

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

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

July 6, 2021

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

² 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, Kavango-Zambezi
Transfrontier Conservation Area, landscape connectivity, *Lycaon pictus*

Abstract

Dispersal is an important process that allows species to avoid inbreeding, colonize new habitats and reinforce non-viable subpopulations. Successful dispersal thus represents a crucial pre-requisite for long-term species persistence in wild animal populations. However, the ability to disperse is contingent a sufficient degree of landscape connectivity, which is why the estimation of connectivity and preservation of dispersal corridors has become a task of extraordinary importance for conservation authorities.

Over the past two decades, ecologists have primarily relied on analytical tools such as least-cost analysis and circuit theory to model and investigate landscape connectivity. Despite their usefulness for a diverse suite of ecological applications, both methods make several restricting assumptions that limit their usefulness in reality. Individual-based dispersal simulations have been proposed to address these shortcomings, yet due to the sheer amount of non-trivial modeling decisions decisions, a unified and objective framework to simulate dispersal is missing.

Recent innovations in movement ecology have brought forward novel opportunities to study animal dispersal and estimate landscape connectivity. In particular, the rich suite of resource selection functions, namely point-, step-, and path-selection functions, have undergone substantial improvements over the past years. Most notably, step-selection functions have been generalized to *integrated* step selection functions, which essentially represent fully mechanistic movement models based on which an individual's movement could be simulated. While such models have been applied to study *steady-state* utilization distribution resident animals, a similar approach may be useful to investigate *transient* movement behavior during dispersal and landscape connectivity.

Here, we showcase the use of integrated step selection functions as simple, individual-based, and spatially explicit movement model to simulate dispersal of the endangered African wild dog across the world's largest transboundary conservation area, the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). For this, we utilize data collected on 16 dispersing wild dog coalitions in combination with relevant habitat covariates. We analyse the data using integrated step selection functions, thereby parametrizing a fully mechanistic movement model describing how dispersing wild dogs move through the available landscape. Based on this model, we simulate 80'000 dispersers moving across the extent of the KAZA-TFCA and generate a set of three connectivity maps, each focused on a different aspect of connectivity. Finally, we discuss the benefits and pitfalls of such a simulation-based approach and highlight potential improvements to be made in the future.

Contents

1	Introduction	1
1.1	Importance of Dispersal & Connectivity (90%)	1
1.2	Advancements in GPS Technology & Movement Ecology (90%)	1
1.3	Resource Selection & Connectivity (90%)	1
1.4	Issues with Least-Cost Paths (90%)	2
1.5	Issues with Circuit Theory (90%)	3
1.6	Issues of Both Methods	3
1.7	What about IBMMs? (90%)	3
1.8	Step Selection Analysis (90%)	4
1.9	Study Species & Study Area (90%)	4
1.10	Previous Paper (90%)	5
2	Methods	5
2.1	Study Area (90%)	5
2.2	GPS Relocation Data (90%)	6
2.3	Covariates (90%)	7
2.4	Movement Model (80%)	7
2.5	Dispersal Simulation (80%)	9
2.6	Source Points (90%)	10
2.7	Convergence (80%)	10
2.8	Heatmap (100%)	11
2.9	Betweenness (80%)	11
2.10	Inter-Patch Connectivity (80%)	11
3	Results	12
3.1	Movement Model (80%)	12
3.2	Dispersal Simulation (80%)	13
3.3	Convergence (80%)	13
3.4	Heatmap (80%)	14
3.5	Betweenness (80%)	14
3.6	Inter-Patch Connectivity (80%)	14
4	Discussion	15
4.1	Short Summary (90%)	15
4.2	Movement Model (80 %)	16
4.3	Simulation (80%)	17
4.4	Maps (70%)	17
4.5	Related Literature (80%)	18
4.6	Benefits & Modeling Decisions with ISSF Simulations (70%)	19
4.7	Further Considerations (70%)	20
4.8	Conclusion (80%)	23
5	Authors' Contributions	23
6	Data Availability	24

1 Introduction

1.1 Importance of Dispersal & Connectivity (90%)

Dispersal is defined as the movement of individuals away from their natal location to the site of first reproduction Howard (1960). It is a vital process governing the social structure of wild animal populations that are distributed in space (Hanski, 1998; Clobert et al., 2012) and may strongly affect population dynamics at different spatial and social scales (Hanski, 1999a; Clobert et al., 2012). Dispersal allows species to maintain genetic diversity (Perrin and Mazalov, 1999, 2000; Frankham et al., 2002; Leigh et al., 2012; Baguette et al., 2013), to rescue small, non-viable populations (Brown and Kodric-Brown, 1977), and to promote the colonization or recolonization of unoccupied habitats (Hanski, 1999b; MacArthur and Wilson, 2001). However, successful dispersal requires a sufficient degree of landscape connectivity (Fahrig, 2003; Clobert et al., 2012), which is why the identification and protection of major dispersal corridors has become a fundamental task in conservation science (Nathan, 2008; Doerr et al., 2011; Rudnick et al., 2012). The ability to pinpoint relevant dispersal hotspots requires information on movement behavior during dispersal and knowledge about factors that limit dispersal and therefore connectivity (Baguette et al., 2013; Vasudev et al., 2015).

1.2 Advancements in GPS Technology & Movement Ecology (90%)

Thanks to novel technologies developed over the past decades, particularly of GPS/Satellite radio-collars, the use of GPS data to study animal dispersal and connectivity has accelerated (Elliot et al., 2014; Jönsson et al., 2016; Williams et al., 2019). Additionally, the advent of publicly accessible satellite imagery and sophisticated remote sensing techniques to represent the physical landscape through which individuals disperse have heralded a “golden age of animal tracking” (Kays et al., 2015). Concurrently, the availability of large amounts of empirical data and an increased computational power have led to the development of numerous techniques to study dispersal and highlight critical corridors between subpopulations (Boyce et al., 2002; Fortin et al., 2005; Cushman and Lewis, 2010; Zeller et al., 2012; Diniz et al., 2020).

1.3 Resource Selection & Connectivity (90%)

Resource selection functions (Boyce et al., 2002) and derived methods such as *step selection functions* (Fortin et al., 2005) and *path selection functions* (Cushman and Lewis, 2010) have

proven particularly useful for studying animal movement (Fieberg et al., 2020) and modeling connectivity (Diniz et al., 2020). These methods allow estimating habitat preferences of the focal species by comparing covariates at locations visited by the animal to the same covariates at locations available to, but not visited by the animal (Boyce et al., 2002; Fortin et al., 2005; Cushman and Lewis, 2010; Thurfjell et al., 2014). The so estimated preferences can then be used to predict a permeability surface, indicating the expected ease at which an animal can traverse a given area (Spear et al., 2010; Zeller et al., 2012; Etherington, 2016). Ultimately, the permeability surface serves as input to a connectivity model that is used to reveal movement corridors (Diniz et al., 2020). Two of the most prominent connectivity models are least-cost analysis (LCPA; Adriaensen et al., 2003) and circuit theory (CT; McRae, 2006; McRae et al., 2008), both graph-based methods that estimate conductance of the landscape to infer likely movement corridors. Despite their intuitive nature and ease of use, both methods make rigorous assumptions about animal movement that are often not fulfilled in reality (Diniz et al., 2020).

1.4 Issues with Least-Cost Paths (90%)

In LCP analysis, for instance, a least costly path always exists, even if associated movement costs are unreasonably high and will never be incurred by a dispersing individual. The method also presumes that animals have an infinite perceptual range and a preconceived endpoint in mind, such that they choose a cost-minimizing route accordingly. These assumptions may be fulfilled by migrating animals that typically move between a discrete set of habitats through familiar landscapes. Dispersers, on the other hand, usually move over long distances into unknown territory and are therefore less likely to be aware of associated movement costs (Koen et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020). Another issue of LCPs analysis concerns the fact that least-costly routes, by their very nature, are only one pixel wide (Pinto and Keitt, 2009). This neglects the fact that alternative routes with similar costs may exist and implies that the width of inferred movement routes depends on the resolution of chosen covariate layers and may not be biologically meaningful (Diniz et al., 2020). Although some of these deficiencies can be addressed using less stringent versions of the least cost algorithm (e.g. least-cost *corridors* (Pinto and Keitt, 2009), *thresholded* least-cost paths (Landguth et al., 2012), and *randomized* least-cost paths (Panzacchi et al., 2016; Van Moorter et al., 2021)), a certain degree of arbitrariness remains.

1.5 Issues with Circuit Theory (90%)

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

1.6 Issues of Both Methods

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

1.7 What about IBMMS? (90%)

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

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

1.8 Step Selection Analysis (90%)

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

1.9 Study Species & Study Area (90%)

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

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

1.10 Previous Paper (90%)

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

2 Methods

2.1 Study Area (90%)

The study area was defined by a bounding box centered at $-17^{\circ}13'9''\text{S}$, $23^{\circ}56'4''\text{E}$ (Figure 2a) stretching over 1.3 Mio. km^2 and encompassed the entire KAZA-TFCA (Figure 2b). The KAZA-TFCA represents the world's largest transboundary conservation area and comprises parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia. It covers a total of 520'000 km^2 and hosts diverse landscapes, ranging from savanna 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. The wet season within the KAZA-

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

2.2 GPS Relocation Data (90%)

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

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

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

2.3 Covariates (90%)

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

Besides habitat covariates, we computed movement metrics that we used as movement covariates in our models. 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 ($\cos(ta)$) (for details see (Avgar et al., 2016; Fieberg et al., 2020)). Because wild dogs follow a diurnal activity pattern (Castelló, 2018), we also coded a binary variable (`LowActivity`) indicating whether a step was realized during periods of low wild dog activity (17:00 to 09:00 local time) or high wild dog activity (09:00 to 17:00 local time). Handling and manipulation of all data, as well as all models and simulations were implemented with the statistical software R, version 3.6.6 (R Core Team, 2019). Several helper functions were written in C++ and imported into R using the Rcpp package (Eddelbuettel and François, 2011; Eddelbuettel, 2013)

2.4 Movement Model (80%)

We used ISSFs to parametrize a mechanistic movement model for dispersing wild dogs (Avgar et al., 2016). To conduct ISSF analysis, we paired each realized step with 24 random steps. An observed step plus its 24 random steps formed a 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 ($-\pi, +\pi$) and step lengths from a gamma

distribution that was fitted to realized steps (scale = 6'308, shape = 0.37). Along each step, we extracted and averaged spatial covariates using the `velox` package (Hunziker, 2021). We also calculated the movement metrics `sl`, `log(sl)`, and `cos(ta)` for each observed and random step. To facilitate model convergence, we standardized all continuous covariates to a mean of zero and a standard deviation of one. Since correlation among covariates was low ($|r| > 0.6$; Latham et al., 2011), we retained all of them for modeling.

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

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

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

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

We ran conditional logistic regression analysis in the r-package `glmmTMB` to estimate preferences of interest. To handle multiple individuals, we applied the mixed effects technique developed by (Muff et al., 2020), which allows to effectively model random slopes. Thus, we treated animal IDs as random effect and modeled random slopes for each covariate.

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

`sl:LowActivity` and `log(sl):LowActivity` to account for the fact that step lengths may differ due to wild dogs' diurnal activity pattern. To compare competing models and assess the most parsimonious movement model, 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 movement model using k-fold cross-validation for case-control studies as suggested by Fortin et al. (2009). For this, we randomly assigned 80% of the strata to a training set and the remaining 20% to a testing set. Using the training data we parametrized a movement model based on which we predicted selection scores $w(x)$ for all steps in the test data. Within each stratum, we then assigned ranks 1-25 to each step based on predicted selection scores, where rank 1 was given to the step with the highest score $w(x)$. Across all strata we determined the realized step's rank and we calculated rank frequencies of realized steps across all strata. Finally, we computed Spearman's rank correlation between ranks and associated frequencies $r_{s,realized}$. We replicated the entire procedure 100 times and computed the mean correlation coefficient ($\bar{r}_{s,realized}$), as well as its 95% confidence interval across all replicates. For comparison, we repeated the same procedure 100 times assuming random preferences, which we implemented by discarding the realized step from all strata and identifying the rank of a random step in each stratum. Again, we calculated Spearman's rank correlation coefficient ($r_{s,random}$), its mean across repetitions ($\bar{r}_{s,random}$), and its 95% confidence interval. This validation ultimately proofs a significant prediction in case the confidence intervals of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ do not overlap.

2.5 Dispersal Simulation (80%)

We used the most parsimonious movement model to simulate 80'000 virtual dispersers moving across the KAZA-TFCA. The simulation 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) Departing 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. Similar to the input data, each random step represented the straight line movement within 4 hours. To prevent unreasonably large steps, we capped sampled step lengths to a maximum of 35 km, which corresponded to the farthest distance ever traveled within 4 hours by one of our dispersers. (3) Along each random step, we extracted and averaged habitat covariates and we calculated movement covariates. To ensure compatible scales, we standardized extracted values using the same parameters applied to our input data. (4)

We applied the parametrized movement model to predict the selection score $w(x)$ for each step and we translated predicted scores into probabilities using Equation (Equation 2). (5) We sampled one of the random steps based on predicted probabilities and determined the animal's new position. We repeated steps (2) to (5) until 2'000 steps were realized, implying a total 160 Mio. simulated steps.

To minimize the influence of 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 adding 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 border of this buffer zone, we resampled transgressing steps until they fully lied within the buffer, thereby forcing simulated individuals to “bounce off” such invisible borders.

2.6 Source Points (90%)

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

2.7 Convergence (80%)

To verify that the number of simulated individuals sufficed to ensure reliable estimates of connectivity, we evaluated how the relative traversal frequency across the landscape changed as we increased the number of simulated individuals. For this, we distributed 1'000 rectangular “checkpoints”, each with an extent of 5 km x 5 km at random locations inside the main study area. We then determined the relative traversal frequency by simulated trajectories through each checkpoint for different numbers of simulations (1 to 50'000). To assess variability in the relative traversal frequency, we repeatedly sampled trajectories 100 times and computed the mean traversal frequency across replicates, as well as the 95% prediction-interval. We deemed that a checkpoint converged as soon as the width of the prediction

interval for the traversal frequency across replicates dropped below a value of 0.01.

2.8 Heatmap (100%)

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

2.9 Betweenness (80%)

To pinpoint areas of exceptional relevance for connecting remote regions inside our study area, we converted simulated trajectories into a network and calculated betweenness scores (Bastille-Rousseau et al., 2018). For this, we overlaid the study area (including the buffer) with a regular raster resolved at 5 x 5 km. The centerpoint of each raster-cell served as node in the final network and we used the simulated trajectories to determine 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). Because `igraph` handles edge weights (ω) as costs, we inverted the traversal frequency in each cell by applying $\omega = \frac{\sum_i^n TraversalFrequency_i/n}{TraversalFrequency_i}$. Consequently, edges that were traversed frequently were assigned low costs. Finally, we used the weighted network to calculate the betweenness score of each raster-cell. Betweenness measures how often a specific raster-cell lies on a shortest path between two other raster-cells and is therefore a useful metric to detect movement corridors (Bastille-Rousseau et al., 2018).

2.10 Inter-Patch Connectivity (80%)

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

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

3 Results

3.1 Movement Model (80%)

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

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

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

When looking at the interactions between movement and habitat kernels, we observe that movement behavior is contingent on habitat conditions. For example, there's strong evidence that dispersers realize smaller steps in areas covered by water or areas covered by

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

The k-fold cross-validation procedure reveals that our model substantially outperforms a random guess (Figure 4b) and therefore correctly assigns a high selection score to realized steps. Confidence intervals of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ do not overlap and therefore proof a reliable prediction. Furthermore, the significant correlation between ranks and corresponding frequencies for realized steps indicates a good fit between predictions and observations (Figure 4b). In comparison to the base model ($\bar{r}_{s,realized} = -0.55$; Hofmann et al., 2021), the inclusion of interactions between movement and habitat covariates slightly improved model performance.

3.2 Dispersal Simulation (80%)

On a machine with an octacore AMD Ryzen 7 2700X processor (8 x 3.6 GHz) and 64 GB of RAM, a batch of 1'000 simulated dispersers moving over 2'000 steps required 90 minutes to compute ($\mu = 88.90$, $\sigma = 1.87$). Consequently, the simulation of all 80'000 dispersers (160 Mio. steps) terminated after 120 hours (i.e. five days). Comparable simulations will be substantially faster for smaller study areas and lower resolution covariates, as the covariate extraction from large and high-resolution rasters was computationally the most demanding task. Out of the 50'000 dispersers initiated inside the main source area Figure 3(a), only 4.5% eventually hit a map boundary, suggesting that we successfully prevented biases due to boundary effects. In contrast, 78% of the 30'000 dispersers originating from the buffer zone eventually hit a map boundary, yet this was to be expected since many of those dispersers originated from source points located close to the map boundary.

3.3 Convergence (80%)

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

3.4 Heatmap (80%)

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

3.5 Betweenness (80%)

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

3.6 Inter-Patch Connectivity (80%)

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

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

4 Discussion

4.1 Short Summary (90%)

We used ISSFs to analyse data of dispersing wild dogs and to parametrize a fully mechanistic movement model describing how dispersers move through the available landscape. We employed the parametrized model as an individual-based movement model to simulate 80'000 dispersing wild dogs moving 2'000 steps across the extent of the KAZA-TFCA, the world's largest transboundary conservation area. Based on simulated dispersal trajectories, we derived three complementary maps, each geared towards a better understanding of dispersal and 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 or absence of functional links between national parks as well as the average dispersal duration required to realize those links. We thereby showcase that ISSFs offer a simple, yet powerful framework to parametrize movement models and simulate dispersal to assess landscape connectivity. Importantly, individual-based simulations from ISSFs overcome several conceptual shortcomings inherent to more traditional connectivity modeling techniques, such as least-cost path analysis and circuit theory.

4.2 Movement Model (80 %)

Our movement model of dispersing wild dogs comprised a habitat kernel, a movement kernel, and their interactions. Thus, the model rendered habitat and movement preferences of dispersers, as well as how their movement preferences were affected by habitat conditions. Parameter estimates from the habitat kernel revealed that dispersers avoid water, prefer its proximity, avoid woodland, prefer shrubs/grassland, and avoid areas dominated by humans. These results are consistent with findings from previous studies on dispersing wild dogs (Davies-Mostert et al., 2012; Masenga et al., 2016; Woodroffe et al., 2019; O'Neill et al., 2020), as well as with a base model that we developed focussing on dispersing wild dogs' habitat kernel (Hofmann et al., 2021).

By expanding the base model by a proper movement kernel, we were able to model several additional complexities inherent to dispersal. For instance, it is well known that dispersers usually move with directional persistence (Cozzi et al., 2018; Hofmann et al., 2021) and that step lengths are typically correlated with turning angles (Morales et al., 2004; Börger and Fryxell, 2012). That is, larger steps usually coincide with smaller turning angles and vice versa. While such behavior could be captured by jointly sampling turning angles and step lengths from copula probability distributions (?), the ISSF framework allowed us to model similar behavior directly using the movement model. Besides accounting for directional persistence and correlations between step lengths and turning angles, we also allowed for interactions that rendered the fact that wild dogs mainly move during the darker morning and evening hours, whereas they tend to rest during the remainder of the day.

By allowing interactions between habitat covariates and movement covariates, we furthermore accounted for the fact that movement and habitat preferences are interdependent. For example, the final model retained an interaction between water cover and step length, showing that dispersers are more likely to realize short steps (i.e. move slower) in areas covered by water and large steps in areas located on dryland. Likewise, the parameter estimate for the interaction between water cover and turning angles revealed that dispersers move less directional across water bodies than across dryland. We believe that this is owed to the fact that wild dogs wade or swim when traversing waterbodies, thus resulting in slower, more tortuous movements. Besides this, our model also suggested that dispersers preferably realize shorter steps when moving through woodland, but larger steps when moving across shrubs/grassland. This can likely be linked to wild dogs' resting behavior, as wild dogs usually use open areas to quickly move over long distances (Abrahms et al., 2017) but seek shade and protection below the woodland canopy when resting (Creel and Creel, 2002).

4.3 Simulation (80%)

Based on the above described movement model, we simulated 80'000 dispersers moving 2'000 steps across the landscapes of the KAZA-TFCA. On a modern desktop machine, this simulation required five days of computation. The long simulation time was primarily caused by the massive extent considered (ca. 1.8 Mio. km² when including the buffer) and the large number of dispersers simulated. Most connectivity studies are limited to much 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 in the study area converged already after 10'500 simulated individuals in our case. The required number of simulated individuals will, however, vary depending on the structure of the landscape and the dispersal ability of the focal species.

4.4 Maps (70%)

The heatmap resulting from our dispersal simulation highlighted that a large portion of simulated dispersers traversed the Moremi NP and the Chobe NP in northern Botswana. We already recognized the same area as dispersal hotspot using least-cost path and least-cost corridor analysis (Hofmann et al., 2021), yet some researchers questioned whether this was just the logical consequence of the region being in the center of the study area and least-costly routes being enforced between pre-defined start and endpoints. Using least-cost approaches, this claim is difficult to disprove, as all identified routes have to completely run within the study area and will always be enforced between a start and endpoint. With our simulation, on the other hand, dispersers were able to leave the study area and were not enforced to move towards a known endpoint. Despite this, a majority of simulated individuals traversed the central region in northern Botswana, so we conclude that this dispersal hotspot is not caused by geometric properties but results from landscape characteristics and the location of source areas.

Overall, the heatmap gives a good overview of the intensity of use in different areas, yet it is not well suited for pinpointing discrete movement corridors, which is why we also computed a betweenness-map. In contrast to the heatmap, the betweenness-map puts stronger emphasis on areas that are used as stepping stones into other regions of the study area and thereby highlights discrete dispersal corridors or bottlenecks (Bastille-Rousseau et al., 2018). Interestingly, the central region in northern Botswana again stands out, implying that the

region is not only frequently visited, but also promotes the relocation of individuals into more remote regions of the KAZA-TFCA. While this is an example of an area where both the traversal frequency *and* the betweenness score is high, there are other instances where only one of the metrics is pronounced. For example, while the area between the Lengue-Luiana NP in Angola and the Kafue NP in Zambia receives a high betweenness-score, we find that the same area is only rarely traversed by dispersers according to the heatmap. Consequently, despite the region's importance for linking Angola's NPs to Zambia's NP, only few simulated dispersers actually manage to successfully traverse it. Conversely, while the area inside the Central Kalahari NP is traversed by many dispersers, the betweenness map indicates that the same region does not serve as major stepping stone into other regions of the study area.

To complete the picture, we also computed inter-patch connectivity between NPs, highlighting functional links and expected dispersal durations between each national park in the study area. The map showed that movements from Angola into Zambia's Kafue NP are not only rare, but they also require many steps until they are realized. Conversely, we find that dispersal between the Moremi NP and Chobe NP are relatively frequent and require fewer steps, which can be expected given that the areas are located close to each other.

Together, these examples nicely illustrate how powerful a combination of different connectivity metrics can be in deepening our understanding of landscape connectivity. Each map that we produced from simulated trajectories accentuated a different aspect of connectivity, together providing a comprehensive view on dispersal and landscape connectivity. The heatmap, for example, put emphasis on areas where movement is concentrated, regardless whether such areas truly contribute to gene flow or whether they represent "dead ends" that do not connect distinct patches. The betweenness map, on the other hand, pronounced those areas that are relevant in connecting different regions in the landscape and highlights potential bottlenecks. Finally, the map of inter-patch connectivity illustrated the frequency at which dispersal between distinct patches occurs, as well as the average dispersal duration required for individuals to move between them.

4.5 Related Literature (80%)

Our approach of simulating movement to assess connectivity is closely related to a series of previously published papers. Clark et al. (2015), for instance, fitted a regular SSFs to American black bears (*Ursus americanus*) and employed the estimated model parameters to simulate movement and identify the most likely movement corridors between four habitat patches. For the same species, Zeller et al. (2020) used regular SSFs and forecasted seasonal

habitat connectivity under changing land-use. As both of these studies relied on *regular* SSFs, rather than *integrated* SSFs, neither of them was able to account the interdependence between habitat and movement preferences. As such, movement behavior was assumed to be independent of habitat conditions. In addition, both studies lacked data collected during dispersal and instead employed data on residents to estimate connectivity. Although preferences during residence and dispersal may coincide for some species (Fattebert et al., 2015), there is compelling evidence suggesting that dispersers more readily cross areas avoided by residents (Elliot et al., 2014; Gastón et al., 2016; Abrahms et al., 2017; Keeley et al., 2017). The use of data collected during residence may therefore result in biased model estimates that distort our view on connectivity, causing a misallocation of scarce conservation funds (Elliot et al., 2014). Another set of related studies that uses simulations from (regular and integrated) SSFs has been conducted by Potts et al. (2013) and Signer et al. (2017), yet the primary focus of these papers lied on the estimation of steady-state utilization distributions and not the investigation of connectivity between habitat patches.

4.6 Benefits & Modeling Decisions with ISSF Simulations (70%)

A simulation-based approach as proposed in this article offers several advantages over traditional connectivity modeling techniques such as LCPA or CT. In contrast to LCPA, for instance, an individual-based simulation does not require to assume known endpoints. Instead, each endpoint emerges naturally from a simulated dispersal trajectory. The ability of not having to provide pre-determined is particularly valuable for dispersal studies, because dispersers often venture into unfamiliar territory and are therefore unlikely to know the destination of their journey (Elliot et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020). Moreover, LCPA always enforces a connection towards the predefined endpoints, even if associated movement costs are unreasonably high. With simulations from ISSFs this is no longer the case. A connectivity model that does not require pre-defined endpoints also ensures that movement corridors are not enforced between certain start- and endpoints, which permits to detect potential routes that do not lead into suitable habitats but into ecological traps (Dwernychuk and Boag, 1972; Van der Meer et al., 2014) or areas with a high susceptibility for human wildlife conflicts (Cushman et al., 2018).

In contrast to LCPA and CT, simulations from ISSFs furthermore yield the advantage of an explicit representation of time. This 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?*” These are important questions that shift the focus from a structural to a

more functional view on connectivity, which is usually desirable because functional connectivity it is directly related to gene flow (Taylor et al., 1993; Tischendorf and Fahrig, 2000). An explicit representation of time also yields opportunities for studying how seasonality affects connectivity and to investigate whether some dispersal corridors are only available temporarily (*dynamic connectivity*; Zeller et al., 2020). With LCPA or CT, incorporating seasonality is currently impractical, as both methods require a static permeability surface as inputs. Hence, the only possibility to study seasonality effects is to repeat the same analysis using different permeability surfaces, each rendering the environment at a different point in time (e.g. Benz et al., 2016; Osipova et al., 2019). With simulations from ISSFs, on the other hand, the environment can be rendered dynamically “as the dispersers move”, such that simulated individuals can respond to seasonal factors directly within the simulation. Hence, rather than employing a set of static habitat layers, each layer would be updated as the dispersers move, thus correctly rendering seasonal changes in the environment.

While an explicit representation of time offers multiple benefits, it requires that step lengths and turning angles are modeled properly (Kanagaraj et al., 2013), so that dispersal durations between areas can be estimated reliably. Correctly rendering step lengths and turning angles under varying environmental conditions is one of the key strengths of ISSFs (Avgar et al., 2016; Prokopenko et al., 2017; Fieberg et al., 2020), which is why we believe that the framework is exceptionally well suited for simulating dispersal and assessing landscape connectivity. In addition, the framework enables to model autocorrelation between step lengths and turning angles, thereby incorporating directional persistence. Here, we only considered first order autocorrelation, i.e. correlation between two consecutive steps. Although higher order autocorrelation is conceivable and might be desirable to model, this requires vast amounts of GPS data that is not intercepted by missing fixes and is therefore often impractical to model in reality.

4.7 Further Considerations (70%)

Although we did not render mortality, animals regularly die during dispersal, mainly due to deadly encounters with predators, road kills, and persecution by humans (Bonnet et al., 1999; Woodroffe and Sillero-Zubiri, 2012; ?). Mortality during dispersal could therefore substantially limit functional connectivity (Bowler and Benton, 2009), especially in areas where the likelihood of encountering competitors and humans is high (Cozzi et al., 2020). If corresponding information is available, mortality can and should be included in ISSF simulations.

The ability to realistically render movement during dispersal not only serves to investigate landscape connectivity, but also forms the foundation for more realistic spatially explicit population models in which dispersal is not merely rendered through dispersal kernels or cellular automata movements (Visintin et al., 2020), but mechanistically based on observed movement and habitat preferences (e.g. Revilla and Wiegand, 2008, Kleinmann and Wang, 2017). Such models can ultimately be employed to conduct population viability analyses (Boyce, 1992) in which species' dispersal abilities are taken into account.

Despite the benefits that simulations from ISSFs offer, we also want to confer some of the non-trivial modeling decisions involved. In particular, we will discuss five modeling decisions (Figure 9): (1) number of simulated individuals, (2) location of source points, (3) dispersal duration, (4) boundary behavior, and (5) how to handle individual variability.

(1) When simulating dispersal using ISSFs, the modeler needs to decide on the number of simulated individuals. This decision includes the *absolute* number of simulated individuals across the entire study area, as well as the *relative* number of simulated individuals per spatial entity (e.g. protected area, habitat patch, source point). With respect to the *absolute* number of simulated individuals, a higher number is always desirable, as each additional disperser provides novel information about landscape connectivity. Of course this comes at the cost of computational efficiency, such that a trade-off needs to be managed. We propose to handle this trade-off by defining a target metric and only simulating additional until convergence in the target metric is observed. Here, we employed the *relative traversal frequency* across checkpoints as target metric and found that convergence across all checkpoints was achieved already after 10'500 simulated individuals. With regards to the *relative* number of simulated individuals, we see several feasible approaches. If corresponding data is available, one could distribute dispersers in relation to known abundances, reflecting that population densities are not necessarily homogeneous across space. Alternatively, one could also distribute dispersers homogeneously, yet after the simulation weigh each simulated trajectory according to population densities at the respective source patch. Again this requires information on the spatial abundance of the focal species. Finally, if such information is missing, one can distribute dispersers homogeneously across space. This is the approach that we employed and resulted in larger source areas generating a larger number of dispersers.

(2) While we simulated dispersal using point estimates from our most parsimonious movement model but did not investigate the sensitivity of our results with respect to those estimates. Uncertainty is rather common in dispersal studies on endangered species, as data tends to be scarce, resulting in model estimates large confidence intervals (Wiegand et al.,

2003; Kramer-Schadt et al., 2007). To address this, one may explore a broader range of preferences instead of using point estimates initiate dispersers with randomized preferences with variability imposed by the uncertainty in the movement model. We therefore urge future studies to investigate the sensitivity of ISSF simulations with respect to estimated preferences.

(3) When employing ISSFs to simulate dispersers, one also needs to decide on meaningful dispersal durations (i.e. number of simulated steps). If corresponding data is available, dispersal durations could be sampled from observed events, such that each individual would only be simulated until its assigned dispersal duration has been achieved. Due to the low number of observed dispersal events and due to the great variability in wild dogs' dispersal distances (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020) we opted against this approach. Instead, we simulated individuals for 2'000 steps, which is at the upper end of observed dispersal durations and may have resulted in an overly optimistic representation of landscape connectivity. Nevertheless, it is relatively straight forward to shorten simulated trajectories in order to investigate the sensitivity of results with regards to the dispersal duration. Alternatively, if detailed information on settlement behavior is available, the dispersal simulation could include a settlement submodel, where after each simulated step the simulated individual decides whether or not to settle, based the number of realized steps, environmental conditions in the landscape, abundance of conspecifics or competitors etc.

(4) Unless simulated individuals are drawn towards a point of attraction, some individuals will inevitably approach a map boundary such that some of the proposed random steps will leave the study area such that no selection score can be computed. One option to handle this situation would be to simply terminate the simulation as soon as one of the random steps leaves the study area, assuming that the simulated animal left the study area and will not return. This can be problematic when many individuals are initiated close to map boundaries, especially since a single random step leaving the study area forces termination of the simulation. As an alternative, one could resample transgressing random steps until all proposed random steps lie fully within the study area. This will force simulated dispersers to bounce off those boundaries and remain within the main study area. Finally, one could also extend the study area by an artificial buffer zone with randomized covariate values through which dispersers are allowed to leave and re-enter the main study area. Although dispersers might still approach the boundary of the buffer, it has been shown that adding an artifical buffer helps to mitigate edge effects Koen et al. (2010). A last solution that only applies in

theoretical applications is to simulate movement on a torus (?).

(5) To initiate the simulation of a disperser, the modeler needs to define a source point. In some cases, exact locations of source populations are known and source points can be placed accordingly (Kanagaraj et al., 2013). Moreover, if abundance estimates are available, these can be used to inform the relative number of dispersers initiated at each location. The selection of source points is thus directly related to the relative number of simulated individuals. Here, we randomly placed source points within protected areas large enough to sustain viable wild dog populations. Given that the species primarily survives in these formally protected areas (Woodroffe and Ginsberg, 1999; Davies-Mostert et al., 2012; Woodroffe and Sillero-Zubiri, 2012; Van der Meer et al., 2014) we consider this decision to be appropriate. In other cases, comparable knowledge may be lacking and it could be more beneficial to delineate likely source patches based on habitat suitability models (e.g. Squires et al., 2013). After all, the challenge of selecting meaningful source points is not unique individual-based simulations also applies to LCPA and CT. However, as highlighted by Signer et al. (2017), the influence of the exact location of source points decreases as the number of simulated steps is increased.

4.8 Conclusion (80%)

To this end, we have used data on dispersing wild dogs to exemplify how ISSFs can be used to parametrize an individual-based movement model that is further employed to simulate dispersal and examine landscape connectivity. We also presented three complementary connectivity maps derived from simulated trajectories, each focused on a different aspect of connectivity. Furthermore, we discussed the potential advantages and disadvantages of the proposed framework compared to traditional connectivity modeling techniques such as LCPA and CT. With this article, we hope to have sparked interest in the uprising framework of step selection functions for investigating dispersal behavior and landscape connectivity. Nevertheless, we do not attempt to dismiss the application of traditional connectivity models by any means. Rather, we propose to use simulations from ISSF-models as a simple but powerful tool to provide a more comprehensive understanding of dispersal and 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 coalitions will be made available on dryad at the time of publication. Access to all R-scripts is provided through Github.

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 are indebted to 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.
- Bonnet, X., Naulleau, G., and Shine, R. (1999). The Dangers of Leaving Home: Dispersal and Mortality in Snakes. *Biological Conservation*, 89(1):39–50.
- Bovet, P. and Benhamou, S. (1991). Optimal Sinuosity in Central Place Foraging Movements. *Animal Behaviour*, 42(1):57–62.
- Bowler, D. E. and Benton, T. G. (2009). Variation in Dispersal Mortality and Dispersal Propensity among Individuals: The Effects of Age, Sex and Resource Availability. *Journal of Animal Ecology*, 78(6):1234–1241.
- Boyce, M. S. (1992). Population Viability Analysis. *Annual Review of Ecology and Systematics*, 23(1):481–497.
- Boyce, M. S., Vernier, P. R., Nielsen, S. E., and Schmiegelow, F. K. A. (2002). Evaluating Resource Selection Functions. *Ecological Modelling*, 157(2-3):281–300.
- 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.
- 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.
- Castelló, J. R. (2018). *Canids of the World: Wolves, Wild dogs, Foxes, Jackals, Coyotes, and their Relatives*. Princeton Field Guides. Princeton University Press, Princeton, NJ.
- 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., Maag, N., Börger, L., Clutton-Brock, T. H., and Ozgul, A. (2018). Socially Informed Dispersal in a Territorial Cooperative Breeder. *Journal of Animal Ecology*, 87(3):838–849.
- Creel, S. and Creel, N. M. (2002). *The African Wild Dog: Behavior, Ecology, and Conservation*. Princeton University Press, Princeton, NJ, USA.
- 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.
- Cushman, S. A. and Lewis, J. S. (2010). Movement Behavior Explains Genetic Differentiation in American Black Bears. *Landscape Ecology*, 25(10):1613–1625.
- 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. (2020). Landscape Connectivity Modeling from the Perspective of Animal Dispersal. *Landscape Ecology*.
- 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.
- 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.
- Etherington, T. R. (2016). Least-Cost Modelling and Landscape Ecology: Concepts, Applications, and Opportunities. *Current Landscape Ecology Reports*, 1(1):40–53.

- Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1):487–515.
- Fattebert, J., Robinson, H. S., Balme, G., Slotow, R., and Hunter, L. (2015). Structural Habitat Predicts Functional Dispersal Habitat of a Large Carnivore: How Leopards Change Spots. *Ecological Applications*, 25(7):1911–1921.
- Fieberg, J., Signer, J., Smith, B., and Avgar, T. (2020). A ‘How-to’ Guide for Interpreting Parameters in Resource- and Step-Selection Analyses. preprint, Ecology.
- 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.
- Gardner, R. H. and Gustafson, E. J. (2004). Simulating Dispersal of Reintroduced Species within Heterogeneous Landscapes. *Ecological Modelling*, 171(4):339–358.
- Gastón, A., Blázquez-Cabrera, S., Garrote, G., Mateo-Sánchez, M. C., Beier, P., Simón, M. A., and Saura, S. (2016). Response to Agriculture by a Woodland Species Depends on Cover Type and Behavioural State: Insights from Resident and Dispersing Iberian Lynx. *Journal of Applied Ecology*, 53(3):814–824.
- Graf, R. F., Kramer-Schadt, S., Fernández, N., and Grimm, V. (2007). What you see is where you go? Modeling Dispersal in Mountainous Landscapes. *Landscape Ecology*, 22(6):853–866.
- 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. (1998). Metapopulation Dynamics. *Nature*, 396(6706):41–49.
- Hanski, I. (1999a). Habitat Connectivity, Habitat Continuity, and Metapopulations in Dynamic Landscapes. *Oikos*, 87(2):209.
- Hanski, I. (1999b). *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. (2020). *raster: Geographic Data Analysis and Modeling*. R package version 3.3-13.
- Hofmann, D. D., Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2021). Bound within Boundaries: How Well Do Protected Areas Match Movement Corridors of their Most Mobile Protected Species? *Journal of Applied Ecology*. (in 2nd review).
- Howard, W. E. (1960). Innate and Environmental Dispersal of Individual Vertebrates. *American Midland Naturalist*, 63(1):152.
- Hunziker, P. (2021). *velox: Fast Raster Manipulation and Extraction*. R package version 0.2.1.
- Jönsson, K. A., Tøttrup, A. P., Borregaard, M. K., Keith, S. A., Rahbek, C., and Thorup, K. (2016). Tracking Animal Dispersal: From Individual Movement to Community Assembly and Global Range Dynamics. *Trends in Ecology & Evolution*, 31(3):204–214.

- 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.
- Kays, R., Crofoot, M. C., Jetz, W., and Wikelski, M. (2015). Terrestrial Animal Tracking as an Eye on Life and Planet. *Science*, 348(6240):aaa2478 – aaa2478.
- Keeley, A. T., Beier, P., Keeley, B. W., and Fagan, M. E. (2017). Habitat Suitability is a Poor Proxy for Landscape Connectivity during Dispersal and Mating Movements. *Landscape and Urban Planning*, 161:90–102.
- Kleinmann, J. U. and Wang, M. (2017). Modeling Individual Movement Decisions of Brown Hare (*Lepus europaeus*) as a Key Concept for Realistic Spatial Behavior and Exposure: A Population Model for Landscape-Level Risk Assessment: Population Modeling of Brown Hare. *Environmental Toxicology and Chemistry*, 36(9):2299–2307.
- 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.
- Kramer-Schadt, S., Revilla, E., Wiegand, T., and Breitenmoser, U. (2004). Fragmented Landscapes, Road Mortality and Patch Connectivity: Modelling Influences on the Dispersal of Eurasian lynx. *Journal of Applied Ecology*, 41(4):711–723.
- Kramer-Schadt, S., Revilla, E., Wiegand, T., and Grimm, V. (2007). Patterns for Parameters in Simulation Models. *Ecological Modelling*, 204(3-4):553–556.
- Landguth, E. L., Hand, B. K., Glassy, J., Cushman, S. A., and Sawaya, M. A. (2012). UNICOR: A Species Connectivity and Corridor Network Simulator. *Ecography*, 35(1):9–14.
- 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.
- 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.
- 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.
- McNutt, J. W. (1995). *Sociality and Dispersal in African Wild Dogs, Lycaon pictus*. PhD Thesis, University of California, Davis.
- 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.

- Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., and Fryxell, J. M. (2004). Extracting More out of Relocation Data: Building Movement Models as Mixtures of Random Walks. *Ecology*, 85(9):2436–2445.
- 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.
- Munden, R., Börger, L., Wilson, R. P., Redcliffe, J., Brown, R., Garel, M., and Potts, J. R. (2020). Why Did the Animal Turn? Time-Varying Step Selection Analysis for Inference Between Observed Turning Points in High Frequency Data.
- 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.
- Osofsky, S. A., McNutt, J. W., and Hirsch, K. J. (1996). Immobilization of Free-Ranging African Wild Dogs (*Lycaon pictus*) Using a Ketamine/Xylazine/Atropine Combination. *Journal of Zoo and Wildlife Medicine*, pages 528–532.
- 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).
- Panzacchi, M., Van Moorter, B., Strand, O., Saerens, M., Kivimäki, I., St. Clair, C. C., Herfindal, I., and Boitani, L. (2016). Predicting the Continuum Between Corridors and Barriers to Animal Movements Using Step Selection Functions and Randomized Shortest Paths. *Journal of Animal Ecology*, 85(1):32–42.
- 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.
- Pinto, N. and Keitt, T. H. (2009). Beyond the Least-Cost Path: Evaluating Corridor Redundancy Using a Graph-Theoretic Approach. *Landscape Ecology*, 24(2):253–266.
- 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.
- Prokopenko, C. M., Boyce, M. S., and Avgar, T. (2017). Characterizing Wildlife Behavioural Responses to Roads Using Integrated Step Selection Analysis. *Journal of Applied Ecology*, 54(2):470–479.
- R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Revilla, E. and Wiegand, T. (2008). Individual Movement Behavior, Matrix Heterogeneity, and the Dynamics of Spatially Structured Populations. *Proceedings of the National Academy of Sciences*, 105(49):19120–19125.

- Revilla, E., Wiegand, T., Palomares, F., Ferreras, P., and Delibes, M. (2004). Effects of Matrix Heterogeneity on Animal Dispersal: From Individual Behavior to Metapopulation-Level Parameters. *The American Naturalist*, 164(5):E130–E153.
- 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*.
- Schultz, C. B. and Crone, E. E. (2001). Edge-Mediated Dispersal Behavior in a Prairie Butterfly. *Ecology*, 82(7):1879–1892.
- Signer, J., Fieberg, J., and Avgar, T. (2017). Estimating Utilization Distributions from Fitted Step-Selection Functions. *Ecosphere*, 8(4):e01771.
- Spear, S. F., Balkenhol, N., Fortin, M.-J., Mcrae, B. H., and Scribner, K. (2010). Use of Resistance Surfaces for Landscape Genetic Studies: Considerations for Parameterization and Analysis. *Molecular Ecology*, 19(17):3576–3591.
- 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.
- Taylor, P. D., Fahrig, L., Henein, K., and Merriam, G. (1993). Connectivity Is a Vital Element of Landscape Structure. *OIKOS*, 68(3):571–573.
- Thurfjell, H., Ciuti, S., and Boyce, M. S. (2014). Applications of Step-Selection Functions in Ecology and Conservation. *Movement Ecology*, 2(4).
- 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.
- Van Moorter, B., Kivimäki, I., Panzacchi, M., and Saerens, M. (2021). Defining and Quantifying Effective Connectivity of Landscapes for Species' Movements. *Ecography*, page ecog.05351.
- 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.
- Vasudev, D., Goswami, V. R., and Oli, M. K. (2021). Detecting Dispersal: A Spatial Dynamic Occupancy Model to Reliably Quantify Connectivity across Heterogeneous Conservation Landscapes. *Biological Conservation*, 253:108874.
- Visintin, C., Briscoe, N. J., Woolley, S. N. C., Lentini, P. E., Tingley, R., Wintle, B. A., and Golding, N. (2020). STEPS: Software for Spatially and Temporally Explicit Population Simulations. *Methods in Ecology and Evolution*, 11(4):596–603.
- Wiegand, T., Jeltsch, F., Hanski, I., and Grimm, V. (2003). Using Pattern-Oriented Modeling for Revealing Hidden Information: A Key for Reconciling Ecological Theory and Application. *Oikos*, 100(2):209–222.
- Williams, H. J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., Grissac, S., Demšar, U., English, H. M., Franconi, N., Gómez-Laich, A., Griffiths, R. C., Kay, W. P., Morales, J. M., Potts, J. R., Rogerson, K. F., Rutz, C., Spelt, A., Trevail, A. M., Wilson, R. P., and Börger, L. (2019). Optimizing the Use of Biologgers for Movement Ecology Research. *Journal of Animal Ecology*.

- 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., 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.

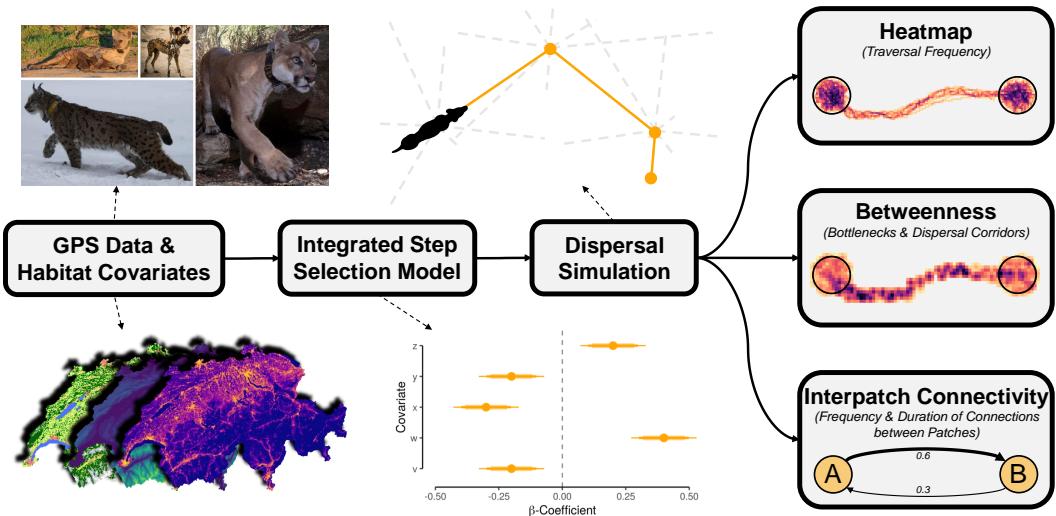


Figure 1: Flowchart of the simulation-based connectivity analysis as proposed in this article. First, GPS data and habitat covariates have to be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement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

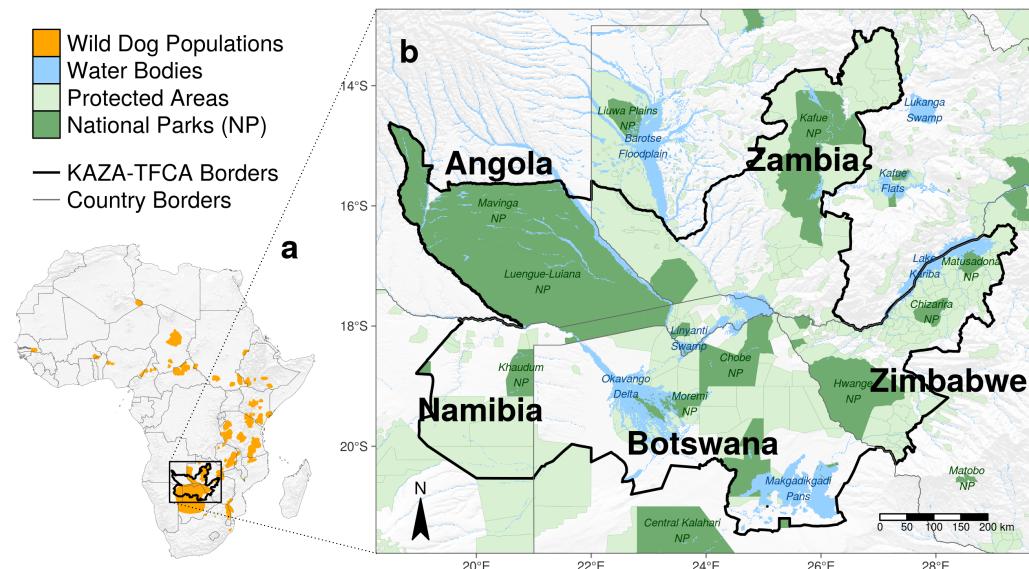


Figure 2: Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA and encompassed parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA represents the world's largest terrestrial conservation area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

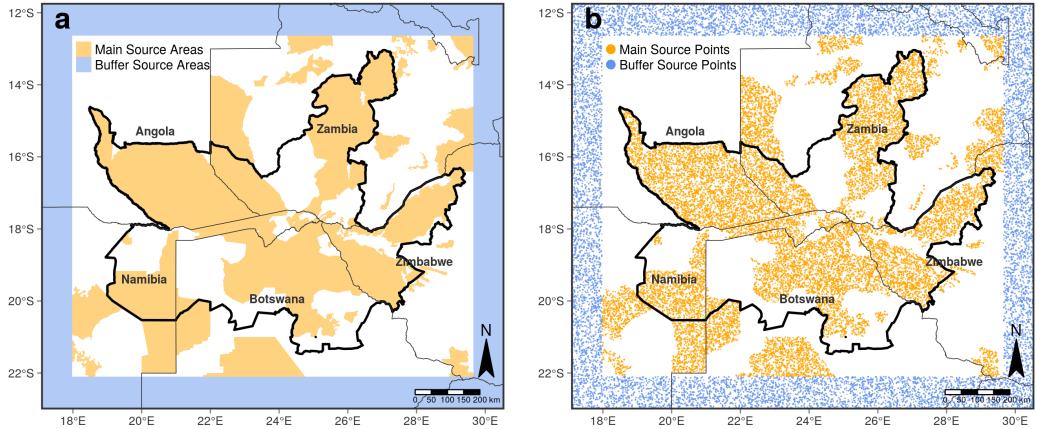


Figure 3: (a) Different source areas from which we released virtual dispersers. We only considered contiguous protected areas (national parks, game reserves, and forest reserves) that were larger than 700 km^2 (green). This area corresponds to the average home range requirement for viable wild dog populations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

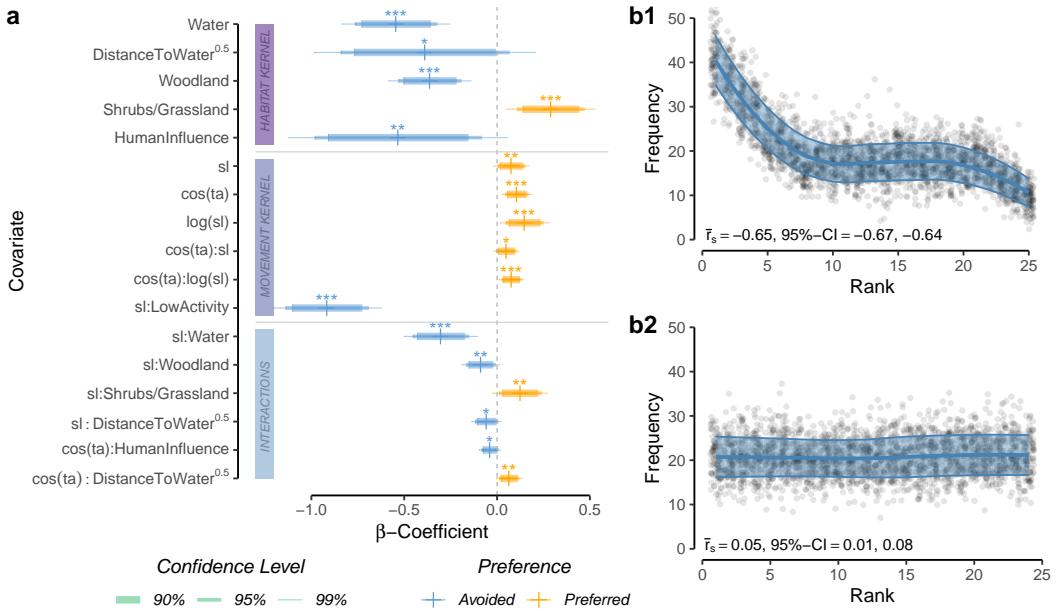


Figure 4: (a) Most parsimonious movement model for dispersing wild dogs. The model includes a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% Confidence-Intervals for the respective β -coefficients. Significance codes: * $p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

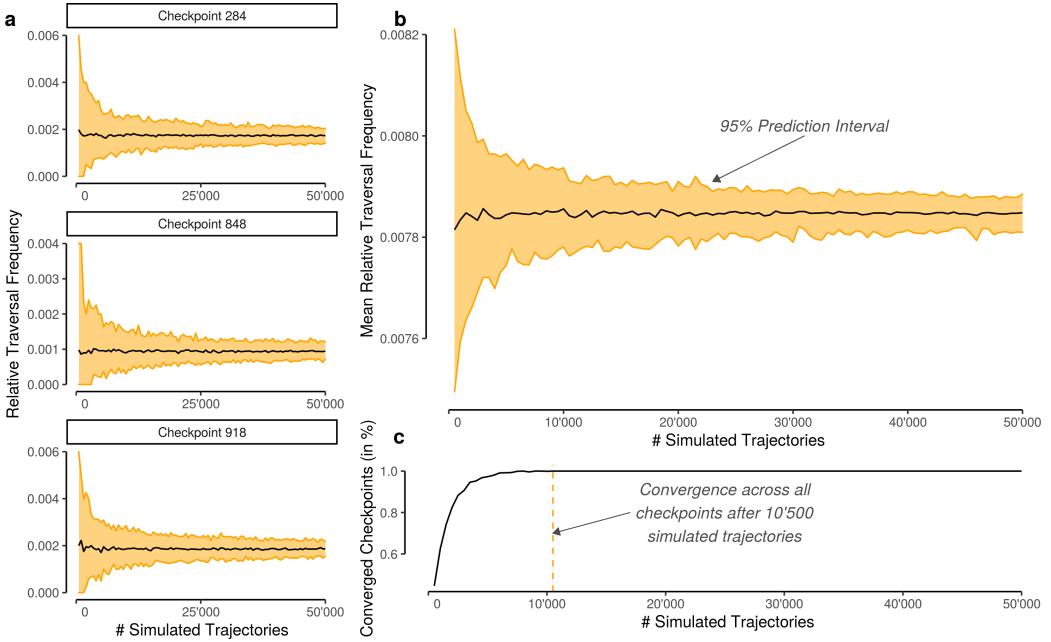


Figure 5: Relative traversal frequency through 1'000 checkpoints (5 km x 5) distributed randomly across the study area. The relative traversal frequency is plotted against the number of simulated individuals to visualize how quickly the metric converges to a steady state. (a) Replicated (100 times) relative traversal frequencies across three randomly chosen checkpoints as well as the corresponding 95% prediction interval (PI). (b) Averaged relative traversal frequency across all checkpoints and replicates including a 95% PI. (c) Width of the PI in relation to the number of simulated dispersers.

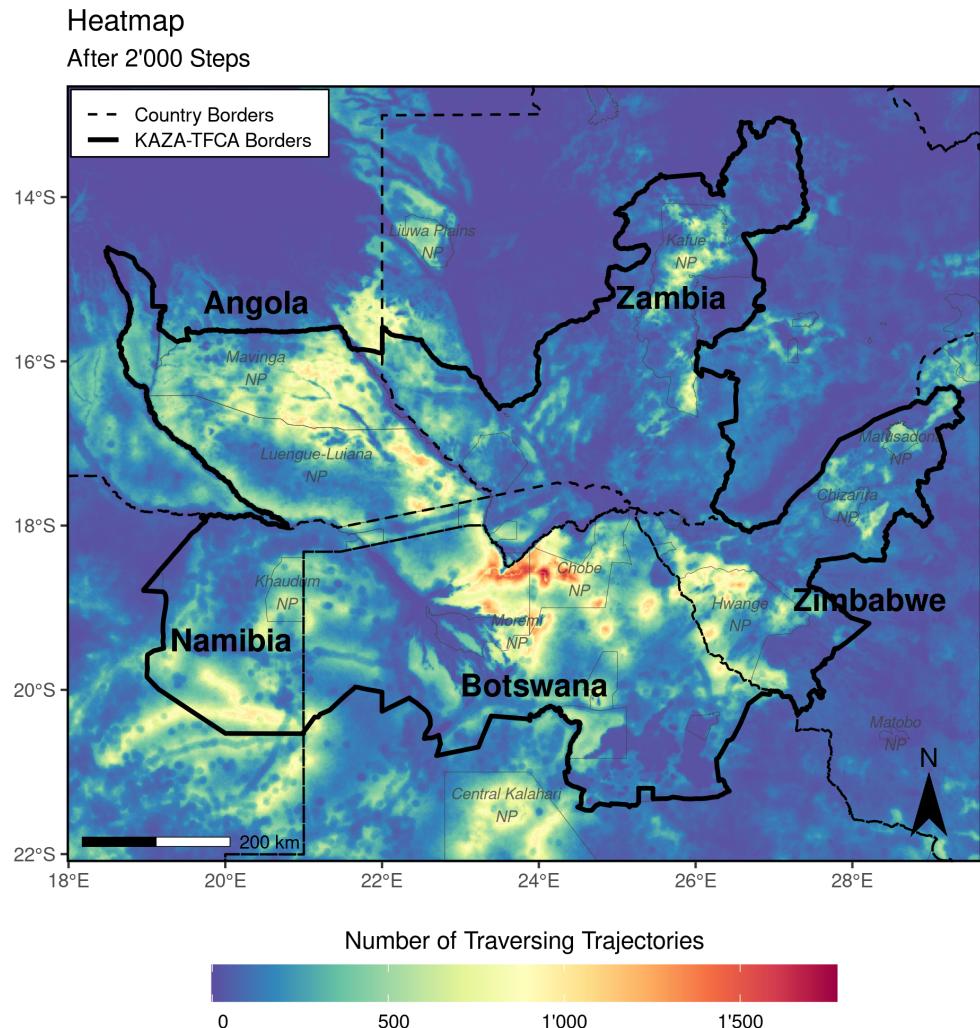


Figure 6: Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step selection model that we fit to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied all simulated trajectories. Consequently, the map highlights areas that are frequently traversed by virtual dispersers. Additional heatmaps showing the traversal frequency for different numbers of simulated steps are provided in Appendix S3.

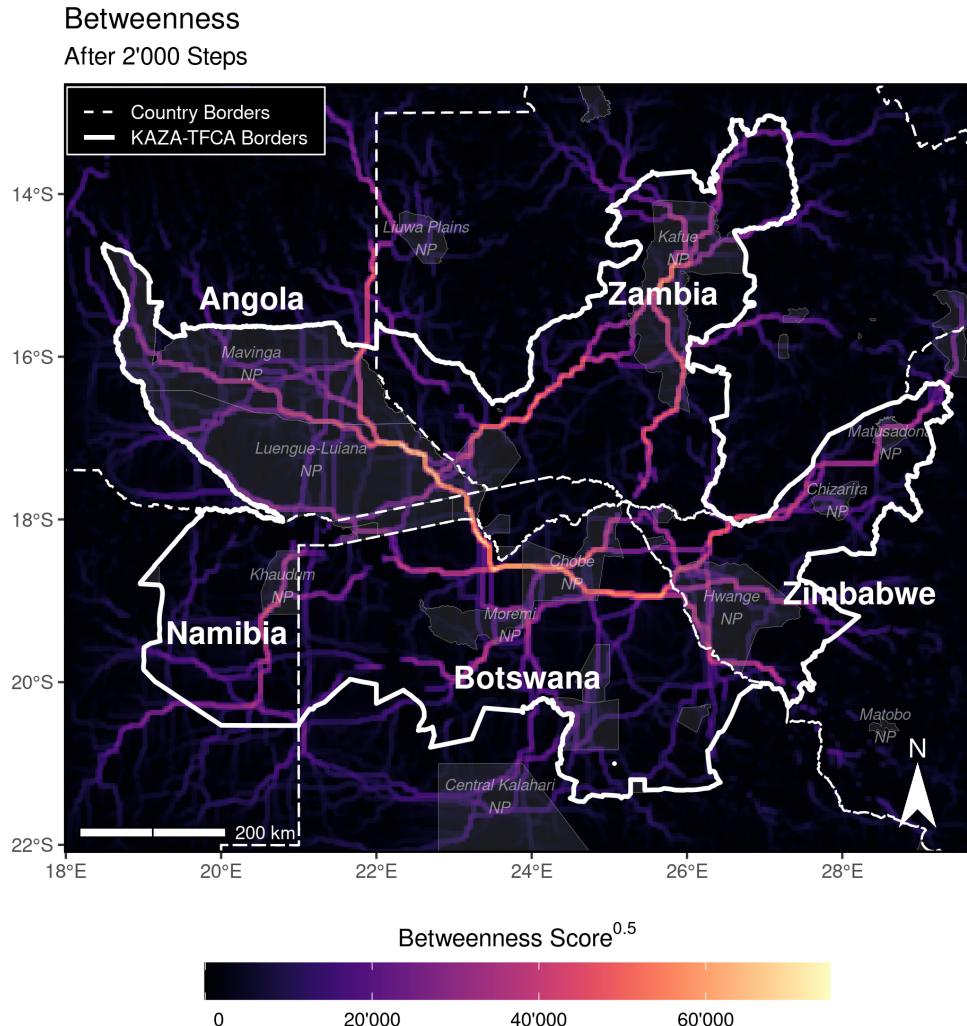


Figure 7: Map of betweenness scores, highlighting distinct dispersal corridors and potential bottlenecks. A high betweenness score indicates that the respective cells are exceptionally relevant in connecting different regions in the study area. That is, the higher the betweenness score, the more often a pixel lies on a shortest path between adjacent areas. In this sense the metric can be used to pinpoint discrete movement corridors. Note that we square-rooted betweenness scores to improve visibility of corridors with low scores. Betweenness scores were determined by converting simulated dispersal trajectories into a large network. Note that we square-rooted betweenness scores to improve the visibility of corridors with low betweenness scores.

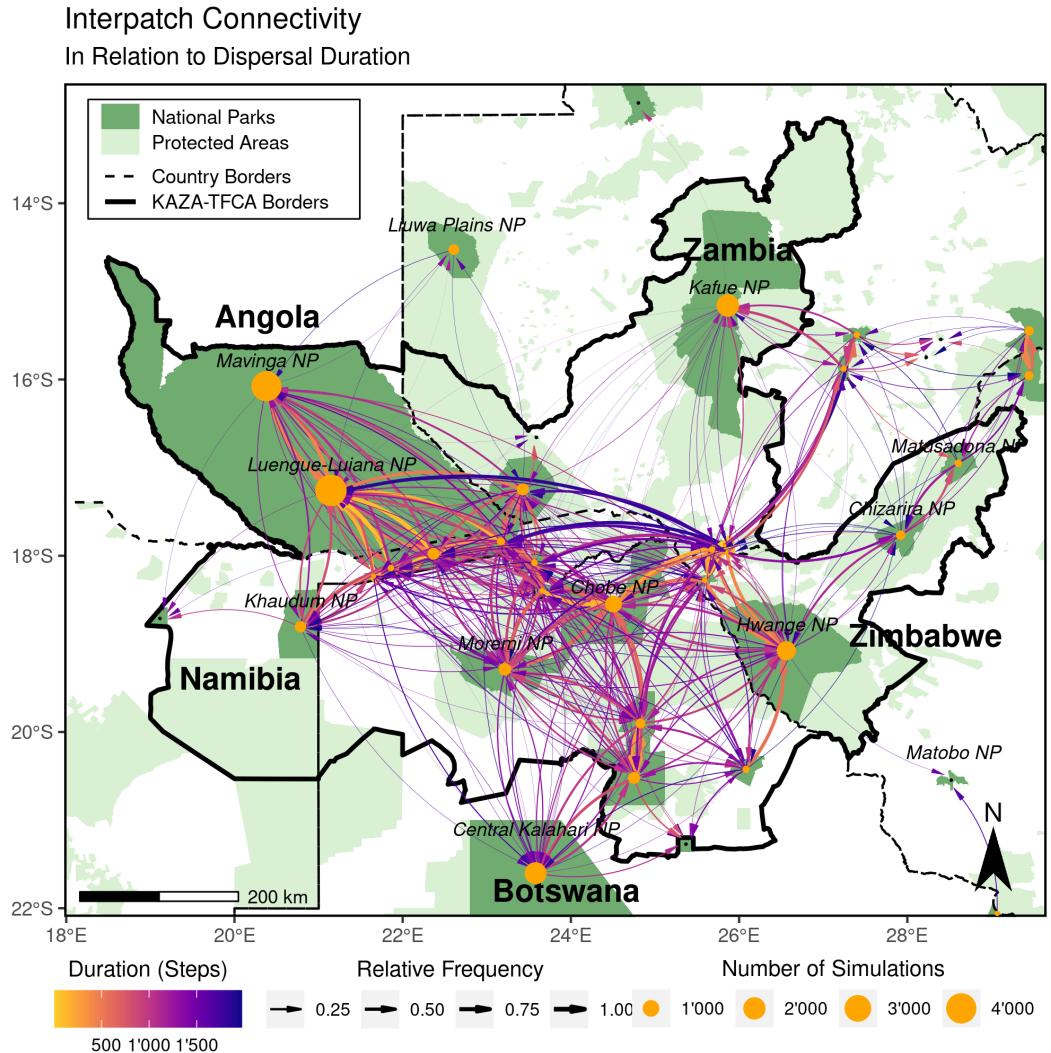


Figure 8: Network on simulated dispersal trajectories highlighting connections between national parks (dark green). Yellow bubbles represent the center of the different national parks and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent national parks that were smaller than 700 km^2 and therefore did not serve as source areas. Arrows between national parks illustrate between which national parks the simulated dispersers successfully moved and the color of each arrow shows the average number of steps (4-hourly movements) that were necessary to realize those connections. Additionally, the line thickness indicates the relative number of dispersers originating from a national park that realized those connections. Note that a similar network view could be adopted to investigate connectivity between other protected areas need not to be restricted to national parks.

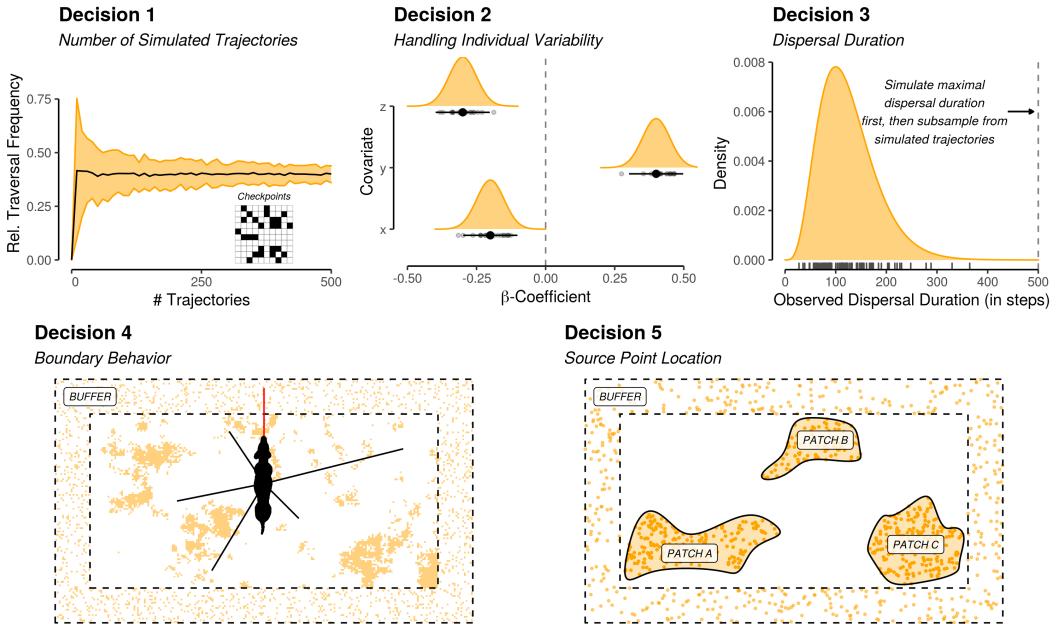


Figure 9: Five major modeling decisions that a researcher needs to consider when simulating dispersers to assess landscape connectivity. (1) Number of simulated trajectories. (2) Handling individual variation: we used point estimates when simulating dispersers, assuming that there was no individual variation.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

Table 1: Most parsimonious movement model for dispersing wild dogs. The model consists of a movement kernel, a habitat kernel, and their interactions. The movement kernel describes preferences with regards to movement behavior, whereas the habitat kernel describes preferences with respect to habitat conditions. Interactions between the two kernels indicate that movement preferences are contingent on habitat conditions. Note that all covariates were standardized to a mean of zero and standard deviation of 1. Plots to aid with the interpretation of this model are given in Appendix S2.

Kernel	Covariate	Coefficient	SE	p-value	Sign.
Habitat Kernel	Water	-0.546	0.112	< 0.001	***
	DistanceToWater ^{0.5}	-0.390	0.231	0.092	*
	Woodland	-0.364	0.086	< 0.001	***
	Shrubs/Grassland	0.288	0.092	0.002	***
	HumanInfluence	-0.535	0.229	0.019	**
Movement Kernel	sl	0.075	0.037	0.042	**
	cos(ta)	0.105	0.031	0.001	***
	log(sl)	0.146	0.051	0.004	***
	cos(ta) : sl	0.049	0.026	0.064	*
	cos(ta) : log(sl)	0.076	0.026	0.003	***
Interactions	sl : LowActivity	-0.917	0.113	< 0.001	***
	sl : Water	-0.305	0.076	< 0.001	***
	sl : Woodland	-0.089	0.039	0.023	**
	sl : Shrubs/Grassland	0.124	0.058	0.032	**
	sl : DistanceToWater ^{0.5}	-0.058	0.031	0.056	*
		cos(ta) : HumanInfluence	-0.040	0.022	0.070
		cos(ta) : DistanceToWater ^{0.5}	0.063	0.026	0.017

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