

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

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September 10, 2020

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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 an increasingly used strategy to maintain and restore connectivity among wildlife populations. Boundaries of such conservation areas are often determined based on expert opinion and socio-political constraints, yet the extent to which they match species' movement corridors is rarely examined. This is mainly due to a lack of data, particularly on wide-ranging movement behavior such as dispersal. Nevertheless, empirically assessing the adequacy of protected areas is key for the implementation of targeted management actions and efficient use of limited conservation funds.
2. Between 2011 and 2019, we collected high-resolution GPS movement data on 16 dispersing African wild dog (*Lycaon pictus*) coalitions from a free-ranging population in the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). Spanning five countries and 520'000 km² the KAZA-TFCA is the world's largest transboundary conservation area and a prime example for international conservation efforts. We used integrated step selection analysis to estimate habitat selection of dispersers and to create a permeability surface for the entire KAZA-TFCA. We compared landscape permeability across different regions within the KAZA-TFCA as well as outside its boundaries. Lastly, we calculated least-cost paths and corridors to verify that major movement routes were adequately encompassed within the KAZA-TFCA.
3. Permeability within the boundaries of the KAZA-TFCA was more than double compared to areas outside it. Furthermore, we observed a five-fold permeability difference among the five KAZA-TFCA countries. We also showed that major movement corridors of wild dogs run within the KAZA-TFCA, although some minor routes remained outside formally protected areas.
4. Differences in permeability were mainly related to different degrees of human activities across regions, and to the presence or absence of rivers, swamps or open water. The relation between permeability and other landscape features was less evident.
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.

Editor indicated that the relationships are correlative and not necessarily causal.

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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). The use of relocation data has shifted the focus
15 from a structural to a functional view on connectivity, taking into account how species
16 respond to environmental features (Taylor et al., 2006; Fattebert et al., 2015). Identification
17 of potential movement corridors typically relies on the estimation of permeability surfaces,
18 which return the ease or willingness at which the focal species traverses a specific landscape
19 (Sawyer et al., 2011). Such surfaces are created based on species' relative selection strengths
20 (Avgar et al., 2017), which can be quantified using a suite of selection functions (Zeller et al.,
21 2012). Specifically, selection strengths are estimated by comparing spatial covariates (e.g.
22 environmental and anthropogenic) at locations visited by the animal to the same spatial
23 covariates at locations available to the animal (Zeller et al., 2012). Importantly, selection
24 functions rely on adequate landscape and relocation data that are representative of the
25 process being studied (Diniz et al., 2019). Although selection during residence and dispersal
26 may coincide (Fattebert et al., 2015), it appears that relocation data collected on dispersing
27 individuals outperforms data collected on resident individuals in the detection of large-scale
28 movement corridors (Elliot et al., 2014; Diniz et al., 2019). Nevertheless, dispersal data is
29 inherently difficult to collect and remains scarce in the connectivity literature (Vasudev et al.,
30 2015). As such, most permeability surfaces upon which movement corridors are identified
31 are created using relocation data collected on resident individuals. This has likely limited
32 our ability to meaningfully assess the effectiveness of protected areas in securing functional
33 connectivity for their protected species.

34 One initiative that aims at restoring and enhancing connectivity across large scales is the

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35 Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA), which constitutes the
36 world's largest transfrontier conservation area, spanning over 520'000 km² and five coun-
37 tries (www.kavangozambezi.org). While the KAZA-TFCA was originally set to facilitate
38 movements of African elephants (*Loxodonta africana*; Tshipa, 2017), it is also key to the con-
39 servation of other wide-ranging species such as African wild dogs (*Lycaon pictus*; Woodroffe
40 and Sillero-Zubiri, 2012; Cozzi et al., 2020), lions (*Panthera leo*; Elliot et al., 2014; Cushman
41 et al., 2018), and cheetahs (*Acinonyx jubatus*; Weise et al., 2017). To date, however, few
42 studies have attempted to assess the adequacy of the KAZA-TFCA using relevant global
43 positioning system (GPS) relocation data of its protected species at large spatial scales (El-
44 liot et al., 2014; Tshipa, 2017). Thus, how well the boundaries of the KAZA-TFCA reflect
45 natural movement patterns and dispersal corridors of its most mobile protected species is
46 virtually unknown.

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

66 Here, we collected and analyzed GPS relocation data on 16 dispersing wild dogs in as
67 many dispersing coalitions from a free-ranging population in northern Botswana to assess
68 the adequacy of the KAZA-TFCA in securing connectivity. We estimated relative selec-

69 tion strengthstowards environmental and anthropogenic landscape features, and used the reviewer 1
70 obtained coefficients to predict a permeability surface spanning the entire KAZA-TFCA.
71 We then investigated how landscape permeability varied regionally and internationally, and
72 we compared permeability within and outside the KAZA-TFCA boundaries. Finally, we
73 calculated least-cost paths and corridors to identify major movement routes and to verify
74 that these were successfully covered by the KAZA-TFCA.

75 **2 Methods**

76 **2.1 Study Area**

77 The study area (centered at $-17^{\circ}13'9''S$, $23^{\circ}56'4''E$; Figure 1a) was outlined by a rectangu-
78 lar bounding box stretching over 1.3 Mio km² and encompassing the entire KAZA-TFCA
79 (Figure 1b). The KAZA-TFCA lies in the basins of the Okavango and Zambezi rivers and
80 includes parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia. With a total area of
81 over 520'000 km² it constitutes the earth's largest transboundary conservation area and is
82 characterized by diverse landscapes, including savanna, grassland, and dry or moist wood-
83 land habitats. Rainfall in the study area is seasonal and lasts from November to March.
84 The KAZA-TFCA also comprises the Okavango Delta, which represents a highly dynamic
85 hydrological flood-pulsing system (McNutt, 1996; Wolski et al., 2017). The extent of the
86 flood in the delta greatly changes within and between years, depending on the amount
87 of rain that descends from the catchment areas in Angola and reaches the distal ends of
88 the delta between July and August (Figure S4). The flood drastically affects surrounding
89 landscapes, so that during maximum extent (ca. 12'000 km²) the delta becomes a patchy
90 conglomerate of swamps, open water, and islands, whereas these structures run dry when
91 the flood retracts to its minimum extent (ca. 5'000 km²; Wolski et al., 2017). Despite 36
92 national parks (NPs) and other protected areas, there is considerable human influence in
93 some regions of the KAZA-TFCA, mainly originating from farms, human density, and road
94 traffic.

95 **2.2 GPS Relocation Data**

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

100 tions of dispersing African wild dogs (7 female and 9 male coalitions). Candidate dispersing
101 individuals were identified based on age, number of same-sex siblings, pack size, and pres-
102 ence of unrelated individuals of the opposite sex in their pack (McNutt, 1996; Behr et al.,
103 2020). Selected individuals were immobilized according to protocols described in Osofsky
104 et al. (1996), and fitted with GPS/Satellite radio collars (*Vertex Lite*; *Vectronic Aerospace*
105 *GmbH, Berlin, Germany*) while still with their natal pack. All required procedures were
106 undertaken and supervised by a Botswana-registered wildlife veterinarian. Collars produced
107 a tag weight of 300 grammes, accounting for 1.2% of a wild dog's average body weight. They
108 were attached using leather belts that included a drop off mechanism, triggered by a de-
109 composing piece of cloth. During dispersal, GPS collars were programmed to record a GPS
110 relocation every 4 hours and to regularly transmit data via Iridium satellite system to a
111 base station.

112 Because we were interested in dispersal behavior only, we discarded any GPS data col-
113 lected while individuals were still with their natal packs and after settlement in a new
114 territory (Cozzi et al., 2020). We identified the exact time of emigration and settlement
115 based on direct field observations and through visual inspection of the net squared displace-
116 ment (NSD) metric. NSD quantifies the squared Euclidean distance of a relocation to a
117 reference point (Börger and Fryxell, 2012), which in our case was the center of the dis-
118 persing coalition's natal home range. Thus, dispersal was deemed to have started when a
119 coalition had left its natal home range and continued until the NSD metric remained sta-
120 tionary, indicating that the coalition had successfully settled (Figure S1). In our analysis,
121 we did not differentiate between male and female dispersing coalitions, for previous research
122 found little differences between sexes during dispersal (Woodroffe et al., 2019; Cozzi et al.,
123 2020).

124 2.3 Spatial Covariates

125 To investigate relative selection strengths of dispersing wild dogs, we used a set of geo-
126 referenced covariates (Figure 2) that we aggregated in the categories *land cover*, *protection*
127 *status*, and *human influence*. Land cover comprised the covariates water cover, distance to
128 water, percentage cover by shrubs/grassland, and percentage cover by trees. To capture
129 the pulsing behavior of the Okavango Delta, we frequently updated layers for water cover
130 and corresponding layers depicting distance to water. Protection status contained a binary
131 indicator of whether an area was protected or not. Human influence included covariates
132 rendering human density, the presence of roads, and the distance to roads. We prepared all

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

139 2.4 Habitat Selection Model

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

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

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

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164 in estimated habitat selection coefficients that may have arisen due to movement behavior
165 (Avgar et al., 2016). To validate the predictive power of the most parsimonious habitat
166 selection model, we ran k-fold cross-validation for case-control studies as described in Fortin
167 et al. (2009) (details in Appendix A.5).

168 2.5 Permeability Surface

169 Using the most parsimonious habitat selection model, we predicted a permeability surface
170 spanning the entire extent of the KAZA-TFCA. That is, we applied Equation 1 to our
171 spatial covariates and calculated the selection score $w(x)$ for each raster cell. Because
172 our representation of water was dynamic (to properly render the pulsing behavior of the
173 Okavango Delta) we collapsed all dynamic water maps into a single static map using areas
174 that were covered by water in at least 10% of the cases. Using the resulting static map
175 we also calculated a layer returning the distance to water. Because the extent of the delta
176 covers merely 6% of the entire KAZA-TFCA, the use of static maps should introduce little
177 bias in predicted permeability. To reduce the influence of outliers in predicted permeability
178 scores, we followed Squires et al. (2013) and curtailed predicted scores between the 1st and
179 99th percentile of their original values. To compare permeability across different regions,
180 we normalized the permeability surface to a range between 0 (most impermeable) and 1
181 (most permeable), and we determined median permeability within and outside the KAZA-
182 TFCA, within and outside formally protected areas, and within each of the five KAZA-TFCA
183 countries.

184 2.6 Least-Cost Paths and Corridors

185 To identify movement corridors of dispersing wild dogs, we specified source points and
186 calculated factorial least-cost paths (LCPs) as well as factorial least-cost corridors (LCCs)
187 among them (Elliot et al., 2014). We generated source points by overlaying the study area
188 with a regular grid of points spaced at 100 km. We only considered those points that fell
189 within protected areas $> 700 \text{ km}^2$, which conforms with home-range requirements of African
190 wild dogs (Pomilia et al., 2015). Finally, we defined centroids as source points for those
191 protected areas $> 700 \text{ km}^2$ that were not assigned any source points from the regular grid.
192 Because wild dogs residing outside of protected areas are rare and likely unviable (Van der
193 Meer et al., 2014), we consider our selection of source points within protected areas to
194 be appropriate. In total, we generated 68 source points, which resulted in 2'278 unique
195 pairwise combinations and therefore 2'278 unique LCPs and LCCs. We computed factorial

¹⁹⁶ LCPs and LCCs between source points using the R-package *gdistance* (further details in
¹⁹⁷ Appendix A.7). After computation, we tallied overlapping LCPs and LCCs, respectively,
¹⁹⁸ into single connectivity maps.

¹⁹⁹ 3 Results

²⁰⁰ 3.1 Dispersal Events

²⁰¹ In total, we collected 4'169 GPS relocations during dispersal (Figure S2 & Table S1), re-
²⁰² sulting in an average of 261 ($SD = 207$) locations per dispersing coalition. Coalitions on
²⁰³ average dispersed for 48 days ($SD = 44$), covered a mean Euclidean distance of 54 km (SD
²⁰⁴ = 71) and a cumulative distance of 597 km ($SD = 508$). One female coalition dispersed far
²⁰⁵ east into the Hwange National Park and covered a cumulative distance of over 360
²⁰⁶ km in under 9 days.

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²⁰⁷ 3.2 Habitat Selection Model

²⁰⁸ Our most parsimonious habitat selection model ($\Delta AIC > 2$ than any alternative model;
²⁰⁹ Table S4) retained the covariates *water*, *distance to water*, *trees*, *shrubs/grassland*, and
²¹⁰ *human influence*, beside the fixed covariates *cos(ta)*, *sl*, and *log(sl)* (Figure 3a). The pos-
²¹¹ itive coefficients for *sl* ($\beta = 0.03$, 95% CI = -0.09 to 0.15) and *log(sl)* ($\beta = 0.12$, 95% CI
²¹² = 0.02 to 0.22) indicated that our initial (selection-biased) gamma distribution produced
²¹³ step-lengths slightly shorter than a selection-free gamma distribution would. Similarly, the
²¹⁴ positive coefficient for *cos(ta)* ($\beta = 0.10$; 95% CI = 0.05 to 0.15) suggested that our uniform
²¹⁵ distribution for turning angles produced turning angles with too little directionality. With
²¹⁶ respect to environmental covariates, dispersers avoided moving through water ($\beta = -0.53$,
²¹⁷ 95% CI -0.79 to -0.27) but selected for locations in its vicinity, although the latter effect
²¹⁸ was not significant ($\beta = -0.33$, 95% CI = -0.73 to 0.08). Dispersers avoided areas that were
²¹⁹ densely covered by trees ($\beta = -0.31$, CI = -0.47 to -0.15) and preferred areas covered by
²²⁰ shrubs/grassland ($\beta = 0.25$, 95% CI = 0.07 to 0.42). Finally, dispersers avoided areas that
²²¹ were influenced by humans ($\beta = -0.45$, 95% CI = -0.82 to -0.08). With the exception of
²²² *distance to water* ($SD_{RE} = 0.57$), random effects revealed little variability between different
²²³ dispersal coalitions' selection strengths (i.e. all with $SD_{RE} \leq 0.22$, Figure S7).

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²²⁴ Results from the k-fold cross-validation suggested that our prediction was significant and
²²⁵ robust, as highlighted by the fact that the 95%-CIs intervals of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ did
²²⁶ not overlap (Figure 3b). Likewise, the significant correlation between ranks and correspond-

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²²⁷ ing frequencies for realized steps suggested a good fit between predictions and observations
²²⁸ (Figure 3b).

²²⁹ **3.3 Permeability Surface**

²³⁰ Our prediction of landscape permeability revealed substantial differences across regions in
²³¹ the study area (Figure 4). Comparisons of median permeability values (Table 1) showed
²³² that permeability inside the KAZA-TFCA was more than two times as high as permeability
²³³ outside it. Permeability varied by country, with a five-fold permeability difference among
²³⁴ them. Angola and Botswana were characterized by comparably highly permeable landscapes,
²³⁵ Zimbabwe and Zambia were relatively impermeable, and Namibia ranged in between the two
²³⁶ extremes (Table 1). Visual inspection of our covariate layers indicated that high permeability
²³⁷ in Angola and Botswana was mainly related to a combination of low human influence, low
²³⁸ tree cover, high shrubs/grassland cover, and a close distance to water. Although swamps,
²³⁹ wetlands, and permanent water themselves provided little permeability, their surroundings
²⁴⁰ acted as strong attractants to dispersers. The low permeability that characterized Zambia
²⁴¹ and Zimbabwe, on the other hand, was mainly caused by substantial human influence.
²⁴² Albeit the KAZA-TFCA covered most permeability hot-spots, several highly permeable
²⁴³ regions remained uncovered by its borders. Across all countries, protected areas provided
²⁴⁴ roughly double the permeability of unprotected landscapes (Table 1).

²⁴⁵ **3.4 Least-Cost Paths & Least-Cost Corridors**

²⁴⁶ Our least-cost analysis revealed three major movement corridors of which all were well-
²⁴⁷ contained within the KAZA-TFCA boundaries (Figure 5). One major corridor ran SE-NW
²⁴⁸ and connected the Okavango-Linyanti ecosystem in Botswana with Luengue-Luiana NP in
²⁴⁹ Angola. A second corridor ran W-E between Chobe NP in Botswana and Zimbabwe's
²⁵⁰ Hwange NP. A third major corridor ran NE-SW, completely across unprotected areas, and
²⁵¹ connected Kafue NP in Zambia with more central regions of the KAZA-TFCA. Several
²⁵² minor corridors branched off from these three major corridors; these included a south-
²⁵³ ward connection between the Okavango-Linyanti and the Central Kalahari Game Reserve,
²⁵⁴ a southwesterly corridor connecting Luengue-Luiana NP with Namibia's Khaudum NP, and
²⁵⁵ a northeasterly extension of the Hwange corridor into Zimbabwe's Matusadona NP. Accord-
²⁵⁶ ing to our predictions, the landscapes in the Okavango-Linyanti region were the highest
²⁵⁷ frequented dispersal routes within the KAZA-TFCA (Figure 5b). Our model did not de-
²⁵⁸ tect any significant direct corridors between Zimbabwe and Zambia or Zambia and Angola,

259 and only a very limited W-E direct connection between the Okavango region and Namibia's
260 Khaudum NP. Except for the corridor into the Central Kalahari National Park, our model
261 did not detect any significant connectivity outside the boundaries of the KAZA-TFCA. Fur-
262 thermore, we found little to no direct connectivity between peripheral points; that is, most
263 paths and corridors connecting two adjacent peripheral points ran through more central
264 regions before heading towards their destination at the periphery (Figure 5).

265 4 Discussion

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

284 Our results emphasize that human influences constitute some of the main barriers to con-
285 nectivity among wild dog populations. According to our model, dispersers avoided corssing
286 human dominated landscapes whenever given the choice. This conforms to findings on dis-
287 persing wild dogs from eastern Africa (Masenga et al., 2016; O'Neill et al., 2020) but conflicts
288 with findings from South Africa by Davies-Mostert et al. (2012), who reported a high will-
289 ingness of dispersers to cross human-dominated landscapes. We believe that such differences
290 are due to the unavailability of alternative routes through natural landscapes, which may
291 have forced dispersers in South Africa to cross human dominated landscapes despite a strong

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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 (Palo-mares et al., 2000; Elliot et al., 2014). Unfortunately, Davies-Mostert et al. (2012) only recorded net dispersal distances, thereby precluding a more indepth understanding of the impact of humans on dispersal behavior. 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).

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

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

Reviewer 1 suggested to add this

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

Locally, we identified the Okavango-Linyanti region as a potential dispersal hub through

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

As per re-
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348 Our approach of identifying movement corridors based on pre-defined start and end
349 points implicitly assumes that individuals know the end point of their dispersal journey and
350 that they have almost complete knowledge of associated movement costs (Panzacchi et al.,
351 2016). Since dispersers often move into unknown territory, this may not necessarily be the
352 case (Abrahms et al., 2017; Cozzi et al., 2020). However, specification of pre-defined end
353 points might not be necessary, as the parametrized iSSF model can be used as mechanistic
354 movement model to simulate dispersal events from known source points, yet without re-
355 stricting the domain of potential end points (Signer et al., 2017). Consequently, movement
356 corridors would emerge more naturally as the result of a myriad of simulated dispersal events
357 (Zeller et al., 2020). Individual based simulations could also serve to generate permeability
358 surfaces that are based on steady state utilistation distributions (Avgar et al., 2016; Signer
359 et al., 2017). Such surfaces have been shown to reduce the risk of overestimating permeabil-

360 ity, particularly in areas that lie far from suitable habitats Signer et al. (2017). While a
361 simulation-based approach is conceptually straightforward, computational requirements are
362 tremendous, especially for such a large extent as constituted by the KAZA-TFCA.

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

377 5 Authors' Contributions

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

383 6 Data Availability

384 GPS movement data of dispersing coalitions will be made available on dryad at the time
385 of publication. We will also provide example R-code on Github to illustrate our least-cost
386 modelling approach (<https://github.com/DavidDHofmann>).

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³⁸⁷ **7 Acknowledgements**

³⁸⁸ We thank the Ministry of Environment and Tourism of Botswana for granting permission to
³⁸⁹ conduct this research. We thank C. Botes, I. Clavadetscher, and G. Camenisch for assisting
³⁹⁰ with wild dog immobilizations. We also thank B. Abrahms for sharing her data of three
³⁹¹ dispersing wild dogs. Furthermore, we are indebted to Prof. J. Fieberg, who consulted all
³⁹² statistical aspects of this work and P. Wolski, from the Okavango Research Institute, who
³⁹³ assisted us in generating dynamic water maps. We also thank the anonymous reviewers for
³⁹⁴ their valuable comments and suggestions. This study was funded by Albert-Heim Stiftung,
³⁹⁵ Basler Stiftung für Biologische Forschung, Claraz Foundation, Idea Wild, Jacot Foundation,
³⁹⁶ National Geographic Society, Parrotia Stiftung, Stiftung Temperatio, Wilderness Wildlife
³⁹⁷ Trust Foundation, Forschungskredit der Universität Zürich, and a Swiss National Science
³⁹⁸ Foundation Grant (31003A_182286) to A. Ozgul.

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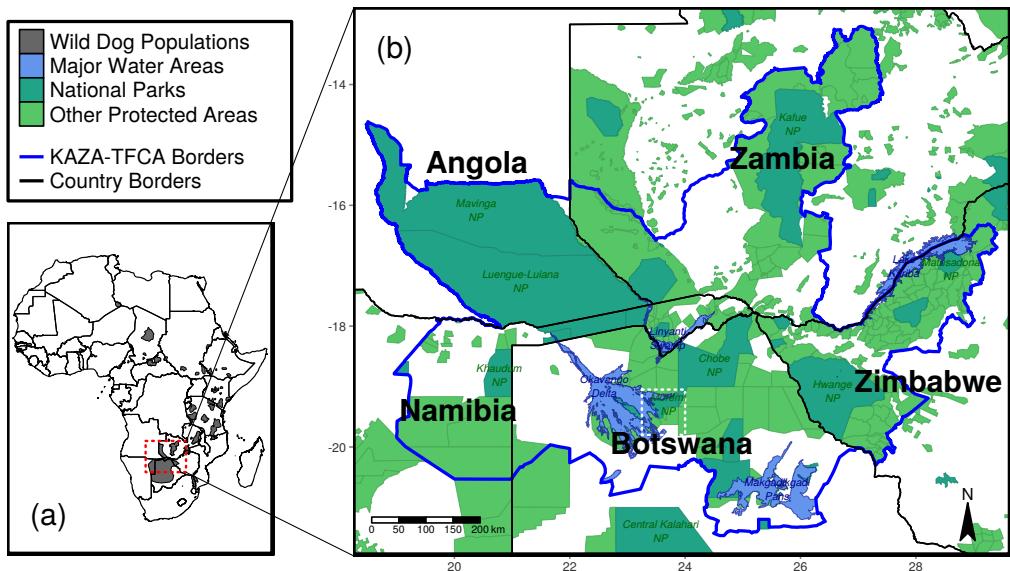


Figure 1: Overview of our study area. (a) The red dotted rectangle depicts the study area, which was confined by a bounding box encompassing the entire KAZA-TFCA. Gray areas indicate remaining wild dog populations according to the IUCN (Woodroffe and Sillero-Zubiri, 2012). (b) The white rectangle illustrates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

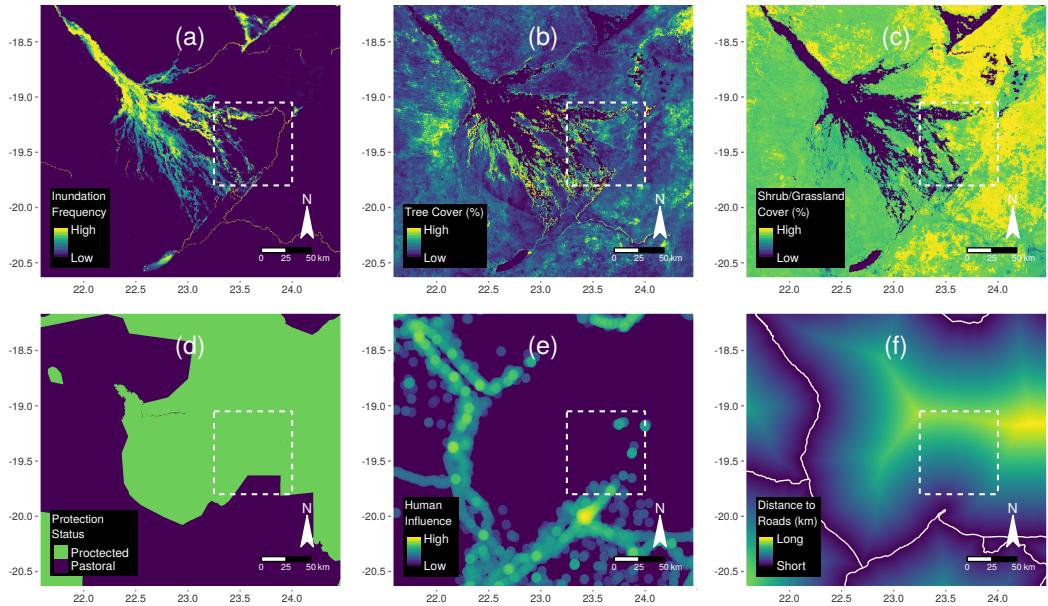


Figure 2: Overview of spatial covariates that we included in our models. We prepared all covariates for the entire study area but for better visibility we only plot them for the surroundings of the Okavango Delta. The white rectangle in each plot depicts the area within which dispersing coalitions were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

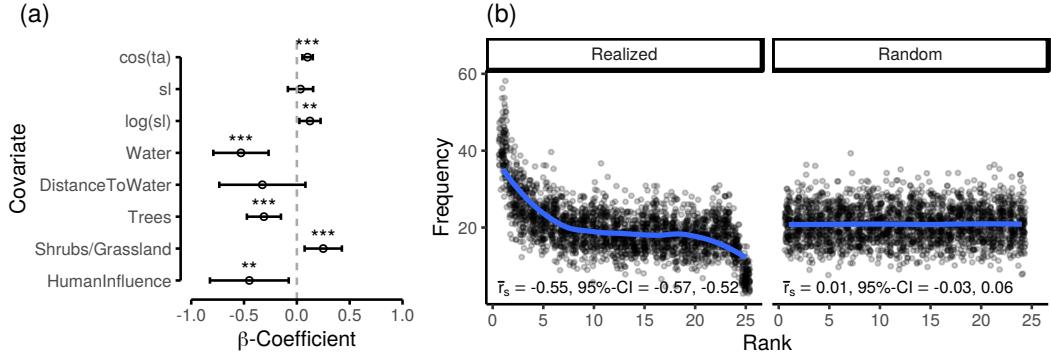


Figure 3: (a) Estimated selection coefficients from the most parsimonious habitat selection model. Negative coefficients indicate avoidance of a covariate, positive coefficients selection of a covariate. Whiskers delineate the 95%-CIs for estimated parameters. Significance codes: ** $p < 0.05$, *** $p < 0.01$. (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.

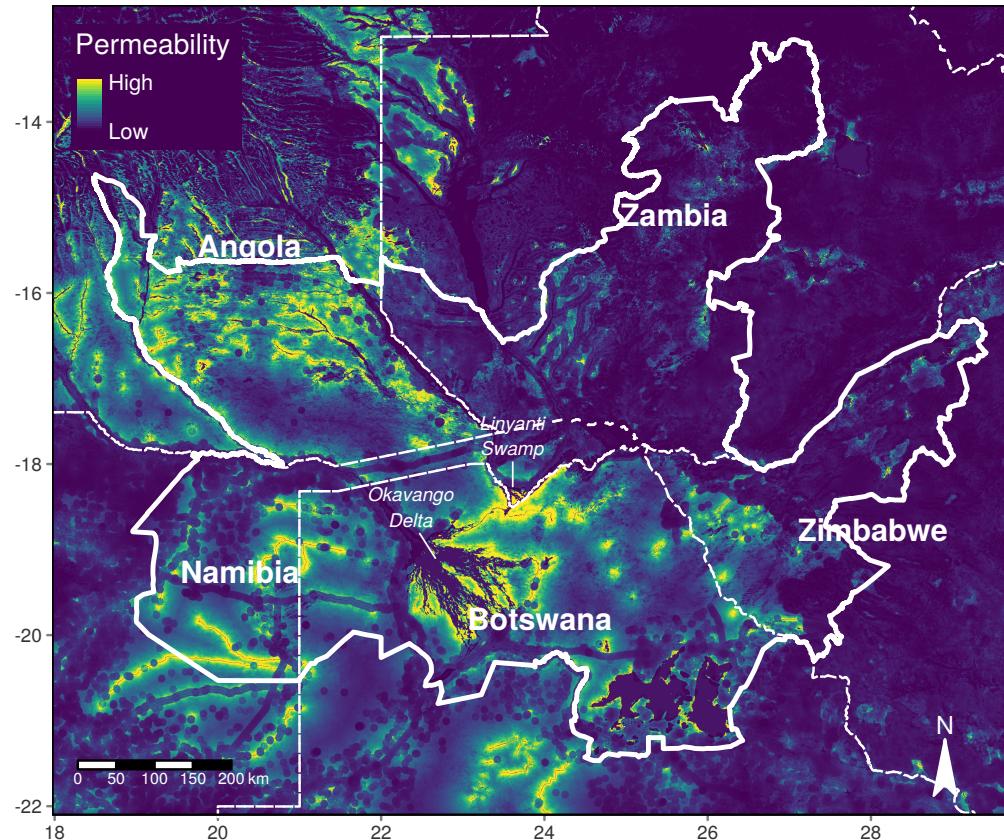


Figure 4: Predicted permeability surface for the extent of the KAZA-TFCA. Permeability was predicted by calculating selection scores $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)$ for each raster cell based on the raster cell's underlying covariates (x_i) and estimated selection strength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

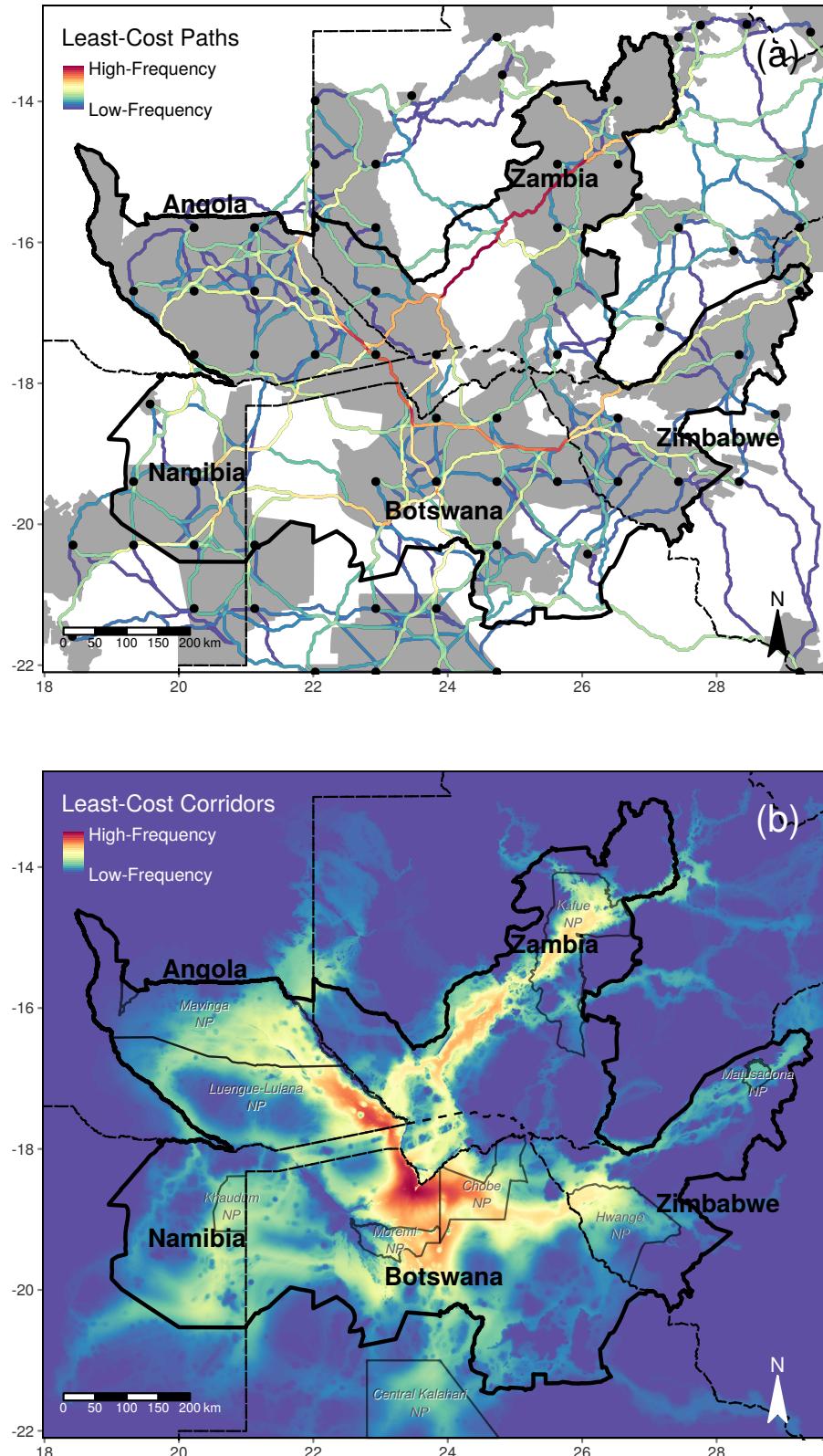


Figure 5: (a) Source points (black dots) and corresponding least-cost paths leaving from protected areas (dark grey borders). Note that only contiguous protected areas covering more than 700 km² are depicted. Continuous thin black lines indicate the borders of the KAZA-TFCA, whereas dashed black lines delineate country-borders. (b) Least-cost corridors between the same source points as illustrated in subfigure (a). For ease of spatial reference, we also labeled some national parks (NPs, in dark-grey).

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

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