

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

David D. Hofmann<sup>1,2,§</sup> Gabriele Cozzi<sup>1,2</sup> John W. McNutt<sup>2</sup> Arpat Ozgul<sup>1</sup>  
Dominik M. Behr<sup>1,2</sup>

September 30, 2021

<sup>1</sup> Department of Evolutionary Biology and Environmental Studies, University of Zurich,  
Winterthurerstrasse 190, 8057 Zurich, Switzerland.

<sup>2</sup> Botswana Predator Conservation, Private Bag 13, Maun, Botswana.

§ Corresponding author (david.hofmann2@uzh.ch)

**Running Title:** Release the Dogs! Simulating Wild Dog Dispersal to Assess Landscape  
Connectivity

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

## Abstract

**Short Version** The ability to disperse is contingent a sufficient degree of landscape connectivity, which is why the identification and preservation of movement corridors that promote connectivity has become a task of extraordinary importance. Currently, ecologists rely on least-cost analysis or circuit theory to investigate connectivity, albeit both methods make several assumptions that are hardly met in reality. To address these issues, simulations from individual-based movement models have been proposed, yet a unified framework to simulate dispersal and quantify connectivity is lacking.

Here, we propose a simple three-step workflow that combines several already-existing methods to assess connectivity using simulated dispersal trajectories. In step one, we use integrated step selection functions to parametrize a mechanistic movement model rendering dispersal behavior. In step two, we apply the parametrized model as an individual-based movement model to simulate dispersal trajectories. In step three, we combine simulated trajectories into three complementary connectivity maps, each focusing on a different aspect of landscape connectivity.

We showcase the application of the proposed workflow using data of dispersing African wild dogs (*Lycaon pictus*) and assess landscape connectivity within the world's largest transboundary conservation area in Southern Africa. We thereby shed light into dispersing wild dogs' habitat and movement preferences, while also uncovering crucial dispersal corridors. With this analysis, we demonstrate that simulations from integrated step selection functions offer a simple, yet powerful alternative to traditional connectivity modeling techniques.

## Abstract

**Long Version** Dispersal of individuals is crucial for long-term species persistence and depends on a sufficient degree of landscape connectivity. To date, researchers primarily investigate connectivity using least-cost analysis and circuit theory, both methods that make assumptions which are hardly met in reality. Least-cost analysis assumes that animals move towards a known endpoint and are knowledgeable about the most favorable route route to reach it. Circuit theory presumes a complete random walk and therefore fails to incorporate directional persistence. These shortcomings can be overcome by spatio-temporally explicitly simulating dispersal, yet a unified approach for such simulations is lacking.

Here, we present a simple three-step workflow to simulate dispersal and assess connectivity starting from empirical GPS movement data. In step one, we use integrated step selection functions to fit a mechanistic movement model describing habitat and movement preferences of dispersers. In step two, we apply the parameterized model to simulate individual dispersal trajectories. In step three, we combine the simulated trajectories into three complementary connectivity maps: a heatmap that highlights frequently traversed areas, a betweenness map that pinpoints dispersal corridors, and a map of inter-patch connectivity that indicates the presence and intensity of functional links between habitat patches. As a case study, we analyse data on the endangered African wild dog and assess landscape connectivity in the Kavango-Zambezi Transfrontier Conservation Area, the world's largest transboundary conservation area.

Our results show that wild dogs preferably disperse with directional persistence in the vicinity to waterbodies and through areas with little human influence and sparse woodland cover. Dispersal simulations and subsequent connectivity maps revealed several dispersal hotspots and corridors across the extent of the KAZA-TFCA. Connectivity between NPs inside the KAZA-TFCA was good, yet few dispersers successfully moved from Zambia's NPs into neighboring areas.

We show that simulations from step-selection functions offer a simple yet powerful alternative to traditional connectivity modeling techniques. In contrast to traditional connect modeling techniques, simulations not only make fewer unrealistic assumptions but also permit a more mechanistic understanding of dispersal and landscape connectivity. This makes our workflow 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 Workflow . . . . .	2
1.5	Case Study . . . . .	3
<b>2</b>	<b>Methods</b>	<b>3</b>
2.1	Study Area . . . . .	3
2.2	Data Collection and Preparation . . . . .	4
2.2.1	GPS Data . . . . .	4
2.2.2	Habitat Covariates . . . . .	4
2.3	Step 1 - Movement Model . . . . .	5
2.4	Step 2 - Dispersal Simulation . . . . .	6
2.5	Step 3 - Connectivity Maps . . . . .	8
2.5.1	Heatmap . . . . .	8
2.5.2	Betweenness Map . . . . .	8
2.5.3	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	Simulation . . . . .	13
4.4	Maps . . . . .	14
4.5	Disadvantages of ISSF Simulations . . . . .	15
4.6	Conclusion . . . . .	17
<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>18</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 colonize unoccupied habitats (Hanski, 1999; MacArthur and Wilson, 2001). Importantly, 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). The identification of 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 two 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), both graph-based methods that quantify conductance of the landscape based on habitat permeability (Zeller et al., 2012). However, both approaches rest on assumptions that appear unsuitable for dispersers, which is why simulating dispersal from individual-based movement models provides a promising alternative approach to investigate connectivity (Diniz et al., 2019).

## 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 fulfilled by migrating animals, it is unlikely to hold for dispersers, as dispersers typically move across unfamiliar territory, so the associated movement costs and potential endpoints are unknown to them (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), implying that dispersal trajectories are usually strongly directional. Moreover, graph-based methods are unable to reflect the temporal dimension of dispersal, so that statements about the expected duration for moving between habitats are impossible

(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 from individual-based movement models (IBMMs) and converting simulated trajectories into meaningful measures of connectivity (Diniz et al., 2019)). In contrast to graph-based methods, 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, thus shifting 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, because simulations from IBMMs generate movement sequentially, the temporal dimension of dispersal becomes explicit and allows to model autocorrelation between subsequent movements (Diniz et al., 2019). Finally, simulations from IBMMs do not enforce connections towards preconceived endpoints, thereby mitigating biases arising from misplaced endpoints. Despite these advantages, a unified framework to simulate dispersal and assess connectivity using IBMMs is lacking.

### 1.4 Proposed Solution: Three-Step Workflow

Here, we draw on recent advancements in movement ecology and propose a simple three-step workflow for simulating dispersal and assessing landscape connectivity (Figure 1). In step one, we combine GPS movement data of dispersing individuals with relevant habitat covariates to fit a mechanistic movement model using integrated step selection functions (ISSFs, Avgar et al., 2016). ISSFs permit inference on the focal species' habitat kernel (i.e. habitat preferences), its movement kernel (i.e. movement preferences/capabilities), and potential interactions between the two (Avgar et al., 2016; Fieberg et al., 2021). In step two, we simulate individual dispersal trajectories using the parametrized movement from step one. Comparable simulations have already been employed to estimate steady-state utilization distributions of residents (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 simulated trajectories into three complementary connectivity maps, each highlighting a different aspect of connectivity. The set of maps includes (i) a heatmap revealing areas that are frequently traversed by simulated dispersers (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 use of specific connections, as well as the average dispersal duration required to connect corresponding habitat patches (e.g. Gustafson and Gardner, 1996; Kanagaraj et al., 2013).

## 1.5 Case Study

We showcase the application of the proposed workflow (Figure 1) using dispersal data collected on the endangered African wild dog (*Lycaon Pictus*). The African wild dog represents a highly mobile species whose persistence hinges on a sufficient degree of landscape connectivity. 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 using LCPA (Hofmann et al., 2021a) or CT (Brennan et al., 2020), a more comprehensive and mechanistic understanding of connectivity is missing for this species (but see Creel et al., 2020). With fewer than 6,000 free-ranging wild dogs remaining in fragmented populations (Woodroffe and Sillero-Zubiri, 2012), reliable information on landscape connectivity is essential for the conservation of this endangered carnivore. Here, we use GPS data of 16 dispersing wild dogs originating from a free-ranging population in northern Botswana to parametrize a mechanistic movement model, which we then employed to simulate 80,000 dispersal trajectories across the landscape of the world's largest transboundary conservation area, the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). We anticipated that simulations based on our three-step workflow would overcome several of the above highlighted conceptual shortcomings of traditional connectivity models and provide a more comprehensive view of landscape connectivity.

## 2 Methods

### 2.1 Study Area

The study area centered at -17°13'9"S, 23°56'4"E (Figure 2a) was located in southern Africa (Figure 2a) and spanned more than 1.3 Mio. km<sup>2</sup>, encompassing the entire KAZA-TFCA (Figure 2b). The KAZA-TFCA comprises parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia and hosts 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 hydrogeographical feature and the world's largest flood-pulsing inland delta. Large portions of the KAZA-TFCA are part of designated national parks (NPs) and other protected areas, yet considerable human influence through roads, agricultural sites, and settlements remains.

## 2.2 Data Collection and Preparation

### 2.2.1 GPS Data

We collected GPS movement data on 16 dispersing wild dogs (7 females and 9 males) between 2011 and 2019 from a free-ranging population in northern Botswana (details on the data collection can be found in Cozzi et al. (2020) and Hofmann et al. (2021a)). Because behavior during dispersal is more pertinent to landscape connectivity than behavior during residence (Elliot et al., 2014; Abrahms et al., 2017), we discarded data collected when individuals were resident. We determined the exact timing of emigration and settlement using direct field observations and through visual inspection of the net squared displacement (NSD) metric. NSD measures the squared Euclidean distance of a GPS relocation to a reference point (Börger and Fryxell, 2012), which we set to the center of each dispersers' natal home range. Thus, dispersal was deemed to have started once an individual left its natal home range and ended once the NSD metric remained constant, indicating settlement. During dispersal, GPS collars recorded a fix every 4 hours and regularly transmitted data over the Iridium satellite system. To ensure regular timespans between GPS fixes, we removed any fix that was not successfully obtained on the aspired 4-hourly schedule (allowing for a tolerance of  $\pm 15$  minutes). We then converted the remaining fixes ( $n = 4'169$ ) into steps, where each step represented the straight-line movement between two consecutive GPS fixes (Turchin, 1998).

### 2.2.2 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 correctly render seasonality in water-cover, we applied a remote sensing algorithm that enabled us to obtain weekly updated raster-layers for water-cover and corresponding layers for distance-to-water from MODIS satellite imagery Wolski et al., 2017; Hofmann et al., 2021a. This algorithm is now implemented in the `floodmapr` package which is available on GitHub (<https://github.com/DavidDHofmann/floodmapr>). Using the frequently updated `floodmpas` we were able to correctly assign the most appropriate covariate layer to each

observed movement step. 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).

Besides habitat covariates, we computed movement metrics that we used as movement covariates in ISSF models (Avgar et al., 2016; Fieberg et al., 2021). Movement metrics were calculated for each step and included the step length (`sl`), its natural logarithm (`log(sl)`), and the cosine of the relative turning angle (`cos(ta)`). Moreover, we created the binary 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, Cozzi et al., 2012). 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).

### 2.3 Step 1 - Movement Model

We used ISSFs to parametrize a mechanistic movement model for dispersing wild dogs (Avgar et al., 2016). More specifically, we paired each realized step with 24 random steps, so that a realized step plus its 24 random steps formed a 25-step-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  $(-\pi, +\pi)$  (which is equivalent to a von Mises distribution with location and concentration parameters;  $\mu = \kappa = 0$ ) and step lengths from a gamma distribution that was fitted to realized steps (scale  $\theta = 6'308$  and shape  $k = 0.37$ ). Along each step, we extracted and averaged values from the habitat covariate layers using the `velox` package (Hunziker, 2021) and calculated the movement metrics `sl`, `log(sl)`, and `cos(ta)` for each realized and random step. To facilitate model convergence, we standardized all continuous covariates to a mean of zero and a standard deviation of one. Since correlation among covariates was low ( $|r| < 0.6$ ; Latham et al., 2011), we retained all of them for modeling.

To contrast realized steps (scored 1) and random steps (scored 0), we assumed that animals assigned a selection score  $w(x)$  of the exponential form to each step (Equation 2; Fortin et al., 2005).  $w(x)$  depended on the step's associated covariates  $(x_1, x_2, \dots, x_n)$  and on the animal's preferences (i.e. relative selection strengths; Avgar et al., 2017) towards these covariates  $(\beta_1, \beta_2, \dots, \beta_n)$ :

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

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

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

To estimate preferences (i.e. the  $\beta$ -coefficients), we used mixed effects conditional logistic regression analysis (Muff et al., 2020) that we implemented using the r-package `glmmTMB` (Brooks et al., 2017). To capitalize on the poisson trick proposed by Muff et al. (2020), we defined random intercepts for each stratum and fixed the intercept variance to an arbitrary high value of  $10^6$ . We also used disperser identity to model random slopes for all covariates.

The covariate structure of the movement model was based on a habitat selection model that we 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. Hence, we expanded the base model and allowed for interactions between all movement covariates and habitat covariates, thus reflecting that movement behavior may 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). Finally, 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 proofs a significant prediction in case the Spearman rank correlation 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).

## 2.4 Step 2 - Dispersal Simulation

We used the most parsimonious movement model to simulate individual dispersal trajectories within the study area. The simulation of a dispersal trajectory resembled an “inverted” ISSF and was set up as follows. (1) We defined a random source point and assumed a random initial orientation of the animal. (2) 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. Like in the empirical data, each random step represented

the straight line movement possible within 4 hours. To prevent unreasonably large steps, we restricted sampled step lengths to a maximum of 35 km (i.e. the farthest dispersal distance traveled within 4 hours in our data). (3) Along each random step, we extracted and averaged values from the different habitat covariate layers and calculated movement covariates. To ensure compatible scales with the fitted movement model, we standardized extracted 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 translated predicted scores into probabilities using Equation 2. (5) We used predicted probabilities to sample one of the random steps and determined the animal's new position. We repeated steps (2) to (5) until 2,000 steps (i.e. 400 consecutive dispersal days) were realized.

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 proposed random steps transgressed the outer border of this buffer zone, we resampled transgressing steps until they fully lied within the buffer zone, forcing individuals to remain within the expanded study area.

For the simulation, we distributed 80,000 unique source points within the study area. Of these, 50,000 were random locations inside protected areas that were larger than the average home range size of wild dogs (i.e.  $> 700 \text{ km}^2$ ; Pomilia et al., 2015), while the remaining 30,000 source points were placed randomly inside the buffer zone, mimicing potential immigration into the study area (Figure S1). Due to the random distribution of source points, the number of source points per  $\text{km}^2$  in selected areas was approximately equal.

To ensure reliable connectivity estimates, we determined the number of simulated dispersal trajectories required for connectivity to reach a “steady state” across the entire study area. For this purpose, we distributed 1,000 rectangular “checkpoints”, each with an 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 dispersers (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 dispersal 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

Since we did not explain the 8-hourly gaps, this might be confusing

the width of the prediction-interval dropped below a value of 0.01 for all checkpoints.

## 2.5 Step 3 - Connectivity Maps

### 2.5.1 Heatmap

To identify dispersal hotspots within the study area, we created a heatmap indicating the absolute frequency at which each raster-cell was traversed by simulated dispersers (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. If the same trajectory crossed a raster-cell twice, we only counted it once, thereby mitigating biases from individuals that moved in circles because they were surrounded by unfavorable habitat. To achieve high performance rasterization, we used the R-package `terra` (Hijmans, 2021).

### 2.5.2 Betweenness Map

To pinpoint discrete 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 (i.e. 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 5 km x 5 km raster, 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 node to another, as well as the frequency at which those transitions occurred. This resulted in an edge-list that we translated into a weighted network using the r-package `igraph` (Csardi and Nepusz, 2006). The weight of each edge was determined by the frequency of transitions, yet because `igraph` handles edge weights ( $\omega$ ) as costs, we had to invert the traversal-frequency through each raster-cell by applying  $\omega = \frac{\text{mean}(\text{TraversalFrequency})}{\text{TraversalFrequency}_i}$ . Consequently, edges that were traversed regularly received small weights (i.e. low costs) and vice versa. Finally, we used the weighted network to calculate betweenness scores for all network nodes.

### 2.5.3 Inter-Patch Connectivity Map

To examine the presence and intensity of functional links (i.e. connections) between specific patches inside the KAZA-TFCA, we calculated inter-patch connectivity between NPs (e.g.

(Gustafson and Gardner, 1996; Kanagaraj et al., 2013)). The decision to only consider NPs as potential “patches” was purely out of simplicity and does not imply that connections between other protected areas are impossible. To quantify inter-patch connectivity, we computed the relative frequency at which dispersers originating from one NP successfully moved into another NP. We considered movements successful if the individuals’ dispersal trajectory intersected with the target NP at least once. We also recorded the number of steps required to reach the first intersection with the respective NP, allowing us to compute the average dispersal durations from one park to another. In summary, we determined *if* and *how often* dispersers moved between certain NPs, as well as *how long* individuals had to move to make these connections.

## 3 Results

### 3.1 Movement Model

The most parsimonious movement model consisted of movement covariates, habitat covariates and several of their interactions, suggesting that movement behavior during dispersal depended on habitat conditions (Figure 3, Table S1 and Table S2). Although multiple models received an AIC weight  $\geq 0$  (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). Plots that facilitate model interpretation are provided in Figure S2. Under average conditions, dispersing wild dogs avoided moving through water, woodlands, and areas dominated by humans, but preferred shrublands or grasslands (Figure 3). 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. Moreover, dispersing wild dogs moved faster during twilight and at night (i.e. between 17:00 and 09:00 o’clock) than during the rest of the day. Although dispersers showed 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.

The k-fold cross-validation of the movement model showed that the final model substantially outperformed a random guess and suggested reliable predictions (confidence intervals of  $\bar{r}_{s,realized}$  and  $\bar{r}_{s,random}$  do not overlap). Moreover, the model correctly assigned high selection scores to realized steps (Figure 3b), indicating a good fit between predictions and observations. Compared to the base model ( $\bar{r}_{s,realized} = -0.55$ ; 95% – CI =  $[-0.57, -0.52]$ ;

Hofmann et al., 2021a), 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]).

### 3.2 Dispersal Simulation

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

### 3.3 Heatmap

The heatmap (Figure 4), which resulted from the summation of all simulated dispersal trajectories, showed that several extensive regions within the KAZA-TFCA were frequently traversed by dispersing wild dogs (mean traversal frequency inside KAZA-TFCA = 166, IQR = 274, Figure S6a), whereas areas beyond the KAZA-TFCA boundary were rarely visited (mean traversal frequency outside KAZA-TFCA = 61, IQR = 133, Figure S6a). Most notably, the region in northern Botswana south of the Linyanti swamp appeared as highly frequented dispersal hotspot (mean traversal frequency = 987, IQR = 558). Nevertheless, the presence of extensive water bodies, such as the Okavango Delta, the Makgadikgadi Pan, and the Linyanti swamp, restricted dispersal movements and limited realized connectivity within the KAZA-TFCA. Similarly, high human density, roads, and agricultural activities in Zambia's and Zimbabwe's part of the KAZA-TFCA limited dispersal movements in those countries. Outside the KAZA-TFCA, the most heavily used regions included the areas inside the Central Kalahari National Park in Botswana, the area south-west of the Khaudum National Park in Namibia, and the area surrounding the Liuwa Plains National Park in Zambia. Although the heatmap facilitated the identification of areas frequently traversed by simulated dispersers, it seemed impractical to pinpoint dispersal corridors.

### 3.4 Betweenness

The betweenness map (Figure 5) revealed distinct dispersal corridors that run within the KAZA-TFCA. Again, the region in northern Botswana emerged as wild dog dispersal hub that connected more remote regions in the study area. Towards east, the extension of this corridor ran through Chobe National Park into Hwange National Park. From there, a further extension connected to Matusadona National Park in Zimbabwe. Northwest of the Linyanyi ecosystem, a major corridor expanded into Angola, where it splitted and finally traversed over a long stretch of unprotected area into Zambia’s Kafue National Park. 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 Mio, IQR = 54.311 Mio, Figure S6b). In general, there were few corridors that directly linked the peripheral regions of the KAZA-TFCA and passed through unprotected areas outside the KAZA-TFCA (mean betweenness outside KAZA-TFCA = 2.685 Mio, IQR = 9.891 Mio, Figure S6b). Compared to the heatmap, the betweenness map facilitated the identification of dispersal corridors between habitat patches.

### 3.5 Inter-Patch Connectivity

The map of inter-patch connectivity showed that the relative frequency at which simulated dispersers moved from one NP to another varied, as did the average dispersal duration required to make these connections (Figure 6). Overall, inter-patch connectivity between NPs in Angola, Namibia, Botswana, and Zimbabwe appeared to be high; between 54% and 87% of individuals originating from a NP in these countries successfully moved into some other NP (Figure S6a). Conversely, only 19% of the dispersers leaving from a NP in Zambia managed to find a route into some other NP (Figure S6b). Prior to reaching another NP, individuals from Angola, Namibia, Botswana, Zimbabwe, and Zambia had to move for an average of 630, 640, 940, 1045, and 890 steps, respectively. For some NPs, we also detected imbalances between the number of ingoing and outgoing links, hinting at possible source-sink dynamics. From Chobe NP, for instance, 510 individuals reached into Moremi NP, yet the opposite route was only realized by 340 individuals. However, relative to the number of simulated individuals in these NPs, these numbers imply fractions of 50% and 68%. Interestingly, it also appears that the dispersal corridor between Angola’s NPs and the Kafue NP in Zambia identified in Figure 6 is only rarely realized.

## 4 Discussion

### 4.1 Short Summary

We presented a three-step workflow to simulate dispersal and assess landscape connectivity. We also demonstrated application of the three steps using empirical dispersal 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 dispersing wild dogs move through the available landscape. In step two, we employed the fitted model to simulate 80,000 dispersing wild dogs moving 2,000 steps across the extent of the KAZA-TFCA, the world’s largest transboundary conservation area. In step three, we converted simulations into three complementary connectivity maps, each emphasizing a different aspect of landscape connectivity. The set of maps included a heatmap revealing frequently traversed areas, a betweenness-map delineating critical dispersal corridors, and a map of inter-patch connectivity indicating the presence and intensity of functional links between NPs and the average dispersal duration required to make those links. With this, we showed that simulations from ISSFs overcome several conceptual shortcomings inherent to more traditional connectivity modeling techniques, such as LCPA and CT.

### 4.2 Movement Model

Our movement model of dispersing wild dogs, which included interactions between habitat and movement covariates, effectively rendered habitat and movement preferences of dispersers, leading to a significant improvement in predictive performance compared to an earlier model that omitted such interactions (Hofmann et al., 2021a). Results on habitat preferences 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), yet by also rendering movement preferences, we were able to model several additional complexities common to dispersal. For instance, by including the appropriate interactions in the movement model we could accommodate that dispersers move with directional persistence and exhibit step lengths that are correlated with turning angles. Albeit the same autocorrelation could be rendered by sampling step lengths and turning angles from copula probability distributions (Hodel and Fieberg, 2021a,b), the ISSF framework allowed us to incorporate correlations directly in the movement model. We only considered first order autocorrelation, i.e. correlation between two consecutive steps, although higher order autocorrelation is conceivable and may be desir-

able to model (Dray et al., 2010; McClintock et al., 2012). 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). Aside from modeling autocorrelation in consecutive movements, we also rendered potential dependencies between movement and habitat preferences by forming interactions between habitat covariates and movement covariates. For example, our final model contained an interaction between water-cover and step lengths showing that dispersers realized shorter steps in areas covered by water or an interaction between turning angles and water-cover highlighting that dispersers moved more tortuous in areas covered by water. The results themselves are not surprising, considering that wild dogs can only cross water by swimming or wading. Nevertheless, the ability of accompanying such effects in a single model is what makes ISSFs such a great and flexible tool for rendering a variety of different movement behaviors (Avgar et al., 2016; Fieberg et al., 2021). For this reason, we believe the method is a perfectly suited framework for individual-based simulations that serve to examine connectivity.

### 4.3 Simulation

Our simulation of 80'000 dispersers moving 2'000 steps across the KAZA-TFCA required five days of computation on a modern desktop machine (AMD Ryzen 7 2700X processor with 8 x 3.6 GHz and 16 logical cores, 64 GB of RAM). The long simulation time was primarily caused by the massive extent considered (ca. 1.8 Mio km<sup>2</sup>) and the large number of dispersers simulated. Most connectivity studies are limited to smaller extents (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 achieve faster simulation times. We also believe that fewer simulated dispersers will often suffice, as the relative traversal frequency by simulated individuals through randomly placed checkpoints across our study area converged already after 10,500 simulated dispersal trajectories. The number of required simulations to achieve reliable estimates of connectivity will, however, vary depending on the structure of the landscape and the dispersal ability of the focal species (Gustafson and Gardner, 1996). For species that disperse short distances through homogeneous environments, already 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.

## 4.4 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. We previously identified the same area as potential dispersal hotspot using LCPA (Hofmann et al., 2021a), yet it was not clear whether this was a consequence of the region being located in the center of the study area and connections being enforced between predefined start and endpoints. Contrary to LCPA, a simulation-based approach as presented in this paper does not require predefined endpoints because endpoints emerge naturally as the result from a simulated dispersal trajectories. Not having to pre-determine endpoints is especially useful for dispersal studies, as known endpoints are usually an unrealistic assumption (Elliot et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020). Simultaneously, simulations permit to detect potential routes that do not necessarily lead into suitable habitats but into ecological traps (Dwernychuk and Boag, 1972; Van der Meer et al., 2014) or into areas with a high susceptibility for human wildlife conflicts (Cushman et al., 2018). Irrespective of the fact that simulated individuals were no longer enforced to move towards known endpoints, a large number of simulated individuals traversed the region in northern Botswana, demonstrating that this hotspot is not merely an artifact but truly results from its favorable landscape characteristics.

In contrast to the heatmap, the betweenness map emphasized relatively narrow and linear movement routes and thus facilitated the identification of discrete movement corridors in the study area. The resulting map reinforced our notion that Botswana plays a central role for the establishment of connections into more remote regions of the KAZA-TFCA. While in this case both the heatmap and the betweenness map attribute high importance to the region in northern Botswana, there are other regions in which the two metrics do not necessarily coincide. The stretch of unprotected land between Luengue-Luiana NP in Angola and the Kafue NP in Zambia, for instance, receives a high betweenness-score, yet is only rarely traversed by dispersers according to the heatmap. This implies that the corridor takes on a crucial role for connecting Luengue-Luiana NP to Kafue NP, yet is in reality only traversed rarely. These contrasts highlight the value of consulting multiple metrics when assessing connectivity.

As a final piece to the trinity of connectivity maps, we produced a map of inter-patch connectivity that strictly focussed on NPs. The map depicted the frequency at which sim-

ulated individuals moved between NPs as well as the average duration (in steps) required to realize them. Calculating dispersal durations was only possible because dispersal trajectories were simulated spatio-temporally explicitly, something that is currently impossible using LCPA or CT. An explicit representation of time enables to answer 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, rendering time explicitly yields opportunities to study how seasonality affects connectivity and to investigate whether dispersal corridors are only available temporarily or all-year round (*dynamic connectivity*; Zeller et al., 2020). With LCPA or CT, seasonality can currently only be incorporated by generating seasonal permeability surfaces and repeating the connectivity analysis for each surface individually (e.g. Benz et al., 2016; Osipova et al., 2019). With simulations from ISSFs, on the other hand, seasonal changes in the environment could be rendered dynamically “as the dispersers move”, so that simulated individuals could directly respond such fluctuations.

## 4.5 Disadvantages of ISSF Simulations

Despite the many benefits and great flexibility offered by simulations from ISSFs, one also must be aware of the associated non-trivial but important modeling decisions. Here, we will elaborate on four modeling decisions concerning: (1) the number of simulated individuals, (2) the location of source points, (3) the simulated dispersal duration, and (4) behavior at map boundaries.

(1) When simulating dispersal, the modeler needs to decide on the number of simulated individuals. A higher number is always desirable, as each additional disperser provides information about landscape connectivity, yet every individual entails computational costs. Consequently, a trade-off needs to be managed and the benefits of simulating additional dispersers needs to be gauged against the cost of computation. Signer et al. (2017) suggests to handle this trade-off by simulating additional individuals only until the metrics of interest converge towards their steady state. We incorporated this idea and employed the relative traversal frequency across randomly placed checkpoints to verify that the number of simulated individuals was large enough. However, the exact number of required individuals might vary depending on the target metric and the anticipated connectivity map. More sophisticated target metrics tailored for each connectivity map will need to be developed in the future.

(2) To initiate dispersers, a modeler needs to provide a set of source points. 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). We lacked precise knowledge about wild dog densities in the different protected areas, so we distributed source points within them randomly. In cases where such data is available (e.g. thanks to a habitat suitability model; Squires et al., 2013), source points can be distributed accordingly, reflecting that the number of dispersers may not strictly scale with the size of the source area. Alternatively, source points can be distributed homogeneously across suitable habitats and only later be weighted when deriving connectivity metrics. After all, the challenge of selecting meaningful source points is not unique to individual-based simulations and also applies to LCPA or CT.

(3) When employing ISSFs to simulate dispersers, it is required to decide on the number of simulated steps (i.e. dispersal durations). If sufficient dispersal data of the focal species has been collected, dispersal durations could be sampled from observed dispersal events. In our case, the low number of observed dispersal events and the high variability in wild dog dispersal durations (see (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020; Hofmann et al., 2021a)) prevented us from sampling from observed dispersal events. Instead, we simulated all individuals for 2'000 steps, which is at the upper end of observed dispersal durations. This allowed us to subsample trajectories to shorter durations after their simulations and to investigate the sensitivity of our connectivity maps with respect to exact dispersal durations (Figures S4 and S5).

(4) Unless simulated individuals are strongly drawn towards a point of attraction (e.g. Signer et al. (2017)), some individuals will inevitably approach a map boundary such that one of their proposed random steps leaves the study area. In theoretical applications, this problem can be circumvented by simulating movement on a torus where no map boundaries exist (?). For real world data, however, other approaches are needed. One possible solution would be to simply terminate the simulation of the respective individual as soon as one of its random steps transgresses a map border. This approach implicitly assumes that the respective animal left the study area and will never return. In cases where individuals are released near map borders, this approach will be problematic, as already a single transgressing random step will break the simulation, thus strongly biasing dispersal from patches near map borders. We tried to mitigate this issue in two complementary ways. First, we artificially increased covariate layers (and therefore the study area) by a buffer zone with randomized covariate values. The same method has already proven effective in mitigating edge-effects for graph-based methods (Koen et al., 2010). In our case, the buffer enabled dispersers to

leave and re-enter the main study area, as well as to initiate potential immigrants into our study system. As a second mitigation measure, we resampled any transgressing random steps until they fully lied within the study area, thus enforcing individuals to always remain within the study area. Given that only very few simulated individuals were repelled by a virtual map boundary, we conclude that the two measures effectively obviated boundary effects.

## 4.6 Conclusion

To this end, we proposed and applied a simple three-step workflow that relies on ISSF-analysis and enables to simulate dispersal and assess landscape connectivity. The proposed workflow 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. In our case study, the workflow proved useful to investigate landscape connectivity for the endangered African wild dog within the KAZA-TFCA ecosystem and allowed us to pinpoint frequently used corridors and dispersal hubs. We hope to have sparked interest in the powerful framework of ISSFs for investigating dispersal connectivity, while at the same time conferring some of the non-trivial modeling decisions involved.

## 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 workflow using simulated data are provided through Github (<https://github.com/DavidDHofmann/DispersalSimulation>). In addition, all codes required for the African wild dog case study will be made available through an online repository at the time of publication.

## 7 Acknowledgements

We thank the Ministry of Environment and Tourism of Botswana for granting permission to conduct this research. We thank C. Botes, I. Clavadetscher, and G. Camenisch for assisting with wild dog immobilizations. We also thank B. Abrahms for sharing her data of three dispersing wild dogs. Furthermore, we would like to thank Johannes Signer for assisting with the simulation algorithm. This study was funded by Basler Stiftung für Biologische Forschung, Claraz Foundation, Idea Wild, Jacot Foundation, National Geographic Society, Parrotia Stiftung, Stiftung Temperatio, Wilderness Wildlife Trust Foundation, Forschungskredit der Universität Zürich, and a Swiss National Science Foundation Grant (31003A\_182286) to A. Ozgul.

## References

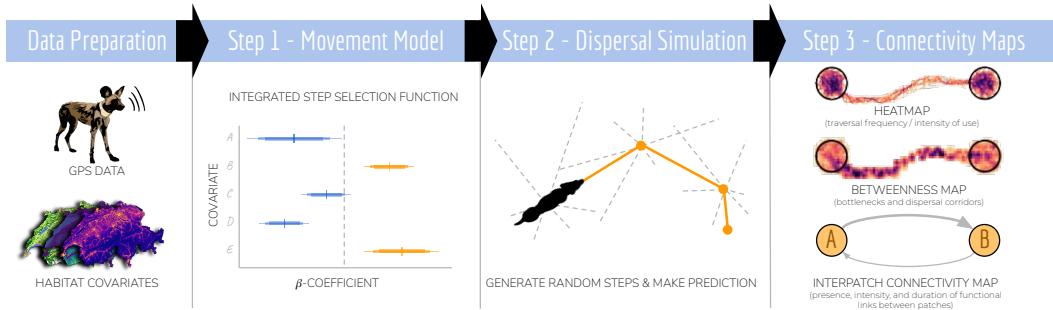
- Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., and Brashares, J. S. (2017). Does Wildlife Resource Selection Accurately Inform Corridor Conservation? *Journal of Applied Ecology*, 54(2):412–422.
- Adriaensen, F., Chardon, J., De Blust, G., Swinnen, E., Villalba, S., Gulinck, 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.
- Börger, L. and Fryxell, J. (2012). Quantifying Individual Differences in Dispersal Using Net Squared Displacement. In Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M., editors, *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.
- 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.

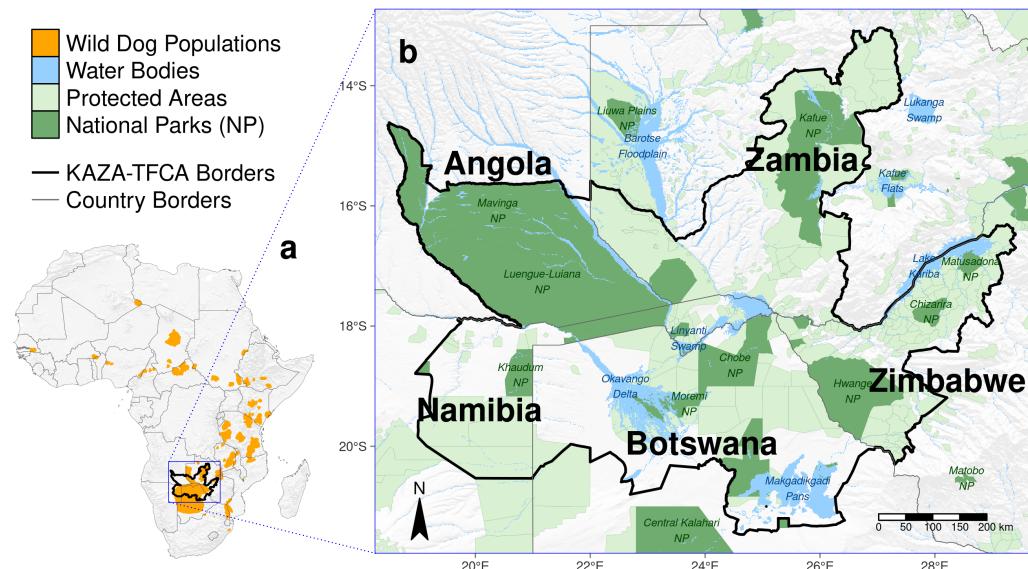
- Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., and Dancose, K. (2009). Group-Size-Mediated Habitat Selection and Group Fusion–Fission Dynamics of Bison under Predation Risk. *Ecology*, 90(9):2480–2490.
- Frankham, R., Briscoe, D. A., and Ballou, J. D. (2002). *Introduction to Conservation 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). Cylcop: 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., Garraway, 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., Hartter, 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*.

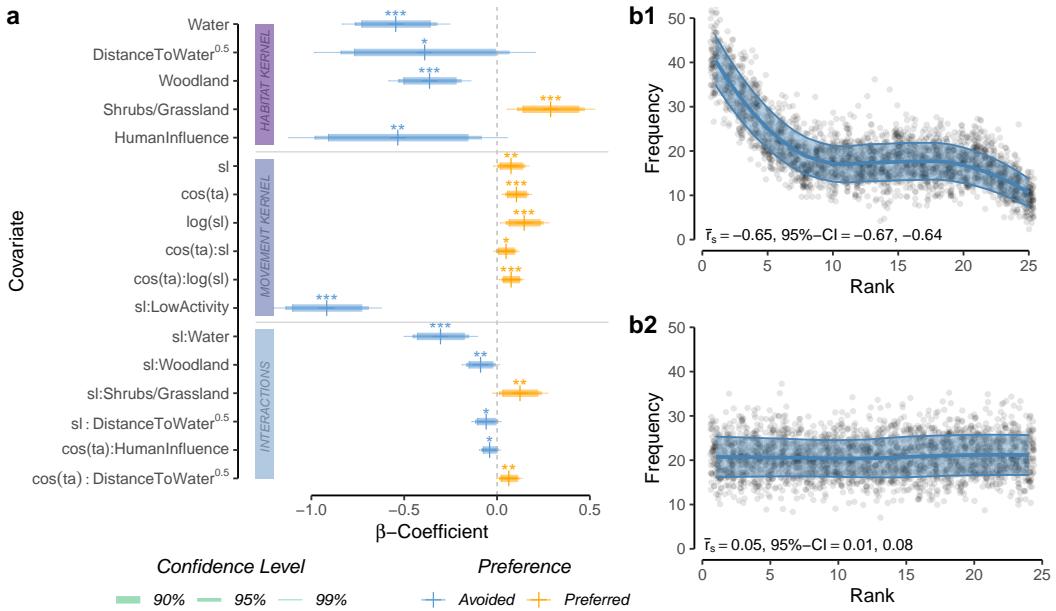
- Sawyer, S. C., Epps, C. W., and Brashares, J. S. (2011). Placing Linkages among Fragmented Habitats: Do Least-Cost Models Reflect How Animals Use Landscapes? *Journal of Applied Ecology*, 48(3):668–678.
- Signer, J., Fieberg, J., and Avgar, T. (2017). Estimating Utilization Distributions from Fitted Step-Selection Functions. *Ecosphere*, 8(4):e01771.
- Squires, J. R., DeCesare, N. J., Olson, L. E., Kolbe, J. A., Hebblewhite, M., and Parks, S. A. (2013). Combining Resource Selection and Movement Behavior to Predict Corridors for Canada Lynx at their Southern Range Periphery. *Biological Conservation*, 157:187–195.
- 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., Strelbel, 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. T12436A1671116.
- Zeller, K. A., McGarigal, K., and Whiteley, A. R. (2012). Estimating Landscape Resistance to Movement: A Review. *Landscape Ecology*, 27(6):777–797.
- 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.



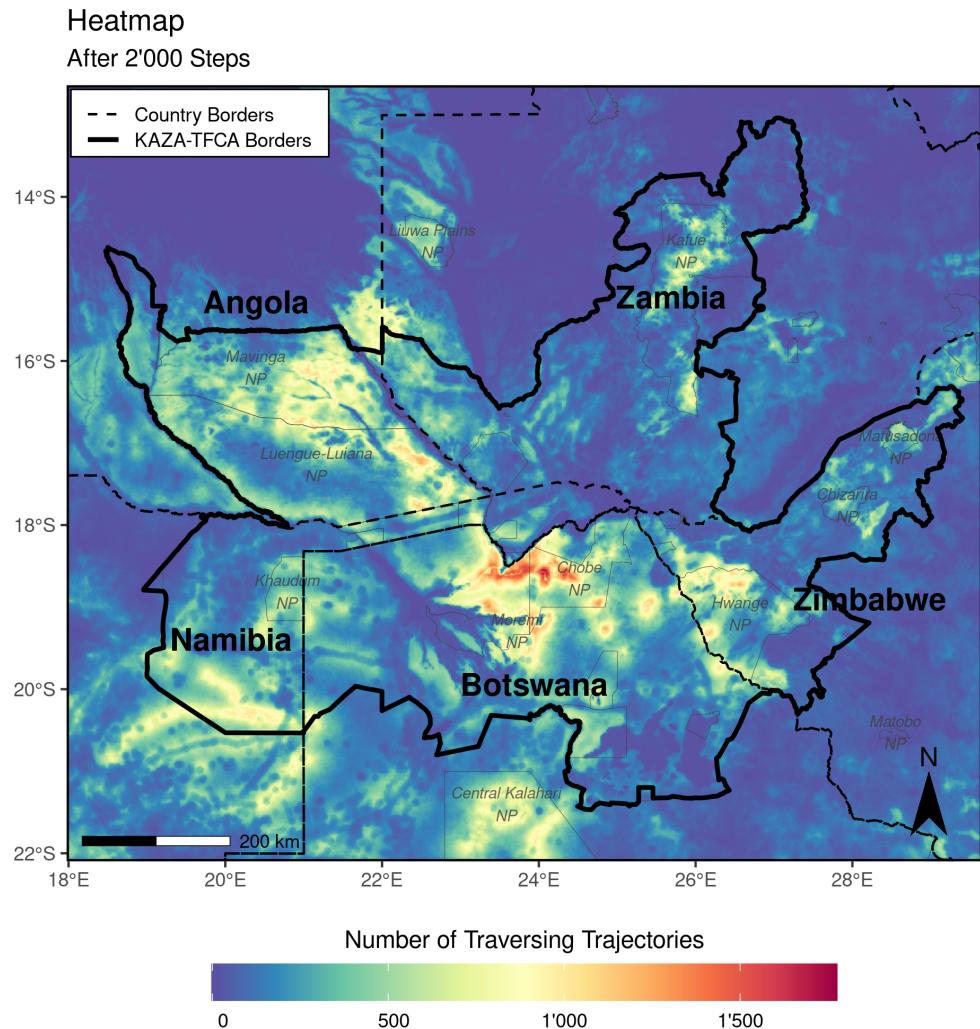
**Figure 1:** Flowchart of the simulation-based connectivity analysis as proposed in this article. First, GPS data and habitat covariates have to be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and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



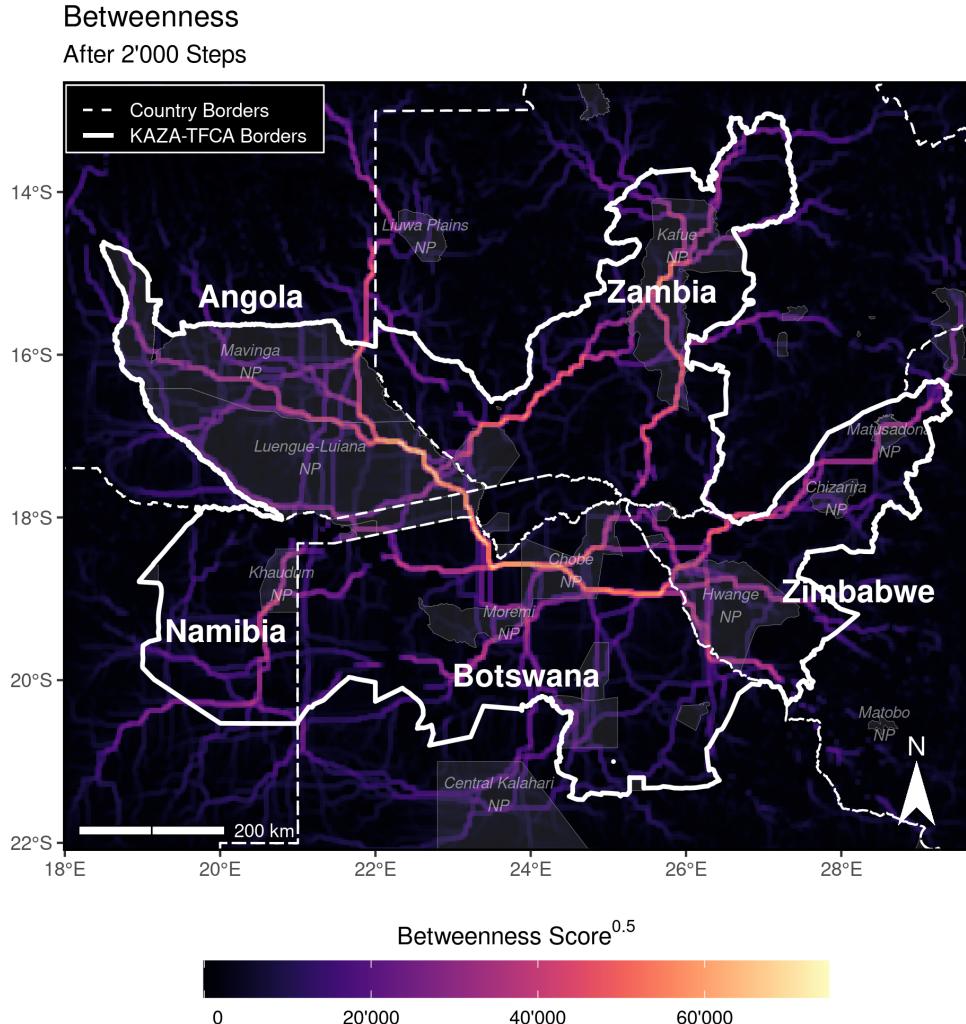
**Figure 2:** Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA which comprises parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA currently represents the world's largest terrestrial transfrontier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



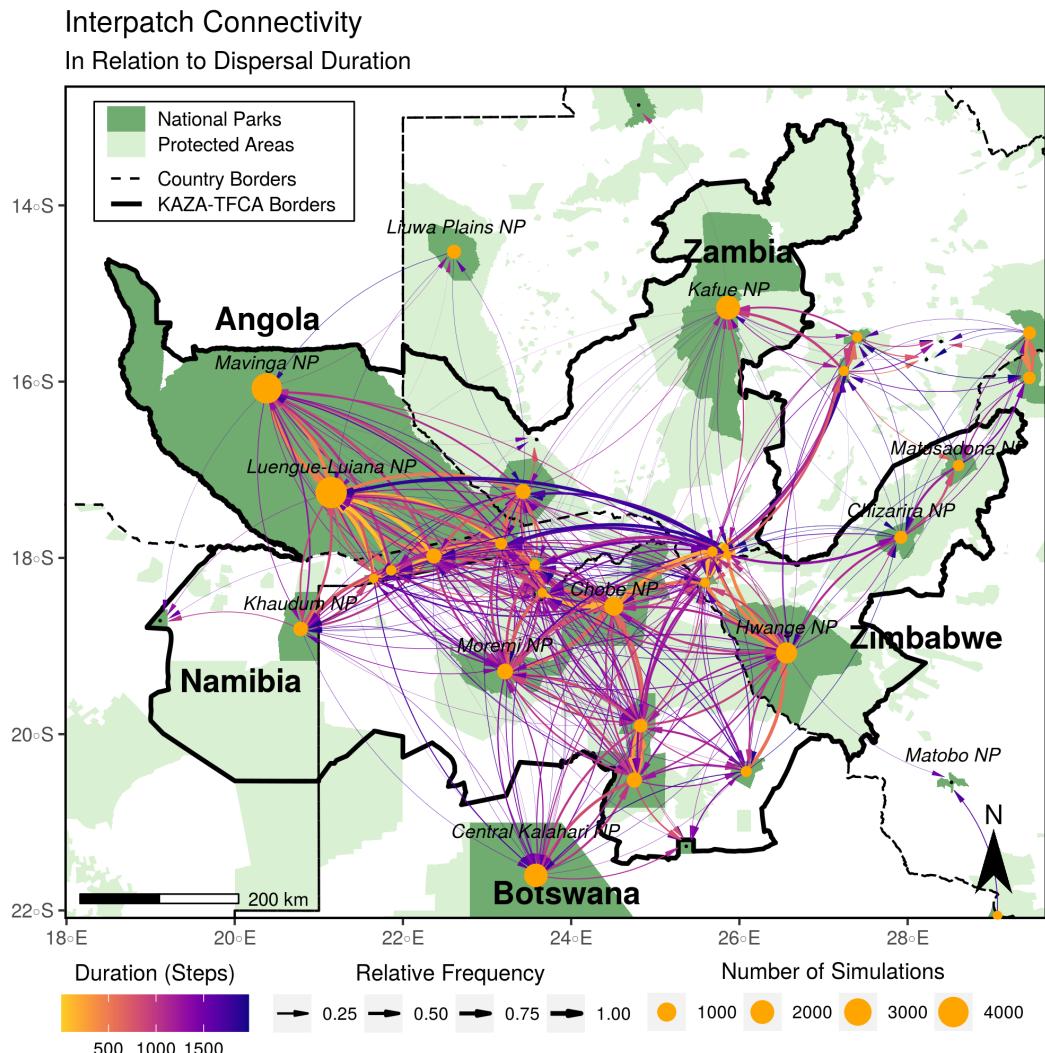
**Figure 3:** (a) Most parsimonious movement model for dispersing wild dogs. The model comprises a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% confidence-intervals for the respective  $\beta$ -coefficients. Significance 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, 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<sup>2</sup> 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.