viable populations (Brown and Kodric-Brown,
¹⁰ 1977), and to promote the colonization of unoccupied habitats (Hanski, 1999b; MacArthur
¹¹ and Wilson, 2001). However, successful dispersal requires a sufficient degree of landscape
¹² connectivity (Fahrig, 2003; Clobert et al., 2012), which is why the identification and pro-
¹³ tection of major dispersal corridors has become a fundamental task in conservation science
¹⁴ (Nathan, 2008; Doerr et al., 2011; Rudnick et al., 2012). Importantly, the ability to pinpoint
¹⁵ relevant dispersal hotspots requires information on movement behavior during dispersal and
¹⁶ knowledge about factors that limit dispersal and therefore connectivity (Baguette et al.,
¹⁷ 2013; Vasudev et al., 2015).

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

¹⁹ Thanks to novel technologies developed over the past decades, particularly of GPS/Satellite
²⁰ radio-collars, the use of GPS data to study animal dispersal and connectivity has accelerated
²¹ (Elliot et al., 2014; Jönsson et al., 2016; Williams et al., 2019). Additionally, the advent
²² of publicly accessible satellite imagery and sophisticated remote sensing techniques to rep-
²³ resent the physical landscape through which individuals disperse have heralded a “golden
²⁴ age of animal tracking” (Kays et al., 2015). Concurrently, the availability of large amounts
²⁵ of empirical data and an increased computational power have led to the development of
²⁶ numerous techniques to study dispersal and highlight critical corridors between subpopula-
²⁷ tions (Boyce et al., 2002; Fortin et al., 2005; Cushman and Lewis, 2010; Zeller et al., 2012;
²⁸ Diniz et al., 2020).

²⁹ 1.3 Resource Selection & Connectivity (90%)

³⁰ *Resource selection functions* (Boyce et al., 2002) and derived methods such as *step selection*
³¹ *functions* (Fortin et al., 2005) and *path selection functions* (Cushman and Lewis, 2010) have

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

46 **1.4 Issues with Least-Cost Paths (90%)**

47 In LCP analysis, for instance, a least costly path always exists, even if associated movement
48 costs are unreasonably high and will never be incurred by a dispersing individual. The
49 method also presumes that animals have an infinite perceptual range and a preconceived end-
50 point in mind, such that they choose a cost-minimizing route accordingly. These assumptions
51 may be reasonable for migrating animals, yet they are unlikely to hold true for dispersers,
52 which typically move over long distances into unknown territory (Koen et al., 2014; Abrahms
53 et al., 2017; Cozzi et al., 2020). Another issue of LCPs analysis concerns the fact that least-
54 costly routes, by their very nature, are only one pixel wide. This implies that the width of
55 inferred movement routes depends on the resolution of chosen covariate layers and may not
56 be biologically meaningful (Diniz et al., 2020). Although some of these deficiencies can be
57 addressed using less stringent versions of the LCP algorithm (e.g. least-cost *corridors* (Pinto
58 and Keitt, 2009), *thresholded* least-cost paths (Landguth et al., 2012), and *randomized* least-
59 cost paths (Panzacchi et al., 2016; Van Moorter et al., 2021)), a certain degree of arbitrariness
60 remains.

61 **1.5 Issues with Circuit Theory (90%)**

62 CT entails similarly unreasonable restrictions that are hardly ever met. Because CT only
63 allows movements from a source cell to its 4 or 8 adjacent cells, it implicitly posits a per-

64 perceptual range of a single pixel. Assuming that covariate layers are usually resolve between
65 30 m and 1 km, this hardly ever renders the true capability of animals to perceive the envi-
66 ronment. Moreover, CT builds on the assumption of a complete random walk (Diniz et al.,
67 2020), implying that directional biases cannot be rendered. Nevertheless, directionality is a
68 commonly observed characteristic in animal movement (Bovet and Benhamou, 1991; Schultz
69 and Crone, 2001), especially in dispersing individuals (Cozzi et al., 2020; Hofmann et al.,
70 2021).

71 **1.6 Issues of Both Methods**

72 Finally, neither LCP analysis nor CT are capable of rendering the temporal dimension of
73 dispersal. Statements about the expected duration required to traverse a certain corridor
74 are therefore impossible. Likewise, because movement is not modeled explicitly, neither of
75 the methods allows to render interactions between movement and habitat preferences of
76 the focal species. Connectivity therefore merely arises in result to the landscape structure,
77 which is usually referred to as structural connectivity. While structural connectivity yields
78 insights in the *potential* of the landscape to be traversed, it does not enable to quantify the
79 *actual* gene flow through the area. Consequently, a functional on connectivity, which also
80 renders the behavioral response of the animal with respect to prevailing habitat conditions,
81 is often more desirable (Tischendorf and Fahrig, 2000; Baguette et al., 2013).

82 **1.7 What about IBMMS? (90%)**

83 To address the issues inherent to LCPs and CT, individual-based movement models (IBMMS)
84 have been proposed and applied (Diniz et al., 2020). In these models, dispersal is simulated
85 spatially explicitly, based on movement rules that determine how individuals move over
86 and interact with the prevailing landscape (Gustafson and Gardner, 1996; Gardner and
87 Gustafson, 2004; Graf et al., 2007; Kramer-Schadt et al., 2004; Revilla et al., 2004; Revilla
88 and Wiegand, 2008; Kanagaraj et al., 2013; Clark et al., 2015; Allen et al., 2016; Hauenstein
89 et al., 2019; Zeller et al., 2020; Vasudev et al., 2021). Using the simulated trajectories, one
90 can calculate a set of connectivity metrics, such as inter-patch connectivity and traversal
91 frequency to reveal major dispersal corridors (Kanagaraj et al., 2013; Bastille-Rousseau
92 et al., 2018; Hauenstein et al., 2019; Zeller et al., 2020). However, while IBMMS can be
93 employed to overcome any of the shortcomings intrinsic to LCPs and CT and provide a more
94 functional view on connectivity, they can be challenging to fit and require vast amounts of
95 data collected during dispersal (Diniz et al., 2020). Moreover, most individual-based models

96 are heavily influenced by subjective decisions, rendering replication and validation of results
97 difficult.

98 **1.8 Step Selection Analysis (90%)**

99 Here, we investigate the usefulness of integrated step selection functions (ISSFs, Avgar et al.,
100 2016), as a relatively simple but powerful IBMM based on which dispersal can be simulated.
101 While regular SSFs were intended to learn about relative habitat preferences of the focal
102 species (Fortin et al., 2005; Thurfjell et al., 2014; Avgar et al., 2017), the method has been
103 generalized and now enables to jointly study habitat and movement preferences, as well as
104 potential interactions between movement and habitat preferences (Avgar et al., 2016; Signer
105 et al., 2017; Fieberg et al., 2020). ISSFs therefore provide a relatively simple method to
106 model complex movement behavior where movement results from two intertwined behavioral
107 kernels (e.g. Prokopenko et al., 2017; Munden et al., 2020). Importantly, a parametrized
108 ISSF model can be viewed as a fully mechanistic movement model based on which individual
109 movement trajectories can be simulated (Avgar et al., 2016; Signer et al., 2017). In fact,
110 Signer et al. (2017) used ISSF to simulate steady state utilization distributions of resident
111 animals. However, the degree to which such simulations are helpful in detecting movement
112 corridors and modeling landscape connectivity is unknown.

113 **1.9 Study Species & Study Area (90%)**

114 One of the species for which long-term viability relies on sufficient landscape connectivity
115 is the endangered African wild dog *Lycon pictus*. While once present across entire sub-
116 Saharan Africa, wild dogs have disappeared from a vast majority of their historic range
117 due to persecution by humans, habitat fragmentation and destruction, and deadly diseases
118 (Woodroffe and Sillero-Zubiri, 2012). As of today, only 6'000 free-ranging individuals remain
119 in small and spatially scattered subpopulations (Woodroffe and Sillero-Zubiri, 2012). Within
120 those subpopulations, wild dogs form cohesive packs comprising 8 to 12 adults and their
121 offspring McNutt (1995). After reaching sexual maturity, male and female offspring form
122 same-sex coalitions and disperse from their natal pack (McNutt, 1996; Behr et al., 2020).
123 New packs are formed when dispersing coalitions join unrelated opposite-sex dispersing
124 coalitions (McNutt, 1996). Dispersing wild dogs can cover several hundred kilometers across
125 a variety of landscapes (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020;
126 Hofmann et al., 2021). One of the few strongholds for this species lies near the Moremi Game
127 Reserve in northern Botswana, which is part of the world's largest transboundary protected

128 area, namely the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). This
129 area has originally been intended to facilitate migration of elephants, but is expected to
130 benefit a multitude of other species (Elliot et al., 2014; Brennan et al., 2020; Hofmann et al.,
131 2021).

132 1.10 Previous Paper (90%)

133 In a previous study, we assessed landscape connectivity for dispersing African wild dogs
134 within the KAZA-TFCA using a least-cost corridor approach (Hofmann et al., 2021). For
135 this, we fitted a basic habitat selection model based on which we predicted landscape per-
136 meability. We now expand on this knowledge and use ISSF to develop a more detailed
137 movement model of dispersing wild dogs (Figure 1). We then use this model to simulate
138 dispersers moving across the KAZA-TFCA. Based on simulations, we compute heatmaps
139 and identify potential dispersal hotspots. We also showcase how network metrics relevant
140 to landscape connectivity can be computed. Our results show that a simulation-based ap-
141 proach yields several major benefits over traditional connectivity modeling techniques. Most
142 importantly, simulations provide a more generic view on how connectivity emerges and to
143 which degree connectivity depends on the dispersal duration. In addition, by generating
144 proper dispersal trajectories, network theory can be applied to calculate network metrics
145 that are pertinent to connectivity analysis.

146 2 Methods

147 2.1 Study Area (90%)

148 The study area was defined by a bounding box centered at -17°13'9"S, 23°56'4"E (Figure 2a)
149 stretching over 1.3 Mio. km² and encompassing the entire KAZA-TFCA (Figure 2b). The
150 KAZA-TFCA represents the world's largest transboundary conservation area and comprises
151 parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia. It covers a total of 520'000
152 km² and hosts a diverse landscape, ranging from savanna to grassland and from dry to moist
153 woodland habitats. In its center lies the Okavango Delta, a dominant hydrogeographical
154 feature and the world's largest flood-pulsing inland delta. The wet season within the KAZA-
155 TFCA lasts from November to March and is out of phase with the flood in the Okavango
156 Delta, which peaks between July and August (McNutt, 1996; Wolski et al., 2017). Although
157 large portions within the KAZA-TFCA are designated national parks or other protected
158 areas, considerable human influence remains due to roads, agricultural sites and settlements

¹⁵⁹ and villages that are distributed across the KAZA-TFCA's landscape.

¹⁶⁰ 2.2 GPS Relocation Data (90%)

¹⁶¹ Between 2011 and 2019, we collected GPS relocation data on dispersing wild dogs from a
¹⁶² free-ranging wild dog population inhabiting the Moremi National Park in northern Botswana
¹⁶³ (Cozzi et al., 2020; Hofmann et al., 2021). We selected potential dispersers based on age,
¹⁶⁴ pack size, number of same-sex siblings within the pack, and presence of unrelated opposite-
¹⁶⁵ sex individuals in the pack (McNutt, 1996; Behr et al., 2020). We immobilized selected
¹⁶⁶ individuals using a cocktail of Ketamine/Xylazine/Atropine (Osofsky et al., 1996; Cozzi
¹⁶⁷ et al., 2020) that was injected by dart, fired from a CO₂-pressurized gun (*DAN-Inject*,
¹⁶⁸ *Denmark*). Immobilized individuals were fitted with GPS/Satellite radio collars (*Vertex*
¹⁶⁹ *Lite*; *Vectronic Aerospace GmbH, Berlin*) that guaranteed automated drop-off through a
¹⁷⁰ decomposable piece of cotton. Handling and collaring of all individuals was supervised by
¹⁷¹ a Botswana-registered wildlife veterinarian and all individuals quickly rejoined their pack
¹⁷² after immobilization.

¹⁷³ 16 collared individuals eventually dispersed, each in a separate same-sex dispersal coalition (7 female and 9 male coalitions). During dispersal, collars were programmed to record
¹⁷⁴ a GPS fix every 4 hours. Collected relocations were regularly transmitted over the Iridium
¹⁷⁵ satellite system, which allowed remote tracking of individuals, even if they left the main
¹⁷⁶ study area and crossed international borders. Because behavior during dispersal is more
¹⁷⁷ pertinent for assessing landscape connectivity (Elliot et al., 2014; Abrahms et al., 2017), we
¹⁷⁸ discarded all data that was collected during residency and only retained GPS data recorded
¹⁷⁹ during dispersal. In some instances, exact dispersal dates were known from field obser-
¹⁸⁰ vations. Where this was not the case, determined dispersal phases using the net-squared
¹⁸¹ displacement metric. Net squared displacement measures the squared Euclidean distance of
¹⁸² a GPS relocation to a reference point (Börger and Fryxell, 2012), which in our case was set
¹⁸³ to the center of each individual's natal home range. As such, dispersal was deemed to have
¹⁸⁴ started when an individual left its natal home range and ended once individuals became
¹⁸⁵ sedentary again. As previous research revealed similar behavior of females and males during
¹⁸⁶ dispersal (Woodroffe et al., 2019; Cozzi et al., 2020), we did not distinguish between sexes.
¹⁸⁷ After collection, we converted collected GPS coordinates (n = 4'169) to steps, where each
¹⁸⁸ step represented the straight-line distance traveled by an individual between two consec-
¹⁸⁹ utive GPS relocations (Turchin, 1998). To ensure a regular sampling interval, we removed
¹⁹⁰ fixes that were not successfully collected on the 4-hourly schedule (\pm 15 minutes).

192 **2.3 Covariates (90%)**

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

203 Besides habitat covariates, we computed movement metrics that we used as movement
204 covariates in our models. Movement metrics were calculated for each step and included the
205 step length (`sl`), its natural logarithm (`log(sl)`), and the cosine of the relative turning angle
206 (`cos(ta)`) (for details see (Avgar et al., 2016; Fieberg et al., 2020)). Because wild dogs follow
207 a diurnal activity pattern, we also coded a binary variable (`LowActivity`) indicating whether
208 a step was realized during periods of low wild dog activity (17:00 to 09:00 local time) or
209 high wild dog activity (09:00 to 17:00 local time). Handling and manipulation of all data, as
210 well as all models and simulations were implemented with the statistical software R, version
211 3.6.6 (R Core Team, 2019). Several helper functions were written in C++ and imported into
212 R using the Rcpp package (Eddelbuettel and François, 2011; Eddelbuettel, 2013)

213 **2.4 Movement Model (80%)**

214 We used ISSFs to parametrize a mechanistic movement model for dispersing wild dogs
215 (Avgar et al., 2016). To conduct ISSF analysis, we paired each realized step with 24 ran-
216 dom steps. An observed and its 24 random steps formed a stratum and received a unique
217 identifier. We generated random steps by sampling random turning angles from a uniform
218 distribution $(-\pi, +\pi)$ and step lengths from a gamma distribution that was fitted to realized
219 steps (scale = 6'308, shape = 0.37). Along each step, we extracted and averaged spatial co-
220 variates using the `velox` package (Hunziker, 2021). We also calculated the movement metrics
221 `sl`, `log(sl)`, and `cos(ta)` for each observed and random step. To facilitate model convergence,
222 we standardized all continuous covariates to a mean of zero and a standard deviation of one.
223 Since correlation among covariates was low ($|r| > 0.6$; Latham et al., 2011), we retained all
224 of them for modeling.

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

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

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

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

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

238 The formula for the movement model was based on the habitat selection model for dis-
 239 persing wild dogs presented in Hofmann et al. (2021). In the original model, no interactions
 240 between habitat covariates (Water, DistanceToWater^{0.5}, Woodland, Shrubs/Grazing, Human
 241 Influence) and movement covariates (sl, log(sl), cos(ta)) were considered. Here, we slightly
 242 expanded this base model and proposed interactions between all movement and habitat
 243 covariates. More specifically, we started with the base model and incrementally increased
 244 model complexity by adding all possible two-way interactions between habitat covariates and
 245 movement covariates. For instance, for the covariate Water, we proposed the interactions Wa-
 246 ter:log(sl), Water:log(sl), and Water:cos(ta). Besides those combinations, we also proposed
 247 the interactions sl:cos(ta) and log(sl):cos(ta) to account for a correlation between turning
 248 angles and step lengths, as well as the interactions sl:LowActivity and log(sl):LowActivity to
 249 account for the fact that step lengths may differ due to wild dogs' diurnal activity pattern.
 250 To compare competing models and assess the most parsimonious movement model, we ran
 251 stepwise forward model selection based on Akaike's Information Criterion (AIC, Burnham
 252 and Anderson, 2002).

We validated the predictive power of the most parsimonious movement model using k-fold cross-validation for case-control studies as suggested by Fortin et al. (2009). For this, we randomly assigned 80% of the strata to a training set and the remaining 20% to a testing set. Using the training data we parametrized a movement model based on which we predicted selection scores $w(x)$ for all steps in the test data. Within each stratum, we then assigned ranks 1-25 to each step based on predicted selection scores, where rank 1 was given to the step with the highest score $w(x)$. Across all strata we determined the realized step's rank and we calculated rank frequencies of realized steps across all strata. Finally, we computed Spearman's rank correlation between ranks and associated frequencies $r_{s,realized}$. We replicated the entire procedure 100 times and computed the mean correlation coefficient ($\bar{r}_{s,realized}$), as well as its 95% confidence interval across all replicates. For comparison, we repeated the same procedure 100 times assuming random preferences, which we implemented by discarding the realized step from all strata and identifying the rank of a random step in each stratum. Again, we calculated Spearman's rank correlation coefficient ($r_{s,random}$), its mean across repetitions ($\bar{r}_{s,random}$), and its 95% confidence interval. This validation ultimately proofs a significant prediction in case the confidence intervals of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ do not overlap.

2.5 Dispersal Simulation (80%)

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

286 Mio. simulated steps.

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

295 **2.6 Source Points (90%)**

296 We released 80'000 virtual dispersers from 80'000 unique source points distributed across
297 the study area. 50'000 virtual dispersers were released from randomly selected source points
298 within contiguous protected areas larger $> 700 \text{ km}^2$ (Figure 3a), which conforms to average
299 home range requirements of resident wild dogs (Pomilia et al., 2015) and allowed us to remove
300 patches too small to host viable populations. By distributing source points randomly, the
301 number of source points per km^2 was approximately equal within protected areas. To render
302 potential immigrants into the study system, we released another 30'000 dispersers at random
303 locations inside the 100 km wide buffer zone surrounding the main study area (Figure 3b).

304 **2.7 Heatmap (100%)**

305 To identify dispersal hotspots across our study area, we created a heatmap indicating the
306 absolute frequency at which each raster-cell in the study area was visited by virtual dis-
307 persers. For this, we rasterized all simulated trajectories and tallied them into a single map.
308 If the same trajectory crossed a raster-cell twice, it was only counted once, thereby miti-
309 gating potential biases resulting from trapped individuals that were moving in circles. To
310 achieve high performance rasterization, we used the R-package `terra` (Hijmans, 2020).

311 **2.8 Betweenness (80%)**

312 To pinpoint areas of exceptional relevance for connecting remote regions inside our study
313 area, we converted simulated trajectories into a network and calculated betweenness scores.
314 For this, we overlaid the study area (including the buffer) with a regular raster resolved at
315 5 x 5 km. The centerpoint of each raster-cell acted as node in the final network and we
316 used the simulated trajectories to determine all transitions occurring from one raster-cell

317 to another, as well as the frequency at which those transitions occurred. This resulted in
318 an edge-list that we translated into a weighted network using the r-package **igraph** (Csardi
319 and Nepusz, 2006). Because **igraph** handles edge weights (ω) as costs, we inverted the
320 traversal frequency in each cell by applying $\omega = \frac{\sum_i^n TraversalFrequency_i/n}{TraversalFrequency_i}$. Finally, we used
321 the weighted network to calculate the betweenness score of each raster-cell. Betweenness
322 measures how often a specific raster-cell lies on a shortest path between two other raster-
323 cells and is therefore a useful metric to detect movement corridors (Bastille-Rousseau et al.,
324 2018).

325 **2.9 Inter-Patch Connectivity (80%)**

326 To exemplify how simulations can be used to provide a network view on connectivity, we
327 assessed inter-patch connectivity between national parks located in our study area. The
328 decision to focus on national parks was purely out of simplicity and does not imply that
329 connections between other regions are impossible. In fact, the same logic could easily be
330 expanded to include other protected areas as well. To quantify inter-patch connectivity,
331 we computed the relative frequency at which dispersers originating from one national park
332 successfully moved into another national park. Successful movement was said to be achieved
333 if the individuals' trajectory ever intersected with the corresponding national park. We also
334 recorded the step-number of the first step that ever intersected with the national park's
335 polygon. This allowed us to determine *if* and *how often* dispersers moved between certain
336 national parks, as well as to estimate *how long* dispersers had to move to realize those
337 connections.

338 **3 Results**

339 **3.1 Movement Model (80%)**

340 Compared to the base model reported in (Hofmann et al., 2021), our most parsimonious
341 movement model included several additional interactions between habitat covariates and
342 movement covariates (Figure 4 and Table 1). Although several models received an AIC
343 weight above zero (Table 1 in Appendix S1), we only considered results from the most
344 parsimonious model for simplicity. All models with positive AIC weight included similar
345 covariates (Table S1), so this decision only marginally influenced subsequent analyses. Plots
346 that aid with the interpretation of the final model are provided in Appendix S2.

347 Assuming that all other covariates are held constant, the habitat kernel reveals that

348 dispersing wild dogs avoid water but prefer its proximity. Similarly, dispersers avoid areas
349 that are covered by woodlands, yet prefer regions covered by shrublands or grasslands.
350 Finally, dispersers avoid movement through landscapes that are dominated by humans.
351 Effect sizes are rather pronounced and, except for effect for **distance to water**, effects were
352 statistically clear on the 5% significance level.

353 With regards to the movement kernel, the positive estimate for **cos(ta)** indicates that dis-
354 persers move with directional persistence, unlike what was proposed by the uniform turning
355 angle distribution. Moreover, directionality is particularly pronounced when dispersers re-
356 alize large steps (move quickly), as indicated by the positive estimates for **cos(ta):sl** and
357 **cos(ta):log(sl)**. Finally, the negative estimate for the interaction **sl:LowActivity** reveals that
358 wild dogs realize shorter steps (move slowly) outside the main activity periods during sunrise
359 and sunset. Aside from the interaction **sl:LowActivity**, which appears to strongly influence
360 movmement behavior, effect sizes are moderate, but mostly significant on the 5% significance
361 level.

362 Finally, when looking at the interactions between the movement and habitat kernels, we
363 observe that movement behavior is contingent on habitat conditions. For example, there's
364 strong evidence that dispersers realize smaller steps in areas covered by water or areas
365 covered by wooldand. Conversely, it appears that steps tend to larger in regions dominated
366 by shrubs/grassland, and shorter when the distance to water is high. Correspondingly,
367 the model suggests that directionality is lower in areas dominated by humans, yet more
368 pronounced when dispersers are far from water. However, except for the effect of **sl:Water**,
369 effect sizes are small.

370 The k-fold cross-validation procedure reveals that our model substantially outperforms a
371 random guess (Figure 4b). Confidence intervals of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ do not overlap and
372 therefore proof a reliable prediction. Furthermore, the significant correlation between ranks
373 and corresponding frequencies for realized steps indicates a good fit between predictions and
374 observations (Figure 4b). In comparison to the base model ($\bar{r}_{s,realized} = -0.55$; Hofmann
375 et al., 2021), the inclusion of interactions between movement and habitat covariates slightly
376 improved model performance.

377 **3.2 Dispersal Simulation (80%)**

378 On a machine with an octacore AMD Ryzen 7 2700X processor (8 x 3.6 GHz) and 64 GB
379 of RAM, the simulation of 1'000 dispersers moving over 2'000 steps required 90 minutes to
380 compute ($\mu = 88.90$, $\sigma = 1.87$). Consequently, the simulation of all 80'000 dispersers (160

381 Mio. steps) terminated after 120 hours, i.e. five days. However, comparable computations
382 will be substantially faster for smaller study areas and lower resolution covariates, as the
383 covariate extraction from large rasters (ca. 1.4 Mio. km²) along each step was computa-
384 tionally the most expensive task. Out of the 50'000 dispersers initiated in the main source
385 area Figure 3(a), only 4.5% eventually hit a map boundary, suggesting that we successfully
386 limited biases due to boundary effects. In contrast, 78% of the 30'000 dispersers originating
387 from the buffer zone eventually hit a map boundary, yet this was to be expected since many
388 of those dispersers originated from source points located close to the map boundary.

389 **3.3 Heatmap (80%)**

390 Figure 5 depicts the heatmap of all 80'000 simulated trajectories resulting after 2'000 steps.
391 The map shows that large portions of land beyond the borders of the KAZA-TFCA are
392 only infrequently visited by dispersers (dark blue areas), whereas within the KAZA-TFCA
393 several extensive regions are regularly traversed (bright yellow and red areas). Most no-
394 tably, the region in northern Botswana south of the Linyanti swamp stands out as highly
395 frequented dispersal hotspot. Still, the presence of several massive water bodies, such as
396 the Okavango Delta, the Makgadikgadi Pan, and the Linyanti swamp, results in consider-
397 able dispersal barriers that limit realized connectivity within the KAZA-TFCA. Similarly,
398 dispersal appears to be very limited in Zambia's and Zimbabwe's part of the KAZA-TFCA,
399 where only few areas are successfully traversed by dispersers. This can largely be attributed
400 to substantial human influences resulting from high human density, roads, and agricultural
401 activities. Outside the KAZA-TFCA, the most heavily used regions include the areas in-
402 side the Central Kalahari National Park in Botswana, the area south-west of the Khaudum
403 National Park in Namibia, and the area around the Liuwa Plains National Park in Zambia.

404 **3.4 Betweenness (80%)**

405 Betweenness scores after 2'000 simulated steps are presented in Figure 6 and reveal a set of
406 discrete dispersal corridors. Again, the dispersal corridor in northern Botswana stands out
407 and receives the highest betweenness score observed across the study area. Consequently,
408 the region serves as crucial dispersal hub that connects more remote regions in the study
409 system. Towards east, the extension of this corridor runs through the Chobe National Park
410 into the Hwange national park. From there, a further extension connects to the distant
411 Matusadona National Park in Zimbabwe. Northwest of the Linyanti ecosystem, a major
412 corridor expands into Angola, where it splits and finally traverses over a long stretch of

413 unprotected area into the Kafue National Park in Zambia. Several additional corridors
414 with slightly lower betweenness scores exist, yet most of them run within the boundaries of
415 the KAZA-TFCA. In general, only few corridors directly link the peripheral regions of the
416 KAZA-TFCA. For instance, there are only few corridors between the Matusadona National
417 Park in Zimbabwe and the Kafue National Park in Zimbabwe. Similarly, there are no direct
418 links between the Zimbabwean and Angolan “spikes” of the KAZA-TFCA.

419 **3.5 Interpatch Connectivity (80%)**

420 Results from the analysis of interpatch connectivity are given in Figure 7, but it is worth
421 pointing out that the figure is only intended as an example, as for clarity we limited the net-
422 work on national parks (NPs) only, albeit plenty of links between other protected areas exist.
423 As can be seen, interpatch connectivity between NPs in Angola, Namibia, and Botswana
424 is comparably high and dispersal durations short. In contrast, it appears that connectivity
425 towards the Kafue NP in Zambia and is low and requires long dispersal events to realize a
426 link. Similarly, there is a lack of connections to Zimbabwe’s Chizarira and Matusadona NP
427 and the more distant Lower Zambezi and Mana Pools NPs.

428 **4 Discussion**

429 **4.1 Short Summary (90%)**

430 We used integrated step selection functions to analyse data of dispersing wild dogs and
431 parametrize a fully mechanistic movement model describing how dispersers move through
432 the available landscape. We employed the parametrized model to simulate 80'000 dispersing
433 wild dogs, moving 2'000 steps across the extent of the KAZA-TFCA, the world’s largest
434 transboundary conservation area. Based on simulated dispersal trajectories, we prepared
435 a set of complementary maps, all geared towards a better understanding of dispersal and
436 landscape connectivity. The set of maps included a heatmap, revealing frequently traversed
437 areas, a betweenness-map, delineating critical dispersal corridors connecting different re-
438 gions, and a map of inter-patch connectivity, indicating presence or absence of functional
439 links between national parks. We thereby showcase that integrated step selection functions
440 offer a simple, yet powerful framework to parametrize movement models, which can further
441 be used simulate animal movement and to assess landscape connectivity. Importantly, such
442 an approach overcomes several conceptual shortcomings inherent to more traditional con-
443 nectivity models, such as least-cost analyses and circuit theory. Nevertheless, we do not

444 suggest to view such simulations as a substitute, but rather as a complement to traditional
445 connectivity modelling techniques.

446 4.2 Movement Model (80 %)

447 Our most parsimonious movement model of dispersing wild dogs comprised of a habitat
448 kernel, a movement kernel, and their interactions. Together, the kernels described in detail
449 how dispersers move through the landscape and how movement behavior is affected by
450 habitat conditions. Parameter estimates from the habitat kernel revealed that dispersing
451 wild dogs avoid water, prefer its proximity, avoid woodland, prefer shrubs/grassland, and
452 avoid areas dominated by humans. These findings are well in line with previous research
453 on dispersing wild dogs (Davies-Mostert et al., 2012; Masenga et al., 2016; Woodroffe et al.,
454 2019; O'Neill et al., 2020), as well as with an earlier dispersal model, were we primarily
455 investigated the habitat kernel of dispersers Hofmann et al. (2021). Nevertheless, expanding
456 the model allowed us to model several complexities inherent to dispersal that would otherwise
457 have gone undetected. For instance, by including the respective interactions, we showed that
458 dispersers are more likely to realize short steps (i.e. they move slower) in areas covered by
459 water than in areas covered by dryland. This may be unsurprising, given that wild dogs
460 have to wade or swim in order to traverse water. Similarly, we found that movement in
461 water-covered areas is much more tortuous and less directional. However, because fixes
462 were recorded only every 4th hour, we could not ascertain whether dispersers truly crossed
463 waterbodies between two fixes or if the reduced step length and lower turning angles resulted
464 from more turuous movements in an attempt to avoid crossing water directly.

465 Our movement model also revealed that dipsersers preferably realize shorter steps when
466 moving through woodland, but larger steps when moving across shrubs/grassland. This
467 finding can likely be attributed to resting periods during which dispersers seek shade and
468 protection below the woodland canopy. To effectively model this behavior, however, one
469 would need to include a three-way interaction between the movement kernel, habitat kernel
470 and a temporal measure. Instead, we generically modeled resting behavior using a binary
471 variable, highlighting that characteristics of the step length distribution changed between
472 17:00 and 09:00 o'clock compared to the rest of the day.

473 Another peculiarity of animal movement, particularly during dispersal, is that turning
474 angles and step lengths tend to be correlated, such that larger steps coincide with lower
475 turning angles, resulting in quick and directional movements. While such behavior could be
476 rendered by sampling turning angles and step lengths from copula distributions (?) when

477 generating random steps, the ISSF framework allowed to readily model similar correlations
478 by including the respective interactions in the movement model, without having to fit cop-
479 ulas.

480 To this end, we showcased how a relatively simple ISSF model can be employed to in-
481 vestigate complex dispersal patterns. Although some of these reported effects may seem
482 biologically irrelevant, their representation in the movement model enabled us to more re-
483 alistically simulate dispersal movements. The ability to accurately render how the habitat
484 (or temporal factors) influences movement behavior is crucial when using simulations to
485 estimate functional connectivity between habitat patches. For example, a certain habitat
486 type may be preferred by a species, yet impose relatively slow and tortuous movements.
487 Consequently, realized connectivity between patches separated by such habitat will be low,
488 even if a purely structural approach would suggest high permeability of this area.

489 4.3 Simulation (80%)

490 Our dispersal simulation comprised 160 Mio. simulated steps and required six days of
491 computation on a modern desktop machine. This was largely owed to the massive extent
492 considered (ca. 1.4 Mio. km² + buffer) and the large number of dispersers simulated
493 (80'000 individuals). Since many connectivity studies focus on much smaller extents (e.g.
494 (Kanagaraj et al., 2013; Abrahms et al., 2017; Zeller et al., 2020)), faster simulation speeds
495 should be attainable for most applications. We also believe that fewer simulated dispersers
496 will often suffice, as the relative traversal frequency by simulated individuals across the study
497 area converged rather quickly in our case, suggesting that additional simulations provided
498 only little novel information (Appendices). By adding a buffer zone through which dispersers
499 were allowed to leave and re-enter the main study area, we effectively mitigated potential
500 biases arising from edge effects (Koen et al., 2010).

501 4.4 Maps (10%)

502 The heatmap produced from all simulated dispersal events suggests that a large number
503 of dispersers traverses the Moremi NP and the Chobe NP in northern Botswana. Since we
504 already highlighted the same area in our previous analysis (Hofmann et al., 2021), this result
505 was to be expected. Nevertheless, we believe it reinforces our notion that the area acts as
506 crucial hub inside the KAZA-TFCA. The very same area is highlighted on the betweenness
507 map, showing that the region is not only frequently traversed, but it actually serves as
508 stepping stone into more remote regions of the KAZA-TFCA. As such, the area exemplifies

509 a region were both, traversal frequency and betweenness scores are high. In contrast, the
510 betweenness map suggests the presence of a corridor moving from Angola into Zambia's
511 Kafue NP, yet when looking at the heatmap, one realizes that the area is not used very
512 often. Consequently, despite the corridor's importance for linking Angola's NPs to Zambia's
513 Np, only very few simulated dispersers successfully traversed it. This is also reflected in
514 the interpatch connectivity map, where the Kafue NP only receives very few links from the
515 central region of the KAZA-TFCA.

516 4.5 General (20%)

517 A simulation-based approached as outlined in this article has several advantages over more
518 traditional connectivity modelling techniques such as least-cost analysis or circuit theory.
519 First of all, an individual-based simulation does not require to specify predetermined end
520 points *a priori*. Instead, each endpoint emerges naturally as the result of a simulated
521 dispersal trajectory. Although predefined endpoints are not a premise for circuit theory,
522 they are required in least-cost analyses. This requirement is particularly unreasonable when
523 modeling dispersers, as dispersers typically do not have a preconceived target in mind when
524 moving. Nevertheless, even if such behavior is exhibited it could be incorporated in the
525 ISSF movement model using attraction points.

526 While endpoints emerge naturally from the dispersal process, startpoints still need to
527 be specified *a priori* by the modeler. Here, we placed source points within protected areas
528 large enough to sustain viable wild dog populations. This was done under the simplifying
529 assumption that wild dogs only survive in formally protected areas, which is in line with
530 scientific findings (Woodroffe and Ginsberg, 1999; Davies-Mostert et al., 2012; Woodroffe
531 and Sillero-Zubiri, 2012; Van der Meer et al., 2014). In some cases, exact locations of source
532 populations are known and source points can easily be placed accordingly (Kanagaraj et al.,
533 2013). In other cases, comparable knowledge may be lacking and it may be more appropriate
534 to delineate likely source patches using habitat suitability models (Squires et al., 2013).
535 Because we did not investigate the sensitivity of our results with respect to the exact location
536 of source points, this is something that needs further investigation in the future.

537 Another advantage of simulation-based approaches is that they render time explicitly.
538 This enables to answer questions such as: "*How long will it take a disperser to move from*
539 *A to B?*" or *Is it possible for a disperser to move from A to B within X days?*. These are
540 interesting questions and they shift the focus from a structural to a more functional point
541 of view. However, an explicit representation of time requires that speed (step length) and

542 directionality during motion is appropriately modeled (Kanagaraj et al., 2013). Because
543 ISSFs enable to model these two components adequately, the method offers a powerful
544 framework for simulations. Besides this, one also needs to decide on a meaningful dispersal
545 duration when simulating movement. We decided to simulate individuals for 2'000 steps,
546 which is at the upper end of observed dispersal durations and likely resulted in overestimated
547 landscape connectivity. Nevertheless, it requires little tweaking to subset from the generated
548 simulations to any dispersal duration desired. In fact, one could randomly sample dispersal
549 durations based on observed dispersal events. In most cases, however, it will be more
550 convenient and insightful to simulate relatively extensive dispersal events and only subsample
551 afterwards.

552 Allows to render directional persistence

553 While we have assumed a set of static covariates when simulating dispersal, an explicit
554 representation theoretically allows to render seasonality in covariate layers. This is an im-
555 portant aspect in ecosystems where seasonality substantially influences landscape connec-
556 tivity. With least-cost analysis and circuit theory, seasonality can merely be incorporated
557 by producing a multitude of permeability surfaces, each depicting landscape permeability
558 in a different season, and then applying the connectivity models to those surfaces (Benz
559 et al., 2016; Osipova et al., 2019). With individual-based simulations, on the other hand,
560 seasonal covariates can be updated as the simulated dispersers move. As such, seasonality
561 would directly influence movement, i.e. the process that ultimately leads to connectivity.
562 For instance, in our simulation we represented the Okavango Delta statically and assumed
563 a relatively extended flood. In this regard, the maps presented in the results section may be
564 most representative of the period shortly after the wet-season, when floodlevels in the Delta
565 are at their maximum. During the dry season, however, the flood considerably retracts
566 and potentially clears the way for wild dogs dispersing from the Moremi-Game reserve into
567 the south-western section of the Delta. Consequently, instead of using a static floodmap,
568 one could render the flood dynamically. Hence, the floodlevels would be updated as the
569 dispersers move, which would allow studying how connectivity evolves as the flood climaxes
570 and retracts again.

571 We simulated dispersal using point estimates from our most parsimonious movement
572 model, yet the degree to which our results depend on those estimates is unknown. Given
573 that data from dispersal studies on endangered species is scarce, point estimates may be
574 quite inaccurate, therefore leading to erroneous inference (Wiegand et al., 2003; Kramer-
575 Schadt et al., 2007). Rather than using point estimates, an alternative may be to simulate

576 dispersers using a set of randomized preferences imposed by the uncertainty reported in the
577 model output. We urge future studies to further investigate investigate the sensitivity of
578 ISSF simulations with respect to estimated habitat preferences.

579 In contrast to least-cost path analysis and circuit theory, a simulation-based approach
580 permits studying inter-patch connectivity. This facilitates the identification of asymmetri-
581 cal links and statements about source-sink dynamics (Ferreras, 2001; Revilla et al., 2004;
582 Kanagaraj et al., 2013).

583 Our results thus are in concert with other recent studies on functional connectivity based
584 on individual-based models that showed that including the behavioral ecology of the target
585 species and the landscape structure are imperative when assessing connectivity (Gustafson
586 and Gardner, 1996; Gardner and Gustafson, 2004; Graf et al., 2007; Kramer-Schadt et al.,
587 2004; Revilla et al., 2004; Revilla and Wiegand, 2008; Kanagaraj et al., 2013) rather than
588 considering it purely a function of distance.

589 We have previously attributed the weak significance of distance to water to the fact that
590 we did not control for the presence or absence of conspecifics. We stick to this reasoning
591 as our expanded model still shows a rather large uncertainty around the respective beta
592 coefficients. To better gauge the importance and influence of this covariate, future studies
593 will need to control for inter- and intra-specific interactions that may explain why and when
594 dispersers are attracted to or afraid of waterbodies. Fortin et al. (2005), for instance, found
595 that elk movement was significantly impacted by the density of wolf in the area, such that
596 habitat preferences strictly differed depending on the presence or absence of wolves.

597 Comparable simulations that are based on empirical data are also a fundamental com-
598 ponent for spatially realistic population models in which dispersal is rendered realistically
599 and does not merely depend on the distance between habitat patches (Revilla and Wiegand,
600 2008). In combination, the models could be employed to determine the required level of
601 dispersal to achieve metapopulation viability (Davies-Mostert et al., 2012).

602 In this regard, our work is most comparable to the analysis conducted by Clark et al.
603 (2015), who used SSFs to simulate dispersing Louisiana black bears and determine move-
604 ment corridors. However, Clark et al. (2015) did not use iSSF, thereby precluding to model
605 interactions between habitat conditions and movement behavior.

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

610 Even though connectivity is generally believed to promote population viability, it has
611 also been pointed out that improved connectivity may cause ecological traps, especially when
612 connectivity into or through human-dominated landscapes is promoted. In such instances,
613 connectivity increases the risk of encountering humans and facilitates persecution by humans.
614 By overlapping simulated trajectories with a map of human influence, such ecological traps
615 could be pinpointed.

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

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

630 A major benefit of individual-based simulations is the ability to make the temporal
631 dimension of movement explicit. This allows to investigate how connectivity depends on
632 the dispersal duration, something that is not possible with traditional least-cost or circuit
633 theory methods.

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

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

644 increase public acceptance of large predators.

645 We do not dismiss the application of least-cost analysis or circuit theory in any way.
646 Rather, we propose to use simulations from IBMMs complementary to least-cost analysis and
647 circuit theory in order to provide a more comprehensive analysis of landscape connectivity.
648 In fact, simulations from IBMMs could be employed to identify likely connections between
649 habitat patches in a first place and only afterwards least-cost paths and corridors can be
650 drawn between such likely connections. Thus far, dispersal kernels or thresholded least cost
651 paths have been used for this.

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

665 **5 Authors' Contributions**

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

670 **6 Data Availability**

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

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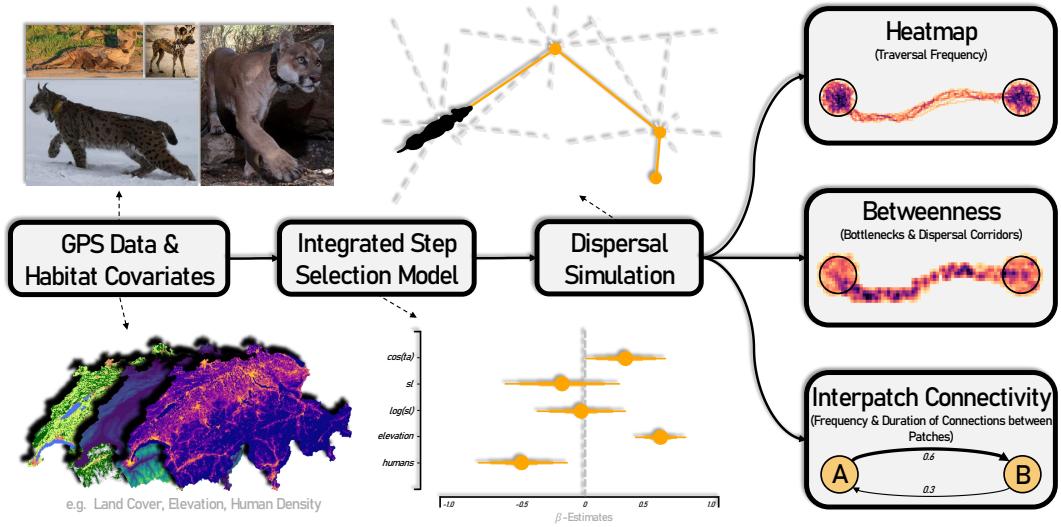


Figure 1: Flowchart of the simulation-based connectivity analysis. First, GPS data and habitat covariates have to be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement kernels. The parametrized 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?

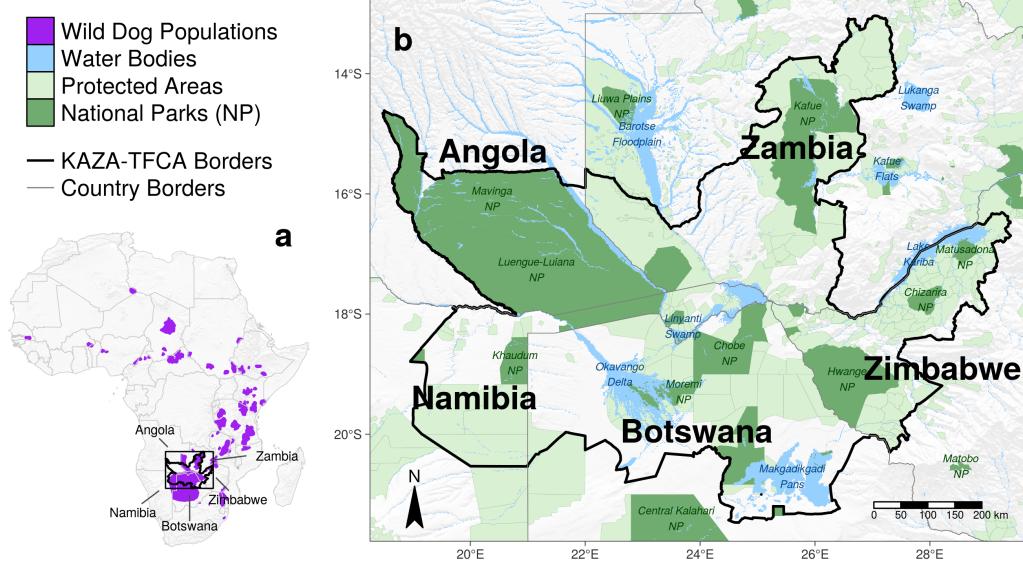


Figure 2: Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA and encompassing parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA represents the world’s largest terrestrial conservation area and covers a total of 520’000 km². 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.

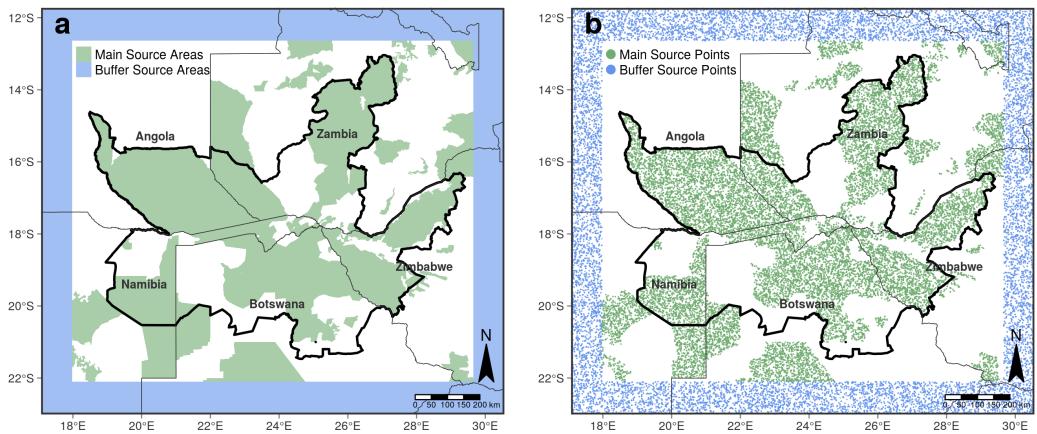


Figure 3: (a) Different source areas from which we released virtual dispersers. We only considered contiguous protected areas (national parks, game reserves, and forest reserves) that were larger than 700 km^2 (green). This area corresponds to the average home range requirement for viable wild dog populations (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).

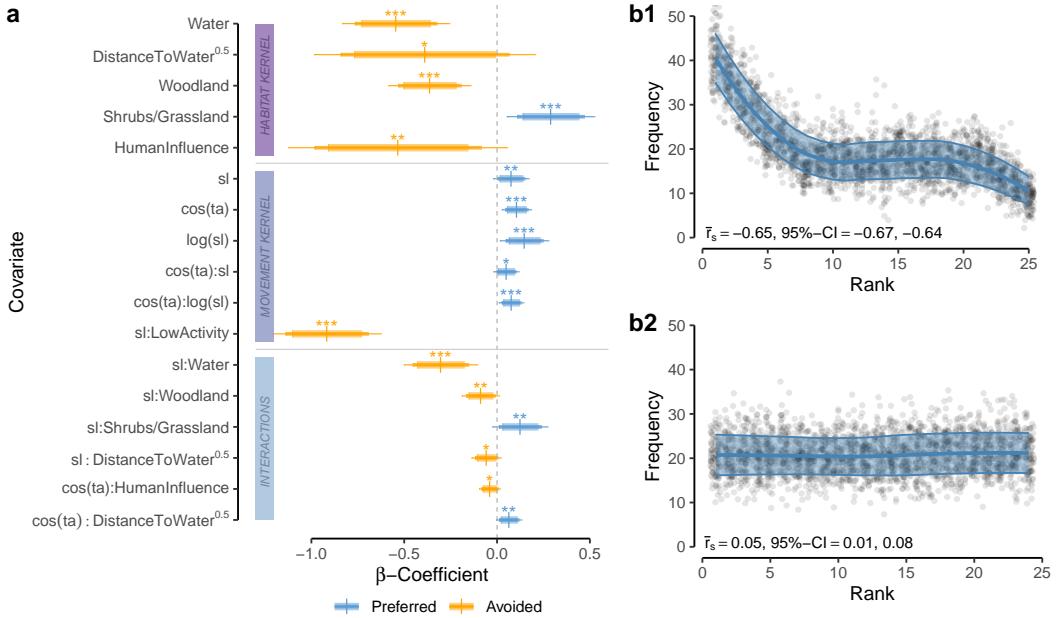


Figure 4: (a) Most parsimonious movement model for dispersing wild dogs. The model includes a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% Confidence-Intervals for the respective β -coefficients. Significance codes: * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$. (b) Results from the k-fold cross validation procedure. The upper plot shows rank frequencies of realized steps according to model predictions with known preferences, whereas the lower plot shows rank frequencies of realized steps 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. The significant correlation between rank and associated frequency in (b1) highlights that the most parsimonious model successfully outperforms a random guess (b2) and assigns comparably high selection scores to realized steps.

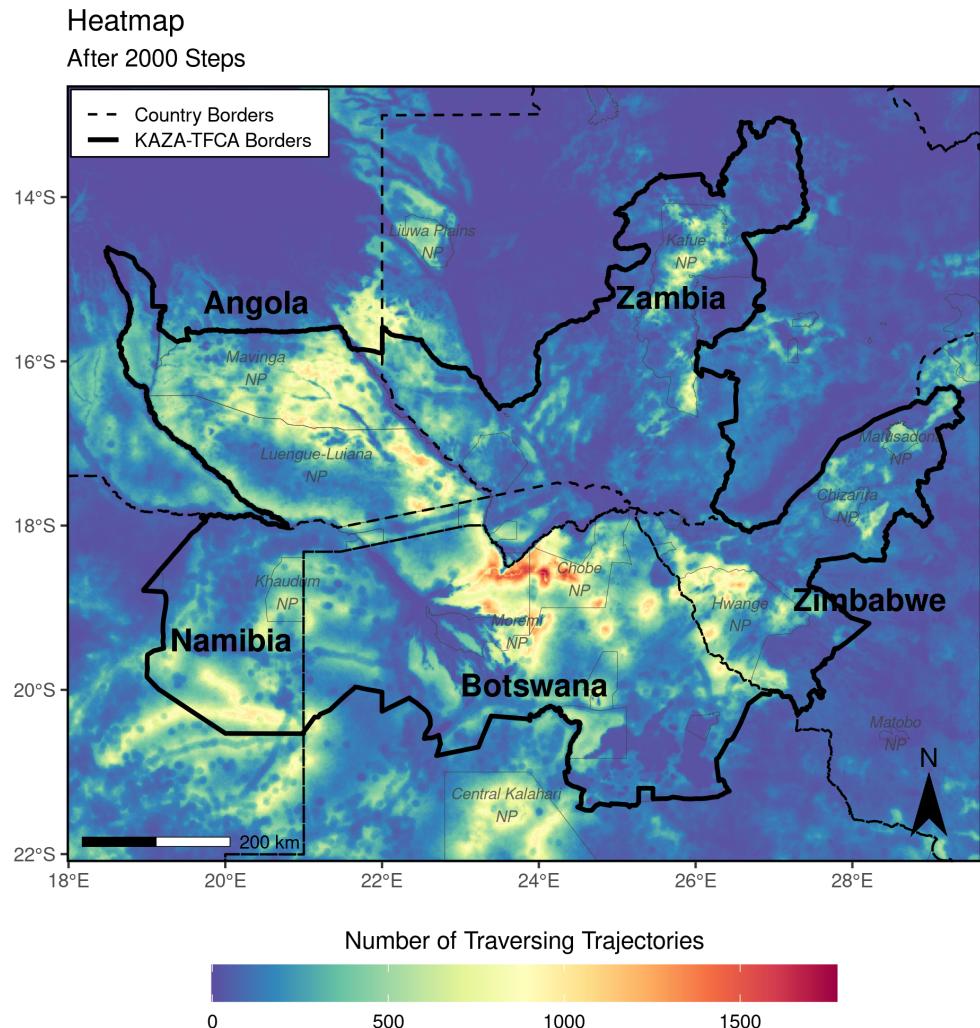


Figure 5: Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step selection model that we fit to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied all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

Betweenness

After 2000 Steps

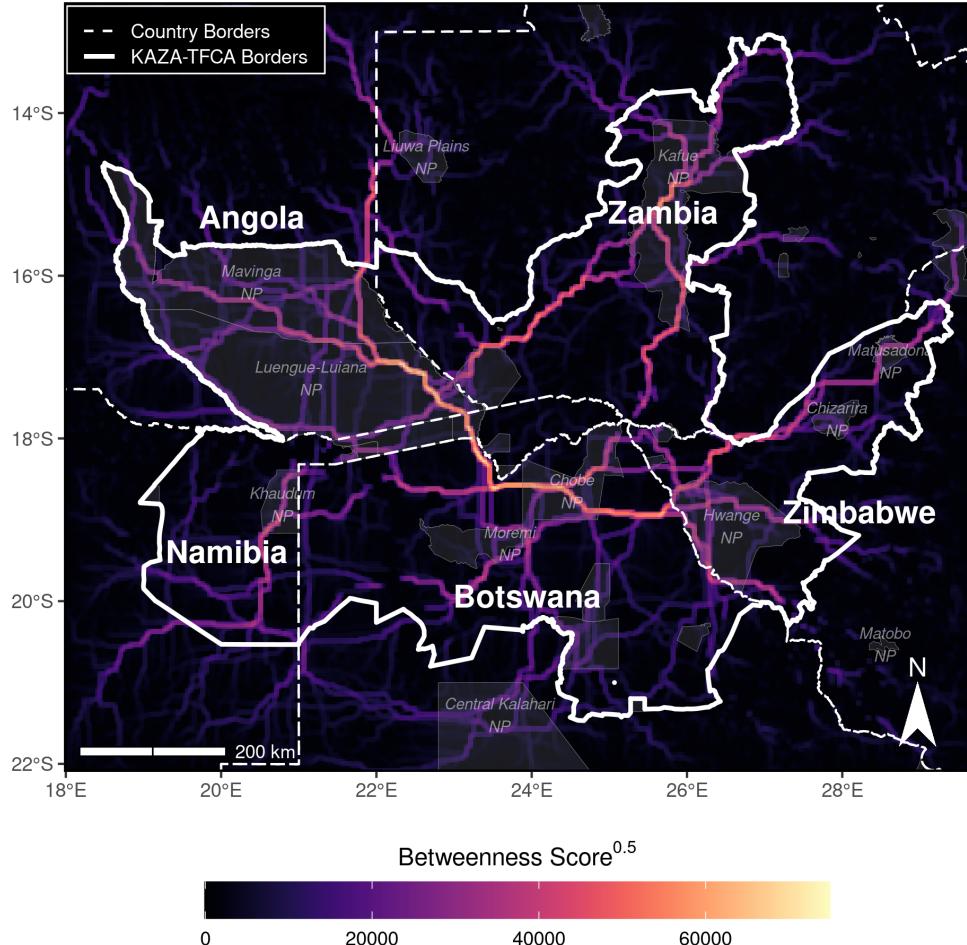


Figure 6: Map of betweenness scores, highlighting distinct dispersal corridors and potential bottlenecks. A high betweenness score indicates that the respective cells are exceptionally relevant in connecting different regions in the study area. That is, the higher the betweenness score, the more often 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. Betweenness scores were determined by converting simulated dispersal trajectories into a large network. Note that we square-rooted betweenness scores to improve the visibility of corridors with low betweenness scores.

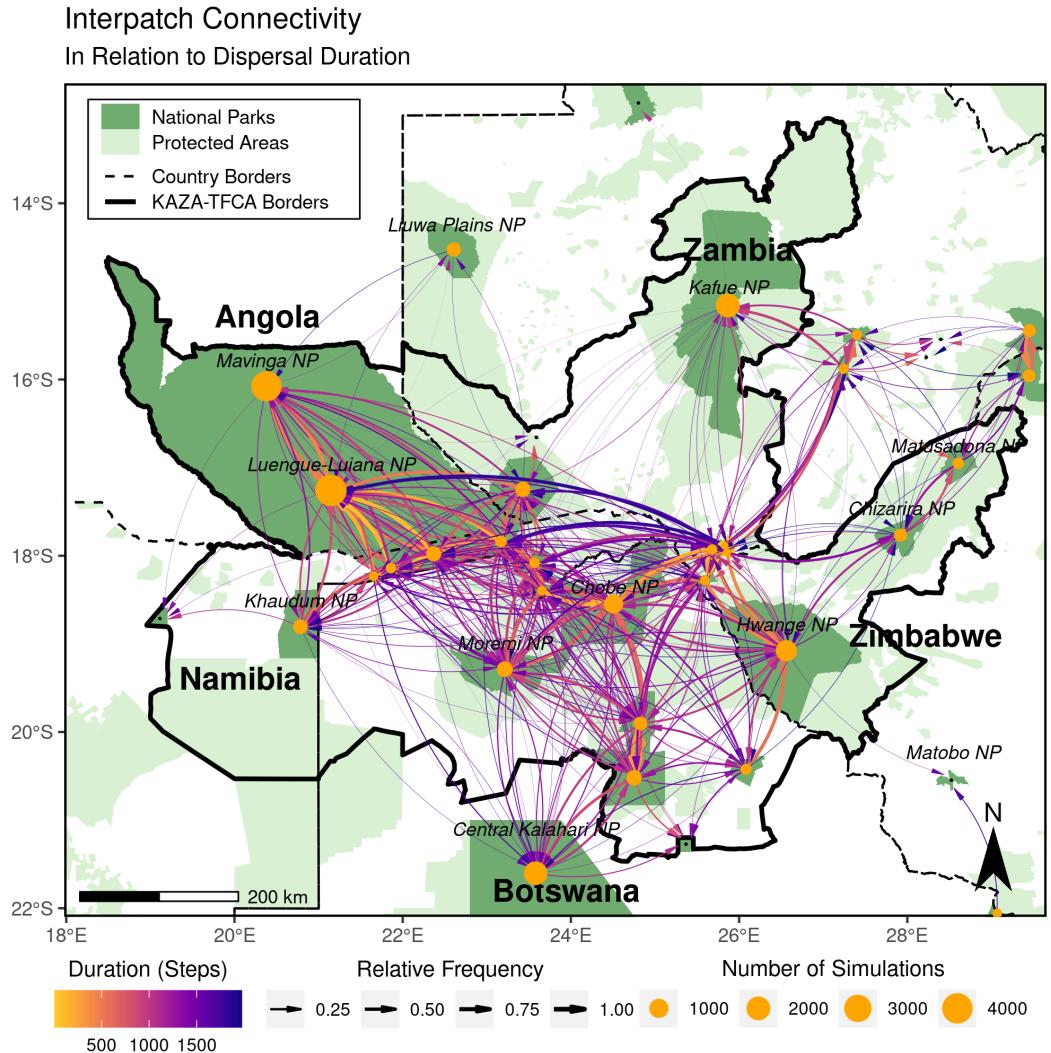


Figure 7: Network on simulated dispersal trajectories highlighting connections between national parks (dark green). Yellow bubbles represent the center of the different national parks and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent national parks that were smaller than 700 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 ^{0.5}	-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 ^{0.5}	-0.058	0.031	0.056	*	
		cos(ta) : HumanInfluence	-0.040	0.022	0.070	*
		cos(ta) : DistanceToWater ^{0.5}	0.063	0.026	0.017	**

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