

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

David D. Hofmann^{1,2,§} Gabriele Cozzi^{1,2} John W. McNutt² Arpat Ozgul¹
Dominik M. Behr^{1,2}

February 7, 2022

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

² Botswana Predator Conservation Program, Private Bag 13, Maun, Botswana.

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

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

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

Abstract

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 simulating dispersal movements explicitly across the landscape, a unified approach for such simulations is lacking.

Here, we present a simple three-step approach to simulate dispersal movements and to assess connectivity using empirical GPS movement data and a set of habitat covariates. In step one, integrated step-selection functions are used to fit a mechanistic movement model describing habitat and movement preferences of dispersing individuals. In step two, the parameterized model is used to simulate dispersal trajectories across the study area. In step three, a set of three complementary connectivity maps is derived: 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 applied the approach to GPS data collected on dispersing individuals of the endangered African wild dog (*Lycaon pictus*) inhabiting the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA) in southern Africa.

Besides providing insights into the movement and habitat preferences of dispersing individuals, our movement model also rendered how movement behavior depended on habitat conditions. The model thereby substantially outperformed a model that omitted such interactions. While we simulated a total of 80,000 dispersal trajectories, metrics of connectivity only marginally changed beyond 10,500 simulations, suggesting that fewer simulations would have sufficed. The three connectivity maps derived from simulations revealed several dispersal hotspots and corridors across the extent of our study area. Each map emphasized a different aspect of landscape connectivity, thus highlighting their complementary nature. Overall, our case study demonstrates that a simulation-based approach utilizing step-selection functions offers a simple yet powerful alternative to traditional connectivity modeling techniques. Our approach not only makes fewer unrealistic assumptions about dispersal but also permits a more mechanistic understanding of dispersal movements and landscape connectivity. It is thus useful for a variety of applications in ecological, evolutionary, and conservation research.

Contents

1	Introduction	1
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
2	Methods	4
2.1	Case Study	4
2.1.1	GPS Data	4
2.1.2	Study Area	4
2.1.3	Covariates	4
2.2	Step 1 - Movement Model	5
2.3	Step 2 - Dispersal Simulation	7
2.4	Step 3 - Connectivity Maps	8
2.4.1	Heatmap	8
2.4.2	Betweenness Map	8
2.4.3	Inter-Patch Connectivity Map	9
3	Results	9
3.1	Movement Model	9
3.2	Dispersal Simulation	10
3.3	Heatmap	10
3.4	Betweenness	11
3.5	Inter-Patch Connectivity	11
4	Discussion	12
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
5	Authors' Contributions	16
6	Data Availability	17
7	Acknowledgements	17

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). 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 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, the large number of subjective modeling decisions required by IBMMs renders 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, such that statements about the expected duration for moving between habitat patches 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 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 consecutive steps (Diniz et al., 2019). Finally, simulations from IBMMs do not enforce movement or connections towards preconceived endpoints, thereby preventing biases arising from misplaced endpoints. Despite these advantages, a unifying framework 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 unifies the application of dispersal simulations to assess connectivity will, however, be critical to safeguard interspecific comparability and reproducibility 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, GPS movement data of dispersing individuals is combined with habitat covariates to fit a mechanistic movement model via integrated step-selection functions (ISSFs, Avgar et al., 2016). ISSFs allow inference on the study species' habitat kernel (i.e. habitat preferences), its movement kernel (i.e. movement preferences/capabilities), as well as potential interactions between the two (Avgar et al., 2016; Fieberg et al., 2021). In step two, the parametrized movement model is used to simulate individual dispersal trajectories starting from randomly placed source points. 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, the simulated trajec-

tories are converted into three complementary connectivity maps; (i) a heatmap revealing areas that are frequently traversed by 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 functional links between habitat patches, as well as the average dispersal duration required for the realization of those connections (e.g. Gustafson and Gardner, 1996; Kanagaraj et al., 2013).

1.5 Case Study

We showcase the application of the proposed approach (Figure 1) using GPS movement data collected on dispersing individuals of the endangered African wild dog (*Lycaan 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) or 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 on our three-step approach would overcome several of the above highlighted conceptual shortcomings of traditional connectivity models, while providing a more detailed view on movement behavior during dispersal.

2 Methods

2.1 Case Study

2.1.1 GPS Data

We applied the three step approach mentioned above 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 (details on the data collection can be found in Cozzi et al. (2020) and Hofmann et al. (2021a)). During dispersal, GPS collars recorded a fix every 4 hours and regularly transmitted data over the Iridium satellite system. To ensure regular 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 ± 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).

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 is still human-dominated (e.g. roads, agricultural sites, and settlements). We used NPs as patches to calculate inter-patch connectivity (cf. Section 2.4.3). The decision to only consider NPs as patches was purely out of simplicity and does not imply that dispersal between other protected areas does not occur.

2.1.3 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 in water-cover of major water bodies 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).

Besides habitat covariates, we computed movement metrics that we used as movement covariates in the ISSF models (Avgar et al., 2016; Fieberg et al., 2021). Specifically, we computed for each step 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). 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). 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 used ISSFs (Avgar et al., 2016) to parametrize a mechanistic movement model starting from GPS movement data collected on dispersing individuals. More specifically, we paired each realized (i.e. observed) step with a set of 24 randomly generated alternative steps. A realized step plus its 24 random steps formed a 25-step-stratum and 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 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. For each step, we further calculated the movement metrics `sl`, `log(sl)`, and `cos(ta)`. 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 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 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 preferences (i.e. the β -coefficients), we used mixed effects conditional logistic regression analysis (Muff et al., 2020), implemented through the r-package `glmmTMB` (Brooks et al., 2017). The method introduced by Muff et al. (2020) allows to model random slopes, yet requires to fix the variance of the stratum specific intercept to a large value. We therefore fixed the variance of the stratum specific intercept to an arbitrary high value of 10^6 and used disperser identity to model random slopes for all covariates.

The structure of 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 interactions between all movement covariates and habitat covariates, thus reflecting that movement behavior 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). 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 80'000 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 different habitat covariate layers and 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.

As source points for the simulations, we distributed 50,000 points at random locations inside protected areas that were larger than the average home range of resident wild dog packs (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 individuals to remain within the expanded study area.

To ensure reliable connectivity estimates, we determined the number of simulated dispersal trajectories required for connectivity 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 (ω) as costs, we inverted the traversal-frequency through each raster-cell by applying $\omega = \frac{\text{mean}(\text{TraversalFrequency})}{\text{TraversalFrequency}_i}$. Consequently, regularly used edges received small weights (i.e. low costs) and vice versa. Finally, 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 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.

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 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 $\bar{r}_{s,\text{realized}}$ and $\bar{r}_{s,\text{random}}$ did not overlap). Moreover, the model correctly assigned high selection scores to realized steps (Figure 3b), indicating a good fit between predictions and observations. Compared to the base model ($\bar{r}_{s,\text{realized}} = -0.55; 95\% - CI = [-0.57, -0.52]$; Hofmann et al., 2021a), the inclusion of several interactions between movement and habitat covariates significantly improved model performance ($\bar{r}_{s,\text{realized}} = -0.65; 95\% - CI = [-0.67, -0.64]$).

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 strong effect for

the variable `LowActivity`, suggesting that dispersing wild dogs moved faster during twilight and at night (i.e. between 17:00 and 09:00 o'clock) in comparison to the rest of the day (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 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 simulating additional trajectories diminished quickly (Figure S3).

3.3 Heatmap

The heatmap (Figure 4), which resulted from the sum of all simulated dispersal trajectories, allowed us to pinpoint areas that were intensely used by simulated dispersers. This enabled us to compare areas inside and outside the KAZA-TFCA borders with respect to the frequency at which they were visited. 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 act as movement barriers. The presence of extensive water bodies, such as, for example, the Okavango Delta, the Makgadikgadi Pan, and the Linyanti swamp, substantially restricted dispersal movements and limited realized connectivity inside the KAZA-TFCA. Although 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 distinct dispersal corridors that run across the study area. In comparison to the heatmap, the betweenness map thus facilitated the identification of narrower and more linear routes that are used to disperse between distinct 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 = 6.947×10^6 , IQR = 54.311×10^6 , 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 = 2.685×10^6 , IQR = 9.891×10^6 , 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 NP to another varied, as did the average dispersal duration required to make these connections (Figure 6). 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 Moremi NP, yet the opposite route was only realized by 340 individuals. However, relative to the number of simulated individuals, these numbers imply fractions of 50% and 68%, respectively. 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 S7a). Conversely, only 19% of the dispersers leaving from a NP in Zambia managed to find their way into some other NP (Figure S7b). 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. Furthermore, it appeared 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

Here, we proposed a three-step approach to assess landscape connectivity via simulated dispersal trajectories, and 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. In step two, we employed the movement model to simulate dispersal trajectories across the landscape. 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). Such simulations from ISSFs overcome several conceptual shortcomings inherent to traditional connectivity modeling techniques, such as LCPA and CT, and enable a more detailed view on landscape connectivity.

4.2 Movement Model

Our results on habitat preferences showed that dispersers avoid areas dominated by humans and covered by water, but select 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, by also accounting for movement preferences, we were able to model several additional complexities common to dispersal. For instance, our model attributed a strong effect to the binary variable `LowActivity`, demonstrating the necessity to consider different activity period of the focal species. By including an interaction between turning angle and step length we could furthermore accommodate that dispersers exhibit step lengths that are correlated with turning angles, meaning turning angles are 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 include correlations 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 desirable to model (Dray et al., 2010; McClintock et al., 2012). This will, however, 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, something that surely was to be expected. 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 LCPA, however, following their analysis it was not clear whether this was the consequence of the central location of the region and connections being enforced between predefined start and endpoints. Contrary to LCPA, a simulation-based approach as presented here does not require predefined endpoints, as endpoints emerge naturally from the simulated dispersal trajectories. Not having to predefine 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). Simulations also enable the detection of potential routes that do not lead into suitable habitats (Dwernychuk and Boag, 1972; Van der Meer et al., 2014) but into 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 and 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, while the stretch of unprotected land between Luengue-Luiana NP in Angola and the Kafue NP in Zambia was characterized by a high betweenness-score, it only received a low score on the heatmap. The reason for this difference can be found in the differential way in which the maps view connectivity. While the heatmap assigns high connectivity to areas that are frequently traversed, it does not distinguish between areas that truly bring individuals into different parts of the study area and regions that lead into ecological traps. The converse is true on the betweenness map, which strictly

highlights regions that promote movement into other areas of the landscape and thus might promote gene-flow. Because neither of the two maps provides insights into functional links between distinct habitat patches or how connections depend on the dispersal duration, we also produced a map of inter-patch connectivity. The map depicted the frequency at which simulated individuals moved between NPs as well as the average duration (in steps) required to realize them. Calculating dispersal durations was possible because dispersal trajectories were simulated spatially and temporally explicitly, something that is currently unfeasible with LCPA or CT. An explicit representation of time enables answering 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 by repeatedly running a connectivity analysis using an array of seasonal permeability surfaces (e.g. Benz et al., 2016; Osipova et al., 2019). In contrast, simulations from ISSFs allow the environment to change “as the dispersers move”, so that simulated trajectories can dynamically respond to seasonal fluctuations in the environment.

Overall, the contrasts highlight the complementary nature of the presented connectivity maps and emphasize the value of consulting multiple metrics when assessing connectivity.

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 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 of the study area considered (ca. 1.8 Mio km²) and the large number of trajectories simulated. 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 number of required simulations to achieve reliable estimates of connectivity will, however,

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 necessary 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 of which 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) 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 entails computational costs, so a trade-off needs to be managed. Here, we followed Signer et al. (2017) who suggested to simulate additional individuals only until the metrics of interest converge towards a steady state. The exact number of required individuals might, however, vary depending on the target metric and the anticipated connectivity map. More sophisticated target metrics tailored to each of the presented 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 disperser will be released. We placed source points within protected areas large enough to sustain viable wild dog populations, implicitly assuming 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 the presence and abundance of wild dogs in the different protected areas, so we distributed source randomly points within them. In cases where such data is available, source points could be distributed accordingly, reflecting that the number of simulated trajectories does not necessarily scale with the size of the source area. Alternatively, source points could be distributed homogeneously and only later be weighted when computing the heatmap, betweenness map, or inter-patch connectivity map. In any case, the challenge of selecting meaningful source points is not unique to individual-based simulations but also applies to LCPA or CT.

(3) The use of ISSFs to simulate dispersers requires deciding on the number of simulated steps (i.e. dispersal durations). If sufficient dispersal data of the focal species has been collected, dispersal durations can be sampled from observed dispersal events. Due to the low

number of observed dispersal events, we opted against this solution and instead simulated all individuals for 2,000 steps, which is at the upper end of observed dispersal durations (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020; Hofmann et al., 2021a). This approach also had the advantage that it allowed us to subsample simulated trajectories to shorter durations 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 (e.g. Signer et al., 2017), some trajectories will inevitably approach a map boundary and one or more of the generated random steps will leave the study area. One solution to deal with such cases would be to simply terminate the simulation of the affected trajectory, implicitly assuming that the respective animal left the study area. However, this approach might produce ambiguous results in cases where individuals are released near map borders, since already a single random step leaving the study area will break the simulation, thus resulting in biased connectivity estimates along map borders. Rather than halting 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. With this work, we hope to have sparked interest in the application, optimization, or creation of methods to investigate dispersal movements 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 simulation 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.

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 Albert-Heim Foundation, 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., Skauge, 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 Røskuft, 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., Harter, 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. *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.

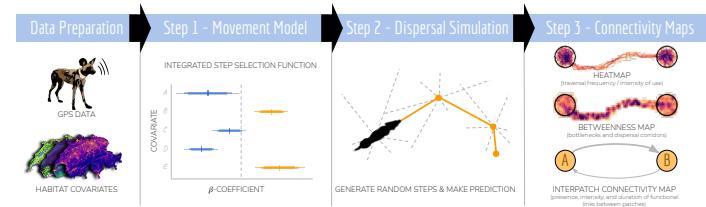


Figure 1: Flowchart of the simulation-based connectivity analysis as proposed in this article. First, GPS data and habitat covariates must be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement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

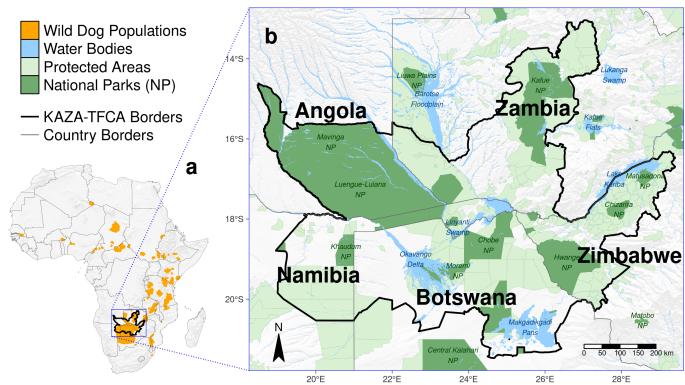
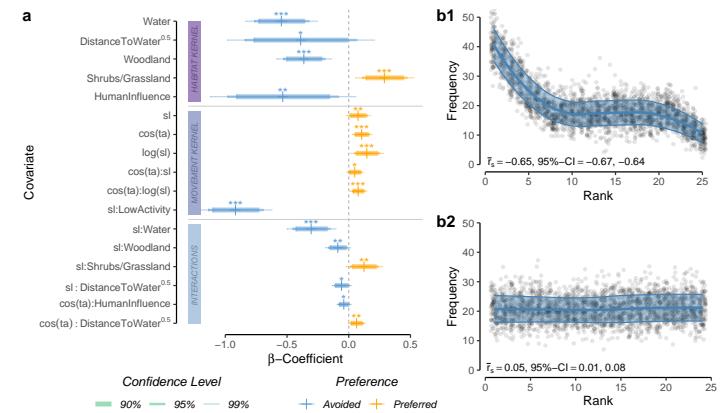


Figure 2: Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA which comprises parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA currently represents the world's largest terrestrial transfrontier conservation area, covering a total area of 520'000 km². Its main purpose is to re-establish connectivity between already-existing NPs (dark green) and other protected areas (light green).



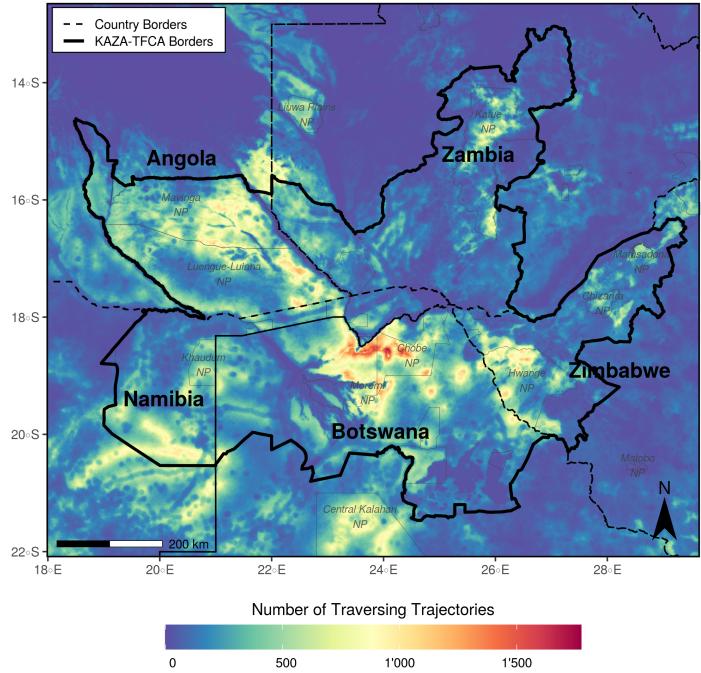
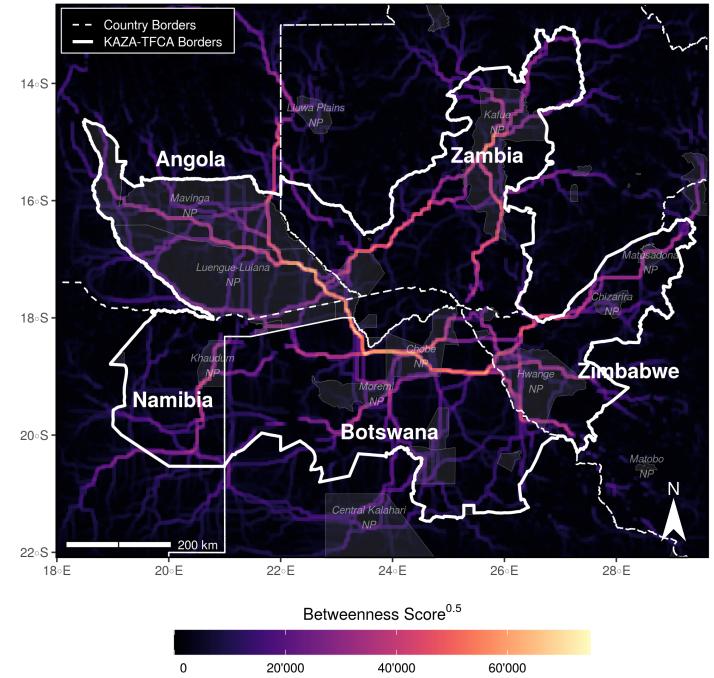


Figure 4: Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step-selection model that we fitted to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied 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.



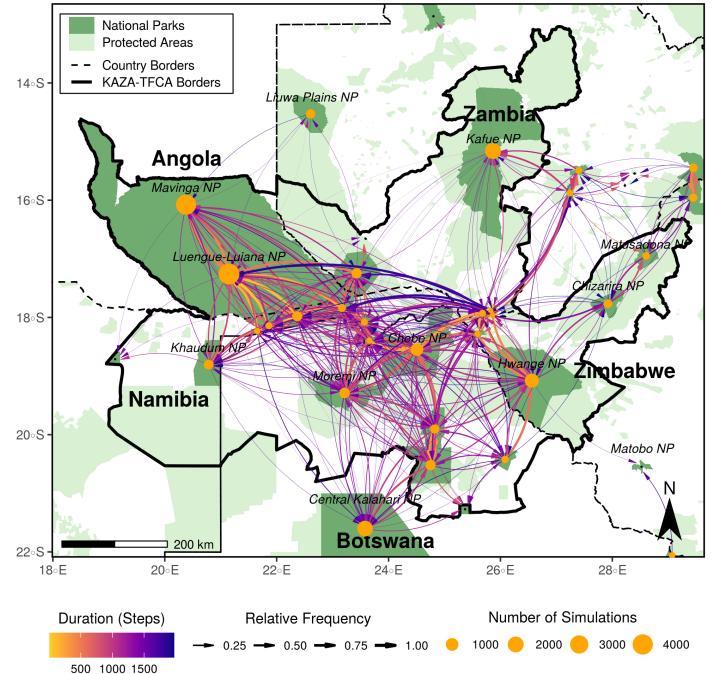


Figure 6: Map of inter-patch connectivity in relation to dispersal duration, highlighting connections between NPs (dark green). Yellow bubbles represent the center of the different NPs and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent NPs that were smaller than 700 km^2 and therefore 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.