

# 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>

February 11, 2021

<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

**Running Title:** Connectivity across a Transfrontier Conservation Area.

**Keywords:** dispersal, habitat selection, integrated step selection function,  
Kavango-Zambezi Transfrontier Conservation Area, landscape connectivity, African wild  
dog, movement

## 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<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 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**

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

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 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

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.,

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

## <sup>167</sup> 2.5 Permeability Surface

<sup>168</sup> Using the most parsimonious habitat selection model, we predicted a permeability surface  
<sup>169</sup> spanning the entire extent of the KAZA-TFCA. That is, we applied Equation 1 to our  
<sup>170</sup> spatial covariates and calculated the selection score  $w(x)$  for each raster cell. Because our  
<sup>171</sup> representation of water was dynamic, we collapsed all dynamic water maps into a single  
<sup>172</sup> map using areas that were covered by water in at least 10% of the cases. We used the  
<sup>173</sup> resulting map to also calculate a layer returning the distance to water. Because the delta  
<sup>174</sup> only covers 5% of the KAZA-TFCA, we considered the use of a single water map to be  
<sup>175</sup> appropriate. To reduce the influence of outliers in predicted permeability scores, we followed  
<sup>176</sup> Squires et al. (2013) and curtailed predicted scores between the 1<sup>st</sup> and 99<sup>th</sup> percentile of  
<sup>177</sup> their original values. To compare permeability across different regions, we normalized the  
<sup>178</sup> permeability surface to a range between 0 (most impermeable) and 1 (most permeable),  
<sup>179</sup> and we determined median permeability within and outside the KAZA-TFCA, within and  
<sup>180</sup> outside formally protected areas, and within each of the five KAZA-TFCA countries.

## <sup>181</sup> 2.6 Least-Cost Paths and Corridors

<sup>182</sup> To identify potential movement corridors of dispersing wild dogs, we specified source points  
<sup>183</sup> and calculated factorial least-cost paths (LCPs) as well as factorial least-cost corridors  
<sup>184</sup> (LCCs) among them (Elliot et al., 2014). To select source points, we followed the om-  
<sup>185</sup> nidirectional *go-through* approach proposed by Koen et al. (2014) and placed 68 regularly  
<sup>186</sup> spaced source points along the map border (Koen et al., 2014; Pitman et al., 2017). While  
<sup>187</sup> this approach tends to identify high connectivity towards the map boundaries, it reduces  
<sup>188</sup> potential biases caused by the selection of unreasonable source points (Koen et al., 2014). To  
<sup>189</sup> assess the sensitivity of our results with respect to the location of source points, we reran the  
<sup>190</sup> same analysis using 68 source points located within protected areas that are large enough to  
<sup>191</sup> sustain viable wild dog populations (further details and corresponding results in Appendix  
<sup>192</sup> A.9). In either case, the 68 source points resulted in 2'278 unique pairwise combinations and  
<sup>193</sup> therefore 2'278 unique LCPs and LCCs. We computed factorial LCPs and LCCs between  
<sup>194</sup> source points using the R-package *gdistance* (details in Appendix A.6). After computation,  
<sup>195</sup> we tallied overlapping LCPs and LCCs, respectively, into single connectivity maps. Because

<sup>196</sup> LCPs return discrete paths, whereas LCCs return continuous corridors, we present both  
<sup>197</sup> methods. R-codes showcasing the main steps for sections 2.5 to 2.6 can be downloaded from  
<sup>198</sup> GitHub (<https://github.com/DavidDHofmann/LeastCostAnalysis>).

## <sup>199</sup> 3 Results

### <sup>200</sup> 3.1 Dispersal Events

<sup>201</sup> In total, we collected 4'169 GPS relocations during dispersal (Figure S2 & Table S1), re-  
<sup>202</sup> sulting in an average of 261 ( $SD = 207$ ) locations per dispersing coalition. Coalitions on  
<sup>203</sup> average dispersed for 48 days ( $SD = 44$ ), covered a mean Euclidean distance of 54 km ( $SD$   
<sup>204</sup> = 71) and a cumulative distance of 597 km ( $SD = 508$ ).

### <sup>205</sup> 3.2 Habitat Selection Model

<sup>206</sup> Our most parsimonious habitat selection model ( $\Delta AIC > 2$  than any alternative model;  
<sup>207</sup> Table S4) retained the covariates *water*, *distance to water*, *trees*, *shrubs/grassland*, and  
<sup>208</sup> *human influence*, beside the fixed covariates *cos(ta)*, *sl*, and *log(sl)* (Figure 3a). Dispersers  
<sup>209</sup> avoided moving through water ( $\beta = -0.53$ , 95% CI -0.79 to -0.27) but selected for locations  
<sup>210</sup> in its vicinity, although the latter effect was not significant ( $\beta = -0.33$ , 95% CI = -0.73 to  
<sup>211</sup> 0.08). Dispersers avoided areas that were densely covered by trees ( $\beta = -0.31$ ,  $CI = -0.47$   
<sup>212</sup> to -0.15) and preferred areas covered by shrubs/grassland ( $\beta = 0.25$ , 95% CI = 0.07 to  
<sup>213</sup> 0.42). Finally, dispersers avoided areas that were influenced by humans ( $\beta = -0.45$ , 95% CI  
<sup>214</sup> = -0.82 to -0.08). Except for *distance to water* ( $SD_{RandomEffect} = 0.57$ ), we observed little  
<sup>215</sup> variation between dispersal coalitions' relative selection strengths ( $SD_{RandomEffect} < 0.22$   
<sup>216</sup> for all other covariates, see also Figure S8).

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

### <sup>222</sup> 3.3 Permeability Surface

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

226 outside it. Permeability varied by country, with a five-fold permeability difference among  
227 them. Angola and Botswana were characterized by comparably highly permeable landscapes,  
228 Zimbabwe and Zambia were relatively impermeable, and Namibia ranged in between the two  
229 extremes (Table 1). Visual inspection of our covariate layers indicated that high permeability  
230 in Angola and Botswana was mainly related to a combination of low human influence, low  
231 tree cover, high shrubs/grassland cover, and a close distance to water. Although swamps,  
232 wetlands, and permanent water themselves provided little permeability, their surroundings  
233 acted as strong attractants to dispersers. The low permeability that characterized Zambia  
234 and Zimbabwe, on the other hand, was mainly caused by substantial human influence.  
235 Albeit the KAZA-TFCA covered most permeability hot-spots, several highly permeable  
236 regions remained uncovered by its borders. Across all countries, protected areas provided  
237 roughly double the permeability of unprotected landscapes (Table 1).

### 238 **3.4 Least-Cost Paths & Least-Cost Corridors**

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

258 **4 Discussion**

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

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

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

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

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

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

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

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

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

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

360 this approach challenging. We therefore urge future studies to optimize the simulation of  
361 movement from iSSFs to capture a more mechanistic model of dispersal.

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

## 376 **5 Authors' Contributions**

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

## 382 **6 Data Availability**

383 GPS movement data of dispersing coalitions is available in the Dryad Digital Repository  
384 doi:10.5061/dryad.dncjsxkzn (Hofmann et al., 2021). R-code showcasing the main steps for  
385 sections 2.5 to 2.6 can be obtained through GitHub (<https://github.com/DavidDHofmann/LeastCostAnalysis>).  
386

<sup>387</sup> **7 Acknowledgements**

<sup>388</sup> We thank the Ministry of Environment and Tourism of Botswana for granting permission to  
<sup>389</sup> conduct this research. We thank C. Botes, I. Clavadetscher, and G. Camenisch for assisting  
<sup>390</sup> with wild dog immobilizations. We also thank B. Abrahms for sharing her data of three  
<sup>391</sup> dispersing wild dogs. Furthermore, we are indebted to Prof. J. Fieberg, who consulted all  
<sup>392</sup> statistical aspects of this work and P. Wolski, from the Okavango Research Institute, who  
<sup>393</sup> assisted us in generating dynamic water maps. We also thank the anonymous reviewers for  
<sup>394</sup> their valuable comments and suggestions. This study was funded by Albert-Heim Stiftung,  
<sup>395</sup> Basler Stiftung für Biologische Forschung, Claraz Foundation, Idea Wild, Jacot Foundation,  
<sup>396</sup> National Geographic Society, Parrotia Stiftung, Stiftung Temperatio, Wilderness Wildlife  
<sup>397</sup> Trust Foundation, Forschungskredit der Universität Zürich, and a Swiss National Science  
<sup>398</sup> Foundation Grant (31003A\_182286) to A. Ozgul.

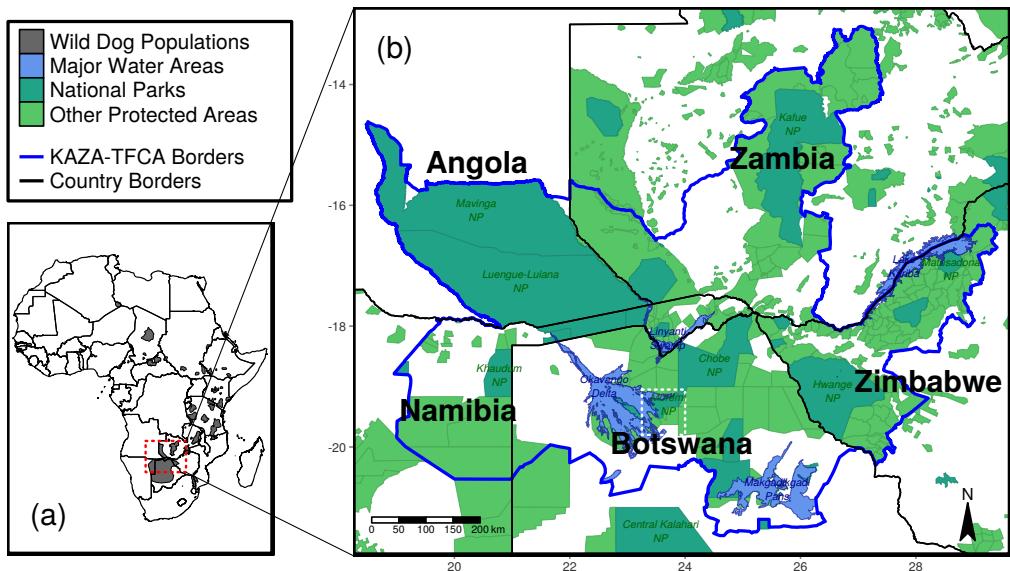
399 **References**

- 400 Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., and Brashares,  
401 J. S. (2017). Does Wildlife Resource Selection Accurately Inform Corridor Conservation?  
402 *Journal of Applied Ecology*, 54(2):412–422.
- 403 Allen, C. H., Parrott, L., and Kyle, C. (2016). An Individual-Based Modelling Approach to  
404 Estimate Landscape Connectivity for Bighorn Sheep (*Ovis canadensis*). *PeerJ*, 4:e2001.
- 405 Armansin, N. C., Stow, A. J., Cantor, M., Leu, S. T., Klarevas-Irby, J. A., Chariton, A. A.,  
406 and Farine, D. R. (2019). Social Barriers in Ecological Landscapes: The Social Resistance  
407 Hypothesis. *Trends in Ecology & Evolution*, pages 137–148.
- 408 Avgar, T., Lele, S. R., Keim, J. L., and Boyce, M. S. (2017). Relative Selection Strength:  
409 Quantifying Effect Size in Habitat- and Step-Selection Inference. *Ecology and Evolution*,  
410 7(14):5322–5330.
- 411 Avgar, T., Potts, J. R., Lewis, M. A., and Boyce, M. S. (2016). Integrated Step Selection  
412 Analysis: Bridging the Gap Between Resource Selection and Animal Movement. *Methods  
413 in Ecology and Evolution*, 7(5):619–630.
- 414 Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2020). When to Stay and When  
415 to Leave? Proximate Causes of Dispersal in an Endangered Social Carnivore. *Journal of  
416 Animal Ecology*. In press.
- 417 Bonyongo, C. M. (2005). Habitat Utilization by Impala (*Aepyceros memmatus*) in the Oka-  
418 vango Delta. *Botswana Notes & Records*, 37(1):227–235.
- 419 Brennan, A., Beytell, P., Aschenborn, O., Du Preez, P., Funston, P., Hanssen, L., Kilian,  
420 J., Stuart-Hill, G., Taylor, R., and Naidoo, R. (2020). Characterizing Multispecies Con-  
421 nectivity Across a Transfrontier Conservation Landscape. *Journal of Applied Ecology*,  
422 57:1700–1710.
- 423 Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen,  
424 A., Skaug, H. J., Maechler, M., and Bolker, B. M. (2017). glmmTMB Balances Speed and  
425 Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling. *The R  
426 Journal*, 9(2):378–400.
- 427 Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A  
428 Practical Information-Theoretic Approach*. Springer Science & Business Media, Ney York,  
429 NY, USA.
- 430 Börger, L. and Fryxell, J. (2012). Quantifying Individual Differences in Dispersal Using Net  
431 Squared Displacement. In Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M.,  
432 editors, *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.
- 433 Chetkiewicz, C.-L. B., St. Clair, C. C., and Boyce, M. S. (2006). Corridors for Conservation:  
434 Integrating Pattern and Process. *Annual Review of Ecology, Evolution, and Systematics*,  
435 37(1):317–342.
- 436 Clevenger, A. P., Wierzchowski, J., Chruszcz, B., and Gunson, K. (2002). GIS-Generated,  
437 Expert-Based Models for Identifying Wildlife Habitat Linkages and Planning Mitigation  
438 Passages. *Conservation Biology*, 16(2):503–514.
- 439 Cozzi, G., Behr, D. M., Webster, H. S., Claase, M., Bryce, C. M., Modise, B., Mcnutt, J. W.,  
440 and Ozgul, A. (2020). African Wild Dog Dispersal and Implications for Management. *The  
441 Journal of Wildlife Management*, 84(4):614–621.
- 442 Cozzi, G., Broekhuis, F., McNutt, J. W., and Schmid, B. (2013). Comparison of the Effects of  
443 Artificial and Natural Barriers on Large African Carnivores: Implications for Interspecific  
444 Relationships and Connectivity. *Journal of Animal Ecology*, 82(3):707–715.

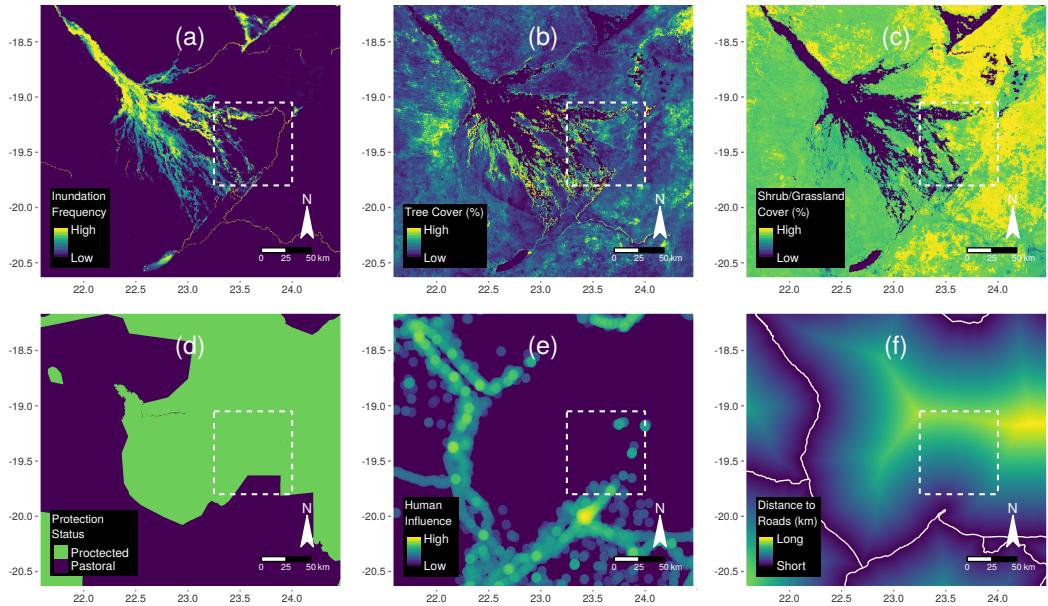
- 445 Cozzi, G., Maag, N., Börger, L., Clutton-Brock, T. H., and Ozgul, A. (2018). Socially  
446 Informed Dispersal in a Territorial Cooperative Breeder. *Journal of Animal Ecology*,  
447 87(3):838–849.
- 448 Creel, S. and Creel, N. M. (2002). *The African Wild Dog: Behavior, Ecology, and Conser-*  
449 *vation*. Princeton University Press, Princeton, NJ, USA.
- 450 Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el din, L., Bothwell, H., Flyman,  
451 M., Mtare, G., Macdonald, D. W., and Loveridge, A. J. (2018). Prioritizing Core Areas,  
452 Corridors and Conflict Hotspots for Lion Conservation in Southern Africa. *PLOS ONE*,  
453 13(7):e0196213.
- 454 Davies-Mostert, H. T., Kamler, J. F., Mills, M. G. L., Jackson, C. R., Rasmussen, G. S. A.,  
455 Groom, R. J., and Macdonald, D. W. (2012). Long-Distance Transboundary Dispersal  
456 of African Wild Dogs among Protected Areas in Southern Africa. *African Journal of*  
457 *Ecology*, 50(4):500–506.
- 458 Diniz, M. F., Cushman, S. A., Machado, R. B., and De Marco Júnior, P. (2019). Landscape  
459 Connectivity Modeling From the Perspective of Animal Dispersal. *Landscape Ecology*,  
460 (35):41–58.
- 461 Doerr, V. A. J., Barrett, T., and Doerr, E. D. (2011). Connectivity, Dispersal Behaviour  
462 and Conservation under Climate Change: A Response to Hodgson et al.: Connectivity  
463 and Dispersal Behaviour. *Journal of Applied Ecology*, 48(1):143–147.
- 464 Elliot, N. B., Cushman, S. A., Macdonald, D. W., and Loveridge, A. J. (2014). The Devil  
465 is in the Dispersers: Predictions of Landscape Connectivity Change with Demography.  
466 51(5):1169–1178.
- 467 Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of*  
468 *Ecology, Evolution, and Systematics*, 34(1):487–515.
- 469 Fattebert, J., Robinson, H. S., Balme, G., Slotow, R., and Hunter, L. (2015). Struc-  
470 tural Habitat Predicts Functional Dispersal Habitat of a Large Carnivore: How Leopards  
471 Change Spots. *Ecological Applications*, 25(7):1911–1921.
- 472 Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., and Mao, J. S. (2005).  
473 Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone  
474 National Park. *Ecology*, 86(5):1320–1330.
- 475 Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., and Dancose, K. (2009).  
476 Group-Size-Mediated Habitat Selection and Group Fusion–Fission Dynamics of Bison  
477 under Predation Risk. *Ecology*, 90(9):2480–2490.
- 478 Hauenstein, S., Fattebert, J., Grüebler, M. U., Naef-Daenzer, B., Pe'er, G., and Hartig, F.  
479 (2019). Calibrating an Individual-Based Movement Model to Predict Functional Connec-  
480 tivity for Little Owls. *[Ecological Applications]*, 29(4):e01873.
- 481 Hofmann, D. D., Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2021). Data from:  
482 Bound within Boundaries: How Well Do Protected Areas Match Movement Corridors of  
483 their Most Mobile Protected Species? Dryad Digital Repository. <https://doi:10.5061/dryad.dncjsxkzn>.
- 485 Koen, E. L., Bowman, J., Sadowski, C., and Walpole, A. A. (2014). Landscape Connectivity  
486 for Wildlife: Development and Validation of Multispecies Linkage Maps. *Methods in*  
487 *Ecology and Evolution*, 5(7):626–633.
- 488 Latham, A. D. M., Latham, M. C., Boyce, M. S., and Boutin, S. (2011). Movement Re-  
489 sponds by Wolves to Industrial Linear Features and Their Effect on Woodland Caribou  
490 in Northeastern Alberta. *Ecological Applications*, 21(8):2854–2865.

- 491 Masenga, E. H., Jackson, C. R., Mjingo, E. E., Jacobson, A., Riggio, J., Lyamuya, R. D.,  
492 Fyumagwa, R. D., Borner, M., and Røskift, E. (2016). Insights into Long-Distance  
493 Dispersal by African Wild Dogs in East Africa. *African Journal of Ecology*, 54(1):95–98.
- 494 McNutt, J. (1996). Sex-Biased Dispersal in African Wild Dogs (*Lycaon pictus*). *Animal  
495 Behaviour*, 52(6):1067–1077.
- 496 Mills, M. G. L. and Gorman, M. L. (1997). Factors Affecting the Density and Distribution  
497 of Wild Dogs in the Kruger National Park. *Conservation Biology*, 11(6):1397–1406.
- 498 Muff, S., Signer, J., and Fieberg, J. (2020). Accounting for Individual-Specific Variation in  
499 Habitat-Selection Studies: Efficient Estimation of Mixed-Effects Models Using Bayesian  
500 or Frequentist Computation. *Journal of Animal Ecology*, 89(1):80–92.
- 501 O'Neill, H. M. K., Durant, S. M., and Woodroffe, R. (2020). What Wild Dogs Want: Habitat  
502 Selection Differs across Life Stages and Orders of Selection in a Wide-Ranging Carnivore.  
503 *BMC Zoology*, 5(1).
- 504 Osofsky, S. A., McNutt, J. W., and Hirsch, K. J. (1996). Immobilization of Free-Ranging  
505 African Wild Dogs (*Lycaon pictus*) Using a Ketamine/xylazine/Atropine Combination.  
506 *Journal of Zoo and Wildlife Medicine*, 27(4):528–532.
- 507 Palomares, F., Delibes, M., Ferreras, P., Fedriani, J. M., Calzada, J., and Revilla, E. (2000).  
508 Iberian Lynx in a Fragmented Landscape: Predispersal, Dispersal, and Postdispersal  
509 Habitats. *Conservation Biology*, 14(3):809–818.
- 510 Panzacchi, M., Van Moorter, B., Strand, O., Saerens, M., Kivimäki, I., St. Clair, C. C.,  
511 Herfindal, I., and Boitani, L. (2016). Predicting the Continuum Between Corridors and  
512 Barriers to Animal Movements Using Step Selection Functions and Randomized Shortest  
513 Paths. *Journal of Animal Ecology*, 85(1):32–42.
- 514 Pitman, R. T., Fattebert, J., Williams, S. T., Williams, K. S., Hill, R. A., Hunter, L.  
515 T. B., Robinson, H., Power, J., Swanepoel, L., Slotow, R., and Balme, G. A. (2017).  
516 Cats, Connectivity and Conservation: Incorporating Data Sets and Integrating Scales for  
517 Wildlife Management. *Journal of Applied Ecology*, 54(6):1687–1698.
- 518 Pullinger, M. G. and Johnson, C. J. (2010). Maintaining or Restoring Connectivity of  
519 Modified Landscapes: Evaluating the Least-Cost Path Model with Multiple Sources of  
520 Ecological Information. *Landscape Ecology*, 25(10):1547–1560.
- 521 R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foun-  
522 dation for Statistical Computing, Vienna, Austria.
- 523 Rudnick, D., Ryan, S., Beier, P., Cushman, S., Dieffenbach, F., Epps, C., Gerber, L., Hart-  
524 ter, J., Jenness, J., Kintsch, J., Merenlender, A., Perkl, R., Perziosi, D., and Trombulack,  
525 S. (2012). The Role of Landscape Connectivity in Planning and Implementing Conserva-  
526 tion and Restoration Priorities. *Issues in Ecology*, 16.
- 527 Sawyer, S. C., Epps, C. W., and Brashares, J. S. (2011). Placing Linkages among Fragmented  
528 Habitats: Do Least-Cost Models Reflect How Animals Use Landscapes? *Journal of  
529 Applied Ecology*, 48(3):668–678.
- 530 Signer, J., Fieberg, J., and Avgar, T. (2017). Estimating Utilization Distributions from  
531 Fitted Step-Selection Functions. *Ecosphere*, 8(4):e01771.
- 532 Squires, J. R., DeCesare, N. J., Olson, L. E., Kolbe, J. A., Hebblewhite, M., and Parks, S. A.  
533 (2013). Combining Resource Selection and Movement Behavior to Predict Corridors for  
534 Canada Lynx at their Southern Range Periphery. *Biological Conservation*, 157:187–195.
- 535 Thurfjell, H., Ciuti, S., and Boyce, M. S. (2014). Applications of Step-Selection Functions  
536 in Ecology and Conservation. *Movement Ecology*, 2(4).

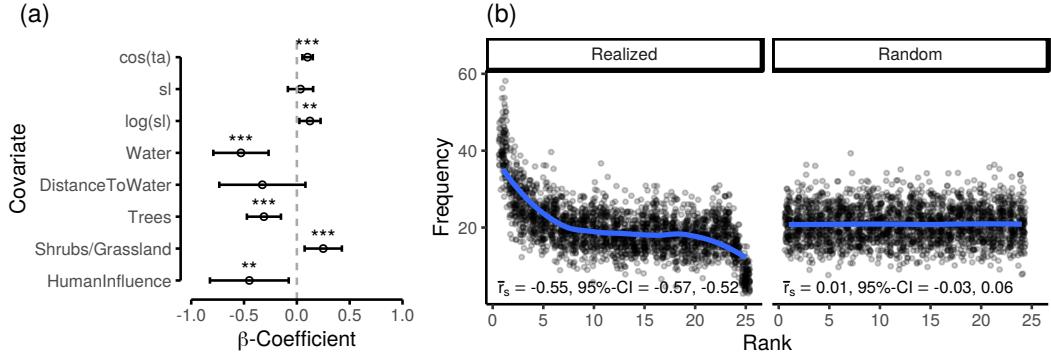
- 537 Tshipa, A. (2017). Partial Migration Links Local Surface-Water Management to Large-Scale  
538 Elephant Conservation in the World's Largest Transfrontier Conservation Area. *Biological  
539 Conservation*, 215:46–50.
- 540 Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population  
541 Redistribution in Plants and Animals*. Sinauer Associates, Sunderland, MA, USA.
- 542 Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., and Macdonald, D. W.  
543 (2010). How Key Habitat Features Influence Large Terrestrial Carnivore Movements: Wa-  
544 terholes and African Lions in a Semi-Arid Savanna of North-Western Zimbabwe. *Landscape  
545 Ecology*, 25(3):337–351.
- 546 Van der Meer, E., Fritz, H., Blinston, P., and Rasmussen, G. S. (2014). Ecological Trap in  
547 the Buffer Zone of a Protected Area: Effects of Indirect Anthropogenic Mortality on the  
548 African Wild Dog (*Lycaon pictus*). *Oryx*, 48(2):285–293.
- 549 Vasudev, D., Fletcher, R. J., Goswami, V. R., and Krishnadas, M. (2015). From Disper-  
550 sal Constraints to Landscape Connectivity: Lessons from Species Distribution Modeling.  
551 *Ecography*, 38(10):967–978.
- 552 Weise, F. J., Vijay, V., Jacobson, A. P., Schoonover, R. F., Groom, R. J., Horgan, J.,  
553 Keeping, D., Klein, R., Marnewick, K., Maude, G., Melzheimer, J., Mills, G., Merwe,  
554 V. v. d., Meer, E. v. d., Vuuren, R. J. v., Wachter, B., and Pimm, S. L. (2017). The  
555 Distribution and Numbers of Cheetah (*Acinonyx jubatus*) in Southern Africa. *PeerJ*,  
556 5:e4096.
- 557 Wolski, P., Murray-Hudson, M., Thito, K., and Cassidy, L. (2017). Keeping it Simple:  
558 Monitoring Flood Extent in Large Data-Poor Wetlands Using MODIS SWIR Data. *In-  
559 ternational Journal of Applied Earth Observation and Geoinformation*, 57:224–234.
- 560 Woodroffe, R. (2011). Ranging behaviour of African Wild Dog Packs in a Human-Dominated  
561 Landscape. *Journal of Zoology*, 283(2):88–97.
- 562 Woodroffe, R. and Ginsberg, J. R. (1999). Conserving the African Wild Dog (*Lycaon pictus*).  
563 Diagnosing and Treating Causes of Decline. *Oryx*, 33(2):132–142.
- 564 Woodroffe, R., Rabaiotti, D., Ngatia, D. K., Smallwood, T. R. C., Strelbel, S., and O'Neill,  
565 H. M. K. (2019). Dispersal Behaviour of African Wild Dogs in Kenya. *African Journal  
566 of Ecology*, 58(1):46–57.
- 567 Woodroffe, R. and Sillero-Zubiri, C. (2012). *Lycaon pictus*. *The IUCN Red List of Threatened  
568 Species*, 2012:e. T12436A16711116.
- 569 Zeller, K. A., McGarigal, K., and Whiteley, A. R. (2012). Estimating Landscape Resistance  
570 to Movement: A Review. *Landscape Ecology*, 27(6):777–797.
- 571 Zeller, K. A., Wattles, D. W., Bauder, J. M., and DeStefano, S. (2020). Forecasting Seasonal  
572 Habitat Connectivity in a Developing Landscape. *Land*, 9(7):233.



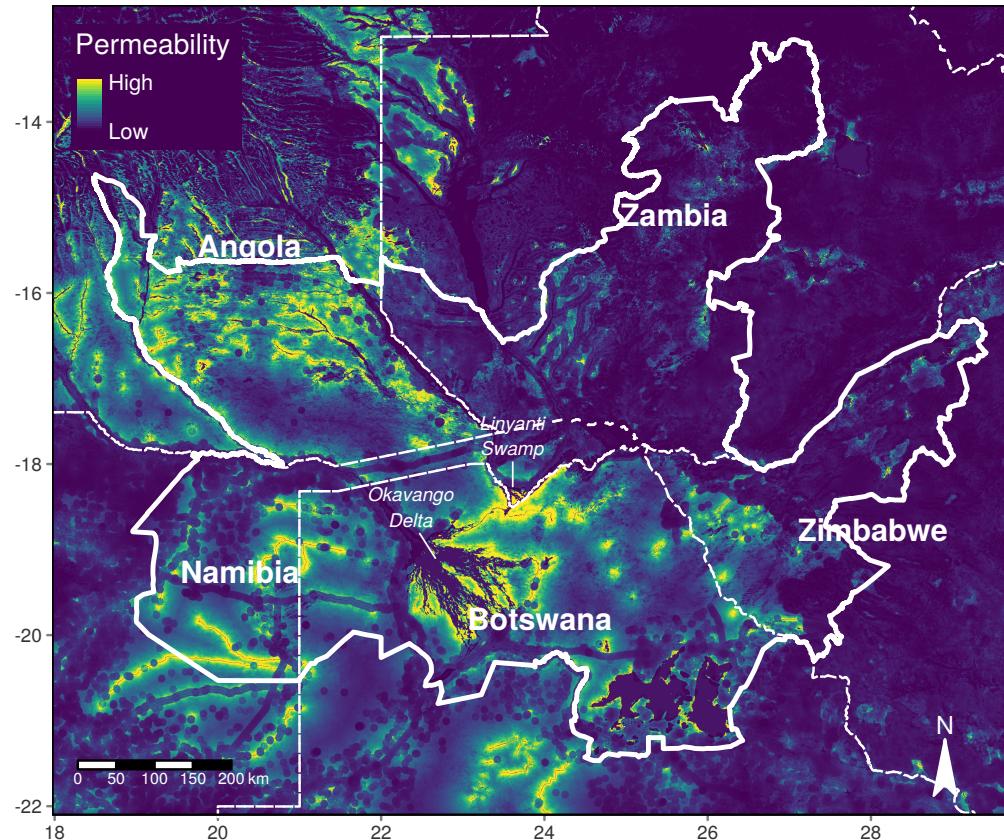
**Figure 1:** Overview of our study area. (a) The red dotted rectangle depicts the study area, which was confined by a bounding box encompassing the entire KAZA-TFCA. Gray areas indicate remaining wild dog populations according to the IUCN (Woodroffe and Sillero-Zubiri, 2012). (b) The white rectangle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



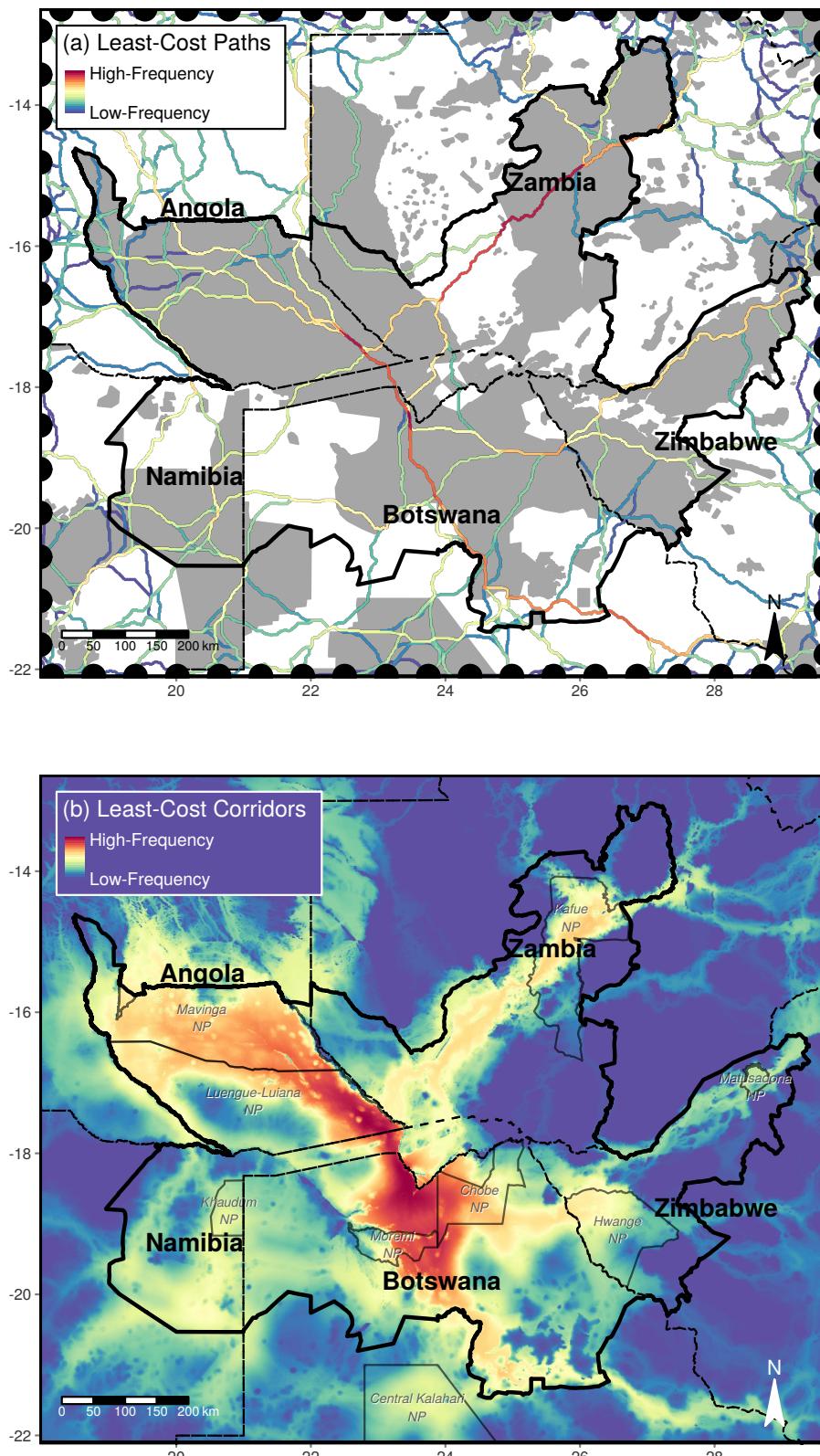
**Figure 2:** Overview of spatial covariates that we included in our models. We prepared all covariates for the entire study area but for better visibility we only plot them for the surroundings of the Okavango Delta. The white rectangle in each plot depicts the area within which dispersing coalitions 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.  $ta$  = 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  $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)$  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 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.

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)