Bound within Boundaries: How Well Do Protected Areas Match Movement Corridors of Their Most Mobile Protected Species?

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Abstract

1. Conserving and managing large portions of land to connect wildlife reserves is an increasingly used strategy to maintain and restore connectivity among wildlife populations. Boundaries of such conservation areas are often determined based on expert opinion and socio-political constraints, yet the extent to which they match species' movement corridors is rarely examined. This is mainly due to a lack of data, particularly on wide-ranging movement behavior such as dispersal. Nevertheless, empirically assessing the adequacy of protected areas is key for the implementation of targeted management actions and efficient use of limited conservation funds.

2. Between 2011 and 2019, we collected high-resolution GPS data on 16 dispersing African wild dog (*Lycaon pictus*) coalitions from a free-ranging population in the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). Spanning five countries and 520'000 km^2 the KAZA-TFCA is the world's largest transboundary conservation area and a prime example for international conservation efforts. We used integrated step selection analysis to estimate habitat selection of dispersers and to create a permeability surface for the KAZA-TFCA. We compared landscape permeability across different regions within the KAZA-TFCA as well as outside its boundaries. Lastly, we calculated least-cost paths and corridors to verify that major movement routes were adequately encompassed within the KAZA-TFCA.

3. Permeability within the boundaries of the KAZA-TFCA was more than double compared to areas outside it. Furthermore, we observed a five-fold permeability difference among the five KAZA-TFCA countries. We also showed that major movement corridors of wild dogs ran within the KAZA-TFCA, although some minor routes remained formally unprotected.

4. Differences in permeability were mainly related to different degrees of human activities across regions, and to the presence or absence of rivers, swamps and open water. The relationship between permeability and other landscape features was less pronounced.

5. *Synthesis and Applications*: In this study, we showed how pertinent dispersal data of a highly mobile species can be used to empirically evaluate the adequacy of already-existing or planned protected areas. Furthermore, we observed regional differences in landscape permeability that highlight the need for a coordinated effort towards maintaining or restoring connectivity, especially where transboundary dispersal occurs.

1 Introduction

Connectivity among subpopulations is a crucial pre-requisite for many species to thrive and persist (Fahrig, 2003). Accordingly, preserving and protecting movement corridors between wildlife reserves has become a task of utmost importance (Doerr et al., 2011; Rudnick et al., 2012), resulting in an ever-growing number of large and often transboundary protected areas. While boundaries of such areas are often drawn according to expert opinion and socio-political needs, subjective assessments have revealed deficiencies in the past (Clevenger et al., 2002; Pullinger and Johnson, 2010). Thus, an empirical evaluation of the adequacy of already-existing or planned protected areas using pertinent animal movement data is paramount for targeted use of valuable and scarce conservation funds (Pullinger and Johnson, 2010).

In recent years, a growing body of research has used animal relocation data to identify movement corridors and assess connectivity at large scales (e.g. Chetkiewicz et al., 2006; Squires et al., 2013; Elliot et al., 2014). Identification of potential movement corridors typically relies on the estimation of permeability surfaces, which return the ease or willingness at which the focal species traverses a specific landscape (Sawyer et al., 2011). Such surfaces are created based on species' relative selection strengths (Avgar et al., 2017), which can be quantified using a suite of selection functions (Zeller et al., 2012). Specifically, selection strengths are estimated by comparing spatial covariates (e.g. environmental and anthropogenic) at locations visited by the animal to the same spatial covariates at locations available to the animal (Zeller et al., 2012). Importantly, selection functions require adequate landscape and relocation data that are representative of the process being studied (Diniz et al., 2019). Altough selection during residence and dispersal may coincide (Fattebert et al., 2015), it appears that relocation data collected on dispersing individuals outperforms data collected on resident individuals in the detection of large-scale movement corridors (Elliot et al., 2014; Abrahms et al., 2017; Diniz et al., 2019). Nevertheless, dispersal data is inherently difficult to collect and remains scarce in the connectivity literature (Vasudev et al., 2015). As such, most permeability surfaces upon which movement corridors are identified are created using relocation data collected on resident individuals. This has likely limited our ability to meaningfully assess the effectiveness of protected areas in securing connectivity for their protected species.

One initiative that aims at restoring and enhancing connectivity across large scales is the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA), which constitutes the world's largest transfrontier conservation area, spanning over 520'000 km^2 and five countries (`www.kavangozambezi.org`). While the KAZA-TFCA was originally set to facilitate movements of African elephants (*Loxodonta africana*; Tshipa, 2017), it is also key to the conservation of other wide-ranging species such as African wild dogs (*Lycaon pictus*; Woodroffe and Sillero-Zubiri, 2012; Cozzi et al., 2020), lions (*Panthera leo*; Elliot et al., 2014; Cushman et al., 2018), and cheetahs (*Acinonyx jubatus*; Weise et al., 2017). To date, however, few studies have attempted to assess the adequacy of the KAZA-TFCA using global positioning system (GPS) relocation data of its protected species at large spatial scales (Elliot et al., 2014; Tshipa, 2017; Brennan et al., 2020). Thus, how well the boundaries of the KAZA-TFCA reflect natural movement patterns and dispersal corridors of its most mobile protected species is virtually unknown.

Across the KAZA-TFCA, the African wild dog (*Lycaon pictus*) represents a highly mobile and endangered flagship species for conservation efforts. Once widespread across the entire Sub-Saharan continent, wild dogs have been widely extirpated through human persecution, habitat destruction, and disease outbreaks (Woodroffe and Sillero-Zubiri, 2012). For these reasons, viable populations mainly occur in spatially scattered subpopulations within protected areas (Woodroffe and Ginsberg, 1999; Woodroffe and Sillero-Zubiri, 2012; Van der Meer et al., 2014). Within these subpopulations, wild dogs form cooperative breeding packs of up to thirty individuals (Creel and Creel, 2002), whose social structure is strongly governed by the process of dispersal (McNutt, 1996; Behr et al., 2020). Both males and females disperse from their natal pack, either alone or in same-sex dispersing coalitions, and search for unrelated mates and a suitable territory to settle (McNutt, 1996; Cozzi et al., 2020; Behr et al., 2020). During dispersal, wild dogs can cover several hundred kilometers and cross international borders (Masenga et al., 2016; Woodroffe et al., 2019; Cozzi et al., 2020). Despite the importance of dispersal for the long-term viability of this species, little empirical information is available on habitat selection and potential movement barriers during dispersal. The few studies that have collected dispersal data have shown that dispersers quickly move over large distances, avoid human-dominated landscapes and areas densely covered by trees, but prefer proximity to water (Masenga et al., 2016; Woodroffe et al., 2019; O'Neill et al., 2020; Cozzi et al., 2020).

Here, we collected and analyzed GPS relocation data on 16 dispersing wild dogs in as many dispersing coalitions from a free-ranging population in northern Botswana to assess the adequacy of the KAZA-TFCA in securing connectivity. We estimated relative selection strengths towards environmental and anthropogenic landscape features, and used the obtained coefficients to predict a permeability surface spanning the entire KAZA-TFCA.

We then investigated how landscape permeability varied regionally and internationally, and we compared permeability within and outside the KAZA-TFCA boundaries. Finally, we calculated least-cost paths and corridors to identify major movement routes and to verify that these were successfully covered by the KAZA-TFCA.

2 Materials and Methods

2.1 Study Area

The study area (centered at -17°13'9"S, 23°56'4"E; Figure 1a) was outlined by a rectangular bounding box stretching over 1.3 Mio km^2 and encompassing the entire KAZA-TFCA (Figure 1b). The KAZA-TFCA lies in the basins of the Okavango and Zambezi rivers and includes parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia. With a total area of over 520'000 km^2 it constitutes the earth's largest transboundary conservation area and is characterized by diverse landscapes, including savanna, grassland, and dry or moist woodland habitats. Rainfall in the study area is seasonal and lasts from November to March. The KAZA-TFCA also comprises the Okavango Delta, which represents a highly dynamic hydrological flood-pulsing system (McNutt, 1996; Wolski et al., 2017). The extent of the flood in the delta greatly changes within and between years, depending on the amount of rain that descends from the catchment areas in Angola and reaches the distal ends of the delta between July and August (Figure S4). The flood drastically affects surrounding landscapes, so that during maximum extent (ca. 12'000 km^2) the delta becomes a patchy conglomerate of swamps, open water, and islands, whereas these structures run dry when the flood retracts to its minimum extent (ca. 5'000 km^2; Wolski et al., 2017). Despite 36 national parks (NPs) and other protected areas, there is considerable human influence in some regions of the KAZA-TFCA, mainly originating from farms, human density, and road traffic.

2.2 GPS Relocation Data

We used a population of free-ranging African wild dogs inhabiting the Okavango Delta in northern Botswana as a source population for dispersing individuals. This population has been extensively studied since 1989 (McNutt, 1996; Cozzi et al., 2013, 2020; Behr et al., 2020). Between 2011 and 2019, we systematically collected GPS relocation data on 16 coalitions of dispersing African wild dogs (7 female and 9 male coalitions). Candidate dispersing individuals were identified based on age, number of same-sex siblings, pack size, and presence of unrelated individuals of the opposite sex in their pack (McNutt, 1996; Behr et al., 2020). Selected individuals were immobilized according to protocols described in Osofsky et al. (1996), and fitted with GPS/Satellite radio collars (*Vertex Lite; Vectronic Aerospace GmbH, Berlin, Germany*) while still with their natal pack. Collars weighed 330g, accounting for about 1.5% of a wild dog's body weight. A 5cm long decomposable cotton piece was added to the collar belt to guarantee collar drop-off after about 12-18 months. All required procedures were undertaken and supervised by a Botswana-registered wildlife veterinarian. During dispersal, GPS collars were programmed to record a GPS relocation every 4 hours and to regularly transmit data via iridium satellite system to a base station.

Because we were interested in dispersal behavior only, we discarded any GPS data collected while individuals were still with their natal packs and after settlement in a new territory (Cozzi et al., 2020). We identified the exact time of emigration and settlement based on direct field observations and through visual inspection of the net squared displacement (NSD) metric. NSD quantifies the squared Euclidean distance of a relocation to a reference point (Börger and Fryxell, 2012), which in our case was the center of the dispersing coalition's natal home range. Thus, dispersal was deemed to have started when a coalition had left its natal home range and continued until the NSD metric remained stationary, indicating that the coalition had successfully settled (Figure S1 in Supporting Information). In our analysis, we did not differentiate between male and female dispersing coalitions, for previous research found little differences between sexes during dispersal (Woodroffe et al., 2019; Cozzi et al., 2020).

2.3 Spatial Covariates

To investigate relative selection strengths of dispersing wild dogs, we used a set of georeferenced covariates (Figure 2) that we aggregated in the categories *land cover*, *protection status*, and *anthropogenic*. *Land cover* comprised the covariates water cover (binary), distance to water (continuous), percentage cover by shrubs/grassland (continuous), and percentage cover by trees (continuous). To capture the pulsing behavior of the Okavango Delta, we classified satellite imagery and frequently updated layers for water cover and corresponding layers depicting distance to water. *Protection status* contained a binary covariate, indicating whether an area was protected or not. *Anthropogenic* included covariates rendering the presence of roads (binary), the distance to roads (continuous), and a proxy for human influence (continuous) that took into account human density, farming, and roads. We prepared all covariates as spatial raster layers from freely available online services and from remotely sensed satellite imagery. To ensure a consistent resolution (i.e. cell-size or grain) across covariates, we coarsened or interpolated all layers to a resolution of 250m x 250m. For further details on the preparation and source of each covariate, see Appendix A.3. We performed processing and manipulation of data as well as all spatial and statistical analyses using R, version 3.6.1 (R Core Team, 2019).

2.4 Habitat Selection Model

We used an integrated step selection function (iSSF; Avgar et al., 2016) to investigate dispersers' relative selection strentghs towards the above-mentioned spatial covariates. That is, we paired each realized step (i.e. the connecting line between two consecutive GPS relocations; Turchin, 1998) with 24 random steps that were generated by sampling turning angles from a uniform distribution $U(-\pi, +\pi)$ and step lengths from a gamma distribution fitted to realized steps (Avgar et al., 2016). A realized step and its 24 associated random steps formed a stratum and received a unique identifier. Along each step, we extracted the above-mentioned covariates (Table S3), standardized extracted values using a z-score transformation, and checked for correlation using Pearson's Correlation Coefficient r. None of the covariates were overly correlated ($|r| > 0.6$; Latham et al., 2011) and we retained all of them for modeling. Our habitat selection model then assumed that dispersing wild dogs assigned a selection score $w(x)$ of the following exponential form to each realized and random step (Fortin et al., 2005):

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

The selection score $w(x)$ of a step depended on its associated covariates $(x_1, x_2, ..., x_n)$, as well as on the animal's relative selection strengths towards these covariates $(\beta_1, \beta_2, ..., \beta_n)$. To estimate relative selection strengths (i.e. the β's) for each covariate, we used mixed effects conditional logistic regression analysis as suggested by Muff et al. (2020). We implemented their method using the R-package *glmmTMB* (Brooks et al., 2017) and used dispersing coalition ID to model random slopes. We also modelled random intercepts with an arbitrary high variance of 10^6 to make use of the poisson trick (see Muff et al., 2020). We defined three movement metrics, namely the cosine of the turning angle ($cos(ta)$), the step length (sl) and the logarithm of the step length ($log(sl)$), as core covariates and ran stepwise forward model selection based on Akaike's Information Criterion (AIC; Burnham and Anderson, 2002) for all other covariates. The inclusion of movement metrics served to reduce biases in estimated habitat selection coefficients that may have arisen due to movement behavior (Avgar et al., 2016). To validate the predictive power of the most parsimonious habitat selection model, we ran k-fold cross-validation for case-control studies as described in Fortin et al. (2009) (details in Appendix A.5).

2.5 Permeability Surface

Using the most parsimonious habitat selection model, we predicted a permeability surface spanning the entire extent of the KAZA-TFCA. That is, we applied Equation 1 to our spatial covariates and calculated the selection score $w(x)$ for each raster cell. Because our representation of water was dynamic, we collapsed all dynamic water maps into a single map using areas that were covered by water in at least 10% of the cases. We used the resulting map to also calculate a layer returning the distance to water. Because the delta only covers 5% of the KAZA-TFCA, we considered the use of a single water map to be appropriate. To reduce the influence of outliers in predicted permeability scores, we followed Squires et al. (2013) and curtailed predicted scores between the 1st and 99th percentile of their original values. To compare permeability across different regions, we normalized the permeability surface to a range between 0 (most impermeable) and 1 (most permeable), and we determined median permeability within and outside the KAZA-TFCA, within and outside formally protected areas, and within each of the five KAZA-TFCA countries.

2.6 Least-Cost Paths and Corridors

To identify potential movement corridors of dispersing wild dogs, we specified source points and calculated factorial least-cost paths (LCPs) as well as factorial least-cost corridors (LCCs) among them (Elliot et al., 2014). To select source points, we followed the omnidirectional *go-through* approach proposed by Koen et al. (2014) and placed 68 regularly spaced source points along the map border (Koen et al., 2014; Pitman et al., 2017). While this approach tends to identify high connectivity towards the map boundaries, it reduces potential biases caused by the selection of unreasonable source points (Koen et al., 2014). To assess the sensitivity of our results with respect to the location of source points, we reran the same analysis using 68 source points located within protected areas that are large enough to sustain viable wild dog populations (further details and corresponding results in Appendix A.9). In either case, the 68 source points resulted in 2'278 unique pairwise combinations and therefore 2'278 unique LCPs and LCCs. We computed factorial LCPs and LCCs between source points using the R-package *gdistance* (details in Appendix A.6). After computation, we tallied overlapping LCPs and LCCs, respectively, into single connectivity maps. Because

LCPs return discrete paths, whereas LCCs return continuous corridors, we present both methods. R-codes showcasing the main steps for sections 2.5 to 2.6 can be downloaded from GitHub (`https://github.com/DavidDHofmann/LeastCostAnalysis`).

3 Results

3.1 Dispersal Events

In total, we collected 4'169 GPS relocations during dispersal (Figure S2 & Table S1), resulting in an average of 261 (SD = 207) locations per dispersing coalition. Coalitions on average dispersed for 48 days (SD = 44), covered a mean Euclidean distance of 54 km (SD = 71) and a cumulative distance of 597 km (SD = 508).

3.2 Habitat Selection Model

Our most parsimonious habitat selection model ($\Delta AIC > 2$ than any alternative model; Table S4) retained the covariates *water*, *distance to water*, *trees*, *shrubs/grassland*, and *human influence*, beside the fixed covariates *cos(ta)*, *sl*, and *log(sl)* (Figure 3a). Dispersers avoided moving through water (β = -0.53, 95% CI -0.79 to -0.27) but selected for locations in its vicinity, although the latter effect was not significant (β = -0.33, 95% CI = -0.73 to 0.08). Dispersers avoided areas that were densely covered by trees (β = -0.31, CI = -0.47 to -0.15) and preferred areas covered by shrubs/grassland (β = 0.25, 95% CI = 0.07 to 0.42). Finally, dispersers avoided areas that were influenced by humans (β = -0.45, 95% CI = -0.82 to -0.08). Except for *distance to water* ($SD_{\text{RandomEffect}} = 0.57$), we observed little variation between dispersal coalitions' relative selection strengths ($SD_{\text{RandomEffect}} < 0.22$ for all other covariates, see also Figure S8).

Results from the k-fold cross-validation suggested that our prediction was significant and robust, as highlighted by the fact that the 95%-CIs intervals of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ did not overlap (Figure 3b). Likewise, the significant correlation between ranks and corresponding frequencies for realized steps suggested a good fit between predictions and observations (Figure 3b).

3.3 Permeability Surface

Our prediction of landscape permeability revealed substantial differences across regions in the study area (Figure 4). Comparisons of median permeability values (Table 1) showed that permeability inside the KAZA-TFCA was more than two times as high as permeability outside it. Permeability varied by country, with a five-fold permeability difference among them. Angola and Botswana were characterized by comparably highly permeable landscapes, Zimbabwe and Zambia were relatively impermeable, and Namibia ranged in between the two extremes (Table 1). Visual inspection of our covariate layers indicated that high permeability in Angola and Botswana was mainly related to a combination of low human influence, low tree cover, high shrubs/grassland cover, and a close distance to water. Although swamps, wetlands, and permanent water themselves provided little permeability, their surroundings acted as strong attractants to dispersers. The low permeability that characterized Zambia and Zimbabwe, on the other hand, was mainly caused by substantial human influence. Albeit the KAZA-TFCA covered most permeability hot-spots, several highly permeable regions remained uncovered by its borders. Across all countries, protected areas provided roughly double the permeability of unprotected landscapes (Table 1).

3.4 Least-Cost Paths & Least-Cost Corridors

Our least-cost analysis revealed three major movement corridors of which all were well-contained within the KAZA-TFCA boundaries (Figure 5). One major corridor ran SE-NW and connected the Okavango-Linyanti ecosystem in Botswana with Luengue-Luiana NP in Angola. A second corridor ran W-E between Chobe NP in Botswana and Zimbabwe's Hwange NP. A third major corridor ran NE-SW, completely across unprotected areas, and connected Kafue NP in Zambia with more central regions of the KAZA-TFCA. Several minor corridors branched off from these three major corridors; these included a southward connection between the Okavango-Linyanti and the Central Kalahari Game Reserve, a southwesterly corridor connecting Luengue-Luiana NP with Namibia's Khaudum NP, and a northeasterly extension of the Hwange corridor into Zimbabwe's Matusadona NP. According to our predictions, the landscapes in the Okavango-Linyanti region were the highest frequented dispersal routes within the KAZA-TFCA (Figure 5b). Our model did not detect any significant direct corridors between Zimbabwe and Zambia or Zambia and Angola, and only a very limited W-E direct connection between the Okavango region and Namibia's Khaudum NP. Except for the corridor into the Central Kalahari National Park, our model did not detect any significant connectivity outside the boundaries of the KAZA-TFCA. Furthermore, we found little to no direct connectivity between peripheral points; that is, most paths and corridors connecting two adjacent peripheral points ran through more central regions before heading towards their destination at the periphery (Figure 5).

4 Discussion

We used GPS relocation data collected on dispersing African wild dogs to investigate whether their main movement corridors are contained within the boundaries of the world's largest transboundary conservation area, namely the KAZA-TFCA. Our analysis suggests that the KAZA-TFCA indeed encompasses all major corridors of African wild dogs, demonstrating the potential value of such an initiative. We thus exemplified how pertinent dispersal data of a highly mobile species can be used to assess the adequacy of already existing or planned protected areas. Our approach is neither limited to the African wild dog, nor to our study area and thus applicable to any study system. All covariates used throughout this study are readily available on a global scale and many of them are likely to be important determinants of movement behavior, landscape permeability, and connectivity for other species (Zeller et al., 2012; Thurfjell et al., 2014). Interestingly, our predicted network of least cost-paths and corridors for African wild dogs shows surprising similarities to corridors of dispersing lions inhabiting the same ecosystem (Elliot et al., 2014; Cushman et al., 2018). This not only reinforces confidence in our own predictions but also suggests potential synergies for the conservation of these two, and possibly more, species. Expanding our analytical framework to additional species will likely yield important insights on the consistency of inter-specific movement corridors, thus highlighting areas that are exceptionally valuable for the conservation of several species (e.g. Brennan et al., 2020).

Our results emphasize that human influences constitute some of the main barriers to connectivity among wild dog populations. This conforms to findings on dispersing wild dogs from eastern Africa (Masenga et al., 2016; O'Neill et al., 2020) but conflicts with findings from South Africa by Davies-Mostert et al. (2012), who reported a high willingness of dispersers to cross human-dominated landscapes. Such differences may arise from the fact that our model infers preferences by comparing *used* and *available* habitats, whereas Davies-Mostert et al. (2012) only recorded net dispersal distances, thereby precluding such an analysis. Thus, we believe that differences to Davies-Mostert et al. (2012) may be explained by the unavailability of alternative routes through natural landscapes, which may have forced dispersers in South Africa to cross human dominated landscapes despite a strong aversion to do so. In this regard, our representation of dispersal corridors and the resulting connectivity appear conservative, as dispersers may be able to make the best out of a bad situation and cross landscapes characterized by considerably unfavorable conditions (Palomares et al., 2000; Elliot et al., 2014). Nevertheless, successful conservation of this species relies on policymakers' and local authorities' willingness and ability to provide and conserve natural areas that remain free from anthropogenic pressures. This is not only paramount in light of increasing connectivity and facilitating dispersal, but also in terms of reducing human-caused mortality during dispersal. In fact, previous studies have shown that human-caused mortality represents a major threat to wild dogs' ability to disperse (Woodroffe et al., 2019; Cozzi et al., 2020).

Besides human influence, we identified water as additional obstacle to dispersal. This corroborates earlier studies showing that water bodies are almost impenetrable to resident packs (Abrahms et al., 2017) and only infrequently crossed by dispersing individuals (Cozzi et al., 2020). An accurate and dynamic representation of water is thus imperative and particularly relevant in seasonal or flood-pulsing ecosystems such as the Okavango Delta.

Although dispersers avoided moving through water, they selected locations in its vicinity. This behavior may be caused by the occurence of prey close to water (Bonyongo, 2005). For the same reason, however, competitors such as lions, spotted hyenas, and resident wild dogs may also use areas close to water (Valeix et al., 2010), thereby occasionally forcing dispersing wild dogs to switch behavior and move into prey-poorer areas away from water (Creel and Creel, 2002; Mills and Gorman, 1997). This may explain the large confidence intervals for the corresponding β-estimate of *distance to water*. Given the influence that resident conspecifics, competitors, and prey can have on dispersers (Cozzi et al., 2018; Armansin et al., 2019) future studies should strive to collect and incorporate intra- and interspecific relationships into analyses of landscape connectivity.

Overall, our findings on habitat selection during dispersal coincide with findings from dipsersing wild dogs in Kenya (O'Neill et al., 2020) and Tanzania (Masenga et al., 2016), suggesting that there are strong commonalities between dispersers from these very different ecosystems. Thus, despite wild dogs' ability to cope with diverse habitats and adapt to changing conditions (Woodroffe, 2011), the fundamental factors included in our study appear to influence wild dogs from other ecosystems alike. Nevertheless, expanding our analysis to dispersers emigrating from other source populations would invaluably contribute to our understanding of dispersal.

Locally, we identified the Okavango-Linyanti region as a potential dispersal hub through which dispersing wild dogs gain access to more peripheral regions of the KAZA-TFCA. It appears that the absence of human activities, the central position within the KAZA-TFCA, and the presence of relatively impermeable water bodies (e.g. Okavango Delta, Linyanti Swamp) funnel dispersal movements, resulting in a highly frequented corridor. Furthermore, the lack of permeable areas between peripheral source points often resulted in corridors stretching longer Euclidean distances, in an arc-shaped route via a stretch of suitable habitat through the Okavango-Linyanty ecosystem. This is an expected outcome in case structural and functional connectivity coincide, i.e. when dispersers follow suitable habitats to disperse (Fattebert et al., 2015; Hauenstein et al., 2019). The key role of the Okavango-Linyanti region for overall connectivity within the KAZA-TFCA thus calls for actions to secure its protection status in the future. While the region is currently a Wildlife Management Area, it has neither the status of a National Park nor that of a Game Reserve. A similar case of non-formally protected but key dispersal landscape is represented by the area south of Kafue NP in Zambia, for which a disruption of its main and narrow dispersal corridor or high disperser mortality due for example to human persecution or vehicle collision would result in considerable isolation of its subpopulations. We also revealed a potential southwards corridor between the Okavango-Linyanti ecosystem and the Central Kalahari National Park. Elliot et al. (2014) and Cushman et al. (2018) identified a similar corridor for dispersing lions, suggesting that upholding and protecting a link between those ecosystems is pivotal. Some areas through which the corridor runs are neither part of the KAZA-TFCA nor profit from any form of protection status. Human presence and activities along the national road that longitudinally traverses this corridor may limit functional connectivity (Cozzi et al., 2020).

Our approach of identifying movement corridors based on pre-defined start and end points implicitly assumes that individuals know the end point of their dispersal journey and that they have almost complete knowledge of associated movement costs (Panzacchi et al., 2016). Since dispersers often move into unknown territory, this may not necessarily be the case (Abrahms et al., 2017; Cozzi et al., 2020). However, specification of pre-defined end points might not be necessary, as the parametrized iSSF model can be used as mechanistic movement model to simulate dispersal from known source points, yet without restricting the domain of potential end points (Signer et al., 2017). Consequently, movement corridors would emerge more naturally as the result of a myriad of simulated dispersal events (Allen et al., 2016; Zeller et al., 2020).

Besides estimating corridors, individual based simulations may be used to generate permeability surfaces (Avgar et al., 2016; Signer et al., 2017). Such simulation based surfaces have been shown to reduce the risk of overestimating permeability ($w(x)$) and conesquently connectivity, particularly in areas that lie far from suitable habitats (Signer et al., 2017). While a simulation-based approach is conceptually straightforward, computational requirements for such a large spatial extent as the KAZA-TFCA are very high, making the use of this approach challenging. We therefore urge future studies to optimize the simulation of movement from iSSFs to capture a more mechanistic model of dispersal.

Our work shows how dispersal data of a highly mobile species can be used to identify movement corridors and to assess the adequacy of protected areas. In our case, the predicted movement corridors of African wild dogs were well contained within the boundaries of the world's largest transboundary conservation area, namely the KAZA-TFCA, suggesting that it will significantly contribute to the long-term viability of this species. Moreover, our connectivity network allowed revealing potential dispersal hubs through which dispersers gain access to more remote regions of the study area. Finally, our investigations showed that human influence constitutes one of the main barriers to dispersal and substantially reduces landscape connectivity. Successful conservation of wide-ranging species, such as exemplified by the African wild dog, will therefore be contingent on the willingness of local authorities, policymakers, and land managers to preserve areas that remain free from human strains. Ultimately, our work contributes to the growing field of connectivity studies and provides and easily expandable framework for assessing the adequacy of already-existing or planned protected areas.

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 Statement

GPS movement data of dispersing coalitions available via the Dryad Digital Repository doi:10.5061/dryad.dncjsxkzn (Hofmann et al., 2021). R-code showcasing the main steps for sections 2.5 to 2.6 can be obtained through GitHub (`https://github.com/DavidDHofmann/LeastCostAnalysis`).

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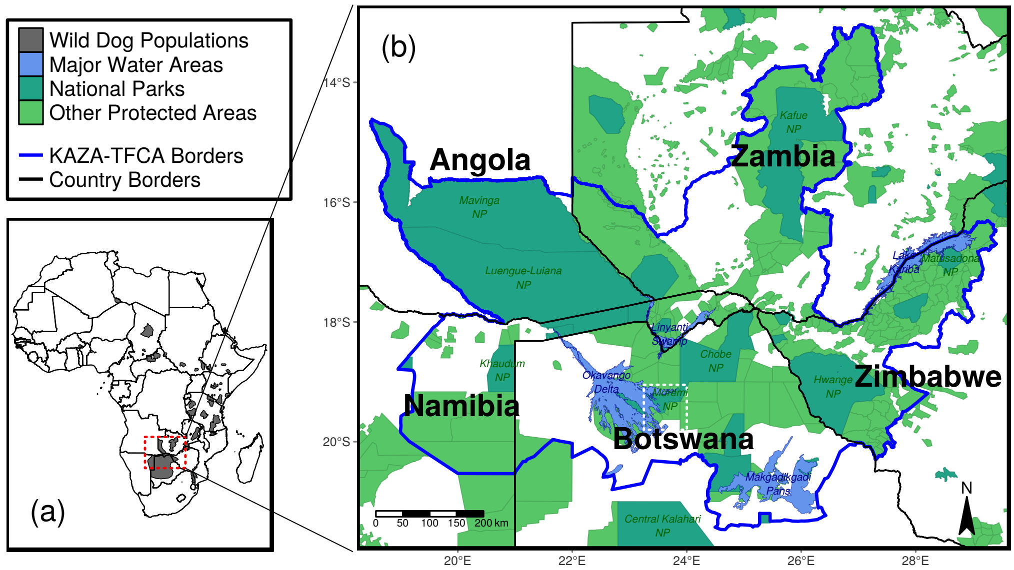

Figure 1: Overview of our study area. (a) The red dotted rectangle depicts the study area, which was confined by a bounding box encompassing the entire KAZA-TFCA. Gray areas indicate remaining wild dog populations according to the IUCN (Woodroffe and Sillero-Zubiri, 2012). (b) The white rectangle illustrates the area within which dispersing coalitions were collared. Since Game Reserves in Botswana virtually serve the same purpose as National Parks, we use the terms interchangeably for this region.

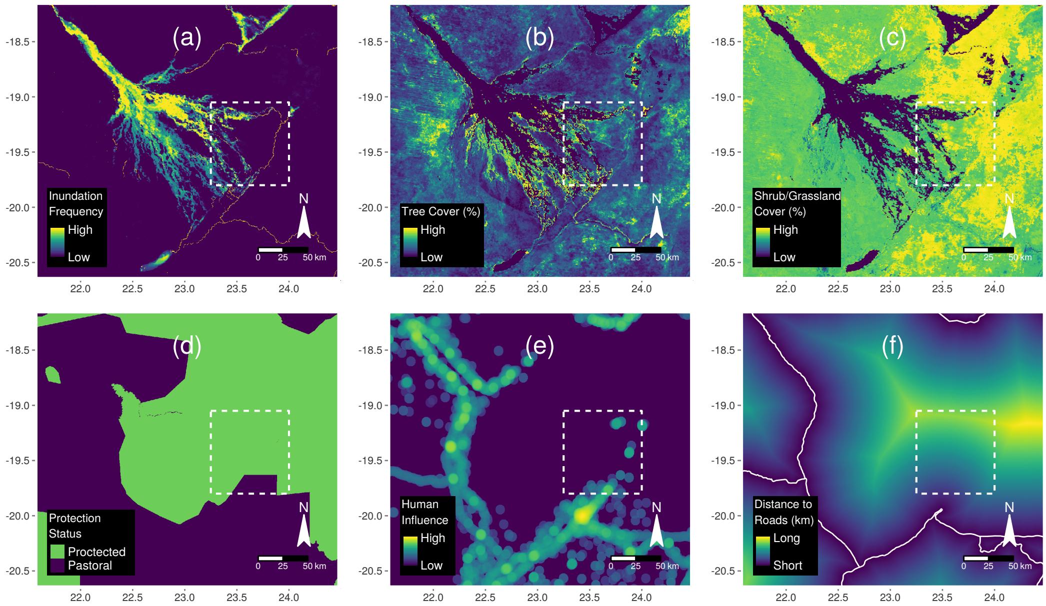

Figure 2: Overview of spatial covariates that we included in our models. We prepared all covariates for the entire study area but for better visibility we only plot them for the surroundings of the Okavango Delta. The white rectangle in each plot depicts the area within which dispersing coalitions were collared. (a) Averaged layer of all dynamic (binary) water maps. (b) Percentage cover of trees. (c) Percentage cover of shrubs/grassland. Anything that was not covered by trees or shrubs/grassland was deemed to be bare land. (d) Protection status of the area. (e) Human influence proxy composed of human density, farms, and roads. (f) Distance to nearest road (white lines depict actual roads).

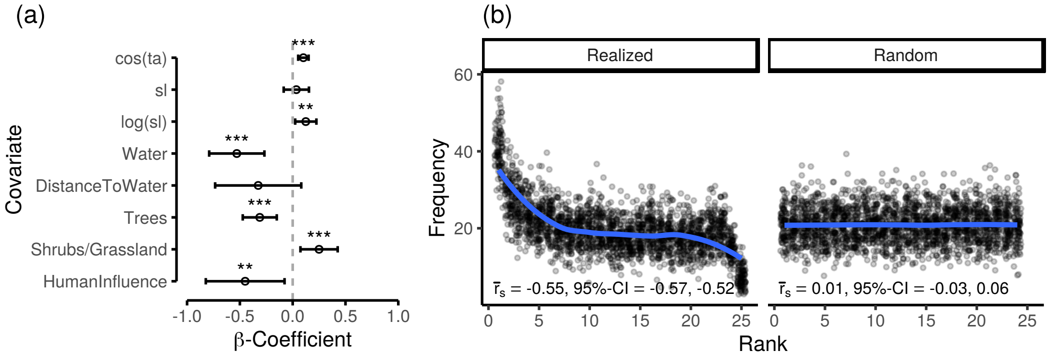

Figure 3: (a) Estimated selection coefficients from the most parsimonious habitat selection model. Negative coefficients indicate avoidance of a covariate, positive coefficients selection of a covariate. ta = turning angle, sl = step length. Whiskers delineate the 95%-CIs for estimated parameters. Significance codes: ** $p < 0.05$, *** $p < 0.01$. (b) Results from the k-fold cross validation for case-control studies. The left graph shows rank frequencies of *realized* steps according to predictions, whereas the right graph shows rank frequencies of *randomly selected* steps according to predictions. $\bar{r}_s$ indicates the mean correlation coefficient resulting from 100 repetitions of the k-fold cross validation. The blue smoothing line was fitted using a locally weighted polynomial regression and serves to aid the eye in detecting the trends. Correlation coefficients suggest that our prediction was significant and robust, evidenced by the fact that the confidence intervals of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ did overlap and by the fact that there was strong and significant correlation between ranks and associated frequency for realized steps.

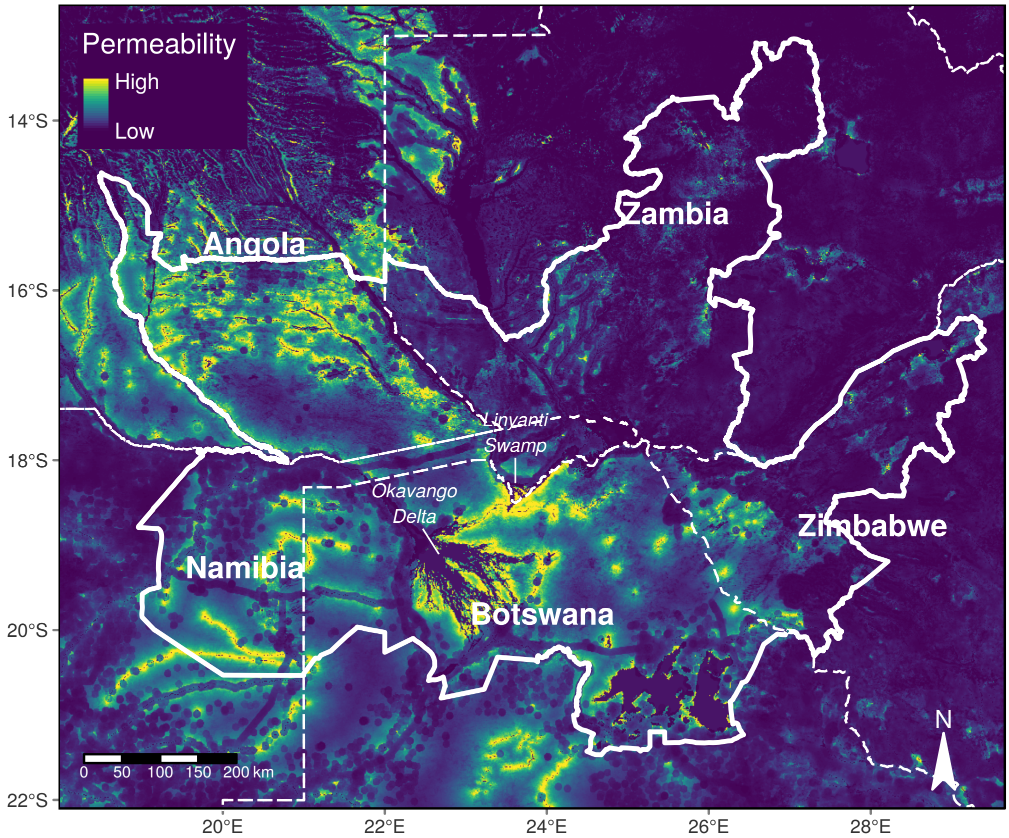

Figure 4: Predicted permeability surface for the extent of the KAZA-TFCA. Permeability was predicted by calculating selection scores $w(x) = exp(\beta_1 x_1 + \beta_2 x_2 + ... + \beta_n x_n)$ for each raster cell based on the raster cell's underlying covariates (x_i) and estimated selection strength (β_i). Areas that dispersers find easy to traverse are depicted in bright colors. Bold white lines delineate the borders of the KAZA-TFCA, whereas dashed white lines show country borders.

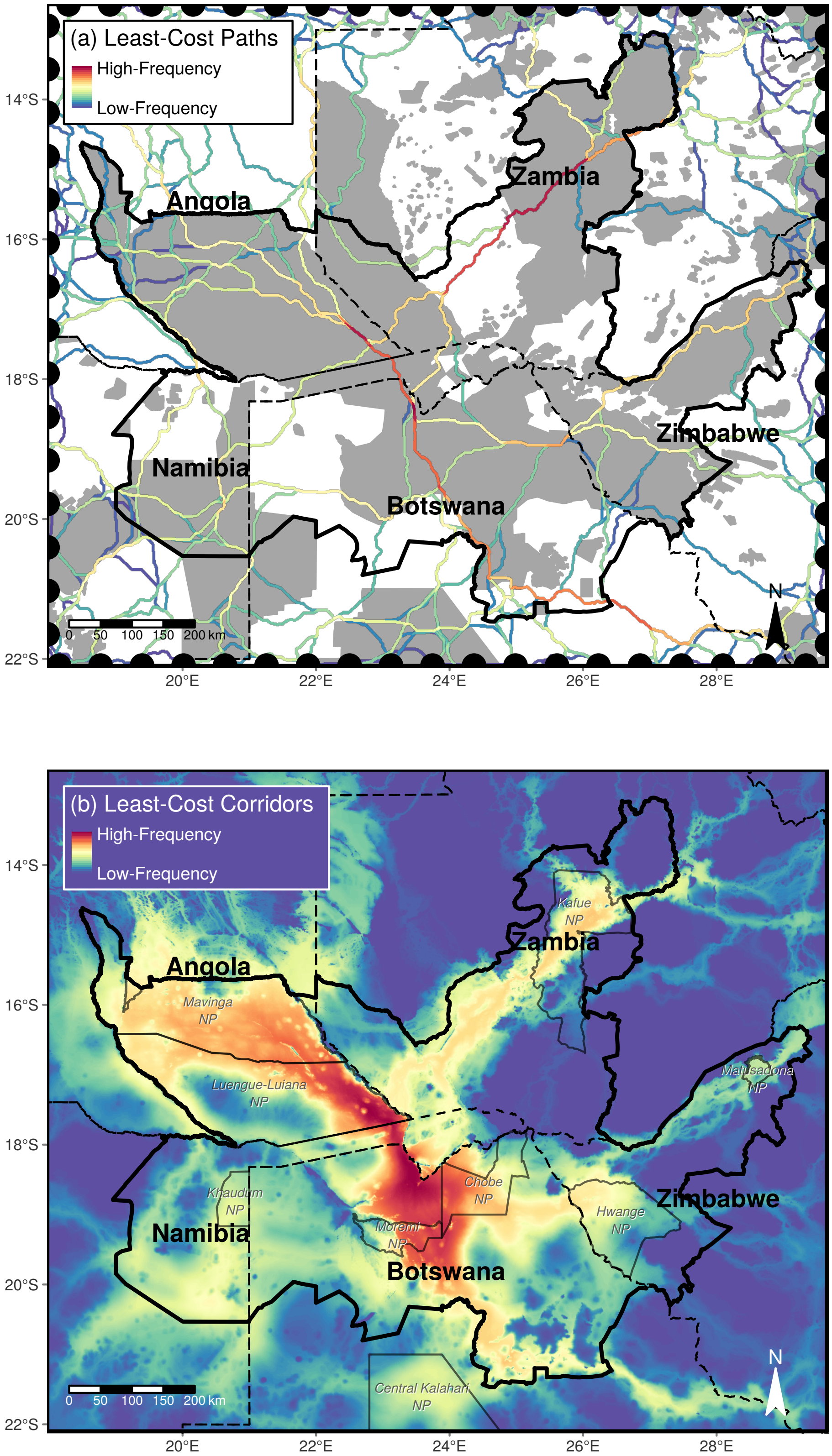

Figure 5: (a) Source points (black semicircles along the map border) and corresponding least-cost paths between them. Continuous black lines indicate the borders of the KAZA-TFCA, whereas dashed black lines delineate country-borders. (b) Least-cost corridors between the same source points as illustrated in subfigure (a). For ease of spatial reference, we also labeled some national parks (NPs, in dark-grey).

Table 1: Comparison of median permeability (interquantile range in brackets) across countries, separated into areas within and outside the KAZA-TFCA, as well as within and outside formally protected areas. High values indicate high permeability, whereas low values correspond to low permeability.

	KAZA-TFCA		Protection Status		
Country	Inside	Outside	Protected	Pastoral	Overall
Angola	0.35 (0.41)	0.12 (0.32)	0.35 (0.41)	0.12 (0.32)	0.19 (0.38)
Botswana	0.24 (0.30)	0.14 (0.16)	0.27 (0.35)	0.14 (0.18)	0.18 (0.25)
Namibia	0.20 (0.30)	0.12 (0.17)	0.22 (0.30)	0.10 (0.14)	0.14 (0.24)
Zambia	0.05 (0.09)	0.02 (0.05)	0.04 (0.09)	0.03 (0.05)	0.03 (0.06)
Zimbabwe	0.06 (0.16)	0.05 (0.04)	0.07 (0.17)	0.04 (0.04)	0.05 (0.06)
Overall	0.15 (0.29)	0.06 (0.14)	0.14 (0.30)	0.06 (0.14)	0.08 (0.21)