

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 maps, each focused on a different aspect of connectivity within the KAZA-TFCA. Finally, we discuss the benefits and pitfalls of such a simulation-based approach 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 methods (Hofmann et al., 2021). Specifically,
135 we fitted a basic habitat selection model using which we predicted a permeability surface
136 and computed least-cost paths and corridors. We now expand this model and use ISSFs to
137 develop a more detailed movement model of dispersing wild dogs (Figure 1). We then employ
138 the model to simulate dispersers moving across the KAZA-TFCA. Based on simulations,
139 we generate three distinct connectivity maps, all shedding light onto a different aspect of
140 connectivity. With this work we hope to show that a simulation-based approach yields
141 several benefits over traditional connectivity modeling techniques such as least-cost analyses
142 and circuit theory. Most importantly, simulations provide a more generic view on how
143 connectivity emerges and to which degree connectivity depends on the dispersal duration.
144 In addition, by generating proper dispersal trajectories, network theory can be applied to
145 calculate network metrics 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 Convergence (80%)**

305 To verify that the number of simulated individuals sufficed to ensure reliable estimates of
306 connectivity, we evaluated how the relative traversal frequency across the landscape de-
307 pended on the number of simulated trajectories. Specifically, we placed 1'000 “checkpoints”
308 each with an extent of 5 km x 5 km at random locations inside the main study area. We then
309 determined the relative traversal frequency by simulated trajectories through each check-
310 point for different numbers of simulations (1 to 50'000). We replicated each random sample
311 100 times and computed the mean across replicates, as well as the 95% xx-interval. Note
312 that we only considered the 50'000 trajectories originating from the main study area.

313 **2.8 Heatmap (100%)**

314 To identify dispersal hotspots across our study area, we created a heatmap indicating the
315 absolute frequency at which each raster-cell in the study area was visited by virtual dis-
316 persers (Hauenstein et al., 2019; Pe'er and Kramer-Schadt, 2008). For this, we rasterized

317 all simulated trajectories and tallied them into a single map. If the same trajectory crossed
318 a raster-cell twice, it was only counted once, thereby mitigating potential biases resulting
319 from individuals that were trapped and moved in circles. To achieve high performance
320 rasterization, we used the R-package `terra` (Hijmans, 2020).

321 2.9 Betweenness (80%)

322 To pinpoint areas of exceptional relevance for connecting remote regions inside our study
323 area, we converted simulated trajectories into a network and calculated betweenness scores
324 (Bastille-Rousseau et al., 2018). For this, we overlaid the study area (including the buffer)
325 with a regular raster resolved at 5 x 5 km. The centerpoint of each raster-cell acted as
326 node in the final network and we used the simulated trajectories to determine all transi-
327 tions occurring from one raster-cell to another, as well as the frequency at which those
328 transitions occurred. This resulted in an edge-list that we translated into a weighted net-
329 work using the r-package `igraph` (Csardi and Nepusz, 2006). Because `igraph` handles
330 edge weights (ω) as costs, we inverted the traversal frequency in each cell by applying
331 $\omega = \frac{\sum_i^n TraversalFrequency_i}{TraversalFrequency_i}/n$. Finally, we used the weighted network to calculate the be-
332 tweenness score of each raster-cell. Betweenness measures how often a specific raster-cell lies
333 on a shortest path between two other raster-cells and is therefore a useful metric to detect
334 movement corridors (Bastille-Rousseau et al., 2018).

335 2.10 Inter-Patch Connectivity (80%)

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

348 **3 Results**

349 **3.1 Movement Model (80%)**

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

357 Assuming that all other covariates are held constant, the habitat kernel reveals that
358 dispersing wild dogs avoid water but prefer its proximity. Similarly, dispersers avoid areas
359 that are covered by woodlands, yet prefer regions covered by shrublands or grasslands.
360 Finally, dispersers avoid movement through landscapes that are dominated by humans.
361 Effect sizes are strong and, except for effect for `distance to water`, statistically clear on the
362 5% significance level.

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

372 When looking at the interactions between the movement and habitat kernels, we observe
373 that movement behavior is contingent on habitat conditions. For example, there's strong
374 evidence that dispersers realize smaller steps in areas covered by water or areas covered
375 by wooldand. Conversely, it appears that steps tend to larger in regions dominated by
376 shrubs/grassland, and shorter when the distance to water is high. Correspondingly, the
377 model suggests that directionality is lower in areas dominated by humans, yet more pro-
378 nounced when dispersers are far from water. However, except for the effect of `sl:Water`, effect
379 sizes are small.

380 The k-fold cross-validation procedure reveals that our model substantially outperforms a

random guess (Figure 4b). Confidence intervals of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ do not overlap and therefore proof a reliable prediction. Furthermore, the significant correlation between ranks and corresponding frequencies for realized steps indicates a good fit between predictions and observations (Figure 4b). In comparison to the base model ($\bar{r}_{s,realized} = -0.55$; Hofmann et al., 2021), the inclusion of interactions between movement and habitat covariates slightly improved model performance.

3.2 Dispersal Simulation (80%)

On a machine with an octacore AMD Ryzen 7 2700X processor (8 x 3.6 GHz) and 64 GB of RAM, a batch of 1'000 simulated dispersers moving over 2'000 steps required 90 minutes to compute ($\mu = 88.90$, $\sigma = 1.87$). Consequently, the simulation of all 80'000 dispersers (160 Mio. steps) terminated after 120 hours or five days. Comparable simulations will be substantially faster for smaller study areas and lower resolution covariates, as the covariate extraction from large and high-resolution rasters was computationally the most demanding task. Out of the 50'000 dispersers initiated inside the main source area Figure 3(a), only 4.5% eventually hit a map boundary, suggesting that we successfully limited biases due to boundary effects. In contrast, 78% of the 30'000 dispersers originating from the buffer zone eventually hit a map boundary, yet this was to be expected since many of those dispersers originated from source points located close to the map boundary.

3.3 Heatmap (80%)

Figure 6 depicts the heatmap of all 80'000 simulated trajectories resulting after 2'000 steps. The map shows that large portions of land beyond the borders of the KAZA-TFCA are only infrequently visited by dispersers (dark blue areas), whereas within the KAZA-TFCA several extensive regions are regularly traversed (bright yellow and red areas). Most notably, the region in northern Botswana south of the Linyanti swamp stands out as highly frequented dispersal hotspot. Still, the presence of several massive water bodies, such as the Okavango Delta, the Makgadikgadi Pan, and the Linyanti swamp, results in considerable dispersal barriers that limit realized connectivity within the KAZA-TFCA. Similarly, dispersal appears to be very limited in Zambia's and Zimbabwe's part of the KAZA-TFCA, where only few areas are successfully traversed by dispersers. This can largely be attributed to substantial human influences resulting from high human density, roads, and agricultural activities. Outside the KAZA-TFCA, the most heavily used regions include the areas inside the Central Kalahari National Park in Botswana, the area south-west of the Khaudum

⁴¹³ National Park in Namibia, and the area around the Liuwa Plains National Park in Zambia.

⁴¹⁴ **3.4 Betweenness (80%)**

⁴¹⁵ Betweenness scores after 2'000 simulated steps are presented in Figure 7 and reveal a set of
⁴¹⁶ discrete dispersal corridors. Again, the region in northern Botswana stands out as crucial
⁴¹⁷ dispersal corridor that receives the highest betweenness score across the study area. Con-
⁴¹⁸ sequently, the region serves as crucial dispersal hub that connects more remote regions in
⁴¹⁹ the study system. Towards east, the extension of this corridor runs through the Chobe Na-
⁴²⁰ tional Park into the Hwange national park. From there, a further extension connects to the
⁴²¹ distant Matusadona National Park in Zimbabwe. Northwest of the Linyanti ecosystem, a
⁴²² major corridor expands into Angola, where it splits and finally traverses over a long stretch
⁴²³ of unprotected area into the Kafue National Park in Zambia. Several additional corridors
⁴²⁴ with slightly lower betweenness scores exist, yet most of them run within the boundaries of
⁴²⁵ the KAZA-TFCA. In general, only few corridors directly link the peripheral regions of the
⁴²⁶ KAZA-TFCA. For instance, there are only few corridors between the Matusadona National
⁴²⁷ Park in Zimbabwe and the Kafue National Park in Zimbabwe. Similarly, there are no direct
⁴²⁸ links between the Zimbabwean and Angolan “spikes” of the KAZA-TFCA.

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

⁴³⁰ Results from the analysis of interpatch connectivity are given in Figure 8, but it is worth
⁴³¹ pointing out that the figure is only intended as an example, as for clarity we limited the
⁴³² network on national parks (NPs), albeit plenty of links between other protected areas exist.
⁴³³ As can be seen, interpatch connectivity between NPs in Angola, Namibia, and Botswana
⁴³⁴ is comparably high and dispersal durations short. In contrast, it appears that connectivity
⁴³⁵ towards the Kafue NP in Zambia and is low and requires long dispersal events to realize a
⁴³⁶ link. Similarly, there is a lack of connections to Zimbabwe’s Chizarira and Matusadona NP
⁴³⁷ and the more distant Lower Zambezi and Mana Pools NPs.

⁴³⁸ **4 Discussion**

⁴³⁹ **4.1 Short Summary (90%)**

⁴⁴⁰ We used integrated step selection analysis to analyse data of dispersing wild dogs and to
⁴⁴¹ parametrize a fully mechanistic movement model describing how dispersers move through the
⁴⁴² available landscape. We employed the parametrized model as an individual-based movement

model and simulated 80'000 dispersing wild dogs moving 2'000 steps across the extent of the KAZA-TFCA, the world's largest transboundary conservation area. Based on simulated dispersal trajectories, we derived a set of three complementary maps, all geared towards a better understanding of dispersal and landscape connectivity. The set of maps included a heatmap, revealing frequently traversed areas, a betweenness-map, delineating critical dispersal corridors and bottlenecks, and a map of inter-patch connectivity, indicating the presence or absence of functional links between national parks. We thereby showcase how integrated step selection functions can be utilized as simple, yet powerful framework to parametrize movement models and simulate animal movement with the aim of assessing landscape connectivity. Such an individual-based simulation overcomes several conceptual shortcomings inherent to more traditional connectivity modeling techniques, such as least-cost analyses and circuit theory. Nevertheless, we suggest to view such individual-based simulations as complement, and not as substitute, to traditional connectivity models.

4.2 Movement Model (80 %)

Our movement model of dispersing wild dogs comprised a habitat kernel, a movement kernel, and their interactions. Together, the kernels described habitat and movement preferences of dispersing individuals, as well as how movement behavior was affected by habitat conditions. Parameter estimates from the habitat kernel revealed that dispersing wild dogs avoid water, prefer its proximity, avoid woodland, prefer shrubs/grassland, and avoid areas dominated by humans. These findings are consistent with the findings of previous studies on dispersing wild dogs (Davies-Mostert et al., 2012; Masenga et al., 2016; Woodroffe et al., 2019; O'Neill et al., 2020), as well as with an earlier dispersal model that we developed primarily to investigate the habitat kernel of dispersers (Hofmann et al., 2021).

By expanding our initial model to include a proper movement kernel, we were able to model several additional complexities inherent to dispersal. It is, for instance, well known that turning angles and step lengths tend to be correlated in dispersing animals due to a preference for directional persistence. That is, larger steps usually coincide with smaller turning angles and vice versa (cite someone). While this correlation structure could be effectively rendered by sampling turning angles and step lengths from copula probability distributions (?), the ISSF framework allowed us to model similar behavior directly in the movement model. Besides accounting for directional persistence, we further exploited the ISSF framework and included interactions between movement covariates to represent the fact that wild dogs mainly move during the more temperate morning and evening hours.

476 The final model thus rendered a pulse-like movement behavior, where dispersers realize
477 larger steps during morning and evening hours, but shorter steps during the rest of the day.

478 By including interactions between habitat and movement covariates, we also acknowled-
479 ged that movement behavior of dispersers may depend on habitat conditions. For example,
480 the final model contained an interaction between water cover and step length, highlighting
481 that dispersers are more likely to realize short steps (i.e. move slower) in areas covered
482 by water. Likewise, the interaction between water cover and turning angles revealed that
483 dispersers move less directional when across water bodies. We believe that this behavior
484 is owed to the fact that wild dogs wade or swim to traverse waterbodies, thus resulting in
485 slower, more tortuous movements. Besides this, our model also suggested that dispersers
486 preferably realize shorter steps when moving through woodland, but larger steps when mov-
487 ing across shrubs/grassland. This can likely be attributed to resting periods during which
488 dispersers seek shade and protection below the woodland canopy. Since we did not include
489 three way interactions, we could not test this hypothesis.

490 4.3 Simulation (80%)

491 Based on the above outlined model results, we simulated 80'000 dispersers moving 2'000 steps
492 across the landscapes of the KAZA-TFCA. Our dispersal simulation thus comprised 160 Mio.
493 simulated steps, which required six days of computation on a modern desktop machine. This
494 rather long simulation duration was primarily owed to the massive extent considered (ca.
495 1.8 Mio. km²) and the large number of dispersers simulated. Most connectivity studies
496 consider a much smaller extent (e.g. Kanagaraj et al., 2013; Abrahms et al., 2017; Zeller
497 et al., 2020) and should be able to attain faster simulation speeds. We also believe that
498 fewer simulated dispersers will often suffice, as the relative traversal frequency of simulated
499 individuals through randomly placed checkpoints in our study area converged rather quickly
500 (Appendices), yet this will vary depending on the structure of the landscape and dispersal
501 ability of the focal species.

502 A simulation-based approach as proposed in this article offers several advantages over
503 more traditional connectivity modeling techniques such as least-cost analyses or circuit the-
504 ory. In contrast to least-cost analyses, for instance, an individual-based simulation does
505 not require predetermined endpoints. Instead, endpoints emerge naturally as the result of
506 simulated dispersal trajectories. Not having to assume known endpoints is particularly im-
507 portant for dispersal studies because dispersers often venture into unfamiliar territory and
508 are therefore unlikely to know the endpoint of their journey. In addition, without known

509 endpoints, movement corridors are no longer enforced between start- and endpoint, per-
510 mitting to detect potential dead ends where dispersers get trapped due to insurmountable
511 obstacles.

512 IBMMs furthermore yield the advantage of an explicit representation of time. This
513 enables to answer questions such as: “*How long will it take a disperser to move from A to B?*”
514 or *Is it possible for a disperser to move from A to B within X days?*”, all undoubtly interesting
515 questions that shift the focus from a structural to a more functional view on connectivity.
516 Similar questions cannot be answered using least-cost methods or circuit theory because the
517 time component is omitted from those models. An explicit representation of time in IBMMs
518 also yields exciting opportunities for studying seasonal changes to connectivity Zeller et al.
519 (2020). With least-cost methods or circuit theory a dynamic analysis of connectivity is
520 impractical because the same analyses needs to be repeated using different permeability
521 surfaces (e.g. Benz et al., 2016; Osipova et al., 2019). With IBMMs, on the other hand,
522 simulated individuals can directly respond to a dynamic environment within the model and
523 the environment is allowed to change “as the dispersers move”.

524 While an explicit representation of time yields several advantages, it also requires that
525 step lengths and turning angles are modeled properly (Kanagaraj et al., 2013), so that dis-
526 persal durations between habitat patches can be reliably approximated. Accounting for
527 and correctly rendering this movement kernel is the main strength of ISSFs, which is why
528 we believe that the framework is particularly well suited for simulating animal dispersal
529 and assessing landscape connectivity. In principle, the ISSF framework allows to define an
530 infinite amount of movement kernels, each representing movement behavior under different
531 conditions (Fieberg et al., 2020). It can therefore accomodate highly diverse movement
532 modes, including fast paced directional movements and slow paced tortuous movements.
533 Compared to models that disregard an animal’s movement kernel, this allows to model di-
534 rectional persistence, a movement characteristic regularly observed in dispersing animals. To
535 date, however, we only accounted for 1. order autocorrelation. That is, we only considered
536 correlations between two subsequent steps. Modeling higher-order autocorrelation may be
537 desirable, yet will require more extensive data.

538 Overall, IBMMs enable to generate a rich insight into the emergence of connectvity
539 when compared to the outputs of least-cost analysis or circuit theory. By generating proper
540 movement trajectories, a broad variety of summary statistics can be derived. Specifically, by
541 turning simulated trajectories into a network, network theoretical metrics relevant to connec-
542 tivity can be applied (Bastille-Rousseau et al., 2018). In contrast to least-cost path analysis

543 and circuit theory, a simulation-based approach permits studying inter-patch connectivity.
544 This facilitates the identification of asymmetrical links and statements about source-sink
545 dynamics (Ferreras, 2001; Revilla et al., 2004; Kanagaraj et al., 2013). Our results are
546 also in concert with previous studies on functional connectivity based on individual-based
547 models that showed that including the behavioral ecology of the target species and the land-
548 scape structure are imperative when assessing connectivity (Gustafson and Gardner, 1996;
549 Gardner and Gustafson, 2004; Graf et al., 2007; Kramer-Schadt et al., 2004; Revilla et al.,
550 2004; Revilla and Wiegand, 2008; Kanagaraj et al., 2013) rather than considering it purely
551 a function of distance.

552 Besides the benefits of IBMMs, we also want to point out some caveats and not so trivial
553 modeling decisions. In particular, we will discuss five modeling challenges: (1) number of
554 simulated individuals, (2) location of source points, (3) dispersal duration, (4) boundary
555 behavior, and (5) individual variability.

556 (1) When simulating dispersal, the modeler needs to decide on the number of simulated
557 individuals. This decision involves the total (absolute) number of simulated individuals
558 across the study area, as well as the relative number of simulated individuals per spatial
559 entity (e.g. protected area, habitat patch, source point). With regards to the total number
560 of simulated individuals, a larger number is usually desirable as it yields a more balanced
561 view on connectivity. However, this comes at the cost of computational efficiency, implying
562 that a trade-off needs to be managed. One simple solution to handle the trade-off would
563 be to simulate only as many individuals as are needed to achieve convergence in the target
564 metric. In our case, examination of the target metric **traversal frequency** revealed that
565 convergence was achieved with relatively few individuals, such that additional dispersers
566 contributed only little additional information to our results. With regards to the relative
567 number of simulated individuals, we see two feasible approaches. First, one could initiate
568 dispersers in relation to population density at the respective area. This would directly
569 reflect the fact that population densities are not homogeneous across space. (Say more)
570 Alternatively, however, one could also distribute dispersers homogeneously, but then weigh
571 simulated trajectories by the population density at the source patch (Say more). Because
572 we lacked reliable information on density estimates for the extent of the KAZA-TFCA, we
573 opted for a solution where dispersers were distributed homogeneously.

574 (2) While endpoints do not need to be defined in IBMMs, source points will still need to
575 be provided by the modeler. Here, we randomly placed source points within protected areas
576 large enough to sustain viable wild dog populations, knowing that the species primarily

survives in these formally protected areas (Woodroffe and Ginsberg, 1999; Davies-Mostert et al., 2012; Woodroffe and Sillero-Zubiri, 2012; Van der Meer et al., 2014). In some cases, exact locations of potential source populations are known and source points can be placed accordingly (Kanagaraj et al., 2013). Moreover, if abundance estimates are available, these can be used to inform the relative number of dispersers initiated at each location. In other cases, comparable knowledge may be lacking and it could be more beneficial to delineate likely source patches based on habitat suitability models (e.g. Squires et al., 2013). Either way, a meaningful selection of source points is not a problem unique to IBMMs and applies to any connectivity modelling technique. As highlighted by Signer et al. (2017) the influence of the exact location of source points decreases as the number of simulated steps is increased, yet their goal was assessing steady state utilization distributions and not to assess landscape connectivity.

(3) When employing IBMMs, one also needs to decide on meaningful dispersal durations (number of simulated steps). We decided to simulate individuals for 2'000 steps, which is at the upper end of observed dispersal durations and may have resulted in an overestimated representation of landscape connectivity. Instead of enforcing homogeneous dispersal durations, one could also sample dispersal durations from observed dispersal events. Alternatively, after each step, individuals could be faced with a probability to settle, where the probability is contingent on the surrounding landscape and cumulative dispersal distance travelled. Because we only observed few dispersal events and due to the wild dog's ability to cover vast dispersal distance (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020) we decided not to apply this approach. Regardless of this, we think that in most cases it will be more insightful to simulate relatively extensive dispersal events and only subsample afterwards.

(4) Unless simulated individuals are strongly drawn towards a point of attraction, some simulated individuals will eventually approach a map boundary and the modeller needs to define a rule to handle such situations. One feasible option would be to terminate the trajectory as soon as it hits a map boundary, implicitly assuming that the simulated animal left the study area and will not return. The downside to this approach is that source points located near map boundaries will inevitably produce many such dead ends. Alternatively, one could remove transgressing random steps from the set of proposed random steps, thereby forcing virtual dispersers to bounce off virtual boundaries and remain within the main study area. This may seem like an elegant solution, yet again, it potentially results in substantial edge effects when source points are located near map boundaries. Finally, one could extend

611 the study area by an artificial buffer zone through which dispersers are allowed to leave
612 and re-enter the main study area. Of course this does not fully mitigate the issue, since
613 some dispersers may still approach the outer map boundary, however, as Koen et al. (2010)
614 have shown, such an artificial buffer can often help to mitigate edge effects. In theoretical
615 applications, this issue can be circumvented by simulating movement on a torus (?), yet this
616 is unfeasible in most real world applications.

617 (5) We simulated dispersal using point estimates from our most parsimonious movement
618 model but did not investigate the sensitivity of our results with respect to those estimates.
619 Uncertainty is rather common in dispersal studies on endangered species, as data tends to be
620 scarce, resulting in model estimates large confidence intervals (Wiegand et al., 2003; Kramer-
621 Schadt et al., 2007). To address this, one may explore a broader range of preferences instead
622 of using point estimates initiate dispersers with randomized preferences with variability
623 imposed by the uncertainty in the movement model. We therefore urge future studies to
624 investigate the sensitivity of ISSF simulations with respect to estimated preferences.

625 **4.4 Maps (10%)**

626 The heatmap resulting from our dispersal simulation suggests that a large portion of dis-
627 persers traverses the Moremi NP and the Chobe NP in northern Botswana. Since we already
628 highlighted the same area in our previous analysis (Hofmann et al., 2021), this result was to
629 be expected. Nevertheless, we believe it reinforces our notion that the area acts as crucial
630 hub inside the KAZA-TFCA. The very same area stands out on the betweenness map, show-
631 ing that the region is not only frequently traversed, but actually serves as stepping stone
632 into more remote regions of the KAZA-TFCA. As such, the area exemplifies a region were
633 both traversal frequency and betweenness scores are high. In contrast, the betweenness map
634 suggests the presence of a corridor moving from Angola into Zambia’s Kafue NP, yet when
635 looking at the heatmap, one realizes that the area is not used very often. Consequently,
636 despite the corridor’s importance for linking Angola’s NPs to Zambia’s Np, only very few
637 simulated dispersers successfully traversed it. This is also reflected in the interpatch con-
638 nectivity map, where the Kafue NP only receives very few links from the central region of
639 the KAZA-TFCA.

640 Each map that we produced from simulated trajectories accentuates a different aspect
641 of connectivity. The heatmap, for example, puts emphasis on areas where movement is
642 concentrated, regardless whether such areas represent “dead ends” that do not necessarily
643 connect distinct patches. Therefore, the heatmap is useful to determine locations where a

644 disperser are likely to move to, yet not necessarily to uncover corridors that link valuable
645 habitats. The betweenness map, on the other hand, brings out those areas that are relevant
646 in connecting different regions in the landscape. In this regard, the betweenness map is
647 most pertinent to the delineation of dispersal corridors and may serve as an alternative to
648 least-cost algorithms. Finally, the inter-patch connectivity map illustrates the frequency at
649 which dispersal between distinct habitat patches occurs, as well as the average dispersal
650 duration that passes when individuals move between those patches. This knowledge serves
651 to gauge the amount of gene flow between habitat patches and can be employed to determine
652 whether two habitats are connected or not.

653 4.5 General (20%)

654 While we did not attempt to model mortality during dispersal, it is well known that dis-
655 persers regularly die, mainly due to deadly encounters with predators, road kills, or perse-
656 cution by humans (Woodroffe and Sillero-Zubiri, 2012; ?). Mortality during dispersal could
657 therefore substantially limit functional connectivity, especially in areas where the likelihood
658 of encountering competitors and humans is high (Cozzi et al., 2020). If corresponding in-
659 formation is available, IBMMs would readily allow to model mortality. Each timestep, a
660 binary draw determines whether the animal survives or not and this probability can depend
661 on landscape characteristics as well as the dispersal duration.

662 Our approach of simulating movement to assess connectivity is most closely related to the
663 works of Clark et al. (2015) and Zeller et al. (2020), who used regular step selection functions
664 to model habitat preferences by black bears and simulated movement to assess connectivity.
665 However, neither of these studies attempted to jointly model habitat and movement kernels,
666 thereby precluding a more mechanistic understanding of movement. Moreover, both studies
667 parametrized models using data of resident black bearsk, which may lead to a biased view on
668 connectivity, as dispersers may move substantially further, thereby improving connectivity
669 among habitat patches (Elliot et al., 2014).

670 Besides enabling a more mechanistic understanding of connectivity, the ability to real-
671 istically render movement during dispersal also forms the foundation for spatially realistic
672 population models. In these models, dispersal is not merely represented by a dispersal ker-
673 nel (e.g. ...) but mechanistically rendered (Revilla and Wiegand, 2008). Such population
674 models can ultimately be employed to determine the required level of dispersal to achieve
675 metapopulation viability (Davies-Mostert et al., 2012).

676 Simulations resulting from IBMMs could furthermore be utilized as simple tool to predict

677 the likely whereabouts of GPS collared animals into the near future. In some European
678 countries, the comeback of large predators, such as bears, lynx, and the wolf, has triggered
679 emotional discussions and raised public concern (Behr et al., 2017), particularly in areas with
680 free-roaming livestock that may be preyed upon by the returned species. An early warning
681 system based on simulations could thus serve to forewarn about potential encounters and
682 and thereby increase public acceptance of large predators.

683 We have previously attributed the weak significance of distance to water to the fact that
684 we did not control for the presence or absence of conspecifics. We stick to this reasoning
685 as our expanded model still shows a rather large uncertainty around the respective beta
686 coefficients. To better gauge the importance and influence of this covariate, future studies
687 will need to control for inter- and intra-specific interactions that may explain why and when
688 dispersers are attracted to or afraid of waterbodies. Fortin et al. (2005), for instance, found
689 that elk movement was significantly impacted by the density of wolf in the area, such that
690 habitat preferences strictly differed depending on the presence or absence of wolves. The
691 decision to settle is likely related to the presence or absence of conspecifics. Hence, the
692 exact dispersal duration and distance will not be independent of current wild dog densities.
693 In dispersing wolves, for instance, the longest dispersal distances have been observed in
694 low-density populations (??). The dispersal duration may thus be determined by the by
695 the amount of isolation between subpopulations and population densities (Davies-Mostert
696 et al., 2012).

697 Even though connectivity is generally thought to promote population viability, it is also
698 related to various aspects that may cause ecological damage, such as increased human-
699 wildlife conflicts or facilitated spread of deadly diseases.

700 To this end, we have exemplified the use of ISSFs as a simple framework based on which
701 researchers can parametrize dispersers' habitat and movement preferences and at the same
702 time use the parametrized model to as an individual-based movement model to simulate
703 dispersal and examine landscape connectivity. Furthermore, we suggest to analyse simu-
704 lated trajectories using three complementary maps, each focused on a different aspect of
705 connectivity. Ultimately, we hope to have sparked interest in the uprising framework of step
706 selection functions for investigating dispersal behavior and landscape connectivity. Never-
707 theless, we do not attempt to dismiss the application of traditional connectivity models such
708 as least-cost methods or circuit theory by any means. Rather, we propose to use simulations
709 from ISSF-IBMMs as a simple but powerful tool that complements earlier methods in an
710 attempt provide a more comprehensive understanding of landscape connectivity.

711 5 Authors' Contributions

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

716 6 Data Availability

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

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729 **References**

- 730 Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., and Brashares,
731 J. S. (2017). Does Wildlife Resource Selection Accurately Inform Corridor Conservation?
732 *Journal of Applied Ecology*, 54(2):412–422.
- 733 Adriaensen, F., Chardon, J., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., and
734 Matthysen, E. (2003). The Application of Least-Cost Modelling as a Functional Landscape
735 Model. *Landscape and Urban Planning*, 64(4):233–247.
- 736 Allen, C. H., Parrott, L., and Kyle, C. (2016). An Individual-Based Modelling Approach to
737 Estimate Landscape Connectivity for Bighorn Sheep (*Ovis canadensis*). *PeerJ*, 4:e2001.
- 738 Avgar, T., Lele, S. R., Keim, J. L., and Boyce, M. S. (2017). Relative Selection Strength:
739 Quantifying Effect Size in Habitat- and Step-Selection Inference. *Ecology and Evolution*,
740 7(14):5322–5330.
- 741 Avgar, T., Potts, J. R., Lewis, M. A., and Boyce, M. S. (2016). Integrated Step Selection
742 Analysis: Bridging the Gap Between Resource Selection and Animal Movement. *Methods
743 in Ecology and Evolution*, 7(5):619–630.
- 744 Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., and Turlure, C. (2013). Indi-
745 vidual Dispersal, Landscape Connectivity and Ecological Networks. *Biological Reviews*,
746 88(2):310–326.
- 747 Bastille-Rousseau, G., Douglas-Hamilton, I., Blake, S., Northrup, J. M., and Wittemyer,
748 G. (2018). Applying Network Theory to Animal Movements to Identify Properties of
749 Landscape Space Use. *Ecological Applications*, 28(3):854–864.
- 750 Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2020). When to Stay and When
751 to Leave? Proximate Causes of Dispersal in an Endangered Social Carnivore. *Journal of
752 Animal Ecology*, 89(10):2356–2366.
- 753 Behr, D. M., Ozgul, A., and Cozzi, G. (2017). Combining Human Acceptance and Habitat
754 Suitability in a Unified Socio-Ecological Suitability Model: A Case Study of the Wolf in
755 Switzerland. *Journal of Applied Ecology*, 54(6):1919–1929.
- 756 Benz, R. A., Boyce, M. S., Thurfjell, H., Paton, D. G., Musiani, M., Dormann, C. F., and
757 Ciuti, S. (2016). Dispersal Ecology Informs Design of Large-Scale Wildlife Corridors.
758 *PLOS ONE*, 11(9):e0162989.
- 759 Bovet, P. and Benhamou, S. (1991). Optimal Sinuosity in Central Place Foraging Move-
760 ments. *Animal Behaviour*, 42(1):57–62.
- 761 Boyce, M. S., Vernier, P. R., Nielsen, S. E., and Schmiegelow, F. K. A. (2002). Evaluating
762 Resource Selection Functions. *Ecological Modelling*, 157(2-3):281–300.
- 763 Brennan, A., Beytell, P., Aschenborn, O., Du Preez, P., Funston, P., Hanssen, L., Kilian,
764 J., Stuart-Hill, G., Taylor, R., and Naidoo, R. (2020). Characterizing Multispecies Con-
765 nectivity Across a Transfrontier Conservation Landscape. *Journal of Applied Ecology*,
766 57:1700–1710.
- 767 Brown, J. H. and Kodric-Brown, A. (1977). Turnover Rates in Insular Biogeography: Effect
768 of Immigration on Extinction. *Ecology*, 58(2):445–449.
- 769 Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A
770 Practical Information-Theoretic Approach*. Springer Science & Business Media, Ney York,
771 NY, USA.
- 772 Börger, L. and Fryxell, J. (2012). Quantifying Individual Differences in Dispersal Using Net
773 Squared Displacement. In Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M.,
774 editors, *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.

- 775 Clark, J. D., Laufenberg, J. S., Davidson, M., and Murrow, J. L. (2015). Connectivity among
776 Subpopulations of Louisiana Black Bears as Estimated by a Step Selection Function. *The*
777 *Journal of Wildlife Management*, 79(8):1347–1360.
- 778 Cloibert, J., Baguette, M., Benton, T. G., and Bullock, J. M. (2012). *Dispersal Ecology and*
779 *Evolution*. Oxford University Press, Oxford, UK.
- 780 Cozzi, G., Behr, D., Webster, H., Claase, M., Bryce, C., Modise, B., McNutt, J., and
781 Ozgul, A. (2020). The Walk of Life: African Wild Dog Dispersal and its Implications for
782 Management and Conservation across Transfrontier Landscapes. In press.
- 783 Csardi, G. and Nepusz, T. (2006). The igraph Software Package for Complex Network
784 Research. *InterJournal*, Complex Systems:1695.
- 785 Cushman, S. A. and Lewis, J. S. (2010). Movement Behavior Explains Genetic Differentiation
786 in American Black Bears. *Landscape Ecology*, 25(10):1613–1625.
- 787 Davies-Mostert, H. T., Kamler, J. F., Mills, M. G. L., Jackson, C. R., Rasmussen, G. S. A.,
788 Groom, R. J., and Macdonald, D. W. (2012). Long-Distance Transboundary Dispersal
789 of African Wild Dogs among Protected Areas in Southern Africa. *African Journal of*
790 *Ecology*, 50(4):500–506.
- 791 Diniz, M. F., Cushman, S. A., Machado, R. B., and De Marco Júnior, P. (2020). Landscape
792 Connectivity Modeling from the Perspective of Animal Dispersal. *Landscape Ecology*.
- 793 Doerr, V. A. J., Barrett, T., and Doerr, E. D. (2011). Connectivity, Dispersal Behaviour
794 and Conservation under Climate Change: A Response to Hodgson et al.: Connectivity
795 and Dispersal Behaviour. *Journal of Applied Ecology*, 48(1):143–147.
- 796 Eddelbuettel, D. (2013). *Seamless R and C++ Integration with Rcpp*. Springer, New York.
797 ISBN 978-1-4614-6867-7.
- 798 Eddelbuettel, D. and François, R. (2011). Rcpp: Seamless R and C++ Integration. *Journal*
799 *of Statistical Software*, 40(8):1–18.
- 800 Elliot, N. B., Cushman, S. A., Macdonald, D. W., and Loveridge, A. J. (2014). The Devil
801 is in the Dispersers: Predictions of Landscape Connectivity Change with Demography.
802 *Journal of Applied Ecology*, 51(5):1169–1178.
- 803 Etherington, T. R. (2016). Least-Cost Modelling and Landscape Ecology: Concepts, Appli-
804 cations, and Opportunities. *Current Landscape Ecology Reports*, 1(1):40–53.
- 805 Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of*
806 *Ecology, Evolution, and Systematics*, 34(1):487–515.
- 807 Ferreras, P. (2001). Landscape Structure and Asymmetrical Inter-Patch Connectivity in a
808 Metapopulation of the Endangered Iberian Lynx. *Biological Conservation*, 100(1):125–
809 136.
- 810 Fieberg, J., Signer, J., Smith, B., and Avgar, T. (2020). A ‘How-to’ Guide for Interpreting
811 Parameters in Resource- and Step-Selection Analyses. preprint, Ecology.
- 812 Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., and Mao, J. S. (2005).
813 Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone
814 National Park. *Ecology*, 86(5):1320–1330.
- 815 Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., and Dancose, K. (2009).
816 Group-Size-Mediated Habitat Selection and Group Fusion–Fission Dynamics of Bison
817 under Predation Risk. *Ecology*, 90(9):2480–2490.
- 818 Frankham, R., Briscoe, D. A., and Ballou, J. D. (2002). *Introduction to Conservation*
819 *Genetics*. Cambridge University Press, Cambridge, UK.

- 820 Gardner, R. H. and Gustafson, E. J. (2004). Simulating Dispersal of Reintroduced Species
821 within Heterogeneous Landscapes. *Ecological Modelling*, 171(4):339–358.
- 822 Graf, R. F., Kramer-Schadt, S., Fernández, N., and Grimm, V. (2007). What you see
823 is where you go? Modeling Dispersal in Mountainous Landscapes. *Landscape Ecology*,
824 22(6):853–866.
- 825 Gustafson, E. J. and Gardner, R. H. (1996). The Effect of Landscape Heterogeneity on the
826 Probability of Patch Colonization. *Ecology*, 77(1):94–107.
- 827 Hanski, I. (1998). Metapopulation Dynamics. *Nature*, 396(6706):41–49.
- 828 Hanski, I. (1999a). Habitat Connectivity, Habitat Continuity, and Metapopulations in Dy-
829 namic Landscapes. *Oikos*, 87(2):209.
- 830 Hanski, I. (1999b). *Metapopulation Ecology*. Oxford University Press.
- 831 Hauenstein, S., Fattebert, J., Grüebler, M. U., Naef-Daenzer, B., Pe'er, G., and Hartig, F.
832 (2019). Calibrating an Individual-Based Movement Model to Predict Functional Connec-
833 tivity for Little Owls. *Ecological Applications*, 29(4):e01873.
- 834 Hijmans, R. J. (2020). *raster: Geographic Data Analysis and Modeling*. R package version
835 3.3-13.
- 836 Hofmann, D. D., Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2021). Bound
837 within Boundaries: How Well Do Protected Areas Match Movement Corridors of their
838 Most Mobile Protected Species? *Journal of Applied Ecology*. (in 2nd review).
- 839 Howard, W. E. (1960). Innate and Environmental Dispersal of Individual Vertebrates.
840 *American Midland Naturalist*, 63(1):152.
- 841 Hunziker, P. (2021). *velox: Fast Raster Manipulation and Extraction*. R package version
842 0.2.1.
- 843 Jönsson, K. A., Tøttrup, A. P., Borregaard, M. K., Keith, S. A., Rahbek, C., and Thorup, K.
844 (2016). Tracking Animal Dispersal: From Individual Movement to Community Assembly
845 and Global Range Dynamics. *Trends in Ecology & Evolution*, 31(3):204–214.
- 846 Kanagaraj, R., Wiegand, T., Kramer-Schadt, S., and Goyal, S. P. (2013). Using Individual-
847 Based Movement Models to Assess Inter-Patch Connectivity for Large Carnivores in Frag-
848 mented Landscapes. *Biological Conservation*, 167:298 – 309.
- 849 Kays, R., Crofoot, M. C., Jetz, W., and Wikelski, M. (2015). Terrestrial Animal Tracking
850 as an Eye on Life and Planet. *Science*, 348(6240):aaa2478 – aaa2478.
- 851 Koen, E. L., Bowman, J., Sadowski, C., and Walpole, A. A. (2014). Landscape Connectivity
852 for Wildlife: Development and Validation of Multispecies Linkage Maps. *Methods in
853 Ecology and Evolution*, 5(7):626–633.
- 854 Koen, E. L., Garroway, C. J., Wilson, P. J., and Bowman, J. (2010). The Effect of Map
855 Boundary on Estimates of Landscape Resistance to Animal Movement. *PLoS ONE*,
856 5(7):e11785.
- 857 Kramer-Schadt, S., Revilla, E., Wiegand, T., and Breitenmoser, U. (2004). Fragmented
858 Landscapes, Road Mortality and Patch Connectivity: Modelling Influences on the Dis-
859 persal of Eurasian lynx. *Journal of Applied Ecology*, 41(4):711–723.
- 860 Kramer-Schadt, S., Revilla, E., Wiegand, T., and Grimm, V. (2007). Patterns for Parameters
861 in Simulation Models. *Ecological Modelling*, 204(3-4):553–556.
- 862 Landguth, E. L., Hand, B. K., Glassy, J., Cushman, S. A., and Sawaya, M. A. (2012).
863 UNICOR: A Species Connectivity and Corridor Network Simulator. *Ecography*, 35(1):9–
864 14.

- 865 Latham, A. D. M., Latham, M. C., Boyce, M. S., and Boutin, S. (2011). Movement Responses by Wolves to Industrial Linear Features and Their Effect on Woodland Caribou in Northeastern Alberta. *Ecological Applications*, 21(8):2854–2865.
- 868 Leigh, K. A., Zenger, K. R., Tammen, I., and Raadsma, H. W. (2012). Loss of Genetic Diversity in an Outbreeding Species: Small Population Effects in the African Wild Dog (*Lycaon pictus*). *Conservation Genetics*, 13(3):767–777.
- 871 MacArthur, R. H. and Wilson, E. O. (2001). *The Theory of Island Biogeography*, volume 1. Princeton University Press, Princeton, New Jersey, USA.
- 873 Masenga, E. H., Jackson, C. R., Mjingo, E. E., Jacobson, A., Riggio, J., Lyamuya, R. D., Fyumagwa, R. D., Borner, M., and Røskuft, E. (2016). Insights into Long-Distance Dispersal by African Wild Dogs in East Africa. *African Journal of Ecology*, 54(1):95–98.
- 876 McNutt, J. (1996). Sex-Biased Dispersal in African Wild Dogs (*Lycaon pictus*). *Animal Behaviour*, 52(6):1067–1077.
- 878 McNutt, J. W. (1995). *Sociality and Dispersal in African Wild Dogs, Lycaon pictus*. PhD Thesis, University of California, Davis.
- 880 McRae, B. H. (2006). Isolation by Resistance. *Evolution*, 60(8):1551–1561.
- 881 McRae, B. H., Dickson, B. G., Keitt, T. H., and Shah, V. B. (2008). Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation. *Ecology*, 89(10):2712–2724.
- 883 Muff, S., Signer, J., and Fieberg, J. (2020). Accounting for Individual-Specific Variation in Habitat-Selection Studies: Efficient Estimation of Mixed-Effects Models Using Bayesian or Frequentist Computation. *Journal of Animal Ecology*, 89(1):80–92.
- 886 Munden, R., Börger, L., Wilson, R. P., Redcliffe, J., Brown, R., Garel, M., and Potts, J. R. (2020). Why Did the Animal Turn? Time-Varying Step Selection Analysis for Inference Between Observed Turning Points in High Frequency Data.
- 889 Nathan, R. (2008). An Emerging Movement Ecology Paradigm. *Proceedings of the National Academy of Sciences*, 105(49):19050–19051.
- 891 Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., and Balkenhol, N. (2019). Using Step-Selection Functions to Model landscape Connectivity for African Elephants: Accounting for Variability across Individuals and Seasons. *Animal Conservation*, 22(1):35–48.
- 895 Osofsky, S. A., McNutt, J. W., and Hirsch, K. J. (1996). Immobilization of Free-Ranging African Wild Dogs (*Lycaon pictus*) Using a Ketamine/Xylazine/Atropine Combination. *Journal of Zoo and Wildlife Medicine*, pages 528–532.
- 898 O'Neill, H. M. K., Durant, S. M., and Woodroffe, R. (2020). What Wild Dogs Want: Habitat Selection Differs across Life Stages and Orders of Selection in a Wide-Ranging Carnivore. *BMC Zoology*, 5(1).
- 901 Panzacchi, M., Van Moorter, B., Strand, O., Saerens, M., Kivimäki, I., St. Clair, C. C., Herfindal, I., and Boitani, L. (2016). Predicting the Continuum Between Corridors and Barriers to Animal Movements Using Step Selection Functions and Randomized Shortest Paths. *Journal of Animal Ecology*, 85(1):32–42.
- 905 Perrin, N. and Mazalov, V. (1999). Dispersal and Inbreeding Avoidance. *The American Naturalist*, 154(3):282–292.
- 907 Perrin, N. and Mazalov, V. (2000). Local Competition, Inbreeding, and the Evolution of Sex-Biased Dispersal. *The American Naturalist*, 155(1):116–127.
- 909 Pe'er, G. and Kramer-Schadt, S. (2008). Incorporating the Perceptual Range of Animals into Connectivity Models. *Ecological Modelling*, 213(1):73–85.

- 911 Pinto, N. and Keitt, T. H. (2009). Beyond the Least-Cost Path: Evaluating Corridor
912 Redundancy Using a Graph-Theoretic Approach. *Landscape Ecology*, 24(2):253–266.
- 913 Pomilia, M. A., McNutt, J. W., and Jordan, N. R. (2015). Ecological Predictors of African
914 Wild Dog Ranging Patterns in Northern Botswana. *Journal of Mammalogy*, 96(6):1214–
915 1223.
- 916 Prokopenko, C. M., Boyce, M. S., and Avgar, T. (2017). Characterizing Wildlife Behavioural
917 Responses to Roads Using Integrated Step Selection Analysis. *Journal of Applied Ecology*,
918 54(2):470–479.
- 919 R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foun-
920 dation for Statistical Computing, Vienna, Austria.
- 921 Revilla, E. and Wiegand, T. (2008). Individual Movement Behavior, Matrix Heterogene-
922 ity, and the Dynamics of Spatially Structured Populations. *Proceedings of the National
923 Academy of Sciences*, 105(49):19120–19125.
- 924 Revilla, E., Wiegand, T., Palomares, F., Ferreras, P., and Delibes, M. (2004). Effects of
925 Matrix Heterogeneity on Animal Dispersal: From Individual Behavior to Metapopulation-
926 Level Parameters. *The American Naturalist*, 164(5):E130–E153.
- 927 Rudnick, D., Ryan, S., Beier, P., Cushman, S., Dieffenbach, F., Epps, C., Gerber, L., Hart-
928 ter, J., Jenness, J., Kintsch, J., Merenlender, A., Perkl, R., Perziosi, D., and Trombulack,
929 S. (2012). The Role of Landscape Connectivity in Planning and Implementing Conserva-
930 tion and Restoration Priorities. *Issues in Ecology*.
- 931 Schultz, C. B. and Crone, E. E. (2001). Edge-Mediated Dispersal Behavior in a Prairie
932 Butterfly. *Ecology*, 82(7):1879–1892.
- 933 Signer, J., Fieberg, J., and Avgar, T. (2017). Estimating Utilization Distributions from
934 Fitted Step-Selection Functions. *Ecosphere*, 8(4):e01771.
- 935 Spear, S. F., Balkenhol, N., Fortin, M.-J., Mcrae, B. H., and Scribner, K. (2010). Use of
936 Resistance Surfaces for Landscape Genetic Studies: Considerations for Parameterization
937 and Analysis. *Molecular Ecology*, 19(17):3576–3591.
- 938 Squires, J. R., DeCesare, N. J., Olson, L. E., Kolbe, J. A., Hebblewhite, M., and Parks, S. A.
939 (2013). Combining Resource Selection and Movement Behavior to Predict Corridors for
940 Canada Lynx at their Southern Range Periphery. *Biological Conservation*, 157:187–195.
- 941 Thurfjell, H., Ciuti, S., and Boyce, M. S. (2014). Applications of Step-Selection Functions
942 in Ecology and Conservation. *Movement Ecology*, 2(4).
- 943 Tischendorf, L. and Fahrig, L. (2000). On the Usage and Measurement of Landscape Con-
944 nnectivity. *Oikos*, 90(1):7–19.
- 945 Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population
946 Redistribution in Plants and Animals*. Sinauer Associates, Sunderland, MA, USA.
- 947 Van der Meer, E., Fritz, H., Blinston, P., and Rasmussen, G. S. (2014). Ecological Trap in
948 the Buffer Zone of a Protected Area: Effects of Indirect Anthropogenic Mortality on the
949 African Wild Dog (*Lycaon pictus*). *Oryx*, 48(2):285–293.
- 950 Van Moorter, B., Kivimäki, I., Panzacchi, M., and Saerens, M. (2021). Defining and Quan-
951 tifying Effective Connectivity of Landscapes for Species’ Movements. *Ecography*, page
952 ecog.05351.
- 953 Vasudev, D., Fletcher, R. J., Goswami, V. R., and Krishnadas, M. (2015). From Disper-
954 sal Constraints to Landscape Connectivity: Lessons from Species Distribution Modeling.
955 *Ecography*, 38(10):967–978.

- 956 Vasudev, D., Goswami, V. R., and Oli, M. K. (2021). Detecting Dispersal: A Spatial Dy-
957 namic Occupancy Model to Reliably Quantify Connectivity across Heterogeneous Con-
958 servation Landscapes. *Biological Conservation*, 253:108874.
- 959 Wiegand, T., Jeltsch, F., Hanski, I., and Grimm, V. (2003). Using Pattern-Oriented Mod-
960 eling for Revealing Hidden Information: A Key for Reconciling Ecological Theory and
961 Application. *Oikos*, 100(2):209–222.
- 962 Williams, H. J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., Grissac, S.,
963 Demšar, U., English, H. M., Franconi, N., Gómez-Laich, A., Griffiths, R. C., Kay, W. P.,
964 Morales, J. M., Potts, J. R., Rogerson, K. F., Rutz, C., Spelt, A., Trevail, A. M., Wilson,
965 R. P., and Börger, L. (2019). Optimizing the Use of Biologgers for Movement Ecology
966 Research. *Journal of Animal Ecology*.
- 967 Wolski, P., Murray-Hudson, M., Thito, K., and Cassidy, L. (2017). Keeping it Simple:
968 Monitoring Flood Extent in Large Data-Poor Wetlands Wsing MODIS SWIR Data. *In-*
969 *ternational Journal of Applied Earth Observation and Geoinformation*, 57:224–234.
- 970 Woodroffe, R. and Ginsberg, J. R. (1999). Conserving the African Wild Dog *Lycaon pictus*.
971 Diagnosing and Treating Causes of Decline. *Oryx*, 33(2):132–142.
- 972 Woodroffe, R., Rabaiotti, D., Ngatia, D. K., Smallwood, T. R. C., Strelak, S., and O'Neill,
973 H. M. K. (2019). Dispersal Behaviour of African Wild Dogs in Kenya. *African Journal
974 of Ecology*.
- 975 Woodroffe, R. and Sillero-Zubiri, C. (2012). *Lycaon pictus*. *The IUCN Red List of Threatened
976 Species*, 2012:e. T12436A16711116.
- 977 Zeller, K. A., McGarigal, K., and Whiteley, A. R. (2012). Estimating Landscape Resistance
978 to Movement: A Review. *Landscape Ecology*, 27(6):777–797.
- 979 Zeller, K. A., Wattles, D. W., Bauder, J. M., and DeStefano, S. (2020). Forecasting Seasonal
980 Habitat Connectivity in a Developing Landscape. *Land*, 9(7):233.

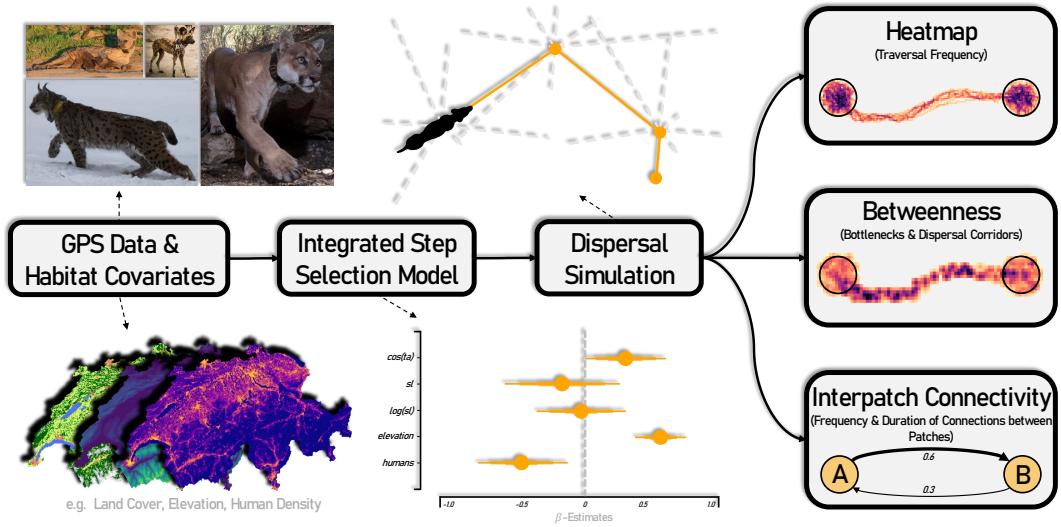


Figure 1: Flowchart of the simulation-based connectivity analysis. First, GPS data and habitat covariates have to be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement kernels. The parametrized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

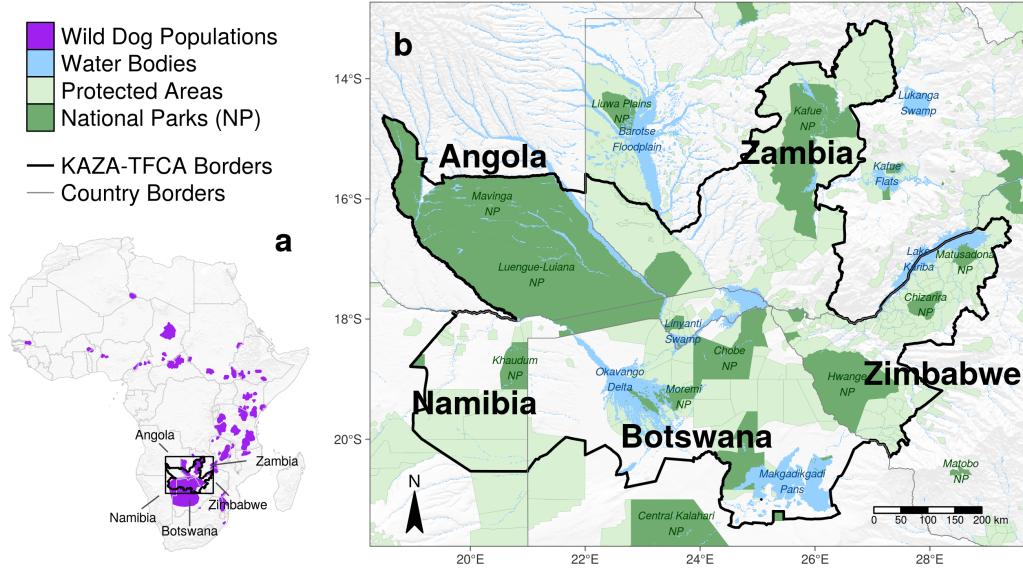


Figure 2: Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA and encompassing parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA represents the world's largest terrestrial conservation area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

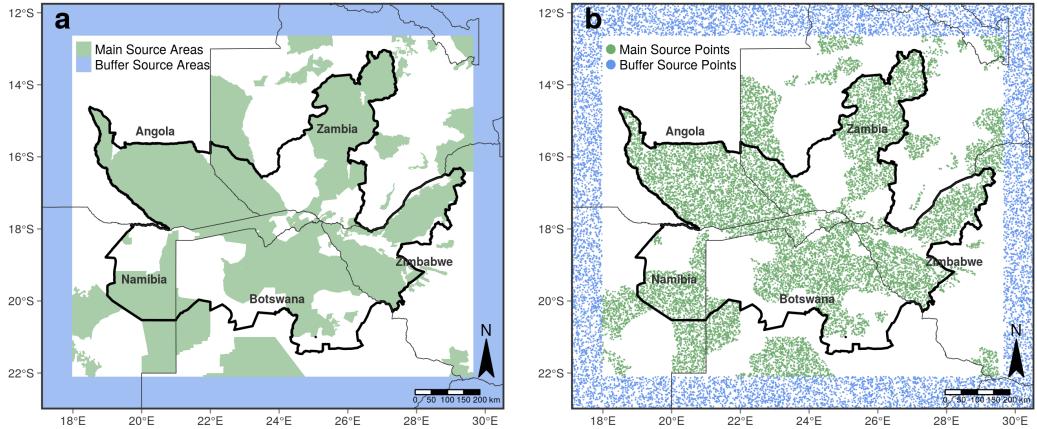


Figure 3: (a) Different source areas from which we released virtual dispersers. We only considered contiguous protected areas (national parks, game reserves, and forest reserves) that were larger than 700 km^2 (green). This area corresponds to the average home range requirement for viable wild dog populations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

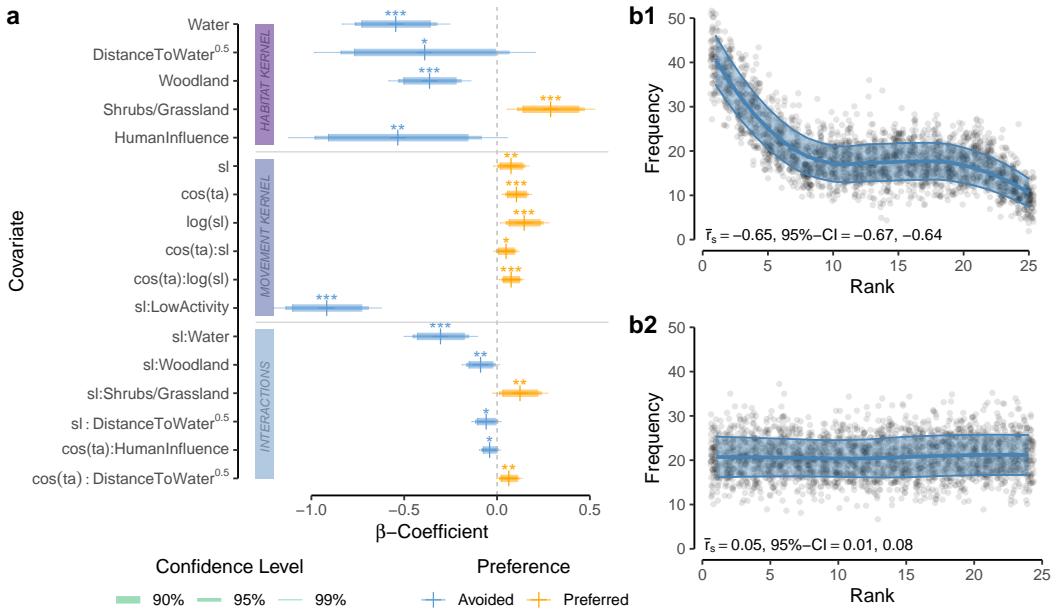


Figure 4: (a) Most parsimonious movement model for dispersing wild dogs. The model includes a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% Confidence-Intervals for the respective β -coefficients. Significance codes: * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$. (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.

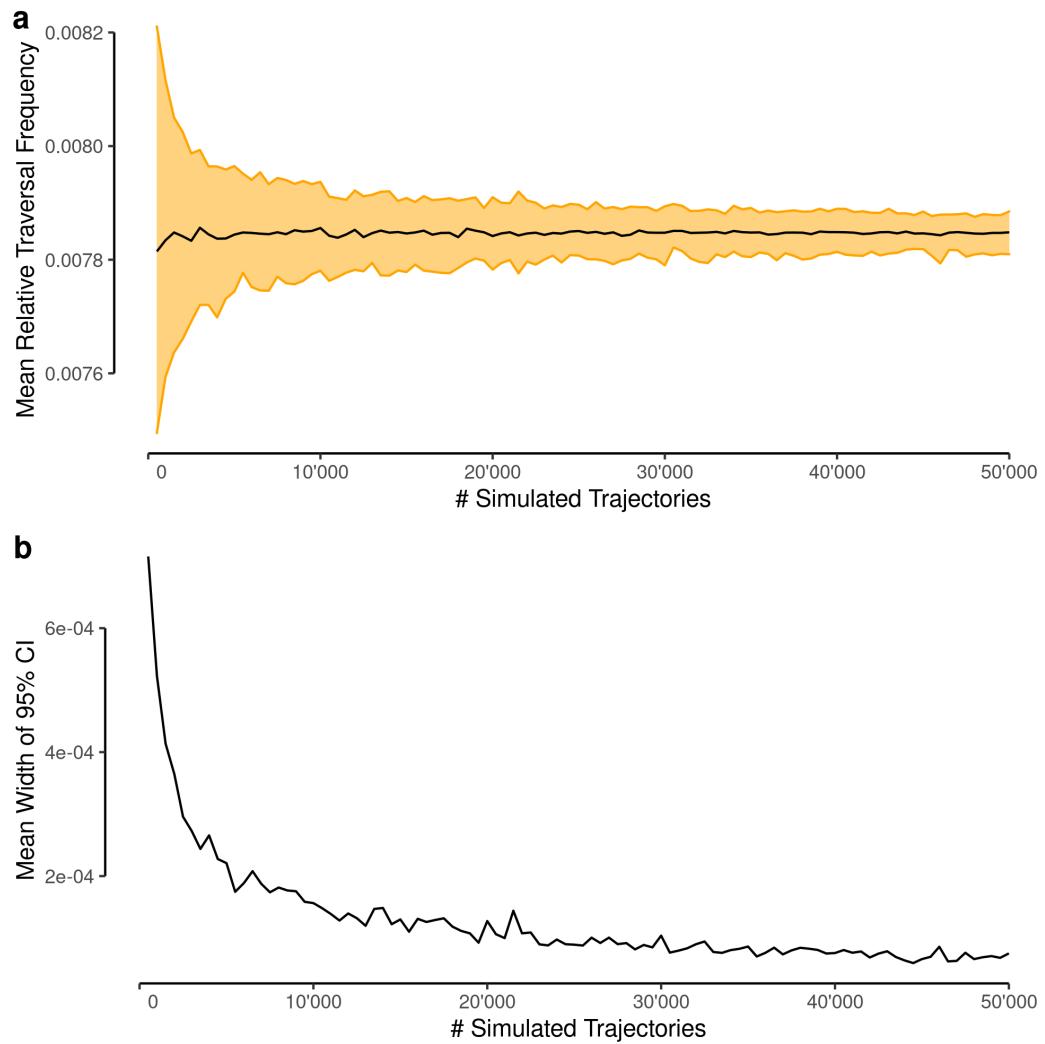


Figure 5: Convergence

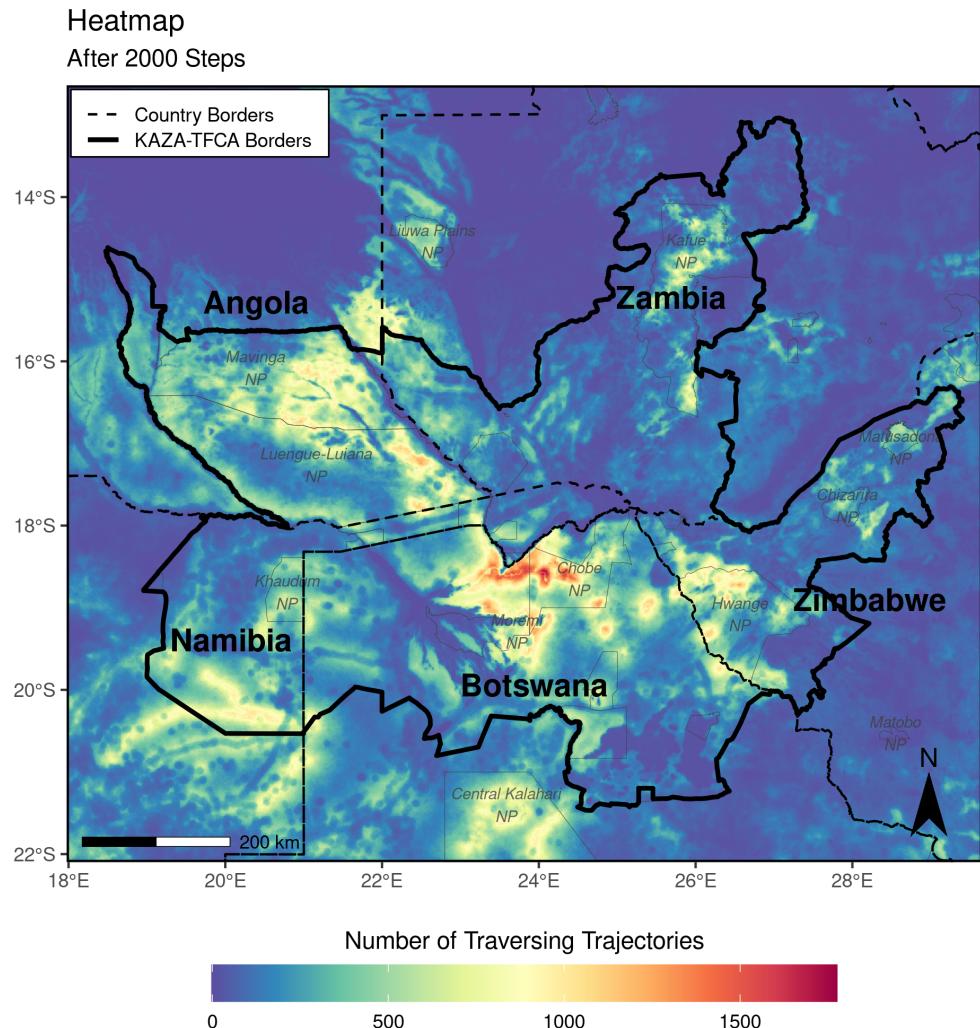


Figure 6: Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step selection model that we fit to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied all 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

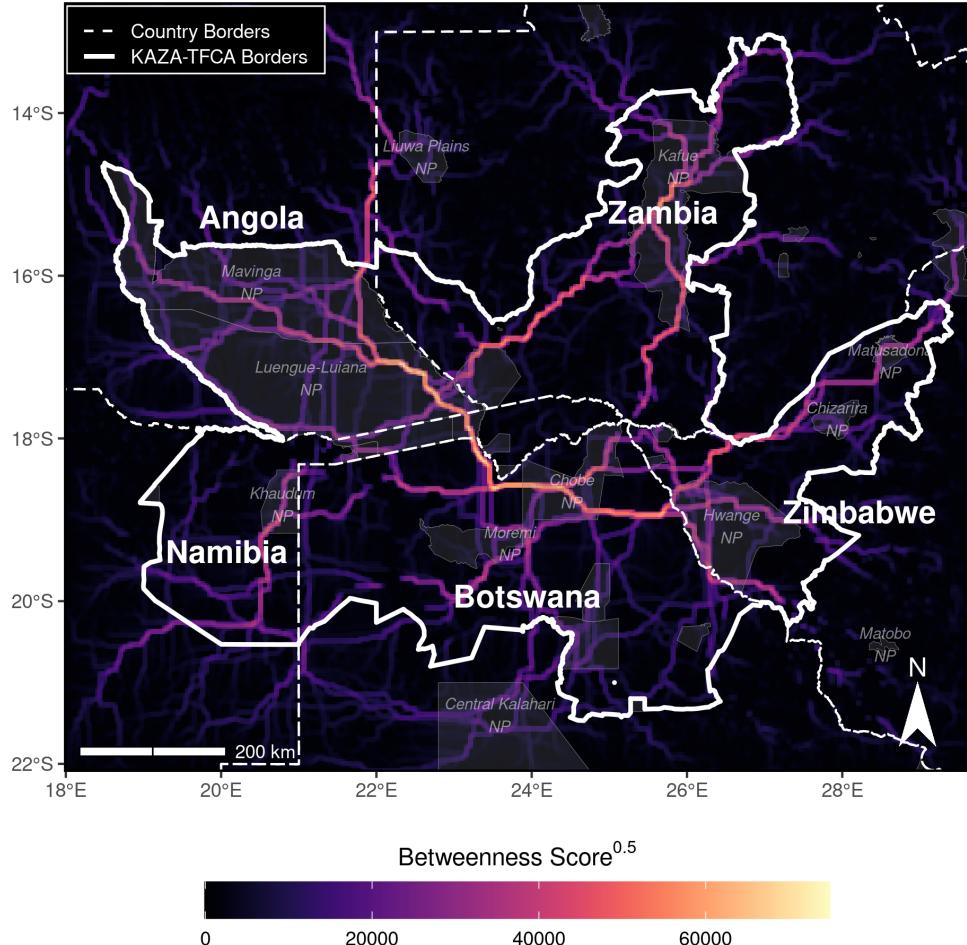


Figure 7: Map of betweenness scores, highlighting distinct dispersal corridors and potential bottlenecks. A high betweenness score indicates that the respective cells are exceptionally relevant in connecting different regions in the study area. That is, the higher the betweenness score, the more often 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.

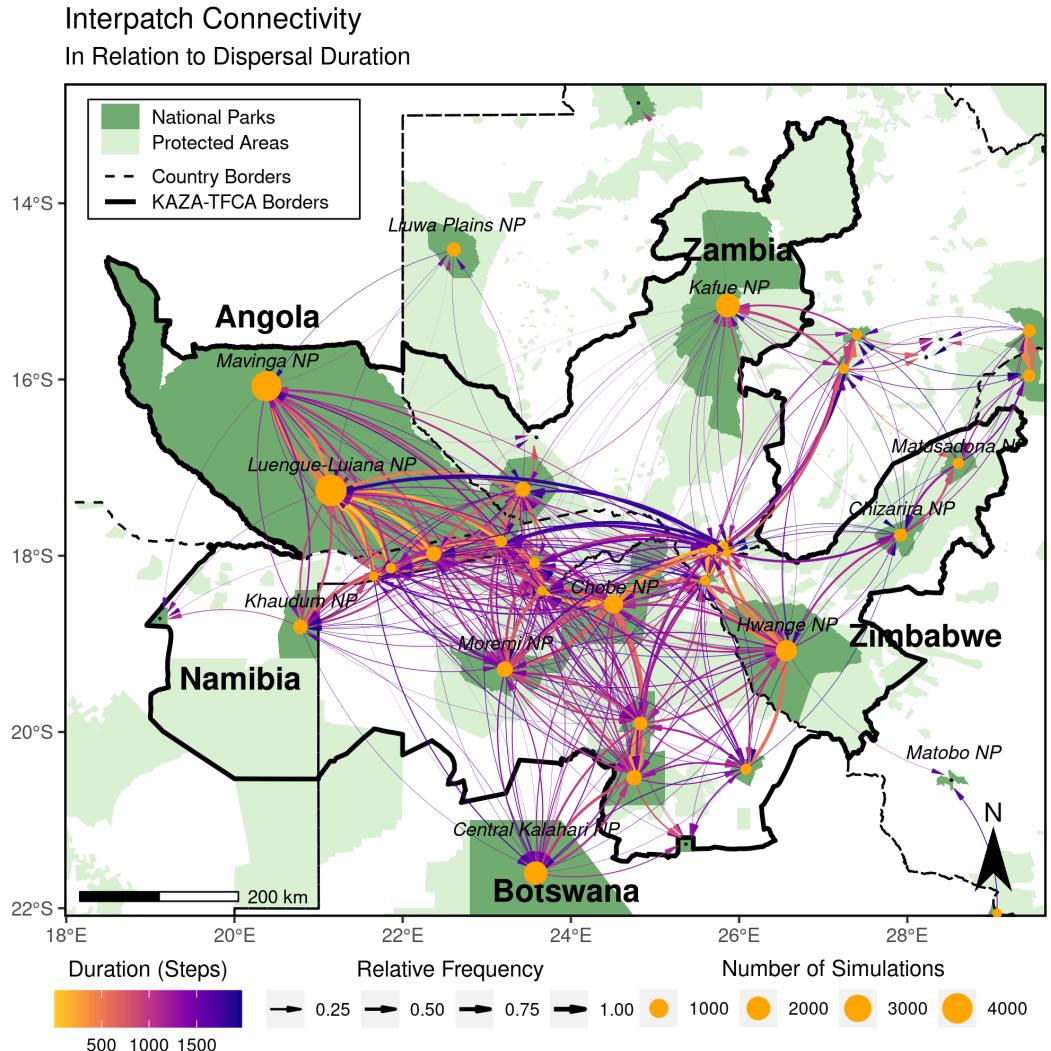


Figure 8: Network on simulated dispersal trajectories highlighting connections between national parks (dark green). Yellow bubbles represent the center of the different national parks and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent national 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: * $p < 0.10$ ** $p < 0.05$ *** $p < 0.01$