

# 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>

August 28, 2020

<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, least-cost  
corridors, *Lycaon pictus*, permeability surface, protected areas, wildlife management

## Abstract

1. Conserving and managing large portions of land to connect wildlife reserves is increasingly used 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 preferences 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 further showed that major movement corridors of wild dogs run within the KAZA-TFCA, although some minor routes remained outside formally protected areas.
4. Differences in permeability were mainly caused by different degrees of human activities across regions, which hampered dispersal. Rivers, swamps or open water also limited dispersal, while other landscape features had a limited effect.
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, observed regional differences in landscape permeability highlight the need for a coordinated effort towards maintaining or restoring connectivity, especially where international effort is required.

# 1 Introduction

2 Connectivity among subpopulations is a crucial pre-requisite for many species to thrive and  
3 persist (Fahrig, 2003). Accordingly, preserving and protecting movement corridors between  
4 wildlife reserves has become a task of utmost importance for conservation management (Do-  
5 err et al., 2011; Rudnick et al., 2012), resulting in an ever-growing number of large and often  
6 transboundary protected areas. While boundaries of such areas are often drawn according  
7 to expert opinion and socio-political needs, subjective assessments have revealed deficien-  
8 cies in the past (Clevenger et al., 2002; Pullinger and Johnson, 2010). Thus, an empirical  
9 assessment of the adequacy of already-existing or planned protected areas using pertinent  
10 animal movement data is paramount for targeted use of valuable and scarce conservation  
11 funds (Pullinger and 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 corridors typically relies  
15 on the estimation of permeability surfaces, which return the ease or willingness at which the  
16 focal species traverses a specific landscape (Sawyer et al., 2011). Such surfaces are created  
17 based on a species' habitat preferences, which can be quantified using a suite of selection  
18 functions (Zeller et al., 2012). Specifically, habitat preferences are estimated by comparing  
19 spatial covariates (e.g. environmental and anthropogenic) at locations visited by the animal  
20 to the same spatial covariates at locations available to, yet unused by the animal (Zeller et al.,  
21 2012). Importantly, selection functions rely on adequate landscape and relocation data that  
22 are representative of the process being studied (Diniz et al., 2019). For instance, relocation  
23 data collected on dispersing individuals has been shown to outperform data collected on  
24 resident individuals in the detection of large-scale movement corridors (Elliot et al., 2014;  
25 Diniz et al., 2019). Nevertheless, dispersal data is inherently difficult to collect and remains  
26 scarce in the connectivity literature (Vasudev et al., 2015). As such, most permeability  
27 surfaces upon which movement corridors are identified are created using relocation data  
28 collected on resident individuals. This introduces severe biases and substantially reduces  
29 the power to reveal meaningful movement corridors, for dispersing individuals have different  
30 needs and drives compared to resident individuals (Elliot et al., 2014; Cozzi et al., 2020).  
31 Such biases have limited our ability to meaningfully assess the effectiveness of protected  
32 areas in securing connectivity for their protected species.

33 One initiative that aims at restoring and enhancing connectivity across large scales is the  
34 Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA), which constitutes the

Reviewer  
one  
pointed  
out an  
awkward  
use of  
the word  
utmost.  
I have  
changed  
it accord-  
ing to his  
suggestion.

Reviewer  
1 pointed  
out cor-  
rectly that  
we should  
talk about  
available  
locations,  
rather  
than ran-  
domly se-  
lected lo-  
cations

35 world's largest transfrontier conservation area, spanning over 520'000 km<sup>2</sup> and five coun-  
36 tries ([www.kavangozambezi.org](http://www.kavangozambezi.org)). While the KAZA-TFCA was originally set to facilitate  
37 movements of African elephants (*Loxodonta africana*; Tshipa, 2017), it is also key to the con-  
38 servation of other wide-ranging species such as African wild dogs (*Lycaon pictus*; Woodroffe  
39 and Sillero-Zubiri, 2012; Cozzi et al., 2020), lions (*Panthera leo*; Elliot et al., 2014; Cushman  
40 et al., 2018), and cheetahs (*Acinonyx jubatus*; Weise et al., 2017). To date, however, few  
41 studies have attempted to assess the adequacy of the KAZA-TFCA using relevant global  
42 positioning system (GPS) relocation data of its protected species at the appropriate spatial  
43 scale (Elliot et al., 2014; Tshipa, 2017). Thus, how well the boundaries of the KAZA-TFCA  
44 reflect natural movement patterns and dispersal corridors of its most mobile protected species  
45 is virtually unknown.

46 Across the KAZA-TFCA, the African wild dog (*Lycaon pictus*) represents a highly mobile  
47 and endangered flagship species for conservation efforts. Once widespread across the entire  
48 Sub-Saharan continent, wild dogs have been widely extirpated through human persecution,  
49 habitat destruction, and disease outbreaks (Woodroffe and Sillero-Zubiri, 2012). As a result,  
50 the species has become one of Africa's most endangered large carnivores, and currently  
51 only survives in small, spatially scattered subpopulations (Woodroffe and Sillero-Zubiri,  
52 2012). Within these subpopulations, wild dogs form cooperative breeding packs of up to  
53 thirty individuals (Creel and Creel, 2002), whose social structure is strongly governed by the  
54 process of dispersal (McNutt, 1996; Behr et al., 2020). Both males and females disperse from  
55 their natal pack, either alone or in same-sex dispersing coalitions, and search for unrelated  
56 mates and a suitable territory to settle (McNutt, 1996; Cozzi et al., 2020; Behr et al., 2020).  
57 During dispersal, wild dogs can cover several hundred kilometers (Masenga et al., 2016;  
58 Woodroffe et al., 2019; Cozzi et al., 2020). Despite the importance of dispersal for the long-  
59 term viability of this species, little empirical information is available on habitat selection and  
60 potential movement barriers during dispersal. The few studies that have collected dispersal  
61 data have shown that dispersers quickly move over large distances, avoid human-dominated  
62 landscapes and areas densely covered by trees, but prefer proximity to water (Masenga et al.,  
63 2016; Woodroffe et al., 2019; O'Neill et al., 2020; Cozzi et al., 2020).

64 Here, we collected GPS relocation data on 16 dispersing wild dogs in as many dispersing  
65 coalitions from a free-ranging population in northern Botswana and analyzed it to assess the  
66 adequacy of the KAZA-TFCA in securing connectivity. We estimated the degree of selection  
67 or avoidance for environmental and anthropogenic landscape features and used the obtained  
68 habitat preferences to predict a permeability surface spanning the entire KAZA-TFCA. We

69 then investigated how landscape permeability varies regionally and internationally and com-  
70 pared permeability within and outside the KAZA-TFCA boundaries. Finally, we calculated  
71 least-cost paths and corridors to identify major movement routes and to verify that these  
72 are 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 of rain  
85 that descends from the catchment areas in Angola and reaches the distal ends of the delta  
86 between July and August (Figure S4). The flood drastically affects surrounding landscapes,  
87 so that during maximum extent (ca. 12'000 km<sup>2</sup>) the delta becomes a patchy conglomerate  
88 of swamps, open water, and islands, whereas these structures run dry when the flood re-  
89 tracts to its minimum extent (ca. 5'000 km<sup>2</sup>; Wolski et al., 2017). Despite 36 national parks  
90 (NPs) and other protected areas, there is considerable human influence in some regions of  
91 the KAZA-TFCA, mainly originating from farms, high human density, and road traffic.

### 92 **2.2 GPS Relocation Data**

93 We used a population of free-ranging African wild dogs inhabiting the Okavango Delta in  
94 northern Botswana as a source population for dispersing individuals. This population has  
95 been extensively studied since 1989 (McNutt, 1996; Cozzi et al., 2013, 2020; Behr et al.,  
96 2020). Between 2011 and 2019, we systematically collected GPS relocation data on 16 coali-  
97 tions of dispersing African wild dogs (7 female and 9 male coalitions). Candidate dispersing  
98 individuals were identified based on age, number of same-sex siblings, pack size, and pres-  
99 ence of unrelated individuals of the opposite sex in the pack (McNutt, 1996; Behr

100 et al., 2020). Individuals were immobilized according to protocols described in Osofsky  
101 et al. (1996), and fitted with GPS/Satellite radio collars (*Vertex Lite*; *Vetricnic Aerospace*  
102 *GmbH, Berlin, Germany*) while still with their natal pack. All procedures were undertaken  
103 and supervised by a Botswana-registered wildlife veterinarian. Fully assembled collars pro-  
104 duced a tag weight of approximately xx kg, which conforms to the proposed threshold of  
105 3% of an animal's body weight (Kenward, 2000). Collars were mounted using leather belts  
106 and included a drop off mechanism triggered by a slowly decomposing piece of cloth. During  
107 dispersal, GPS collars were programmed to record GPS relocation data every 4 hours and  
108 to regularly transmit them via Iridium satellite system to a base station.

109 Because we were interested in dispersal behavior only, we discarded any GPS data col-  
110 lected while individuals were still with their natal packs and after settlement in a new  
111 territory (Cozzi et al., 2020). We identified the exact time of emigration and settlement  
112 based on direct field observations and through visual inspection of the net squared displace-  
113 ment (NSD) metric. NSD quantifies the squared Euclidean distance of a relocation to a  
114 reference point (Börger and Fryxell, 2012), which in our case was the center of the dis-  
115 persing coalition's natal home range. Thus, dispersal was deemed to have started when a  
116 coalition had left its natal home range and continued until the NSD metric remained sta-  
117 tionary, implying that the coalition had successfully settled (Figure S1). In our analysis,  
118 we did not differentiate between male and female dispersing coalitions, for previous research  
119 found little differences between sexes during dispersal (Woodroffe et al., 2019; Cozzi et al.,  
120 2020).

### 121 2.3 Spatial Covariates

122 To investigate habitat preferences of dispersing wild dogs, we used a set of geo-referenced  
123 covariates (Figure 2) that we aggregated in the categories *land cover* (which included water  
124 cover, distance to water, shrubs/grassland cover, and tree cover), *protection status* (pro-  
125 tected vs. unprotected), and *human pressure* (which included human influence, presence of  
126 roads, and distance to roads). For each of these covariates we prepared spatial raster layers  
127 from freely available online services or from remotely sensed satellite imagery. To ensure a  
128 consistent resolution (i.e. cell-size or grain) across covariates, we coarsened or interpolated  
129 all layers to match a resolution of 250m x 250m. For further details on the preparation of  
130 each covariate, see Appendix A.3. We performed processing and manipulation of data as  
131 well as all spatial and statistical analyses using R, version 3.6.1 (R Core Team, 2019).

We origi-  
nally only  
pointed to  
Behr and  
did not in-  
clude the  
criteria.  
The edi-  
tor desired  
to include  
those

Editor de-  
sired more  
infor-  
ma-  
tion on  
GPS collar

Reviewer  
1 pointed  
out cor-  
rectly that  
we need  
to talk  
about the  
*squared*  
euclidean  
distance

132 **2.4 Habitat Selection Model**

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

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

146 The selection score  $w(x)$  of a step depended on its associated covariates  $(x_1, x_2, \dots, x_n)$ , as  
147 well as on the animal's relative selection strength for these covariates  $(\beta_1, \beta_2, \dots, \beta_n)$ . To  
148 estimate relative selection strengths (i.e. the  $\beta$ 's), we used mixed effects conditional logistic  
149 regression analysis as suggested by Muff et al. (2020). We implemented their method using  
150 the R-package *glmmTMB* (Brooks et al., 2017) and used dispersing coalition ID to model  
151 random intercepts and slopes. We defined two movement metrics, namely the cosine of the  
152 turning angle ( $\cos(ta)$ ) and the log of the step length ( $\log(sl)$ ), as core covariates and ran  
153 stepwise forward model selection based on Akaike's Information Criterion (AIC; Burnham  
154 and Anderson, 2002) for all other covariates. The inclusion of movement metrics served  
155 to reduce biases in estimated habitat preferences that may have arisen due to movement  
156 preferences (Avgar et al., 2016). To validate the predictive power of the most parsimonious  
157 habitat selection model, we ran k-fold cross-validation for case-control studies as described  
158 in Fortin et al. (2009) (details in Appendix A.5).

159 **2.5 Permeability Surface**

160 Using the most parsimonious habitat selection model, we predicted a permeability surface  
161 spanning the entire extent of the KAZA-TFCA. That is, we applied Equation 1 to our

Reviewer 1  
suggested  
to use rel-  
ative se-  
lection  
strength,  
rather  
than pref-  
erence

As per re-  
viewer 1

As per re-  
viewer 1

162 spatial covariates and calculated the selection score  $w(x)$  for each raster cell. Because  
163 our representation of water was dynamic (to properly render the pulsing behavior of the  
164 Okavango Delta) we collapsed all dynamic water maps into a single static map using areas  
165 that were covered by water in at least 10% of the cases. Using the resulting static map we  
166 also calculated a layer returning the distance to water. To reduce the influence of outliers  
167 in predicted permeability scores we followed Squires et al. (2013) and curtailed predicted  
168 scores between the 1<sup>st</sup> and 99<sup>th</sup> percentile of their original values. To compare permeability  
169 across different regions, we normalized the permeability surface to a range between 0 (most  
170 impermeable) and 1 (most permeable). We then determined median permeability within  
171 and outside the KAZA-TFCA, within and outside formally protected areas, and within each  
172 of the five KAZA-TFCA countries.

## 173 2.6 Least-Cost Paths and Corridors

174 To identify movement corridors of dispersing wild dogs, we specified source points and  
175 calculated factorial least-cost paths (LCPs) as well as factorial least-cost corridors (LCCs)  
176 among them (Elliot et al., 2014). We generated source points by overlaying the study area  
177 with a regular grid of points spaced at 100 km. We only considered those points that  
178 fell within protected areas  $> 700 \text{ km}^2$ , which conforms with home-range requirements of  
179 African wild dogs reported in Pomilia et al. (2015). Finally, we defined centroids as source  
180 points for those protected areas  $> 700 \text{ km}^2$  that were not assigned any source points from  
181 the regular grid. In total, we generated 68 source points, which resulted in 2'278 unique  
182 pairwise combinations and therefore 2'278 unique LCPs and LCCs. We computed factorial  
183 LCPs and LCCs between source points using the R-package *gdistance* (for further details see  
184 Appendix A.6). After computation, we tallied overlapping LCPs and LCCs, respectively,  
185 into single connectivity maps.

## 186 3 Results

### 187 3.1 Dispersal Events

188 In total, we collected 4'169 GPS relocations during dispersal (Figure S2 & Table S1), re-  
189 sulting in an average of 261 ( $SD = 207$ ) locations per dispersing coalition. Dispersers on  
190 dispersed on average for 48 days ( $SD = 44$ ), covered a mean euclidean distance of 54 km  
191 ( $SD = 71$ ) and a cumulative distance of 597 km ( $SD = 508$ ). One female coalition dispersed  
192 far east into the Hwange National Park and covered a cumulative distance of over

Editor  
desired a  
quick sum-  
mary of  
the disper-  
sal data.

193 360 km in under 9 days.

### 194 3.2 Habitat Selection Model

195 Our most parsimonious habitat selection model ( $\Delta AIC > 2$  than any alternative model;  
196 Table S4) retained the covariates *water*, *distance to water*, *trees*, *shrubs/grassland*, and  
197 *human influence*, beside the fixed covariates *cos(ta)* and *log(sl)* (Figure 3a). Parameter  
198 estimates showed that dispersing wild dogs moved in a directional and fast manner, as  
199 indicated by a positive selection for small turning angles, i.e. high *cos(ta)* ( $\beta = 0.14$ ; 95%  
200 CI = 0.07 to 0.21) and longer steps, i.e. high *log(sl)* ( $\beta = 0.06$ , 95% CI = 0.02 to 0.09).  
201 Dispersers avoided moving through water ( $\beta = -0.52$ , 95% CI -0.77 to -0.26) but selected  
202 for locations in its vicinity, although the latter effect was not significant ( $\beta = -0.32$ , 95% CI  
203 = -0.72 to 0.08). Dispersers avoided areas that were densely covered by trees ( $\beta = -0.31$ ,  
204 CI = -0.46 to -0.15) and preferred areas covered by shrubs/grassland ( $\beta = 0.25$ , 95% CI =  
205 0.07 to 0.42). Finally, dispersers avoided areas that were influenced by humans ( $\beta = -0.41$ ,  
206 95% CI = -0.78 to -0.05).

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

### 212 3.3 Permeability Surface

213 Our prediction of landscape permeability revealed substantial differences across regions in  
214 the study area (Figure 4). Comparisons of median permeability values (Table 1) showed  
215 that permeability inside the KAZA-TFCA is more than two times as high as permeability  
216 outside it. Permeability varies by country, with a five-fold permeability difference among  
217 them. Angola and Botswana are characterized by comparably highly permeable landscapes,  
218 Zimbabwe and Zambia are relatively impermeable, and Namibia ranges in between the two  
219 extremes (Table 1). Visual inspection of our covariate layers indicated that high permeability  
220 in Angola and Botswana is mainly caused by a combination of low human influences, low  
221 tree cover, high shrubs/grassland cover, and a close distance to water. Although swamps,  
222 wetlands, and permanent water themselves provide little permeability, their surroundings  
223 act as strong attractants to dispersers. The low permeability that characterizes Zambia and  
224 Zimbabwe, on the other hand, is mainly caused by substantial human influences. Albeit the

225 KAZA-TFCA covers most permeability hot-spots, several highly permeable regions remain  
226 uncovered by its borders. Across all countries, protected areas provide roughly double the  
227 permeability of unprotected landscapes (Table 1).

### 228 3.4 Least-Cost Paths & Least-Cost Corridors

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

## 248 4 Discussion

249 We used GPS relocation data collected on dispersing African wild dogs to investigate whether  
250 their main movement corridors are contained within the boundaries of the world's largest  
251 transboundary conservation area, namely the KAZA-TFCA. Our analysis suggests that the  
252 KAZA-TFCA indeed encompasses all major corridors of African wild dogs, demonstrating  
253 the potential value of such an initiative. We thus exemplified how pertinent dispersal data  
254 of a highly mobile species can be used to assess the adequacy of already existing or planned  
255 protected areas. Our approach is neither limited to the African wild dog, nor to our study  
256 area and thus applicable to any study system. All covariates used throughout this study are

readily available on a global scale and many of them are likely to be important determinants of movement behavior, landscape permeability, and connectivity for other species (Thurfjell et al., 2014; Zeller et al., 2012). Interestingly, our predicted network of least cost-paths and corridors for African wild dogs shows surprising similarities to corridors of dispersing lions inhabiting the same ecosystem (Elliot et al., 2014; Cushman et al., 2018). This not only reinforces confidence in our own predictions but also suggests potential synergies for the conservation of these two, and possibly more, species. Expanding our analytical framework to additional species will likely yield important insights on the consistency of inter-specific movement corridors, thus highlighting areas that are exceptionally valuable for the conservation of several species.

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

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

Although dispersers avoided moving through water, they selected locations in its vicinity. This preference may be caused by the occurrence of prey close to water (Bonyongo, 2005).

291 For the same reason, however, competitors such as lions, spotted hyenas, and resident wild  
292 dogs may also use areas close to water (Valeix et al., 2010), thereby occasionally forcing  
293 dispersing wild dogs to move into prey-poorer areas away from water. Given the influence  
294 that resident conspecifics, competitors, and prey can have on dispersers (Cozzi et al., 2018;  
295 Armansin et al., 2019) future studies should strive to collect and incorporate intra- and  
296 interspecific relationships into analyses of landscape connectivity.

297 Locally, we identified the Okavango-Linyanti region as a potential dispersal hub through  
298 which dispersing wild dogs gain access to more peripheral regions of the KAZA-TFCA. It  
299 appears that the absence of human activities, the central position within the KAZA-TFCA,  
300 and the presence of relatively impermeable water bodies (e.g. Okavango Delta, Linyanti  
301 Swamp) funnel dispersal movements, resulting in a highly frequented corridor. The key  
302 role of the Okavango-Linyanti region for overall connectivity within the KAZA-TFCA thus  
303 calls for actions to secure its protection status in the future. While the region is currently  
304 a Wildlife Management Area, it has neither the status of a National Park nor that of a  
305 Game Reserve. A similar case of non-formally protected but key dispersal landscape is  
306 represented by the area south of Kafue NP in Zambia, for which a disruption of its main  
307 and narrow dispersal corridor would result in considerable isolation of its subpopulations.  
308 We also revealed a potential southwards corridor between the Okavango-Linyanti ecosystem  
309 and the Central Kalahari National Park. Elliot et al. (2014) and Cushman et al. (2018)  
310 identified a similar corridor for dispersing lions, suggesting that upholding and protecting a  
311 link between those ecosystems is pivotal. Some areas through which the corridor runs are  
312 neither part of the KAZA-TFCA nor profit from any form of protection status. In fact,  
313 human presence and activities along the national road that longitudinally traverses this  
314 corridor may limit realized connectivity (Cozzi et al., 2020).

315 Our approach of identifying movement corridors based on pre-defined start and end  
316 points implicitly assumes that individuals know the end point of their dispersal journey and  
317 that they have almost complete knowledge of associated movement costs (Panzacchi et al.,  
318 2016). Since dispersers often move into unknown territory, this may not necessarily be the  
319 case (Abrahms et al., 2017; Cozzi et al., 2020). However, specification of pre-defined end  
320 points might not be necessary, as the parametrized iSSF model can be used as mechanistic  
321 movement model to simulate dispersal events from known source points, yet without re-  
322 stricting the domain of potential end points (Signer et al., 2017). Consequently, movement  
323 corridors would emerge more naturally as the result of a myriad of simulated dispersal events.  
324 While a simulation-based approach is conceptually straightforward, it requires a comprehen-

325 sive mechanistic understanding of dispersal movements, which is conditional on our ability  
326 to collect additional dispersal data and adequately represent the landscape through which  
327 individuals move.

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

to in-  
stead of  
t, pointed  
out by the  
editor and  
reviewer 1

## 342 5 Authors' Contributions

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

## 348 6 Data Availability

349 GPS movement data of dispersing coalitions will be made available on dryad at the time of  
350 publication.

## 351 7 Acknowledgements

352 We thank the Ministry of Environment and Tourism of Botswana for granting permission  
353 to conduct this research. We thank C. Botes, I. Clavadetscher, and G. Camenisch for

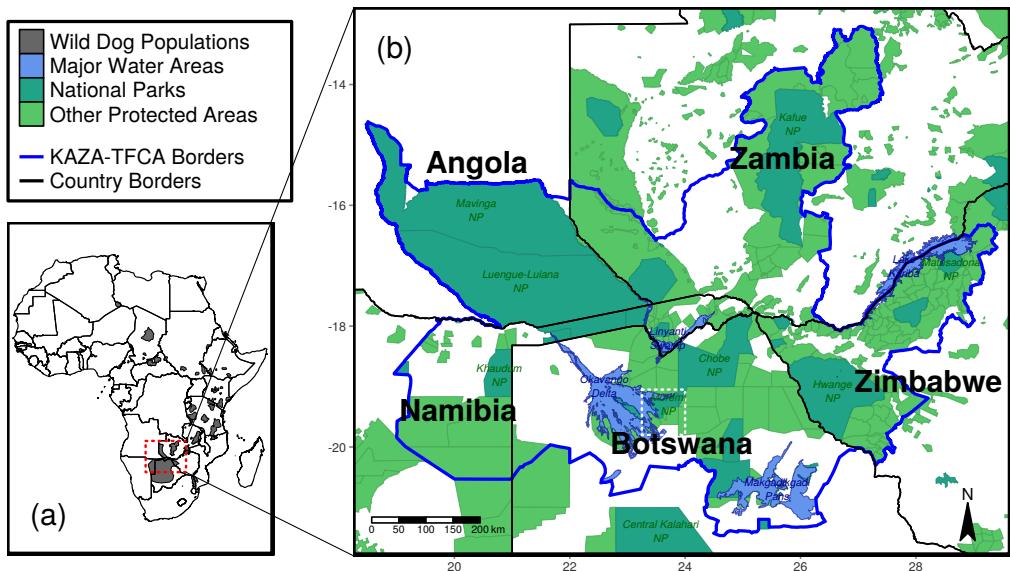
354 assisting with wild dog immobilizations. We also thank B. Abrahms for sharing her data  
355 of three dispersing wild dogs. Furthermore, we are indebted to Prof. J. Fieberg, who  
356 consulted all statistical aspects of this work and P. Wolski, from the Okavango Research  
357 Institute, who assisted us in generating dynamic water maps. This study was funded by  
358 Basler Stiftung für Biologische Forschung, Claraz Foundation, Idea Wild, Jacot Foundation,  
359 National Geographic Society, Parrotia Stiftung, Stiftung Temperatio, Wilderness Wildlife  
360 Trust Foundation, Forschungskredit der Universität Zürich, and a Swiss National Science  
361 Foundation Grant (31003A\_182286) to A. Ozgul.

## 362 References

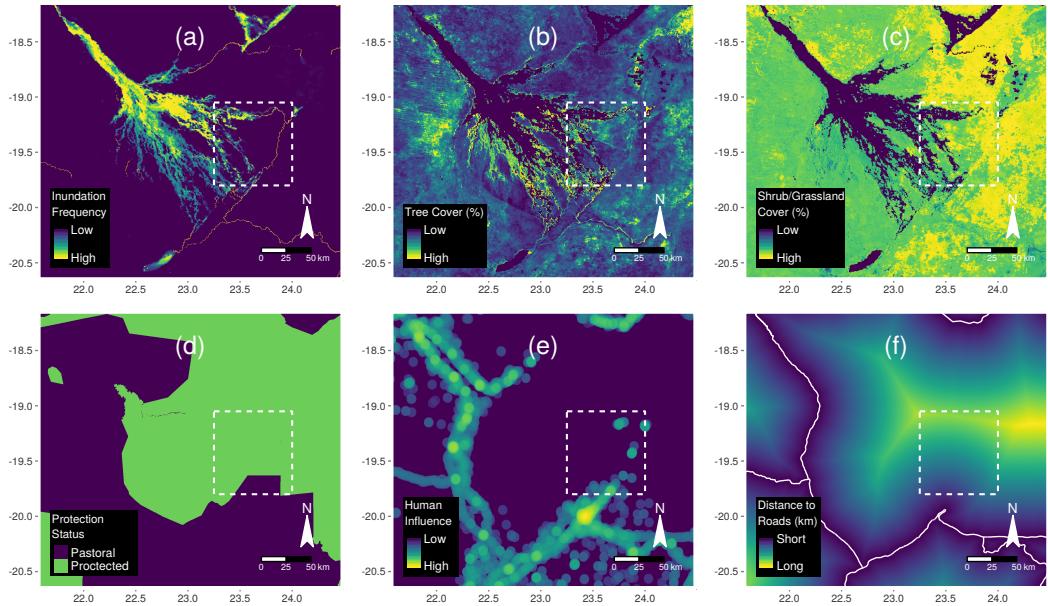
- 363 Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., and Brashares,  
364 J. S. (2017). Does Wildlife Resource Selection Accurately Inform Corridor Conservation?  
365 *Journal of Applied Ecology*, 54(2):412–422.
- 366 Armansin, N. C., Stow, A. J., Cantor, M., Leu, S. T., Klarevas-Irby, J. A., Chariton, A. A.,  
367 and Farine, D. R. (2019). Social Barriers in Ecological Landscapes: The Social Resistance  
368 Hypothesis. *Trends in Ecology & Evolution*, pages 137–148.
- 369 Avgar, T., Potts, J. R., Lewis, M. A., and Boyce, M. S. (2016). Integrated Step Selection  
370 Analysis: Bridging the Gap Between Resource Selection and Animal Movement. *Methods  
371 in Ecology and Evolution*, 7(5):619–630.
- 372 Behr, D. M., McNutt, J. W., Ozgul, A., and Cozzi, G. (2020). When to Stay and When  
373 to Leave? Proximate Causes of Dispersal in an Endangered Social Carnivore. *Journal of  
374 Animal Ecology*. In press.
- 375 Bonyongo, C. M. (2005). Habitat Utilization by Impala (*Aepyceros memmatus*) in the Oka-  
376 vango Delta. *Botswana Notes & Records*, 37(1):227–235.
- 377 Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen,  
378 A., Skaug, H. J., Maechler, M., and Bolker, B. M. (2017). glmmTMB Balances Speed and  
379 Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling. *The R  
380 Journal*, 9(2):378–400.
- 381 Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A  
382 Practical Information-Theoretic Approach*. Springer Science & Business Media, Ney York,  
383 NY, USA.
- 384 Börger, L. and Fryxell, J. (2012). Quantifying Individual Differences in Dispersal Using Net  
385 Squared Displacement. In Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M.,  
386 editors, *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.
- 387 Chetkiewicz, C.-L. B., St. Clair, C. C., and Boyce, M. S. (2006). Corridors for Conservation:  
388 Integrating Pattern and Process. *Annual Review of Ecology, Evolution, and Systematics*,  
389 37(1):317–342.
- 390 Clevenger, A. P., Wierzchowski, J., Chruszcz, B., and Gunson, K. (2002). GIS-Generated,  
391 Expert-Based Models for Identifying Wildlife Habitat Linkages and Planning Mitigation  
392 Passages. *Conservation Biology*, 16(2):503–514.
- 393 Cozzi, G., Behr, D. M., Webster, H. S., Claase, M., Bryce, C. M., Modise, B., Mcnutt, J. W.,  
394 and Ozgul, A. (2020). African Wild Dog Dispersal and Implications for Management. *The  
395 Journal of Wildlife Management*, 84(4):614–621.
- 396 Cozzi, G., Broekhuis, F., McNutt, J. W., and Schmid, B. (2013). Comparison of the Effects of  
397 Artificial and Natural Barriers on Large African Carnivores: Implications for Interspecific  
398 Relationships and Connectivity. *Journal of Animal Ecology*, 82(3):707–715.
- 399 Cozzi, G., Maag, N., Börger, L., Clutton-Brock, T. H., and Ozgul, A. (2018). Socially  
400 Informed Dispersal in a Territorial Cooperative Breeder. *Journal of Animal Ecology*,  
401 87(3):838–849.
- 402 Creel, S. and Creel, N. M. (2002). *The African Wild Dog: Behavior, Ecology, and Conser-  
403 vation*. Princeton University Press, Princeton, NJ, USA.
- 404 Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el din, L., Bothwell, H., Flyman,  
405 M., Mtare, G., Macdonald, D. W., and Loveridge, A. J. (2018). Prioritizing Core Areas,  
406 Corridors and Conflict Hotspots for Lion Conservation in Southern Africa. *PLOS ONE*,  
407 13(7):e0196213.

- 408 Davies-Mostert, H. T., Kamler, J. F., Mills, M. G. L., Jackson, C. R., Rasmussen, G. S. A.,  
409 Groom, R. J., and Macdonald, D. W. (2012). Long-Distance Transboundary Dispersal  
410 of African Wild Dogs among Protected Areas in Southern Africa. *African Journal of  
411 Ecology*, 50(4):500–506.
- 412 Diniz, M. F., Cushman, S. A., Machado, R. B., and De Marco Júnior, P. (2019). Landscape  
413 Connectivity Modeling From the Perspective of Animal Dispersal. *Landscape Ecology*,  
414 (35):41–58.
- 415 Doerr, V. A. J., Barrett, T., and Doerr, E. D. (2011). Connectivity, Dispersal Behaviour  
416 and Conservation under Climate Change: A Response to Hodgson et al.: Connectivity  
417 and Dispersal Behaviour. *Journal of Applied Ecology*, 48(1):143–147.
- 418 Elliot, N. B., Cushman, S. A., Macdonald, D. W., and Loveridge, A. J. (2014). The Devil  
419 is in the Dispersers: Predictions of Landscape Connectivity Change with Demography.  
420 51(5):1169–1178.
- 421 Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of  
422 Ecology, Evolution, and Systematics*, 34(1):487–515.
- 423 Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., and Mao, J. S. (2005).  
424 Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone  
425 National Park. *Ecology*, 86(5):1320–1330.
- 426 Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., and Dancose, K. (2009).  
427 Group-Size-Mediated Habitat Selection and Group Fusion–Fission Dynamics of Bison  
428 under Predation Risk. *Ecology*, 90(9):2480–2490.
- 429 Kenward, R. E. (2000). *A Manual for Wildlife Radio Tagging*. Academic Press.
- 430 Latham, A. D. M., Latham, M. C., Boyce, M. S., and Boutin, S. (2011). Movement Re-  
431 sponses by Wolves to Industrial Linear Features and Their Effect on Woodland Caribou  
432 in Northeastern Alberta. *Ecological Applications*, 21(8):2854–2865.
- 433 Masenga, E. H., Jackson, C. R., Mjingo, E. E., Jacobson, A., Riggio, J., Lyamuya, R. D.,  
434 Fyumagwa, R. D., Borner, M., and Røskraft, E. (2016). Insights into Long-Distance  
435 Dispersal by African Wild Dogs in East Africa. *African Journal of Ecology*, 54(1):95–98.
- 436 McNutt, J. (1996). Sex-Biased Dispersal in African Wild Dogs (*Lycaon pictus*). *Animal  
437 Behaviour*, 52(6):1067–1077.
- 438 Muff, S., Signer, J., and Fieberg, J. (2020). Accounting for Individual-Specific Variation in  
439 Habitat-Selection Studies: Efficient Estimation of Mixed-Effects Models Using Bayesian  
440 or Frequentist Computation. *Journal of Animal Ecology*, 89(1):80–92.
- 441 O'Neill, H. M. K., Durant, S. M., and Woodroffe, R. (2020). What Wild Dogs Want: Habitat  
442 Selection Differs across Life Stages and Orders of Selection in a Wide-Ranging Carnivore.  
443 *BMC Zoology*, 5(1).
- 444 Osofsky, S. A., McNutt, J. W., and Hirsch, K. J. (1996). Immobilization of Free-Ranging  
445 African Wild Dogs (*Lycaon pictus*) Using a Ketamine/xylazine/Atropine Combination.  
446 *Journal of Zoo and Wildlife Medicine*, 27(4):528–532.
- 447 Palomares, F., Delibes, M., Ferreras, P., Fedriani, J. M., Calzada, J., and Revilla, E. (2000).  
448 Iberian Lynx in a Fragmented Landscape: Predispersal, Dispersal, and Postdispersal  
449 Habitats. *Conservation Biology*, 14(3):809–818.
- 450 Panzacchi, M., Van Moorter, B., Strand, O., Saerens, M., Kivimäki, I., St. Clair, C. C.,  
451 Herfindal, I., and Boitani, L. (2016). Predicting the Continuum Between Corridors and  
452 Barriers to Animal Movements Using Step Selection Functions and Randomized Shortest  
453 Paths. *Journal of Animal Ecology*, 85(1):32–42.

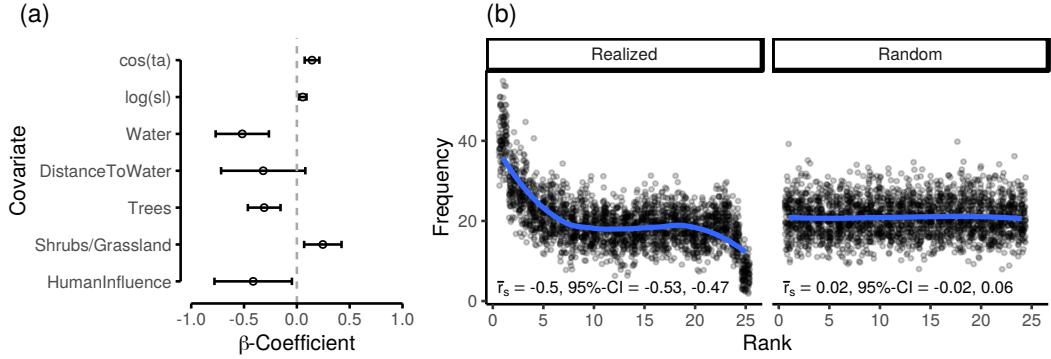
- 454 Pomilia, M. A., McNutt, J. W., and Jordan, N. R. (2015). Ecological Predictors of African  
455 Wild Dog Ranging Patterns in Northern Botswana. *Journal of Mammalogy*, 96(6):1214–  
456 1223.
- 457 Pullinger, M. G. and Johnson, C. J. (2010). Maintaining or Restoring Connectivity of  
458 Modified Landscapes: Evaluating the Least-Cost Path Model with Multiple Sources of  
459 Ecological Information. *Landscape Ecology*, 25(10):1547–1560.
- 460 R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foun-  
461 dation for Statistical Computing, Vienna, Austria.
- 462 Rudnick, D., Ryan, S., Beier, P., Cushman, S., Dieffenbach, F., Epps, C., Gerber, L., Hart-  
463 ter, J., Jenness, J., Kintsch, J., Merenlender, A., Perkl, R., Perziosi, D., and Trombulack,  
464 S. (2012). The Role of Landscape Connectivity in Planning and Implementing Conserva-  
465 tion and Restoration Priorities. *Issues in Ecology*, 16.
- 466 Sawyer, S. C., Epps, C. W., and Brashares, J. S. (2011). Placing Linkages among Fragmented  
467 Habitats: Do Least-Cost Models Reflect How Animals Use Landscapes? *Journal of*  
468 *Applied Ecology*, 48(3):668–678.
- 469 Signer, J., Fieberg, J., and Avgar, T. (2017). Estimating Utilization Distributions from  
470 Fitted Step-Selection Functions. *Ecosphere*, 8(4):e01771.
- 471 Squires, J. R., DeCesare, N. J., Olson, L. E., Kolbe, J. A., Hebblewhite, M., and Parks, S. A.  
472 (2013). Combining Resource Selection and Movement Behavior to Predict Corridors for  
473 Canada Lynx at their Southern Range Periphery. *Biological Conservation*, 157:187–195.
- 474 Thurfjell, H., Ciuti, S., and Boyce, M. S. (2014). Applications of Step-Selection Functions  
475 in Ecology and Conservation. *Movement Ecology*, 2(4).
- 476 Tshipa, A. (2017). Partial Migration Links Local Surface-Water Management to Large-Scale  
477 Elephant Conservation in the World's Largest Transfrontier Conservation Area. *Biological*  
478 *Conservation*, 215:46–50.
- 479 Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population*  
480 *Redistribution in Plants and Animals*. Sinauer Associates, Sunderland, MA, USA.
- 481 Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., and Macdonald, D. W.  
482 (2010). How Key Habitat Features Influence Large Terrestrial Carnivore Movements: Wa-  
483 terholes and African Lions in a Semi-Arid Savanna of North-Western Zimbabwe. *Landscape*  
484 *Ecology*, 25(3):337–351.
- 485 Vasudev, D., Fletcher, R. J., Goswami, V. R., and Krishnadas, M. (2015). From Disper-  
486 sal Constraints to Landscape Connectivity: Lessons from Species Distribution Modeling.  
487 *Ecography*, 38(10):967–978.
- 488 Weise, F. J., Vijay, V., Jacobson, A. P., Schoonover, R. F., Groom, R. J., Horgan, J.,  
489 Keeping, D., Klein, R., Marnewick, K., Maude, G., Melzheimer, J., Mills, G., Merwe,  
490 V. v. d., Meer, E. v. d., Vuuren, R. J. v., Wachter, B., and Pimm, S. L. (2017). The  
491 Distribution and Numbers of Cheetah (*Acinonyx jubatus*) in Southern Africa. *PeerJ*,  
492 5:e4096.
- 493 Wolski, P., Murray-Hudson, M., Thito, K., and Cassidy, L. (2017). Keeping it Simple:  
494 Monitoring Flood Extent in Large Data-Poor Wetlands Using MODIS SWIR Data. *In-*  
495 *ternational Journal of Applied Earth Observation and Geoinformation*, 57:224–234.
- 496 Woodroffe, R., Rabaiotti, D., Ngatia, D. K., Smallwood, T. R. C., Strelbel, S., and O'Neill,  
497 H. M. K. (2019). Dispersal Behaviour of African Wild Dogs in Kenya. *African Journal*  
498 *of Ecology*, 58(1):46–57.
- 499 Woodroffe, R. and Sillero-Zubiri, C. (2012). *Lycaon pictus*. *The IUCN Red List of Threatened*  
500 *Species*, 2012:e. T12436A16711116.
- 501 Zeller, K. A., McGarigal, K., and Whiteley, A. R. (2012). Estimating Landscape Resistance  
502 to Movement: A Review. *Landscape Ecology*, 27(6):777–797.



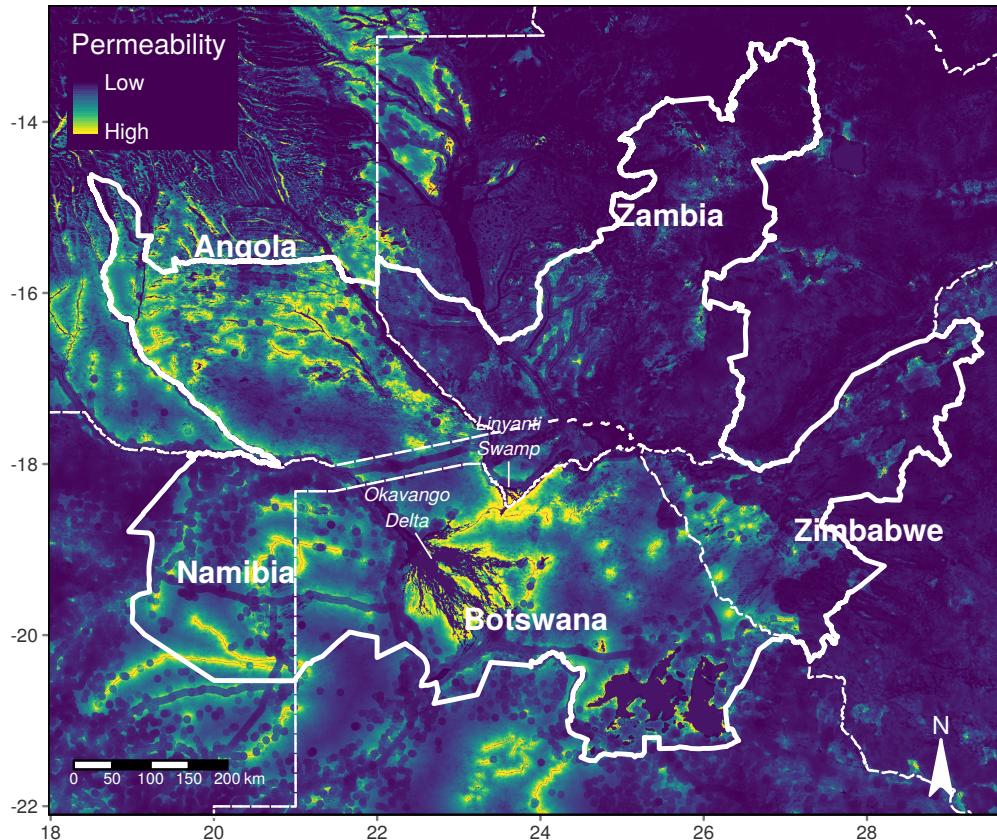
**Figure 1:** Overview of our study area. (a) The red dotted rectangle depicts the study area, which was confined by a bounding box encompassing the entire KAZA-TFCA. Gray areas indicate remaining wild dog populations according to the IUCN (Woodroffe and Sillero-Zubiri, 2012). (b) The white rectangle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



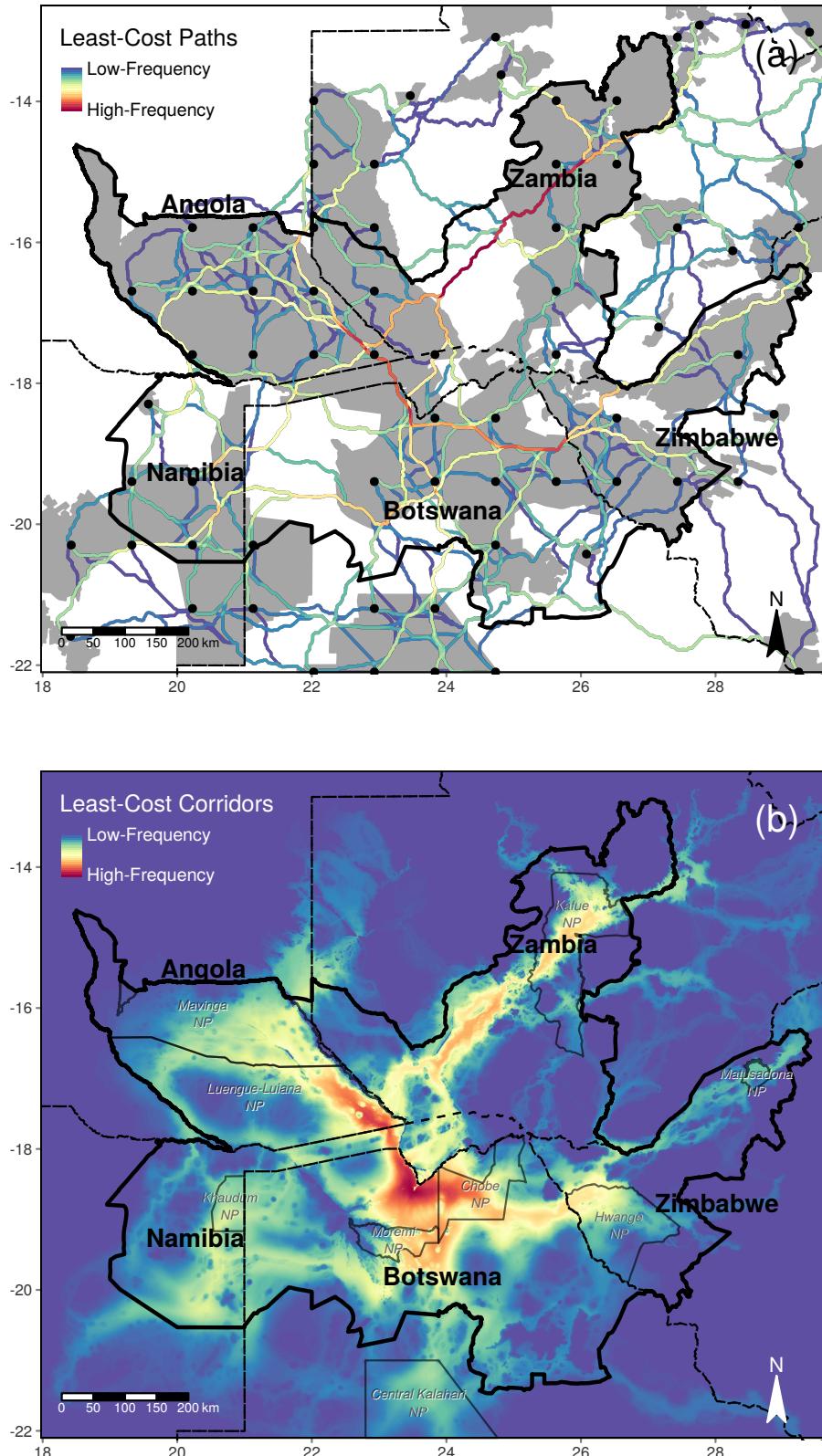
**Figure 2:** Overview of spatial covariates that we included in our models. We prepared all covariates for the entire study area but for better visibility we only plot them for the surroundings of the Okavango Delta. The white rectangle in each plot depicts the area within which dispersing coalitions 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. (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 habitat preferences ( $\beta_i$ ). 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 (light grey). 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	0.36 (0.41)	0.12 (0.32)	0.36 (0.41)	0.12 (0.33)	0.20 (0.39)
Botswana	0.25 (0.30)	0.15 (0.16)	0.28 (0.35)	0.15 (0.18)	0.19 (0.25)
Namibia	0.22 (0.30)	0.13 (0.18)	0.24 (0.30)	0.11 (0.15)	0.16 (0.24)
Zambia	0.05 (0.09)	0.03 (0.06)	0.04 (0.10)	0.03 (0.05)	0.03 (0.07)
Zimbabwe	0.07 (0.16)	0.06 (0.05)	0.08 (0.17)	0.05 (0.05)	0.06 (0.07)
Overall	0.16 (0.30)	0.07 (0.15)	0.15 (0.30)	0.07 (0.15)	0.10 (0.22)