

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

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## Abstract

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. Least-cost analysis assumes that animals move towards a known endpoint and are knowledgeable about the most favorable route. Circuit theory presumes a complete random walk and fails to incorporate directional persistence. While these assumptions can be relaxed by explicitly simulating dispersal trajectories across the landscape, a unified approach for such simulations is lacking.

Here, we present a simple three-step approach to simulate dispersal and to assess connectivity using empirical GPS movement data and a set of habitat covariates. In step one, 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 a set of 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. As a case study, we apply the three-step approach to GPS data collected on dispersing African wild dogs (*Lycaon pictus*) inhabiting the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA) in southern Africa.

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. By explicitly simulating individuals, this approach not only requires fewer unrealistic assumptions about dispersal, but also permits the calculation of a rich suite of connectivity metrics that together provide a comprehensive view on landscape connectivity. The three derived connectivity maps revealed several dispersal hotspots and corridors across the extent of our study area, yet 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. The approach is therefore useful for a variety of applications in ecological, evolutionary, and conservation research.

# Contents

<b>1</b>	<b>Introduction</b>	<b>1</b>
1.1	Importance of Connectivity & Connectivity Models . . . . .	1
1.2	Issues with Traditional Connectivity Models . . . . .	1
1.3	What about IBMMs? . . . . .	2
1.4	Proposed Solution: Three-Step Approach . . . . .	2
1.5	Case Study . . . . .	3
<b>2</b>	<b>Methods</b>	<b>3</b>
2.1	Case Study . . . . .	3
2.1.1	GPS Data . . . . .	3
2.1.2	Study Area . . . . .	4
2.1.3	Habitat Covariates . . . . .	4
2.2	Step 1 - Movement Model . . . . .	5
2.3	Step 2 - Dispersal Simulation . . . . .	6
2.4	Step 3 - Connectivity Maps . . . . .	7
2.4.1	Heatmap . . . . .	7
2.4.2	Betweenness Map . . . . .	8
2.4.3	Inter-Patch Connectivity Map . . . . .	8
<b>3</b>	<b>Results</b>	<b>9</b>
3.1	Movement Model . . . . .	9
3.2	Dispersal Simulation . . . . .	10
3.3	Heatmap . . . . .	10
3.4	Betweenness . . . . .	11
3.5	Inter-Patch Connectivity . . . . .	11
<b>4</b>	<b>Discussion</b>	<b>12</b>
4.1	Short Summary . . . . .	12
4.2	Movement Model . . . . .	12
4.3	Maps . . . . .	13
4.4	Disadvantages of ISSF Simulations . . . . .	14
4.5	Conclusion . . . . .	16
<b>5</b>	<b>Authors' Contributions</b>	<b>17</b>
<b>6</b>	<b>Data Availability</b>	<b>17</b>
<b>7</b>	<b>Acknowledgements</b>	<b>17</b>

# 1 Introduction

## 1.1 Importance of Connectivity & Connectivity Models

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

## 1.2 Issues with Traditional Connectivity Models

Traditional connectivity models make assumptions that are rarely met for dispersers. LCPA, for instance, assumes that individuals move towards a preconceived endpoint and choose a cost-minimizing route accordingly (Sawyer et al., 2011; Abrahms et al., 2017). While this assumption may be justifiable for migrating animals, it is unlikely to hold for dispersers, as dispersers typically move across unfamiliar territory towards an unknown endpoint (Koen et al., 2014; Cozzi et al., 2020). CT, on the contrary, posits that animals move according to a random walk, entailing that autocorrelation between subsequent movements cannot be rendered (Diniz et al., 2019). For dispersers, however, autocorrelated movements are regularly observed (Cozzi et al., 2020; Hofmann et al., 2021a), meaning that dispersal trajectories are usually strongly directional. Moreover, because both models require static permeability or resistance surfaces as input, they are unable to reflect the temporal dimension of dispersal and therefore fail to allow statements about the expected duration for moving between

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

### 1.3 What about IBMMs?

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

### 1.4 Proposed Solution: Three-Step Approach

Here, we propose and exemplify a simple three-step approach for simulating dispersal and assessing landscape connectivity (Figure 1). In step one, we combine GPS movement data of dispersing individuals with habitat covariates to fit a mechanistic movement model via integrated step-selection functions (ISSFs, Avgar et al., 2016). We chose to use ISSFs because the framework not only allows inference on the study species’ habitat kernel (i.e. its habitat preferences), but also its movement kernel (i.e. its movement preferences/capabilities) and potential interactions among the two (Avgar et al., 2016; Fieberg et al., 2021). In step two, we use the parametrized movement model to simulate dispersal across the study area. Comparable simulations have already been applied to estimate steady-state utilization distributions of resident individuals (Potts et al., 2013; Signer et al., 2017) and to model landscape connectivity, yet disregarding interdependencies between habitat and movement

kernels (Clark et al., 2015; Zeller et al., 2020). Finally, in step three, we convert the simulated trajectories into three complementary connectivity maps; (i) a heatmap revealing frequently traversed areas (e.g. Hauenstein et al., 2019; Zeller et al., 2020), (ii) a betweenness-map delineating dispersal corridors and bottlenecks (e.g. Bastille-Rousseau et al., 2018), (iii) and a map of inter-patch connectivity, depicting the presence and intensity of functional links between habitat patches, as well as the average dispersal duration required to realize those connections (e.g. Gustafson and Gardner, 1996; Kanagaraj et al., 2013).

## 1.5 Case Study

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

## 2 Methods

### 2.1 Case Study

#### 2.1.1 GPS Data

We applied the three step approach presented in Figure 1 to GPS movement data from 16 dispersing African wild dog coalitions (7 female and 9 male coalitions). This data has

been collected between 2011 and 2019 from a free-ranging wild dog population in northern Botswana. During dispersal, GPS collars recorded a fix every 4 hours and regularly transmitted data over the Iridium satellite system. To ensure comparable time intervals between GPS fixes, we removed any fixes that were not successfully obtained at the desired 4-hour schedule (allowing for a tolerance of  $\pm$  15 minutes). To prepare the data for step-selection analysis, we converted the fixes ( $n = 4'169$ ) into steps, where each step represented the straight-line movement between two consecutive GPS fixes (Turchin, 1998). We only considered steps with equal step-durations (i.e. 4 hours) for further analysis. We will refer to these steps as “realized steps”. Additional details on the data collection and preparation can be found in Cozzi et al. (2020) and Hofmann et al. (2021a).

### 2.1.2 Study Area

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

### 2.1.3 Habitat Covariates

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

We performed all data preparations, spatial computations, and statistical analysis in R,

version 3.6.6 (R Core Team, 2020). Some helper functions were written in C++ and imported into R using the Rcpp package (Eddelbuettel and François, 2011; Eddelbuettel, 2013).

## 2.2 Step 1 - Movement Model

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

Along each realized and random step, we extracted values from underlying habitat covariate layers using the `velox` package (Hunziker, 2021) and we computed averages of each covariate along the steps. Besides extracting *habitat covariates*, we also computed movement metrics that we used as *movement covariates* in the ISSF models (Avgar et al., 2016; Fieberg et al., 2021). Specifically, we computed the step length (`sl`), its natural logarithm (`log(sl)`), and the cosine of the relative turning angle (`cos(ta)`), which is a measure of directionality (Turchin, 1998), for each step. Because wild dog activity is low during the hot midday hours (Cozzi et al., 2012), we additionally created the variable `LowActivity`, indicating whether a step was realized during periods of low wild dog activity (09:00 to 17:00 local time) or high wild dog activity (17:00 to 09:00 local time). To facilitate model convergence, we standardized all continuous covariates to a mean of zero and a standard deviation of one. Correlations among covariates were low ( $|r| < 0.6$ ; Latham et al., 2011), so 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  $w(x)$  to each step (Equation 1; Fortin et al., 2005), where  $w(x)$  depended on the step's associated covariates  $(x_1, x_2, \dots, x_n)$  and on the animal's 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  $i$  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:

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

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

Our movement model was based on a habitat selection model that was previously developed for dispersing wild dogs (hereafter referred to as *base model*, Hofmann et al., 2021a). In the base model, no interactions among habitat covariates and movement covariates were considered, so we here expanded the model and allowed for such interactions, acknowledging that movement preferences during dispersal could depend on habitat conditions (details in Appendix A1). To determine the most parsimonious movement model among model candidates, we ran stepwise forward model selection based on Akaike's Information Criterion (AIC, Burnham and Anderson, 2002). More specifically, we started with the base model and iteratively increased model complexity by adding all possible interactions between movement and habitat covariates. We validated the predictive power of the most parsimonious model using k-fold cross-validation for case-control studies as described in Fortin et al. (2009). This validation proves a significant prediction in case the Spearman rank correlation coefficient of predicted step-ranks and associated frequencies under the movement model is significantly greater than under the assumption of random preferences (details in Appendix A2).

### 2.3 Step 2 - Dispersal Simulation

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

standardized covariate values using means and standard deviations from the empirical data.

(4) We applied the parametrized movement model to predict the selection score  $w(x)$  for each step using Equation 1 and we converted predicted scores into probabilities using Equation 2.

(5) We randomly sampled one of the generated random steps based on assigned probabilities and determined the animal's new position. We repeated steps (2) to (5) until 2,000 steps were realized and we repeated the simulation until a total of 80'000 dispersal trajectories was reached.

As source points for the simulations, we distributed 50,000 points at random locations inside protected areas that were large enough to host an average size wild dog home range (i.e.  $> 700 \text{ km}^2$ ; Pomilia et al., 2015). We placed another 30,000 points randomly inside the buffer zone, mimicking potential immigration into the study area (Figure S1).

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

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

## 2.4 Step 3 - Connectivity Maps

### 2.4.1 Heatmap

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

(e.g. Pe'er and Kramer-Schadt, 2008; 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).

#### 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 5 km x 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. 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 ( $\omega$ ) 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 movements between patches as successful if an individual’s dispersal trajectory originating from the source patch intersected with the target patch at least once. For each trajectory we also recorded the number of steps required to reach the first intersection with the respective

patch, allowing us to compute the average dispersal durations from one patch to another. In summary, we determined *if* and *how often* dispersers moved between certain patches, as well as *how long* individuals had to move to make these connections. In our case study, we used NPs as patches to determine inter-patch connectivity, hence we'll use the terms interchangeably from here on. The decision to focus on NPs was purely out of simplicity and should not imply that dispersal between other areas is impossible.

## 3 Results

### 3.1 Movement Model

The most parsimonious movement model consisted of movement covariates, habitat covariates, as well as several of their interactions, thus suggesting that movement behavior during dispersal depended on habitat conditions (Figure 3a, Table S1 and Table S2). Although multiple models received an AIC weight  $> 0$  (Table S1), we only considered results from the most parsimonious model for simplicity. This decision only marginally influenced subsequent steps as all models with positive AIC weights retained similar covariates (Table S1). The k-fold cross-validation showed that the final model substantially outperformed a random guess and provided reliable predictions (i.e. confidence intervals of  $\bar{r}_{s,realized}$  and  $\bar{r}_{s,random}$  did not overlap). Moreover, the model correctly assigned high selection scores to realized steps (Figure 3b), indicating a good fit between predictions and observations. As can be taken from the Spearman rank correlation coefficient, the inclusion of several interactions between movement and habitat covariates significantly improved model performance ( $\bar{r}_{s,realized} = -0.65; 95\% - CI = [-0.67, -0.64]$ ), compared to the base model ( $\bar{r}_{s,realized} = -0.55; 95\% - CI = [-0.57, -0.52]$ ; Hofmann et al., 2021a)

Plots that aid with the interpretation of the most parsimonious movement model are provided in Figure S2 and suggest that, under average conditions, dispersing wild dogs avoided moving through water, woodlands, and areas dominated by humans, but preferred moving across shrublands or grasslands (Figure 3a). Dispersers realized shorter steps (indicating slower movements) in areas covered by water or woodland, while realizing larger steps in areas dominated by shrubs or grass (Figure 3a). We found a particularly large effect for the variable **LowActivity**, suggesting that dispersing wild dogs moved substantially faster during twilight and at night (i.e. between 17:00 and 09:00 o'clock; Figure 3a). Although dispersers revealed a preference for directional movements (i.e. low turning angles), especially when moving quickly, they did less so in proximity to humans or water, resulting in more tortuous

movements in such areas (Figure 3a).

### 3.2 Dispersal Simulation

Dispersal simulations based on the most parsimonious movement model proved useful for assessing landscape connectivity. Of the 50,000 simulated dispersal trajectories with starting point within the main study area, only 4.5% reached a map boundary, suggesting that we successfully mitigated biases from boundary effects. Moreover, our examination of the relative traversal frequency across all checkpoints showed that the relative traversal frequency reached a steady state after 10,500 simulated dispersal trajectories (Figure S3). Although variability in the relative traversal frequency kept decreasing as we increased the number of simulated dispersers, the marginal benefit of simulating additional trajectories diminished quickly (Figure S3).

### 3.3 Heatmap

The heatmap (Figure 4), which resulted from the summation of all simulated dispersal trajectories, allowed us to pinpoint areas that were frequently visited and enabled us to compare areas inside and outside the KAZA-TFCA borders with respect to the intensity at which they were used for dispersal. For instance, we could deduct that areas inside the KAZA-TFCA were frequently traversed by dispersers (median traversal frequency inside KAZA-TFCA = 166, IQR = 274, Figure S6a), whereas areas beyond the KAZA-TFCA boundary were comparatively rarely visited (median traversal frequency outside KAZA-TFCA = 61, IQR = 133, Figure S6a). Most notably, the region in northern Botswana south of the Linyanti swamp appeared to serve as highly frequented dispersal hotspot (median traversal frequency = 987, IQR = 558). Aside from revealing movement hotspots, the heatmap also provided information on areas that appeared to hinder movement. For example, extensive water bodies, such as the Okavango Delta, the Makgadikgadi Pan, and the Linyanti swamp, substantially restricted dispersal movements and limited realized connectivity inside the KAZA-TFCA. Similarly, the landscapes of Zambia and Zimbabwe were only rarely used for dispersal, even within the KAZA-TFCA boundaries (Figure S7a). Despite the fact that the heatmap improved our understanding of the frequency at which areas were traversed by simulated dispersers, it seemed impractical to pinpoint dispersal corridors.

### 3.4 Betweenness

The betweenness map (Figure 5) revealed several distinct dispersal corridors that run across the study area. In comparison to the heatmap, the betweenness map was less biased towards areas with many dispersers and pronounced narrower, more linear routes that were used by simulated individuals to move between regions. Again, northern Botswana emerged as a wild dog dispersal corridor that connected more remote regions in the study area. Towards east, the extension of this corridor ran through Chobe NP into Hwange NP. From there, a further extension connected to Matusadona NP in Zimbabwe. Northwest of the Linyanti ecosystem, a major corridor expanded into Angola, where it split and finally traversed over a long stretch of unprotected area into Zambia’s Kafue NP. Several additional corridors with lower betweenness scores emerged, yet most of them ran within the KAZA-TFCA boundaries (median betweenness inside KAZA-TFCA =  $6.947 \times 10^6$ , IQR =  $54.311 \times 10^6$ , Figure S6b). Consequently, only few corridors directly linked the peripheral regions of the KAZA-TFCA and passed through unprotected areas outside its borders (mean betweenness outside KAZA-TFCA =  $2.685 \times 10^6$ , IQR =  $9.891 \times 10^6$ , Figure S6b).

### 3.5 Inter-Patch Connectivity

The inter-patch connectivity map showed that the relative frequency at which simulated dispersal trajectories moved from one patch to another varied, as did the average dispersal duration between patches (Figure 6). The map thereby completed the picture on connectivity and provided valuable insights into the frequency and duration of connections between patches. For some patches, we also detected imbalances between the number of incoming and outgoing links, hinting at possible source-sink dynamics. From Chobe NP, for instance, 510 individuals reached the Moremi NP, yet the opposite route was only realized by 340 individuals. Relative to the number of simulated individuals, however, these numbers correspond to fractions of 50% and 68%, respectively. Overall, inter-patch connectivity between patches in Angola, Namibia, Botswana, and Zimbabwe appeared to be high; between 54% and 87% of individuals originating from a patch in these countries successfully moved into at least one other patch (Figure S8a). Conversely, only 19% of the dispersers leaving from a patch in Zambia managed to find their way into some other patch (Figure S8b). Prior to reaching another patch, individuals from Angola, Namibia, Botswana, Zimbabwe, and Zambia had to move for an average of 630, 640, 940, 1045, and 890 steps, respectively. Furthermore, it appeared that the corridor previously identified on Figure 6 between Angola’s NPs and the Kafue NP in Zambia is only rarely realized.

## 4 Discussion

### 4.1 Short Summary

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

### 4.2 Movement Model

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, 2021a,b), 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).

### 4.3 Maps

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 LCRA, 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 LCRA, a simulation-based approach as presented 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 (Dwernychuk and Boag, 1972; Van der Meer et al., 2014) or areas with a high susceptibility for human wildlife conflicts (Cushman et al., 2018).

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 An-

gola 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 X days?*”. Moreover, it yields opportunities to incorporate seasonality and to investigate whether dispersal corridors exist seasonally or all-year round (*dynamic connectivity*; Zeller et al., 2020). With LCPA or CT, seasonality can currently only be incorporated through the preparation of multiple permeability surfaces on which the same connectivity model is repeatedly applied (e.g. Benz et al., 2016; Osipova et al., 2019). With simulations from ISSFs, in contrast, the environment could change “as the dispersers move”, so that simulated trajectories would dynamically respond to seasonal fluctuations in the environment.

#### 4.4 Disadvantages of ISSF Simulations

Despite the many benefits and great flexibility offered by simulations from ISSFs, one must also be aware of the associated limitations. For example, while our approach of simulating dispersal proved useful to assess landscape connectivity, it was computationally costly. Simulating 80,000 dispersal trajectories for 2'000 steps across the KAZA-TFCA required five days of computation on a regular desktop machine (AMD Ryzen 7 2700X octa-core processor with 3.6 GHz, 64 GB of RAM). The long simulation time was primarily caused by the massive extent of the study area considered (ca. 1.8 Mio km<sup>2</sup>) and the large number of simulated trajectories. Most connectivity studies focus on smaller study areas (e.g. Kanagaraj et al., 2013; Clark et al., 2015; McClure et al., 2016; Abrahms et al., 2017; Zeller et al., 2020) and will therefore require fewer simulations and achieve faster simulation times

(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.

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 (Woodroffe and Ginsberg, 1999; 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 distribution and abundance are available, source points could be distributed accordingly. Alternatively, source points could be distributed homogeneously but later be weighted when computing connectivity metrics. In any case, the challenge of selecting meaningful source

points is not unique to individual-based simulations but also applies to LCPA and CT.

(3) The use of ISSFs to simulate dispersers requires deciding on the number of simulated steps (i.e. the simulated dispersal durations). If sufficient dispersal data of the focal species has been collected, dispersal durations could be sampled from observed dispersal events or from parametric distributions fit to observed data. Due to the low number of observed dispersal events, we opted against this solution and instead simulated all individuals for 2,000 steps, which was at the upper end of observed dispersal durations in African wild dogs (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020; Hofmann et al., 2021a). This approach had the advantage that it allowed us to systematically shorten the simulated trajectories after their simulation and thereby to investigate the sensitivity of our results with respect to exact dispersal durations (Figures S4 and S5).

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

## 4.5 Conclusion

In summary, we proposed and applied a simple three-step approach that relies on ISSF-analysis and enables the simulation of dispersal trajectories and the assessment of landscape connectivity. The proposed approach overcomes several of the conceptual shortcomings inherent to LCPA and CT, such as the assumption of known endpoints, and provides a highly flexible tool for investigating connectivity. Moreover, the simulation of dispersal opens up new avenues for incorporating interactions between habitat and movement covariates and provides the foundation for a rich suite of complementary connectivity measures. With this work, we hope to have sparked interest in the application, optimization, or creation of methods to investigate dispersal and connectivity via individual-based simulations, while

at the same time stressing some of the non-trivial modeling decisions involved. We also hope to provide a useful framework that helps unifying and streamlining the application of individual-based simulations for assessing landscape connectivity.

## 5 Authors' Contributions

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

## 6 Data Availability

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

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## References

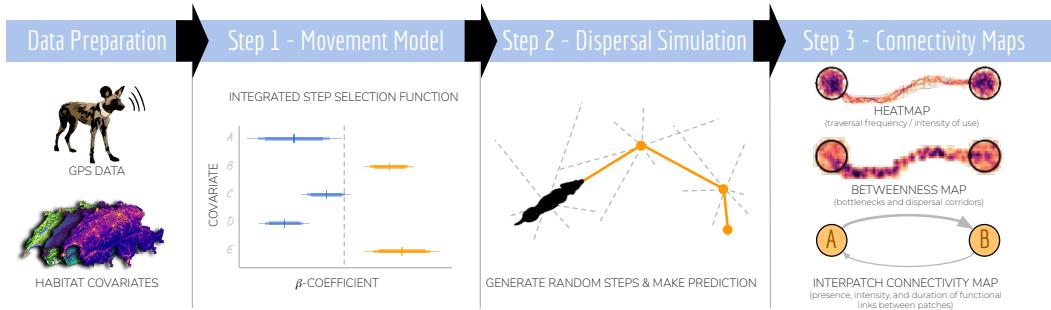
- Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., and Brashares, J. S. (2017). Does Wildlife Resource Selection Accurately Inform Corridor Conservation? *Journal of Applied Ecology*, 54(2):412–422.
- Adriaensen, F., Chardon, J., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., and Matthysen, E. (2003). The Application of Least-Cost Modelling as a Functional Landscape Model. *Landscape and Urban Planning*, 64(4):233–247.
- Allen, C. H., Parrott, L., and Kyle, C. (2016). An Individual-Based Modelling Approach to Estimate Landscape Connectivity for Bighorn Sheep (*Ovis canadensis*). *PeerJ*, 4:e2001.
- Avgar, T., Lele, S. R., Keim, J. L., and Boyce, M. S. (2017). Relative Selection Strength: Quantifying Effect Size in Habitat- and Step-Selection Inference. *Ecology and Evolution*, 7(14):5322–5330.
- Avgar, T., Potts, J. R., Lewis, M. A., and Boyce, M. S. (2016). Integrated Step Selection Analysis: Bridging the Gap Between Resource Selection and Animal Movement. *Methods in Ecology and Evolution*, 7(5):619–630.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., and Turlure, C. (2013). Individual Dispersal, Landscape Connectivity and Ecological Networks. *Biological Reviews*, 88(2):310–326.
- Bastille-Rousseau, G., Douglas-Hamilton, I., Blake, S., Northrup, J. M., and Wittemyer, G. (2018). Applying Network Theory to Animal Movements to Identify Properties of Landscape Space Use. *Ecological Applications*, 28(3):854–864.
- Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2020). When to Stay and When to Leave? Proximate Causes of Dispersal in an Endangered Social Carnivore. *Journal of Animal Ecology*, 89(10):2356–2366.
- Benz, R. A., Boyce, M. S., Thurfjell, H., Paton, D. G., Musiani, M., Dormann, C. F., and Ciuti, S. (2016). Dispersal Ecology Informs Design of Large-Scale Wildlife Corridors. *PLOS ONE*, 11(9):e0162989.
- Brennan, A., Beytell, P., Aschenborn, O., Du Preez, P., Funston, P., Hanssen, L., Kilian, J., Stuart-Hill, G., Taylor, R., and Naidoo, R. (2020). Characterizing Multispecies Connectivity Across a Transfrontier Conservation Landscape. *Journal of Applied Ecology*, 57:1700–1710.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., and Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling. *The R Journal*, 9(2):378–400.
- Brown, J. H. and Kodric-Brown, A. (1977). Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology*, 58(2):445–449.
- Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science & Business Media, Ney York, NY, USA.
- Clark, J. D., Laufenberg, J. S., Davidson, M., and Murrow, J. L. (2015). Connectivity among Subpopulations of Louisiana Black Bears as Estimated by a Step Selection Function. *The Journal of Wildlife Management*, 79(8):1347–1360.
- Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M. (2012). *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.
- Cozzi, G., Behr, D., Webster, H., Claase, M., Bryce, C., Modise, B., McNutt, J., and Ozgul, A. (2020). The Walk of Life: African Wild Dog Dispersal and its Implications for Management and Conservation across Transfrontier Landscapes. In press.

- Cozzi, G., Broekhuis, F., McNutt, J. W., Turnbull, L. A., Macdonald, D. W., and Schmid, B. (2012). Fear of the Dark or Dinner by Moonlight? Reduced Temporal Partitioning among Africa's Large Carnivores. *Ecology*, 93(12):2590–2599.
- Creel, S., Merkle, J., Mweetwa, T., Becker, M. S., Mwape, H., Simpamba, T., and Simukonda, C. (2020). Hidden Markov Models Reveal a clear Human Footprint on the Movements of Highly Mobile African Wild Dogs. *Scientific reports*, 10(1):1–11.
- Csardi, G. and Nepusz, T. (2006). The igraph Software Package for Complex Network Research. *InterJournal, Complex Systems*:1695.
- Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el din, L., Bothwell, H., Flyman, M., Mtare, G., Macdonald, D. W., and Loveridge, A. J. (2018). Prioritizing Core Areas, Corridors and Conflict Hotspots for Lion Conservation in Southern Africa. *PLOS ONE*, 13(7):e0196213.
- Davies-Mostert, H. T., Kamler, J. F., Mills, M. G. L., Jackson, C. R., Rasmussen, G. S. A., Groom, R. J., and Macdonald, D. W. (2012). Long-Distance Transboundary Dispersal of African Wild Dogs among Protected Areas in Southern Africa. *African Journal of Ecology*, 50(4):500–506.
- Diniz, M. F., Cushman, S. A., Machado, R. B., and De Marco Júnior, P. (2019). Landscape Connectivity Modeling from the Perspective of Animal Dispersal. *Landscape Ecology*, 35:41–58.
- Doerr, V. A. J., Barrett, T., and Doerr, E. D. (2011). Connectivity, Dispersal Behaviour and Conservation under Climate Change: A Response to Hodgson et al.: Connectivity and Dispersal Behaviour. *Journal of Applied Ecology*, 48(1):143–147.
- Dray, S., Royer-Carenzi, M., and Calenge, C. (2010). The Exploratory Analysis of Autocorrelation in Animal-Movement Studies. *Ecological Research*, 25(3):673–681.
- Dwernychuk, L. W. and Boag, D. A. (1972). Ducks Nesting in Association with Gulls - An Ecological Trap? *Canadian Journal of Zoology*, 50(5):559–563. Publisher: NRC Research Press.
- Eddelbuettel, D. (2013). *Seamless R and C++ Integration with Rcpp*. Springer, New York. ISBN 978-1-4614-6867-7.
- Eddelbuettel, D. and François, R. (2011). Rcpp: Seamless R and C++ Integration. *Journal of Statistical Software*, 40(8):1–18.
- Elliot, N. B., Cushman, S. A., Macdonald, D. W., and Loveridge, A. J. (2014). The Devil is in the Dispersers: Predictions of Landscape Connectivity Change with Demography. *Journal of Applied Ecology*, 51(5):1169–1178.
- Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1):487–515.
- Fieberg, J., Signer, J., Smith, B., and Avgar, T. (2021). A ‘How to’ Guide for Interpreting Parameters in Habitat-Selection Analyses. *Journal of Animal Ecology*, 90(5):1027–1043.
- Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., and Mao, J. S. (2005). Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone National Park. *Ecology*, 86(5):1320–1330.
- Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., and Dancose, K. (2009). Group-Size-Mediated Habitat Selection and Group Fusion–Fission Dynamics of Bison under Predation Risk. *Ecology*, 90(9):2480–2490.
- Frankham, R., Briscoe, D. A., and Ballou, J. D. (2002). *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK.

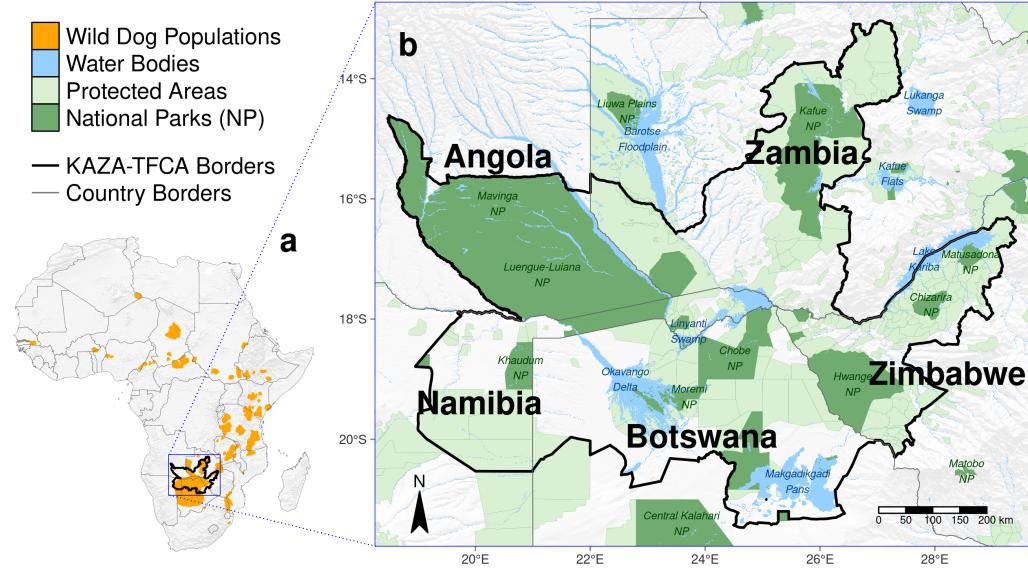
- Graves, T. A. and Waller, J. S. (2006). Understanding the Causes of Missed Global Positioning System Telemetry Fixes. *Journal of Wildlife Management*, 70(3):844–851.
- Gustafson, E. J. and Gardner, R. H. (1996). The Effect of Landscape Heterogeneity on the Probability of Patch Colonization. *Ecology*, 77(1):94–107.
- Hanski, I. (1999). *Metapopulation Ecology*. Oxford University Press.
- Hauenstein, S., Fattebert, J., Grüebler, M. U., Naef-Daenzer, B., Pe'er, G., and Hartig, F. (2019). Calibrating an Individual-Based Movement Model to Predict Functional Connectivity for Little Owls. *Ecological Applications*, 29(4):e01873.
- Hijmans, R. J. (2021). *terra: Spatial Data Analysis*. R package version 1.2-10.
- Hodel, F. H. and Fieberg, J. R. (2021a). Circular-linear copulae for animal movement data. *bioRxiv*.
- Hodel, F. H. and Fieberg, J. R. (2021b). Cyclop: An r package for circular-linear copulae with angular symmetry. *bioRxiv*.
- Hofmann, D. D., Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2021a). Bound within boundaries: Do protected areas cover movement corridors of their most mobile, protected species? *Journal of Applied Ecology*, 58(6):1133–1144. Publisher: Wiley Online Library.
- Hofmann, D. D., Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2021b). Data from: Bound within Boundaries: Do Protected Areas Cover Movement Corridors of their Most Mobile, Protected Species? Dryad Digital Repository. <https://doi:10.5061/dryad.dncjsxkzn>.
- Hunziker, P. (2021). *velox: Fast Raster Manipulation and Extraction*. R package version 0.2.1.
- Kanagaraj, R., Wiegand, T., Kramer-Schadt, S., and Goyal, S. P. (2013). Using Individual-Based Movement Models to Assess Inter-Patch Connectivity for Large Carnivores in Fragmented Landscapes. *Biological Conservation*, 167:298 – 309.
- Koen, E. L., Bowman, J., Sadowski, C., and Walpole, A. A. (2014). Landscape Connectivity for Wildlife: Development and Validation of Multispecies Linkage Maps. *Methods in Ecology and Evolution*, 5(7):626–633.
- Koen, E. L., Garroway, C. J., Wilson, P. J., and Bowman, J. (2010). The Effect of Map Boundary on Estimates of Landscape Resistance to Animal Movement. *PLoS ONE*, 5(7):e11785.
- Latham, A. D. M., Latham, M. C., Boyce, M. S., and Boutin, S. (2011). Movement Responses by Wolves to Industrial Linear Features and Their Effect on Woodland Caribou in Northeastern Alberta. *Ecological Applications*, 21(8):2854–2865.
- Leigh, K. A., Zenger, K. R., Tammen, I., and Raadsma, H. W. (2012). Loss of Genetic Diversity in an Outbreeding Species: Small Population Effects in the African Wild Dog (*Lycaon pictus*). *Conservation Genetics*, 13(3):767–777.
- MacArthur, R. H. and Wilson, E. O. (2001). *The Theory of Island Biogeography*, volume 1. Princeton University Press, Princeton, New Jersey, USA.
- Martensen, A. C., Saura, S., and Fortin, M. (2017). Spatio-Temporal Connectivity: Assessing the Amount of Reachable Habitat in Dynamic Landscapes. *Methods in Ecology and Evolution*, 8(10):1253–1264.
- Masenga, E. H., Jackson, C. R., Mjingo, E. E., Jacobson, A., Riggio, J., Lyamuya, R. D., Fyumagwa, R. D., Borner, M., and Røskraft, E. (2016). Insights into Long-Distance Dispersal by African Wild Dogs in East Africa. *African Journal of Ecology*, 54(1):95–98.

- McClintock, B. T., King, R., Thomas, L., Matthiopoulos, J., McConnell, B. J., and Morales, J. M. (2012). A General Discrete-Time Modeling Framework for Animal Movement Using Multistate Random Walks. *Ecological Monographs*, 82(3):335–349.
- McClure, M. L., Hansen, A. J., and Inman, R. M. (2016). Connecting Models to Movements: Testing Connectivity Model Predictions against Empirical Migration and Dispersal Data. *Landscape Ecology*, 31(7):1419–1432.
- McNutt, J. (1996). Sex-Biased Dispersal in African Wild Dogs (*Lycaon pictus*). *Animal Behaviour*, 52(6):1067–1077.
- McRae, B. H. (2006). Isolation by Resistance. *Evolution*, 60(8):1551–1561.
- McRae, B. H., Dickson, B. G., Keitt, T. H., and Shah, V. B. (2008). Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation. *Ecology*, 89(10):2712–2724.
- Muff, S., Signer, J., and Fieberg, J. (2020). Accounting for Individual-Specific Variation in Habitat-Selection Studies: Efficient Estimation of Mixed-Effects Models Using Bayesian or Frequentist Computation. *Journal of Animal Ecology*, 89(1):80–92.
- Nathan, R. (2008). An Emerging Movement Ecology Paradigm. *Proceedings of the National Academy of Sciences*, 105(49):19050–19051.
- Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., and Balkenhol, N. (2019). Using Step-Selection Functions to Model landscape Connectivity for African Elephants: Accounting for Variability across Individuals and Seasons. *Animal Conservation*, 22(1):35–48.
- O'Neill, H. M. K., Durant, S. M., and Woodroffe, R. (2020). What Wild Dogs Want: Habitat Selection Differs across Life Stages and Orders of Selection in a Wide-Ranging Carnivore. *BMC Zoology*, 5(1).
- Perrin, N. and Mazalov, V. (1999). Dispersal and Inbreeding Avoidance. *The American Naturalist*, 154(3):282–292.
- Perrin, N. and Mazalov, V. (2000). Local Competition, Inbreeding, and the Evolution of Sex-Biased Dispersal. *The American Naturalist*, 155(1):116–127.
- Pe'er, G. and Kramer-Schadt, S. (2008). Incorporating the Perceptual Range of Animals into Connectivity Models. *Ecological Modelling*, 213(1):73–85.
- Pomilia, M. A., McNutt, J. W., and Jordan, N. R. (2015). Ecological Predictors of African Wild Dog Ranging Patterns in Northern Botswana. *Journal of Mammalogy*, 96(6):1214–1223.
- Potts, J. R., Bastille-Rousseau, G., Murray, D. L., Schaefer, J. A., and Lewis, M. A. (2013). Predicting local and non-local effects of resources on animal space use using a mechanistic step selection model. *Methods in Ecology and Evolution*, 5(3):253–262.
- R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rudnick, D., Ryan, S., Beier, P., Cushman, S., Dieffenbach, F., Epps, C., Gerber, L., Hartner, J., Jenness, J., Kintsch, J., Merenlender, A., Perkl, R., Perziosi, D., and Trombulack, S. (2012). The Role of Landscape Connectivity in Planning and Implementing Conservation and Restoration Priorities. *Issues in Ecology*.
- Sawyer, S. C., Epps, C. W., and Brashares, J. S. (2011). Placing Linkages among Fragmented Habitats: Do Least-Cost Models Reflect How Animals Use Landscapes? *Journal of Applied Ecology*, 48(3):668–678.
- Signer, J., Fieberg, J., and Avgar, T. (2017). Estimating Utilization Distributions from Fitted Step-Selection Functions. *Ecosphere*, 8(4):e01771.

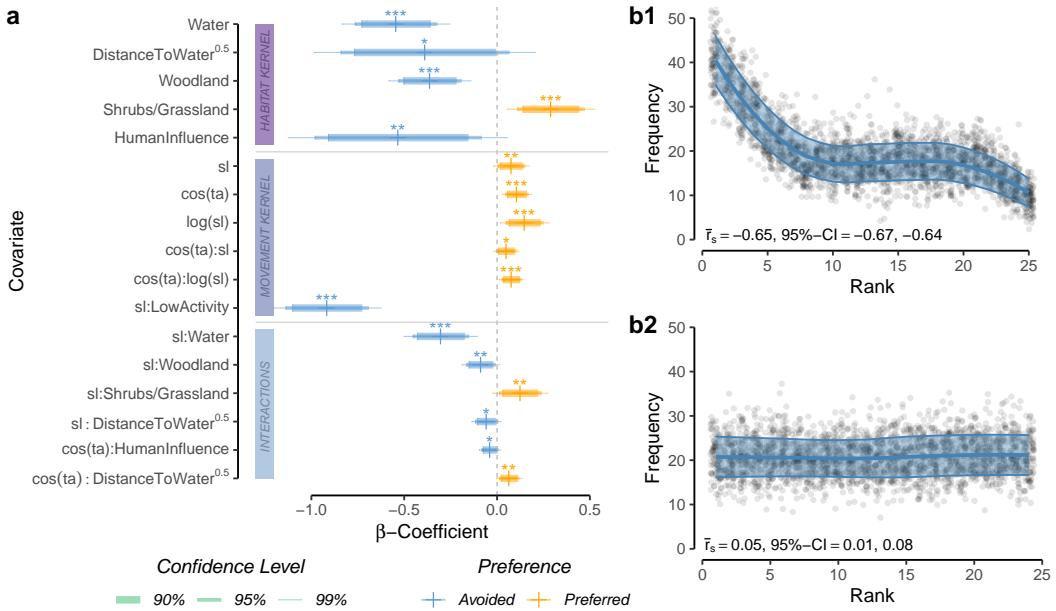
- Tischendorf, L. and Fahrig, L. (2000). On the Usage and Measurement of Landscape Connectivity. *Oikos*, 90(1):7–19.
- Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Plants and Animals*. Sinauer Associates, Sunderland, MA, USA.
- Van der Meer, E., Fritz, H., Blinston, P., and Rasmussen, G. S. (2014). Ecological Trap in the Buffer Zone of a Protected Area: Effects of Indirect Anthropogenic Mortality on the African Wild Dog (*Lycaon pictus*). *Oryx*, 48(2):285–293.
- Vasudev, D., Fletcher, R. J., Goswami, V. R., and Krishnadas, M. (2015). From Dispersal Constraints to Landscape Connectivity: Lessons from Species Distribution Modeling. *Ecography*, 38(10):967–978.
- Wolski, P., Murray-Hudson, M., Thito, K., and Cassidy, L. (2017). Keeping it Simple: Monitoring Flood Extent in Large Data-Poor Wetlands Using MODIS SWIR Data. *International Journal of Applied Earth Observation and Geoinformation*, 57:224–234.
- Woodroffe, R. and Ginsberg, J. R. (1999). Conserving the African Wild Dog *Lycaon pictus*. Diagnosing and Treating Causes of Decline. *Oryx*, 33(2):132–142.
- Woodroffe, R., Rabaiotti, D., Ngatia, D. K., Smallwood, T. R. C., Strelak, S., and O'Neill, H. M. K. (2019). Dispersal Behaviour of African Wild Dogs in Kenya. *African Journal of Ecology*.
- Woodroffe, R. and Sillero-Zubiri, C. (2012). *Lycaon pictus*. *The IUCN Red List of Threatened Species*, 2012:e. T12436A16711116.
- Zeller, K. A., Wattles, D. W., Bauder, J. M., and DeStefano, S. (2020). Forecasting Seasonal Habitat Connectivity in a Developing Landscape. *Land*, 9(7):233.



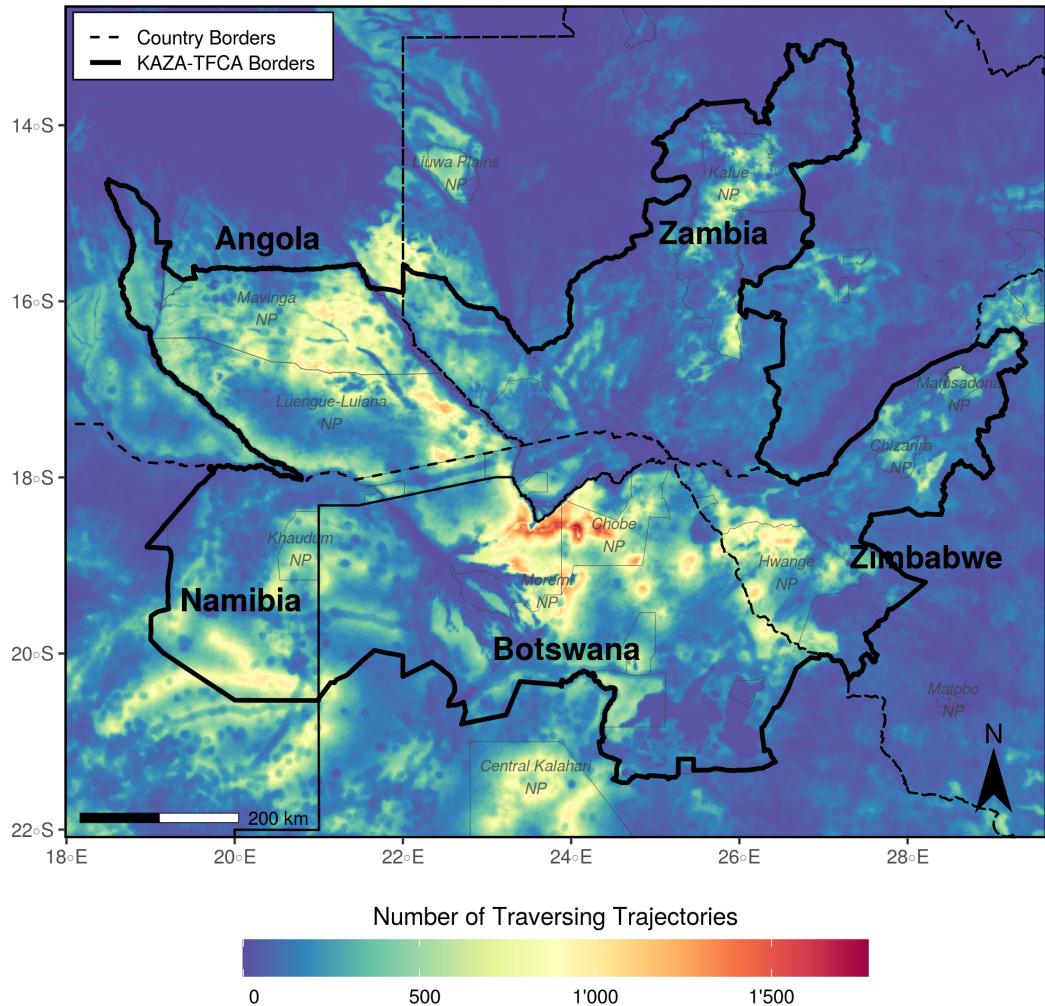
**Figure 1:** Flowchart of the simulation-based connectivity analysis as proposed in this article. First, GPS data and habitat covariates must be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement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



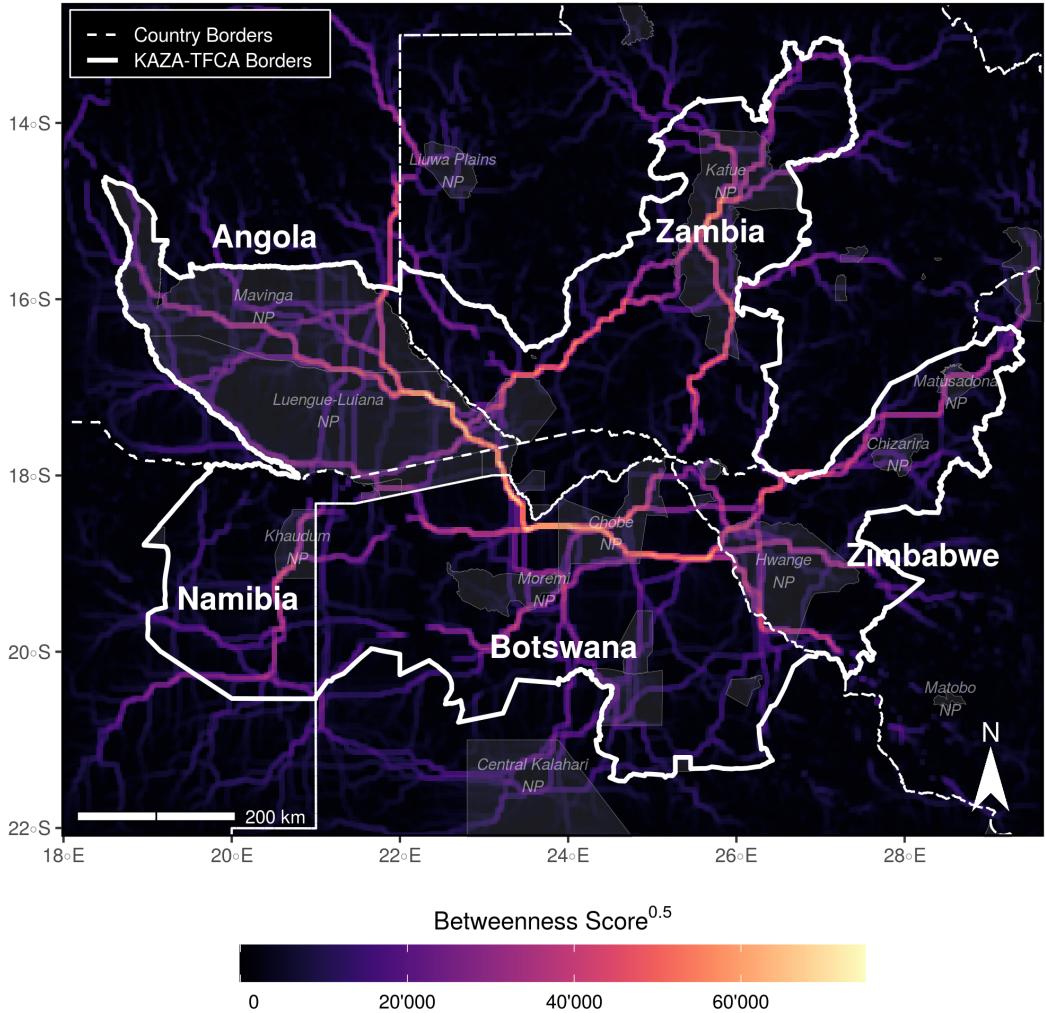
**Figure 2:** Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA which comprises parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. Data on remaining wild dog populations has been sourced from Woodroffe and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



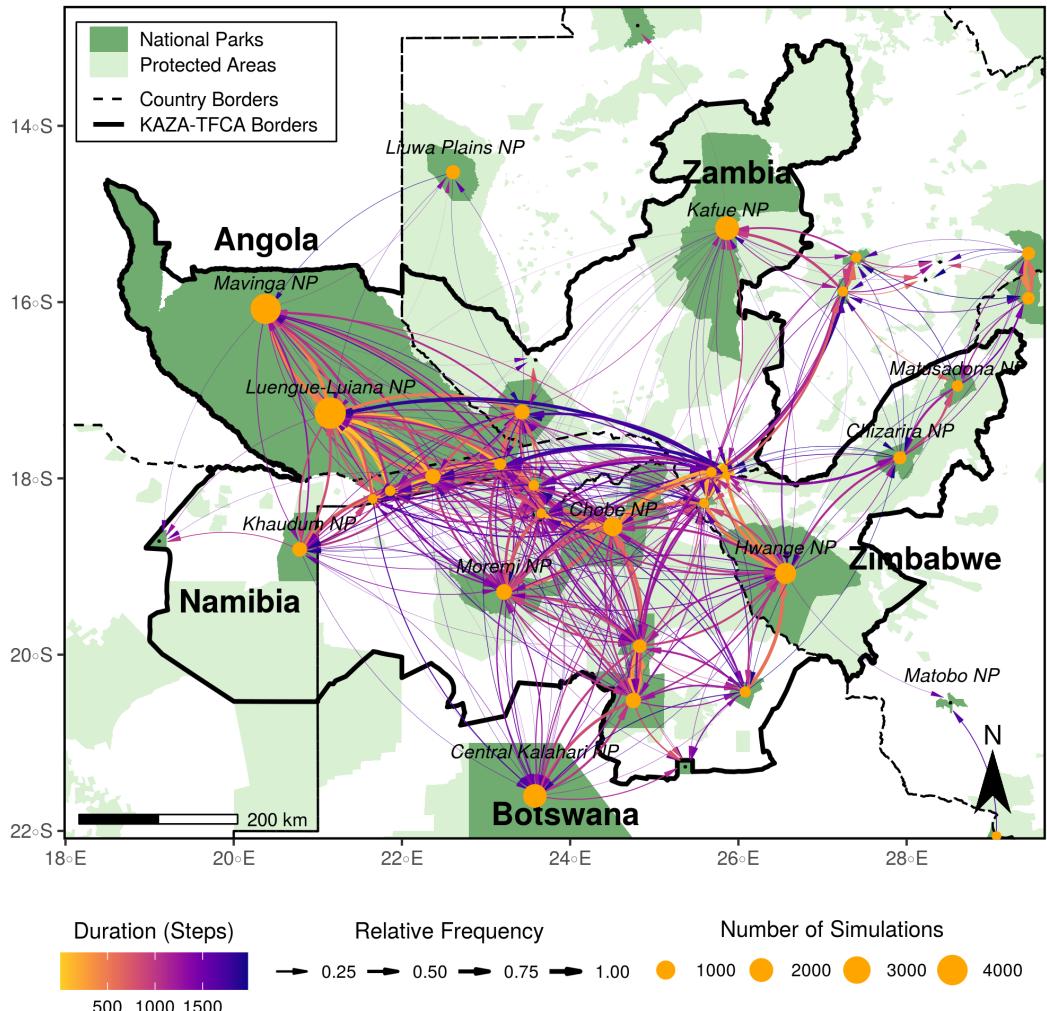
**Figure 3:** (a) Most parsimonious movement model for dispersing wild dogs. The model comprises a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% confidence-intervals for the respective  $\beta$ -coefficients. Significance codes: \*  $p < 0.10$ , \*\*  $p < 0.05$ , \*\*\*  $p < 0.01$ . (b) Results from the k-fold cross validation procedure. The upper plot shows rank frequencies of realized steps according to model predictions with known preferences, whereas the lower plot shows rank frequencies of realized steps when assuming random preferences. The blue ribbon shows the prediction interval around a loess smoothing regression that we fitted to ease the interpretation of the plots. The significant correlation between rank and associated frequency in (b1) highlights that the most parsimonious model successfully outperforms a random guess (b2) and assigns comparably high selection scores to realized steps.



**Figure 4:** 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 by virtual dispersers. 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 S4.



**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 S4.



**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  $700 \text{ km}^2$  and therefore did not serve 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 (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. Note that a similar network view could be adopted to investigate connectivity between other protected areas need not to be restricted to NPs.