

# Step by Step: Using Step Selection Functions to Simulate Dispersal and Assess Landscape Connectivity

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## Abstract

Dispersal is an important process that allows species to avoid inbreeding, colonize new habitats and reinforce non-viable subpopulations. Successful dispersal thus represents a crucial pre-requisite for long-term species persistence in wild animal populations. However, the ability to disperse is contingent a sufficient degree of landscape connectivity, which is why the estimation of connectivity and preservation of dispersal corridors has become a task of extraordinary importance for conservation authorities worldwide.

Over the past two decades, ecologists have primarily relied on analytical tools such as least-cost analysis and circuit theory to model and investigate landscape connectivity. Despite their usefulness for a diverse suite of ecological applications, both methods make several restricting assumptions that limit their suitability in reality. Individual-based dispersal simulations have been proposed to address these shortcomings, yet due to the sheer amount of non-trivial modeling decisions required, a unified and objective framework to simulate dispersal is missing.

Recent innovations in movement ecology have brought forward novel opportunities to study animal dispersal and estimate landscape connectivity. In particular, the rich suite of resource selection functions, namely point-, step-, and path-selection functions, have undergone substantial improvements over the past years. Most notably, step-selection functions have been generalized to *integrated* step selection functions, which essentially represent fully mechanistic movement models based on which an individual's movement could be simulated. While such models have been applied to study *steady-state* utilization distribution resident animals, a similar approach may be useful to investigate *transient* movement behavior and landscape connectivity.

Here, we showcase the use of integrated step selection functions as a simple individual-based and spatially explicit model to simulate dispersal of the endangered African wild dog across the world's largest transboundary conservation area, the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). For this, we utilize data collected on 16 dispersing wild dog coalitions in combination with relevant habitat covariates. We analyse the data using integrated step selection functions, thereby parametrizing a fully mechanistic movement model describing how dispersing wild dogs move through the landscape. Based on this model, we simulate 80'000 dispersers moving across the extent of the KAZA-TFCA, and generate a set of maps, each focused on a different aspect of connectivity. Finally, we discuss the benefits and pitfalls of such a simulation-based approach and highlight potential improvements to be made in the future.

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# <sup>1</sup> 1 Introduction

## <sup>2</sup> 1.1 Importance of Dispersal & Connectivity (90%)

<sup>3</sup> Dispersal is defined as the movement of individuals away from their natal location to the  
<sup>4</sup> site of first reproduction Howard (1960). It is a vital process governing the social structure  
<sup>5</sup> of wild animal populations that are distributed in space (Hanski, 1998; Clobert et al., 2012)  
<sup>6</sup> and may strongly affect population dynamics at different spatial and social scales (Hanski,  
<sup>7</sup> 1999a; Clobert et al., 2012). Dispersal allows species to maintain genetic diversity (Perrin  
<sup>8</sup> and Mazalov, 1999, 2000; Frankham et al., 2002; Leigh et al., 2012; Baguette et al., 2013),  
<sup>9</sup> to rescue small, non-viable populations (Brown and Kodric-Brown, 1977), and to promote  
<sup>10</sup> the colonization or recolonization of unoccupied habitats (Hanski, 1999b; MacArthur and  
<sup>11</sup> Wilson, 2001). However, successful dispersal requires a sufficient degree of landscape con-  
<sup>12</sup>nectivity (Fahrig, 2003; Clobert et al., 2012), which is why the identification and protection  
<sup>13</sup>of major dispersal corridors has become a fundamental task in conservation science (Nathan,  
<sup>14</sup> 2008; Doerr et al., 2011; Rudnick et al., 2012). The ability to pinpoint relevant dispersal  
<sup>15</sup> hotspots requires information on movement behavior during dispersal and knowledge about  
<sup>16</sup> factors that limit dispersal and therefore connectivity (Baguette et al., 2013; Vasudev et al.,  
<sup>17</sup> 2015).

## <sup>18</sup> 1.2 Advancements in GPS Technology & Movement Ecology (90%)

<sup>19</sup> Thanks to novel technologies developed over the past decades, particularly of GPS/Satellite  
<sup>20</sup> radio-collars, the use of GPS data to study animal dispersal and connectivity has accelerated  
<sup>21</sup> (Elliot et al., 2014; Jönsson et al., 2016; Williams et al., 2019). Additionally, the advent  
<sup>22</sup> of publicly accessible satellite imagery and sophisticated remote sensing techniques to rep-  
<sup>23</sup>resent the physical landscape through which individuals disperse have heralded a “golden  
<sup>24</sup> age of animal tracking” (Kays et al., 2015). Concurrently, the availability of large amounts  
<sup>25</sup> of empirical data and an increased computational power have led to the development of  
<sup>26</sup> numerous techniques to study dispersal and highlight critical corridors between subpopula-  
<sup>27</sup>tions (Boyce et al., 2002; Fortin et al., 2005; Cushman and Lewis, 2010; Zeller et al., 2012;  
<sup>28</sup> Diniz et al., 2020).

## <sup>29</sup> 1.3 Resource Selection & Connectivity (90%)

<sup>30</sup> *Resource selection functions* (Boyce et al., 2002) and derived methods such as *step selection*  
<sup>31</sup> *functions* (Fortin et al., 2005) and *path selection functions* (Cushman and Lewis, 2010) have

32 proven particularly useful for studying animal movement (Fieberg et al., 2020) and modeling  
33 connectivity (Diniz et al., 2020). These methods allow estimating habitat preferences of the  
34 focal species by comparing covariates at locations visited by the animal to the same covariates  
35 at locations available to, but not visited by the animal (Boyce et al., 2002; Fortin et al., 2005;  
36 Cushman and Lewis, 2010; Thurfjell et al., 2014). The so estimated preferences can then be  
37 used to predict a permeability surface, indicating the expected ease at which an animal can  
38 traverse a given area (Spear et al., 2010; Zeller et al., 2012; Etherington, 2016). Ultimately,  
39 the permeability surface serves as input to a connectivity model that is used to reveal  
40 movement corridors (Diniz et al., 2020). Two of the most prominent connectivity models  
41 are least-cost path analysis (LCP analysis; Adriaensen et al., 2003) and circuit theory (CT  
42 McRae, 2006; McRae et al., 2008), both graph-based methods that estimate conductance of  
43 the landscape to infer likely movement corridors. Despite their intuitive nature and ease of  
44 use, both methods make rigorous assumptions about animal movement that are often not  
45 fulfilled in reality (Diniz et al., 2020).

#### 46 1.4 Issues with Least-Cost Paths (90%)

47 In LCP analysis, for instance, a least costly path always exists, even if associated movement  
48 costs are unreasonably high and will never be incurred by a dispersing individual. The  
49 method also presumes that animals have an infinite perceptual range and a preconceived end-  
50 point in mind, such that they choose a cost-minimizing route accordingly. These assumptions  
51 may be fulfilled by migrating animals that typically move between a discrete set of habitats  
52 through familiar landscapes. Dispersers, on the other hand, usually move over long distances  
53 into unknown territory and are therefore less likely to be aware of associated movement costs  
54 (Koen et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020). Another issue of LCPs analysis  
55 concerns the fact that least-costly routes, by their very nature, are only one pixel wide (Pinto  
56 and Keitt, 2009). This neglects the fact that alternative routes with similar costs may exist  
57 and implies that the width of inferred movement routes depends on the resolution of chosen  
58 covariate layers and may not be biologically meaningful (Diniz et al., 2020). Although some  
59 of these deficiencies can be addressed using less stringent versions of the LCP algorithm (e.g.  
60 least-cost *corridors* (Pinto and Keitt, 2009), *thresholded* least-cost paths (Landguth et al.,  
61 2012), and *randomized* least-cost paths (Panzacchi et al., 2016; Van Moorter et al., 2021)),  
62 a certain degree of arbitrariness remains.

63 **1.5 Issues with Circuit Theory (90%)**

64 CT entails similarly unreasonable restrictions that are hardly ever met. For example, because  
65 CT only allows movements from a source cell to its 4 or 8 adjacent cells, it implicitly posits  
66 that animals exhibit a perceptual range of a single pixel. Given that covariate layers are  
67 usually resolved with a pixel size between 30 m x 30 m and 1 km x 1 km, this hardly  
68 ever renders the true capability of animals to perceive the environment. Moreover, CT is  
69 built around the assumption of a complete random walk (Diniz et al., 2020), entailing that  
70 directional biases cannot be rendered. Nevertheless, directionality is a common characteristic  
71 in animal movement (Bovet and Benhamou, 1991; Schultz and Crone, 2001), especially in  
72 dispersing individuals (Cozzi et al., 2020; Hofmann et al., 2021).

73 **1.6 Issues of Both Methods**

74 Finally, neither LCP analysis nor CT are capable of rendering the temporal dimension of  
75 dispersal (Diniz et al., 2020). Statements about the expected duration required to traverse  
76 a certain corridor are therefore impossible. Likewise, because movement is not modeled  
77 explicitly, interactions between movement and habitat preferences of the focal species cannot  
78 be rendered. Connectivity therefore merely arises in result to the landscape structure, which  
79 is usually referred to as structural connectivity. While structural connectivity yields insights  
80 in the *potential* of the landscape to be traversed, it does not enable to quantify the *actual*  
81 gene flow through the area. Consequently, a functional view on connectivity, which also  
82 renders the behavioral response of the animal with respect to prevailing habitat conditions,  
83 is often more desirable (Tischendorf and Fahrig, 2000; Baguette et al., 2013).

84 **1.7 What about IBMMS? (90%)**

85 To address the issues inherent to LCPs and CT, individual-based movement models (IBMMS)  
86 have been proposed and applied (Diniz et al., 2020). In these models, dispersal trajectories  
87 are simulated spatially explicitly, based on movement rules that determine how individuals  
88 move over and interact with the prevailing landscape (Gustafson and Gardner, 1996; Gardner  
89 and Gustafson, 2004; Graf et al., 2007; Kramer-Schadt et al., 2004; Revilla et al., 2004;  
90 Revilla and Wiegand, 2008; Kanagaraj et al., 2013; Clark et al., 2015; Allen et al., 2016;  
91 Hauenstein et al., 2019; Zeller et al., 2020; Vasudev et al., 2021). Using the simulated  
92 trajectories, one can calculate a set of connectivity metrics, such as inter-patch connectivity  
93 and traversal frequency, to reveal major dispersal corridors (Kanagaraj et al., 2013; Bastille-  
94 Rousseau et al., 2018; Hauenstein et al., 2019; Zeller et al., 2020). However, while IBMMS

95 can be employed to overcome any of the shortcomings intrinsic to LCPs and CT, they are  
96 subject to a vast amount of subjective, non-trivial modeling decisions. Moreover, they can  
97 be challenging to fit and require vast amounts of movement data, ideally collected during  
98 dispersal (Diniz et al., 2020). Consequently, alternative methods that require fewer modeling  
99 decisions and are straight forward to apply are desirable.

## 100 **1.8 Step Selection Analysis (90%)**

101 Here, we investigate the usefulness of integrated step selection functions (ISSFs, Avgar  
102 et al., 2016), as a relatively simple but powerful IBMM based on which dispersal can be  
103 simulated. While regular SSFs were intended to learn about relative habitat preferences of  
104 the focal species (Fortin et al., 2005; Thurfjell et al., 2014; Avgar et al., 2017), the method  
105 has recently been generalized to *integrated* SSFs and now enables to jointly study habitat  
106 and movement preferences, as well as potential interactions between them (Avgar et al.,  
107 2016; Signer et al., 2017; Fieberg et al., 2020). ISSFs therefore provide a relatively simple  
108 means to model complex movement behavior, where movement is viewed as the result of  
109 two intertwined behavioral kernels (e.g. Prokopenko et al., 2017; Munden et al., 2020).  
110 Importantly, a parametrized ISSF model can be employed as a fully mechanistic movement  
111 model based on which individual movement trajectories can be simulated (Avgar et al.,  
112 2016; Signer et al., 2017). In fact, Signer et al. (2017) used ISSF to simulate steady state  
113 utilization distributions of resident animals that were moving around a point of attraction.  
114 However, the degree to which such simulations are helpful in detecting movement corridors  
115 and modeling landscape connectivity remains to be investigated.

## 116 **1.9 Study Species & Study Area (90%)**

117 One of the species for which long-term viability relies on sufficient landscape connectivity  
118 is the endangered African wild dog *Lycon pictus*. While once present across entire sub-  
119 Saharan Africa, wild dogs have disappeared from a vast majority of their historic range  
120 due to persecution by humans, habitat fragmentation and destruction, and deadly diseases  
121 (Woodroffe and Sillero-Zubiri, 2012). As of today, only 6'000 free-ranging individuals remain  
122 in small and spatially scattered subpopulations (Woodroffe and Sillero-Zubiri, 2012). Within  
123 those subpopulations, wild dogs form cohesive packs comprising 8 to 12 adults and their  
124 offspring McNutt (1995). After reaching sexual maturity, male and female offspring form  
125 same-sex coalitions and disperse from their natal pack in search for potential mating partners  
126 and a suitable territory to settle (McNutt, 1996; Behr et al., 2020). New packs are formed

<sup>127</sup> when dispersing coalitions join unrelated opposite-sex dispersing coalitions (McNutt, 1996).  
<sup>128</sup> Dispersing wild dogs can cover several hundred kilometers across a variety of landscapes  
<sup>129</sup> (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020; Hofmann et al., 2021).  
<sup>130</sup> One of the few strongholds for this species lies near the Moremi Game Reserve in northern  
<sup>131</sup> Botswana, which is part of the world's largest transboundary protected area, namely the  
<sup>132</sup> Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). This area has originally  
<sup>133</sup> been intended to facilitate migration of elephants, but is expected to provide benefits to a  
<sup>134</sup> multitude of other species (Elliot et al., 2014; Brennan et al., 2020; Hofmann et al., 2021).

## <sup>135</sup> **1.10 Previous Paper (90%)**

<sup>136</sup> In a previous study, we assessed landscape connectivity for dispersing African wild dogs  
<sup>137</sup> within the KAZA-TFCA using least-cost methods (Hofmann et al., 2021). Specifically, we  
<sup>138</sup> fitted a basic habitat selection model and predicted a permeability surface that we used to  
<sup>139</sup> compute least-cost paths and corridors. We now expand on this knowledge and use ISSFs to  
<sup>140</sup> develop a more mechanistic movement model of dispersing wild dogs (Figure 1). We employ  
<sup>141</sup> the model to simulate dispersers moving across the KAZA-TFCA and generate three distinct  
<sup>142</sup> connectivity maps, each shedding light onto a different aspect of connectivity. With this  
<sup>143</sup> work, we exemplify how ISSFs can be utilized for dispersal simulations and we discuss several  
<sup>144</sup> benefits of this approach over traditional connectivity modeling techniques such as least-cost  
<sup>145</sup> analyses and circuit theory. Most importantly, simulations based on ISSFs provide a more  
<sup>146</sup> generic view on how connectivity emerges and to which degree connectivity depends on the  
<sup>147</sup> dispersal duration. In addition, by generating proper dispersal trajectories, network theory  
<sup>148</sup> can be applied to calculate network metrics that are pertinent to connectivity analysis.

## <sup>149</sup> **2 Methods**

### <sup>150</sup> **2.1 Study Area (90%)**

<sup>151</sup> The study area was defined by a bounding box centered at -17°13'9"S, 23°56'4"E (Figure 2a)  
<sup>152</sup> stretching over 1.3 Mio. km<sup>2</sup> and encompassing the entire KAZA-TFCA (Figure 2b). The  
<sup>153</sup> KAZA-TFCA represents the world's largest transboundary conservation area and comprises  
<sup>154</sup> parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia. It covers a total of 520'000  
<sup>155</sup> km<sup>2</sup> and hosts diverse landscapes, ranging from savanna to grassland and from dry to moist  
<sup>156</sup> woodland habitats. In its center lies the Okavango Delta, a dominant hydrogeographical  
<sup>157</sup> feature and the world's largest flood-pulsing inland delta. The wet season within the KAZA-

158 TFCA lasts from November to March and is out of phase with the flood in the Okavango  
159 Delta, which peaks between July and August (McNutt, 1996; Wolski et al., 2017). Although  
160 large portions within the KAZA-TFCA are designated national parks or other protected  
161 areas, considerable human influence remains due to roads, agricultural sites and settlements  
162 and villages that are distributed across the KAZA-TFCA's landscape.

## 163 2.2 GPS Relocation Data (90%)

164 Between 2011 and 2019, we collected GPS relocation data on dispersing wild dogs from a  
165 free-ranging wild dog population inhabiting the Moremi National Park in northern Botswana  
166 (Cozzi et al., 2020; Hofmann et al., 2021). We selected potential dispersers based on age,  
167 pack size, number of same-sex siblings within the pack, and presence of unrelated opposite-  
168 sex individuals in the pack (McNutt, 1996; Behr et al., 2020). We immobilized selected  
169 individuals using a cocktail of Ketamine/Xylazine/Atropine (Osofsky et al., 1996; Cozzi  
170 et al., 2020) that was injected by dart, fired from a CO<sub>2</sub>-pressurized gun (*DAN-Inject*,  
171 *Denmark*). Immobilized individuals were fitted with GPS/Satellite radio collars (*Vertex*  
172 *Lite*; *Vectronic Aerospace GmbH, Berlin*) that guaranteed automated drop-off through a  
173 decomposable piece of cotton. Handling and collaring of all individuals was supervised by  
174 a Botswana-registered wildlife veterinarian and all individuals quickly rejoined their pack  
175 after immobilization.

176 16 collared individuals eventually dispersed, each in a separate same-sex dispersal coali-  
177 tion (7 female and 9 male coalitions). During dispersal, collars were programmed to record  
178 a GPS fix every 4 hours, all of which were regularly transmitted over the Iridium satellite  
179 system, thereby allowing to remotely track individuals, even if they left the main study area  
180 and crossed international borders. Because behavior during dispersal is more pertinent for  
181 assessing landscape connectivity (Elliot et al., 2014; Abrahms et al., 2017), we discarded all  
182 data that was collected during residency and only retained GPS data recorded during dis-  
183 persal. In some instances, exact dispersal dates were known from field observations, whereas  
184 in other cases we determined dispersal phases using the net-squared displacement metric.  
185 Net squared displacement measures the squared Euclidean distance of a GPS relocation to  
186 a reference point (Börger and Fryxell, 2012), which in our case was set to the center of  
187 each individual's natal home range. Thus, dispersal was deemed to have started when an  
188 individual left its natal home range and ended once individuals became sedentary again. As  
189 previous research found no differences in behaviors of females and males during dispersal  
190 (Woodroffe et al., 2019; Cozzi et al., 2020), we did not distinguish between sexes. After

191 collection, we converted collected GPS coordinates ( $n = 4'169$ ) to steps, where each step  
192 represented the straight-line distance traveled by an individual between two consecutive  
193 GPS relocations (Turchin, 1998). To ensure a regular sampling interval, we removed fixes  
194 that were not successfully collected on the 4-hourly schedule ( $\pm 15$  minutes).

### 195 2.3 Covariates (90%)

196 We represented the physical landscape across the study area using a set of habitat covariates  
197 that included water-cover, distance to water, woodland-cover, and shrub/grassland-cover.  
198 Because water cover greatly changes within and between years in the Okavango Delta, we  
199 applied a remote sensing algorithm and generated frequently updated water cover layers  
200 and corresponding distance to water layers (see Wolski et al., 2017 and Appendix A3 in  
201 Hofmann et al., 2021). Resulting water layers thus temporally aligned with our dispersal  
202 events. We furthermore computed a proxy for human influence, rendering anthropogenic  
203 pressures stemming from human-density, agricultural sites, and roads. All spatial layers  
204 were coarsened or interpolated to a target resolution of 250 m by 250 m. Further details on  
205 the sources and preparation of each habitat covariate are given in Hofmann et al. (2021).

206 Besides habitat covariates, we computed movement metrics that we used as movement  
207 covariates in our models. Movement metrics were calculated for each step and included the  
208 step length ( $sl$ ), its natural logarithm ( $\log(sl)$ ), and the cosine of the relative turning angle  
209 ( $\cos(ta)$ ) (for details see (Avgar et al., 2016; Fieberg et al., 2020)). Because wild dogs follow  
210 a diurnal activity pattern, we also coded a binary variable (**LowActivity**) indicating whether  
211 a step was realized during periods of low wild dog activity (17:00 to 09:00 local time) or  
212 high wild dog activity (09:00 to 17:00 local time). Handling and manipulation of all data, as  
213 well as all models and simulations were implemented with the statistical software R, version  
214 3.6.6 (R Core Team, 2019). Several helper functions were written in C++ and imported into  
215 R using the Rcpp package (Eddelbuettel and François, 2011; Eddelbuettel, 2013)

### 216 2.4 Movement Model (80%)

217 We used ISSFs to parametrize a mechanistic movement model for dispersing wild dogs  
218 (Avgar et al., 2016). To conduct ISSF analysis, we paired each realized step with 24 random  
219 steps. An observed step plus its 24 random steps formed a stratum and received a unique  
220 identifier. As suggested by Avgar et al. (2016), we generated random steps by sampling  
221 random turning angles from a uniform distribution  $(-\pi, +\pi)$  and step lengths from a gamma  
222 distribution that was fitted to realized steps (scale = 6'308, shape = 0.37). Along each step,

223 we extracted and averaged spatial covariates using the `velox` package (Hunziker, 2021). We  
 224 also calculated the movement metrics `sl`, `log(sl)`, and `cos(ta)` for each observed and random  
 225 step. To facilitate model convergence, we standardized all continuous covariates to a mean of  
 226 zero and a standard deviation of one. Since correlation among covariates was low ( $|r| > 0.6$ ;  
 227 Latham et al., 2011), we retained all of them for modeling.

228 To contrast realized steps (scored 1) and random steps (scored 0), we assumed that  
 229 animals assigned a selection score  $w(x)$  of the exponential form to each step (Fortin et al.,  
 230 2005). The selection score  $w(x)$  of each step thus depended on its associated covariates  
 231 ( $x_1, x_2, \dots, x_n$ ) and on the animal's preferences (i.e. relative selection strengths; Avgar et al.,  
 232 2017) towards these covariates ( $\beta_1, \beta_2, \dots, \beta_n$ ):

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

233 The probability of a step being realized was then contingent on the step's selection score,  
 234 as well as on the selection scores of all other step in the same stratum:

$$P(Y_i = 1 | Y_1 + Y_2 + \dots + Y_i = 1) = \frac{w(x_i)}{w(x_1) + w(x_2) + \dots + w(x_i)} \quad (\text{Equation 2})$$

235 We ran conditional logistic regression analysis in the r-package `glmmTMB` to estimate pref-  
 236 erences of interest. To handle multiple individuals, we applied the mixed effects technique  
 237 developed by (Muff et al., 2020), which allows to effectively model random slopes. Thus,  
 238 we treated animal IDs as random effect and modeled random slopes for each covariate. We  
 239 fixed the random intercept variance at an arbitrary high value of  $10^6$  to make use of the  
 240 "poission"-trick (Muff et al., 2020).

241 The structure of the movement model was based on the habitat selection model for dis-  
 242 persing wild dogs presented in Hofmann et al. (2021). In the original model (referred to as  
 243 base model hereafter), no interactions between habitat covariates (`Water`, `DistanceToWater0.5`,  
 244 `Woodland`, `Shrubs/Grazing`, `Human Influence`) and movement covariates (`sl`, `log(sl)`, `cos(ta)`)  
 245 were considered. Hence, we slightly expanded this base model and proposed interactions  
 246 between all movement and habitat covariates. More specifically, we started with the base  
 247 model and incrementally increased model complexity by adding all possible two-way inter-  
 248 actions between habitat covariates and movement covariates. For instance, for the covariate  
 249 `Water`, we proposed the interactions `Water:log(sl)`, `Water:log(sl)`, and `Water:cos(ta)`. Besides  
 250 those combinations, we also proposed the interactions `sl:cos(ta)` and `log(sl):cos(ta)` to ac-

251 count for a correlation between turning angles and step lengths, as well as the interactions  
252 `sl:LowActivity` and `log(sl):LowActivity` to account for the fact that step lengths may differ due  
253 to wild dogs' diurnal activity pattern. To compare competing models and assess the most  
254 parsimonious movement model, we ran stepwise forward model selection based on Akaike's  
255 Information Criterion (AIC, Burnham and Anderson, 2002).

256 We validated the predictive power of the most parsimonious movement model using k-  
257 fold cross-validation for case-control studies as suggested by Fortin et al. (2009). For this,  
258 we randomly assigned 80% of the strata to a training set and the remaining 20% to a  
259 testing set. Using the training data we parametrized a movement model based on which  
260 we predicted selection scores  $w(x)$  for all steps in the test data. Within each stratum, we  
261 then assigned ranks 1-25 to each step based on predicted selection scores, where rank 1 was  
262 given to the step with the highest score  $w(x)$ . Across all strata we determined the realized  
263 step's rank and we calculated rank frequencies of realized steps across all strata. Finally, we  
264 computed Spearman's rank correlation between ranks and associated frequencies  $r_{s,realized}$ .  
265 We replicated the entire procedure 100 times and computed the mean correlation coefficient  
266 ( $\bar{r}_{s,realized}$ ), as well as its 95% confidence interval across all replicates. For comparison, we  
267 repeated the same procedure 100 times assuming random preferences, which we implemented  
268 by discarding the realized step from all strata and identifying the rank of a random step  
269 in each stratum. Again, we calculated Spearman's rank correlation coefficient ( $r_{s,random}$ ),  
270 its mean across repetitions ( $\bar{r}_{s,random}$ ), and its 95% confidence interval. This validation  
271 ultimately proofs a significant prediction in case the confidence intervals of  $\bar{r}_{s,realized}$  and  
272  $\bar{r}_{s,random}$  do not overlap.

## 273 2.5 Dispersal Simulation (80%)

274 We used the most parsimonious movement model to simulate 80'000 virtual dispersers mov-  
275 ing across the KAZA-TFCA. The simulation resembled an inverted ISSF and was set up as  
276 follows. (1) We defined a random source point and assumed a random initial orientation of  
277 the animal. (2) Departing from the source point, we generated 25 random steps by sampling  
278 turning angles from a uniform distribution  $(-\pi, +\pi)$  and step lengths from our fitted gamma  
279 distribution. Similar to the input data, each random step represented the straight line move-  
280 ment within 4 hours. To prevent unreasonably large steps, we capped sampled step lengths  
281 to a maximum of 35 km, which corresponded to the farthest distance ever traveled within  
282 4 hours by one of our dispersers. (3) Along each random step, we extracted and averaged  
283 habitat covariates and we calculated movement covariates. To ensure compatible scales, we

284 standardized extracted values using the same parameters applied to our input data. (4)  
285 We applied the parametrized movement model to predict the selection score  $w(x)$  for each  
286 step and we translated predicted scores into probabilities using Equation (Equation 2). (5)  
287 We sampled one of the random steps based on predicted probabilities and determined the  
288 animal's new position. We repeated steps (2) to (5) until 2'000 steps were realized, implying  
289 a total 160 Mio. simulated steps.

290 To minimize the influence of edge effects and to deal with random steps leaving the  
291 study area, we followed (Koen et al., 2010) and artificially expanded all covariate layers by  
292 adding a 100 km wide buffer zone. Within the buffer zone, we randomized covariate values  
293 by resampling values from the original covariate layers. Through this buffer zone, simulated  
294 dispersers were able to leave and re-enter the main study area. In cases where proposed  
295 random steps transgressed the border of this buffer zone, we resampled transgressing steps  
296 until they fully lied within the buffer, thereby forcing simulated individuals to "bounce off"  
297 such invisible borders.

## 298 2.6 Source Points (90%)

299 We released 80'000 virtual dispersers from 80'000 unique source points distributed across  
300 the study area. 50'000 virtual dispersers were released from randomly selected source points  
301 within contiguous protected areas larger  $> 700 \text{ km}^2$  (Figure 3a), which conforms to average  
302 home range requirements of resident wild dogs (Pomilia et al., 2015) and allowed us to remove  
303 patches too small to host viable populations. By distributing source points randomly, the  
304 number of source points per  $\text{km}^2$  was approximately equal within protected areas. To render  
305 potential immigrants into the study system, we released another 30'000 dispersers at random  
306 locations inside the 100 km wide buffer zone surrounding the main study area (Figure 3b).

## 307 2.7 Convergence (80%)

308 To verify that the number of simulated individuals sufficed to ensure reliable estimates of  
309 connectivity, we evaluated how the relative traversal frequency across the landscape de-  
310 pended on the number of simulated trajectories. Specifically, we distributed 1'000 squared  
311 "checkpoints", each with an extent of 5 km x 5 km at random locations inside the main study  
312 area. We then determined the relative traversal frequency by simulated trajectories through  
313 each checkpoint for different numbers of simulations (1 to 50'000). We repeatedly sampled  
314 trajectories 100 times and computed the mean traversal frequency across replicates, as well  
315 as the 95% prediction-interval. We expected that the mean traversal frequency converges

316 towards a steady state with increasing simulations.

## 317 **2.8 Heatmap (100%)**

318 To identify dispersal hotspots across our study area, we created a heatmap indicating the  
319 absolute frequency at which each raster-cell in the study area was visited by virtual dis-  
320 persers (Hauenstein et al., 2019; Pe'er and Kramer-Schadt, 2008). For this, we rasterized all  
321 simulated trajectories and tallied them into a single map. If the same trajectory crossed a  
322 raster-cell twice, we only counted it once, thereby mitigating potential biases caused by indi-  
323 viduals that were trapped and moved in circles. To achieve high performance rasterization,  
324 we used the R-package `terra` (Hijmans, 2020).

## 325 **2.9 Betweenness (80%)**

326 To pinpoint areas of exceptional relevance for connecting remote regions inside our study  
327 area, we converted simulated trajectories into a network and calculated betweenness scores  
328 (Bastille-Rousseau et al., 2018). For this, we overlaid the study area (including the buffer)  
329 with a regular raster resolved at 5 x 5 km. The centerpoint of each raster-cell served as node  
330 in the final network and we used the simulated trajectories to determine all transitions occur-  
331 ring from one node to another, as well as the frequency at which those transitions occurred.  
332 This resulted in an edge-list that we translated into a weighted network using the r-package  
333 `igraph` (Csardi and Nepusz, 2006). Because `igraph` handles edge weights ( $\omega$ ) as costs, we  
334 inverted the traversal frequency in each cell by applying  $\omega = \frac{\sum_i^n TraversalFrequency_i/n}{TraversalFrequency_i}$ . Con-  
335 sequently, edges that were traversed frequently were assigned low costs. Finally, we used  
336 the weighted network to calculate the betweenness score of each raster-cell. Betweenness  
337 measures how often a specific raster-cell lies on a shortest path between two other raster-  
338 cells and is therefore a useful metric to detect movement corridors (Bastille-Rousseau et al.,  
339 2018).

## 340 **2.10 Inter-Patch Connectivity (80%)**

341 We assessed inter-patch connectivity between national parks located in our study area to  
342 examine functional links between distinct patches in the KAZA-TFCA. The decision to focus  
343 on national parks was purely out of simplicity and does not imply that connections between  
344 other regions are impossible. In fact, the same logic could easily be expanded to include other  
345 protected areas. To quantify inter-patch connectivity, we computed the relative frequency at  
346 which dispersers originating from one national park successfully moved into another national

347 park. Successful movement was said to be achieved if the individuals' trajectory intersected  
348 with the corresponding national park at least once. We also recorded the number of steps  
349 required until the first intersection with the polygon of the respective national park. This  
350 allowed us to determine *if* and *how often* dispersers moved between certain national parks,  
351 as well as *how long* dispersers had to move to realize those connections.

### 352 3 Results

#### 353 3.1 Movement Model (80%)

354 Compared to the base model reported in (Hofmann et al., 2021), our most parsimonious  
355 movement model retained several additional interactions between habitat covariates and  
356 movement covariates (Figure 4 and Table 1). Although several models received an AIC  
357 weight above zero (Table 1 in Appendix S1), we only considered results from the most  
358 parsimonious model for simplicity. All models with positive AIC weight included similar  
359 covariates (Table S1), so this decision only marginally influenced subsequent analyses. Plots  
360 that aid with the interpretation of the final model are provided in Appendix S2.

361 Assuming that all other covariates are held constant at their means, the habitat kernel  
362 reveals that dispersing wild dogs avoid water but prefer its proximity. Similarly, dispersers  
363 avoid areas that are covered by woodlands, yet prefer regions covered by shrublands or  
364 grasslands. Finally, dispersers avoid movement through landscapes that are dominated by  
365 humans. Effect sizes are strong and, except for effect of *distance to water*, statistically clear  
366 on the 5% significance level.

367 With regards to the movement kernel, the positive estimate for  $\cos(\text{ta})$  indicates that dis-  
368 persers move with directional persistence, unlike what was proposed by the uniform turning  
369 angle distribution. Moreover, directionality is particularly pronounced when dispersers re-  
370 alize large steps (move quickly), as indicated by the positive estimates for  $\cos(\text{ta}):sl$  and  
371  $\cos(\text{ta}):\log(sl)$ . Finally, the negative estimate for the interaction *sl:LowActivity* reveals that  
372 wild dogs realize shorter steps (move slower) outside the main activity periods (during  
373 sunrise and sunset). Aside from the interaction *sl:LowActivity*, which appears to strongly  
374 influence movmement behavior, effect sizes are moderate, but mostly significant on the 5%  
375 significance level.

376 When looking at the interactions between movement and habitat kernels, we observe  
377 that movement behavior is contingent on habitat conditions. For example, there's strong  
378 evidence that dispersers realize smaller steps in areas covered by water or areas covered by

379 woodland, yet it appears that steps are larger in regions dominated by shrubs/grassland,  
380 and shorter when the distance to water is high. Correspondingly, the model suggests that  
381 directionality is lower in areas dominated by humans but more pronounced when dispersers  
382 are far from water. However, except for the effect of sl:Water, effect sizes and statistical  
383 significance are moderate.

384 The k-fold cross-validation procedure reveals that our model substantially outperforms  
385 a random guess (Figure 4b) and therefore correctly assigns a high selection score to realized  
386 steps. Confidence intervals of  $\bar{r}_{s,realized}$  and  $\bar{r}_{s,random}$  do not overlap and therefore proof a  
387 reliable prediction. Furthermore, the significant correlation between ranks and correspond-  
388 ing frequencies for realized steps indicates a good fit between predictions and observations  
389 (Figure 4b). In comparison to the base model ( $\bar{r}_{s,realized} = -0.55$ ; Hofmann et al., 2021),  
390 the inclusion of interactions between movement and habitat covariates slightly improved  
391 model performance.

### 392 **3.2 Dispersal Simulation (80%)**

393 On a machine with an octacore AMD Ryzen 7 2700X processor (8 x 3.6 GHz) and 64 GB  
394 of RAM, a batch of 1'000 simulated dispersers moving over 2'000 steps required 90 minutes  
395 to compute ( $\mu = 88.90$ ,  $\sigma = 1.87$ ). Consequently, the simulation of all 80'000 dispersers  
396 (160 Mio. steps) terminated after 120 hours (i.e. five days). Comparable simulations will be  
397 substantially faster for smaller study areas and lower resolution covariates, as the covariate  
398 extraction from large and high-resolution rasters was computationally the most demanding  
399 task. Out of the 50'000 dispersers initiated inside the main source area Figure 3(a), only  
400 4.5% eventually hit a map boundary, suggesting that we successfully prevented biases due to  
401 boundary effects. In contrast, 78% of the 30'000 dispersers originating from the buffer zone  
402 eventually hit a map boundary, yet this was to be expected since many of those dispersers  
403 originated from source points located close to the map boundary.

### 404 **3.3 Convergence (50%)**

405 Our examination of the traversal frequency as a function of the number of simulated dis-  
406 persers shows that already after a few simulations the mean traversal frequency remains  
407 stable and on average changes only little when adding further dispersers (Figure 5 (a) and  
408 (b)). While variability keeps decreasing with additional dispersers, the marginal benefit of  
409 having further dispersers decreases following a negative-exponential trend (Figure 5 (c)).

<sup>410</sup> **3.4 Heatmap (80%)**

<sup>411</sup> Figure 6 depicts the heatmap of all 80'000 simulated trajectories resulting after 2'000 steps.  
<sup>412</sup> The map shows that large portions of land beyond the borders of the KAZA-TFCA are only  
<sup>413</sup> infrequently visited by dispersers (dark blue areas), whereas within the KAZA-TFCA several  
<sup>414</sup> extensive regions are regularly traversed (bright yellow and red areas). Most notably, the  
<sup>415</sup> region in northern Botswana south of the Linyanti swamp stands out as highly frequented  
<sup>416</sup> dispersal hotspot. Still, the presence of several massive water bodies, such as the Okavango  
<sup>417</sup> Delta, the Makgadikgadi Pan, and the Linyanti swamp, poses considerable dispersal barriers  
<sup>418</sup> that limit realized connectivity within the KAZA-TFCA. Similarly, dispersal across Zambia's  
<sup>419</sup> and Zimbabwe's part of the KAZA-TFCA appears to be limited, as only few areas are  
<sup>420</sup> successfully traversed by dispersers. This can largely be attributed to substantial human  
<sup>421</sup> influences resulting from high human density, roads, and agricultural activities in these  
<sup>422</sup> areas. Outside the KAZA-TFCA, the most heavily used regions include the areas inside the  
<sup>423</sup> Central Kalahari National Park in Botswana, the area south-west of the Khaudum National  
<sup>424</sup> Park in Namibia, and the area around the Liuwa Plains National Park in Zambia.

<sup>425</sup> **3.5 Betweenness (80%)**

<sup>426</sup> Betweenness scores after 2'000 simulated steps are presented in Figure 7 and reveal a set of  
<sup>427</sup> discrete dispersal corridors. Again, the region in northern Botswana stands out as crucial  
<sup>428</sup> dispersal hub that connects more remote regions in the study system. Towards east, the  
<sup>429</sup> extension of this corridor runs through the Chobe National Park into the Hwange national  
<sup>430</sup> park. From there, a further extension connects to the distant Matusadona National Park  
<sup>431</sup> in Zimbabwe. Northwest of the Linyanty ecosystem, a major corridor expands into Angola,  
<sup>432</sup> where it splits and finally traverses over a long stretch of unprotected area into the Kafue  
<sup>433</sup> National Park in Zambia. Several additional corridors with slightly lower betweenness scores  
<sup>434</sup> exist, yet most of them run within the boundaries of the KAZA-TFCA. In general, only few  
<sup>435</sup> corridors directly link the peripheral regions of the KAZA-TFCA. For instance, there are  
<sup>436</sup> only few corridors between the Matusadona National Park in Zimbabwe and the Kafue  
<sup>437</sup> National Park in Zimbabwe. Similarly, there are no direct links between the Zimbabwean  
<sup>438</sup> and Angolan “spikes” of the KAZA-TFCA.

<sup>439</sup> **3.6 Inter-Patch Connectivity (80%)**

<sup>440</sup> Results from the analysis of inter-patch connectivity are given in Figure 8. It is again  
<sup>441</sup> worth pointing out that the figure is only intended as an example and for clarity only

442 focuses on connectivity between national parks (NPs), albeit plenty of links between other  
443 protected areas exist. As can be seen from the number and thicknesses of arrows, inter-  
444 patch connectivity between NPs in Angola, Namibia, and Botswana is comparably high.  
445 In addition, the bright colors highlight that most dispersal events between those areas are  
446 short. In contrast, we see that connections into the Kafue NP in Zambia require more steps  
447 and are fewer in general. Similarly, there is a lack of connections into Zimbabwe's Chizarira  
448 and Matusadona NP and the more distant Lower Zambezi and Mana Pools NPs.

## 449 **4 Discussion**

### 450 **4.1 Short Summary (90%)**

451 We used ISSFs to analyse data of dispersing wild dogs and parametrize a fully mechanis-  
452 tic movement model describing how dispersers move through the available landscape. We  
453 employed the parametrized model as an individual-based movement model and simulated  
454 80'000 dispersing wild dogs moving 2'000 steps across the extent of the KAZA-TFCA, the  
455 world's largest transboundary conservation area. Based on simulated dispersal trajectories,  
456 we derived a set of three complementary maps, all geared towards a better understanding  
457 of dispersal and landscape connectivity. The set of maps included a heatmap, revealing  
458 frequently traversed areas, a betweenness-map, delineating critical dispersal corridors and  
459 bottlenecks, and a map of inter-patch connectivity, indicating the presence or absence of  
460 functional links between national parks. We thereby showcase how ISSFs can be utilized  
461 as simple, yet powerful framework to parametrize movement models and simulate animal  
462 movement with the aim of assessing landscape connectivity. Such an individual-based simu-  
463 lation overcomes several conceptual shortcomings inherent to more traditional connectivity  
464 modeling techniques, such as least-cost analyses and circuit theory. Nevertheless, we sug-  
465 gest to view similar individual-based simulations as complement, and not as substitute, to  
466 traditional connectivity models.

### 467 **4.2 Movement Model (80 %)**

468 Our movement model of dispersing wild dogs comprised a habitat kernel, a movement kernel,  
469 and their interactions. Together, the kernels described habitat and movement preferences of  
470 dispersing individuals, as well as how movement behavior was affected by habitat conditions.  
471 Parameter estimates from the habitat kernel revealed that dispersing wild dogs avoid water,  
472 prefer its proximity, avoid woodland, prefer shrubs/grassland, and avoid areas dominated

473 by humans. These findings are consistent with the findings of previous studies on dispersing  
474 wild dogs (Davies-Mostert et al., 2012; Masenga et al., 2016; Woodroffe et al., 2019; O'Neill  
475 et al., 2020), as well as with an earlier dispersal model that we developed to investigate the  
476 habitat kernel of dispersers (Hofmann et al., 2021).

477 By expanding our initial model to include a proper movement kernel, we were able to  
478 model several additional complexities inherent to dispersal. It is, for instance, well known  
479 that dispersers typically move with directional persistence and that step lengths are corre-  
480 lated with turning angles. That is, larger steps usually coincide with smaller turning angles  
481 and vice versa (cite someone). While this correlation structure could be rendered by sam-  
482 pling turning angles and step lengths from copula probability distributions (?), the ISSF  
483 framework allowed us to model similar behavior directly in the movement model. Besides  
484 accounting for directional persistence, we further exploited the ISSF framework and included  
485 interactions between movement covariates to represent the fact that wild dogs mainly move  
486 during the more temperate morning and evening hours but tend to rest during the remainder  
487 of the day. The final model thus rendered a pulse-like movement behavior, where dispersers  
488 realize larger steps during morning and evening hours, but shorter steps during the rest of  
489 the day.

490 By including interactions between habitat and movement covariates, we also acknowl-  
491 edged that movement behavior of dispersers depends on habitat conditions. For example,  
492 the final model contained an interaction between water cover and step length, highlighting  
493 that dispersers are more likely to realize short steps (i.e. move slower) in areas covered  
494 by water. Likewise, the interaction between water cover and turning angles revealed that  
495 dispersers move less directional when moving across water bodies. We believe that this  
496 behavior is owed to the fact that wild dogs wade or swim to traverse waterbodies, thus  
497 resulting in slower, more tortuous movements. Besides this, our model also suggested that  
498 dispersers preferably realize shorter steps when moving through woodland, but larger steps  
499 when moving across shrubs/grassland. This can likely be attributed to resting periods dur-  
500 ing which dispersers seek shade and protection below the woodland canopy. Since we did  
501 not include three way interactions, we could not test this hypothesis.

### 502 **4.3 Simulation (80%)**

503 Based on the above outlined model results, we simulated 80'000 dispersers moving 2'000 steps  
504 across the landscapes of the KAZA-TFCA. Our dispersal simulation thus comprised 160 Mio.  
505 simulated steps, which required five days of computation on a modern desktop machine.

506 This rather long simulation duration was primarily owed to the massive extent considered  
507 (including the buffer ca. 1.8 Mio. km<sup>2</sup>) and the large number of dispersers simulated. Most  
508 connectivity studies consider much smaller extents (e.g. Kanagaraj et al., 2013; Clark et al.,  
509 2015; McClure et al., 2016; Abrahms et al., 2017; Zeller et al., 2020) and will therefore be  
510 able to attain faster simulation speeds. We also believe that fewer simulated dispersers will  
511 often suffice, as the relative traversal frequency of simulated individuals through randomly  
512 placed checkpoints in our study area converged rather quickly (Appendices), yet this will  
513 vary depending on the structure of the landscape and dispersal ability of the focal species.

514 A simulation-based approach as proposed in this article offers several advantages over  
515 more traditional connectivity modeling techniques such as least-cost analyses or circuit the-  
516 ory. In contrast to least-cost analyses, for instance, an individual-based simulation does  
517 not require predetermined endpoints. Instead, endpoints emerge naturally as the result of  
518 simulated dispersal trajectories. Not having to assume known endpoints is particularly im-  
519 portant for dispersal studies because dispersers often venture into unfamiliar territory and  
520 are therefore unlikely to know the endpoint of their journey. In addition, without known  
521 endpoints, movement corridors are no longer enforced between start- and endpoint, per-  
522 mitting to detect potential dead ends where dispersers get trapped due to insurmountable  
523 obstacles.

524 IBMMs furthermore yield the advantage of an explicit representation of time. This  
525 enables to answer questions such as: “*How long will it take a disperser to move from A to B?*”  
526 or *Is it possible for a disperser to move from A to B within X days?*”, all undoubtly interesting  
527 questions that shift the focus from a structural to a more functional view on connectivity.  
528 Similar questions cannot be answered using least-cost methods or circuit theory because the  
529 time component is omitted from those models. An explicit representation of time in IBMMs  
530 also yields exciting opportunities for studying seasonal changes to connectivity Zeller et al.  
531 (2020). With least-cost methods or circuit theory a dynamic analysis of connectivity is  
532 impractical because the same analyses needs to be repeated using different permeability  
533 surfaces (e.g. Benz et al., 2016; Osipova et al., 2019). With IBMMs, on the other hand,  
534 simulated individuals can directly respond to a dynamic environment within the model and  
535 the environment is allowed to change “as the dispersers move”.

536 While an explicit representation of time yields several advantages, it also requires that  
537 step lengths and turning angles are modeled properly (Kanagaraj et al., 2013), so that dis-  
538 persal durations between habitat patches can be reliably approximated. Accounting for  
539 and correctly rendering this movement kernel is the main strength of ISSFs, which is why

540 we believe that the framework is particularly well suited for simulating animal dispersal  
541 and assessing landscape connectivity. In principle, the ISSF framework allows to define an  
542 infinite amount of movement kernels, each representing movement behavior under different  
543 conditions (Fieberg et al., 2020). It can therefore accomodate highly diverse movement  
544 modes, including fast paced directional movements and slow paced tortuous movements.  
545 Compared to models that disregard an animal's movement kernel, this allows to model di-  
546 rectional persistence, a movement characteristic regularly observed in dispersing animals. To  
547 date, however, we only accounted for 1. order autocorrelation. That is, we only considered  
548 correlations between two subsequent steps. Modeling higher-order autocorrelation may be  
549 desirable, yet will require more extensive data.

550 Overall, IBMMs enable to generate a rich insight into the emergence of connectivty  
551 when compared to the outputs of least-cost analysis or circuit theory. By generating proper  
552 movement trajectories, a broad variety of summary statistics can be derived. Specifically, by  
553 turning simulated trajectories into a network, network theoretical metrics relevant to connec-  
554 tivity can be applied (Bastille-Rousseau et al., 2018). In contrast to least-cost path analysis  
555 and circuit theory, a simulation-based approach permits studying inter-patch connectivity.  
556 This facilitates the identification of asymmetrical links and statements about source-sink  
557 dynamics (Ferreras, 2001; Revilla et al., 2004; Kanagaraj et al., 2013). Our results are  
558 also in concert with previous studies on functional connectivity based on individual-based  
559 models that showed that including the behavioral ecology of the target species and the land-  
560 scape structure are imperative when assessing connectivity (Gustafson and Gardner, 1996;  
561 Gardner and Gustafson, 2004; Graf et al., 2007; Kramer-Schadt et al., 2004; Revilla et al.,  
562 2004; Revilla and Wiegand, 2008; Kanagaraj et al., 2013) rather than considering it purely  
563 a function of distance.

564 Besides the benefits of IBMMs, we also want to point out some caveats and not so trivial  
565 modeling decisions. In particular, we will discuss five modeling challenges: (1) number of  
566 simulated individuals, (2) location of source points, (3) dispersal duration, (4) boundary  
567 behavior, and (5) individual variability.

568 (1) When simulating dispersal, the modeler needs to decide on the number of simulated  
569 individuals. This decision involves the total (absolute) number of simulated individuals  
570 across the study area, as well as the relative number of simulated individuals per spatial  
571 entity (e.g. protected area, habitat patch, source point). With regards to the total number  
572 of simulated individuals, a larger number is usually desirable as it yields a more balanced  
573 view on connectivity. However, this comes at the cost of computational efficiency, implying

574 that a trade-off needs to be managed. One simple solution to handle the trade-off would  
575 be to simulate only as many individuals as are needed to achieve convergence in the target  
576 metric. In our case, examination of the target metric **traversal frequency** revealed that  
577 convergence was achieved with relatively few individuals, such that additional dispersers  
578 contributed only little additional information to our results. With regards to the relative  
579 number of simulated individuals, we see two feasible approaches. First, one could initiate  
580 dispersers in relation to population density at the respective area. This would directly  
581 reflect the fact that population densities are not homogeneous across space. (Say more)  
582 Alternatively, however, one could also distribute dispersers homogeneously, but then weigh  
583 simulated trajectories by the population density at the source patch (Say more). Because  
584 we lacked reliable information on density estimates for the extent of the KAZA-TFCA, we  
585 opted for a solution where dispersers were distributed homogeneously.

586 (2) While endpoints do not need to be defined in IBMMs, source points will still need to  
587 be provided by the modeler. Here, we randomly placed source points within protected areas  
588 large enough to sustain viable wild dog populations, knowing that the species primarily  
589 survives in these formally protected areas (Woodroffe and Ginsberg, 1999; Davies-Mostert  
590 et al., 2012; Woodroffe and Sillero-Zubiri, 2012; Van der Meer et al., 2014). In some cases,  
591 exact locations of potential source populations are known and source points can be placed  
592 accordingly (Kanagaraj et al., 2013). Moreover, if abundance estimates are available, these  
593 can be used to inform the relative number of dispersers initiated at each location. In other  
594 cases, comparable knowledge may be lacking and it could be more beneficial to delineate  
595 likely source patches based on habitat suitability models (e.g. Squires et al., 2013). Either  
596 way, a meaningful selection of source points is not a problem unique to IBMMs and applies  
597 to any connectivity modelling technique. As highlighted by Signer et al. (2017) the influence  
598 of the exact location of source points decreases as the number of simulated steps is increased,  
599 yet their goal was assessing steady state utilization distributions and not to assess landscape  
600 connectivity.

601 (3) When employing IBMMs, one also needs to decide on meaningful dispersal durations  
602 (number of simulated steps). We decided to simulate individuals for 2'000 steps, which  
603 is at the upper end of observed dispersal durations and may have resulted in an overesti-  
604 mated representation of landscape connectivity. Instead of enforcing homogeneous dispersal  
605 durations, one could also sample dispersal durations from on observed dispersal events. Al-  
606 ternatively, after each step, individuals could be faced with a probability to settle, where the  
607 probability is contingent on the surrounding landscape and cumulative dispersal distance

608 travelled. Because we only observed few dispersal events and due to the wild dog's ability  
609 to cover vast dispersal distance (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi  
610 et al., 2020) we decided not to apply this approach. Regardless of this, we think that in  
611 most cases it will be more insightful to simulate relatively extensive dispersal events and  
612 only subsample afterwards.

613 (4) Unless simulated individuals are strongly drawn towards a point of attraction, some  
614 simulated individuals will eventually approach a map boundary and the modeller needs  
615 to define a rule to handle such situations. One feasible option would be to terminate the  
616 trajectory as soon as it hits a map boundary, implicitly assuming that the simulated animal  
617 left the study area and will not return. The downside to this approach is that source points  
618 located near map boundaries will inevitably produce many such dead ends. Alternatively,  
619 one could remove transgressing random steps from the set of proposed random steps, thereby  
620 forcing virtual dispersers to bounce off virtual boundaries and remain within the main study  
621 area. This may seem like an elegant solution, yet again, it potentially results in substantial  
622 edge effects when source points are located near map boundaries. Finally, one could extend  
623 the study area by an artificial buffer zone through which dispersers are allowed to leave  
624 and re-enter the main study area. Of course this does not fully mitigate the issue, since  
625 some dispersers may still approach the outer map boundary, however, as Koen et al. (2010)  
626 have shown, such an artificial buffer can often help to mitigate edge effects. In theoretical  
627 applications, this issue can be circumvented by simulating movement on a torus (?), yet this  
628 is unfeasible in most real world applications.

629 (5) We simulated dispersal using point estimates from our most parsimonious movement  
630 model but did not investigate the sensitivity of our results with respect to those estimates.  
631 Uncertainty is rather common in dispersal studies on endangered species, as data tends to be  
632 scarce, resulting in model estimates large confidence intervals (Wiegand et al., 2003; Kramer-  
633 Schadt et al., 2007). To address this, one may explore a broader range of preferences instead  
634 of using point estimates initiate dispersers with randomized preferences with variability  
635 imposed by the uncertainty in the movement model. We therefore urge future studies to  
636 investigate the sensitivity of ISSF simulations with respect to estimated preferences.

#### 637 **4.4 Maps (10%)**

638 The heatmap resulting from our dispersal simulation suggests that a large portion of dis-  
639 persers traverses the Moremi NP and the Chobe NP in northern Botswana. Since we already  
640 highlighted the same area in our previous analysis (Hofmann et al., 2021), this result was to

641 be expected. Nevertheless, we believe it reinforces our notion that the area acts as crucial  
642 hub inside the KAZA-TFCA. The very same area stands out on the betweenness map, show-  
643 ing that the region is not only frequently traversed, but actually serves as stepping stone  
644 into more remote regions of the KAZA-TFCA. As such, the area exemplifies a region were  
645 both traversal frequency and betweenness scores are high. In contrast, the betweenness map  
646 suggests the presence of a corridor moving from Angola into Zambia's Kafue NP, yet when  
647 looking at the heatmap, one realizes that the area is not used very often. Consequently,  
648 despite the corridor's importance for linking Angola's NPs to Zambia's Np, only very few  
649 simulated dispersers successfully traversed it. This is also reflected in the interpatch con-  
650 nectivity map, where the Kafue NP only receives very few links from the central region of  
651 the KAZA-TFCA.

652 Each map that we produced from simulated trajectories accentuates a different aspect  
653 of connectivity. The heatmap, for example, puts emphasis on areas where movement is  
654 concentrated, regardless whether such areas represent “dead ends” that do not necessarily  
655 connect distinct patches. Therefore, the heatmap is useful to determine locations where a  
656 disperser are likely to move to, yet not necessarily to uncover corridors that link valuable  
657 habitats. The betweenness map, on the other hand, brings out those areas that are relevant  
658 in connecting different regions in the landscape. In this regard, the betweenness map is  
659 most pertinent to the delineation of dispersal corridors and may serve as an alternative to  
660 least-cost algorithms. Finally, the inter-patch connectivity map illustrates the frequency at  
661 which dispersal between distinct habitat patches occurs, as well as the average dispersal  
662 duration that passes when individuals move between those patches. This knowledge serves  
663 to gauge the amount of geneflow between habitat patches and can be employed to determine  
664 whether two habitats are connected or not.

## 665 **4.5 General (20%)**

666 While we did not attempt to model mortality during dispersal, it is well known that dis-  
667 persers regularly die, mainly due to deadly encounters with predators, road kills, or perse-  
668 cution by humans (Woodroffe and Sillero-Zubiri, 2012; ?). Mortality during dispersal could  
669 therefore substantially limit functional connectivity, especially in areas where the likelihood  
670 of encountering competitors and humans is high (Cozzi et al., 2020). If corresponding in-  
671 formation is available, IBMMs would readily allow to model mortality. Each timestep, a  
672 binary draw determines whether the animal survives or not and this probability can depend  
673 on landscape characteristics as well as the dispersal duration.

674 Our approach of simulating movement to assess connectivity is most closely related to the  
675 works of Clark et al. (2015) and Zeller et al. (2020), who used regular step selection functions  
676 to model habitat preferences by black bears and simulated movement to assess connectivity.  
677 However, neither of these studies attempted to jointly model habitat and movement kernels,  
678 thereby precluding a more mechanistic understanding of movement. Moreover, both studies  
679 parametrized models using data of resident black bearsk, which may lead to a biased view on  
680 connectivity, as dispersers may move substantially further, thereby improving connectivity  
681 among habitat patches (Elliot et al., 2014).

682 Besides enabling a more mechanistic understanding of connectivity, the ability to real-  
683 istically render movement during dispersal also forms the foundation for spatially realistic  
684 population models. In these models, dispersal is not merely represented by a dispersal ker-  
685 nel (e.g. ...) but mechanistically rendered (Revilla and Wiegand, 2008). Such population  
686 models can ultimately be employed to determine the required level of dispersal to achieve  
687 metapopulation viability (Davies-Mostert et al., 2012).

688 Simulations resulting from IBMMS could furthermore be utilized as simple tool to predict  
689 the likely whereabouts of GPS collared animals into the near future. In some European  
690 countries, the comeback of large predators, such as bears, lynx, and the wolf, has triggered  
691 emotional discussions and raised public concern (Behr et al., 2017), particularly in areas with  
692 free-roaming livestock that may be preyed upon by the returned species. An early warning  
693 system based on simulations could thus serve to forewarn about potential encounters and  
694 and thereby increase public acceptance of large predators.

695 We have previously attributed the weak significance of distance to water to the fact that  
696 we did not control for the presence or absence of conspecifics. We stick to this reasoning  
697 as our expanded model still shows a rather large uncertainty around the respective beta  
698 coefficients. To better gauge the importance and influence of this covariate, future studies  
699 will need to control for inter- and intra-specific interactions that may explain why and when  
700 dispersers are attracted to or afraid of waterbodies. Fortin et al. (2005), for instance, found  
701 that elk movement was significantly impacted by the density of wolf in the area, such that  
702 habitat preferences strictly differed depending on the presence or absence of wolves. The  
703 decision to settle is likely related to the presence or absence of conspecifics. Hence, the  
704 exact dispersal duration and distance will not be independent of current wild dog densities.  
705 In dispersing wolves, for instance, the longest dispersal distances have been observed in  
706 low-density populations (??). The dispersal duration may thus be determined by the by  
707 the amount of isolation between subpopulations and population densities (Davies-Mostert

<sup>708</sup> et al., 2012).

<sup>709</sup> Even though connectivity is generally thought to promote population viability, it is also  
<sup>710</sup> related to various aspects that may cause ecological damage, such as increased human-  
<sup>711</sup> wildlife conflicts or facilitated spread of deadly diseases.

<sup>712</sup> To this end, we have exemplified the use of ISSFs as a simple framework based on which  
<sup>713</sup> researchers can parametrize dispersers' habitat and movement preferences and at the same  
<sup>714</sup> time use the parametrized model to as an individual-based movement model to simulate  
<sup>715</sup> dispersal and examine landscape connectivity. Furthermore, we suggest to analyse simu-  
<sup>716</sup> lated trajectories using three complementary maps, each focused on a different aspect of  
<sup>717</sup> connectivity. Ultimately, we hope to have sparked interest in the uprising framework of step  
<sup>718</sup> selection functions for investigating dispersal behavior and landscape connectivity. Never-  
<sup>719</sup> theless, we do not attempt to dismiss the application of traditional connectivity models such  
<sup>720</sup> as least-cost methods or circuit theory by any means. Rather, we propose to use simulations  
<sup>721</sup> from ISSF-IBMMs as a simple but powerful tool that complements earlier methods in an  
<sup>722</sup> attempt provide a more comprehensive understanding of landscape connectivity.

## <sup>723</sup> 5 Authors' Contributions

<sup>724</sup> D.D.H., D.M.B., A.O. and G.C. conceived the study and designed methodology; D.M.B.,  
<sup>725</sup> G.C., and J.W.M. collected the data; D.D.H. and D.M.B. analysed the data; G.C. and A.O.  
<sup>726</sup> assisted with modeling; D.D.H., D.M.B., and G.C. wrote the first draft of the manuscript and  
<sup>727</sup> all authors contributed to the drafts at several stages and gave final approval for publication.

## <sup>728</sup> 6 Data Availability

<sup>729</sup> GPS movement data of dispersing coalitions will be made available on dryad at the time of  
<sup>730</sup> publication. Access to all R-scripts for our analyses is provided through Github.

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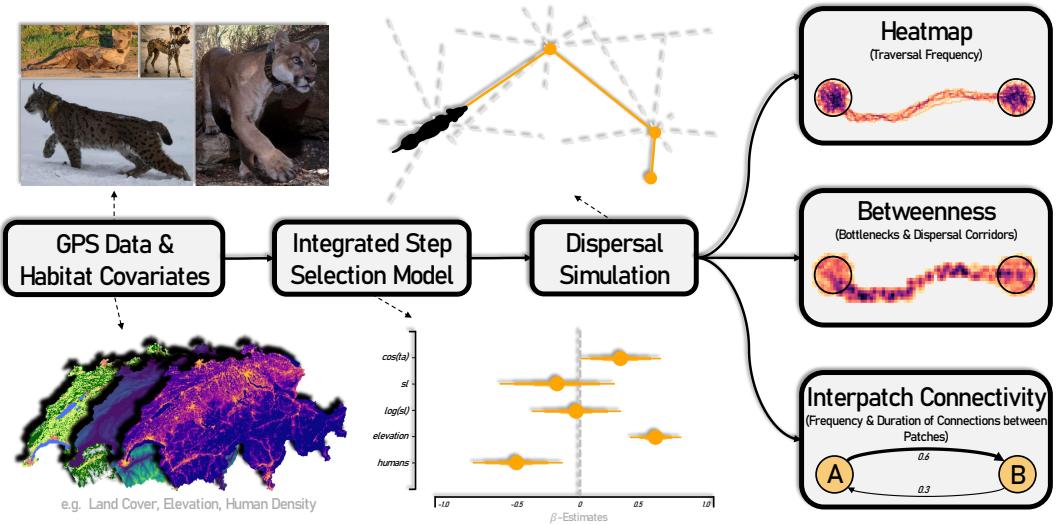
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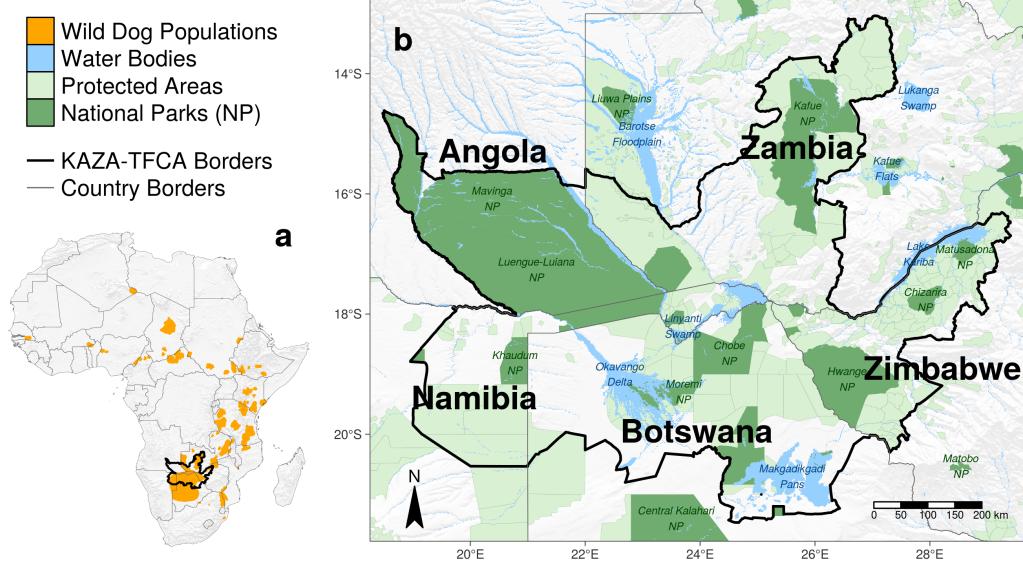
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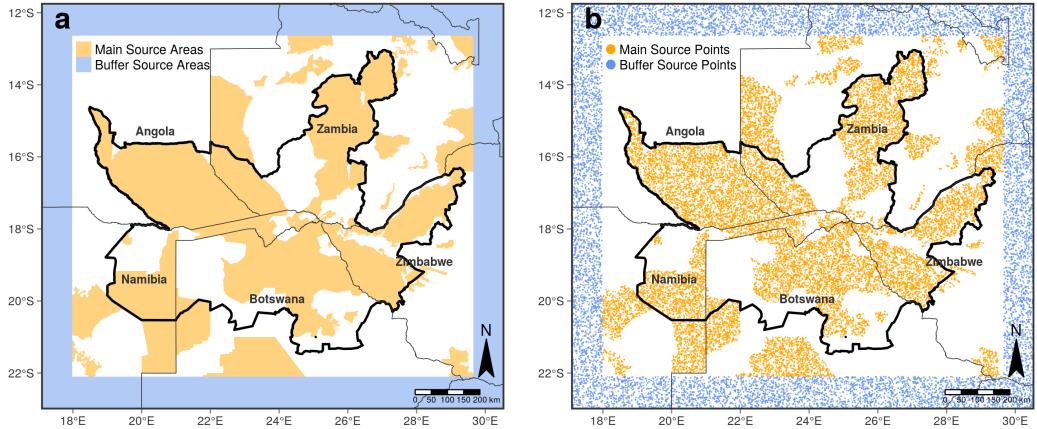
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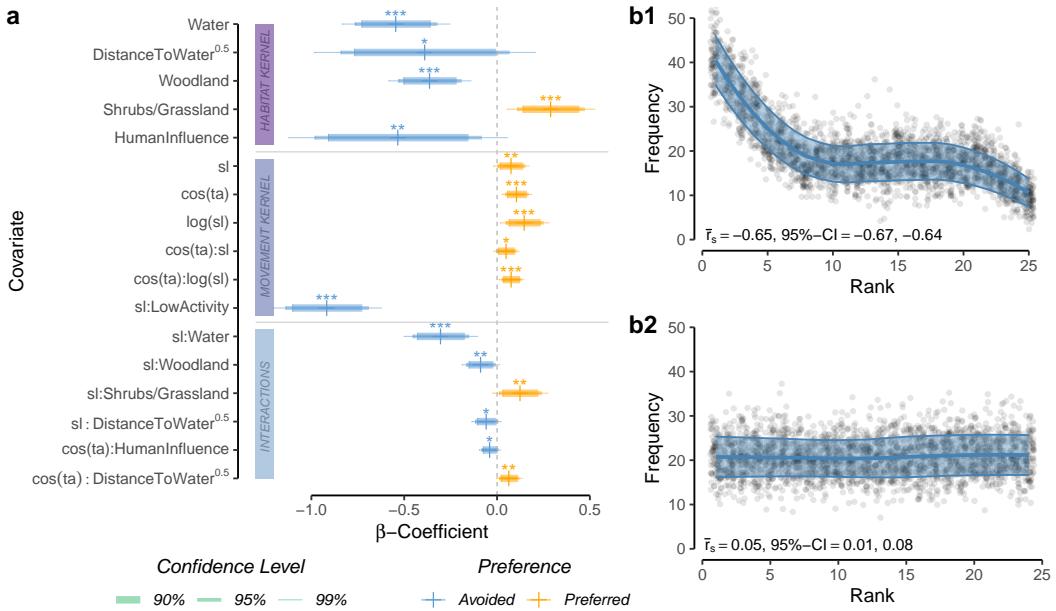
**Figure 1:** Flowchart of the simulation-based connectivity analysis. First, GPS data and habitat covariates have to be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement kernels. The parametrized model is then treated as an individual-based movement model and used to simulate dispersal trajectories. Ultimately, simulated trajectories serve to produce a set of maps that are pertinent to landscape connectivity. This includes a heatmap, indicating the relative traversal frequency across the study area, a betweenness map, highlighting movement corridors and bottlenecks, and, finally, an inter-patch connectivity map, where the frequency of connections and their average duration can be depicted. Photos: Whom to cite? Vectronics or Photographers?



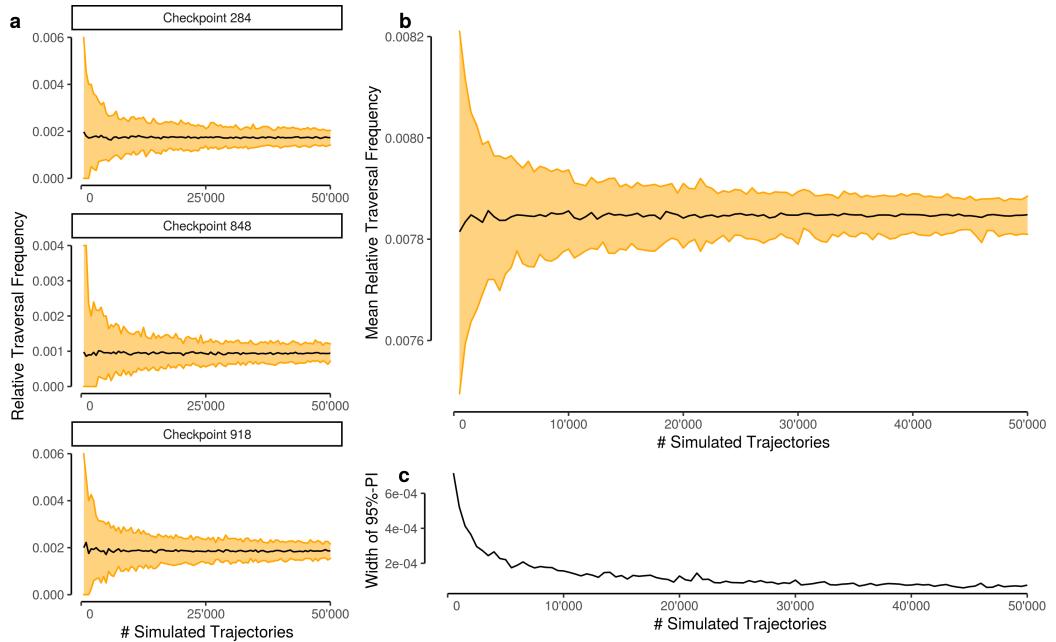
**Figure 2:** Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA and encompassing parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA represents the world’s largest terrestrial conservation area and covers a total of 520’000 km<sup>2</sup>. Its purpose is to re-establish connectivity between already-existing national parks (dark green) and other protected areas (light green). The dispersal data used in this study was collected on a free-ranging African wild dog population inhabiting the Moremi National Park in northern Botswana.



**Figure 3:** (a) Different source areas from which we released virtual dispersers. We only considered contiguous protected areas (national parks, game reserves, and forest reserves) that were larger than  $700 \text{ km}^2$  (green). This area corresponds to the average home range requirement for viable wild dog populations (Pomilia et al., 2015). To render potential immigrants into the study system, we also initiated dispersers within a buffer zone (blue) surrounding the main study area. (b) Source points from which dispersers were released. 50'000 dispersers were released from the main study area (green dots) and another 30'000 dispersers within the virtual buffer (blue dots).

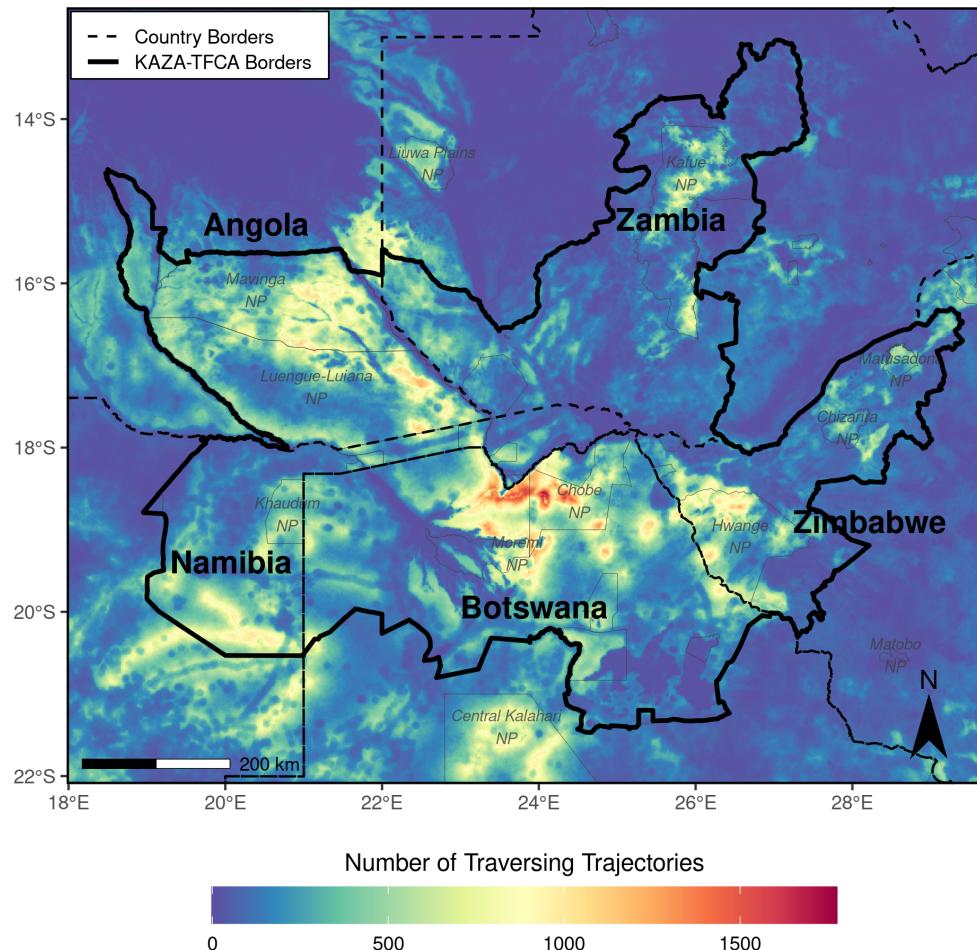


**Figure 4:** (a) Most parsimonious movement model for dispersing wild dogs. The model includes a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% Confidence-Intervals for the respective  $\beta$ -coefficients. Significance codes: \*  $p < 0.10$ , \*\*  $p < 0.05$ , \*\*\*  $p < 0.01$ . (b) Results from the k-fold cross validation procedure. The upper plot shows rank frequencies of realized steps according to model predictions with known preferences, whereas the lower plot shows rank frequencies of realized steps when assuming random preferences. The blue ribbon shows the prediction interval around a loess smoothing regression that we fitted to ease the interpretation of the plots. The significant correlation between rank and associated frequency in (b1) highlights that the most parsimonious model successfully outperforms a random guess (b2) and assigns comparably high selection scores to realized steps.

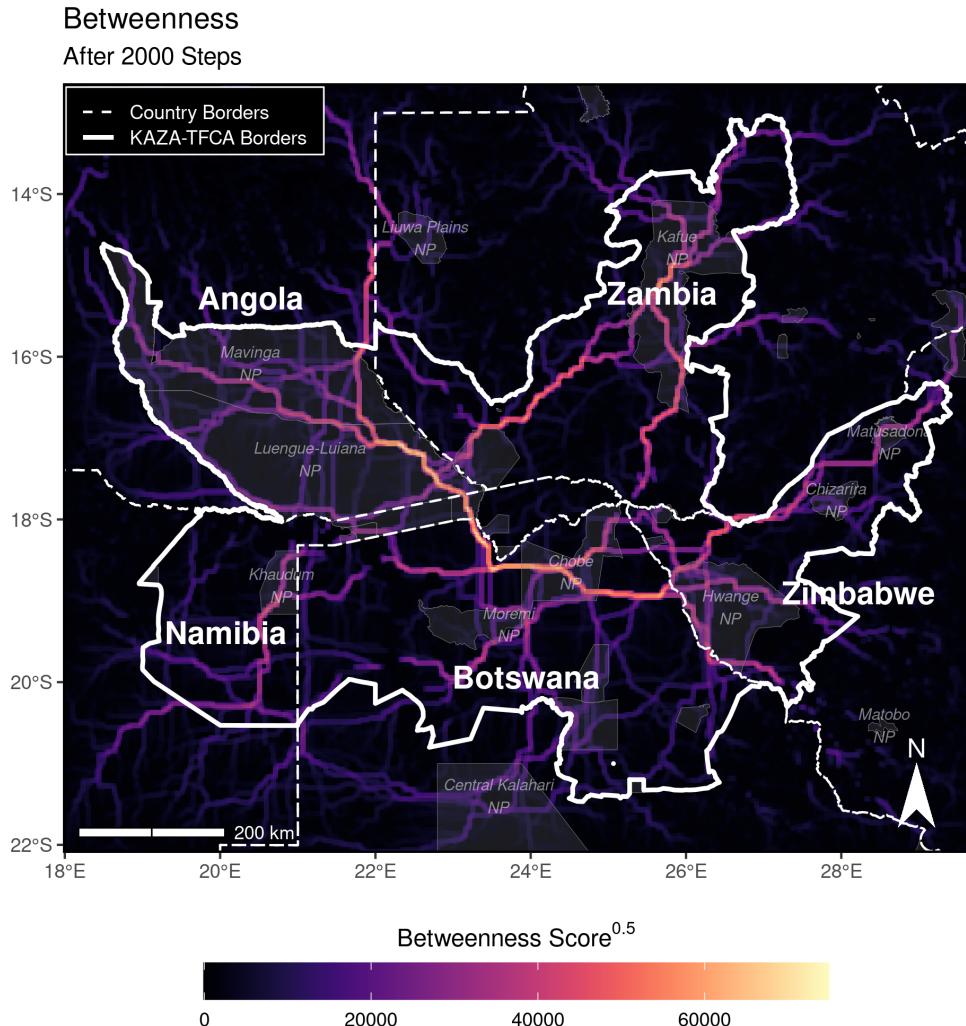


**Figure 5:** Relative traversal frequency across 1'000 checkpoints ( $5 \text{ km} \times 5$ ) distributed in the study area. The relative traversal frequency is plotted against the number of simulated individuals to visualize how quickly the metric converges to a steady state. (a) Replicated (100 times) relative traversal frequencies across three randomly chosen checkpoints as well as the corresponding 95% prediction interval (PI). (b) Averaged relative traversal frequency across all checkpoints and replicates including a 95% PI. (c) Width of the PI in relation to the number of simulated dispersers.

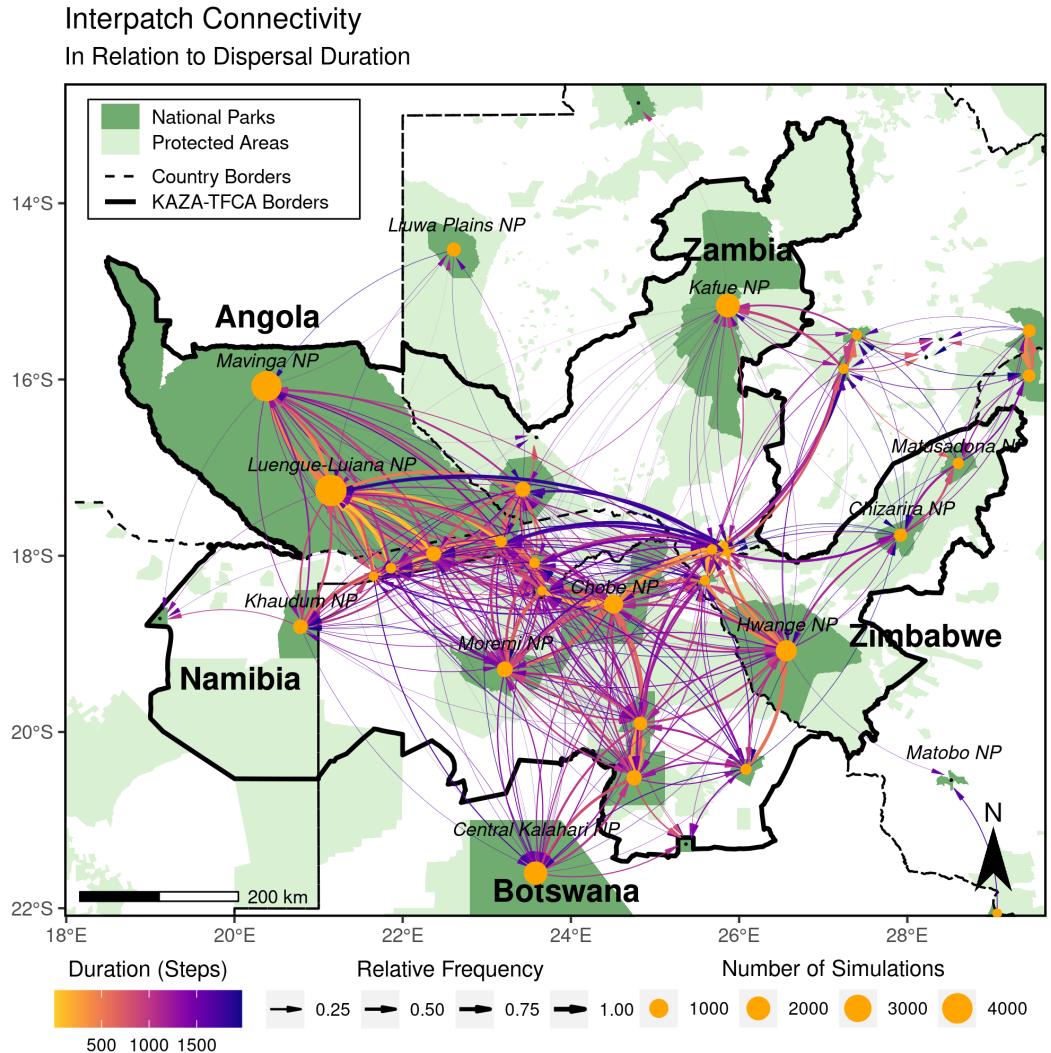
Heatmap  
After 2000 Steps



**Figure 6:** Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step selection model that we fit to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied all simulated trajectories. Consequently, the map highlights areas that are frequently traversed by virtual dispersers. Additional heatmaps showing the traversal frequency for different numbers of simulated steps are provided in Appendix S3.



**Figure 7:** Map of betweenness scores, highlighting distinct dispersal corridors and potential bottlenecks. A high betweenness score indicates that the respective cells are exceptionally relevant in connecting different regions in the study area. That is, the higher the betweenness score, the more often a pixel lies on a shortest path between adjacent areas. In this sense the metric can be used to pinpoint discrete movement corridors. Note that we square-rooted betweenness scores to improve visibility of corridors with low scores. Betweenness scores were determined by converting simulated dispersal trajectories into a large network. Note that we square-rooted betweenness scores to improve the visibility of corridors with low betweenness scores.



**Figure 8:** Network on simulated dispersal trajectories highlighting connections between national parks (dark green). Yellow bubbles represent the center of the different national parks and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent national parks that were smaller than  $700 \text{ km}^2$  and therefore did not serve as source areas. Arrows between national parks illustrate between which national parks the simulated dispersers successfully moved and the color of each arrow shows the average number of steps (4-hourly movements) that were necessary to realize those connections. Additionally, the line thickness indicates the relative number of dispersers originating from a national park that realized those connections. Note that a similar network view could be adopted to investigate connectivity between other protected areas need not to be restricted to national parks.

**Table 1:** Most parsimonious movement model for dispersing wild dogs. The model consists of a movement kernel, a habitat kernel, and their interactions. The movement kernel describes preferences with regards to movement behavior, whereas the habitat kernel describes preferences with respect to habitat conditions. Interactions between the two kernels indicate that movement preferences are contingent on habitat conditions. Note that all covariates were standardized to a mean of zero and standard deviation of 1. Plots to aid with the interpretation of this model are given in Appendix S2.

Kernel	Covariate	Coefficient	SE	p-value	Sign.	
Habitat Kernel	Water	-0.546	0.112	< 0.001	***	
	DistanceToWater <sup>0.5</sup>	-0.390	0.231	0.092	*	
	Woodland	-0.364	0.086	< 0.001	***	
	Shrubs/Grassland	0.288	0.092	0.002	***	
	HumanInfluence	-0.535	0.229	0.019	**	
Movement Kernel	sl	0.075	0.037	0.042	**	
	cos(ta)	0.105	0.031	0.001	***	
	log(sl)	0.146	0.051	0.004	***	
	cos(ta) : sl	0.049	0.026	0.064	*	
	cos(ta) : log(sl)	0.076	0.026	0.003	***	
Interactions	sl : LowActivity	-0.917	0.113	< 0.001	***	
	sl : Water	-0.305	0.076	< 0.001	***	
	sl : Woodland	-0.089	0.039	0.023	**	
	sl : Shrubs/Grassland	0.124	0.058	0.032	**	
	sl : DistanceToWater <sup>0.5</sup>	-0.058	0.031	0.056	*	
		cos(ta) : HumanInfluence	-0.040	0.022	0.070	*
		cos(ta) : DistanceToWater <sup>0.5</sup>	0.063	0.026	0.017	**

Significance codes: \*  $p < 0.10$    \*\*  $p < 0.05$    \*\*\*  $p < 0.01$