

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, colonize new habitats and 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 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. Individual-based dispersal simulations have been proposed to address these shortcomings, yet due to the sheer amount of non-trivial modeling decisions required, a unified and objective framework to simulate dispersal 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 to investigate *transient* movement behavior and 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, thereby parametrizing a fully mechanistic movement 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, and generate a set of maps, each focused on a different aspect of connectivity. 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 maintain genetic diversity (Perrin
⁸ and Mazalov, 1999, 2000; Frankham et al., 2002; Leigh et al., 2012; Baguette et al., 2013),
⁹ to rescue small, non-viable populations (Brown and Kodric-Brown, 1977), and to promote
¹⁰ the colonization or recolonization of unoccupied habitats (Hanski, 1999b; MacArthur and
¹¹ Wilson, 2001). However, successful dispersal requires a sufficient degree of landscape con-
¹²nectivity (Fahrig, 2003; Clobert et al., 2012), which is why the identification and protection
¹³of major dispersal corridors has become a fundamental task in conservation science (Nathan,
¹⁴ 2008; Doerr et al., 2011; Rudnick et al., 2012). The ability to pinpoint relevant dispersal
¹⁵ hotspots requires information on movement behavior during dispersal and knowledge about
¹⁶ factors that limit dispersal and therefore connectivity (Baguette et al., 2013; Vasudev et al.,
¹⁷ 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-
²³resent 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-
²⁷tions (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., 2005;
36 Cushman and Lewis, 2010; Thurfjell et al., 2014). The so estimated preferences can then be
37 used to predict a permeability surface, indicating the expected ease at which an animal can
38 traverse a given area (Spear et al., 2010; Zeller et al., 2012; Etherington, 2016). Ultimately,
39 the permeability surface serves as input to a connectivity model that is used to reveal
40 movement corridors (Diniz et al., 2020). Two of the most prominent connectivity models
41 are least-cost path analysis (LCP analysis; Adriaensen et al., 2003) and circuit theory (CT;
42 McRae, 2006; McRae et al., 2008), both graph-based methods that estimate conductance of
43 the landscape to infer likely movement corridors. Despite their intuitive nature and ease of
44 use, both methods make rigorous assumptions about animal movement that are often not
45 fulfilled in 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 fulfilled by migrating animals that typically move between a discrete set of habitats
52 through familiar landscapes. Dispersers, on the other hand, usually move over long distances
53 into unknown territory and are therefore less likely to be aware of associated movement costs
54 (Koen et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020). Another issue of LCPs analysis
55 concerns the fact that least-costly routes, by their very nature, are only one pixel wide (Pinto
56 and Keitt, 2009). This neglects the fact that alternative routes with similar costs may exist
57 and implies that the width of inferred movement routes depends on the resolution of chosen
58 covariate layers and may not be biologically meaningful (Diniz et al., 2020). Although some
59 of these deficiencies can be addressed using less stringent versions of the LCP algorithm (e.g.
60 least-cost *corridors* (Pinto and Keitt, 2009), *thresholded* least-cost paths (Landguth et al.,
61 2012), and *randomized* least-cost paths (Panzacchi et al., 2016; Van Moorter et al., 2021)),
62 a certain degree of arbitrariness remains.

63 **1.5 Issues with Circuit Theory (90%)**

64 CT entails similarly unreasonable restrictions that are hardly ever met. For example, because
65 CT only allows movements from a source cell to its 4 or 8 adjacent cells, it implicitly posits
66 that animals exhibit a perceptual range of a single pixel. Given that covariate layers are
67 usually resolved with a pixel size between 30 m x 30 m and 1 km x 1 km, this hardly
68 ever renders the true capability of animals to perceive the environment. Moreover, CT is
69 built around the assumption of a complete random walk (Diniz et al., 2020), entailing that
70 directional biases cannot be rendered. Nevertheless, directionality is a common characteristic
71 in animal movement (Bovet and Benhamou, 1991; Schultz and Crone, 2001), especially in
72 dispersing individuals (Cozzi et al., 2020; Hofmann et al., 2021).

73 **1.6 Issues of Both Methods**

74 Finally, neither LCP analysis nor CT are capable of rendering the temporal dimension of
75 dispersal (Diniz et al., 2020). Statements about the expected duration required to traverse
76 a certain corridor are therefore impossible. Likewise, because movement is not modeled
77 explicitly, interactions between movement and habitat preferences of the focal species cannot
78 be rendered. Connectivity therefore merely arises in result to the landscape structure, which
79 is usually referred to as structural connectivity. While structural connectivity yields insights
80 in the *potential* of the landscape to be traversed, it does not enable to quantify the *actual*
81 gene flow through the area. Consequently, a functional view on connectivity, which also
82 renders the behavioral response of the animal with respect to prevailing habitat conditions,
83 is often more desirable (Tischendorf and Fahrig, 2000; Baguette et al., 2013).

84 **1.7 What about IBMMS? (90%)**

85 To address the issues inherent to LCPs and CT, individual-based movement models (IBMMS)
86 have been proposed and applied (Diniz et al., 2020). In these models, dispersal trajectories
87 are simulated spatially explicitly, based on movement rules that determine how individuals
88 move over and interact with the prevailing landscape (Gustafson and Gardner, 1996; Gardner
89 and Gustafson, 2004; Graf et al., 2007; Kramer-Schadt et al., 2004; Revilla et al., 2004;
90 Revilla and Wiegand, 2008; Kanagaraj et al., 2013; Clark et al., 2015; Allen et al., 2016;
91 Hauenstein et al., 2019; Zeller et al., 2020; Vasudev et al., 2021). Using the simulated
92 trajectories, one can calculate a set of connectivity metrics, such as inter-patch connectivity
93 and traversal frequency, to reveal major dispersal corridors (Kanagaraj et al., 2013; Bastille-
94 Rousseau et al., 2018; Hauenstein et al., 2019; Zeller et al., 2020). However, while IBMMS

95 can be employed to overcome any of the shortcomings intrinsic to LCPs and CT, they are
96 subject to a vast amount of subjective, non-trivial modeling decisions. Moreover, they can
97 be challenging to fit and require vast amounts of movement data, ideally collected during
98 dispersal (Diniz et al., 2020). Consequently, alternative methods that require fewer modeling
99 decisions and are straight forward to apply are desirable.

100 **1.8 Step Selection Analysis (90%)**

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

116 **1.9 Study Species & Study Area (90%)**

117 One of the species for which long-term viability relies on sufficient landscape connectivity
118 is the endangered African wild dog *Lycon pictus*. While once present across entire sub-
119 Saharan Africa, wild dogs have disappeared from a vast majority of their historic range
120 due to persecution by humans, habitat fragmentation and destruction, and deadly diseases
121 (Woodroffe and Sillero-Zubiri, 2012). As of today, only 6'000 free-ranging individuals remain
122 in small and spatially scattered subpopulations (Woodroffe and Sillero-Zubiri, 2012). Within
123 those subpopulations, wild dogs form cohesive packs comprising 8 to 12 adults and their
124 offspring McNutt (1995). After reaching sexual maturity, male and female offspring form
125 same-sex coalitions and disperse from their natal pack in search for potential mating partners
126 and a suitable territory to settle (McNutt, 1996; Behr et al., 2020). New packs are formed

¹²⁷ when dispersing coalitions join unrelated opposite-sex dispersing coalitions (McNutt, 1996).
¹²⁸ Dispersing wild dogs can cover several hundred kilometers across a variety of landscapes
¹²⁹ (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020; Hofmann et al., 2021).
¹³⁰ One of the few strongholds for this species lies near the Moremi Game Reserve in northern
¹³¹ Botswana, which is part of the world's largest transboundary protected area, namely the
¹³² Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). This area has originally
¹³³ been intended to facilitate migration of elephants, but is expected to provide benefits to a
¹³⁴ multitude of other species (Elliot et al., 2014; Brennan et al., 2020; Hofmann et al., 2021).

¹³⁵ **1.10 Previous Paper (90%)**

¹³⁶ In a previous study, we assessed landscape connectivity for dispersing African wild dogs
¹³⁷ within the KAZA-TFCA using least-cost methods (Hofmann et al., 2021). Specifically, we
¹³⁸ fitted a basic habitat selection model and predicted a permeability surface that we used to
¹³⁹ compute least-cost paths and corridors. We now expand on this knowledge and use ISSFs to
¹⁴⁰ develop a more mechanistic movement model of dispersing wild dogs (Figure 1). We employ
¹⁴¹ the model to simulate dispersers moving across the KAZA-TFCA and generate three distinct
¹⁴² connectivity maps, each shedding light onto a different aspect of connectivity. With this
¹⁴³ work, we exemplify how ISSFs can be utilized for dispersal simulations and we discuss several
¹⁴⁴ benefits of this approach over traditional connectivity modeling techniques such as least-cost
¹⁴⁵ analysis and circuit theory. Most importantly, simulations based on ISSFs provide a more
¹⁴⁶ generic view on how connectivity emerges and to which degree connectivity depends on the
¹⁴⁷ dispersal duration. In addition, by generating proper dispersal trajectories, network theory
¹⁴⁸ can be applied to calculate network metrics that are pertinent to connectivity analysis.

¹⁴⁹ **2 Methods**

¹⁵⁰ **2.1 Study Area (90%)**

¹⁵¹ The study area was defined by a bounding box centered at -17°13'9"S, 23°56'4"E (Figure 2a)
¹⁵² stretching over 1.3 Mio. km² and encompassing the entire KAZA-TFCA (Figure 2b). The
¹⁵³ KAZA-TFCA represents the world's largest transboundary conservation area and comprises
¹⁵⁴ parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia. It covers a total of 520'000
¹⁵⁵ km² and hosts diverse landscapes, ranging from savanna to grassland and from dry to moist
¹⁵⁶ woodland habitats. In its center lies the Okavango Delta, a dominant hydrogeographical
¹⁵⁷ feature and the world's largest flood-pulsing inland delta. The wet season within the KAZA-

158 TFCA lasts from November to March and is out of phase with the flood in the Okavango
159 Delta, which peaks between July and August (McNutt, 1996; Wolski et al., 2017). Although
160 large portions within the KAZA-TFCA are designated national parks or other protected
161 areas, considerable human influence remains due to roads, agricultural sites and settlements
162 and villages that are distributed across the KAZA-TFCA's landscape.

163 2.2 GPS Relocation Data (90%)

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

176 16 collared individuals eventually dispersed, each in a separate same-sex dispersal coali-
177 tion (7 female and 9 male coalitions). During dispersal, collars were programmed to record
178 a GPS fix every 4 hours, all of which were regularly transmitted over the Iridium satellite
179 system, thereby allowing to remotely track individuals, even if they left the main study area
180 and crossed international borders. Because behavior during dispersal is more pertinent for
181 assessing landscape connectivity (Elliot et al., 2014; Abrahms et al., 2017), we discarded all
182 data that was collected during residency and only retained GPS data recorded during dis-
183 persal. In some instances, exact dispersal dates were known from field observations, whereas
184 in other cases we determined dispersal phases using the net-squared displacement metric.
185 Net squared displacement measures the squared Euclidean distance of a GPS relocation to
186 a reference point (Börger and Fryxell, 2012), which in our case was set to the center of
187 each individual's natal home range. Thus, dispersal was deemed to have started when an
188 individual left its natal home range and ended once individuals became sedentary again. As
189 previous research found no differences in behaviors of females and males during dispersal
190 (Woodroffe et al., 2019; Cozzi et al., 2020), we did not distinguish between sexes. After

191 collection, we converted collected GPS coordinates ($n = 4'169$) to steps, where each step
192 represented the straight-line distance traveled by an individual between two consecutive
193 GPS relocations (Turchin, 1998). To ensure a regular sampling interval, we removed fixes
194 that were not successfully collected on the 4-hourly schedule (± 15 minutes).

195 2.3 Covariates (90%)

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

206 Besides habitat covariates, we computed movement metrics that we used as movement
207 covariates in our models. Movement metrics were calculated for each step and included
208 the step length (sl), its natural logarithm ($\log(sl)$), and the cosine of the relative turning
209 angle ($\cos(ta)$) (for details see (Avgar et al., 2016; Fieberg et al., 2020)). Because wild
210 dogs follow a diurnal activity pattern (Castelló, 2018), we also coded a binary variable
211 (**LowActivity**) indicating whether a step was realized during periods of low wild dog activity
212 (17:00 to 09:00 local time) or high wild dog activity (09:00 to 17:00 local time). Handling
213 and manipulation of all data, as well as all models and simulations were implemented with
214 the statistical software R, version 3.6.6 (R Core Team, 2019). Several helper functions were
215 written in C++ and imported into R using the Rcpp package (Eddelbuettel and François,
216 2011; Eddelbuettel, 2013)

217 2.4 Movement Model (80%)

218 We used ISSFs to parametrize a mechanistic movement model for dispersing wild dogs
219 (Avgar et al., 2016). To conduct ISSF analysis, we paired each realized step with 24 random
220 steps. An observed step plus its 24 random steps formed a stratum and received a unique
221 identifier. As suggested by Avgar et al. (2016), we generated random steps by sampling
222 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:

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

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 developed by (Muff et al., 2020), which allows to effectively model random slopes. Thus, we treated animal IDs as random effect and modeled random slopes for each covariate. We fixed the random intercept variance at an arbitrary high value of 10^6 to make use of the "poission"-trick (Muff et al., 2020).

The structure of the movement model was based on the habitat selection model for dispersing wild dogs presented in Hofmann et al. (2021). In the original model (referred to as base model hereafter), no interactions between habitat covariates (`Water`, `DistanceToWater0.5`, `Woodland`, `Shrubs/Grassland`, `Human Influence`) and movement covariates (`sl`, `log(sl)`, `cos(ta)`) were considered. Hence, we slightly expanded this base model and proposed interactions between all movement and habitat covariates. More specifically, we started with the base model and incrementally increased model complexity by adding all possible two-way interactions between habitat covariates and movement covariates. For instance, for the covariate `Water`, we proposed the interactions `Water:log(sl)`, `Water:log(sl)`, and `Water:cos(ta)`. Besides

251 those combinations, we also proposed the interactions `sl:cos(ta)` and `log(sl):cos(ta)` to ac-
252 count for a correlation between turning angles and step lengths, as well as the interactions
253 `sl:LowActivity` and `log(sl):LowActivity` to account for the fact that step lengths may differ due
254 to wild dogs' diurnal activity pattern. To compare competing models and assess the most
255 parsimonious movement model, we ran stepwise forward model selection based on Akaike's
256 Information Criterion (AIC, Burnham and Anderson, 2002).

257 We validated the predictive power of the most parsimonious movement model using k-
258 fold cross-validation for case-control studies as suggested by Fortin et al. (2009). For this,
259 we randomly assigned 80% of the strata to a training set and the remaining 20% to a
260 testing set. Using the training data we parametrized a movement model based on which
261 we predicted selection scores $w(x)$ for all steps in the test data. Within each stratum, we
262 then assigned ranks 1-25 to each step based on predicted selection scores, where rank 1 was
263 given to the step with the highest score $w(x)$. Across all strata we determined the realized
264 step's rank and we calculated rank frequencies of realized steps across all strata. Finally, we
265 computed Spearman's rank correlation between ranks and associated frequencies $r_{s,realized}$.
266 We replicated the entire procedure 100 times and computed the mean correlation coefficient
267 ($\bar{r}_{s,realized}$), as well as its 95% confidence interval across all replicates. For comparison, we
268 repeated the same procedure 100 times assuming random preferences, which we implemented
269 by discarding the realized step from all strata and identifying the rank of a random step
270 in each stratum. Again, we calculated Spearman's rank correlation coefficient ($r_{s,random}$),
271 its mean across repetitions ($\bar{r}_{s,random}$), and its 95% confidence interval. This validation
272 ultimately proofs a significant prediction in case the confidence intervals of $\bar{r}_{s,realized}$ and
273 $\bar{r}_{s,random}$ do not overlap.

274 2.5 Dispersal Simulation (80%)

275 We used the most parsimonious movement model to simulate 80'000 virtual dispersers mov-
276 ing across the KAZA-TFCA. The simulation resembled an inverted ISSF and was set up as
277 follows. (1) We defined a random source point and assumed a random initial orientation of
278 the animal. (2) Departing from the source point, we generated 25 random steps by sampling
279 turning angles from a uniform distribution $(-\pi, +\pi)$ and step lengths from our fitted gamma
280 distribution. Similar to the input data, each random step represented the straight line move-
281 ment within 4 hours. To prevent unreasonably large steps, we capped sampled step lengths
282 to a maximum of 35 km, which corresponded to the farthest distance ever traveled within
283 4 hours by one of our dispersers. (3) Along each random step, we extracted and averaged

284 habitat covariates and we calculated movement covariates. To ensure compatible scales, we
285 standardized extracted values using the same parameters applied to our input data. (4)
286 We applied the parametrized movement model to predict the selection score $w(x)$ for each
287 step and we translated predicted scores into probabilities using Equation (Equation 2). (5)
288 We sampled one of the random steps based on predicted probabilities and determined the
289 animal's new position. We repeated steps (2) to (5) until 2'000 steps were realized, implying
290 a total 160 Mio. simulated steps.

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

299 **2.6 Source Points (90%)**

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

308 **2.7 Convergence (80%)**

309 To verify that the number of simulated individuals sufficed to ensure reliable estimates of
310 connectivity, we evaluated how the relative traversal frequency across the landscape de-
311 pended on the number of simulated trajectories. Specifically, we distributed 1'000 squared
312 "checkpoints", each with an extent of 5 km x 5 km at random locations inside the main study
313 area. We then determined the relative traversal frequency by simulated trajectories through
314 each checkpoint for different numbers of simulations (1 to 50'000). We repeatedly sampled
315 trajectories 100 times and computed the mean traversal frequency across replicates, as well

316 as the 95% prediction-interval. We expected that the mean traversal frequency converges
317 towards a steady state with increasing simulations.

318 2.8 Heatmap (100%)

319 To identify dispersal hotspots across our study area, we created a heatmap indicating the
320 absolute frequency at which each raster-cell in the study area was visited by virtual dis-
321 persers (Hauenstein et al., 2019; Pe'er and Kramer-Schadt, 2008). For this, we rasterized all
322 simulated trajectories and tallied them into a single map. If the same trajectory crossed a
323 raster-cell twice, we only counted it once, thereby mitigating potential biases caused by indi-
324 viduals that were trapped and moved in circles. To achieve high performance rasterization,
325 we used the R-package `terra` (Hijmans, 2020).

326 2.9 Betweenness (80%)

327 To pinpoint areas of exceptional relevance for connecting remote regions inside our study
328 area, we converted simulated trajectories into a network and calculated betweenness scores
329 (Bastille-Rousseau et al., 2018). For this, we overlaid the study area (including the buffer)
330 with a regular raster resolved at 5 x 5 km. The centerpoint of each raster-cell served as node
331 in the final network and we used the simulated trajectories to determine all transitions occur-
332 ring from one node to another, as well as the frequency at which those transitions occurred.
333 This resulted in an edge-list that we translated into a weighted network using the r-package
334 `igraph` (Csardi and Nepusz, 2006). Because `igraph` handles edge weights (ω) as costs, we
335 inverted the traversal frequency in each cell by applying $\omega = \frac{\sum_i^n TraversalFrequency_i}{TraversalFrequency_i}/n$. Con-
336 sequently, edges that were traversed frequently were assigned low costs. Finally, we used
337 the weighted network to calculate the betweenness score of each raster-cell. Betweenness
338 measures how often a specific raster-cell lies on a shortest path between two other raster-
339 cells and is therefore a useful metric to detect movement corridors (Bastille-Rousseau et al.,
340 2018).

341 2.10 Inter-Patch Connectivity (80%)

342 We assessed inter-patch connectivity between national parks located in our study area to
343 examine functional links between distinct patches in the KAZA-TFCA. The decision to focus
344 on national parks was purely out of simplicity and does not imply that connections between
345 other regions are impossible. In fact, the same logic could easily be expanded to include other
346 protected areas. To quantify inter-patch connectivity, we computed the relative frequency at

347 which dispersers originating from one national park successfully moved into another national
348 park. Successful movement was said to be achieved if the individuals' trajectory intersected
349 with the corresponding national park at least once. We also recorded the number of steps
350 required until the first intersection with the polygon of the respective national park. This
351 allowed us to determine *if* and *how often* dispersers moved between certain national parks,
352 as well as *how long* dispersers had to move to realize those connections.

353 3 Results

354 3.1 Movement Model (80%)

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

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

368 With regards to the movement kernel, the positive estimate for $\cos(\text{ta})$ indicates that dis-
369 persers move with directional persistence, unlike what was proposed by the uniform turning
370 angle distribution. Moreover, directionality is particularly pronounced when dispersers re-
371 alize large steps (move quickly), as indicated by the positive estimates for $\cos(\text{ta}):sl$ and
372 $\cos(\text{ta}):log(sl)$. Finally, the negative estimate for the interaction *sl:LowActivity* reveals that
373 wild dogs realize shorter steps (move slower) outside the main activity periods (during
374 sunrise and sunset). Aside from the interaction *sl:LowActivity*, which appears to strongly
375 influence movmement behavior, effect sizes are moderate, but mostly significant on the 5%
376 significance level.

377 When looking at the interactions between movement and habitat kernels, we observe
378 that movement behavior is contingent on habitat conditions. For example, there's strong

evidence that dispersers realize smaller steps in areas covered by water or areas covered by woodland, yet it appears that steps are larger in regions dominated by shrubs/grassland, and shorter when the distance to water is high. Correspondingly, the model suggests that directionality is lower in areas dominated by humans but more pronounced when dispersers are far from water. However, except for the effect of sl:Water, effect sizes and statistical significance are moderate.

The k-fold cross-validation procedure reveals that our model substantially outperforms a random guess (Figure 4b) and therefore correctly assigns a high selection score to realized steps. 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 (i.e. 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 prevented 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 Convergence (80%)

Our examination of the traversal frequency as a function of the number of simulated dispersers shows that the mean traversal frequency stabilizes already after very few simulations and changes only little when adding further dispersers (Figure 5 (a) and (b)). While variability keeps decreasing with additional dispersers, the marginal benefit of adding further dispersers steeply decreases with a negative-exponential trend (Figure 5 (c)).

⁴¹¹ **3.4 Heatmap (80%)**

⁴¹² Figure 6 depicts the heatmap of all 80'000 simulated trajectories resulting after 2'000 steps.
⁴¹³ The map shows that large portions of land beyond the borders of the KAZA-TFCA are only
⁴¹⁴ infrequently visited by dispersers (dark blue areas), whereas within the KAZA-TFCA several
⁴¹⁵ extensive regions are regularly traversed (bright yellow and red areas). Most notably, the
⁴¹⁶ region in northern Botswana south of the Linyanti swamp stands out as highly frequented
⁴¹⁷ dispersal hotspot. Still, the presence of several massive water bodies, such as the Okavango
⁴¹⁸ Delta, the Makgadikgadi Pan, and the Linyanti swamp, poses considerable dispersal barriers
⁴¹⁹ that limit realized connectivity within the KAZA-TFCA. Similarly, dispersal across Zambia's
⁴²⁰ and Zimbabwe's part of the KAZA-TFCA appears to be limited, as only few areas are
⁴²¹ successfully traversed by dispersers. This can largely be attributed to substantial human
⁴²² influences resulting from high human density, roads, and agricultural activities in these
⁴²³ areas. Outside the KAZA-TFCA, the most heavily used regions include the areas inside the
⁴²⁴ Central Kalahari National Park in Botswana, the area south-west of the Khaudum National
⁴²⁵ Park in Namibia, and the area around the Liuwa Plains National Park in Zambia.

⁴²⁶ **3.5 Betweenness (80%)**

⁴²⁷ Betweenness scores after 2'000 simulated steps are presented in Figure 7 and reveal a set of
⁴²⁸ discrete dispersal corridors. Again, the region in northern Botswana stands out as crucial
⁴²⁹ dispersal hub that connects more remote regions in the study system. Towards east, the
⁴³⁰ extension of this corridor runs through the Chobe National Park into the Hwange national
⁴³¹ park. From there, a further extension connects to the distant Matusadona National Park
⁴³² in Zimbabwe. Northwest of the Linyanty ecosystem, a major corridor expands into Angola,
⁴³³ where it splits and finally traverses over a long stretch of unprotected area into the Kafue
⁴³⁴ National Park in Zambia. Several additional corridors with slightly lower betweenness scores
⁴³⁵ exist, yet most of them run within the boundaries of the KAZA-TFCA. In general, only few
⁴³⁶ corridors directly link the peripheral regions of the KAZA-TFCA. For instance, there are
⁴³⁷ only few corridors between the Matusadona National Park in Zimbabwe and the Kafue
⁴³⁸ National Park in Zimbabwe. Similarly, there are no direct links between the Zimbabwean
⁴³⁹ and Angolan “spikes” of the KAZA-TFCA.

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

⁴⁴¹ Results from the analysis of inter-patch connectivity are given in Figure 8. The figure shows
⁴⁴² all realized links by simulated dispersers between national parks and indicates the average

duration a disperser had to move to realize those links. It is again worth pointing out that the figure is only intended as an example and for clarity we only consider connectivity between national parks (NPs), albeit plenty of links between other protected areas exist. As can be seen from the number and thicknesses of arrows, inter-patch connectivity between NPs in Angola, Namibia, and Botswana is comparably high. In addition, the bright colors highlight that most dispersal events between those areas are short. In contrast, we see that connections into the Kafue NP in Zambia require more steps and are fewer in general. Similarly, there is a lack of connections into Zimbabwe's Chizarira and Matusadona NP and the more distant Lower Zambezi and Mana Pools NPs. In some cases, one can also detect imbalances between ingoing and outgoing links, hinting at potential source-sink dynamics that occur due to asymmetries in landscape permeability depending on the origin. For instance, while a large portion of dispersers from the Chizaria NP in Zimbabwe manage to move into the Hwange NP, there are comparably few dispersers that succeed in the opposite direction.

4 Discussion

4.1 Short Summary (90%)

We used ISSFs to analyse data of dispersing wild dogs and to parametrize a fully mechanistic movement model describing how dispersers move through the available landscape. We employed the parametrized model as an individual-based movement model to simulate 80'000 dispersing wild dogs moving 2'000 steps across the extent of the KAZA-TFCA, the world's largest transboundary conservation area, located in southern Africa. Based on simulated dispersal trajectories, we derived three complementary maps, all geared towards a better understanding of dispersal and landscape connectivity. These maps included a heatmap, revealing frequently traversed areas, a betweenness-map, delineating critical dispersal corridors, and a map of inter-patch connectivity, indicating the presence or absence of functional links between national parks. We thereby showcase that ISSFs offer a simple, yet powerful framework to parametrize movement models and simulate dispersal to assess landscape connectivity. Importantly, individual-based simulations from ISSFs overcome several conceptual shortcomings inherent to more traditional connectivity modeling techniques, such as least-cost path analysis and circuit theory.

473 **4.2 Movement Model (80 %)**

474 Our movement model of dispersing wild dogs consisted of a habitat kernel, a movement
475 kernel, and their interactions. Together, the kernels in detail described habitat and move-
476 ment preferences of dispersing wild dogs, as well as how movement behavior was affected
477 by habitat conditions. Parameter estimates from the habitat kernel revealed that dispersing
478 wild dogs avoid water, prefer its proximity, avoid woodland, prefer shrubs/grassland, and
479 avoid areas dominated by humans. These findings are consistent with findings from previous
480 studies on dispersing wild dogs (Davies-Mostert et al., 2012; Masenga et al., 2016; Woodroffe
481 et al., 2019; O'Neill et al., 2020), as well as with a base model that we developed with a
482 main focus on dispersers' habitat kernel (Hofmann et al., 2021).

483 By expanding our base model by a proper movement kernel, we were able to model
484 several additional complexities inherent to dispersal. For instance, it is well known that
485 dispersers move with directional persistence and that their step lengths are correlated with
486 turning angles (Morales et al., 2004; Börger and Fryxell, 2012). That is, larger steps usually
487 imply smaller turning angles and vice versa. While this behavior could be captured by
488 sampling turning angles and step lengths from copula probability distributions (?), the ISSF
489 framework allowed us to model similar behavior directly in the movement model. Besides
490 accounting for directional persistence and correlations between step lengths and turning
491 angles, we also allowed for interactions that rendered the fact that wild dogs mainly move
492 during the morning and evening hours, whereas they tend to rest during the remainder of
493 the day. The final model thus rendered a burst-like movement behavior, where dispersers
494 realize larger steps during the darker morning and evening hours, but shorter steps during
495 the rest of the day. While we accounted for 1. order autocorrelation (i.e. correlation
496 between two subsequent steps), higher order autocorrelation is conceivable and might be
497 desirable to model. While ISSFs are conceptually capable of rendering such behavior, it
498 unfortunately requires vast amounts of GPS data that is not intercepted by missing fixes,
499 making it impractical to model higher-order autocorrelation using ISSFs in reality.

500 By allowing interactions between habitat covariates and movement covariates, we fur-
501 thermore accounted for the fact that movement and habitat preferences are interdependent.
502 For example, the final model retained an interaction between water cover and step length,
503 showing that dispersers are more likely to realize short steps (i.e. move slower) in areas
504 covered by water. Likewise, the parameter estimate for the interaction between water cover
505 and turning angles revealed that dispersers move less directional when moving across water
506 bodies. We believe that this behavior is owed to the fact that wild dogs wade or swim when

507 traversing waterbodies, thus resulting in slower, more tortuous movements. Besides this, our
508 model also suggested that dispersers preferably realize shorter steps when moving through
509 woodland, but larger steps when moving across shrubs/grassland. This can likely be linked
510 to wild dogs' resting behavior, as wild dogs usually use open areas to quickly move over long
511 distances (Abrahms et al., 2017) but seek shade and protection below the woodland canopy
512 when resting (Creel and Creel, 2002). However, we did not consider three way interactions
513 and could therefore not test this hypothesis.

514 4.3 Simulation (80%)

515 Based on the above described movement model, we simulated 80'000 dispersers moving 2'000
516 steps across the landscapes of the KAZA-TFCA. This simulation of 160 Mio. steps required
517 five days of computation on a modern desktop machine. The long simulation time was
518 primarily caused by the massive extent considered (ca. 1.8 Mio. km² when including the
519 buffer) and the large number of dispersers simulated. Most connectivity studies are limited
520 to much smaller extents (e.g. Kanagaraj et al., 2013; Clark et al., 2015; McClure et al., 2016;
521 Abrahms et al., 2017; Zeller et al., 2020) and will therefore require shorter simulation times.
522 We also believe that fewer simulated dispersers will often suffice, as the relative traversal
523 frequency by simulated individuals through randomly placed checkpoints converged rather
524 quickly. In any case, the exact number of required simulations will vary depending on the
525 structure of the landscape and the dispersal ability of the focal species.

526 A simulation-based approach as proposed in this article offers several advantages over
527 traditional connectivity modeling techniques such as LCP analysis or CT. In contrast to
528 LCP analysis, for instance, an individual-based simulation does not require to assume known
529 endpoints. Instead, each endpoint emerges naturally from a simulated dispersal trajectory.
530 This is particularly valuable for dispersal studies, because dispersers often venture into
531 unfamiliar territory and are unlikely to know the destination of their journey (Elliot et al.,
532 2014; Abrahms et al., 2017; Cozzi et al., 2020). A connectivity model that does not require
533 pre-defined endpoints also ensures that movement corridors are not enforced between certain
534 start- and endpoints and permits to reveal frequently used routes that potentially lead into
535 ecological traps (Dwernychuk and Boag, 1972; Van der Meer et al., 2014).

536 In comparison to LCP and CT approaches, IBMMs furthermore yield the advantage of
537 an explicit representation of time. The ability to render time enables to answer questions
538 such as: "*How long will it take a disperser to move from A to B?*" or *Is it possible for a*
539 *disperser to move from A to B within X days?*. These are important questions that shift the

540 focus from a structural to a more functional view on connectivity. An explicit representation
541 of time also yields opportunities to study how connectivity depends on seasonal changes in
542 the environment (*dynamic connectivity*; Zeller et al., 2020). With LCP or CT, a dynamic
543 connectivity analysis is currently impractical because the same analysis needs to be repeated
544 for different permeability surfaces, each resembling a snapshot in time for a different seasonal
545 state of the environment (e.g. Benz et al., 2016; Osipova et al., 2019). With IBMMs, on the
546 other hand, the environment is allowed to change dynamically “as the dispersers move” such
547 that simulated individuals can respond to seasonal factors directly within the simulation.

548 While an explicit representation of time appears beneficial, it also requires that step
549 lengths and turning angles are modeled correctly (Kanagaraj et al., 2013), so that the time
550 required to move between areas can be reliably estimated. Correctly rendering movement
551 behavior under varying environmental conditions is one of the main strength of ISSFs (Avgar
552 et al., 2016; Prokopenko et al., 2017; Fieberg et al., 2020), which is why we believe that
553 the framework is exceptionally well suited for simulating animal dispersal and assessing
554 landscape connectivity. In fact, the ISSF framework allows to define an infinite amount of
555 movement kernels, each representing movement preferences under different environmental
556 conditions (Fieberg et al., 2020). ISSFs can therefore accommodate highly diverse movement
557 modes, including fast paced directional movements and slow paced tortuous movements.

558 Whereas the results of LCP analysis and CT are usually restricted to single “conduc-
559 tance” maps, individual-based simulations can be processed using a diverse suite of different
560 approaches, each enabling to focus on a different aspect of connectivity. By turning simulated
561 trajectories into a network, for instance, researchers can capitalize on concepts from network
562 theory and calculate network metrics that are pertinent to landscape connectivity (Bastille-
563 Rousseau et al., 2018). Here, we have exemplified this by calculating the betweenness
564 metric, highlighting major movement corridors. Alternatively, can learn about inter-patch
565 connectivity and potential source-sink dynamics between patches (Ferreras, 2001; Revilla
566 et al., 2004; Kanagaraj et al., 2013) based on simulated dispersal trajectories. Ultimately,
567 by accounting for habitat- and movement preferences of the focal species, simulations from
568 ISSFs are capable of rendering the behavioral ecology of the focal species in detail, thereby
569 permitting a more functional view on connectivity that is not solely driven by the land-
570 scape structure and distances between patches (Gustafson and Gardner, 1996; Gardner and
571 Gustafson, 2004; Graf et al., 2007; Kramer-Schadt et al., 2004; Revilla et al., 2004; Revilla
572 and Wiegand, 2008; Kanagaraj et al., 2013).

573 Despite the benefits that ISSF simulations offer, we also want to confer some of the non-

574 trivial modeling decisions involved. In particular, we will discuss five modeling decisions
575 (Figure 9): (1) number of simulated individuals, (2) location of source points, (3) dispersal
576 duration, (4) boundary behavior, and (5) how to handle individual variability.

577 (1) When simulating dispersal, the modeler needs to decide on the number of simulated
578 individuals. This decision includes the *absolute* number of simulated individuals across
579 the study area, as well as the *relative* number of simulated individuals per spatial entity
580 (e.g. protected area, habitat patch, source point). Because each additionally simulated
581 individual adds information about landscape connectivity and potential movement routes, a
582 larger absolute number of simulated individuals is always desirable, yet this comes at the cost
583 of computational efficiency. Consequently, a trade-off needs to be managed. One solution
584 to handle the trade-off would be to define a target metric and to only simulate so many
585 individuals until convergence in the target metric is achieved. Here, we used the *relative*
586 *traversal frequency* across checkpoints as target metric and revealed that convergence was
587 achieved already after few simulated individuals. With regards to the relative number of
588 simulated individuals, we see two feasible approaches. First, one could initiate dispersers in
589 relation to population density at the respective area. This would directly reflect the fact that
590 population densities are not homogeneous across space. (Say more) Alternatively, however,
591 one could also distribute dispersers homogeneously, but then weigh simulated trajectories
592 by the population density at the source patch (Say more). Because we lacked reliable
593 information on density estimates for the extent of the KAZA-TFCA, we opted for a solution
594 where dispersers were distributed homogeneously.

595 (2) While endpoints do not need to be defined in IBMMs, source points will still need to
596 be provided by the modeler. Here, we randomly placed source points within protected areas
597 large enough to sustain viable wild dog populations, knowing that the species primarily
598 survives in these formally protected areas (Woodroffe and Ginsberg, 1999; Davies-Mostert
599 et al., 2012; Woodroffe and Sillero-Zubiri, 2012; Van der Meer et al., 2014). In some cases,
600 exact locations of potential source populations are known and source points can be placed
601 accordingly (Kanagaraj et al., 2013). Moreover, if abundance estimates are available, these
602 can be used to inform the relative number of dispersers initiated at each location. In other
603 cases, comparable knowledge may be lacking and it could be more beneficial to delineate
604 likely source patches based on habitat suitability models (e.g. Squires et al., 2013). Either
605 way, a meaningful selection of source points is not a problem unique to IBMMs and applies
606 to any connectivity modeling technique. As highlighted by Signer et al. (2017) the influence
607 of the exact location of source points decreases as the number of simulated steps is increased,

608 yet their goal was assessing steady state utilization distributions and not to assess landscape
609 connectivity.

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

622 (4) Unless simulated individuals are strongly drawn towards a point of attraction, some
623 simulated individuals will eventually approach a map boundary and the modeler needs to
624 define a rule to handle such situations. One feasible option would be to terminate the
625 trajectory as soon as it hits a map boundary, implicitly assuming that the simulated animal
626 left the study area and will not return. The downside to this approach is that source points
627 located near map boundaries will inevitably produce many such dead ends. Alternatively,
628 one could remove transgressing random steps from the set of proposed random steps, thereby
629 forcing virtual dispersers to bounce off virtual boundaries and remain within the main study
630 area. This may seem like an elegant solution, yet again, it potentially results in substantial
631 edge effects when source points are located near map boundaries. Finally, one could extend
632 the study area by an artificial buffer zone through which dispersers are allowed to leave
633 and re-enter the main study area. Of course this does not fully mitigate the issue, since
634 some dispersers may still approach the outer map boundary, however, as Koen et al. (2010)
635 have shown, such an artificial buffer can often help to mitigate edge effects. In theoretical
636 applications, this issue can be circumvented by simulating movement on a torus (?), yet this
637 is unfeasible in most real world applications.

638 (5) We simulated dispersal using point estimates from our most parsimonious movement
639 model but did not investigate the sensitivity of our results with respect to those estimates.
640 Uncertainty is rather common in dispersal studies on endangered species, as data tends to be
641 scarce, resulting in model estimates large confidence intervals (Wiegand et al., 2003; Kramer-

642 Schadt et al., 2007). To address this, one may explore a broader range of preferences instead
643 of using point estimates initiate dispersers with randomized preferences with variability
644 imposed by the uncertainty in the movement model. We therefore urge future studies to
645 investigate the sensitivity of ISSF simulations with respect to estimated preferences.

646 4.4 Maps (10%)

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

661 Each map that we produced from simulated trajectories accentuates a different aspect
662 of connectivity. The heatmap, for example, puts emphasis on areas where movement is
663 concentrated, regardless whether such areas represent “dead ends” that do not necessarily
664 connect distinct patches. Therefore, the heatmap is useful to determine locations where a
665 disperser are likely to move to, yet not necessarily to uncover corridors that link valuable
666 habitats. The betweenness map, on the other hand, brings out those areas that are relevant
667 in connecting different regions in the landscape. In this regard, the betweenness map is
668 most pertinent to the delineation of dispersal corridors and may serve as an alternative to
669 least-cost algorithms. Finally, the inter-patch connectivity map illustrates the frequency at
670 which dispersal between distinct habitat patches occurs, as well as the average dispersal
671 duration that passes when individuals move between those patches. This knowledge serves
672 to gauge the amount of gene flow between habitat patches and can be employed to determine
673 whether two habitats are connected or not.

674 **4.5 General (20%)**

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

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

691 Approach also similar to Potts et al. (2013), yet they used regular SSFs and examined
692 steady state UDs.

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

699 Simulations resulting from IBMMs could furthermore be utilized as simple tool to predict
700 the likely whereabouts of GPS collared animals into the near future. In some European
701 countries, the comeback of large predators, such as bears, lynx, and the wolf, has triggered
702 emotional discussions and raised public concern (Behr et al., 2017), particularly in areas with
703 free-roaming livestock that may be preyed upon by the returned species. An early warning
704 system based on simulations could thus serve to forewarn about potential encounters and
705 and thereby increase public acceptance of large predators.

706 We have previously attributed the weak significance of distance to water to the fact that
707 we did not control for the presence or absence of conspecifics. We stick to this reasoning

708 as our expanded model still shows a rather large uncertainty around the respective beta
709 coefficients. To better gauge the importance and influence of this covariate, future studies
710 will need to control for inter- and intra-specific interactions that may explain why and when
711 dispersers are attracted to or afraid of waterbodies. Fortin et al. (2005), for instance, found
712 that elk movement was significantly impacted by the density of wolf in the area, such that
713 habitat preferences strictly differed depending on the presence or absence of wolves. The
714 decision to settle is likely related to the presence or absence of conspecifics. Hence, the
715 exact dispersal duration and distance will not be independent of current wild dog densities.
716 In dispersing wolves, for instance, the longest dispersal distances have been observed in
717 low-density populations (??). The dispersal duration may thus be determined by the by
718 the amount of isolation between subpopulations and population densities (Davies-Mostert
719 et al., 2012).

720 Even though our simulations generated several interesting results, most of them need
721 to be validated using independent data. We learned that between some national parks
722 asymmetries between the number of ingoing and outgoing dispersers exist, suggesting that
723 some patches act as sinks, whereas others serve as sources for dispersers.

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

736 5 Authors' Contributions

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

6 Data Availability

⁷⁴¹ GPS movement data of dispersing coalitions will be made available on dryad at the time of
⁷⁴² publication. Access to all R-scripts for our analyses is provided through Github.

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⁷⁵³ Ozgul.

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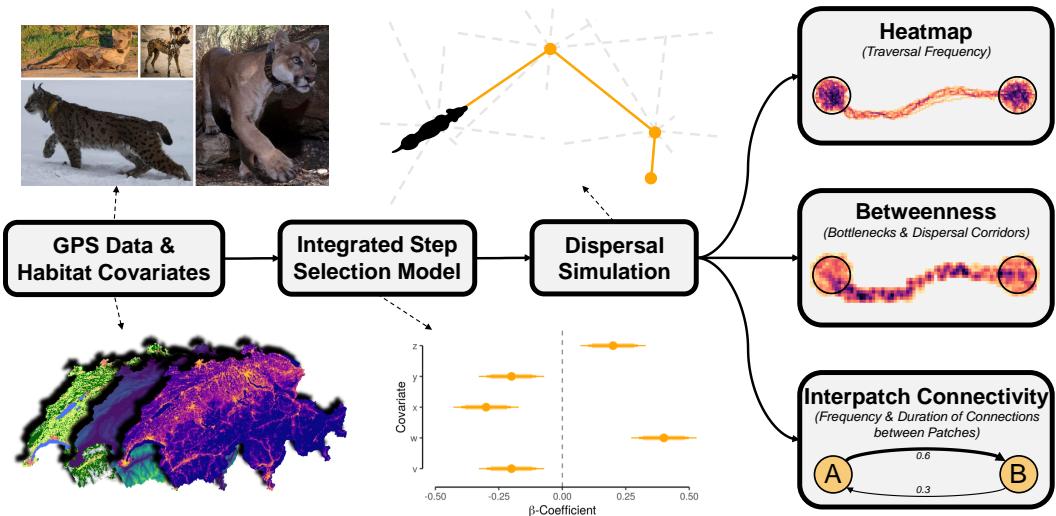


Figure 1: Flowchart of the simulation-based connectivity analysis. First, GPS data and habitat covariates have to be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement kernels. The parametrized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

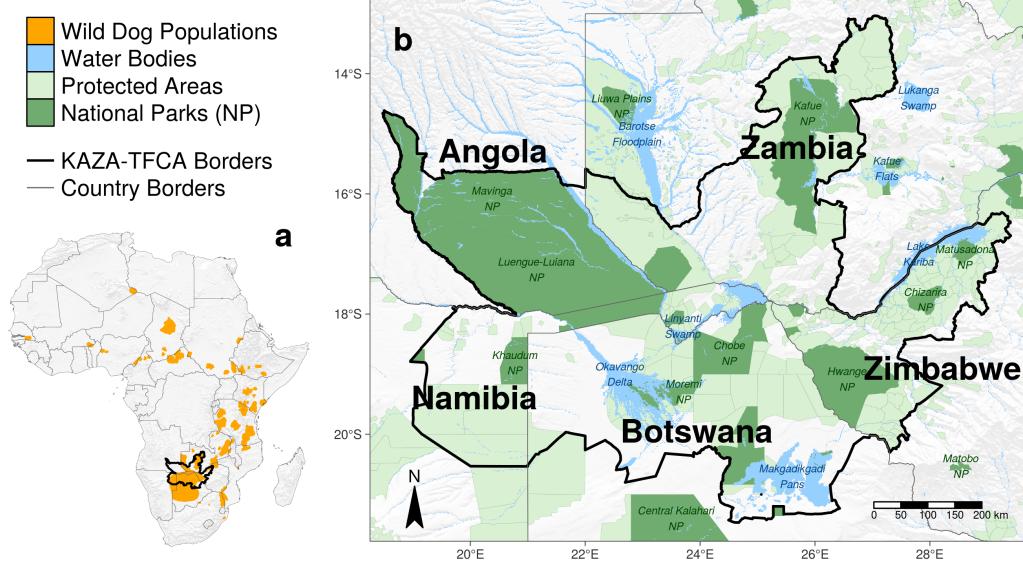


Figure 2: Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA and encompassing parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA represents the world’s largest terrestrial conservation area and covers a total of 520’000 km². Its purpose is to re-establish connectivity between already-existing national parks (dark green) and other protected areas (light green). The dispersal data used in this study was collected on a free-ranging African wild dog population inhabiting the Moremi National Park in northern Botswana.

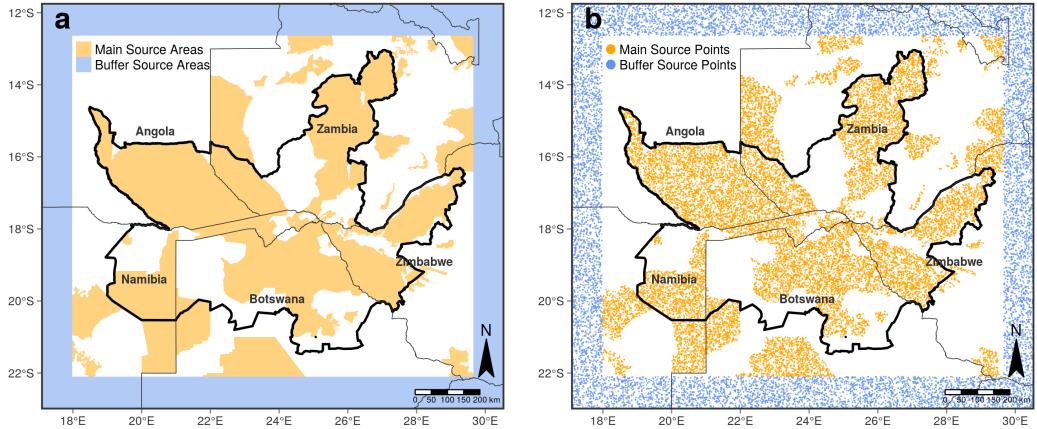


Figure 3: (a) Different source areas from which we released virtual dispersers. We only considered contiguous protected areas (national parks, game reserves, and forest reserves) that were larger than 700 km^2 (green). This area corresponds to the average home range requirement for viable wild dog populations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

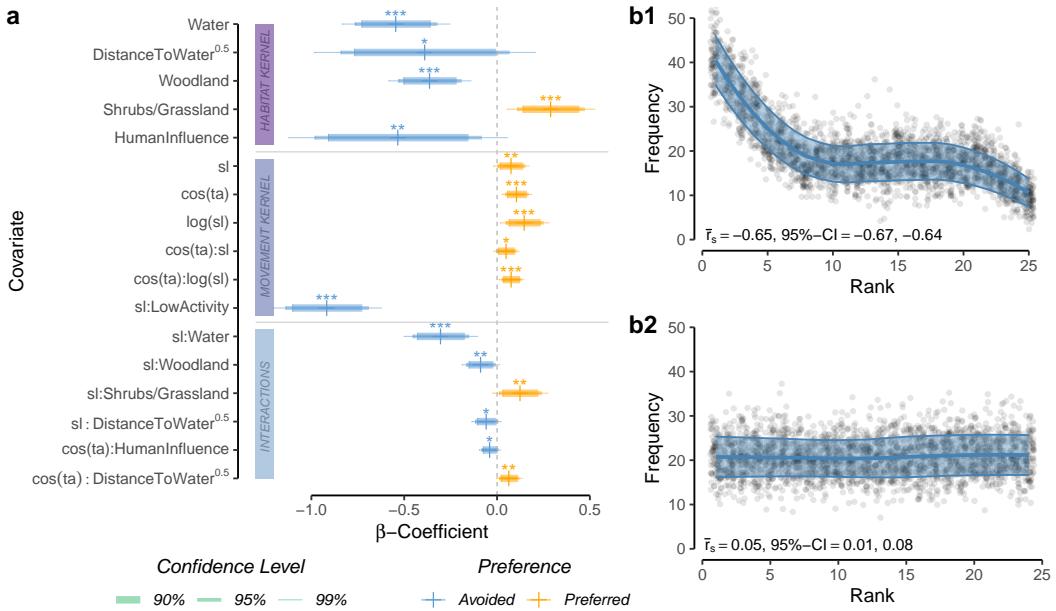


Figure 4: (a) Most parsimonious movement model for dispersing wild dogs. The model includes a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% Confidence-Intervals for the respective β -coefficients. Significance codes: * $p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

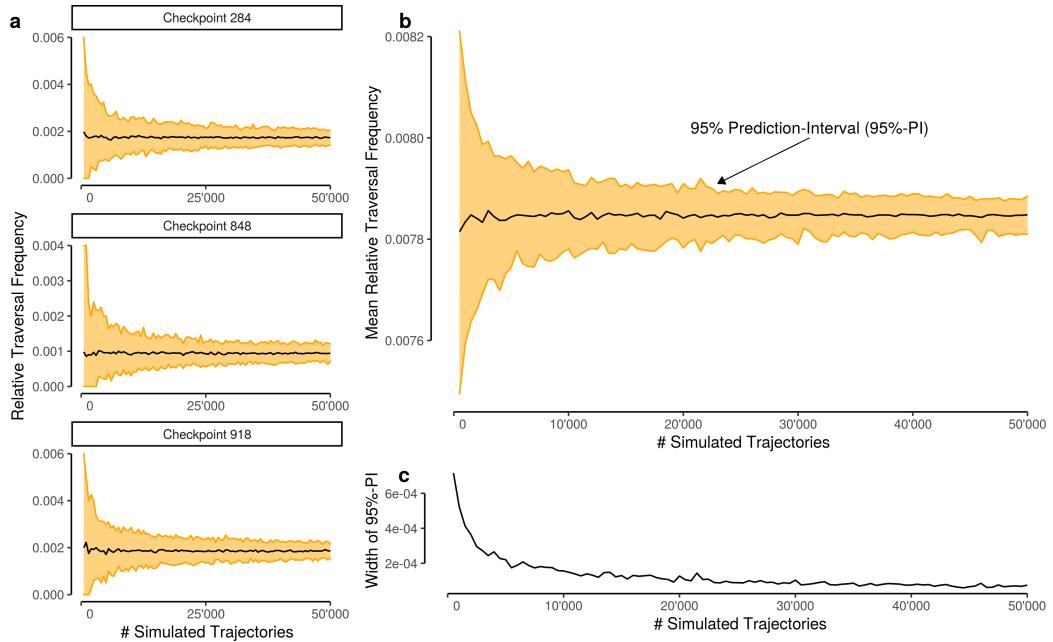


Figure 5: Relative traversal frequency through 1'000 checkpoints (5 km x 5) distributed randomly across the study area. The relative traversal frequency is plotted against the number of simulated individuals to visualize how quickly the metric converges to a steady state. (a) Replicated (100 times) relative 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.

Heatmap
After 2000 Steps

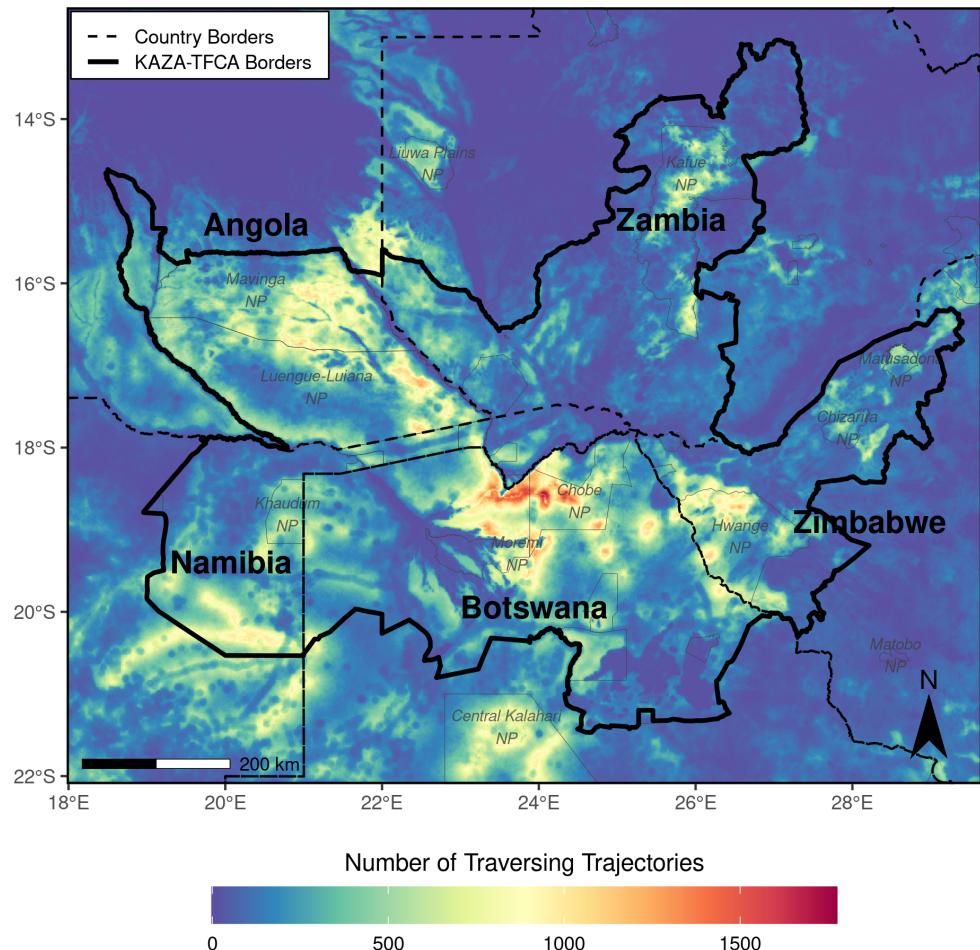


Figure 6: Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step selection model that we fit to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied all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

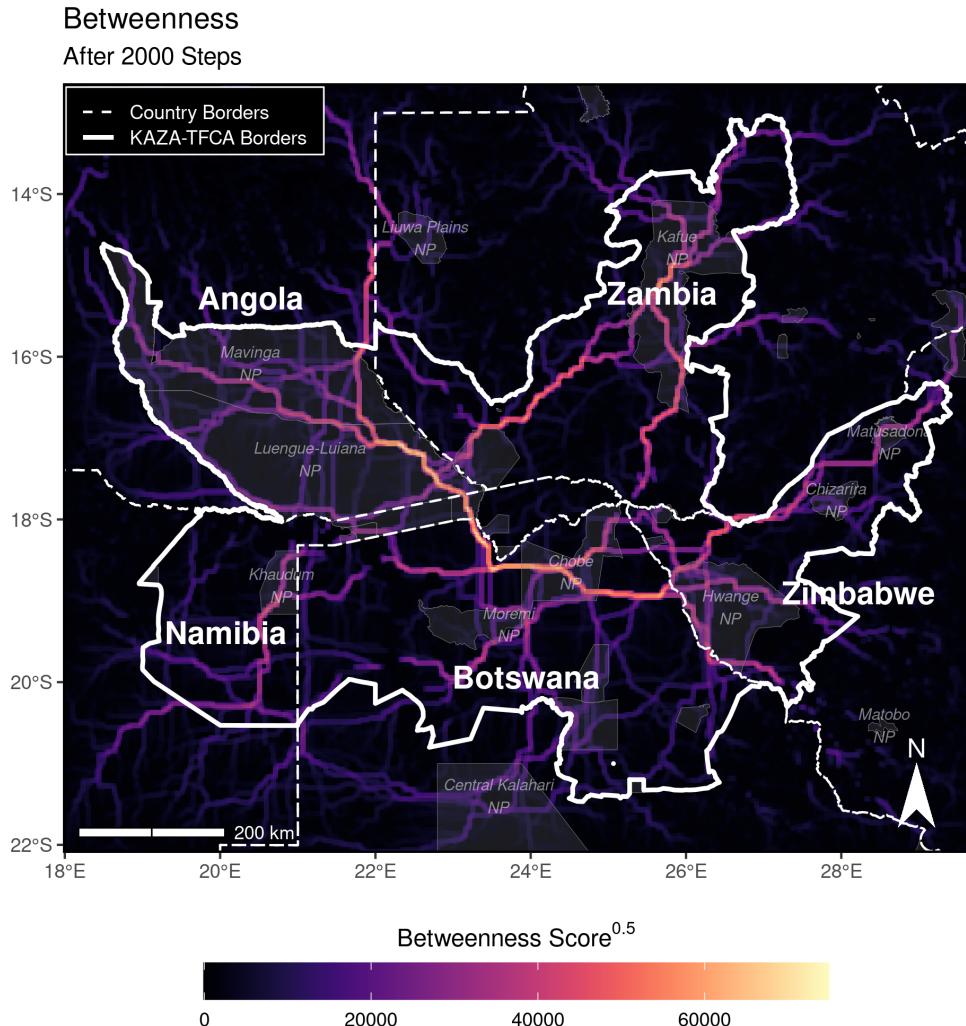


Figure 7: Map of betweenness scores, highlighting distinct dispersal corridors and potential bottlenecks. A high betweenness score indicates that the respective cells are exceptionally relevant in connecting different regions in the study area. That is, the higher the betweenness score, the more often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

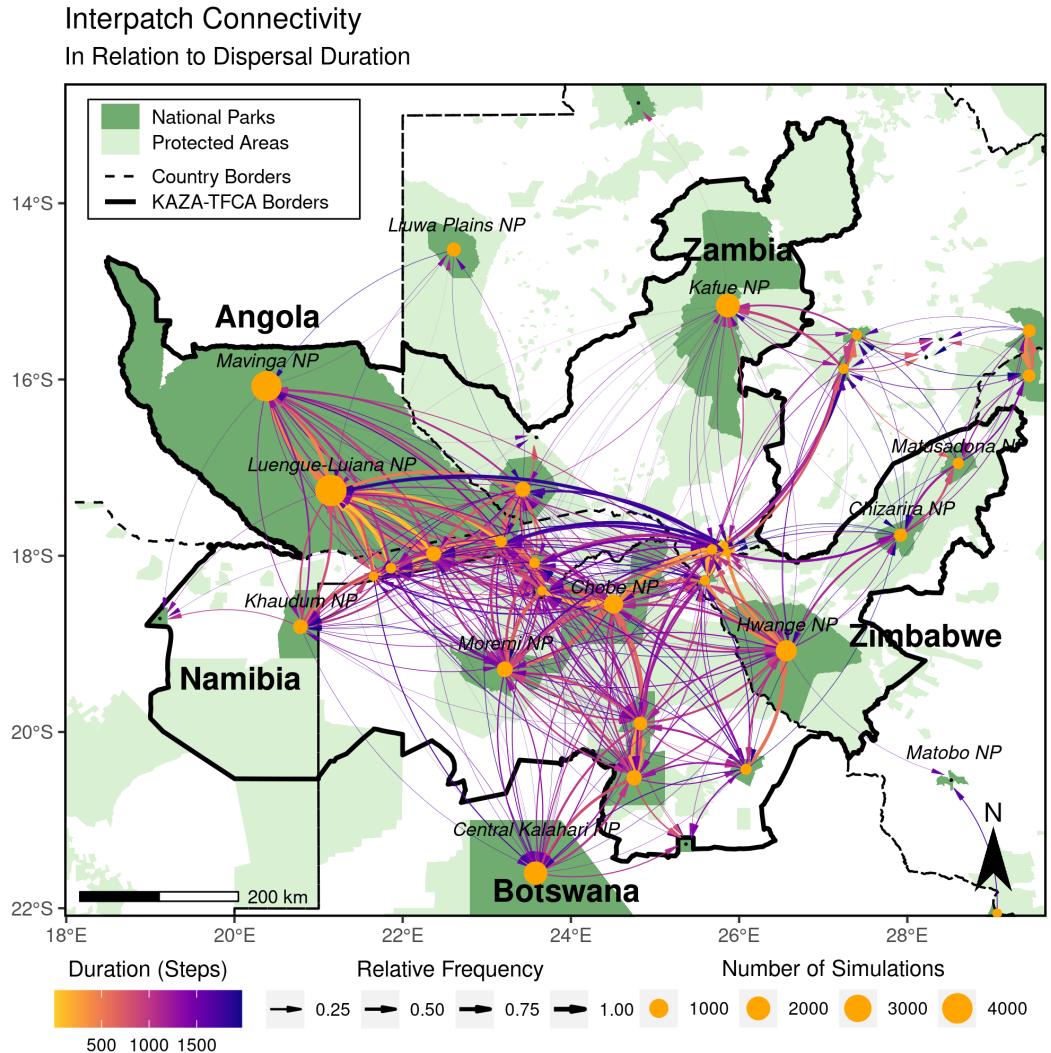


Figure 8: Network on simulated dispersal trajectories highlighting connections between national parks (dark green). Yellow bubbles represent the center of the different national parks and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent national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

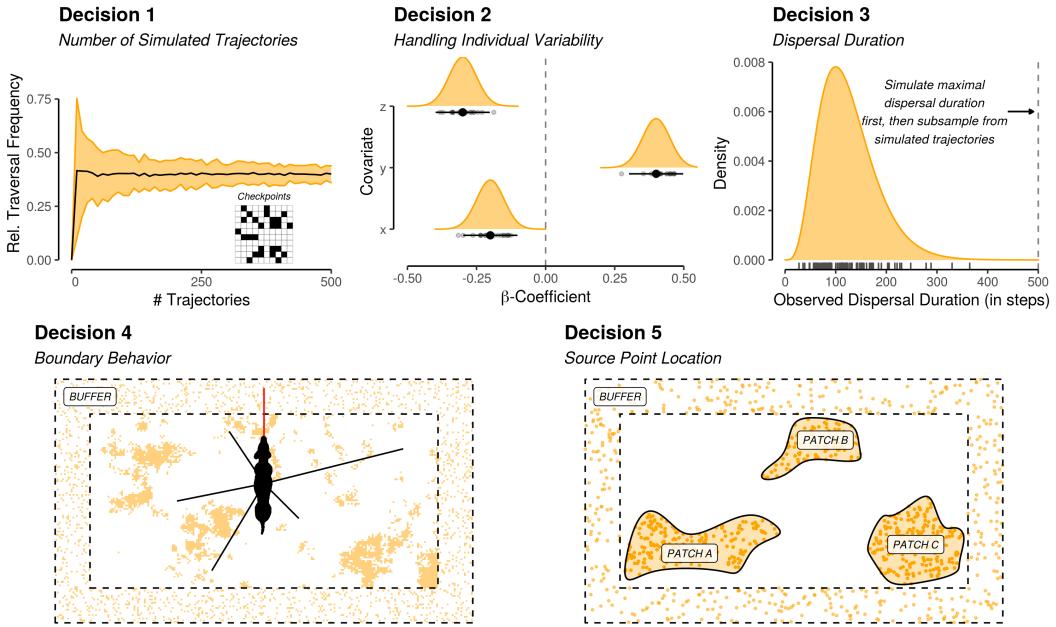


Figure 9: Five major modeling decisions that a researcher needs to consider when simulating dispersers to assess landscape connectivity. (1) Number of simulated trajectories. (2) Handling individual variation: we used point estimates when simulating dispersers, assuming that there was no individual variation. Alternatively, however, one could draw preferences for each simulated individually based on model uncertainty. (3) Dispersal duration. While one could draw the number of simulated steps based on observed dispersal events, we opted for an alternative and simulated each individual for 2'000 steps, which was at the upper end of observed dispersal durations. This allows to easily shorten the generated trajectories afterwards and to investigate the sensitivity of results with regards to the dispersal duration. (4) Boundary behavior. We allowed dispersers to leave and re-enter the main study area through a buffer zone with randomized covariate values. Alternatively, one could discard transgressing random steps, thereby forcing dispersers to remain within the study area or simply terminate the simulation, assuming the individual has disappeared. (5) Source point location. The location of source points should optimally be biologically informed. For our simulation, we placed source points within protected areas large enough to sustain viable wild dog populations. Conceivable alternatives include placing source points according to a habitat suitability model or based on abundance information. Importantly, one must also consider potential immigrants from outside the main study area.

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