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

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March 24, 2021

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

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 transboundary 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 simualtions and highlight potential improvements to be made in the future.

1 Introduction

Dispersal of individuals is an important process governing the dynamics 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). Successfull 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 (Jønsson 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 (**?**). These methods allow estimating habitat preferences of the focal species by comparing covariates at locations visited by the animal to the scame 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). Utimately, 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 θ (Panzacchi et al., 2016; ?).

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 analyes 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 (**?**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:

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

The selection score $w(x)$ of each step depends on its associated covariates $(x_1, x_2, ..., x_n)$ and on the animal's relative selection strengths (i.e. preferences) towards these covariates $(\beta_1, \beta_2, ..., \beta_n)$. 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:

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

Preferences of interest, i.e. the β'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 β-coefficients indicate selection of a covariate, whereas negative β-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 seen 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 pre-

vailing 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 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 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 throughout the KAZA. 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 suggest 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 addtion, 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^2. 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 a 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 (centered at -17°13'9"S, 23°56'4"E; Figure 1a) stretched over 1.3 Mio km^2 and ecompassed 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 area of over 520'000 km^2. 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 Okavango Delta, the earth's largest inland delta. The delta and its surroundings are considered a stronghold for African wild dogs and may act as a source for the recolonization of surrounding habitats. The wet season within our study area 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).
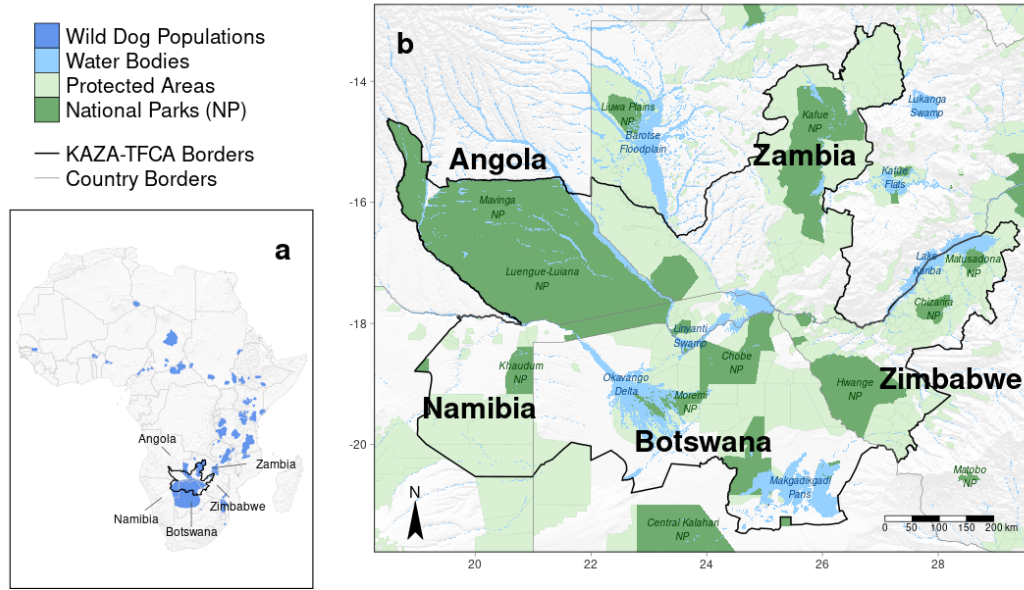
Figure 1: Study area

2.2 GPS Relocation Data

Between 2011 and 2020, we collected GPS relocation data on dispersing wild dogs from a free-ranging wild dog population inhabiting the Okavango Delta in northern Botswana. We identified potential dispersers based on age, number of same-sex siblings, pack size, and presence of unrelated opposite-sex individuals in the pack (McNutt, 1996; Behr et al., 2020). We immobilized individuals using a cocktail of Ketamine/Xylazine/Atropine (Osofsky et al., 1996; Cozzi et al., 2020), injected with a dart that was fired from a CO_2-pressurized gun (*DAN-Inject, Denmark*). Protocols for the anesthization protocols were approved by the Ministry of Environment, Natural Resources Conservation and Tourism of Botswana (permit EWT 8/36/4 XXXVI). After immobilization, individuals were fitted with GPS/Satellite radio collars (*Vertex Lite; Vectronic Aerospace GmbH, Berlin*) that included an automated drop-off mechanism. Handling and collaring of all individuals was carried out and supervised by a Botswana-registered wildlife veterinarian. All of the immobilized individuals quickly rejoined their pack within one hour after the procedure. Out of all collared individuals, 16 eventually dispersed in separate same-sex coalitions and their trajectories were successfully recorded (7 female and 9 male coalitions).

During dispersal, collars were programmed to record a GPS fix every 4 hours. Recorded relocations were regularly transmitted over the Iridium satellite system, which allowed re-

mote tracking of individuals, even if they left the main study area and crossed international borders. To effectively distinguish between periods of residency and dispersal, we applied the net-squared displacement metric to the observed movement data. This metric measures the squared Euclidean distance of a collared individual to a reference point (Börger and Fryxell, 2012), which we set at the center of each disperser's natal home range. Hence, dispersal was deemed to have started when an individual left its natal home range and ended when the individual became stationary again. For the purpose of this study, we discarded andy data that was collected during residency. Because previous research could not find any differences between males and females during dispersal (Woodroffe et al., 2019; Cozzi et al., 2020), we did not distinguish sexes for the sake of our analyses. Ultimately, we converted the collected GPS relocations to steps, where each step represented the straight-line distance travelled between two consequtive GPS relocations (Turchin, 1998).

2.3   Covariates

To represent habitat covariates, we prepared a set of spatial raster layers depicting water-cover (dynamically updated), distance to water (dynamically updated), tree-cover, and shrub/grassland-cover. To render a decreasing impact with increasing distance, we square rooted the distance to water covariate layer. We also created a proxy for human influence, rendering anthropogenic pressures stemming from human-density, agricultural sites, and roads. We rendered all layers at a resolution of 250m by 250m for the entire extent of the KAZA-TFCA. Further details on the derivation and preparation of each environmental covariate is given in Hofmann (2020).

Besides habitat covariates, we also computed movement metrics that we used as movement covariates in our models. These covariates included the step length (sl), its natural logarithm ($log(sl)$), as well as the cosine of the relative turning angle ($cos(ta)$). Because wild dogs follow a diurnal activity pattern, we furthermore coded a binary variable indicating whether an observed step was realized during main activity (xx to xx) or low activity (xx to xx).

2.4   Movement Model

We used integrated step selection functions (iSSF) to parametrize a mechanistic movement model of dispersing wild dogs. In this framework, observed steps are contrasted to random steps that the animal could have realized, but decided not to. To compare steps, it is assumed that animals assign a relative selection score $w(x)$ to each step. The score depends

on the covariates X experienced along a step, as well as the animals preferences towards these covariates β. The probability of a step being realized is then contingent on the step's selection score, as well as the selection scores of all other step in the same stratum. In contrast to regular step selection analysis, *integrated* step selection analysis allows simulatneous inference on movement and habitat preferences of the studied animal. Moreover, potential interactions between habitat and movement preferences can be included to investigate how movement behavior depends on habitat characteristics. In result, the method produces less biased selection estimates and allows to apply the resulting model as a fully mechanistic movement model based on which movement can be simulated. To conduct iSSF analysis, we paired each observed step with 24 random steps. Random steps basically resembled potential alternatives 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 distirbution that was fitted to observed steps (scale = 6'308, shape = 0.37). While the number of random steps is inversely proportional to the sampling error (Avgar et al., 2016), we found only minor differences in model performance when sampling additional random steps and deemed 24 random steps sufficient. Along each step, we extracted spatial covariates using the *velox* package and 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. We then used the r-package *glmmTMB* to fit mixed effects conditional logistic regression models as proposed by (Muff et al., 2020).

Our movement model was and extension of the habitat model presented in Hofmann et al 2021. We will refer to it as the base model. Because the base model was used to predict landscape permeability, no interactions between the habitat and movement metrics were modeled. Thus, we expanded the base model and by proposing additional interactions between movement metrics and environmental covariates. For this, we started with the base model and iteratively increased model complexity by adding all proposed 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 $Water : cos(ta)$. Furthermore, we 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 $sl : MainActivity$ and $log(sl) : MainActivity$ to account for the fact that step lengths diffuer due to the diurnal activity pattern. We then ran stepwise model forward selection based on Akaike's Information Criterion (AIC, Burnham and Anderson, 2002) values and

identified the most parsimonious movement model. Although several models received an AIC weight above one, we decided to only consider the "best" model for simplicity. In either way, the models with positive weights contained almost identical covariates and an averaged model would have only given weak support to additional covariates.

2.5   Source Points

We randomly placed source points within protected areas larger (> 700 km^2), which conforms to the average home range requirement of resident wild dogs (Pomilia et al., 2015). By distributing source points randomly, the number of source points per km^2 within protected areas was approximately equal across our study area. In total, we distributed 50'000 source points across all protected areas, each representing the starting point of a dispersal trajectory. To render potential immigrants into the study system, we randomly placed 10'000 additional source points inside a xx km buffer around the study area. Hence, a total of 60'000 source points were generated, thereby resulting in 60'000 simulated dispersers. It is worth pointing out that our choice of placing source points completely random is arbitrary, as one as well adjust the sampling frequency based on the density of dispersers in the respective source area.

2.6   Dispersal Simulation

We used the most parsimonious movement model to simulate a total 80'000 dispersing wild dogs across the KAZA-TFCA. The simulation basically resembled an inverted iSSF and was set up as follows. First, we sampled a source point at which a disperser was initiated and assumed a random initial orientation of the animal. The orientation was essential to permit calculation of relative turning angles. Second, we generated a set of 25 random steps by sampling turning angles from a uniform distribution $(-\pi, +\pi)$ and step lengths from the fitted gamma distribution. Similarly to our input data, each step corresponded to a temporal difference of 4 hours. To prevent unrealistically large steps, we capped sampled step lengths at 35km, which corresponds to the farthest distance travelled by one of our dispersers within 4 hours. Third, along each random step we extracted habitat covariates and calculated movement covariates. Fourth, we applied the parametrized movement model to predict the selection scores $w(x)$ for all steps. Fifth, we translated selection scores into probabilities by applying Equation (Equation 2). Sixth, we sampled one of the random steps based on assigned probabilities and determined the animal's new position. We then repeated steps two to six until a total of 2'000 steps were realized.
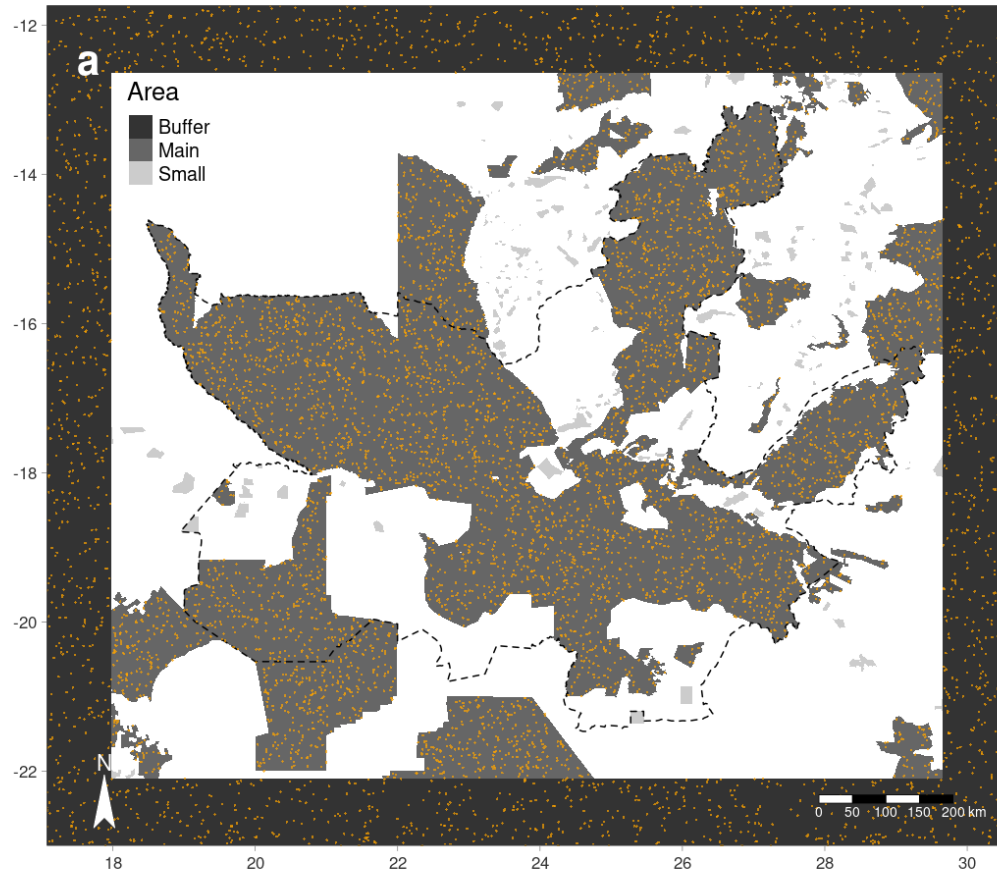
Figure 2: Illustration of source points from which dispersal was simulated. Although in reality we simulated 1'000 per source point, we illustrate an example assuming 10 dispersers from each source point. (a) Static source points similar to the source points reported in ... (b) Source points that were randomized within the catchment areas (dark gray, delinated by solid black lines).

Inevitably, some simulated dispersers would approach a map boundary and one of the generated random steps would leave the study area. However, beyond the study area no covariates could be extracted and no selection scores can be calculated. To mitigate the influence of such edge effects, we buffered all covariate layers by xx percent and filled the buffer zone with covariate values resampled from the observed data. As such, simulated dispersers were allowed to leave and reenter the study area through this buffer zone. In case one of the proposed random steps left the buffer, we resampled the corresponding step until it lied fully within the buffer zone. This implies that we forced the disperser to bounce off the borders of the buffer zone.

To meaningfully select source points, we randomly sampled coordinates within protected areas larger (> 700 km^2), which conforms to the average home range requirement of resident wild dogs (Pomilia et al., 2015). By distributing source points randomly, the number of source points per km^2 within protected areas was approximately equal. In total, we distributed 50'000 source points across protected areas. To render potential immigrants into the study area, we placed 10'000 additional random points inside a xx km buffer around the study area. In total, we generated 80'000 source points, thereby resulting in 80'000 simulated dispersers, each of which moved 2'000 steps. Overall, this implied 160 Mio. simulated steps.

2.7 Heatmaps

Using the simulated trajectories, we created heatmaps that indicate the frequency at which each raster-cell in the study area was visited. If the same trajectory crossed a pixel twice, it was only counted once, i.e. we did not consider revisits. We achieved high performance rasterization of all simulated trajectories using the recently developed R-package *terra* (Hijmans, 2020).

To examine if and how "heat" changes in response to changes in the location of source points and the number of simulated steps, we followed a 2 x 6 design and created heatmaps for both point sampling regimes, as well as for 68, 125, 250, 500, 1000, and 2000 dispersal steps. We quantified the similarity of the resulting 12 heatmaps to the permeability and least-cost corridor maps presented in (Hofmann ...) we used Bhattacharyya's affinity. Bhattacharyya's affinity ranges from zero (complete separation) to one (perfect match) and has earlier been proposed to compare the overlap of utilisation distributions (Fieberg).

2.8 Network Analysis

We coerced all simulated trajectories into a network consisting of vertices (relocations) and edges (connections between relocations). To do so, we created raster layers at multiple resolutions and identified each trajectory's transition matrix on these rasters see figure xx (Bastille-Rousseau et al., 2018). We then merged the transition matrices of all trajectories and calculated cumulative transitions between all raster-cells. This resulted in an edge-list, containing all observed from-to connections as well as their frequency. Using this edge-list, we generated a weighted graph using the r-package *igraph*. Based on this graph we calculated betweenness scores as well as the degree of each raster cell. Betweenness indicates how often a specific raster-cell lies on a shortest path between two other raster-cells and is a useful metric to detect movement corridors. Degree, on the other hand, indicates how many connections a raster cell has and therefore serves to illustrate the xxx of specific nodes. When calculating betweenness, we used the transition frequency as weighting factor. That is, a higher transition frequency contributed to a higher betweenness score.

3 Results

3.1 Movement Model

Compared to the base model, the most parsimonious movement model included several additional interactions (Figure 3 and Table S1). The model indicates that dispersers move directional, particularly when distant to water, yet less so in human dominated landscapes. Furthermore, dispersers prefer large steps, especially during main activity. In contrast, step lengths tend to be shorter when water- or tree-cover is high. In general, dispersers avoid water, prefer proximity to water, avoid dense tree-cover, prefer shrubs/grassland, and, finally, avoid human dominated landscapes.

3.2 Dispersal Simulation

3.3 Heatmaps

Six of the twelve rasterized dispersal trajectories are presented as heatmaps in Figure 4. As can be seen, differences that stem from the method of point sampling disappear as more steps are simulated. This is to be expected as the influence of the origin becomes smaller and smaller as the animal moves through the landscape. However, there are striking differences when simualtions are only run for few iterations.
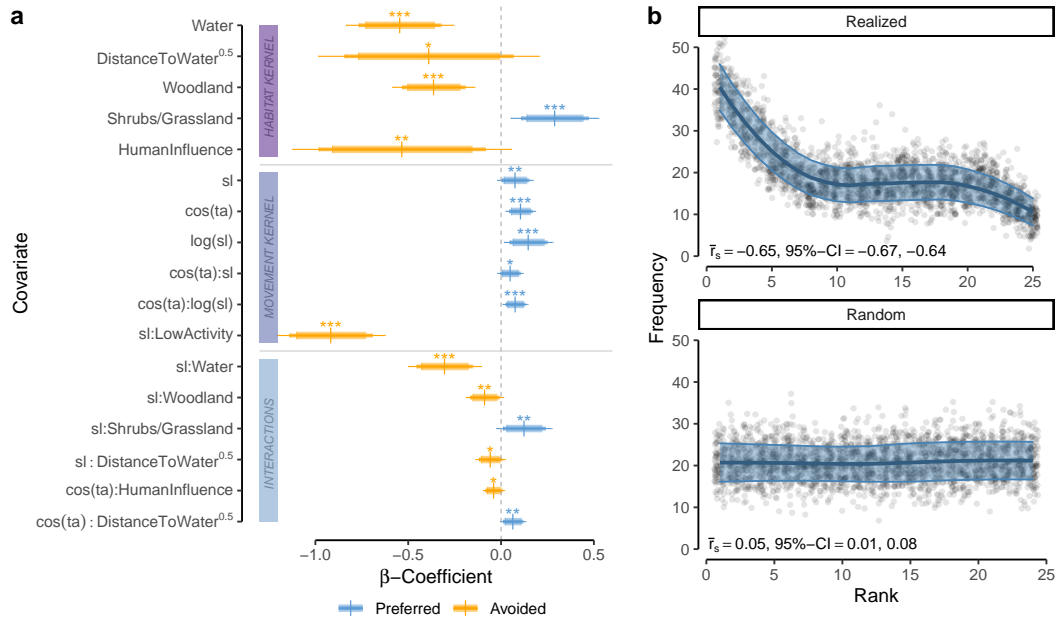
Figure 3: (a) Most parsimonious movement model for dispersing wild dogs. The model includes a habitat kernel, a movement kernel, as well as their interactions. The orange and blue line segments delineate the 90%, 95%, and 99% Confidence-Intervals around the respective β coefficients. Significance codes: * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$. (b) Results from the k-fold cross validation procedure. The upper plot shows rank frequencies of predicted realized scroes 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.
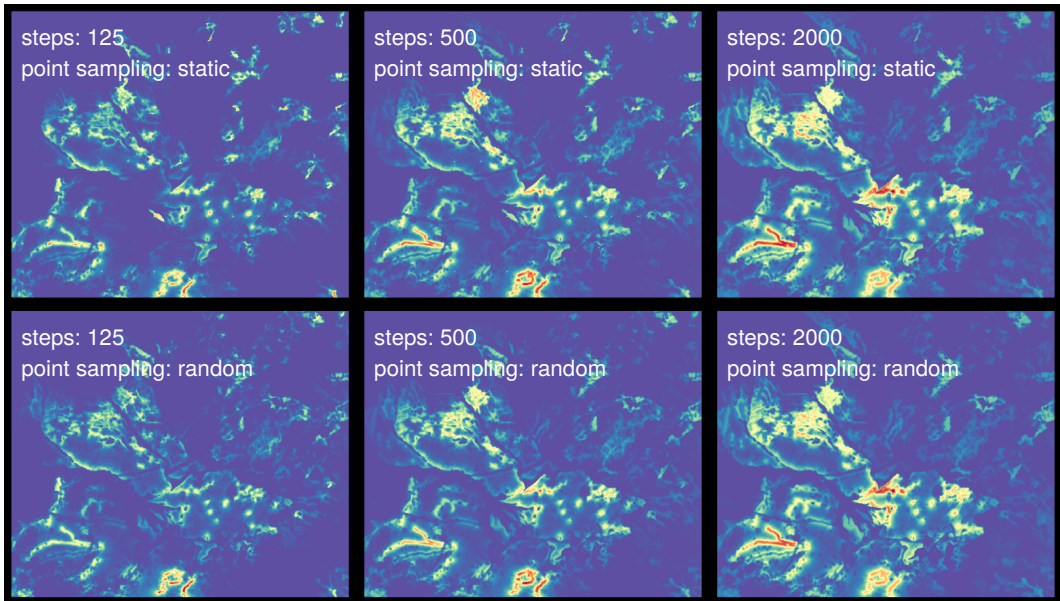

Figure 4

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Bhattacharyya's affinity index supports the notion that heatmaps become more similar to the earlier developed permeability and corridor maps as the number of simulated steps increases. Furthermore, it appears that randomly sampled source points contribute to a higher similarity too, albeit differences due to the sampling regime vanish as the number of simulated steps increases. In fact, both maps are almost identical to each other after 2000 steps. Furthermore, the connectivity networks become increasingly similar to the previously published permeability and corridor maps. Still, some differences remain even after 2000 simulated steps, highlighting that some severe impediments in the landscape exist.

3.4 Network Analysis

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 detal's western part.

Empircally informed dispersal models will also be invaluable in spatially explicit population models in which dispersal is actually rendered mechanistically.

In addition, individual based simulations will allow to explicitly model dispersal between subpopulations in models of population dynamics.

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 weigth.

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 attraciton. 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.

Comparable simulations could also serve to predict the likely whereabouts of dispersers as they move. This information can then be utilized as an "early warning" system, such that potential encounters can be gauged ad hoc.

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 modelling; 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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