

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

David D. Hofmann<sup>1,§,\*</sup> Dominik M. Behr<sup>1,2,\*</sup> John W. McNutt<sup>2</sup>  
Arpat Ozgul<sup>1</sup> Gabriele Cozzi<sup>1,2</sup>

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

<sup>2</sup> Botswana Predator Conservation Trust, Private Bag 13, Maun, Botswana.

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

\* Shared first authorship

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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 movement 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<sup>2</sup> 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 entire 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 outside formally protected areas.
4. Differences in permeability were mainly related to different degrees of human activities across regions, and to the presence or absence of rivers, swamps or 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**

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

12 In recent years, a growing body of research has used animal relocation data to iden-  
13 tify movement corridors and assess connectivity at large scales (e.g. Chetkiewicz et al.,  
14 2006; Squires et al., 2013; Elliot et al., 2014). Identification of potential movement corri-  
15 dors typically relies on the estimation of permeability surfaces, which return the ease or  
16 willingness at which the focal species traverses a specific landscape (Sawyer et al., 2011).  
17 Such surfaces are created based on species' relative selection strengths (Avgar et al., 2017),  
18 which can be quantified using a suite of selection functions (Zeller et al., 2012). Specifically,  
19 selection strengths are estimated by comparing spatial covariates (e.g. environmental and  
20 anthropogenic) at locations visited by the animal to the same spatial covariates at locations  
21 available to the animal (Zeller et al., 2012). Importantly, selection functions require adequate  
22 landscape and relocation data that are representative of the process being studied (Diniz  
23 et al., 2019). Altough selection during residence and dispersal may coincide (Fattebert et al.,  
24 2015), it appears that relocation data collected on dispersing individuals outperforms data  
25 collected on resident individuals in the detection of large-scale movement corridors (Elliot  
26 et al., 2014; Abrahms et al., 2017; Diniz et al., 2019). Nevertheless, dispersal data is inher-  
27 ently difficult to collect and remains scarce in the connectivity literature (Vasudev et al.,  
28 2015). As such, most permeability surfaces upon which movement corridors are identified  
29 are created using relocation data collected on resident individuals. This has likely limited  
30 our ability to meaningfully assess the effectiveness of protected areas in securing functional  
31 connectivity for their protected species.

32 One initiative that aims at restoring and enhancing connectivity across large scales is the  
33 Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA), which constitutes the  
34 world's largest transfrontier conservation area, spanning over 520'000 km<sup>2</sup> and five coun-

tries ([www.kavangozambezi.org](http://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). As a result, the species has become one of Africa's most endangered large carnivores, and currently only survives in small, spatially scattered subpopulations (Woodroffe and Sillero-Zubiri, 2012). 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.

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

## 73 **2 Methods**

### 74 **2.1 Study Area**

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

### 93 **2.2 GPS Relocation Data**

94 We used a population of free-ranging African wild dogs inhabiting the Okavango Delta in  
95 northern Botswana as a source population for dispersing individuals. This population has  
96 been extensively studied since 1989 (McNutt, 1996; Cozzi et al., 2013, 2020; Behr et al.,  
97 2020). Between 2011 and 2019, we systematically collected GPS relocation data on 16  
98 coalitions of dispersing African wild dogs (7 female and 9 male coalitions). Candidate  
99 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 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

133 from remotely sensed satellite imagery. To ensure a consistent resolution (i.e. cell-size or  
134 grain) across covariates, we coarsened or interpolated all layers to a resolution of 250m x  
135 250m. For further details on the preparation and source of each covariate, see Appendix  
136 A.3. We performed processing and manipulation of data as well as all spatial and statistical  
137 analyses using R, version 3.6.1 (R Core Team, 2019).

138 **2.4 Habitat Selection Model**

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

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

152 The selection score  $w(x)$  of a step depended on its associated covariates  $(x_1, x_2, \dots, x_n)$ , as  
153 well as on the animal's relative selection strengths towards these covariates  $(\beta_1, \beta_2, \dots, \beta_n)$ .  
154 To estimate relative selection strengths (i.e. the  $\beta$ 's) for each covariate, we used mixed effects  
155 conditional logistic regression analysis as suggested by Muff et al. (2020). We implemented  
156 their method using the R-package *glmmTMB* (Brooks et al., 2017) and used dispersing  
157 coalition ID to model random slopes. We also modelled random intercepts with an arbitrary  
158 high variance of  $10^6$  to make use of the poisson trick (see Muff et al., 2020). We defined three  
159 movement metrics, namely the cosine of the turning angle ( $\cos(ta)$ ), the step length ( $sl$ ) and  
160 the logarithm of the step length ( $\log(sl)$ ), as core covariates and ran stepwise forward model  
161 selection based on Akaike's Information Criterion (AIC; Burnham and Anderson, 2002) for  
162 all other covariates. The inclusion of movement metrics served to reduce biases in estimated  
163 habitat selection coefficients that may have arisen due to movement behavior (Avgar et al.,

164 2016). To validate the predictive power of the most parsimonious habitat selection model,  
165 we ran k-fold cross-validation for case-control studies as described in Fortin et al. (2009)  
166 (details in Appendix A.5).

## 167 2.5 Permeability Surface

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

## 180 2.6 Least-Cost Paths and Corridors

181 To identify movement corridors of dispersing wild dogs, we specified source points and  
182 calculated factorial least-cost paths (LCPs) as well as factorial least-cost corridors (LCCs)  
183 among them (Elliot et al., 2014). We generated source points by overlaying the study area  
184 with a regular grid of points spaced at 100 km. We only considered those points that  
185 fell within protected areas  $> 700 \text{ km}^2$ , which conforms with home-range requirements of  
186 African wild dogs (Pomilia et al., 2015). Finally, we defined centroids as source points  
187 for those protected areas  $> 700 \text{ km}^2$  that were not assigned any source points from the  
188 regular grid. Because wild dogs residing outside of protected areas are rare and unviable  
189 (Van der Meer et al., 2014), we consider our selection of source points within protected areas  
190 to be appropriate. In total, we generated 68 source points, which resulted in 2'278 unique  
191 pairwise combinations and therefore 2'278 unique LCPs and LCCs. We computed factorial  
192 LCPs and LCCs between source points using the R-package *gdistance* (further details in  
193 Appendix A.7). After computation, we tallied overlapping LCPs and LCCs, respectively,  
194 into single connectivity maps. Because LCPs return discrete paths, whereas LCCs return  
195 continuous corridors, we present both methods. R-codes showcasing the main steps for

196 sections 2.5 to 2.6 can be downloaded from GitHub (<https://github.com/DavidDHofmann/LeastCostAnalysis>).  
197

## 198 3 Results

### 199 3.1 Dispersal Events

200 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 201 202 average dispersed for 48 days ( $SD = 44$ ), covered a mean Euclidean distance of 54 km ( $SD = 71$ ) and a cumulative distance of 597 km ( $SD = 508$ ).  
203

### 204 3.2 Habitat Selection Model

205 Our most parsimonious habitat selection model ( $\Delta AIC > 2$  than any alternative model; 206 Table S4) retained the covariates *water*, *distance to water*, *trees*, *shrubs/grassland*, and 207 *human influence*, beside the fixed covariates *cos(ta)*, *sl*, and *log(sl)* (Figure 3a). With respect 208 to environmental covariates, dispersers avoided moving through water ( $\beta = -0.53$ , 95% CI 209 -0.79 to -0.27,  $SD_{RE} = 0.17$ ) but selected for locations in its vicinity, although the latter 210 effect was not significant ( $\beta = -0.33$ , 95% CI = -0.73 to 0.08,  $SD_{RE} = 0.57$ ). Dispersers 211 avoided areas that were densely covered by trees ( $\beta = -0.31$ , CI = -0.47 to -0.15,  $SD_{RE} = 0.14$ ) and preferred areas covered by shrubs/grassland ( $\beta = 0.25$ , 95% CI = 0.07 to 0.42, 212  $SD_{RE} < 0.01$ ). Finally, dispersers avoided areas that were influenced by humans ( $\beta = -0.45$ , 213 95% CI = -0.82 to -0.08,  $SD_{RE} = 0.22$ ). With the exepction of *distance to water*, random 214 effects revealed little variability between dispersal coalitions (Appendix A6).  
215

216 Results from the k-fold cross-validation suggested that our prediction was significant and 217 robust, as highlighted by the fact that the 95%-CIs intervals of  $\bar{r}_{s,realized}$  and  $\bar{r}_{s,random}$  did 218 not overlap (Figure 3b). Likewise, the significant correlation between ranks and corresponding 219 frequencies for realized steps suggested a good fit between predictions and observations 220 (Figure 3b).  
221

### 3.3 Permeability Surface

222 Our prediction of landscape permeability revealed substantial differences across regions in 223 the study area (Figure 4). Comparisons of median permeability values (Table 1) showed 224 that permeability inside the KAZA-TFCA was more than two times as high as permeability 225 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).

## 257 4 Discussion

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

276 Our results emphasize that human influences constitute some of the main barriers to  
277 connectivity among wild dog populations. This conforms to findings on dispersing wild  
278 dogs from eastern Africa (Masenga et al., 2016; O'Neill et al., 2020) but conflicts with  
279 findings from South Africa by Davies-Mostert et al. (2012), who reported a high willingness  
280 of dispersers to cross human-dominated landscapes. Such differences may arise from the fact  
281 that our model infers preferences by comparing *used* and *available* habitats, whereas Davies-  
282 Mostert et al. (2012) only recorded net dispersal distances, thereby precluding such an  
283 analysis. Thus, we believe that differences to Davies-Mostert et al. (2012) may be explained  
284 by the unavailability of alternative routes through natural landscapes, which may have forced  
285 dispersers in South Africa to cross human dominated landscapes despite a strong aversion to  
286 do so. In this regard, our representation of dispersal corridors and the resulting connectivity  
287 appear conservative, as dispersers may be able to make the best out of a bad situation and  
288 cross landscapes characterized by considerably unfavorable conditions (Palomares et al.,  
289 2000; Elliot et al., 2014). Nevertheless, successful conservation of this species relies on  
290 policymakers' and local authorities' willingness and ability to provide and conserve natural

291 areas that remain free from anthropogenic pressures. This is not only paramount in light  
292 of increasing connectivity and facilitating dispersal, but also in terms of reducing human-  
293 caused mortality during dispersal. In fact, previous studies have shown that human-caused  
294 mortality represents a major threat to wild dogs' ability to disperse (Woodroffe et al., 2019;  
295 Cozzi et al., 2020).

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

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

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

319 Locally, we identified the Okavango-Linyanti region as a potential dispersal hub through  
320 which dispersing wild dogs gain access to more peripheral regions of the KAZA-TFCA.  
321 It appears that the absence of human activities, the central position within the KAZA-  
322 TFCA, and the presence of relatively impermeable water bodies (e.g. Okavango Delta,  
323 Linyanti Swamp) funnel dispersal movements, resulting in a highly frequented corridor.  
324 Furthermore, the lack of permeable areas between peripheral source points often resulted

325 in corridors stretching longer Euclidean distances, in an arc-shaped route via a stretch of  
326 suitable habitat through the Okavango-Linyanti ecosystem. This is an expected outcome  
327 in case structural and functional connectivity coincide, i.e. when dispersers follow suitable  
328 habitats to disperse (Fattebert et al., 2015; Hauenstein et al., 2019). The key role of the  
329 Okavango-Linyanti region for overall connectivity within the KAZA-TFCA thus calls for  
330 actions to secure its protection status in the future. While the region is currently a Wildlife  
331 Management Area, it has neither the status of a National Park nor that of a Game Reserve. A  
332 similar case of non-formally protected but key dispersal landscape is represented by the area  
333 south of Kafue NP in Zambia, for which a disruption of its main and narrow dispersal corridor  
334 would result in considerable isolation of its subpopulations. We also revealed a potential  
335 southwards corridor between the Okavango-Linyanti ecosystem and the Central Kalahari  
336 National Park. Elliot et al. (2014) and Cushman et al. (2018) identified a similar corridor for  
337 dispersing lions, suggesting that upholding and protecting a link between those ecosystems  
338 is pivotal. Some areas through which the corridor runs are neither part of the KAZA-TFCA  
339 nor profit from any form of protection status. Human presence and activities along the  
340 national road that longitudinally traverses this corridor may limit functional connectivity  
341 (Cozzi et al., 2020).

342 Our approach of identifying movement corridors based on pre-defined start and end  
343 points implicitly assumes that individuals know the end point of their dispersal journey and  
344 that they have almost complete knowledge of associated movement costs (Panzacchi et al.,  
345 2016). Since dispersers often move into unknown territory, this may not necessarily be the  
346 case (Abrahms et al., 2017; Cozzi et al., 2020). However, specification of pre-defined end  
347 points might not be necessary, as the parametrized iSSF model can be used as mechanistic  
348 movement model to simulate dispersal events from known source points, yet without re-  
349 stricting the domain of potential end points (Signer et al., 2017). Consequently, movement  
350 corridors would emerge more naturally as the result of a myriad of simulated dispersal events  
351 (Zeller et al., 2020).

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

359 model of dispersal.

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

## 374 **5 Authors' Contributions**

375 D.D.H., D.M.B., A.O. and G.C. conceived the study and designed methodology; D.M.B.,  
376 G.C., and J.W.M. collected the data; D.D.H. and D.M.B. analysed the data; G.C. and A.O.  
377 assisted with modelling; D.D.H., D.M.B., and G.C. wrote the first draft of the manuscript  
378 and all authors contributed to the drafts at several stages and gave final approval for pub-  
379 lication.

## 380 **6 Data Availability**

381 GPS movement data of dispersing coalitions will be made available on dryad at the time of  
382 publication. R-code showcasing the main steps for sections 2.5 to 2.6 can be downloaded  
383 from GitHub (<https://github.com/DavidDHofmann/LeastCostAnalysis>).

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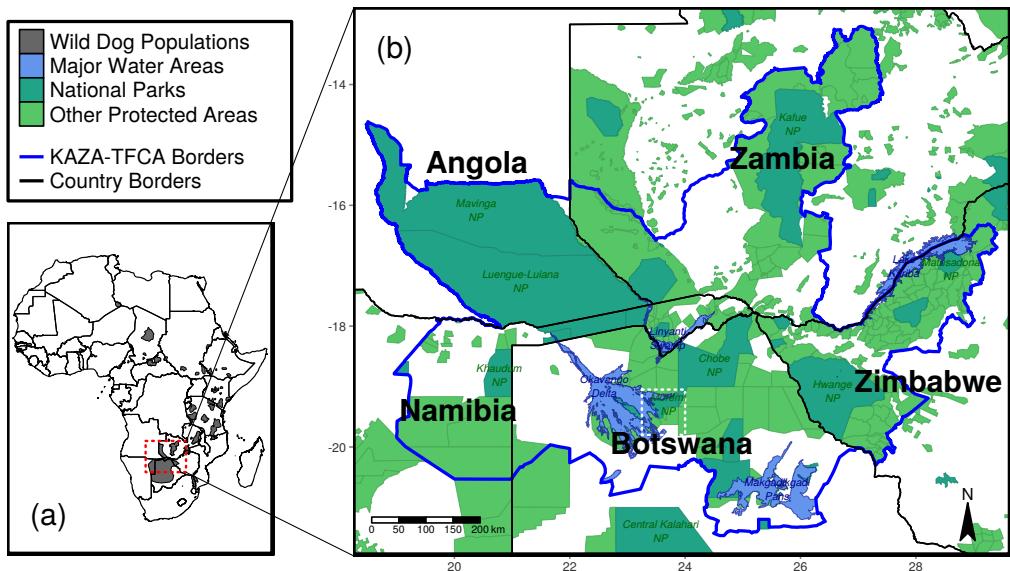
396 **References**

- 397 Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., and Brashares,  
398 J. S. (2017). Does Wildlife Resource Selection Accurately Inform Corridor Conservation?  
399 *Journal of Applied Ecology*, 54(2):412–422.
- 400 Armansin, N. C., Stow, A. J., Cantor, M., Leu, S. T., Klarevas-Irby, J. A., Chariton, A. A.,  
401 and Farine, D. R. (2019). Social Barriers in Ecological Landscapes: The Social Resistance  
402 Hypothesis. *Trends in Ecology & Evolution*, pages 137–148.
- 403 Avgar, T., Lele, S. R., Keim, J. L., and Boyce, M. S. (2017). Relative Selection Strength:  
404 Quantifying Effect Size in Habitat- and Step-Selection Inference. *Ecology and Evolution*,  
405 7(14):5322–5330.
- 406 Avgar, T., Potts, J. R., Lewis, M. A., and Boyce, M. S. (2016). Integrated Step Selection  
407 Analysis: Bridging the Gap Between Resource Selection and Animal Movement. *Methods  
408 in Ecology and Evolution*, 7(5):619–630.
- 409 Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2020). When to Stay and When  
410 to Leave? Proximate Causes of Dispersal in an Endangered Social Carnivore. *Journal of  
411 Animal Ecology*. In press.
- 412 Bonyongo, C. M. (2005). Habitat Utilization by Impala (*Aepyceros memmatus*) in the Oka-  
413 vango Delta. *Botswana Notes & Records*, 37(1):227–235.
- 414 Brennan, A., Beytell, P., Aschenborn, O., Du Preez, P., Funston, P., Hanssen, L., Kilian,  
415 J., Stuart-Hill, G., Taylor, R., and Naidoo, R. (2020). Characterizing Multispecies  
416 Connectivity Across a Transfrontier Conservation Landscape. *Journal of Applied Ecology*,  
417 57:1700–1710.
- 418 Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen,  
419 A., Skaug, H. J., Maechler, M., and Bolker, B. M. (2017). glmmTMB Balances Speed and  
420 Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling. *The R  
421 Journal*, 9(2):378–400.
- 422 Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A  
423 Practical Information-Theoretic Approach*. Springer Science & Business Media, Ney York,  
424 NY, USA.
- 425 Börger, L. and Fryxell, J. (2012). Quantifying Individual Differences in Dispersal Using Net  
426 Squared Displacement. In Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M.,  
427 editors, *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.
- 428 Chetkiewicz, C.-L. B., St. Clair, C. C., and Boyce, M. S. (2006). Corridors for Conservation:  
429 Integrating Pattern and Process. *Annual Review of Ecology, Evolution, and Systematics*,  
430 37(1):317–342.
- 431 Clevenger, A. P., Wierzchowski, J., Chruszcz, B., and Gunson, K. (2002). GIS-Generated,  
432 Expert-Based Models for Identifying Wildlife Habitat Linkages and Planning Mitigation  
433 Passages. *Conservation Biology*, 16(2):503–514.
- 434 Cozzi, G., Behr, D. M., Webster, H. S., Claase, M., Bryce, C. M., Modise, B., Mcnutt, J. W.,  
435 and Ozgul, A. (2020). African Wild Dog Dispersal and Implications for Management. *The  
436 Journal of Wildlife Management*, 84(4):614–621.
- 437 Cozzi, G., Broekhuis, F., McNutt, J. W., and Schmid, B. (2013). Comparison of the Effects of  
438 Artificial and Natural Barriers on Large African Carnivores: Implications for Interspecific  
439 Relationships and Connectivity. *Journal of Animal Ecology*, 82(3):707–715.
- 440 Cozzi, G., Maag, N., Börger, L., Clutton-Brock, T. H., and Ozgul, A. (2018). Socially  
441 Informed Dispersal in a Territorial Cooperative Breeder. *Journal of Animal Ecology*,  
442 87(3):838–849.

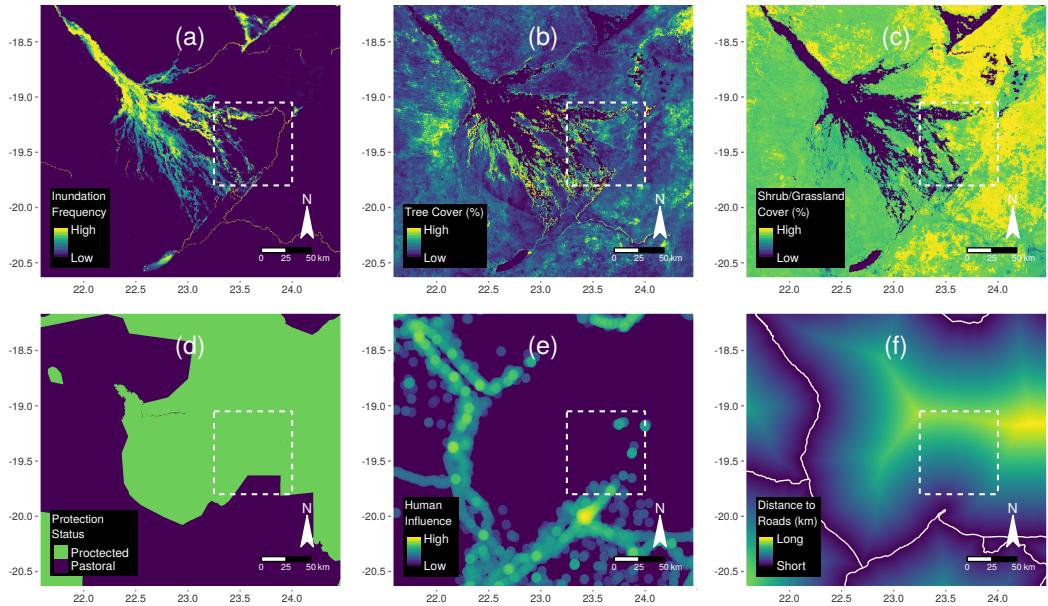
- 443 Creel, S. and Creel, N. M. (2002). *The African Wild Dog: Behavior, Ecology, and Conservation*. Princeton University Press, Princeton, NJ, USA.
- 444
- 445 Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el din, L., Bothwell, H., Flyman, M., Mtare, G., Macdonald, D. W., and Loveridge, A. J. (2018). Prioritizing Core Areas, Corridors and Conflict Hotspots for Lion Conservation in Southern Africa. *PLOS ONE*, 13(7):e0196213.
- 446
- 447
- 448
- 449 Davies-Mostert, H. T., Kamler, J. F., Mills, M. G. L., Jackson, C. R., Rasmussen, G. S. A., Groom, R. J., and Macdonald, D. W. (2012). Long-Distance Transboundary Dispersal of African Wild Dogs among Protected Areas in Southern Africa. *African Journal of Ecology*, 50(4):500–506.
- 450
- 451
- 452
- 453 Diniz, M. F., Cushman, S. A., Machado, R. B., and De Marco Júnior, P. (2019). Landscape Connectivity Modeling From the Perspective of Animal Dispersal. *Landscape Ecology*, 35(35):41–58.
- 454
- 455
- 456 Doerr, V. A. J., Barrett, T., and Doerr, E. D. (2011). Connectivity, Dispersal Behaviour and Conservation under Climate Change: A Response to Hodgson et al.: Connectivity and Dispersal Behaviour. *Journal of Applied Ecology*, 48(1):143–147.
- 457
- 458
- 459 Elliott, N. B., Cushman, S. A., Macdonald, D. W., and Loveridge, A. J. (2014). The Devil is in the Dispersers: Predictions of Landscape Connectivity Change with Demography. 51(5):1169–1178.
- 460
- 461
- 462 Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1):487–515.
- 463
- 464 Fattebert, J., Robinson, H. S., Balme, G., Slotow, R., and Hunter, L. (2015). Structural Habitat Predicts Functional Dispersal Habitat of a Large Carnivore: How Leopards Change Spots. *Ecological Applications*, 25(7):1911–1921.
- 465
- 466
- 467 Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., and Mao, J. S. (2005). Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone National Park. *Ecology*, 86(5):1320–1330.
- 468
- 469
- 470 Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., and Dancose, K. (2009). Group-Size-Mediated Habitat Selection and Group Fusion–Fission Dynamics of Bison under Predation Risk. *Ecology*, 90(9):2480–2490.
- 471
- 472
- 473 Hauenstein, S., Fattebert, J., Grüebler, M. U., Naef-Daenzer, B., Pe'er, G., and Hartig, F. (2019). Calibrating an Individual-Based Movement Model to Predict Functional Connectivity for Little Owls. *[Ecological Applications]*, 29(4):e01873.
- 474
- 475
- 476 Latham, A. D. M., Latham, M. C., Boyce, M. S., and Boutin, S. (2011). Movement Responses by Wolves to Industrial Linear Features and Their Effect on Woodland Caribou in Northeastern Alberta. *Ecological Applications*, 21(8):2854–2865.
- 477
- 478
- 479 Masenga, E. H., Jackson, C. R., Mjingo, E. E., Jacobson, A., Riggio, J., Lyamuya, R. D., Fyumagwa, R. D., Borner, M., and Røskraft, E. (2016). Insights into Long-Distance Dispersal by African Wild Dogs in East Africa. *African Journal of Ecology*, 54(1):95–98.
- 480
- 481
- 482 McNutt, J. (1996). Sex-Biased Dispersal in African Wild Dogs (*Lycaon pictus*). *Animal Behaviour*, 52(6):1067–1077.
- 483
- 484 Mills, M. G. L. and Gorman, M. L. (1997). Factors Affecting the Density and Distribution of Wild Dogs in the Kruger National Park. *Conservation Biology*, 11(6):1397–1406.
- 485
- 486 Muff, S., Signer, J., and Fieberg, J. (2020). Accounting for Individual-Specific Variation in Habitat-Selection Studies: Efficient Estimation of Mixed-Effects Models Using Bayesian or Frequentist Computation. *Journal of Animal Ecology*, 89(1):80–92.
- 487
- 488

- 489 O'Neill, H. M. K., Durant, S. M., and Woodroffe, R. (2020). What Wild Dogs Want: Habitat  
490 Selection Differs across Life Stages and Orders of Selection in a Wide-Ranging Carnivore.  
491 *BMC Zoology*, 5(1).
- 492 Osofsky, S. A., McNutt, J. W., and Hirsch, K. J. (1996). Immobilization of Free-Ranging  
493 African Wild Dogs (*Lycaon pictus*) Using a Ketamine/xylazine/Atropine Combination.  
494 *Journal of Zoo and Wildlife Medicine*, 27(4):528–532.
- 495 Palomares, F., Delibes, M., Ferreras, P., Fedriani, J. M., Calzada, J., and Revilla, E. (2000).  
496 Iberian Lynx in a Fragmented Landscape: Predispersal, Dispersal, and Postdispersal  
497 Habitats. *Conservation Biology*, 14(3):809–818.
- 498 Panzacchi, M., Van Moorter, B., Strand, O., Saerens, M., Kivimäki, I., St. Clair, C. C.,  
499 Herfindal, I., and Boitani, L. (2016). Predicting the Continuum Between Corridors and  
500 Barriers to Animal Movements Using Step Selection Functions and Randomized Shortest  
501 Paths. *Journal of Animal Ecology*, 85(1):32–42.
- 502 Pomilia, M. A., McNutt, J. W., and Jordan, N. R. (2015). Ecological Predictors of African  
503 Wild Dog Ranging Patterns in Northern Botswana. *Journal of Mammalogy*, 96(6):1214–  
504 1223.
- 505 Pullinger, M. G. and Johnson, C. J. (2010). Maintaining or Restoring Connectivity of  
506 Modified Landscapes: Evaluating the Least-Cost Path Model with Multiple Sources of  
507 Ecological Information. *Landscape Ecology*, 25(10):1547–1560.
- 508 R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foun-  
509 dation for Statistical Computing, Vienna, Austria.
- 510 Rudnick, D., Ryan, S., Beier, P., Cushman, S., Dieffenbach, F., Epps, C., Gerber, L., Hart-  
511 ter, J., Jenness, J., Kintsch, J., Merenlender, A., Perkl, R., Perziosi, D., and Trombulack,  
512 S. (2012). The Role of Landscape Connectivity in Planning and Implementing Conserva-  
513 tion and Restoration Priorities. *Issues in Ecology*, 16.
- 514 Sawyer, S. C., Epps, C. W., and Brashares, J. S. (2011). Placing Linkages among Fragmented  
515 Habitats: Do Least-Cost Models Reflect How Animals Use Landscapes? *Journal of*  
516 *Applied Ecology*, 48(3):668–678.
- 517 Signer, J., Fieberg, J., and Avgar, T. (2017). Estimating Utilization Distributions from  
518 Fitted Step-Selection Functions. *Ecosphere*, 8(4):e01771.
- 519 Squires, J. R., DeCesare, N. J., Olson, L. E., Kolbe, J. A., Hebblewhite, M., and Parks, S. A.  
520 (2013). Combining Resource Selection and Movement Behavior to Predict Corridors for  
521 Canada Lynx at their Southern Range Periphery. *Biological Conservation*, 157:187–195.
- 522 Thurfjell, H., Ciuti, S., and Boyce, M. S. (2014). Applications of Step-Selection Functions  
523 in Ecology and Conservation. *Movement Ecology*, 2(4).
- 524 Tshipa, A. (2017). Partial Migration Links Local Surface-Water Management to Large-Scale  
525 Elephant Conservation in the World's Largest Transfrontier Conservation Area. *Biological*  
526 *Conservation*, 215:46–50.
- 527 Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population*  
528 *Redistribution in Plants and Animals*. Sinauer Associates, Sunderland, MA, USA.
- 529 Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., and Macdonald, D. W.  
530 (2010). How Key Habitat Features Influence Large Terrestrial Carnivore Movements: Wa-  
531 terholes and African Lions in a Semi-Arid Savanna of North-Western Zimbabwe. *Landscape*  
532 *Ecology*, 25(3):337–351.
- 533 Van der Meer, E., Fritz, H., Blinston, P., and Rasmussen, G. S. (2014). Ecological Trap in  
534 the Buffer Zone of a Protected Area: Effects of Indirect Anthropogenic Mortality on the  
535 African Wild Dog (*Lycaon pictus*). *Oryx*, 48(2):285–293.

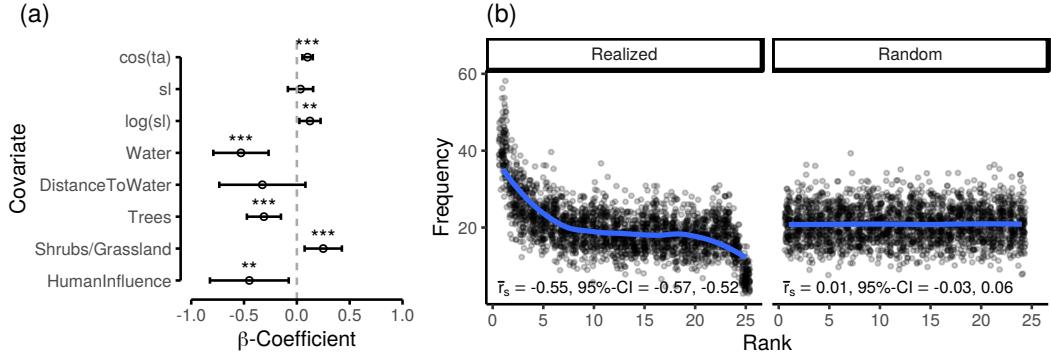
- 536 Vasudev, D., Fletcher, R. J., Goswami, V. R., and Krishnadas, M. (2015). From Disper-  
537 sal Constraints to Landscape Connectivity: Lessons from Species Distribution Modeling.  
538 *Ecography*, 38(10):967–978.
- 539 Weise, F. J., Vijay, V., Jacobson, A. P., Schoonover, R. F., Groom, R. J., Horgan, J.,  
540 Keeping, D., Klein, R., Marnewick, K., Maude, G., Melzheimer, J., Mills, G., Merwe,  
541 V. v. d., Meer, E. v. d., Vuuren, R. J. v., Wachter, B., and Pimm, S. L. (2017). The  
542 Distribution and Numbers of Cheetah (*Acinonyx jubatus*) in Southern Africa. *PeerJ*,  
543 5:e4096.
- 544 Wolski, P., Murray-Hudson, M., Thito, K., and Cassidy, L. (2017). Keeping it Simple:  
545 Monitoring Flood Extent in Large Data-Poor Wetlands Using MODIS SWIR Data. *In-*  
546 *ternational Journal of Applied Earth Observation and Geoinformation*, 57:224–234.
- 547 Woodroffe, R. (2011). Ranging behaviour of African Wild Dog Packs in a Human-Dominated  
548 Landscape. *Journal of Zoology*, 283(2):88–97.
- 549 Woodroffe, R., Rabaiotti, D., Ngatia, D. K., Smallwood, T. R. C., Strebel, S., and O'Neill,  
550 H. M. K. (2019). Dispersal Behaviour of African Wild Dogs in Kenya. *African Journal*  
551 *of Ecology*, 58(1):46–57.
- 552 Woodroffe, R. and Sillero-Zubiri, C. (2012). *Lycaon pictus*. *The IUCN Red List of Threatened*  
553 *Species*, 2012:e. T12436A1671116.
- 554 Zeller, K. A., McGarigal, K., and Whiteley, A. R. (2012). Estimating Landscape Resistance  
555 to Movement: A Review. *Landscape Ecology*, 27(6):777–797.
- 556 Zeller, K. A., Wattles, D. W., Bauder, J. M., and DeStefano, S. (2020). Forecasting Seasonal  
557 Habitat Connectivity in a Developing Landscape. *Land*, 9(7):233.



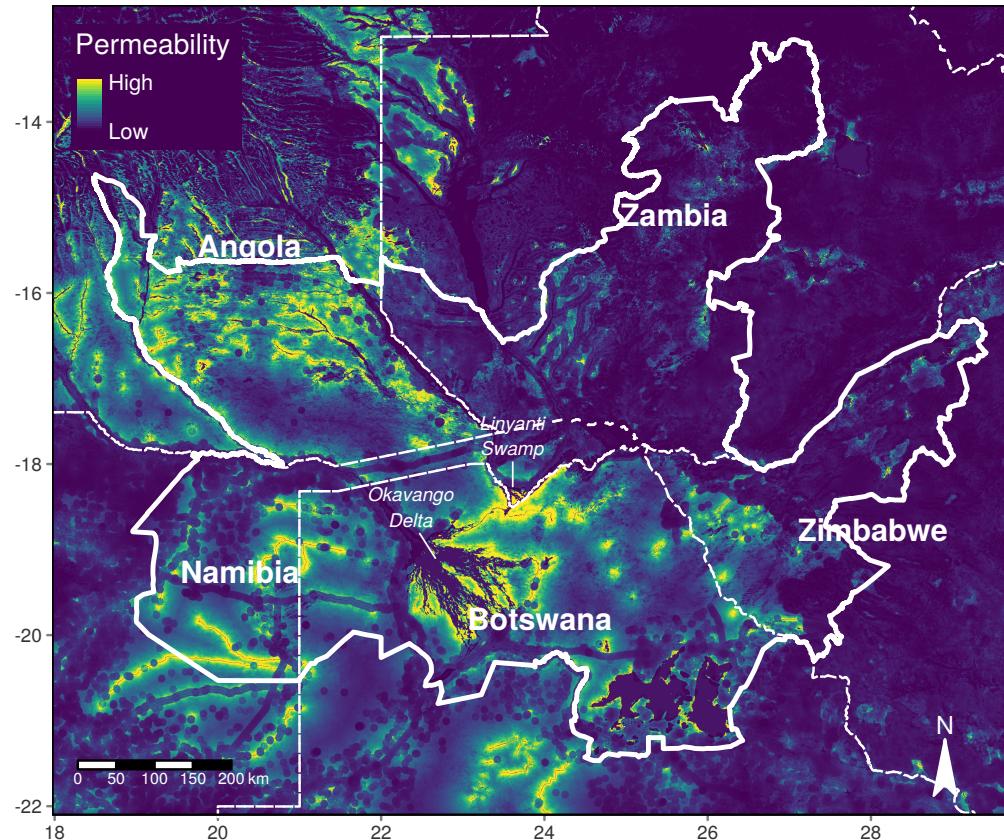
**Figure 1:** Overview of our study area. (a) The red dotted rectangle depicts the study area, which was confined by a bounding box encompassing the entire KAZA-TFCA. Gray areas indicate remaining wild dog populations according to the IUCN (Woodroffe and Sillero-Zubiri, 2012). (b) The white rectangle 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.



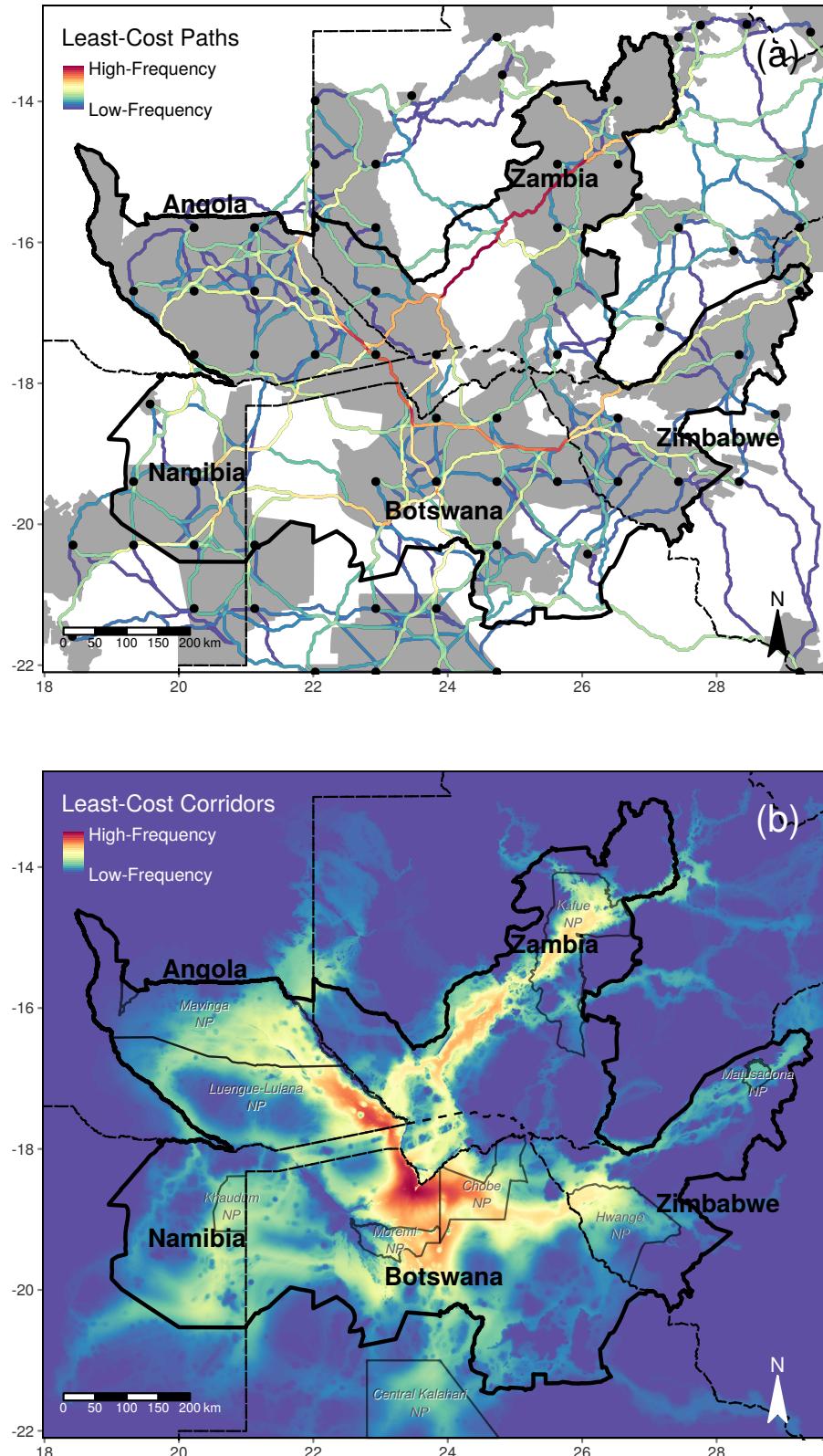
**Figure 2:** Overview of spatial covariates that we included in our models. We prepared all covariates for the entire study area but for better visibility we only plot them for the surroundings of the Okavango Delta. The white rectangle in each plot depicts the area within which dispersing coalitions 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. 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  $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)$  for each raster cell based on the raster cell's underlying covariates ( $x_i$ ) and estimated selection strength ( $\beta_i$ ). 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 dots) and corresponding least-cost paths leaving from protected areas (dark grey borders). Note that only contiguous protected areas covering more than 700 km<sup>2</sup> are depicted. Continuous thin 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.

Country	KAZA-TFCA		Protection Status		
	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)