

A Three-Step Approach for Assessing Landscape Connectivity via Simulated Dispersal: African Wild Dog Case Study

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November 20, 2023

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Running Title: Simulating Wild Dog Dispersal Trajectories to Assess Landscape
Connectivity

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

Abstract

Context Dispersal of individuals contributes to long-term population persistence, yet requires a sufficient degree of landscape connectivity. To date, connectivity has mainly been investigated using least-cost analysis and circuit theory, two methods that make assumptions that are hardly applicable to dispersal. While these assumptions can be relaxed by explicitly simulating dispersal trajectories across the landscape, a unified approach for such simulations is lacking.

Objectives Here, we propose and apply a simple three-step approach to simulate dispersal and to assess connectivity using empirical GPS movement data and a set of habitat covariates.

Methods In step one of the proposed approach, we use integrated step-selection functions to fit a mechanistic movement model describing habitat and movement preferences of dispersing individuals. In step two, we apply the parameterized model to simulate dispersal across the study area. In step three, we derive three complementary connectivity maps; a heatmap highlighting frequently traversed areas, a betweenness map pinpointing dispersal corridors, and a map of inter-patch connectivity indicating the presence and intensity of functional links between habitat patches. We demonstrate the applicability of the proposed three-step approach in a case study in which we use GPS data collected on dispersing African wild dogs (*Lycaon pictus*) inhabiting northern Botswana.

Results Using step-selection functions we successfully parametrized a detailed dispersal model that described dispersing individuals' habitat and movement preferences, as well as potential interactions among the two. The model substantially outperformed a model that omitted such interactions and enabled us to simulate 80,000 dispersal trajectories across the study area.

Conclusion By explicitly simulating dispersal trajectories, our approach not only requires fewer unrealistic assumptions about dispersal, but also permits the calculation of multiple connectivity metrics that together provide a comprehensive view of landscape connectivity. In our case study, the three derived connectivity maps revealed several wild dog dispersal hotspots and corridors across the extent of our study area. Each map highlighted a different aspect of landscape connectivity, thus emphasizing their complementary nature. Overall, our case study demonstrates that a simulation-based approach offers a simple yet powerful alternative to traditional connectivity modeling techniques. It is therefore useful for a variety of applications in ecological, evolutionary, and conservation research.

1 Introduction

2 Dispersal of individuals is a vital process that allows species to maintain genetic diversity
3 (Perrin and Mazalov, 2000; Frankham et al., 2002; Leigh et al., 2012; Baguette et al., 2013;
4 LaPoint et al., 2013), rescue non-viable populations (Brown and Kodric-Brown, 1977), and
5 to colonize unoccupied habitats (Hanski, 1999; MacArthur and Wilson, 2001). However, the
6 ability to disperse depends on a sufficient degree of landscape connectivity (Fahrig, 2003;
7 Clobert et al., 2012), making the identification and protection of dispersal corridors that
8 promote connectivity a task of fundamental importance (Doerr et al., 2011; Rudnick et al.,
9 2012). Identifying dispersal corridors not only necessitates a comprehensive understanding
10 of the factors that limit dispersal, but also an appropriate model to estimate connectivity
11 (Baguette et al., 2013; Vasudev et al., 2015; Hofmann et al., 2021a). To date, the most
12 commonly used connectivity models are least-cost path analysis (LCPA; Adriaensen et al.,
13 2003) and circuit theory (CT; McRae, 2006; McRae et al., 2008). Unfortunately, both models
14 rest on assumptions that appear unsuitable for dispersers, thus calling for the development
15 of alternative approaches. One promising alternative is to assess landscape connectivity via
16 simulated dispersal trajectories generated from individual-based movement models (IBMMs,
17 Diniz et al., 2019). However, IBMMs require a large number of subjective modeling decisions,
18 thus making among-system comparisons difficult.

19 Traditional connectivity models make assumptions that are rarely met for dispersers.
20 LCPA, for instance, assumes that individuals move towards a preconceived endpoint and
21 choose a cost-minimizing route accordingly (Sawyer et al., 2011; Abrahms et al., 2017).
22 While this assumption may be justifiable for migrating animals, it is unlikely to hold for
23 dispersers, as dispersers typically move across unfamiliar territory towards an unknown end-
24 point (Koen et al., 2014; Cozzi et al., 2020). CT, on the contrary, posits that animals move
25 according to a random walk, entailing that autocorrelation between subsequent movements
26 cannot be rendered (Diniz et al., 2019). For dispersers, however, autocorrelated movements
27 are regularly observed (Cozzi et al., 2020; Hofmann et al., 2021a), meaning that dispersal
28 trajectories are usually strongly directional. An interesting generalization that bridges the
29 continuum between LCPA and CT has been proposed by Panzacchi et al. (2016) and enables
30 to capitalize on the merits of both approaches. Despite these and several other generaliza-
31 tions of LCPA and CT (e.g. Pinto and Keitt, 2009; Landguth et al., 2012; Panzacchi et al.,
32 2016; Brennan et al., 2020), some shortcomings remain. Most notably, all of these methods
33 rely on static permeability or resistance surfaces that can't reflect the temporal dimension of
34 dispersal. This permits statements about the expected duration for moving between habitat

35 patches (Martensen et al., 2017; Diniz et al., 2019).

36 The shortcomings inherent to LCPA and CT can be overcome by simulating dispersal
37 using IBMMs and by converting simulated trajectories into meaningful measures of connec-
38 tivity (Diniz et al., 2019). In contrast to LCPA and CT, IBMMs allow to explicitly simulate
39 how individuals move across and interact with the encountered landscape (Kanagaraj et al.,
40 2013; Clark et al., 2015; Allen et al., 2016; Hauenstein et al., 2019; Zeller et al., 2020), as
41 well as to render potential interactions between movement behavior and habitat conditions
42 (Avgar et al., 2016). This shifts the focus towards a more functional view on connectivity
43 (Tischendorf and Fahrig, 2000). Furthermore, IBMMs generate movement sequentially, i.e.
44 they generate a series of steps, so that the temporal dimension of dispersal becomes explicit
45 and allows modeling autocorrelation between successive steps (Diniz et al., 2019). Finally,
46 simulations from IBMMs do not enforce movement or connections towards preconceived
47 endpoints but allow individuals to adjust their route “on the go”, thereby preventing biases
48 arising from misplaced endpoints. Despite these advantages, a unifying approach to simu-
49 late dispersal and assess connectivity using IBMMs is lacking. Considering the large number
50 of subjective decisions entailed by IBMMs, an approach that streamlines and standardizes
51 the application of dispersal simulations to assess connectivity will, however, be critical to
52 safeguard comparability among studies.

53 Here, we propose and exemplify a simple three-step approach for simulating dispersal and
54 assessing landscape connectivity (Figure 1). In step one, we combine GPS movement data
55 of dispersing individuals with habitat covariates to fit a mechanistic movement model via in-
56 tegrated step-selection functions (ISSFs, Avgar et al., 2016). We chose to use ISSFs because
57 the framework not only allows inference on the study species’ habitat kernel (i.e. its habi-
58 tat preferences), but also its movement kernel (i.e. its movement preferences/capabilities)
59 and potential interactions among the two (Avgar et al., 2016; Fieberg et al., 2021). In
60 step two, we use the parametrized movement model to simulate dispersal across the study
61 area. Comparable simulations have already been applied to estimate steady-state utilization
62 distributions of resident individuals (Potts et al., 2013; Signer et al., 2017) and to model
63 landscape connectivity, yet disregarding interdependencies between habitat and movement
64 kernels (Clark et al., 2015; Zeller et al., 2020). Finally, in step three, we convert the simulated
65 trajectories into three complementary connectivity maps; (i) a heatmap revealing frequently
66 traversed areas (e.g. Hauenstein et al., 2019; Zeller et al., 2020), (ii) a betweenness-map
67 delineating dispersal corridors and bottlenecks (e.g. Bastille-Rousseau et al., 2018), (iii) and
68 a map of inter-patch connectivity, depicting the presence and intensity of functional links

69 between habitat patches, as well as the average dispersal duration required to realize those
70 connections (e.g. Gustafson and Gardner, 1996; Kanagaraj et al., 2013).

71 We showcase the application of the proposed approach using GPS movement data col-
72 lected on dispersing African wild dogs (*Lycaon pictus*). The African wild dog is a highly
73 mobile species whose population persistence heavily relies on the availability of large, natural
74 or semi-natural landscapes and a sufficient degree of connectivity among remaining subpop-
75 ulations. Once common throughout sub-Saharan Africa, this species has disappeared from
76 much of its historic range, largely due to human persecution, habitat fragmentation, and
77 disease outbreaks (Woodroffe and Sillero-Zubiri, 2012). Wild dogs typically disperse in
78 single-sex coalitions (McNutt, 1996; Behr et al., 2020) and are capable of dispersing several
79 hundred kilometers (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020).
80 Although previous studies have investigated connectivity for this species using LCPA (Hof-
81 mann et al., 2021a) and CT (Brennan et al., 2020), a more comprehensive and mechanistic
82 understanding of dispersal and connectivity is missing (but see Creel et al., 2020). Nev-
83 ertheless, with about 6,000 free-ranging wild dogs remaining in fragmented subpopulations
84 (Woodroffe and Sillero-Zubiri, 2012), reliable information on dispersal behavior and land-
85 scape connectivity is essential for the conservation of this endangered carnivore. We antic-
86 ipated that a connectivity assessment based upon our three-step approach would overcome
87 several of the conceptual shortcomings of traditional connectivity models, while providing
88 a more detailed view on movement behavior during dispersal its implications for landscape
89 connectivity.

90 **2 Methods**

91 **2.1 Case Study**

92 **2.1.1 GPS Data**

93 We applied the three step approach presented in Figure 1 to GPS movement data from
94 16 dispersing African wild dog coalitions (7 female and 9 male coalitions). This data has
95 been collected between 2011 and 2019 from a free-ranging wild dog population in northern
96 Botswana. During dispersal, GPS collars recorded a fix every 4 hours and regularly trans-
97 mitted data over the Iridium satellite system. To ensure comparable time intervals between
98 GPS fixes, we removed any fixes that were not successfully obtained at the desired 4-hour
99 schedule (allowing for a tolerance of \pm 15 minutes). To prepare the data for step-selection
100 analysis, we converted the fixes ($n = 4'169$) into steps, where each step represented the

101 straight-line movement between two consecutive GPS fixes (Turchin, 1998). We only con-
102 sidered steps with equal step-durations (i.e. 4 hours) for further analysis. We will refer to
103 these steps as “realized steps”. We did not differentiate between sexes, for previous research
104 found little differences between sexes during dispersal (Woodroffe et al., 2019; Cozzi et al.,
105 2020). Additional details on the data collection and preparation can be found in Cozzi et al.
106 (2020) and Hofmann et al. (2021a).

107 **2.1.2 Study Area**

108 Our simulation of dispersal trajectories and assessment of connectivity spanned across the
109 entire Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA, Figure 2a and b)
110 and encompassed a rectangular extent of roughly 1.3 Mio. km². With an area of 520'000
111 km², the KAZA-TFCA is the world’s largest transboundary conservation area and comprises
112 parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia, thus hosting a rich diversity
113 of landscapes, ranging from savannah to grassland and from dry to moist woodland habitats.
114 In its center lies the Okavango Delta, a dominant hydro-geographical feature and the world’s
115 largest flood-pulsing inland delta. Large portions of the KAZA-TFCA are formally protected
116 in the form of national parks (NPs) or other protected areas, yet a considerable portion of
117 the landscape remains human-dominated (e.g. roads, agricultural sites, and settlements).

118 **2.1.3 Habitat Covariates**

119 We represented the physical landscape in our study area by the habitat covariates `water-`
120 `cover`, `distance-to-water`, `woodland-cover`, `shrub/grassland-cover`, and `human-influence`. To
121 render the seasonal dynamics of water-cover for the extent of the Okavango Delta, we
122 applied an algorithm that enabled us to obtain weekly updated raster-layers for `water-`
123 `cover` and `distance-to-water` from MODIS satellite imagery (Wolski et al., 2017; Hofmann
124 et al., 2021a). This algorithm is now implemented in the `floodmapr` package (available on
125 GitHub; <https://github.com/DavidDHofmann/floodmapr>). To ensure a consistent resolu-
126 tion across habitat covariates, we coarsened or interpolated all layers to a resolution of 250
127 m x 250 m. A detailed description of how we prepared each habitat covariate is provided in
128 Hofmann et al. (2021a).

129 We performed all data preparations, spatial computations, and statistical analysis in
130 R, version 4.2.2 (R Core Team, 2022). Some helper functions were written in C++ and
131 imported into R using the Rcpp package (Eddelbuettel and François, 2011; Eddelbuettel,
132 2013; Eddelbuettel and Balamuta, 2018).

¹³³ **2.2 Step 1 - Movement Model**

¹³⁴ We combined the collected GPS data with habitat covariates and used ISSFs (Avgar et al.,
¹³⁵ 2016) to parametrize a mechanistic movement model. More specifically, we paired each
¹³⁶ realized step with a set of 24 randomly generated alternative steps. A realized and its 24
¹³⁷ random steps together formed a stratum that received a unique identifier. As suggested by
¹³⁸ Avgar et al. (2016), we generated random steps by sampling random turning angles from a
¹³⁹ uniform distribution $(-\pi, +\pi)$ and step lengths from a gamma distribution that was fitted
¹⁴⁰ to realized steps (scale $\theta = 6'308$ and shape $k = 0.37$). Note that our approach of sampling
¹⁴¹ turning angles from a uniform distribution does not imply that we assume uniform turning
¹⁴² angles, as we will account for directionality later in the model (Avgar et al., 2016; Fieberg
¹⁴³ et al., 2021).

¹⁴⁴ Along each realized and random step, we extracted values from underlying habitat covari-
¹⁴⁵ ate layers and we computed averages of each covariate along the steps. Besides extracting
¹⁴⁶ *habitat covariates*, we also computed movement metrics that we used as *movement covari-
147 ates* in the ISSF models (Avgar et al., 2016; Fieberg et al., 2021). Specifically, we computed
¹⁴⁸ the step length (`sl`), its natural logarithm (`log(sl)`), and the cosine of the relative turning
¹⁴⁹ angle (`cos(ta)`), which is a measure of directionality (Turchin, 1998), for each step. Because
¹⁵⁰ wild dog activity is low during the hot midday hours (Cozzi et al., 2012), we additionally
¹⁵¹ created the variable `LowActivity`, indicating whether a step was realized during periods of
¹⁵² low wild dog activity (09:00 to 17:00 local time) or high wild dog activity (17:00 to 09:00
¹⁵³ local time). To facilitate model convergence, we standardized all continuous covariates to
¹⁵⁴ a mean of zero and a standard deviation of one. Correlations among covariates were low
¹⁵⁵ ($|r| < 0.6$; Latham et al., 2011), so we retained all of them for modeling.

¹⁵⁶ To contrast realized steps (scored 1) and random steps (scored 0), we assumed that
¹⁵⁷ animals assigned a selection score $w(x)$ to each step (Equation 1; Fortin et al., 2005), where
¹⁵⁸ $w(x)$ depended on the step's associated covariates (x_1, x_2, \dots, x_n) and on the animal's relative
¹⁵⁹ selection strengths (Avgar et al., 2017) towards these covariates $(\beta_1, \beta_2, \dots, \beta_n)$:

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

¹⁶⁰ The probability of a step i being realized was then contingent on the step's selection score,
¹⁶¹ as well as on the selection scores of all other steps in the same stratum:

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

162 To estimate relative selection strengths (i.e. the β -coefficients), we used mixed effects
163 conditional logistic regression analysis, implemented through the r-package `glmmTMB` (Brooks
164 et al., 2017). The implementation of conditional logistic regression has been proposed by
165 Muff et al. (2020) and allows to model random slopes. The method requires to fix the vari-
166 ance of the stratum specific intercept to a large value, so we fixed it to an arbitrary high
167 value of 10^6 and used disperser identity to model random slopes for all covariates.

168 Our movement model was based on a habitat selection model that was previously devel-
169 oped for dispersing wild dogs (hereafter referred to as *base model*, Hofmann et al., 2021a).
170 In the base model, no interactions among habitat covariates and movement covariates were
171 considered, so we here expanded the model and allowed for such interactions, acknowledging
172 that movement preferences during dispersal could depend on habitat conditions (details in
173 Appendix A1). To determine the most parsimonious movement model among model can-
174 didates, we ran stepwise forward model selection based on Akaike's Information Criterion
175 (AIC, Burnham and Anderson, 2002). More specifically, we started with the base model
176 and iteratively increased model complexity by adding all possible interactions between move-
177 ment and habitat covariates. Given that the focus of our analysis lied on predicting dispersal
178 patterns and all model candidates were biologically intuitive, we deemed the use of model
179 selection appropriate. However, caution should be employed if causal relationships are of
180 interest, as model selection may lead to biased parameter estimate (Whittingham et al.,
181 2006). We validated the predictive power of the most parsimonious model using k-fold
182 cross-validation for case-control studies as described in Fortin et al. (2009). This valida-
183 tion attests significant prediction ability to the movement model if the model outperforms a
184 random guess and systematically assigns low ranks (high selection scores) to observed steps
185 (details in Appendix A2).

186 2.3 Step 2 - Dispersal Simulation

187 We used the most parsimonious movement model to simulate individual dispersal trajectories
188 across the study area. The simulation of a dispersal trajectory resembled an “inverted”
189 ISSF and was set up as follows. (1) We defined a source point and assumed a random initial
190 orientation of the simulated animal. (2) Starting from the source point, we generated 25
191 random steps by sampling turning angles from a uniform distribution $(-\pi, +\pi)$ and step
192 lengths from our fitted gamma distribution. (3) Along each random step, we extracted and
193 averaged values from the habitat covariate layers and we computed the movement metrics
194 sl , $\log(sl)$, and $\cos(ta)$. To ensure compatible scales with the fitted movement model, we

195 standardized covariate values using means and standard deviations from the empirical data.
196 (4) We applied the parametrized movement model to predict the selection score $w(x)$ for each
197 step using Equation 1 and we converted predicted scores into probabilities using Equation 2.
198 (5) We randomly sampled one of the generated random steps based on assigned probabilities
199 and determined the animal's new position. We repeated steps (2) to (5) until 2,000 steps
200 were realized and we repeated the simulation until a total of 80'000 dispersal trajectories
201 was reached.

202 As source points for the simulations, we distributed 50,000 points at random locations
203 inside protected areas that were large enough to host an average size wild dog home range
204 (i.e. > 700 km²; Pomilia et al., 2015). We placed another 30,000 points randomly inside the
205 buffer zone, mimicking potential immigration into the study area (Figure S1).

206 To mitigate edge effects and to deal with random steps leaving the study area, we followed
207 Koen et al. (2010) and artificially expanded all covariate layers by a 100 km wide buffer
208 zone. Within the buffer zone, we randomized covariate values by resampling values from the
209 original covariate layers. Through this buffer zone, simulated dispersers were able to leave
210 and re-enter the main study area. In cases where random steps crossed the outer border of
211 this buffer zone, we resampled steps until they fully lied within the buffer zone, essentially
212 forcing simulated individuals to remain within the expanded study area.

213 To ensure reliable connectivity estimates, we determined the number of simulated dis-
214 persal trajectories required to reach a “steady state”. For this purpose, we distributed 1,000
215 rectangular “checkpoints”, each with an arbitrary extent of 5 km x 5 km, at random co-
216 ordinates within the study area (excluding the buffer). We then determined the relative
217 frequency at which each checkpoint was traversed by simulated dispersal trajectories (here-
218 after referred to as relative traversal frequency) as we gradually increased the number of
219 simulated trajectories from 1 to 50'000. To assess variability in the relative traversal fre-
220 quency, we repeatedly subsampled 100 times from all 50'000 trajectories and computed the
221 mean traversal frequency across replicates, as well as its 95% prediction-interval for each
222 checkpoint. We considered connectivity to have reached a steady state once the width of
223 the prediction-interval dropped below a value of 0.01 for all checkpoints.

224 **2.4 Step 3 - Connectivity Maps**

225 **2.4.1 Heatmap**

226 To identify dispersal hotspots within the study area, we created a heatmap indicating the
227 absolute frequency at which different areas were traversed by simulated dispersal trajectories

(e.g. Hauenstein et al., 2019; Zeller et al., 2020). Specifically, we rasterized all simulated trajectories onto a raster with 1 km x 1 km resolution and tallied resulting layers into a single map. This procedure ensured that every trajectory was only counted once, even if it traversed the same raster-cell multiple times, thus reducing potential biases caused by individuals that were surrounded by unfavorable habitat and “moved in circles”. To achieve high performance rasterization, we used the R-package `terra` (Hijmans, 2021). For a subset of the study area, we also generated heatmaps at 250 m x 250 m, yet found little qualitative differences to the coarser resolution, thus suggesting the choice of 1 km x 1 km to be appropriate.

2.4.2 Betweenness Map

To pinpoint movement corridors and bottlenecks, we converted simulated trajectories into a network and calculated betweenness scores for all raster-cells in the study area (Bastille-Rousseau et al., 2018). Betweenness is a pertinent metric for connectivity as it measures how often a specific network-node (in our case a raster-cell) lies on a shortest path between any other pair of nodes (Bastille-Rousseau et al., 2018). To convert simulated trajectories into a network, we followed Bastille-Rousseau et al. (2018) and overlaid the study area (including the buffer) with a raster containing 2.5 km x 2.5 km raster-cells, where the center of each raster-cell served as node in the final network. To identify edges (i.e. connections) between the nodes, we used the simulated trajectories and determined all transitions occurring from one cell to another, as well as the frequency at which those transitions occurred (see also Appendix A4). This resulted in an edge-list that we translated into a weighted network using the r-package `igraph` (Csardi and Nepusz, 2006). The final weight of each edge was determined by the frequency of transitions, yet because `igraph` handles edge weights (ω) as costs, we inverted the traversal-frequency through each raster-cell by applying $\omega = \frac{\text{mean}(\text{TraversalFrequency})}{\text{TraversalFrequency}_i}$. Consequently, regularly used edges received small weights (i.e. low costs) and vice versa. We used the weighted network to calculate betweenness scores for all network nodes.

2.4.3 Inter-Patch Connectivity Map

To examine the presence and intensity of functional links (i.e. connections) between patches within the study area, we calculated inter-patch connectivity (e.g. Gustafson and Gardner, 1996, Kanagaraj et al., 2013). For this, we computed the relative frequency at which dispersers originating from one patch successfully moved into another patch. We considered

260 movements between patches as successful if an individual's dispersal trajectory originating
261 from the source patch intersected with the target patch at least once. For each trajectory we
262 also recorded the number of steps required to reach the first intersection with the respective
263 patch, allowing us to compute the average dispersal durations from one patch to another.
264 In summary, we determined *if* and *how often* dispersers moved between certain patches, as
265 well as *how long* individuals had to move to make these connections. In our case study,
266 we used NPs as patches to determine inter-patch connectivity, hence we'll use the terms
267 interchangeably from here on. The decision to focus on NPs was purely out of simplicity
268 and should not imply that dispersal between other areas is impossible.

269 **2.4.4 Validation**

270 To validate our predictions of connectivity, we utilized additional dispersal data that was
271 collected on eight dispersing coalitions between 2019 and 2022 (totalling to 2'668 GPS
272 locations). We used a path selection function (PSF, Cushman and Lewis, 2010) to assess
273 if observed dispersal trajectories followed areas of high predicted connectivity. Similar to
274 SSF, PSF enables to detect selection for certain features by comparing observed paths to
275 randomly generated paths. Here, we paired each observed path with 50 random paths
276 that we generated by randomly rotating and shifting observed paths by a random angle
277 $\alpha \sim U(-\pi, +\pi)$ and a random distance $d \sim U(0 \text{ km}, 50 \text{ km})$. Along each path, we then
278 extracted connectivity values from the heatmap (see above) generated after 68, 125, 250,
279 500, and 2'000 simulated steps, respectively. Finally, we ran conditional logistic regression
280 to contrast observed and random paths. In case of systematic selection for high-connectivity
281 areas, the regression coefficients from the corresponding conditional logistic regression model
282 should be positive.

283 **3 Results**

284 The most parsimonious movement model consisted of movement covariates, habitat covari-
285 ates, as well as several of their interactions, thus suggesting that movement behavior during
286 dispersal depended on habitat conditions (Figure 3a, Table S1 and Table S2). Although
287 multiple models received an AIC weight > 0 (Table S1), we only considered results from
288 the most parsimonious model for simplicity. This decision only marginally influenced sub-
289 sequent steps as all models with positive AIC weights retained similar covariates (Table
290 S1). The k-fold cross-validation showed that the final model substantially outperformed a
291 random guess and provided reliable predictions (i.e. confidence intervals of $\bar{r}_{s,realized}$ and

292 $\bar{r}_{s,random}$ did not overlap). Moreover, the model correctly assigned high selection scores
293 to realized steps (Figure 3b), indicating a good fit between predictions and observations.
294 As can be taken from the Spearman rank correlation coefficient, the inclusion of several
295 interactions between movement and habitat covariates significantly improved model per-
296 formance ($\bar{r}_{s,realized} = -0.65; 95\% - CI = [-0.67, -0.64]$), compared to the base model
297 ($\bar{r}_{s,realized} = -0.55; 95\% - CI = [-0.57, -0.52]$; Hofmann et al., 2021a). Our validation
298 of the resulting connectivity maps using independent dispersal data showed that dispersers
299 preferentially followed areas of high predicted connectivity, as coefficients from the PSF
300 models were all significantly greater than zero (Figure 3c). The movement model thus
301 successfully predicted functional connectivity.

302 Plots that aid with the interpretation of the most parsimonious movement model are pro-
303 vided in Figure S3 and suggest that, under average conditions, dispersing wild dogs avoided
304 moving through water, woodlands, and areas dominated by humans, but preferred moving
305 across shrublands or grasslands (Figure 3a). Dispersers realized shorter steps (indicating
306 slower movements) in areas covered by water or woodland, while realizing larger steps in
307 areas dominated by shrubs or grass (Figure 3a). We found a particularly large effect for the
308 variable **LowActivity**, suggesting that dispersing wild dogs moved substantially faster during
309 twilight and at night (i.e. between 17:00 and 09:00 o'clock; Figure 3a). Although dispersers
310 revealed a preference for directional movements (i.e. low turning angles), especially when
311 moving quickly, they did less so in proximity to humans or water, resulting in more tortuous
312 movements in such areas (Figure 3a).

313 3.1 Dispersal Simulation

314 Dispersal simulations based on the most parsimonious movement model proved useful for
315 assessing landscape connectivity. Of the 50'000 simulated dispersal trajectories that orig-
316 inated from the main study area, only 4.5% reached a map boundary, suggesting that we
317 successfully mitigated biases from boundary effects. Moreover, our examination of the rel-
318 ative traversal frequency across all checkpoints showed that the relative traversal frequency
319 reached a steady state after 10'500 simulated dispersal trajectories (Figure S4). Although
320 variability in the relative traversal frequency kept decreasing as we increased the number of
321 simulated dispersers, the marginal benefit of simulating additional trajectories diminished
322 quickly (Figure S4).

323 **3.2 Heatmap**

324 The heatmap (Figure 4), which resulted from the summation of all simulated dispersal tra-
325 jectories, allowed us to pinpoint areas that were frequently visited and enabled us to compare
326 areas inside and outside the KAZA-TFCA borders with respect to the intensity at which they
327 were used for dispersal. For instance, we could deduct that areas inside the KAZA-TFCA
328 were frequently traversed by dispersers (median traversal frequency inside KAZA-TFCA
329 = 166, IQR = 274, Figure S7a), whereas areas beyond the KAZA-TFCA boundary were
330 comparatively rarely visited (median traversal frequency outside KAZA-TFCA = 61, IQR
331 = 133, Figure S7a). Most notably, the region in northern Botswana south of the Linyanti
332 swamp appeared to serve as highly frequented dispersal hotspot (median traversal frequency
333 = 987, IQR = 558). Aside from revealing movement hotspots, the heatmap also provided in-
334 formation on areas that appeared to hinder movement. For example, extensive water bodies,
335 such as the Okavango Delta, the Makgadikgadi Pan, and the Linyanti swamp, substantially
336 restricted dispersal movements and limited realized connectivity inside the KAZA-TFCA.
337 Similarly, the landscapes of Zambia and Zimbabwe were only rarely used for dispersal,
338 even within the KAZA-TFCA boundaries (Figure S8a). Despite the fact that the heatmap
339 improved our understanding of the frequency at which areas were traversed by simulated
340 dispersers, it seemed impractical to pinpoint dispersal corridors.

341 **3.3 Betweenness**

342 The betweenness map (Figure 5) revealed several distinct dispersal corridors that run across
343 the study area. In comparison to the heatmap, the betweenness map was less biased towards
344 areas with many dispersers and pronounced narrower, more linear routes that were used by
345 simulated individuals to move between regions. Again, northern Botswana emerged as a
346 wild dog dispersal corridor that connected more remote regions in the study area. Towards
347 east, the extension of this corridor ran through Chobe NP into Hwange NP. From there,
348 a further extension connected to Matusadona NP in Zimbabwe. Northwest of the Linyanti
349 ecosystem, a major corridor expanded into Angola, where it split and finally traversed over
350 a long stretch of unprotected area into Zambia's Kafue NP. Several additional corridors
351 with lower betweenness scores emerged, yet most of them ran within the KAZA-TFCA
352 boundaries (median betweenness inside KAZA-TFCA = 6.947×10^6 , IQR = 54.311×10^6 ,
353 Figure S7b). Consequently, only few corridors directly linked the peripheral regions of the
354 KAZA-TFCA and passed through unprotected areas outside its borders (mean betweenness
355 outside KAZA-TFCA = 2.685×10^6 , IQR = 9.891×10^6 , Figure S7b).

356 **3.4 Inter-Patch Connectivity**

357 The inter-patch connectivity map showed that the relative frequency at which simulated
358 dispersal trajectories moved from one patch to another varied, as did the average dispersal
359 duration between patches (Figure 6). The map thereby completed the picture on connectiv-
360 ity and provided valuable insights into the frequency and duration of connections between
361 patches. For some patches, we also detected imbalances between the number of incoming
362 and outgoing links, hinting at possible source-sink dynamics. From Chobe NP, for instance,
363 510 individuals reached the Moremi NP, yet the opposite route was only realized by 340
364 individuals. Relative to the number of simulated individuals, however, these numbers corre-
365 spond to fractions of 50% and 68%, respectively. Overall, inter-patch connectivity between
366 patches in Angola, Namibia, Botswana, and Zimbabwe appeared to be high; between 54%
367 and 87% of individuals originating from a patch in these countries successfully moved into
368 at least one other patch (Figure S9a). Conversely, only 19% of the dispersers leaving from
369 a patch in Zambia managed to find their way into some other patch (Figure S9b). Prior
370 to reaching another patch, individuals from Angola, Namibia, Botswana, Zimbabwe, and
371 Zambia had to move for an average of 630, 640, 940, 1045, and 890 steps, respectively. Fur-
372 thermore, it appeared that the corridor previously identified on Figure 6 between Angola’s
373 NPs and the Kafue NP in Zambia is only rarely realized.

374 **4 Discussion**

375 Here, we presented a simple three-step approach to assess landscape connectivity via simu-
376 lated dispersal trajectories and we demonstrated its application using empirical data from
377 a free-ranging population of African wild dogs. In step one, we used ISSFs to parametrize a
378 fully mechanistic movement model describing how individuals move through the landscape.
379 Aside from rendering habitat preferences, the model also encapsulated movement prefer-
380 ences and potential interactions between movement and habitat preferences. In step two,
381 we employed the movement model and simulated dispersal trajectories across the landscape.
382 In comparison to more traditional connectivity modeling techniques, such simulations re-
383 quire fewer unrealistic assumptions about dispersal and enable the derivation of multiple
384 connectivity metrics. Hence, in step three, we translated the simulated trajectories into
385 three complementary connectivity maps, each emphasizing a different aspect of landscape
386 connectivity (e.g. frequently traversed areas, critical dispersal corridors and bottlenecks,
387 and the presence and intensity of functional links between suitable patches).

Results on the habitat kernel from our model showed that dispersers avoided areas dominated by humans and covered by water, but selected for regions with open grassland in the vicinity to water bodies. This largely complied with previous studies that investigated habitat selection by dispersing wild dogs (Davies-Mostert et al., 2012; Masenga et al., 2016; Woodroffe et al., 2019; O'Neill et al., 2020; Hofmann et al., 2021a). However, instead of merely generating insights on dispersers' habitat preferences, the ISSF framework also permitted us to model several additional complexities common to dispersal. For instance, by including the interactions $\cos(\text{ta}):sl$ and $\cos(\text{ta}):\log(sl)$, we could accommodate that dispersers exhibit turning angles that are correlated with step lengths, meaning that turning angles tend to be smaller when individuals move fast. Although similar autocorrelations could be incorporated by sampling step lengths and turning angles from copula probability distributions (Hodel and Fieberg, 2022), the ISSF framework allowed us to conveniently model such peculiarities directly in the movement model. While we only considered first order autocorrelation, i.e. correlation between two consecutive steps, higher order autocorrelation is conceivable and may be desirable to model (Dray et al., 2010; McClintock et al., 2012). However, this will require vast amounts of GPS data that are not interrupted by missing fixes; something that is rarely achieved in reality (Graves and Waller, 2006). The power and flexibility of ISSFs to model additive effects between habitat and movement covariates (Avgar et al., 2016; Signer et al., 2017) furthermore allowed us to formally capture that dispersing wild dogs move slower and more tortuous in areas covered by water. Such effects may be of limited interest and novelty from a biological perspective, yet they are important to be considered when simulating dispersal, in particular if one is interested in estimating dispersal durations between habitat patches. Overall, the inclusion of interactions between habitat and movement covariates in our movement model lead to a significant improvement in predictive performance compared to an earlier model that omitted such interactions (Hofmann et al., 2021a).

Each of the three connectivity maps derived from simulated dispersal trajectories highlighted a different aspect of landscape connectivity. The heatmap was most suitable for pinpointing frequently traversed areas and showed that an exceptionally large number of dispersers moved through the regions of the Moremi NP and the Chobe NP in northern Botswana. Hofmann et al. (2021a) previously identified the same area as potential dispersal hotspot using LCPA, however, following their analysis it was not clear whether this was the consequence of the central location of the region and connections being enforced between predefined start and endpoints. Contrary to LCPA, a simulation-based approach as pre-

sented here does not require predefined endpoints, as endpoints emerge naturally from the simulated dispersal trajectories. This is especially useful for dispersal studies, where known endpoints are usually an unrealistic assumption (Elliot et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020). The fact that the same region was emphasized using vastly different methods to model connectivity thus reinforces our notion that the area is of exceptional importance to dispersing wild dogs. Because simulated individuals are not forced to move towards certain endpoints, a simulation-based approach not only lends itself to study landscape connectivity, but also to uncover potential dispersal traps (Van der Meer et al., 2014) or areas with a high susceptibility for human wildlife conflicts (Cushman et al., 2018). Using independent dispersal data we showed that dispersers indeed followed areas of high predicted connectivity. Importantly, however, these predictions were based on a scenario of a relatively extended flood, which may not have accurately represented environmental conditions for dispersers moving through areas affected by the flood. Accounting for such differences would have improved the predictive performance of our model.

In contrast to the heatmap, the betweenness map emphasized relatively narrow and linear movement routes. It thus facilitated the identification of discrete movement corridors. While in some cases both the heatmap and the betweenness map attributed a high importance to the same areas (e.g. northern Botswana), little consensus was found for other regions. For instance, the stretch of unprotected land between Luengue-Luiana NP in Angola and the Kafue NP in Zambia was characterized by a high betweenness-scores, yet it only received low scores on the heatmap. This is due to the differential way in which the maps view connectivity. While the heatmap attributes a high connectivity to areas that are frequently traversed, it does not distinguish between areas that truly bring individuals into other regions of the study area and regions that lead into ecological traps. The converse is true on the betweenness map, as it strictly highlights regions that promote movement into other areas of the landscape and thus promote gene-flow. However, neither of the two maps provides insights into functional links between distinct habitat patches or how connections depend on the dispersal duration. For this reason, we also produced a map of inter-patch connectivity. This map depicted the frequency at which simulated individuals moved between patches as well as the average dispersal duration (in steps) required to realize them. Calculating dispersal durations was only possible because trajectories were simulated spatially and temporally explicitly, something that is currently unfeasible with LCPA or CT. An explicit representation of time enables answerings questions such as: “*How long will it take a disperser to move from A to B?*” or “*Is it possible for a disperser to move from A to B within*

456 *X days?*”. Moreover, it yields opportunities to incorporate seasonality and to investigate
457 whether dispersal corridors exist seasonally or all-year round (*dynamic connectivity*; Zeller
458 et al., 2020). With LCPA or CT, seasonality can currently only be incorporated through
459 the preparation of multiple permeability surfaces on which the same connectivity model is
460 repeatedly applied (e.g. Osipova et al., 2019). With simulations from ISSFs, in contrast, the
461 environment could change “as the dispersers move”, so that simulated trajectories would
462 dynamically respond to seasonal fluctuations in the environment.

463 Our approach enabled us to translate a simple set of small-scale behavioral rules into
464 large scale patterns of connectivity, something previously deemed computationally unfea-
465 sible, yet critical for linking structural and functional connectivity (Doerr et al., 2011).
466 Structural connectivity focuses purely on the spatial arrangement of suitable habitat in the
467 landscape, whereas functional connectivity also takes into account a species dispersal ability
468 and behavioral response to the landscape (Tischendorf and Fahrig, 2000). Functional con-
469 nectivity is of greater interest to conservation scientists, yet is difficult to quantify (Baguette
470 et al., 2013), which is why structural connectivity often serves as surrogate (Doerr et al.,
471 2011; Fattebert et al., 2015). LCPA and CT incorporate functional aspects of connectivity
472 through the permeability surface, which reflects a species habitat preferences and thus ren-
473 ders behavioral impacts of the landscape on the focal species. Aside from rendering habitat
474 preferences, our model also integrates peculiarities of the focal species movement behavior,
475 thus adding further insights on functional connectivity. In addition, we successfully used in-
476 dependent dispersal data to prove that our predictions of connectiviy aligned with observed
477 functional connectivity patterns.

478 Despite the many benefits and great flexibility offered by simulations from ISSFs, one
479 must also be aware of the associated limitations. For example, while our approach of simulat-
480 ing dispersal proved useful to assess landscape connectivity, it was computationally costly.
481 Simulating 80'000 dispersal trajectories for 2'000 steps across the KAZA-TFCA required
482 five days of computation on a regular desktop machine (AMD Ryzen 7 2700X octa-core
483 processor with 3.6 GHz, 64 GB of RAM). The long simulation time was primarily caused
484 by the massive extent of the study area considered (ca. 1.3 Mio km²), the large number of
485 simulated trajectories, and the fact that we extracted covariates along each step, rather than
486 just at their start or endpoints. Most connectivity studies focus on smaller study areas (e.g.
487 Kanagaraj et al., 2013; Clark et al., 2015; McClure et al., 2016; Abrahms et al., 2017; Zeller
488 et al., 2020) and will therefore require fewer simulations and achieve faster simulation times
489 (given the same spatial resolution). We also believe that fewer simulated trajectories will

often suffice, as the relative traversal frequency by simulated trajectories through randomly placed checkpoints across our study area converged already after 10'500 runs. The exact number of required simulations to achieve reliable estimates of connectivity will, of course, vary depending on the structure of the landscape and the dispersal capabilities of the focal species (Gustafson and Gardner, 1996). For species that disperse short distances through homogeneous environments, few simulations may suffice to gauge connectivity, whereas for species that disperse over long distances through heterogeneous habitats, a large number of simulations will be required to sufficiently explore the spectrum of possible routes. Finally, it may often suffice to extract covariates at each step's start or endpoints, thus considerably speeding up simulation times (Signer et al., 2017).

Aside from the computational requirements, simulations further entail several non-trivial but important modeling decisions. On four such decisions we would like to further elaborate: (1) the number of simulated individuals, (2) the location of source points, (3) the simulated dispersal duration, and (4) the behavior at map boundaries.

(1) When simulating dispersal trajectories, the modeler needs to decide on the number of simulated individuals. A higher number is always desirable, as each additional trajectory provides information about landscape connectivity. However, each additional simulation imposes computational costs, so a trade-off needs to be managed. Signer et al. (2017) proposed to handle the trade-off by simulating additional individuals only until the metrics of interest converge towards a steady state. Here, we used the relative traversal frequency as target metric and found that it converged already after 10'500 simulated individuals. The exact number of required individuals might, however, vary depending on the employed target metric and the anticipated connectivity map. More sophisticated target metrics than the relative traversal frequency, preferably tailored to different connectivity maps, need to be developed in the future.

(2) To initiate dispersers, a modeler needs to provide a set of source points at which the virtual dispersers are released. We placed source points within protected areas large enough to sustain viable wild dog populations, implicitly assuming that wild dogs primarily survive in large, formally protected areas (Davies-Mostert et al., 2012; Woodroffe and Sillero-Zubiri, 2012; Van der Meer et al., 2014). Moreover, we lacked precise knowledge about the distribution and abundance of wild dogs across protected areas, so we placed source points randomly within them. In cases where more detailed data about the distribution and abundance of the focal species are available, source points could be distributed accordingly. Alternatively, source points could be distributed homogeneously but later be weighted when

524 computing connectivity metrics. In any case, the challenge of selecting meaningful source
525 points is not unique to individual-based simulations but also applies to LCPA and CT.

526 (3) The use of ISSFs to simulate dispersers requires deciding on the number of simulated
527 steps (i.e. the simulated dispersal durations). If sufficient dispersal data of the focal species
528 has been collected, dispersal durations could be sampled from observed dispersal events or
529 from parametric distributions fit to observed data. Due to the low number of observed
530 dispersal events, we opted against this solution and instead simulated all individuals for
531 2,000 steps, which was at the upper end of observed dispersal durations in African wild
532 dogs (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020; Hofmann et al.,
533 2021a). This approach had the advantage that it allowed us to systematically shorten the
534 simulated trajectories after their simulation and thereby to investigate the sensitivity of our
535 results with respect to exact dispersal durations (Figures S5 and S6).

536 (4) Unless simulated dispersal trajectories are strongly drawn towards a point of attraction
537 inside the study area(e.g. Signer et al., 2017), some trajectories will inevitably approach
538 one of the map boundaries. In this case, one or more of the generated random steps might
539 leave the study area, making it impossible to compute a selection score. A possible solution
540 is to simply terminate the simulation of the affected trajectory, assuming that the simulated
541 individual has left the study area. However, this approach might produce ambiguous results
542 in cases where many individuals are released near map borders, especially because already a
543 single random step leaving the study area will break the simulation, thus resulting in biased
544 connectivity estimates along map borders. Rather than breaking the simulation, we created
545 a buffer zone (Koen et al., 2010) and resampled random steps until they fully lied within
546 the study area. This proved to be an effective solution to overcome problems with boundary
547 effects.

548 In summary, we proposed and applied a simple three-step approach that relies on ISSF-
549 analysis and enables the simulation of dispersal trajectories and the assessment of landscape
550 connectivity. The proposed approach overcomes several of the conceptual shortcomings
551 inherent to LCPA and CT, such as the assumption of known endpoints, and provides a highly
552 flexible tool for investigating connectivity. Moreover, the simulation of dispersal opens up
553 new avenues for incorporating interactions between habitat and movement covariates and
554 provides the foundation for a rich suite of complementary connectivity measures. With
555 this work, we hope to have sparked interest in the application, optimization, or creation
556 of methods to investigate dispersal and connectivity via individual-based simulations, while
557 at the same time stressing some of the non-trivial modeling decisions involved. We also

558 hope to provide a useful framework that helps unifying and streamlining the application of
559 individual-based simulations for assessing landscape connectivity.

560 **5 Authors' Contributions**

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

565 **6 Data Availability**

566 GPS movement data of dispersing wild dogs is available on dryad (Hofmann et al., 2021b).
567 Access to R-scripts that exemplify the application of the proposed approach using simulated
568 data are provided through Github (<https://github.com/DavidDHofmann/DispersalSimulation>).
569 In addition, all codes required to reproduce the African wild dog case study will be made
570 available through an online repository at the time of publication.

571 **7 Acknowledgements**

572 We thank the Ministry of Environment and Tourism of Botswana for granting permission
573 to conduct this research. We thank C. Botes, I. Clavadetscher, and G. Camenisch for
574 assisting with wild dog immobilizations. We also thank B. Abrahms for sharing her data
575 of three dispersing wild dogs. Furthermore, we would like to thank Johannes Signer for
576 assisting with the simulation algorithm. This study was funded by Albert-Heim Foundation,
577 Basler Stiftung für Biologische Forschung, Claraz Foundation, Idea Wild, Jacot Foundation,
578 National Geographic Society, Parrotia Stiftung, Stiftung Temperatio, Wilderness Wildlife
579 Trust, Forschungskredit of the University of Zürich (grant no. FK-21-091), and a Swiss
580 National Science Foundation grant (no. 31003A_182286) to A. Ozgul.

581 **8 Conflict of Interest**

582 All authors declare that they have no conflicts of interest.

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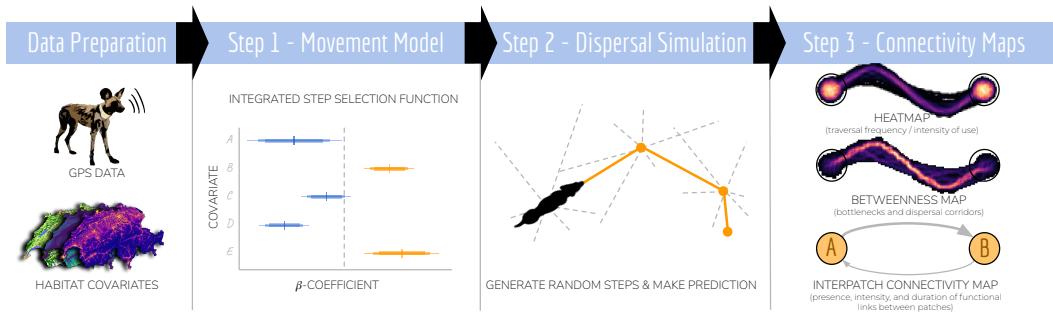


Figure 1: Flowchart of the simulation-based connectivity analysis. First, GPS data and habitat covariates must be collected. The combined data is then analyzed using an integrated step selection model (step 1). The parametrized model is then treated as an individual-based movement model and used to simulate dispersal trajectories (step 2). Ultimately, simulated trajectories are translated into a set of maps that are pertinent to landscape connectivity (step 3). This includes a heatmap, indicating the traversal frequency across each spatial unit of 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.

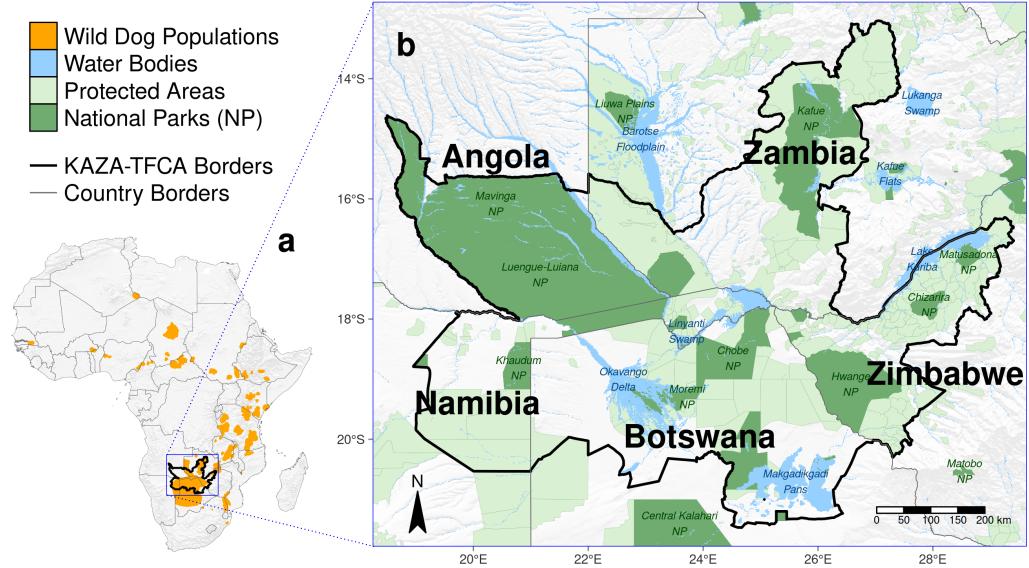


Figure 2: Illustration of the study area in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA which comprises parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. Data on remaining wild dog populations (orange) has been sourced from Woodroffe and Sillero-Zubiri (2012). (b) The KAZA-TFCA represents the world's largest terrestrial transfrontier conservation area and covers a total area of 520'000 km². Its main purpose is to re-establish connectivity between already-existing NPs (dark green) and other protected areas (light green).

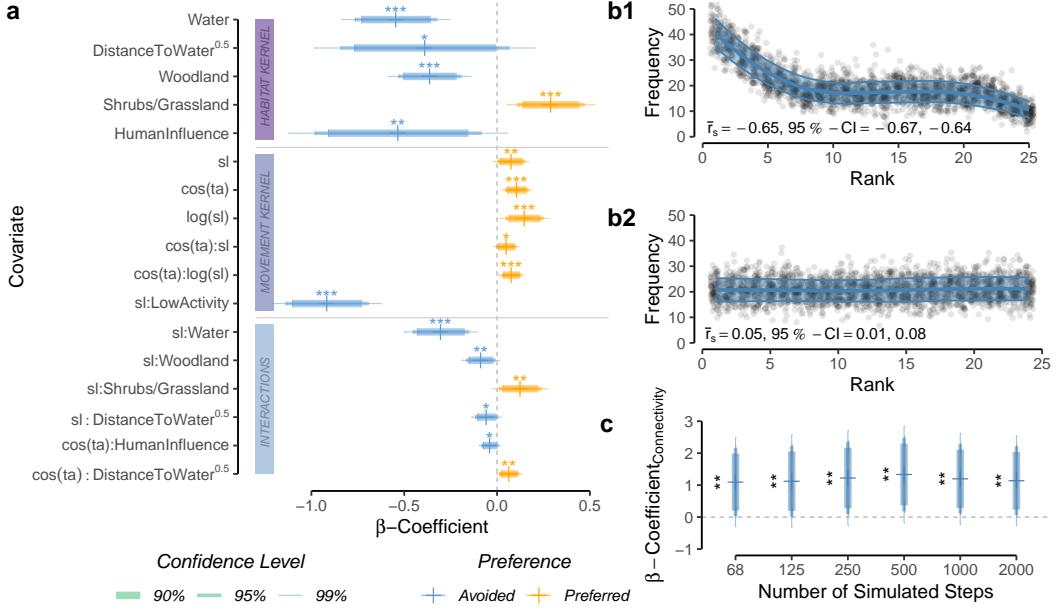


Figure 3: (a) Most parsimonious movement model for dispersing wild dogs. The model comprises a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% confidence-intervals for the respective β -coefficients. Significance codes: * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$. (b) Results from the k-fold cross-validation procedure. Subfigure b1 shows rank frequencies of realized steps according to model predictions with known preferences, whereas subfigure b2 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 outperformed a random guess (b2) and frequently assigned low ranks (i.e. high selection scores) to realized steps but only rarely high ranks (i.e. low selection scores). (c) Results from the PSF analysis using independent dispersal data show that dispersers preferably moved through areas where our heatmaps predicted high connectivity. Results are shown for heatmaps realized after 68, 125, 250, 500, and 2'000 simulated steps, respectively.

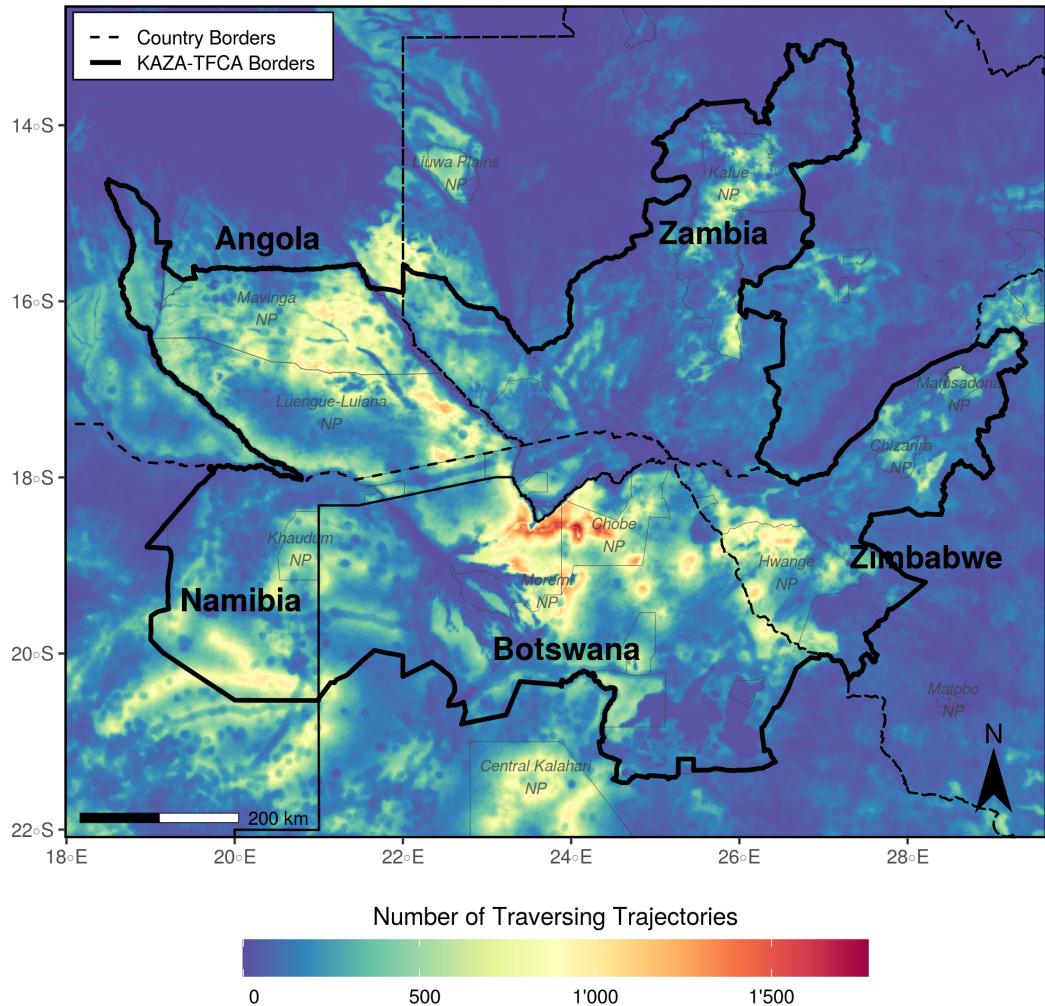


Figure 4: Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step-selection model that we fitted to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied all simulated trajectories. Consequently, the map highlights areas that are frequently traversed. For spatial reference we plotted a few selected NPs (dark gray). Additional heatmaps showing the traversal frequency when individuals move fewer than 2'000 steps are provided in Figure S5.

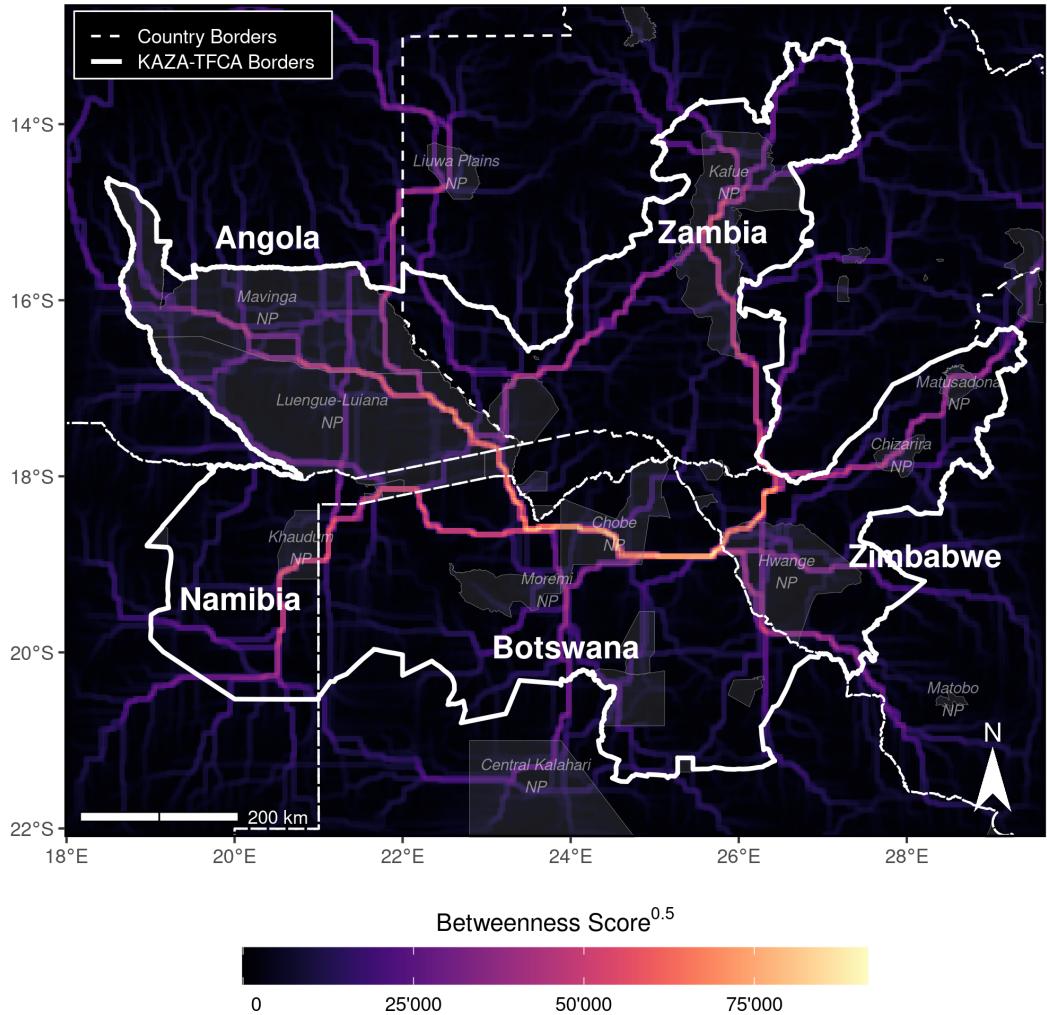


Figure 5: Map of betweenness scores, highlighting distinct dispersal corridors and potential bottlenecks across the extent of the KAZA-TFCA. Betweenness measures the number of shortest paths traversing through each node (raster-cell). Hence, a high betweenness score indicates that the respective area is exceptionally important for connecting different regions in the study area. The metric is therefore useful to pinpoint discrete movement corridors (Bastille-Rousseau et al., 2018). Note that we square-rooted betweenness scores to improve visibility of corridors with comparably low scores. Additional betweenness maps showing betweenness scores when individuals move fewer than 2'000 steps are provided in Figure S6.

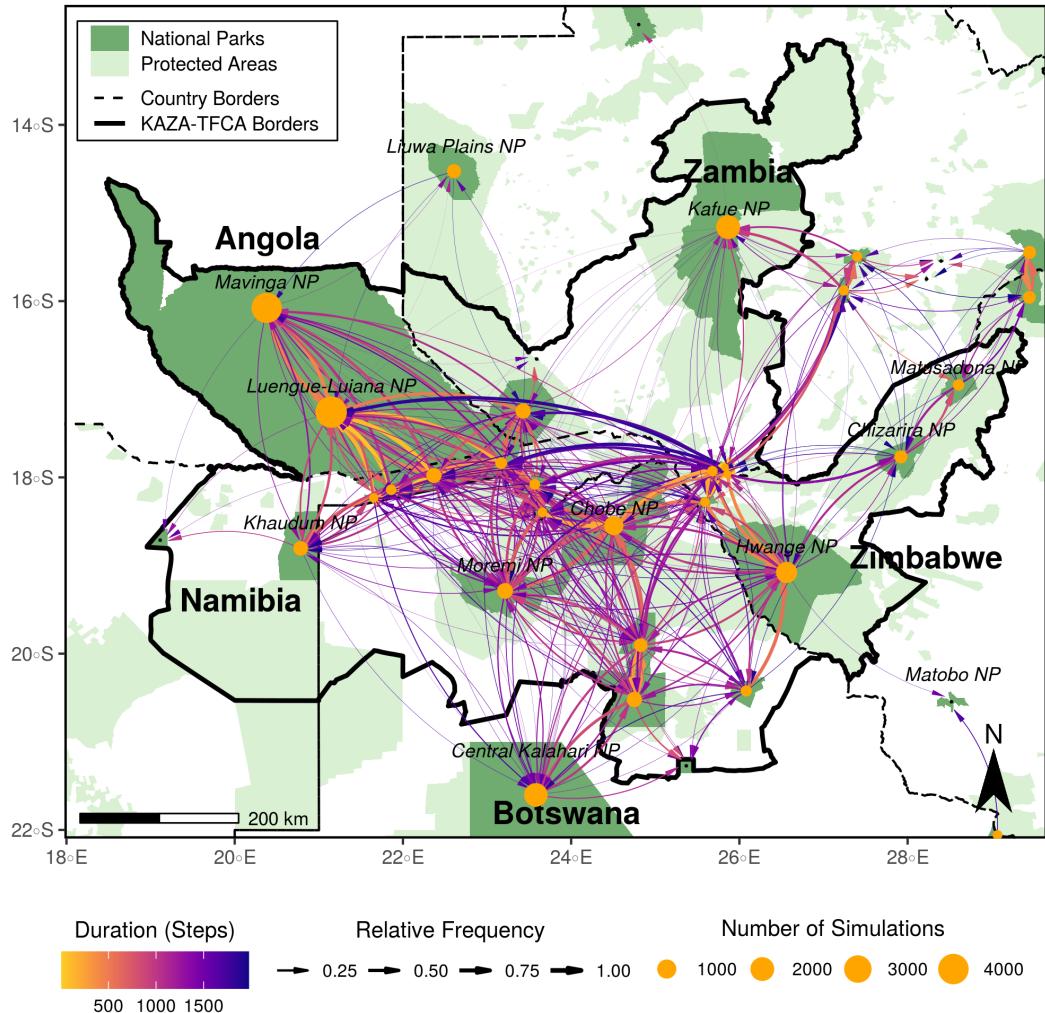


Figure 6: Map of inter-patch connectivity in relation to dispersal duration, highlighting connections between NPs (dark green). Yellow bubbles represent the center of the different NPs and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent NPs that were smaller than 700 km^2 and therefore were not used as source areas. Arrows between NPs illustrate between which NPs the simulated dispersers successfully moved and the color of each arrow shows the average number of steps (i.e. 4-hourly movements) that were necessary to realize those connections. Additionally, the line thickness indicates the relative number of dispersers originating from a NP that realized those connections.