

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

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## Abstract

For many species, a sufficient degree of landscape connectivity is a crucial prerequisite for long-term species persistence. This is especially true for animals that exhibit long-distance dispersal, as dispersers typically cross a variety of habitats and potentially move into unfamiliar territory. Estimating habitat permeability and quantifying landscape connectivity have therefore become two major tasks in conservation ecology. For this, least-cost analysis and circuit theory have been the two workhorses during the past two decades. This is largely owed to their ease of use and intuitive nature which has facilitated the application of the methods across a broad range of the animal kingdom. However, both methods make several restricting assumptions that limit their usefulness in reality.

Recent innovations in movement ecology, particularly on step selection analysis, have brought forward novel ways to look at connectivity. For instance, integrated step selection functions provide a means to parametrize a fully mechanistic movement model based on which virtual dispersers could be simulated. While this approach has been used to infer habitat utilization, it may also serve to highlight landscape connectivity and pinpoint dispersal corridors.

Here, we propose the simulation of dispersal trajectories as a much more generic way to identify dispersal barriers and potential movement corridors. To achieve this, we applied integrated step selection analysis and uses data from 16 dispersing wild dogs to parametrize a fully mechanistic movement model for dispersing African wild dogs. The model rendered dispersers' habitat and movement preferences, as well as potential interactions between them. Based on the model, we simulated myriads of dispersal trajectories and inferred dispersal corridors across the earth's largest trans-boundary conservation area, the Kavango-Zambezi Transfrontier Conservation Area. We also exemplify how such simulations could be analysed using network theory. Finally, we discuss the benefits and pitfalls of dispersal simulations and highlight potential improvements to be made in the future.

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# 1 Introduction

Dispersal of individuals is an important process governing the dynamics of wild animal populations that are distributed in space (Clobert et al., 2012). It is defined as the movement of individuals from their natal location to the site of first reproduction Howard (1960) and allows species to avoid inbreeding (Perrin and Mazalov, 1999, 2000; Frankham et al., 2002; Leigh et al., 2012), to rescue small and unviable populations (Brown and Kodric-Brown, 1977), and to promote the colonization of unoccupied habitats (Hanski, 1998; MacArthur and Wilson, 2001). Successful dispersal requires a sufficient degree of landscape connectivity, which is why the protection of dispersal corridors has become a major goal in conservation science. Information on movement behavior during dispersal and knowledge about the factors that limit dispersal is therefore critical for a comprehensive understanding of landscape connectivity and population viability (Baguette et al., 2013; Vasudev et al., 2015). In addition, reliable modelling techniques to identify dispersal corridors based on empirical data are necessary (Diniz et al., 2019).

Thanks to novel technologies developed over the past decades, particularly of GPS/Satellite radio-collars, the study of dispersal and connectivity using telemetry data has accelerated (Jónsson 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 the “golden age of animal tracking” (Kays et al., 2015). Concurrently, the increased availability of large amounts of empirical data and an increased computational power have led to the development of several modelling techniques that allow studying movement behavior during dispersal and highlighting major movement corridors (Boyce et al., 2002; Fortin et al., 2005; Cushman and Lewis, 2010; Zeller et al., 2012; Diniz et al., 2019).

*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). 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. 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 (Zeller et al., 2012). Ultimately, the permeability surface serves as input to a connectivity model that is used to reveal movement corridors. In this regard, two of the most prominent connectivity models in the literature are least-cost path analysis (Adriaensen et al., 2003)

and circuit theory (McRae, 2006; McRae et al., 2008).

In least-cost path analysis, connectivity is estimated by identifying least-costly routes between pre-defined start- and endpoints (Adriaensen et al., 2003). For this, the permeability surface is converted into a network graph and permeability scores are translated into probabilities for moving from one cell to another. Least-costly routes between start- and endpoints can then be computed using Dijkstra's algorithm (Dijkstra, 1959). Although intuitively appealing, the method suffers from several weaknesses. First of all, a least-cost path always exist, even if the associated costs are unreasonably high. Second, it assumes that animals have a preconceived end-point in mind and choose a cost-minimizing route accordingly. While this assumption may be reasonable for migrating animals that move between a limited number of habitats, it is unlikely to hold for dispersers that move over long distances into unknown territory (Koen et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020). Finally, the method also requires that animals have an infinite perceptual range, otherwise they could not compute an optimal path. Some of these issues have been addressed using alternative least-cost approaches. For instance, instead of computing a least-cost path, a least cost-corridor that also considers slightly suboptimal routes (Pinto and Keitt, 2009) can be calculated. The corridor relaxes the assumption of perfect knowledge and overcomes the single pixel width issue. Alternatively, the randomized least-cost path has been proposed, which allows animals to deviate from the least-cost route by a pre-defined factor  $\theta$  (Panzacchi et al., 2016; Van Moorter et al., 2021).

In contrast to least-cost approaches, circuit theory makes use of electrical circuit theory to quantify landscape connectivity (McRae, 2006; McRae et al., 2008). Here, the permeability surface is converted into an electrical circuit containing nodes and resistor, where resistance values depend on habitat permeability. A source point is connected to a current source, whereas an endpoint is grounded. Hence, the current flowing through each node in the circuit can be computed and is supposed to resemble the relative frequency at which each location in the study area is being visited. By revealing not only a single path or corridor, circuit theory overcomes the single-pixel width issue inherent to least-cost approaches. Intrinsically, circuit theory is based on the assumption that animals follow a random walk and can therefore not render directional biases. In reality, however, dispersers often move in a very directional fashion as they want to cover as much ground in as little time as possible. Furthermore, it is assumed that individuals have a perceptual range of a single pixel, which rarely captures the true spatial scale of selection (cite someone).

Neither least-cost analyses or circuit theory are capable of rendering the temporal di-

mension of movement. Such influences could, however, be studied using individual based movement models. Still, only few have explored these possibilities (Kanagaraj et al., 2013; Hauenstein et al., 2019; Zeller et al., 2020).

While step selection functions were initially intended to learn about habitat preferences of the focal species (Fortin et al., 2005), recent improvements may elevate its applicability into other areas. Originally, Fortin et al. (2005) proposed step selection functions to account for serial autocorrelation inherent to GPS relocation data. In this method, covariates along realized steps (the connecting lines between two consecutive relocations; ; Turchin, 1998) are contrasted to covariates along “alternative” or “random steps” that are generated by randomly sampling turning angles and step lengths based on observed movement characteristics. It is then assumed that animals assign a selection score  $w(x)$  of the following form to each step:

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

The selection score  $w(x)$  of each step depends on its associated covariates ( $x_1, x_2, \dots, x_n$ ) and on the animal’s relative selection strengths (i.e. preferences) towards these covariates ( $\beta_1, \beta_2, \dots, \beta_n$ ). The probability that a step  $i$  is realized  $P(Y_i = 1)$  then depends on the step’s selection score, as well as on the selection scores of all alternative steps:

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

Preferences of interest, i.e. the  $\beta$ ’s, can be estimated by comparing realized (scored 1) and random (scored 0) steps in a conditional logistic regression model (Fortin et al., 2005). In this model, positive  $\beta$ -coefficients indicate selection of a covariate, whereas negative  $\beta$ -coefficients indicate avoidance of a covariate. To deal with multiple individuals, one can either average estimates of individual models (Murtaugh, 2007; Fieberg et al., 2010) or apply mixed effects conditional logistic regression analysis as recently proposed by Muff et al. (2020).

An animals movement trajectory can be viewed as the result of an interplay between habitat and movement preferences. Traditional step selection functions cannot account for a correlation between turning angles and step lengths, unless the two are sampled jointly from a copula distribution (?). Recently, however, SSFs have been generalized to *integrated* SSFs (iSSFs), which tear apart movement and habitat preferences of the studied animals (Avgar et al., 2016). The method thus allows to render an animals preferences with respect

to prevailing habitat conditions, as well as with respect to movement characteristics. This reduces potential biases in estimated preferences and enables parametrization of a fully mechanistic movement model from which movement and space use can be simulated (Avgar et al., 2016; Signer et al., 2017). Signer et al. (2017) used integrated step selection analysis to simulate steady state utilization distributions of resident animals. However, the degree to which such simulations could be used to simulate dispersers and infer movement corridors is unknown.

One of the species for which long-term species persistence relies on sufficient landscape connectivity is the endangered African wild dog *Lycon pictus*. This species has once been wide-spread across sub-Saharan Africa but disappeared from a vast majority of its historic range due to ongoing persecution by humans, habitat destruction, and deadly diseases. As of today, only 6'000 free-ranging individuals remain in small and spatially scattered subpopulations. 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 (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 trans-boundary 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 benefit a multitude of other species (Elliot et al., 2014; Brennan et al., 2020; Hofmann et al., 2021).

In a previous paper, we assessed landscape connectivity within the KAZA-TFCA for dispersing African wild dogs using a least-cost corridor approach. For this, we fitted a basic habitat selection model based on which we predicted landscape permeability. We now expand on this knowledge and develop a more detailed movement model of dispersing wild dogs. We then use this model to simulate thousands of dispersers moving across the KAZA-TFCA. Based on said simulations, we compute heatmaps and identify potential dispersal hotspots and compare them to the dispersal routes identified in (Hofmann et al., 2021). We also showcase how simulated dispersal data can be analysed using network-analysis and how network metrics relevant to landscape connectivity can be computed. Our results show that a simulation based approach yields several major benefits over traditional connectivity

modelling techniques. Most importantly, simulations 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. Finally, we put forward additional opportunities using simulations that go beyond the scope of this paper.

Reliable identification of dispersal corridors will become increasingly important with the uprise of ever-growing and often transboundary conservation areas. One such instance is the KAZA-TFCA, a massive conservation area spanning five countries and over 520'000 km<sup>2</sup>. The KAZA holds the potential of re-establishing dispersal routes for many of its protected species, including the African wild dog *Lycaon pictus*. Persecution by humans, habitat loss, and reduced connectivity are major causes of the decline of the species (Woodroffe and Sillero-Zubiri, 2012). In result, the species currently marks the KAZA's most endangered large carnivore and has been assigned a very high conservation priority. Importantly, due to their inherent mobility and intrinsic need for vast undisturbed landscapes, AWDs have been proposed as surrogate species for landscape connectivity (see recent paper on multispecies connectivity). Nevertheless, the species has received little attention in the connectivity literature, mainly due to the difficulty in observing wild dog dispersal.

## 2 Methods

### 2.1 Study Area

The study area was centered at -17°13'9"S, 23°56'4"E (Figure 1a) and was represented by a rectangular bounding box that stretched over 1.3 Mio. km<sup>2</sup>, encompassing the entire KAZA-TFCA (Figure 1b). The KAZA-TFCA is the world's largest transboundary conservation area and comprises parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia, covering a total of 520'000 km<sup>2</sup>. Its landscape varies regionally and ranges from savanna, to grassland and from dry to moist woodland habitats. A dominant hydrogeographical feature in its center is the flood-pulsing Okavango Delta. The delta and its surroundings are considered a stronghold for African wild dogs that may act as a source for the recolonization of surrounding habitats (Cozzi, 2013). The wet season within the KAZA-TFCA lasts from November to March and is out of phase with the main flooding of the Okavango Delta which peaks between July and August (McNutt, 1996; Wolski et al., 2017). While large portions of land within the KAZA-TFCA are designated national parks or other protected areas, substantial human influence remains due to roads, agricultural sites and settlements and villages.

## 2.2 GPS Relocation Data

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. 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 CO<sub>2</sub>-pressurized gun (*DAN-Inject, Denmark*). Anesthesia protocols were approved by the Ministry of Environment, Natural Resources Conservation and Tourism of Botswana (permit EWT 8/36/4 XXXVI). 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 rejoined their pack within one hour after immobilization. 16 collared individuals eventually dispersed, each in a separate same-sex coalition (7 female and 9 male coalitions).

During dispersal, collars were programmed to record a GPS fix every 4 hours. Collected relocations were regularly transmitted over the Iridium satellite system, which allowed remote tracking of individuals, even if they left the main study area and crossed international borders. In some instances exact dispersal dates were known from field observations. In other cases, we distinguished between residency and dispersal using the net-squared displacement metric. This metric measures the squared Euclidean distance 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. As such, dispersal was deemed to have started when an individual left its natal home range and ended once individuals became sedentary again. Because behavior during dispersal is more pertinent for assessing connectivity, we discarded all data that was collected during residency and only retained GPS data recorded during dispersal. As previous research revealed similar behavior 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 collected on the 4-hourly schedule.

## 2.3 Covariates

We represented the physical landscape across the study area using a set of habitat covariates including water-cover, distance to water, tree-cover, and shrub/grassland-cover. Because water cover greatly changes within and between years around the Okavango Delta, we applied a remote sensing technique that allowed us to generate frequently updated water cover layers and corresponding distance to water layers for the close surroundings of the Delta (see Wolski et al., 2017 and Hofmann et al., 2021). Thus, those layers temporally aligned with our dispersal events. We also computed a proxy for human influence, depicting anthropogenic pressures stemming from human-density, agricultural sites, and roads. All obtained layers were coarsened or interpolated to a target resolution of 250 m by 250 m and cropped slightly beyond the extent of the KAZA-TFCA. Further details on the sources and preparation of each habitat covariate are given in Hofmann et al. (2021).

Besides habitat covariates, we also 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 ( $\cos(ta)$ ). Because wild dogs follow a diurnal activity pattern, we also coded a binary variable (`LowActivity`) indicating whether a step was realized during periods of low wild dog activity (17:00 to 07:00 local time) or high wild dogactivity (09:00 to 17:00 local time). Handling and manipulation of all data, as well as all modelling and simulating was achieved with statistical software R, version 3.6.6 (R Core Team, 2019). R-scripts to reproduce the analyses are provided on Github.

## 2.4 Movement Model

We used integrated step selection functions (iSSF) to parametrize a mechanistic movement model of dispersing wild dogs. In contrast to regular step selection functions, *integrated* step selection functions allow simultaneous inference on movement and habitat preferences of the studied animal, as well as on potential interactions between the two. This results in less biased selection estimates and allows to treat the resulting model as a fully mechanistic movement model based on which movement can be simulated (Avgar et al., 2016). To conduct iSSF analysis, we paired each observed step with 24 random steps. Together, an observed and its random steps formed a stratum that received a unique identifier. The 24 random steps served as pseudeo-absence and represented a potential alternative that the animal could have realized but decided not to. 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 observed steps (scale = 6'308, shape = 0.37). Although a larger number of random steps reduces the sampling error (Avgar et al., 2016), preliminary analyses revealed that 24 steps were sufficient in our case. Along each step, we extracted and averaged spatial covariates using the `velox` package and we calculated the movement metrics `sl`, `log(sl)`, and `cos(ta)`. To facilitate model convergence, we standardized all continuous covariates to a mean of zero and a standard deviation of one. 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 2) and fit a movement model, we assumed that animals assigned a selection score  $w(x)$  to each step. The score depended on the step's covariates  $X$ , as well as the animals preferences  $\beta$  towards these covariates. 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. To estimate the preferences of interest, we ran conditional logistic regression models in the r-package `glmmTMB`. More specifically, we applied the method developed by (Muff et al., 2020), which allows to fit random slopes. Here, we treated animal IDs as random effect and modelled random slopes for each covariate and we fixed the random intercept variance at an arbitrary high value of  $10^6$  to make use of the “poission”-trick (Muff et al., 2020).

The movement model was based on a habitat selection model for dispersing wild dogs presented in Hofmann et al. (2021). In the original model, no interactions between the habitat and movement covariates were considered, so we slightly expanded this base model by proposing interactions between 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 presented Fortin et al. (2009). We randomly split the input data into training and testing data with an 80:20 ratio. 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 such that rank 1 was given to the step with the highest score  $w(x)$ . Across all strata we determined the realized step's rank and calculated rank frequencies for realized steps. 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. Random preferences were 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 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

We used the most parsimonious movement model to simulate 80'000 dispersing wild dogs moving across the KAZA-TFCA. The simulation resembled an inverted iSSF and worked 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 relative turning angles from a uniform distribution  $(-\pi, +\pi)$  and step lengths from our fitted gamma distribution. As such, each step corresponded to the straight line movement conducted within 4 hours. To prevent unreasonably large steps, we capped sampled values to a maximum of 35 km, which corresponds 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 calculated movement covariates. Extracted values were again standardized using the same transformations that were used on the input data. (4) We applied the parameterized movement model and predicted the selection score  $w(x)$  for each of the proposed steps and translated selection scores into probabilities by applying Equation (Equation 2). (5) We randomly sampled one of the random steps based on predicted probabilities and used it to determine the animal's new position. We repeated steps (2) to (5) until a total of 2'000 steps were realized.

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 buffer zone. Within the buffer zone, we randomized covariate values by resampling values from the original covariate layers. In result, simulated dispersers were

able to leave and reenter the main study area through this buffer zone. In cases where a disperser approached the outer map boundary such that one of the proposed random steps transgressed its border, we resampled transgressing steps until they fully lied within the buffer zone. Although the algorithm for the simulation was mainly coded in R, we wrote a few helper functions in C++ and imported them into R using the Rcpp package (Eddelbuettel and François, 2011; Eddelbuettel, 2013).

## 2.6 Source Points

We initiated virtual dispersers at 50'000 randomly selected source points within contiguous protected areas larger  $> 700 \text{ km}^2$  (Figure 2 (a)). This conforms to the average home range requirement of resident wild dogs (Pomilia et al., 2015) and allowed us to remove areas too small to host viable wild dog populations. By distributing source points randomly, the number of source points per  $\text{km}^2$  within protected areas was approximately equal across the study area. To render potential immigrants into the study system, we placed additional 30'000 source points inside the buffer zone around the main study area (Figure 2 (b)). This resulted in a total of 80'000 source points, each representing the start point of an individual disperser.

## 2.7 Heatmap

To identify dispersal hotspots across our study area using the simulated dispersal events, we rasterized all simulated trajectories and created a heatmap indicating the absolute frequency at which each raster-cell in the study area was visited by our virtual dispersers. If the same trajectory crossed a raster-cell twice, it was only counted once, meaning that we did not consider revisits. This mitigated biases arising due to trapped individuals that were moving in circles. To achieve high performance rasterization of all simulated trajectories, we used the R-package `terra` (Hijmans, 2020).

## 2.8 Network Analysis I: Betweenness

To pinpoint areas of exceptional relevance for connecting remote regions in our study area, we converted simulated trajectories into a network and calculated betweenness scores. More specifically, we overlaid the study area (including the buffer) with a regular raster that was resolved at 5 x 5 km and where each raster-cell represented a node in the final network. We then used the simulated trajectories to determine all transitions occurring from one cell to another, as well as their frequency. This resulted in an edge-list that we translated into a weighted

network using the r-package `igraph`. Because `igraph` handles the weights  $\omega$  as costs, we inverted the traversal frequency at each cell by applying  $\omega = \frac{\sum_i^n TraversalFrequency_i/n}{TraversalFrequency_i}$ . Finally, we calculated the betweenness metric for each node in the final network. This metric indicates 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).

## 2.9 Network Analysis II: Interpatch-Connectivity

We also adopted an alternative network view and assessed interpatch connectivity between national parks. The decision to focus on national parks was purely out of simplicity and could easily be expanded to any other patch of interest. To determine interpatch-connectivity, we identified the relative frequency at which dispersers originating from one national park successfully moved into another national park. This allowed us to determine *if* and *how often* dispersers moved between certain national parks, as well as to estimate the average number of steps that was necessary for those movements.

## 3 Results

### 3.1 Movement Model

Compared to the base model reported in (Hofmann et al., 2021), our most parsimonious movement model included several additional interactions between habitat and movement covariates (Figure 3 and Table 1). Although multiple models received an AIC weight above zero (T1 in Appendix S1), we only considered results from the “best” model for further analyses. Since all models with positive AIC weight contained similar covariates, this decision only marginally influenced subsequent results. Results from the selected model are given in Table 1 and illustrated in Figure 3 (a). Additional plots to ease with the interpretation of the model are provided in Appendix XX.

When holding constant for movement behavior, we find that dispersing wild dogs avoid water, but prefer its proximity. Dispersers also avoid densely forested woodlands, yet prefer open shrublands or grasslands. Finally, dispersers avoid moving through landscapes that are influenced by humans.

When looking at the movement kernel, we observe several significant interactions. However, except for the interaction `sl:LowActivity`, estimated slopes are relatively flat, suggesting that our initial distributions for step lengths and turning angles were only marginally biased.

For instance, the positive effect for  $\cos(\text{ta})$  indicates that observed turning angles are slightly more directional compared to the turning angles proposed by our uniform distribution. On the other hand, the strongly significant and negative interaction `sl:LowActivity` reveals that our fitted gamma distribution produced steps lengths that were substantially larger than those realized by the dispersers during low wild dog activity.

However, we also find a strongly significant and negative interaction between the step length and main-activity indicator, showing that realized step lengths tended to be much shorter during periods of activity in comparison to the steps proposed by our fitted gamma distribution.

Finally, the significant interactions `cos(ta):HumanInfluence` and `cos(ta):DistanceToWater2` indicate that dispersers move much more tortuous in areas influenced by humans but more directed when distant to water.

Results from the k-fold cross-validation procedure show that our model substantially outperforms a random guess, as the confidence intervals of  $r_{..}$  and  $r_{..}$  do not overlap. Additionally, we find that the rank correlation slightly improved in comparison to the base model reported in (Hofmann et al., 2021).

### 3.2 Dispersal Simulation

On a machine with an AMD Ryzen 7 2700X processor with 8 x 3.6 GHz and 64 GB of RAM, a single batch of 1'000 simulated dispersers took roughly 90 minutes to compute ( $\mu = 88.90$ ,  $\sigma = 1.87$ ). As such, the simulation of all 80'000 dispersers terminated after 120 hours, i.e. five days. However, comparable computations will be substantially quicker for smaller study areas, as the covariate extraction from large rasters was computationally the most expensive task.

On average, step lengths realized by the simulated dispersers ( $\mu = 2'093$  m,  $\sigma = 3'067$ ) were slightly shorter than those by observed dispersers ( $\mu = 2'326$  m,  $\sigma = 3'323$ ). Simultaneously, a slightly smaller  $\cos(\text{ta})$  indicated that simulated dispersers moved with marginally lower directionality ( $\mu = 0.057$ ,  $\sigma = 0.071$ ) compared to observed dispersers ( $\mu = 0.078$ ,  $\sigma = 0.072$ ). These differences in step lengths and turning angles can be attributed to minor disparities between habitat conditions at the area within which we collected training data and habitat conditions within the entire study area.

Out of the 50'000 dispersers initiated in protected areas, only 4.5% eventually hit a map boundary, highlighting that boundary effects should be neglectable. In contrast, 78% of the 30'000 dispersers originating from the buffer zone hit a map boundary at least once.

### 3.3 Heatmaps

Figure 4 depicts the heatmap rendering the traversal frequency at each pixel of the study area across all simulated individuals and steps. The map illustrates that large portions of land beyond the borders of the KAZA-TFCA are only infrequently visited by dispersers (dark blue areas). On the contrary, we observe that within the KAZA-TFCA extensive regions are regularly visited by dispersers (bright yellow and red areas). Most notably, the region in northern Botswana south of the Linyanti swamp glows in rich red and stands out as highly frequented dispersal hub. Nevertheless, massive water bodies such as the Okavango Delta, the Makgadikgadi Pan, and the Linyanti swamp, pose considerable dispersal barriers within and therefore limit realized connectivity the KAZA-TFCA.

### 3.4 Network Analysis I

The results of our first network analyses are presented in Figure 5. In contrast to the heatmap, Figure 5 puts much more emphasis on discrete dispersal corridors. Nonetheless, the dispersal hub in northern Botswana stands out again and is traversed by a corridor that receives a comparably high betweenness score. This implies that the region is particularly crucial for connecting other pixels in the study system and hence represents a proper dispersal hub. Towards east, the corridor runs through the Chobe National Park into the Hwange national park, where it branches out and further extends into the distant Matusadona National Park in Zimbabwe. Northwest of the Linyanty ecosystem, the same 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 appear to directly link the peripheral regions of the KAZA-TFCA. For instance, there are no viable dispersal 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.

### 3.5 Network Analysis II

The results from the second network analysis that was focused on connectivity between national parks are given in Figure 6. The map shows between which national parks direct links exist and how frequent they are, as well as the average duration a disperser had to move to realize those links. For instance, 6.8 % of the simulated dispersers originating from the Moremi National Park successfully reached the Chobe National Park and 4.2 % reached

the Hwange National Park in Zimbabwe. On average, dispersers moved for 623 steps before arriving at Chobe ( $SD = 520$ ) and for 1'413 steps before arriving at Hwange ( $SD = 371$ ).

## 4 Discussion

Our connectivity network further suggests that dispersers from the Okavango Delta more likely disperse towards east than west. Indeed, only  $x$  out of our  $y$  observed dispersers ever reached the western part of the delta. Only when the flood retracts a small pathway between the city of Maun and the floodwaters of the delta emerges and enables dispersers to move towards the delta's western part.

All of our findings are well in line with our previous work, where we have highlighted dispersal corridors for wild dogs using least-cost approaches. This suggests that qualitative results are quite insensitive to the exact methodological approach. Still, we believe that a simulation based approach offers possibilities for much richer inferences compared to traditional approaches. This is largely due to the fact that proper movement trajectories are generated that can be analysed *as if* they were generated by real dispersers. This is of course contingent on the assumption that underlying models are adequately representing movement behavior of the focal species and calls for further methods to validate the predictive power of such simulations.

While the segment running into Kafue receives a high betweenness score, it was actually only rarely traversed by our simulated dispersers, as can be seen from the dark colors in this region in Figure 4. It is therefore worth noting that the betweenness metric highlights crucial bottlenecks that are relevant for connecting remote regions, yet does not directly yield information about the absolute frequency at which these bottlenecks are used.

We have previously attributed the weak significance of distance to water to the fact that we did not control for the presence or absence of conspecifics. We stick to this reasoning as our expanded model still shows a rather large uncertainty around the respective beta coefficients. To better gauge the importance and influence of this covariate, future studies will need to control for inter- and intra-specific interactions that may explain why and when dispersers are attracted to or afraid of waterbodies.

For our simulations, we represented the Okavango Delta statically and assumed a relatively extended flood. This resulted in a quasi-barrier, formed by the Okavango-Delta and the adjacent city of Maun, which was rarely traversed by simulated individuals. Out of the 499 dispersers initiated inside the Moremi National Park, only 101 managed to reach the south-western section of the Delta, whereas 284 eventually reached the equally distant

Linyanti swamp. In this regard, the heatmap presented in Figure 4 may be most representative of the period shortly after the wet-season, when floodlevels in the Delta are at their maximum. During the dry season, however, the flood considerably retracts and potentially clears the way for wild dogs dispersing from the Moremi-Game reserve into the south-western section of the Delta. Future studies could relax the assumption of a static flood and attempt to update floodlevels as the dispersers move. This would allow studying how connectivity within the ecosystem evolves over time as the flood climaxes and retracts again. In fact, one of the major advantages of such simulation based approaches is that a dynamic environment can be rendered, as time is explicit in these models (Zeller et al., 2020). This contrasts with traditional modelling approaches such least-cost analysis or circuit theory, where the temporal dimension cannot be made explicit. An explicit view on time also directly translates in insights on the duration required by dispersers to move between distinct patches such as national parks or spatially segregated subpopulations.

Comparable simulations that are based on empirical data are also a fundamental component for spatially realistic population models in which dispersal is rendered more realistically and does not merely depend on the distance between habitat patches.

We did not model mortality during dispersal in our simulations. This was a simplifying assumption and only inaccurately reflects dispersal in reality. It is well known that wild dogs often die during dispersal in result of deadly encounters with other predators, but also due to road kills and illegal shootings by humans. In result, mortality during dispersal may limit realized connectivity, especially in areas that wild dogs are unfamiliar with or in areas with high potential for human-wildlife conflict (Cozzi et al., 2020). Interestingly though, ? have recently demonstrated that mortality during dispersal is lower compared to residency, suggesting the presence some fitness benefits to dispering individuals.

In this regard, our approach is rather similar to dispersal kernels, yet it enables to render directional biases, which are currently difficult to implement using such methods.

We completely randomized the location of source points within protected areas. However, in some cases prior knowledge about the density of potential dispersers is available and can be used to adjust the number of simulated individuals accordingly. Alternatively, instead of tweaking the number of simulated individuals, one could assign a weight to each trajectory that depends on the density of potential dispersers in the source areas. As such, trajectories from areas with high density would enter the heatmap with above average weight.

The parametrized movement model could also be manipulated to investigate how different habitat preferences influence landscape connectivity and to test the sensitivity of results

with respect to the exact preferences of individuals.

One of the major benefits of individual-based simulations is the ability to make the temporal dimension of movement explicit. This allows to investigate how connectivity depends on the dispersal duration, something that is not possible with traditional least-cost or circuit theory methods.

Optimally, one should simulate additional dispersers until the amount of newly gained information lies beyond a certain threshold, i.e. until some sort of convergence is achieved. However, due to the myriad of outcomes in movement behavior, this would often imply countless repetitions for each source points at each location where dispersal is possibly initiated. This is computationally infeasible.

Our work suggests that the selection of source points significantly impacts resulting connectivity networks. Especially when dispersal durations are short, wrongly placed source points lead to vastly different results. Signer et al. used estimated utilisation distributions by means of simulated movements. They used a rather long burn in period prior to alleviate the problem of selecting meaningful source points. However, this approach only works when individuals move around a point of attractor. This is typically not the case when simulating dispersers, introducing an important trade-off. The researcher can decide to increase the number of simulated steps, hence reducing the influence of starting locations, yet this also inevitably increases estimated connectivity.

In some European countries, the comeback of large predators, such as bears, lynx, and the wolf, has triggered emotional discussions and raised public concern (Behr et al., 2017), particularly in areas with free-roaming livestock that may be preyed upon by the returned species. In cases where recent locations of such predators are known, an early warning system based on simulations could serve to forewarn about potential encounters and thereby increase public acceptance of large predators.

## 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.

## **7 Acknowledgements**

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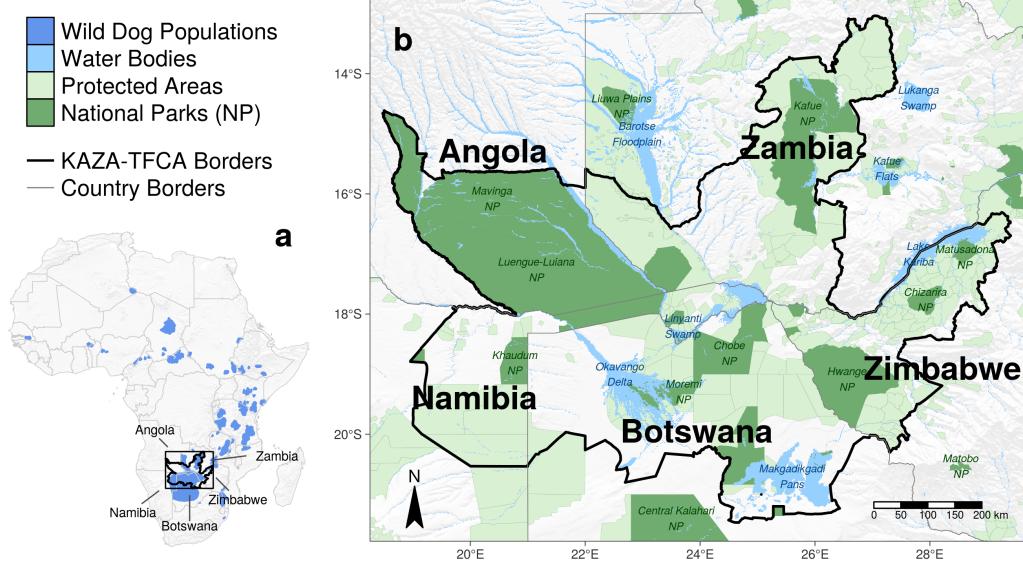
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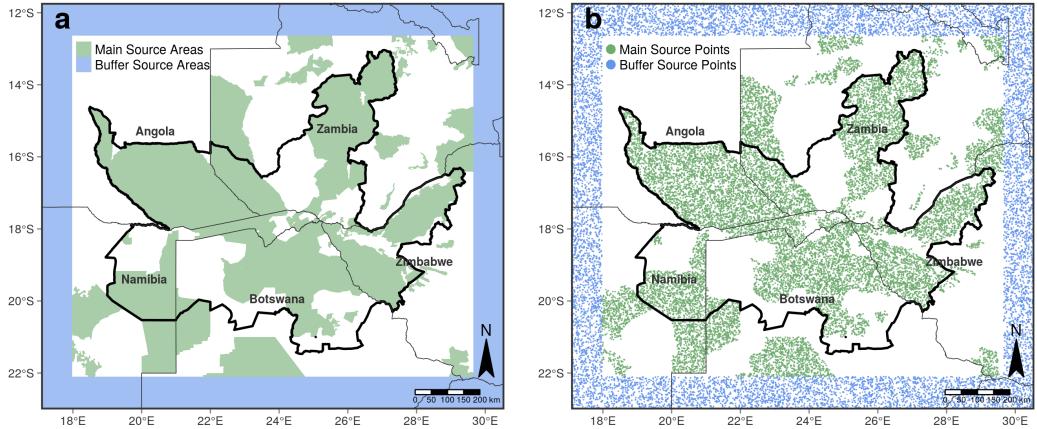
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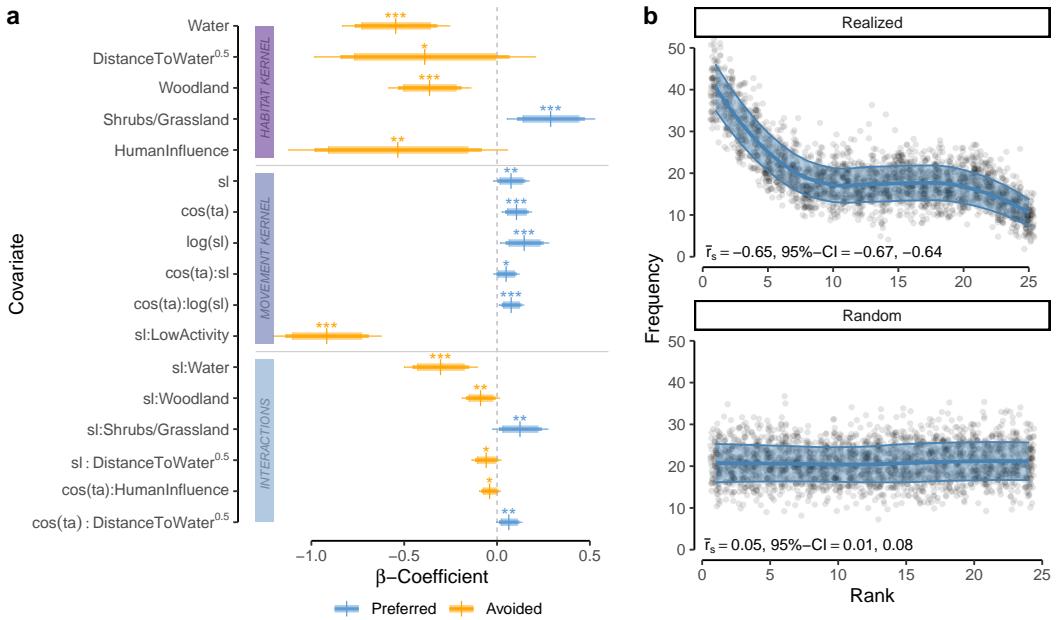
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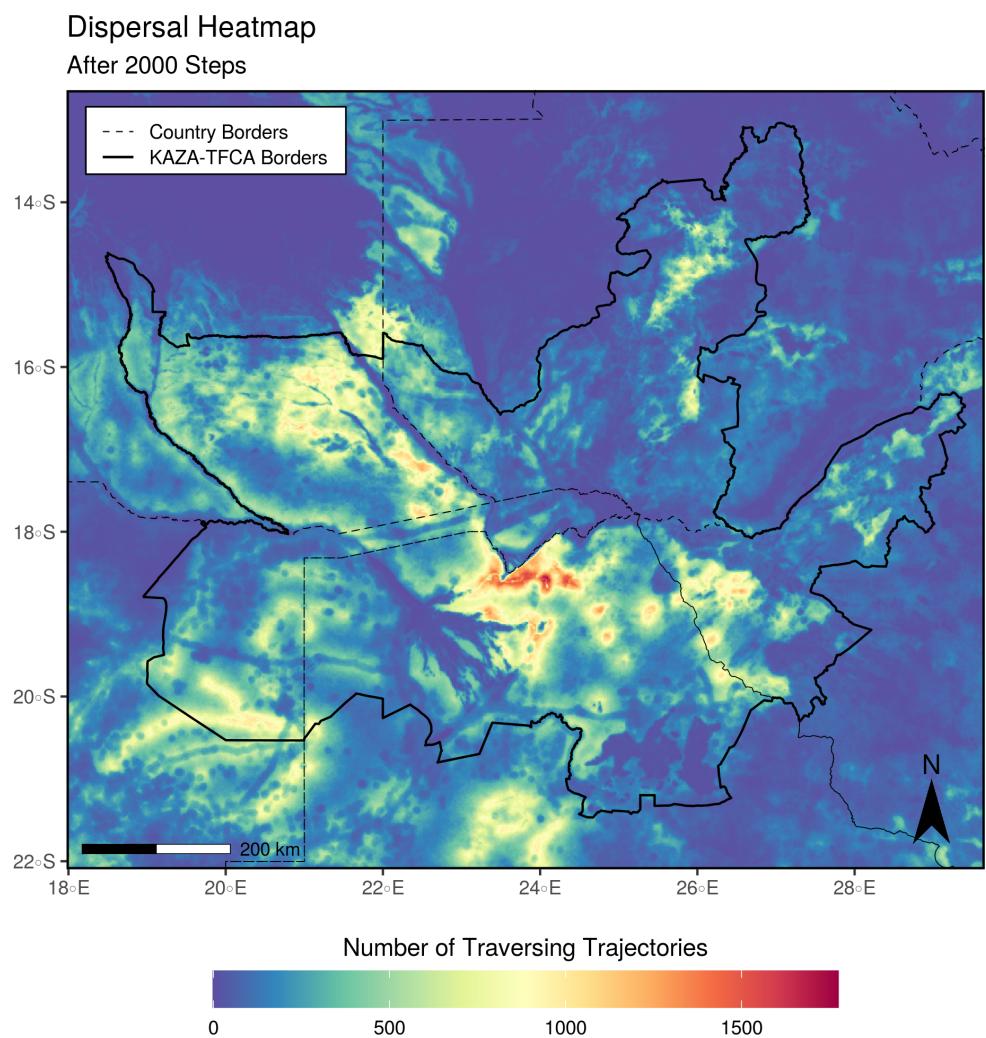
**Figure 1:** (a) The study area of our research was confined by a bounding box encompassing the entire KAZA-TFCA, which comprises parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA represents the world's largest terrestrial conservation area and covers a total of 520'000 km<sup>2</sup>. Its purpose is to re-establish connectivity between already-existing national parks and other protected areas (green polygons). The dispersal data used in this study was collected on a free-ranging African wild dog population inhabiting the Moremi National Park in northern Botswana.



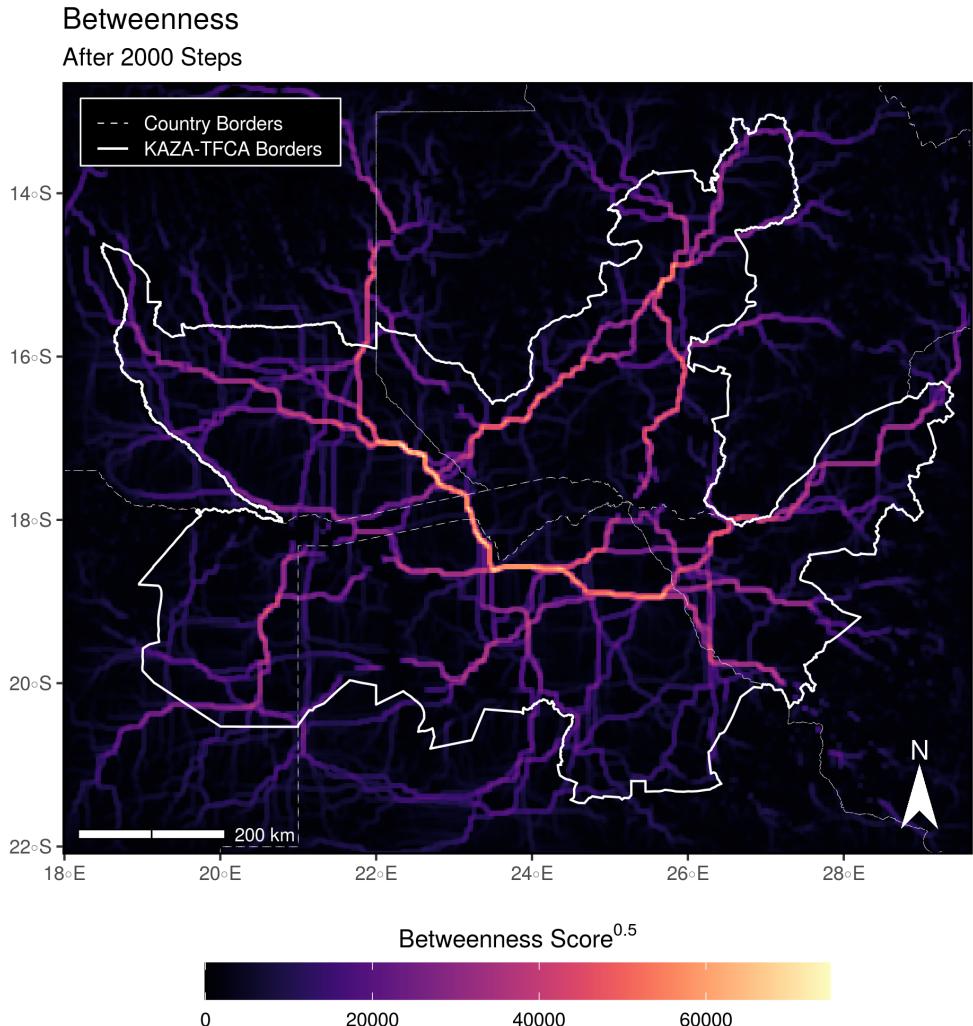
**Figure 2:** (a) Different source areas from which we released virtual dispersers. We only considered contiguous protected areas (national parks, game reserves, and forest reserves) that were larger than  $700 \text{ km}^2$  (green). This area corresponds to the average home range requirement for viable 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 3:** (a) Most parsimonious movement model for dispersing wild dogs. The model includes a habitat kernel, a movement kernel, as well as their interactions. The orange and blue line segments delineate the 90%, 95%, and 99% Confidence-Intervals around the respective  $\beta$  coefficients. Significance codes: \*  $p < 0.10$ , \*\*  $p < 0.05$ , \*\*\*  $p < 0.01$ . (b) Results from the k-fold cross validation procedure. The upper plot shows rank frequencies of predicted realized scores according to model predictions with known preferences, whereas the lower plot shows rank frequencies 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.



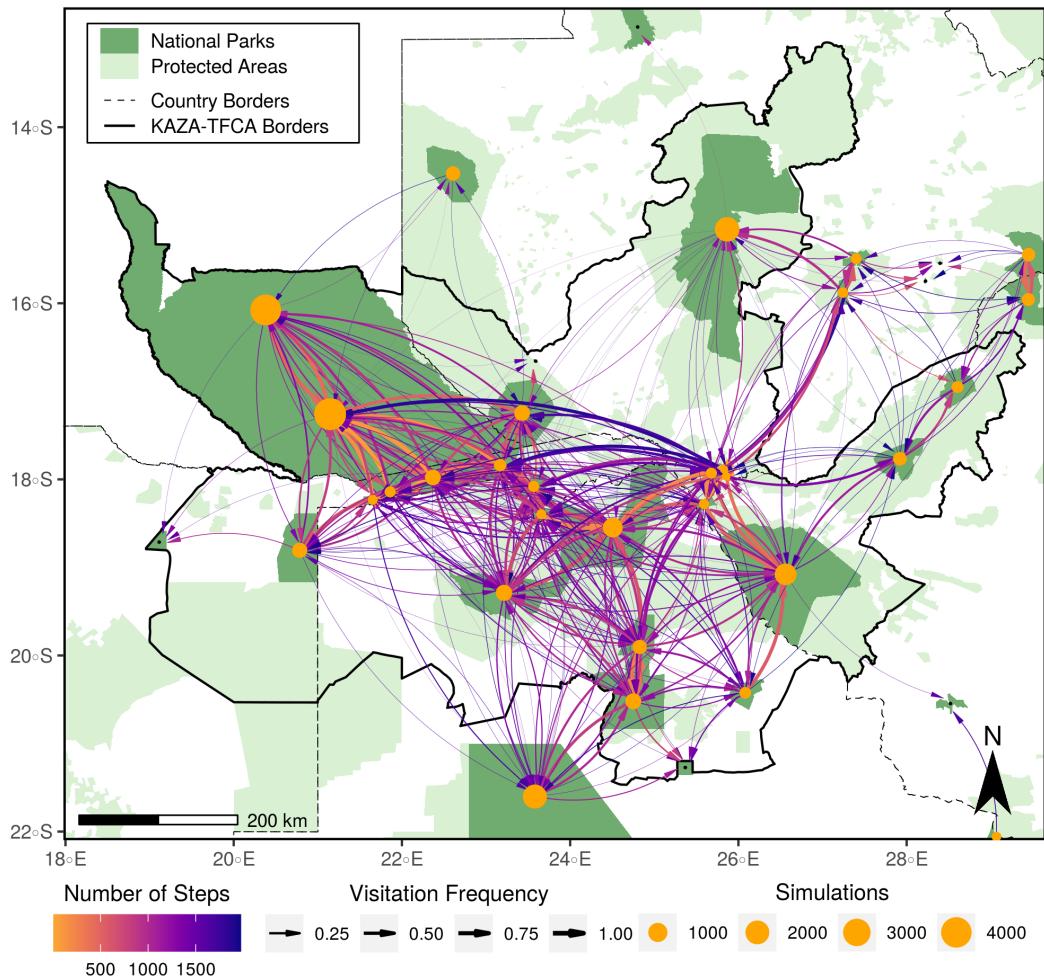
**Figure 4**



**Figure 5:** Betweenness scores of each raster cell in a raster with  $5 \times 5$  km resolution. Betweenness scores were determined based on simulated dispersal events. A high betweenness score highlights cells that 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.

## Areas Reached and Visitation Frequency

In Relation to Number of Steps



**Figure 6:** Network on simulated dispersal trajectories highlighting the 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. Colored 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 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.

**Table 1:** Most parsimonious movement model for dispersing wild dogs. The model comprises of a movement and habitat kernel, where the movement kernels describes preferences with regards to movement behavior, whereas the habitat kernel describes preferences with respect to the habitat. Finally, the two kernels can interact, such that movement preferences are contingent on habitat conditions.

Kernel	Covariate	Coefficient	SE	pvalue	Significance
Habitat Kernel	Water	-0.546	0.112	< 0.001	***
	DistanceToWater <sup>0.5</sup>	-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	***
Interaction	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 <sup>0.5</sup>	-0.058	0.031	0.056	*
<i>Significance codes:</i> * $p < 0.10$ ** $p < 0.05$ *** $p < 0.01$					