

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

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Abstract

Dispersal of individuals is a crucial pre-requisite for long-term species persistence. However, the ability to disperse is contingent a sufficient degree of landscape connectivity, which is why the identification and preservation of movement corridors that promote connectivity has become a task of exceptional importance.

Over the past two decades, ecologists have primarily relied on least-cost analysis and circuit theory to investigate connectivity. Unfortunately, both methods make several restrictive assumptions that limit their usefulness in reality. Least-cost analysis, for instance, assumes that animals move towards a pre-conceived endpoint and choose a cost-minimizing route accordingly. Circuit theory, in contrast, presumes a random walk without any directional persistence. To address these shortcomings, simulations from individual-based movement models have been proposed and applied, yet a unified framework to simulate dispersal and to derive connectivity maps based on simulated dispersal events is lacking.

Here, we combine several already-existing methods to simulate dispersal and investigate landscape connectivity in three distinct steps. In the first step, integrated step selection functions are used to parametrize a mechanistic movement model. In the second step, the parametrized model is applied as an individual-based movement model to simulate dispersal trajectories. In the third step, simulated trajectories are consolidated and synthesized into three complementary connectivity maps, each focusing on a different aspect of landscape connectivity. The set of maps includes a heatmap, revealing frequently traversed areas, a betweenness-map, delineating critical dispersal corridors, and a map of inter-patch connectivity, depicting the presence or absence of functional links between distinct habitat patches.

As a case study, we apply the proposed workflow to assess landscape connectivity for dispersing African wild dogs (*Lycaon pictus*) in the Kavango-Zambezi Transfrontier Conservation Area, the world's largest transboundary conservation area. With this, we demonstrate that the outlined workflow offers a simple, yet powerful alternative to traditional connectivity modeling techniques. Although such individual-based simulations necessitate informed decisions about the number of simulated individuals and the duration of simulated dispersal events, they enable to relax several of the unrealistic assumptions inherent to least-cost analysis or circuit theory.

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1 Introduction

1.1 Dispersal & Connectivity Models (90%)

Successful dispersal of individuals requires a sufficient degree of landscape connectivity (Fahrig, 2003; Clobert et al., 2012), which is why the identification and protection of major dispersal corridors has become a fundamental task in conservation science (Nathan, 2008; Doerr et al., 2011; Rudnick et al., 2012). To pinpoint relevant dispersal corridors, a comprehensive understanding of the factors that limit dispersal of the focal species and an adequate connectivity model are required (Baguette et al., 2013; Vasudev et al., 2015; Hofmann et al., 2021). To date, the two most prominent connectivity models are least-cost path analysis (LCPA; Adriaensen et al., 2003) and circuit theory (CT; McRae, 2006; McRae et al., 2008), both graph-based approaches that estimate conductance of the landscape based on predicted habitat permeability (Zeller et al., 2012).

1.2 Issues with Traditional Methods (90%)

Despite their intuitive nature and ease of use, both methods make several assumptions that are hardly ever met in reality (Diniz et al., 2020). With LCPA, for instance, a least costly route always exists, even if associated movement costs are unreasonably high and will never be incurred by a dispersing individual. The method also presumes that animals move towards a pre-conceived endpoint and choose a cost-minimizing route accordingly. While these assumptions may be fulfilled by migrating animals, dispersers usually move into unfamiliar territory and are therefore less likely to be aware of associated movement costs (Koen et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020). CT relaxes these assumptions, yet posits that animals move according to a random walk, entailing that directional biases cannot be rendered (Diniz et al., 2020). In reality, however, directional persistence is regularly observed (Bovet and Benhamou, 1991; Schultz and Crone, 2001), especially in dispersing individuals (Cozzi et al., 2020; Hofmann et al., 2021). Some of these deficiencies can be addressed using alternative graph-based approaches, such as least-cost *corridors* (Pinto and Keitt, 2009), *thresholded* least-cost paths (Landguth et al., 2012), or *randomized* least-cost paths (Panzacchi et al., 2016), yet a certain degree of arbitrariness remains. Finally, none of the methods is capable of rendering the temporal dimension of dispersal (Diniz et al., 2020), meaning that statements about the expected duration required to traverse a certain corridor are impossible.

³² **1.3 What about IBMMs? (90%)**

³³ To overcome the unrealistic assumptions inherent to traditional connectivity modeling tech-
³⁴ niques, simulations from individual-based movement models (IBMMs) have been proposed
³⁵ and applied (Diniz et al., 2020). In these models, dispersal trajectories are simulated based
³⁶ on movement rules that determine how individuals move across or interact with the pre-
³⁷ vailing landscape (Gustafson and Gardner, 1996; Gardner and Gustafson, 2004; Graf et al.,
³⁸ 2007; Kramer-Schadt et al., 2004; Revilla et al., 2004; Revilla and Wiegand, 2008; Kanagaraj
³⁹ et al., 2013; Clark et al., 2015; Allen et al., 2016; Hauenstein et al., 2019; Zeller et al., 2020;
⁴⁰ Vasudev et al., 2021). Instead of enforcing connections towards a known endpoint, IBMMs
⁴¹ allow individuals to choose their route as they move and enable to render potential inter-
⁴² actions between movement behavior and environmental conditions. IBMMs furthermore
⁴³ enable to model directional persistence and to study the temporal dimension of dispersal
⁴⁴ (Diniz et al., 2020). Despite these advantages, however, a unified framework to simulate
⁴⁵ dispersal and to derive connectivity maps based on simulated dispersal events is lacking.

⁴⁶ **1.4 Step Selection Functions (90%)**

⁴⁷ A promising framework that has been developed more recently... Over the past decade, the
⁴⁸ increased availability of large amounts of data and an increased computational power have
⁴⁹ led to the development of numerous techniques to study animal movement and resource
⁵⁰ selection during dispersal (Boyce et al., 2002; Fortin et al., 2005; Cushman and Lewis,
⁵¹ 2010; Zeller et al., 2012). Especially *resource selection functions* (Boyce et al., 2002), *step*
⁵² *selection functions* (Fortin et al., 2005), and *path selection functions* (Cushman and Lewis,
⁵³ 2010) have pushed the field of movement ecology forward. These methods allow estimating
⁵⁴ habitat preferences of the focal species by comparing covariates at locations visited by the
⁵⁵ animal to the same covariates at locations available to, but not visited by the animal (Boyce
⁵⁶ et al., 2002; Fortin et al., 2005; Cushman and Lewis, 2010; Thurfjell et al., 2014). While
⁵⁷ regular SSFs were intended to learn about relative habitat preferences of the focal species
⁵⁸ (Fortin et al., 2005; Thurfjell et al., 2014; Avgar et al., 2017), the method has recently
⁵⁹ been generalized to *integrated* SSFs and now enables to jointly study habitat and movement
⁶⁰ preferences, as well as potential interactions between them (Avgar et al., 2016; Signer et al.,
⁶¹ 2017; Fieberg et al., 2020). ISSFs therefore provide a relatively simple means to model
⁶² complex movement behavior, where movement is viewed as the result of two intertwined
⁶³ behavioral kernels (e.g. Prokopenko et al., 2017; Munden et al., 2020). Importantly, a
⁶⁴ parametrized ISSF model represents a fully mechanistic movement model based on which

65 individual movement trajectories can be simulated (Avgar et al., 2016; Signer et al., 2017).
66 In fact, Signer et al. (2017) used ISSF to simulate steady state utilization distributions of
67 resident animals that were moving around a point of attraction. However, the degree to
68 which such simulations are helpful in detecting movement corridors and modeling landscape
69 connectivity remains to be investigated.

70 **1.5 Proposed Framework (90%)**

71 Here, we therefore propose to combine several already-existing methods into a simple three-
72 step workflow to simulate dispersal and investigate landscape connectivity. In the first step,
73 integrated step selection functions are used to parametrize a mechanistic movement model
74 rendering dispersal behavior. In the second step, the parametrized model is applied as an
75 individual-based movement model to simulate dispersal trajectories. Finally, in the third
76 step, simulated trajectories are consolidated into three complementary connectivity maps,
77 each focusing on a different aspect of landscape connectivity. The set of maps includes
78 a heatmap, revealing frequently traversed areas, a betweenness-map, delineating critical
79 dispersal corridors, and a map of inter-patch connectivity, depicting the presence or absence
80 of functional links between distinct habitat patches.

81 **1.6 Study Species & Study Area (90%)**

82 We exemplify application of the proposed workflow by investigating landscape connectivity
83 for the endangered African wild dog (*Lycon pictus*). While once present across entire sub-
84 Saharan Africa, wild dogs have disappeared from a vast majority of their historic range,
85 mainly due to persecution by humans, habitat fragmentation and destruction, and deadly
86 diseases (Woodroffe and Sillero-Zubiri, 2012). Within the few remaining subpopulations,
87 wild dogs form cohesive packs comprising 8 to 12 adults and their offspring McNutt (1995).
88 After reaching sexual maturity, male and female offspring form same-sex coalitions and
89 disperse from their natal pack in search for potential mating partners and a suitable territory
90 to settle (McNutt, 1996; Behr et al., 2020). New packs are formed when dispersing coalitions
91 join unrelated opposite-sex dispersing coalitions (McNutt, 1996). During dispersal, wild
92 dogs can cover several hundred kilometers across a variety of landscapes (Davies-Mostert
93 et al., 2012; Masenga et al., 2016; Cozzi et al., 2020; Hofmann et al., 2021). One of the main
94 strongholds for this species lies near the Moremi Game Reserve in northern Botswana, which
95 is part of the world's largest transboundary protected area, namely the Kavango-Zambezi
96 Transfrontier Conservation Area (KAZA-TFCA). This area was originally devoted towards

⁹⁷ facilitating the migration of elephants, yet it can be expected to yield benefits to a great
⁹⁸ multitude of other species (Elliot et al., 2014; Brennan et al., 2020; Hofmann et al., 2021).

⁹⁹ 1.7 Previous Paper (90%)

¹⁰⁰ We previously assessed landscape connectivity for dispersing African wild dogs within the
¹⁰¹ KAZA-TFCA using least-cost methods (Hofmann et al., 2021). More specifically, we fitted
¹⁰² a habitat selection model and predicted a permeability surface based on which we computed
¹⁰³ least-cost paths and corridors between protected areas. We now expand on this knowledge
¹⁰⁴ and use ISSFs to develop a more detailed, mechanistic movement model of dispersing wild
¹⁰⁵ dogs (Figure 1). We then employ the model to simulate 80'000 dispersers moving 2'000
¹⁰⁶ steps across the KAZA-TFCA. Finally, we generate a heatmap, betweenness map and a
¹⁰⁷ map of interpatch connectivity. We thereby exemplify how ISSFs can be utilized for disper-
¹⁰⁸ sal simulations and we discuss several benefits of this approach over traditional connectivity
¹⁰⁹ modeling techniques such as least-cost analysis and circuit theory. Most importantly, sim-
¹¹⁰ ulations based on ISSFs provide a more generic view on how connectivity emerges and to
¹¹¹ which degree connectivity depends on the dispersal duration. In addition, by generating
¹¹² proper dispersal trajectories, network theory can be applied to calculate network metrics
¹¹³ that are pertinent to connectivity analysis.

¹¹⁴ 2 Methods

¹¹⁵ 2.1 Study Area (90%)

¹¹⁶ The study area was defined by a bounding box centered at -17°13'9"S, 23°56'4"E (Figure 2a)
¹¹⁷ stretching over 1.3 Mio. km² and encompassed the entire KAZA-TFCA (Figure 2b). The
¹¹⁸ KAZA-TFCA represents the world's largest transboundary conservation area and comprises
¹¹⁹ parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia. It covers a total of 520'000
¹²⁰ km² and hosts diverse landscapes, ranging from savanna to grassland and from dry to moist
¹²¹ woodland habitats. In its center lies the Okavango Delta, a dominant hydrogeographical
¹²² feature and the world's largest flood-pulsing inland delta. The wet season within the KAZA-
¹²³ TFCA lasts from November to March and is out of phase with the flood in the Okavango
¹²⁴ Delta, which peaks between July and August (McNutt, 1996; Wolski et al., 2017). Although
¹²⁵ large portions within the KAZA-TFCA are designated national parks or other protected
¹²⁶ areas, considerable human influence remains due to roads, agricultural sites and settlements
¹²⁷ and villages that are distributed across the KAZA-TFCA's landscape.

₁₂₈ **2.2 GPS Relocation Data (90%)**

₁₂₉ GPS data of 16 dispersing wild dogs was obtained as described in (Cozzi et al., 2020; Hof-
₁₃₀ mann et al., 2021). We collected data on 7 female and 9 male dispersing coalitions between
₁₃₁ 2011 and 2019 from a free-ranging population inhabiting the Moremi National Park in north-
₁₃₂ ern Botswana. In some instances, exact dispersal dates were known from field observations,
₁₃₃ in other cases we determined dispersal phases using the net-squared displacement metric.
₁₃₄ Net squared displacement measures the squared Euclidean distance of a GPS relocation to
₁₃₅ a reference point (Börger and Fryxell, 2012), which in our case was set to the center of
₁₃₆ each individual's natal home range. Thus, dispersal was deemed to have started when an
₁₃₇ individual left its natal home range and ended once individuals became sedentary again.
₁₃₈ Because behavior during dispersal is more pertinent to landscape connectivity (Elliot et al.,
₁₃₉ 2014; Abrahms et al., 2017), we discarded all data that was collected during residency. Dur-
₁₄₀ ing dispersal, collars were programmed to record a GPS fix every four hours and regularly
₁₄₁ transmitted over the Iridium satellite system. As previous research found no differences in
₁₄₂ behaviors of females and males during dispersal (Woodroffe et al., 2019; Cozzi et al., 2020),
₁₄₃ we did not distinguish between sexes. After collection, we converted GPS coordinates ($n =$
₁₄₄ 4'169) to steps, where each step represented the straight-line distance traveled by an individ-
₁₄₅ ual between two consecutive GPS relocations (Turchin, 1998). To ensure a regular sampling
₁₄₆ interval, we removed fixes that were not successfully collected on the 4-hourly schedule (\pm
₁₄₇ 15 minutes).

₁₄₈ **2.3 Covariates (90%)**

₁₄₉ We represented the physical landscape across the study area using a set of habitat covariates
₁₅₀ that included water-cover, distance to water, woodland-cover, and shrub/grassland-cover.
₁₅₁ Because water cover greatly changes within and between years in the Okavango Delta, we
₁₅₂ applied a remote sensing algorithm and generated frequently updated water cover layers
₁₅₃ and corresponding distance to water layers (see Wolski et al., 2017 and Appendix A3 in
₁₅₄ Hofmann et al., 2021). Resulting layers thus temporally aligned with each dispersal event,
₁₅₅ ensuring minimal temporal lag between observed movements and corresponding water layer.
₁₅₆ We furthermore computed a proxy for human influence, rendering anthropogenic pressures
₁₅₇ stemming from human-density, agricultural sites, and roads. All spatial layers were coars-
₁₅₈ ened or interpolated to a target resolution of 250 m by 250 m. A detailed description of the
₁₅₉ preparation of each habitat covariate is given in Hofmann et al. (2021).

₁₆₀ Besides habitat covariates, we computed movement metrics that we used as movement

covariates in our models. Movement metrics were calculated for each step and included the step length (`sl`), its natural logarithm (`log(sl)`), and the cosine of the relative turning angle (`cos(ta)`) (for details see (Avgar et al., 2016; Fieberg et al., 2020)). Because wild dogs follow a diurnal activity pattern (Castelló, 2018), we also coded a binary variable (`LowActivity`) indicating whether a step was realized during periods of low wild dog activity (17:00 to 09:00 local time) or high wild dog activity (09:00 to 17:00 local time). Handling and manipulation of all data, as well as all models and simulations were implemented with the statistical software R, version 3.6.6 (R Core Team, 2019). Several helper functions were written in C++ and imported into R using the `Rcpp` package (Eddelbuettel and François, 2011; Eddelbuettel, 2013).

2.4 Movement Model (80%)

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

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

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

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

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

190 We ran conditional logistic regression analysis in the r-package `glmmTMB` to estimate preferences of interest. To handle multiple individuals, we applied the mixed effects technique
 191 developed by (Muff et al., 2020), which allows to effectively model random slopes. Thus, we
 192 treated animal IDs as random effect and modeled random slopes for each covariate.
 193

194 The structure of the movement model was based on the habitat selection model for
 195 dispersing wild dogs presented in Hofmann et al. (2021). In the original model (hereafter re-
 196 ferred to as base model), no interactions between habitat covariates (`Water`, `DistanceToWater`^{0.5},
 197 `Woodland`, `Shrubs/Grazing`, `Human Influence`) and movement covariates (`sl`, `log(sl)`, `cos(ta)`)
 198 were considered. Hence, we slightly expanded this base model and proposed interactions
 199 between all movement and habitat covariates. More specifically, we started with the base
 200 model and incrementally increased model complexity by adding all possible two-way inter-
 201 actions between habitat covariates and movement covariates. For instance, for the covariate
 202 `Water`, we proposed the interactions `Water:log(sl)`, `Water:log(sl)`, and `Water:cos(ta)`. Besides
 203 those combinations, we also proposed the interactions `sl:cos(ta)` and `log(sl):cos(ta)` to ac-
 204 count for a correlation between turning angles and step lengths, as well as the interactions
 205 `sl:LowActivity` and `log(sl):LowActivity` to account for the fact that step lengths may differ due
 206 to wild dogs' diurnal activity pattern. To compare competing models and assess the most
 207 parsimonious movement model, we ran stepwise forward model selection based on Akaike's
 208 Information Criterion (AIC, Burnham and Anderson, 2002).

209 We validated the predictive power of the most parsimonious movement model using k-
 210 fold cross-validation for case-control studies as suggested by Fortin et al. (2009). For this,
 211 we randomly assigned 80% of the strata to a training set and the remaining 20% to a
 212 testing set. Using the training data we parametrized a movement model based on which
 213 we predicted selection scores $w(x)$ for all steps in the test data. Within each stratum, we
 214 then assigned ranks 1-25 to each step based on predicted selection scores, where rank 1 was
 215 given to the step with the highest score $w(x)$. Across all strata we determined the realized
 216 step's rank and we calculated rank frequencies of realized steps across all strata. Finally, we
 217 computed Spearman's rank correlation between ranks and associated frequencies $r_{s,realized}$.
 218 We replicated the entire procedure 100 times and computed the mean correlation coefficient
 219 ($\bar{r}_{s,realized}$), as well as its 95% confidence interval across all replicates. For comparison, we
 220 repeated the same procedure 100 times assuming random preferences, which we implemented

221 by discarding the realized step from all strata and identifying the rank of a random step
222 in each stratum. Again, we calculated Spearman's rank correlation coefficient ($r_{s,random}$),
223 its mean across repetitions ($\bar{r}_{s,random}$), and its 95% confidence interval. This validation
224 ultimately proofs a significant prediction in case the confidence intervals of $\bar{r}_{s,realized}$ and
225 $\bar{r}_{s,random}$ do not overlap.

226 **2.5 Dispersal Simulation (80%)**

227 We used the most parsimonious movement model to simulate 80'000 virtual dispersers mov-
228 ing across the KAZA-TFCA. The simulation resembled an inverted ISSF and was set up as
229 follows. (1) We defined a random source point and assumed a random initial orientation of
230 the animal. (2) Departing from the source point, we generated 25 random steps by sampling
231 turning angles from a uniform distribution $(-\pi, +\pi)$ and step lengths from our fitted gamma
232 distribution (similar to the input data, each random step represented the straight line move-
233 ment within 4 hours). To prevent unreasonably large steps, we capped sampled step lengths
234 to a maximum of 35 km, which corresponded to the farthest distance ever traveled within
235 4 hours by one of our dispersers. (3) Along each random step, we extracted and averaged
236 habitat covariates and we calculated movement covariates. To ensure compatible scales, we
237 standardized extracted values using the same parameters applied to our input data. (4)
238 We applied the parametrized movement model to predict the selection score $w(x)$ for each
239 step and we translated predicted scores into probabilities using Equation (Equation 2). (5)
240 We sampled one of the random steps based on predicted probabilities and determined the
241 animal's new position. We repeated steps (2) to (5) until 2'000 steps were realized, implying
242 a total 160 Mio. simulated steps.

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

251 **2.6 Source Points (90%)**

252 We released 80'000 virtual dispersers from 80'000 unique source points distributed across
253 the study area. 50'000 virtual dispersers were released from randomly selected source points
254 within contiguous protected areas that were large enough to sustain viable wild dog popula-
255 tions ($> 700 \text{ km}^2$; Pomilia et al., 2015) and another 30'000 were released at random locations
256 inside the 100 km wide buffer to render potential immigrants into the study system. By dis-
257 tributing source points randomly, the number of source points per km^2 was approximately
258 equal within protected areas and the buffer zone.

259 **2.7 Convergence (80%)**

260 To verify that the number of simulated individuals sufficed to ensure reliable estimates of
261 connectivity, we evaluated how the relative traversal frequency across the landscape changed
262 as we increased the number of simulated individuals. For this, we distributed 1'000 rectan-
263 gular “checkpoints”, each with an extent of 5 km x 5 km at random locations inside the main
264 study area. We then determined the relative traversal frequency by simulated trajectories
265 through each checkpoint as we increased the number of simulated individuals (1 to 50'000).
266 To assess variability in the relative traversal frequency, we repeatedly sampled trajectories
267 100 times and computed the mean traversal frequency across replicates, as well as the 95%
268 prediction-interval. We deemed that a checkpoint converged as soon as the width of the
269 prediction interval for the traversal frequency across replicates dropped below a value of
270 0.01.

271 **2.8 Heatmap (100%)**

272 To identify dispersal hotspots across our study area, we created a heatmap indicating the
273 absolute frequency at which each raster-cell in the study area was visited by virtual dis-
274 persers (Hauenstein et al., 2019; Pe'er and Kramer-Schadt, 2008). For this, we rasterized
275 all simulated trajectories and tallied them into a single map. If the same trajectory crossed
276 a raster-cell twice, we only counted it once, thereby mitigating potential biases caused by
277 individuals that moved in circles because they were trapped by dispersal barriers. To achieve
278 high performance rasterization, we used the R-package **terra** (Hijmans, 2020).

279 **2.9 Betweenness (80%)**

280 To pinpoint areas of exceptional relevance for connecting remote regions inside our study
281 area, we converted simulated trajectories into a network and calculated betweenness scores

(Bastille-Rousseau et al., 2018). For this, we overlaid the study area (including the buffer) with a regular raster resolved at 5 x 5 km. The centerpoint of each raster-cell served as node in the final network and we used the simulated trajectories to determine all transitions occurring from one node to another, as well as the frequency at which those transitions occurred. This resulted in an edge-list that we translated into a weighted network using the r-package `igraph` (Csardi and Nepusz, 2006). Because `igraph` handles edge weights (ω) as costs, we inverted the traversal frequency in each cell by applying $\omega = \frac{\sum_i^n TraversalFrequency_i/n}{TraversalFrequency_i}$. Consequently, edges that were traversed frequently were assigned low costs. Finally, we used the weighted network to calculate the betweenness score of each raster-cell. Betweenness measures how often a specific raster-cell lies on a shortest path between two other raster-cells and is therefore a useful metric to detect movement corridors (Bastille-Rousseau et al., 2018).

2.10 Inter-Patch Connectivity (80%)

We assessed inter-patch connectivity between national parks located in our study area to examine functional links between distinct patches in the KAZA-TFCA. The decision to focus on national parks was purely out of simplicity and does not imply that connections between other regions are impossible. In fact, the same process could easily be expanded to include other protected areas. To quantify inter-patch connectivity, we computed the relative frequency at which dispersers originating from one national park successfully moved into another national park. Successful movement was said to be achieved if the individuals' trajectory intersected with the corresponding national park at least once. We also recorded the number of steps required until the first intersection with the respective national park. This allowed us to determine *if* and *how often* dispersers moved between certain national parks, as well as *how long* dispersers had to move to realize those connections.

3 Results

3.1 Movement Model (80%)

Compared to the base model reported in (Hofmann et al., 2021), our most parsimonious movement model retained several additional interactions between habitat covariates and movement covariates (Figure 3 and Table 1). Although several models received an AIC weight above zero (Table 1 in Appendix S1), we only considered results from the most parsimonious model for simplicity. All models with positive AIC weight included similar

313 covariates (Table S1), so this decision only marginally influenced subsequent analyses. Plots
314 that aid with the interpretation of the final model are provided in Appendix S2.

315 Assuming that all other covariates are held at their means, the habitat kernel reveals
316 that dispersing wild dogs avoid water but prefer its proximity. Similarly, dispersers avoid
317 areas that are covered by woodlands, yet prefer regions covered by shrublands or grasslands.
318 Finally, dispersers avoid movement through landscapes that are dominated by humans.
319 Effect sizes are strong and, except for effect of **distance to water**, statistically clear on the
320 5% significance level.

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

330 When looking at the interactions between movement and habitat kernels, we observe
331 that movement behavior is contingent on habitat conditions. For example, there's strong
332 evidence that dispersers realize smaller steps in areas covered by water or areas covered by
333 wooldand, yet it appears that steps are larger in regions dominated by shrubs/grassland,
334 and shorter when the distance to water is high. Correspondingly, the model suggests that
335 directionality is lower in areas dominated by humans but more pronounced when dispersers
336 are far from water. However, except for the effect of **sl:Water**, effect sizes and statistical
337 significance are moderate.

338 The k-fold cross-validation procedure reveals that our model substantially outperforms
339 a random guess (Figure 3b) and therefore correctly assigns a high selection score to realized
340 steps. Confidence intervals of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ do not overlap and therefore proof a
341 reliable prediction. Furthermore, the significant correlation between ranks and correspond-
342 ing frequencies for realized steps indicates a good fit between predictions and observations
343 (Figure 3b). In comparison to the base model ($\bar{r}_{s,realized} = -0.55$; Hofmann et al., 2021),
344 the inclusion of interactions between movement and habitat covariates slightly improved
345 model performance.

346 **3.2 Dispersal Simulation (80%)**

347 On a machine with an octacore AMD Ryzen 7 2700X processor (8 x 3.6 GHz) and 64 GB
348 of RAM, a batch of 1'000 simulated dispersers moving over 2'000 steps required 90 minutes
349 to compute ($\mu = 88.90$, $\sigma = 1.87$). Consequently, the simulation of all 80'000 dispersers
350 (160 Mio. steps) terminated after 120 hours (i.e. five days). Comparable simulations will be
351 substantially faster for smaller study areas and lower resolution covariates, as the covariate
352 extraction from large and high-resolution rasters was computationally the most demanding
353 task. Out of the 50'000 dispersers initiated inside the main source area ??(a), only 4.5%
354 eventually hit a map boundary, suggesting that biases due to boundary effects are moderate.
355 In contrast, 78% of the 30'000 dispersers originating from the buffer zone eventually hit a
356 map boundary, yet this was to be expected since many of those dispersers originated from
357 source points located close to the map boundary.

358 **3.3 Convergence (80%)**

359 Our examination of the traversal frequency as a function of the number of simulated dis-
360 persers shows that the mean traversal frequency stabilizes already after very few simulations
361 and changes only little when adding further dispersers (Figure 4 (a) and (b)). While vari-
362 ability keeps decreasing with additional dispersers, the marginal benefit of adding further
363 dispersers steeply decreases with a negative-exponential trend (Figure 4 (c)).

364 **3.4 Heatmap (80%)**

365 Figure 5 depicts the heatmap of all 80'000 simulated trajectories resulting after 2'000 steps.
366 The map shows that large portions of land beyond the borders of the KAZA-TFCA are only
367 infrequently visited by dispersers (dark blue areas), whereas within the KAZA-TFCA several
368 extensive regions are regularly traversed (bright yellow and red areas). Most notably, the
369 region in northern Botswana south of the Linyanti swamp stands out as highly frequented
370 dispersal hotspot. Still, the presence of several massive water bodies, such as the Okavango
371 Delta, the Makgadikgadi Pan, and the Linyanti swamp, poses considerable dispersal barriers
372 that limit realized connectivity within the KAZA-TFCA. Similarly, dispersal across Zambia's
373 and Zimbabwe's part of the KAZA-TFCA appears to be limited, as only few areas are
374 successfully traversed by dispersers. This can largely be attributed to substantial human
375 influences resulting from high human density, roads, and agricultural activities in these
376 areas. Outside the KAZA-TFCA, the most heavily used regions include the areas inside the
377 Central Kalahari National Park in Botswana, the area south-west of the Khaudum National

³⁷⁸ Park in Namibia, and the area around the Liuwa Plains National Park in Zambia.

³⁷⁹ **3.5 Betweenness (80%)**

³⁸⁰ Betweenness scores after 2'000 simulated steps are presented in Figure 6 and reveal a set of
³⁸¹ discrete dispersal corridors. Again, the region in northern Botswana stands out as crucial
³⁸² dispersal hub that connects more remote regions in the study system. Towards east, the
³⁸³ extension of this corridor runs through the Chobe National Park into the Hwange national
³⁸⁴ park. From there, a further extension connects to the distant Matusadona National Park
³⁸⁵ in Zimbabwe. Northwest of the Linyanti ecosystem, a major corridor expands into Angola,
³⁸⁶ where it splits and finally traverses over a long stretch of unprotected area into the Kafue
³⁸⁷ National Park in Zambia. Several additional corridors with slightly lower betweenness scores
³⁸⁸ exist, yet most of them run within the boundaries of the KAZA-TFCA. In general, only few
³⁸⁹ corridors directly link the peripheral regions of the KAZA-TFCA. For instance, there are
³⁹⁰ only few corridors between the Matusadona National Park in Zimbabwe and the Kafue
³⁹¹ National Park in Zimbabwe. Similarly, there are no direct links between the Zimbabwean
³⁹² and Angolan “spikes” of the KAZA-TFCA.

³⁹³ **3.6 Inter-Patch Connectivity (80%)**

³⁹⁴ Results from the analysis of inter-patch connectivity are given in Figure 7. The figure shows
³⁹⁵ all realized links by simulated dispersers between national parks and indicates the average
³⁹⁶ duration a disperser had to move to realize those links. It is again worth pointing out that
³⁹⁷ the figure is only intended as an example, as for clarity we only considered connectivity
³⁹⁸ between national parks (NPs), albeit plenty of links between other protected areas exist.
³⁹⁹ As can be seen from the number, thickness, and color of arrows, inter-patch connectivity
⁴⁰⁰ between NPs in Angola, Namibia, and Botswana is comparably high and dispersal events
⁴⁰¹ between those areas short. In contrast, we see that connections into the Kafue NP in Zambia
⁴⁰² require more steps and are fewer in general. Similarly, there is a lack of connections into
⁴⁰³ Zimbabwe’s Chizarira and Matusadona NP and the more distant Lower Zambezi and Mana
⁴⁰⁴ Pools NPs. In some cases, one can also detect imbalances between ingoing and outgoing
⁴⁰⁵ links, hinting at potential source-sink dynamics that occur due to asymmetries in landscape
⁴⁰⁶ permeability depending on the origin. For instance, while a large portion of dispersers from
⁴⁰⁷ the Chizaria NP in Zimbabwe manage to move into the Hwange NP, there are comparably
⁴⁰⁸ few dispersers that succeed in the opposite direction.

409 **4 Discussion**

410 **4.1 Short Summary (90%)**

411 We used ISSFs to analyse data of dispersing wild dogs and to parametrize a fully mech-
412 anistic movement model describing how dispersers move through the available landscape.
413 We employed the parametrized model as an individual-based movement model to simulate
414 80'000 dispersing wild dogs moving 2'000 steps across the extent of the KAZA-TFCA, the
415 world's largest transboundary conservation area. Based on simulated dispersal trajec-
416 tories, we derived three complementary maps, each geared towards a better understanding
417 of dispersal and landscape connectivity. The set of maps included a heatmap, revealing
418 frequently traversed areas, a betweenness-map, delineating critical dispersal corridors, and
419 a map of inter-patch connectivity, indicating the presence or absence of functional links be-
420 tween national parks as well as the average dispersal duration required to realize those links.
421 We thereby showcase that ISSFs offer a simple, yet powerful framework to parametrize
422 movement models and simulate dispersal to assess landscape connectivity. Importantly,
423 individual-based simulations from ISSFs overcome several conceptual shortcomings inherent
424 to more traditional connectivity modeling techniques, such as least-cost path analysis and
425 circuit theory.

426 **4.2 Movement Model (80 %)**

427 Our movement model of dispersing wild dogs comprised a habitat kernel, a movement kernel,
428 and their interactions. Thus, the model rendered habitat and movement preferences of
429 dispersers, as well as how their movement preferences were affected by habitat conditions.
430 Parameter estimates from the habitat kernel revealed that dispersers avoid water, prefer its
431 proximity, avoid woodland, prefer shrubs/grassland, and avoid areas dominated by humans.
432 These results are consistent with findings from previous studies on dispersing wild dogs
433 (Davies-Mostert et al., 2012; Masenga et al., 2016; Woodroffe et al., 2019; O'Neill et al.,
434 2020), as well as with a base model that we developed focussing on dispersing wild dogs'
435 habitat kernel (Hofmann et al., 2021).

436 By expanding the base model by a proper movement kernel, we were able to model several
437 additional complexities inherent to dispersal. For instance, it is well known that dispersers
438 usually move with directional persistence (Cozzi et al., 2018; Hofmann et al., 2021) and that
439 step lengths are typically correlated with turning angles (Morales et al., 2004; Börger and
440 Fryxell, 2012). That is, larger steps usually coincide with smaller turning angles and vice

441 versa. While such behavior could be captured by jointly sampling turning angles and step
442 lengths from copula probability distributions (?), the ISSF framework allowed us to model
443 similar behavior directly using the movement model. Besides accounting for directional
444 persistence and correlations between step lengths and turning angles, we also allowed for
445 interactions that rendered the fact that wild dogs mainly move during the darker morning
446 and evening hours, whereas they tend to rest during the remainder of the day.

447 By allowing interactions between habitat covariates and movement covariates, we fur-
448 thermore accounted for the fact that movement and habitat preferences are interdependent.
449 For example, the final model retained an interaction between water cover and step length,
450 showing that dispersers are more likely to realize short steps (i.e. move slower) in areas cov-
451 ered by water and large steps in areas located on dryland. Likewise, the parameter estimate
452 for the interaction between water cover and turning angles revealed that dispersers move
453 less directional across water bodies than across dryland. We believe that this is owed to
454 the fact that wild dogs wade or swim when traversing waterbodies, thus resulting in slower,
455 more tortuous movements. Besides this, our model also suggested that dispersers preferably
456 realize shorter steps when moving through woodland, but larger steps when moving across
457 shrubs/grassland. This can likely be linked to wild dogs' resting behavior, as wild dogs
458 usually use open areas to quickly move over long distances (Abrahms et al., 2017) but seek
459 shade and protection below the woodland canopy when resting (Creel and Creel, 2002).

460 4.3 Simulation (80%)

461 Based on the above described movement model, we simulated 80'000 dispersers moving
462 2'000 steps across the landscapes of the KAZA-TFCA. On a modern desktop machine, this
463 simulation required five days of computation. The long simulation time was primarily caused
464 by the massive extent considered (ca. 1.8 Mio. km² when including the buffer) and the
465 large number of dispersers simulated. Most connectivity studies are limited to much smaller
466 extents (e.g. Kanagaraj et al., 2013; Clark et al., 2015; McClure et al., 2016; Abrahms
467 et al., 2017; Zeller et al., 2020) and will therefore achieve faster simulation times. We also
468 believe that fewer simulated dispersers will often suffice, as the relative traversal frequency
469 by simulated individuals through randomly placed checkpoints in the study area converged
470 already after 10'500 simulated individuals in our case. The required number of simulated
471 individuals will, however, vary depending on the structure of the landscape and the dispersal
472 ability of the focal species.

473 **4.4 Maps (70%)**

474 The heatmap resulting from our dispersal simulation highlighted that a large portion of
475 simulated dispersers traversed the Moremi NP and the Chobe NP in northern Botswana.
476 We already recognized the same area as dispersal hotspot using least-cost path and least-cost
477 corridor analysis (Hofmann et al., 2021), yet some researchers questioned whether this was
478 just the logical consequence of the region being in the center of the study area and least-costly
479 routes being enforced between pre-defined start and endpoints. Using least-cost approaches,
480 this claim is difficult to disprove, as all identified routes have to completely run within the
481 study area and will always be enforced between a start and endpoint. With our simulation,
482 on the other hand, dispersers were able to leave the study area and were not enforced to
483 move towards a known endpoint. Despite this, a majority of simulated individuals traversed
484 the central region in northern Botswana, so we conclude that this dispersal hotspot is not
485 caused by geometric properties but results from landscape characteristics and the location
486 of source areas.

487 Overall, the heatmap gives a good overview of the intensity of use in different areas, yet
488 it is not well suited for pinpointing discrete movement corridors, which is why we also com-
489 puted a betweenness-map. In contrast to the heatmap, the betweenness-map puts stronger
490 emphasis on areas that are used as stepping stones into other regions of the study area and
491 thereby highlights discrete dispersal corridors or bottlenecks (Bastille-Rousseau et al., 2018).
492 Interestingly, the central region in northern Botswana again stands out, implying that the
493 region is not only frequently visited, but also promotes the relocation of individuals into
494 more remote regions of the KAZA-TFCA. While this is an example of an area where both the
495 traversal frequency *and* the betweenness score is high, there are other instances where only
496 one of the metrics is pronounced. For example, while the area between the Lengue-Luiana
497 NP in Angola and the Kafue NP in Zambia receives a high betweenness-score, we find that
498 the same area is only rarely traversed by dispersers according to the heatmap. Consequently,
499 despite the region's importance for linking Angola's NPs to Zambia's NP, only few simulated
500 dispersers actually manage to successfully traverse it. Conversely, while the area inside the
501 Central Kalahari NP is traversed by many dispersers, the betweenness map indicates that
502 the same region does not serve as major stepping stone into other regions of the study area.

503 To complete the picture, we also computed inter-patch connectivity between NPs, high-
504 lighting functional links and expected dispersal durations between each national park in the
505 study area. The map showed that movements from Angola into Zambia's Kafue NP are not
506 only rare, but they also require many steps until they are realized. Conversely, we find that

507 dispersal between the Moremi NP and Chobe NP are relatively frequent and require fewer
508 steps, which can be expected given that the areas are located close to each other.

509 Together, these examples nicely illustrate how powerful a combination of different con-
510 nectivity metrics can be in deepening our understanding of landscape connectivity. Each
511 map that we produced from simulated trajectories accentuated a different aspect of con-
512 nectivity, together providing a comprehensive view on dispersal and landscape connectivity.
513 The heatmap, for example, put emphasis on areas where movement is concentrated, regard-
514 less whether such areas truly contribute to geneflow or whether they represent “dead ends”
515 that do not connect distinct patches. The betweenness map, on the other hand, pronounced
516 those areas that are relevant in connecting different regions in the landscape and highlights
517 potential bottlenecks. Finally, the map of inter-patch connectivity illustrated the frequency
518 at which dispersal between distinct patches occurs, as well as the average dispersal duration
519 required for individuals to move between them.

520 4.5 Related Literature (80%)

521 Our approach of simulating movement to assess connectivity is closely related to a series
522 of previously published papers. Clark et al. (2015), for instance, fitted a regular SSF to
523 American black bears (*Ursus americanus*) and employed the estimated model parameters
524 to simulate movement and identify the most likely movement corridors between four habitat
525 patches. For the same species, Zeller et al. (2020) used regular SSFs and forecasted seasonal
526 habitat connectivity under changing land-use. As both of these studies relied on *regular*
527 SSFs, rather than *integrated* SSFs, neither of them was able to account the interdependence
528 between habitat and movement preferences. As such, movement behavior was assumed to
529 be independent of habitat conditions. In addition, both studies lacked data collected during
530 dispersal and instead employed data on residents to estimate connectivity. Although prefer-
531 ences during residence and dispersal may coincide for some species (Fattebert et al., 2015),
532 there is compelling evidence suggesting that dispersers more readily cross areas avoided by
533 residents (Elliot et al., 2014; Gastón et al., 2016; Abrahms et al., 2017; Keeley et al., 2017).
534 The use of data collected during residence may therefore result in biased model estimates
535 that distort our view on connectivity, causing a misallocation of scarce conservation funds
536 (Elliot et al., 2014). Another set of related studies that uses simulations from (regular and
537 integrated) SSFs has been conducted by Potts et al. (2013) and Signer et al. (2017), yet the
538 primary focus of these papers lied on the estimation of steady-state utilization distributions
539 and not the investigation of connectivity between habitat patches.

540 **4.6 Benefits & Modeling Decisions with ISSF Simulations (70%)**

541 A simulation-based approach as proposed in this article offers several advantages over tra-
542 ditional connectivity modeling techniques such as LCPA or CT. In contrast to LCPA, for
543 instance, an individual-based simulation does not require to assume known endpoints. In-
544 stead, each endpoint emerges naturally from a simulated dispersal trajectory. The ability of
545 not having to provide pre-determined is particularly valuable for dispersal studies, because
546 dispersers often venture into unfamiliar territory and are therefore unlikely to know the
547 destination of their journey (Elliot et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020).
548 Moreover, LCPA always enforces a connection towards the predefined endpoints, even if
549 associated movement costs are unreasonably high. With simulations from ISSFs this is no
550 longer the case. A connectivity model that does not require pre-defined endpoints also en-
551 sures that movement corridors are not enforced between certain start- and endpoints, which
552 permits to detect potential routes that do not lead into suitable habitats but into ecolog-
553 ical traps (Dwernychuk and Boag, 1972; Van der Meer et al., 2014) or areas with a high
554 susceptibility for human wildlife conflicts (Cushman et al., 2018).

555 In contrast to LCPA and CT, simulations from ISSFs furthermore yield the advantage of
556 an explicit representation of time. This enables to answer questions such as: “*How long will*
557 *it take a disperser to move from A to B?*” or “*Is it possible for a disperser to move from A to*
558 *B within X days?*” These are important questions that shift the focus from a structural to a
559 more functional view on connectivity, which is usually desirable because functional connec-
560 tivity it is directly related to geneflow (Taylor et al., 1993; Tischendorf and Fahrig, 2000).
561 An explicit representation of time also yields opportunities for studying how seasonality
562 affects connectivity and to investigate whether some dispersal corridors are only available
563 temporarily (*dynamic connectivity*; Zeller et al., 2020). With LCPA or CT, incorporating
564 seasonality is currently impractical, as both methods require a static permeability surface as
565 inputs. Hence, the only possibility to study seasonality effects is to repeat the same analysis
566 using different permeability surfaces, each rendering the environment at a different point in
567 time (e.g. Benz et al., 2016; Osipova et al., 2019). With simulations from ISSFs, on the
568 other hand, the environment can be rendered dynamically “as the dispersers move”, such
569 that simulated individuals can respond to seasonal factors directly within the simulation.
570 Hence, rather than employing a set of static habitat layers, each layer would be updated as
571 the dispersers move, thus correctly rendering seasonal changes in the environment.

572 While an explicit representation of time offers multiple benefits, it requires that step
573 lengths and turning angles are modeled properly (Kanagaraj et al., 2013), so that dispersal

574 durations between areas can be estimated reliably. Correctly rendering step lengths and
575 turning angles under varying environmental conditions is one of the key strengths of ISSFs
576 (Avgar et al., 2016; Prokopenko et al., 2017; Fieberg et al., 2020), which is why we believe
577 that the framework is exceptionally well suited for simulating dispersal and assessing land-
578 scape connectivity. In addition, the framework enables to model autocorrelation between
579 step lengths and turning angles, thereby incorporating directional persistence. Here, we
580 only considered first order autocorrelation, i.e. correlation between two consecutive steps.
581 Although higher order autocorrelation is conceivable and might be desirable to model, this
582 requires vast amounts of GPS data that is not intercepted by missing fixes and is therefore
583 often impractical to model in reality.

584 **4.7 Further Considerations (70%)**

585 Although we did not render mortality, animals regularly die during dispersal, mainly due
586 to deadly encounters with predators, road kills, and persecution by humans (Bonnet et al.,
587 1999; Woodroffe and Sillero-Zubiri, 2012; ?). Mortality during dispersal could therefore
588 substantially limit functional connectivity (Bowler and Benton, 2009), especially in areas
589 where the likelihood of encountering competitors and humans is high (Cozzi et al., 2020).
590 If corresponding information is available, mortality can and should be included in ISSF
591 simulations.

592 The ability to realistically render movement during dispersal not only serves to investigate
593 landscape connectivity, but also forms the foundation for more realistic spatially explicit
594 population models in which dispersal is not merely rendered through dispersal kernels or
595 cellular automata movements (Visintin et al., 2020), but mechanistically based on observed
596 movement and habitat preferences (e.g. Revilla and Wiegand, 2008, Kleinmann and Wang,
597 2017). Such models can ultimately be employed to conduct population viability analyses
598 (Boyce, 1992) in which species' dispersal abilities are taken into account.

599 Despite the benefits that simulations from ISSFs offer, we also want to confer some of
600 the non-trivial modeling decisions involved. In particular, we will discuss five modeling
601 decisions: (1) number of simulated individuals, (2) location of source points, (3) dispersal
602 duration, (4) boundary behavior, and (5) how to handle individual variability.

603 (1) When simulating dispersal using ISSFs, the modeler needs to decide on the number
604 of simulated individuals. This decision includes the *absolute* number of simulated individ-
605 uals across the entire study area, as well as the *relative* number of simulated individuals
606 per spatial entity (e.g. protected area, habitat patch, source point). With respect to the

607 *absolute* number of simulated individuals, a higher number is always desirable, as each ad-
608 ditional disperser provides novel information about landscape connectivity. Of course this
609 comes at the cost of computational efficiency, such that a trade-off needs to be managed. We
610 propose to handle this trade-off by defining a target metric and only simulating additional
611 until convergence in the target metric is observed. Here, we employed the *relative traversal*
612 *frequency* across checkpoints as target metric and found that convergence across all check-
613 points was achieved already after 10'500 simulated individuals. With regards to the *relative*
614 number of simulated individuals, we see several feasible approaches. If corresponding data
615 is available, one could distribute dispersers in relation to known abundances, reflecting that
616 population densities are not necessarily homogeneous across space. Alternatively, one could
617 also distribute dispersers homogeneously, yet after the simulation weigh each simulated tra-
618 jectory according to population densities at the respective source patch. Again this requires
619 information on the spatial abundance of the focal speciesl. Finally, if such information is
620 missing, one can distribute dispersers homogeneously across space. This is the approach that
621 we employed and resulted in larger source areas generating a larger number of dispersers.

622 (2) While we simulated dispersal using point estimates from our most parsimonious
623 movement model but did not investigate the sensitivity of our results with respect to those
624 estimates. Uncertainty is rather common in dispersal studies on endangered species, as data
625 tends to be scarce, resulting in model estimates large confidence intervals (Wiegand et al.,
626 2003; Kramer-Schadt et al., 2007). To address this, one may explore a broader range of
627 preferences instead of using point estimates initiate dispersers with randomized preferences
628 with variability imposed by the uncertainty in the movement model. We therefore urge
629 future studies to investigate the sensitivity of ISSF simulations with respect to estimated
630 preferences.

631 (3) When employing ISSFs to simulate dispersers, one also needs to decide on meaningful
632 dispersal durations (i.e. number of simulated steps). If corresponding data is available,
633 dispersal durations could be sampled from observed events, such that each individual would
634 only be simulated until its assigned dispersal duration has been achieved. Due to the low
635 number of observed dispersal events and due to the great variability in wild dogs' dispersal
636 distances (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020) we opted
637 against this approach. Instead, we simulated individuals for 2'000 steps, which is at the
638 upper end of observed dispersal durations and may have resulted in an overly optimistic
639 representation of landscape connectivity. Nevertheless, it is relatively straight forward to
640 shorten simulated trajectories in order to investigate the sensitivity of results with regards

641 to the dispersal duration. Alternatively, if detailed information on settlement behavior is
642 available, the dispersal simulation could include a settlement submodel, where after each
643 simulated step the simulated individual decides whether or not to settle, based the number
644 of realized steps, environmental conditions in the landscape, abundance of conspecifics or
645 competitors etc.

646 (4) Unless simulated individuals are drawn towards a point of attraction, some individuals
647 will inevitably approach a map boundary such that some of the proposed random steps will
648 leave the study area such that no selection score can be computed. One option to handle
649 this situation would be to simply terminate the simulation as soon as one of the random
650 steps leaves the study area, assuming that the simulated animal left the study area and
651 will not return. This can be problematic when many individuals are initiated close to map
652 boundaries, especially since a single random step leaving the study area forces termination
653 of the simulation. As an alternative, one could resample transgressing random steps until all
654 proposed random steps lie fully within the study area. This will force simulated dispersers to
655 bounce off those boundaries and remain within the main study area. Finally, one could also
656 extend the study area by an artificial buffer zone with randomized covariate values through
657 which dispersers are allowed to leave and re-enter the main study area. Although dispersers
658 might still approach the boundary of the buffer, it has been shown that adding an artificial
659 buffer helps to mitigate edge effects Koen et al. (2010). A last solution that only applies in
660 theoretical applications is to simulate movement on a torus (?).

661 (5) To initiate the simulation of a disperser, the modeler needs to define a source point.
662 In some cases, exact locations of source populations are known and source points can be
663 placed accordingly (Kanagaraj et al., 2013). Moreover, if abundance estimates are available,
664 these can be used to inform the relative number of dispersers initiated at each location. The
665 selection of source points is thus directly related to the relative number of simulated individu-
666 als. Here, we randomly placed source points within protected areas large enough to sustain
667 viable wild dog populations. Given that the species primarily survives in these formally
668 protected areas (Woodroffe and Ginsberg, 1999; Davies-Mostert et al., 2012; Woodroffe and
669 Sillero-Zubiri, 2012; Van der Meer et al., 2014) we consider this decision to be appropriate.
670 In other cases, comparable knowledge may be lacking and it could be more beneficial to de-
671 lineate likely source patches based on habitat suitability models (e.g. Squires et al., 2013).
672 After all, the challenge of selecting meaningful source points is not unique individual-based
673 simulations also applies to LCPA and CT. However, as highlighted by Signer et al. (2017),
674 the influence of the exact location of source points decreases as the number of simulated

675 steps is increased.

676 **4.8 Conclusion (80%)**

677 To this end, we have used data on dispersing wild dogs to exemplify how ISSFs can be
678 used to parametrize an individual-based movement model that is further employed to simu-
679 late dispersal and examine landscape connectivity. We also presented three complementary
680 connectivity maps derived from simulated trajectories, each focused on a different aspect
681 of connectivity. Furthermore, we discussed the potential advantages and disadvantages of
682 the proposed framework compared to traditional connectivity modeling techniques such as
683 LCPA and CT. With this article, we hope to have sparked interest in the uprising framework
684 of step selection functions for investigating dispersal behavior and landscape connectivity.
685 Nevertheless, we do not attempt to dismiss the application of traditional connectivity mod-
686 els by any means. Rather, we propose to use simulations from ISSF-models as a simple but
687 powerful tool to provide a more comprehensive understanding of dispersal and landscape
688 connectivity.

689 **5 Authors' Contributions**

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

694 **6 Data Availability**

695 GPS movement data of dispersing coalitions will be made available on dryad at the time of
696 publication. Access to all R-scripts is provided through Github.

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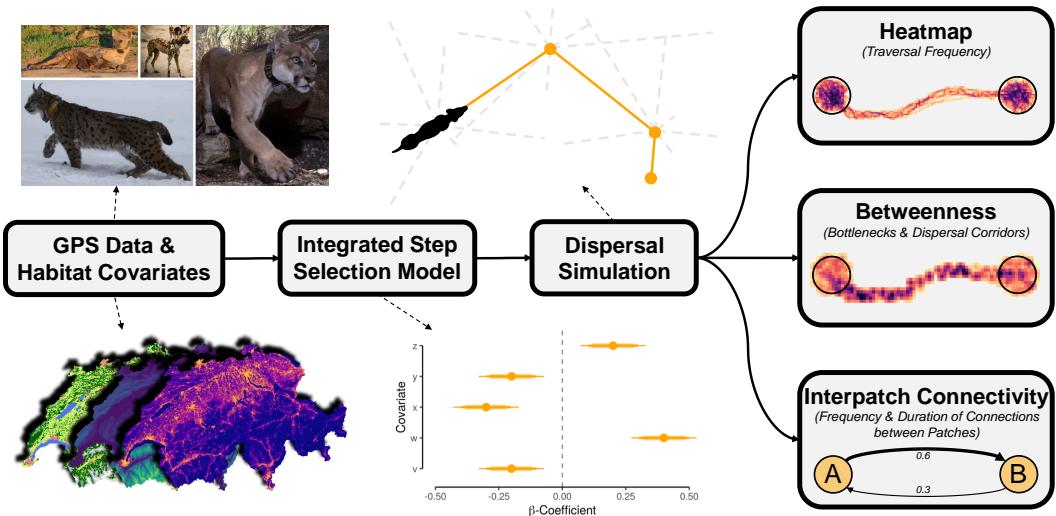


Figure 1: Flowchart of the simulation-based connectivity analysis as proposed in this article. First, GPS data and habitat covariates have to be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement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

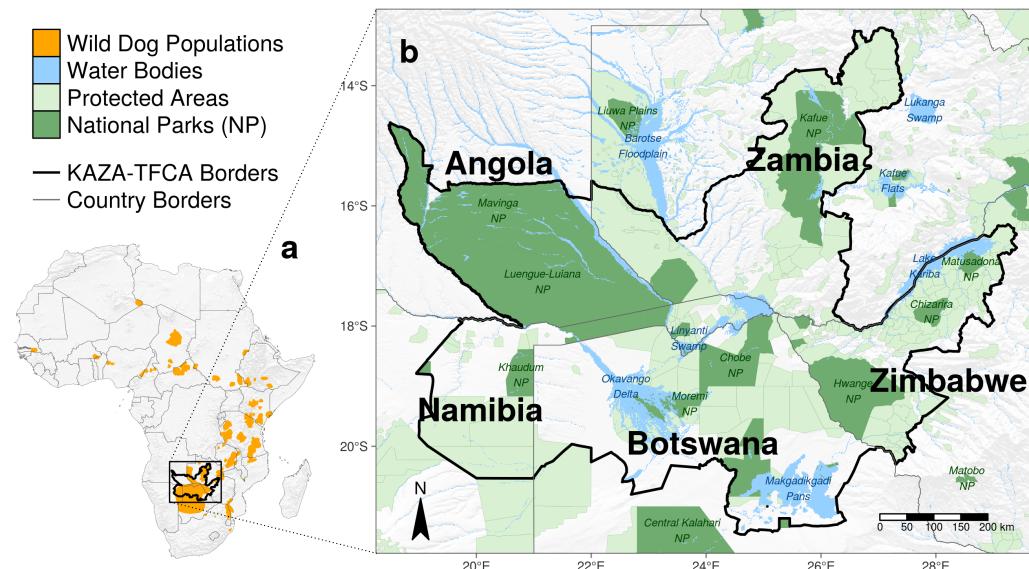


Figure 2: Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA and encompassed parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA represents the world's largest terrestrial conservation area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

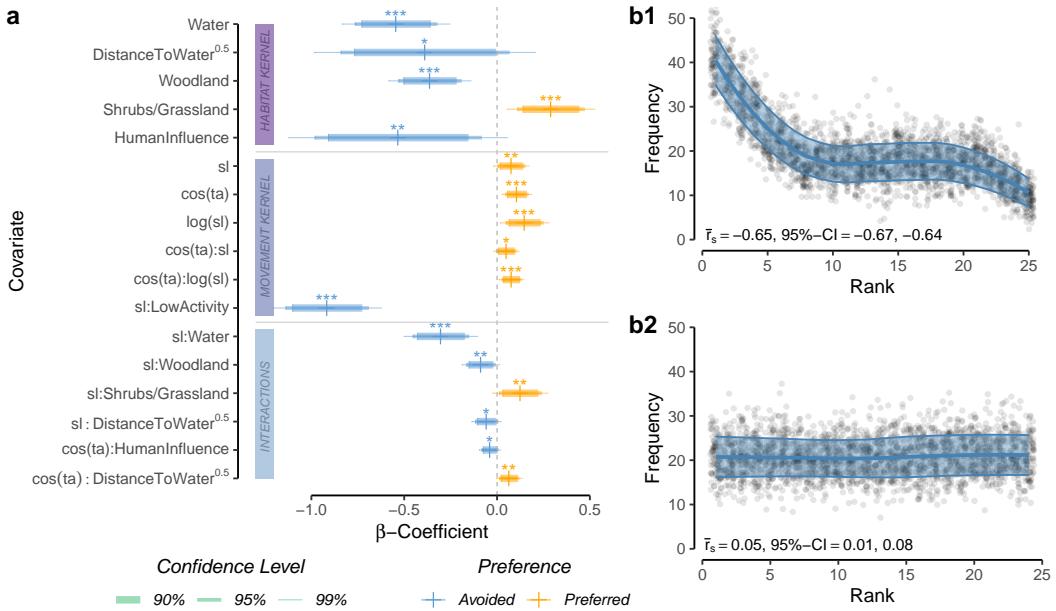


Figure 3: (a) Most parsimonious movement model for dispersing wild dogs. The model includes a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% Confidence-Intervals for the respective β -coefficients. Significance codes: * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$. (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.

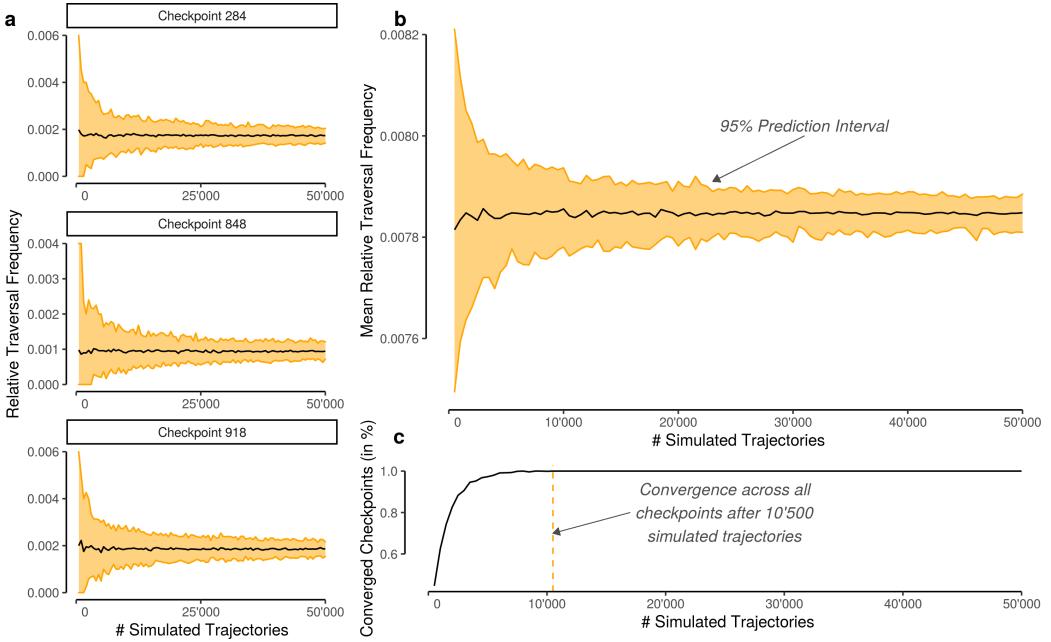


Figure 4: Relative traversal frequency through 1'000 checkpoints (5 km x 5) distributed randomly across the study area. The relative traversal frequency is plotted against the number of simulated individuals to visualize how quickly the metric converges to a steady state. (a) Replicated (100 times) relative traversal frequencies across three randomly chosen checkpoints as well as the corresponding 95% prediction interval (PI). (b) Averaged relative traversal frequency across all checkpoints and replicates including a 95% PI. (c) Width of the PI in relation to the number of simulated dispersers.

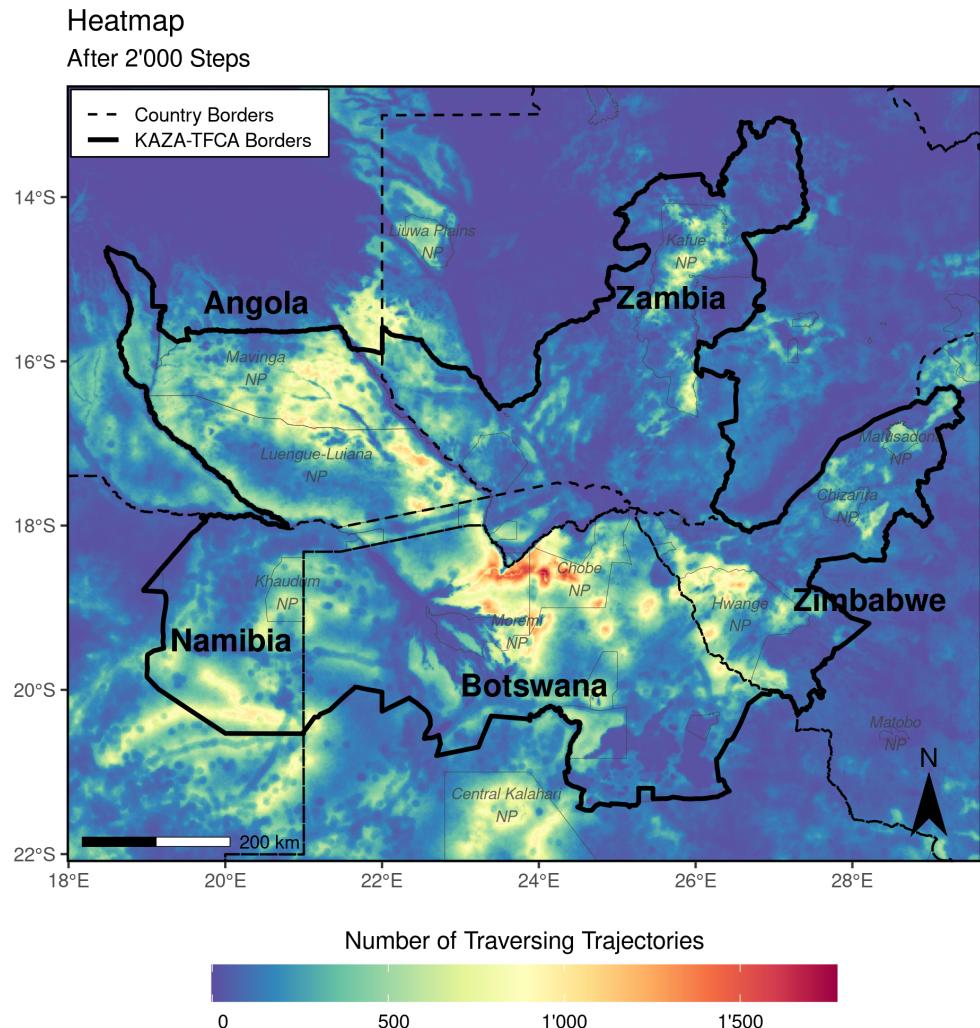


Figure 5: Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step selection model that we fit to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied all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

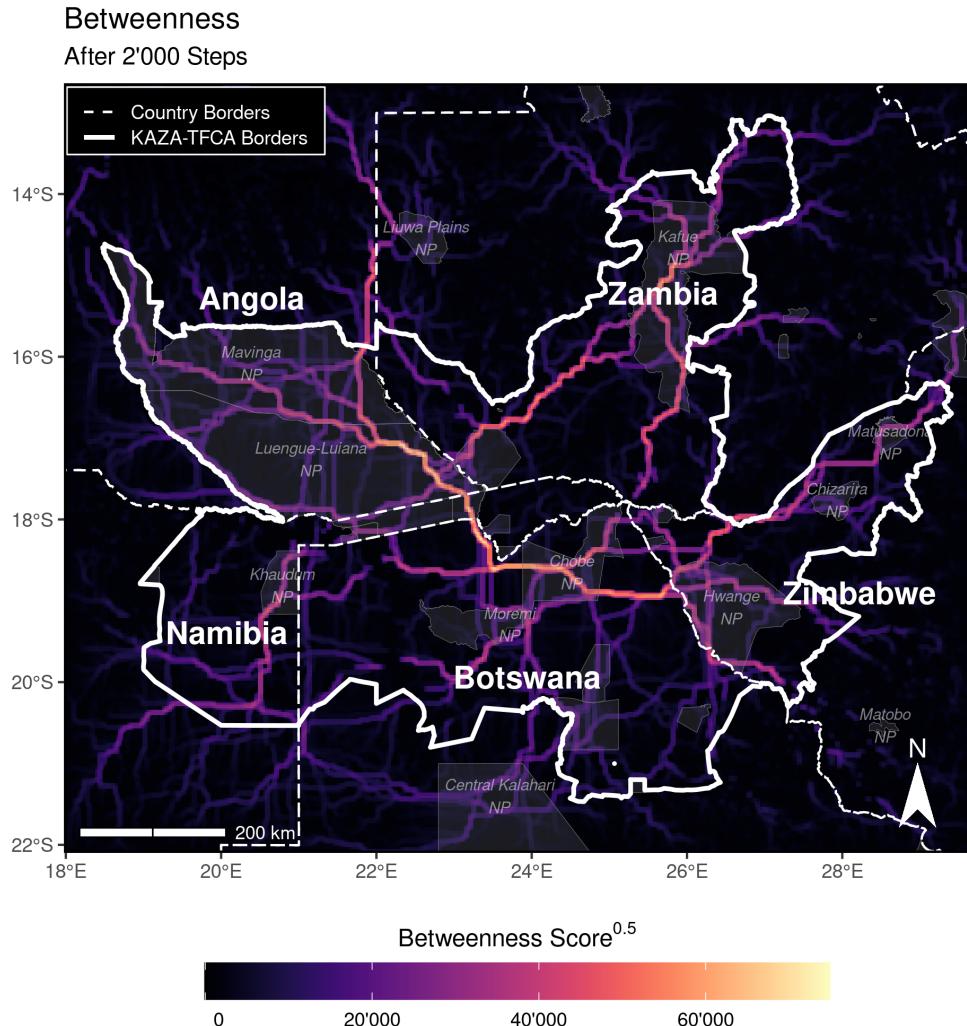


Figure 6: Map of betweenness scores, highlighting distinct dispersal corridors and potential bottlenecks. A high betweenness score indicates that the respective cells are exceptionally relevant in connecting different regions in the study area. That is, the higher the betweenness score, the more often a pixel lies on a shortest path between adjacent areas. In this sense the metric can be used to pinpoint discrete movement corridors. Note that we square-rooted betweenness scores to improve visibility of corridors with low scores. Betweenness scores were determined by converting simulated dispersal trajectories into a large network. Note that we square-rooted betweenness scores to improve the visibility of corridors with low betweenness scores.

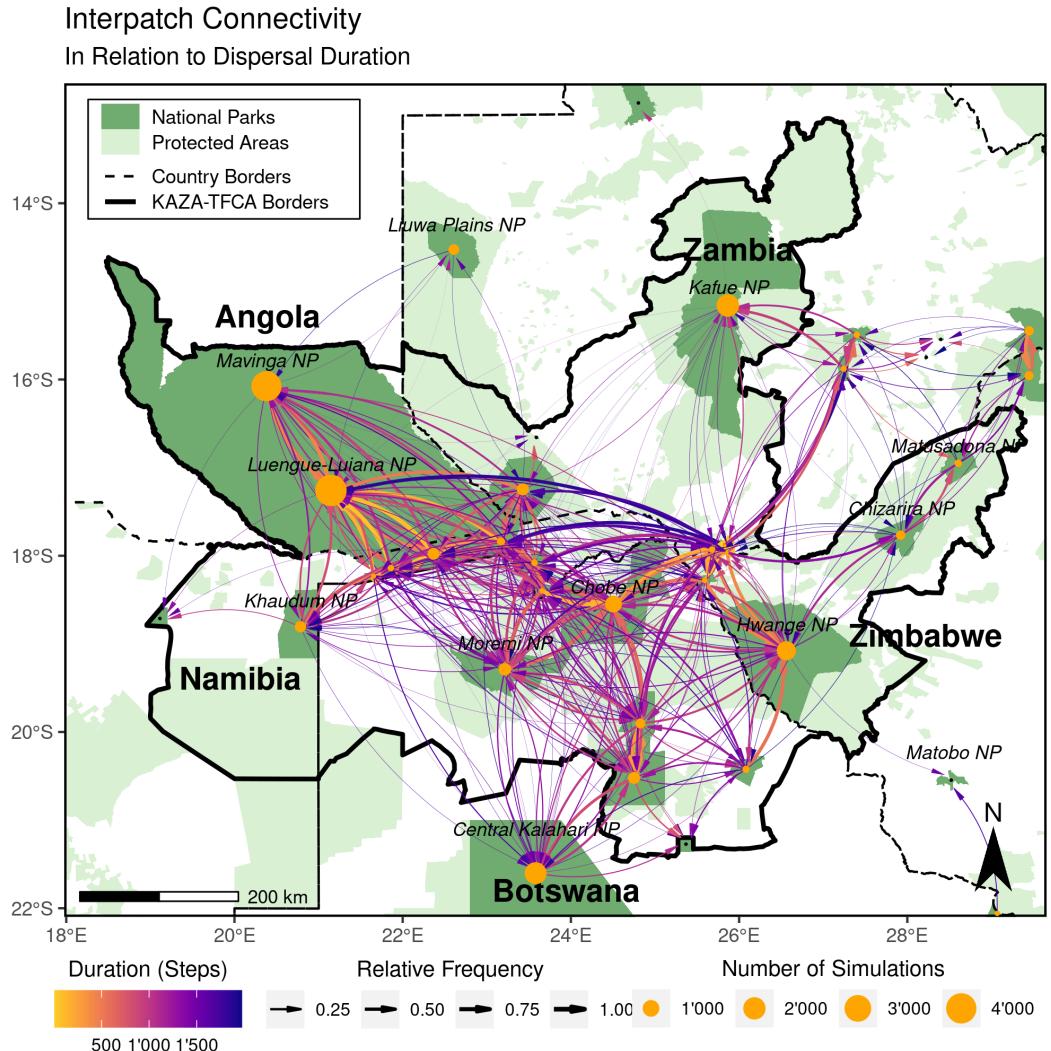


Figure 7: Network on simulated dispersal trajectories highlighting connections between national parks (dark green). Yellow bubbles represent the center of the different national parks and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent national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

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

Kernel	Covariate	Coefficient	SE	p-value	Sign.
Habitat Kernel	Water	-0.546	0.112	< 0.001	***
	DistanceToWater ^{0.5}	-0.390	0.231	0.092	*
	Woodland	-0.364	0.086	< 0.001	***
	Shrubs/Grassland	0.288	0.092	0.002	***
	HumanInfluence	-0.535	0.229	0.019	**
Movement Kernel	sl	0.075	0.037	0.042	**
	cos(ta)	0.105	0.031	0.001	***
	log(sl)	0.146	0.051	0.004	***
	cos(ta) : sl	0.049	0.026	0.064	*
	cos(ta) : log(sl)	0.076	0.026	0.003	***
Interactions	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: * $p < 0.10$ ** $p < 0.05$ *** $p < 0.01$