

Dispersal and Connectivity in Increasingly Extreme Climatic Conditions

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Abstract

While climate change has been shown to impact several life-history traits of wild-living animal populations, little is known about its effects on dispersal and connectivity.

Here, we capitalize on the highly variable flooding regime of the Okavango Delta to investigate impacts of changing environmental conditions on dispersal and connectivity of the endangered African wild dog (*Lycaon pictus*). Based on remote sensed flood extents observed over 20 years, we derive two extreme flood scenarios: a minimum and a maximum flood extent; representative of very dry and very wet environmental periods. These conditions are akin to those anticipated under increased climatic variability, as it is expected under climate change. Using a movement model parametrized with GPS data from dispersing individuals, we simulate 12,000 individual dispersal trajectories across the ecosystem under both scenarios and investigate patterns of connectivity.

Across the entire ecosystem, surface water coverage during maximum flood extent reduces dispersal success (i.e., the propensity of individuals to disperse between adjacent subpopulations) by 12% and increases dispersal durations by 17%. Locally, however, dispersal success diminishes by as much as 78%. Depending on the flood extent, alternative dispersal corridors emerge, some of which in the immediate vicinity of human-dominated landscapes. Notably, under maximum flood extent, the number of dispersing trajectories moving into human-dominated landscapes decreases by 41% at the Okavango Delta's inflow, but increases by 126% at the Delta's distal end. This may drive the amplification of human-wildlife conflict.

Whilst predicting the impacts of climate change on environmental conditions on-the-ground remains challenging, our results highlight that environmental change may have significant consequences for dispersal patterns and connectivity, and ultimately, population viability. Acknowledging and anticipating such impacts will be key to effective conservation strategies and to preserve vital dispersal corridors in light of climate change and other human-related landscape alterations.

1 Introduction

Climate change is expected to impact ecosystems across the globe with far-reaching consequences for the species living therein (Paniw et al., 2019; Radchuk et al., 2019; IPCC, 2022; Ozgul et al., 2023). By altering environmental conditions, climate change has been shown to affect animal behavior (Fuller et al., 2016), resource availability (Durant et al., 2007), demographic rates of local populations (Paniw et al., 2021), range distribution of wild-living animals (Thomas et al., 2004; Thuiller et al., 2006), and the potential for human-wildlife conflict (hereafter referred to as HWC; Abrahms et al., 2023), thus threatening the viability of most wildlife species. An important life-history trait known to influence the persistence of wild living populations across large spatial scales is dispersal (Hanski, 1999; Bowler & Benton, 2005; Kokko, 2006), which is defined as the movement of individuals away from their natal location to the site of first reproduction (Clobert et al., 2012). Despite the crucial role of dispersal in maintaining population viability, little is known about the impacts of climate change on long-distance dispersal and landscape connectivity. Nevertheless, assessing the consequences of climate change for dispersal is essential to anticipate potential shifts in range distributions and population dynamics.

Predicting how dispersal and connectivity respond to environmental change remains challenging (Littlefield et al., 2019). This is mainly due to insufficient data on dispersing animals at the appropriate spatial and temporal scales (Graves et al., 2014; Vasudev et al., 2015), coupled with limited insights into potential differences in environmental conditions under climate change (Scheiter & Higgins, 2009; IPCC, 2022). To address these shortcomings, one approach has been to combine climate projections and species distribution models with the aim of predicting future species ranges and investigating the impacts of such range shifts on structural connectivity (Wasserman et al., 2012; Ashrafzadeh et al., 2019; Luo et al., 2021). However, this approach fails to translate predicted atmospheric conditions into ground-level landscape characteristics (e.g., vegetation cover, surface-water). An alternative approach, albeit not primarily focusing on climate change, is to investigate how seasonality affects functional connectivity (e.g., Mui et al., 2017; Osipova et al., 2019; Zeller et al., 2020; Kaszta et al., 2021). This is usually achieved using seasonally updated resistance surfaces that depict the ease or difficulty at which the focal species can traverse a particular environment in a specific season (Zeller et al., 2012). Despite its biological relevance for understanding seasonal variability, this approach suffers from the short time-span at which processes are investigated and hinders drawing inferences on the long-term effects of climate change on dispersal and connectivity. Recently, alternative approaches for investi-

gating landscape connectivity that combine empirical GPS movement data with a modeling framework to reconstruct and predict movement trajectories at the level of the individual have been suggested (Signer et al., 2017; Hofmann et al., 2023; Signer et al., 2023). Such predicted trajectories are uncoupled from any temporal constraint and therefore suitable to investigate the effects of changing landscapes, as observed or predicted under the influence of climate change, on dispersal and connectivity. Given that climate change will shift systems towards conditions that currently represent extremes (Stott, 2016; Ummenhofer & Meehl, 2017; IPCC, 2022), we argue that a focus on extreme, rather than seasonal, variations could serve as a robust way to learn about the impacts of climate change on patterns of dispersal and connectivity. Such an approach appears particularly useful in cases where data on future environmental conditions are difficult to obtain or plagued by uncertainty (Collins et al., 2012).

One ecosystem that offers a unique opportunity to study the impacts of extreme environmental conditions on dispersal and connectivity in a large-scale natural experiment is the Okavango Delta in Botswana. The Okavango Delta (henceforth “Delta”) is the world’s largest inland delta and characterized by striking variability in its flood extent within and between years (Gumbricht et al., 2004; Wolski et al., 2017). The area covered by the Delta’s floodwaters can fluctuate between 3,500 km² during particularly dry and 14,000 km² during particularly wet periods (McCarthy et al., 2003; Gumbricht et al., 2004). The region is among the most vulnerable to climate change, as temperature increases of 4 to 6°C above pre-industrial levels are expected within the 21st century (Engelbrecht et al., 2015; Akinyemi & Abiodun, 2019); a prediction that goes far beyond the global average (IPCC, 2022). The rise in ambient temperature is likely to elevate evapotranspiration rates across the Delta’s alluvial fan, yet it is unclear whether water-losses to the atmosphere will be offset or exceeded by an increase in precipitation across the Delta’s catchment areas in Angola (Wolski & Murray-Hudson, 2008; IPCC, 2022). Despite the importance of the Delta as a driver of ecosystem functioning (Wolski & Murray-Hudson, 2008), species distribution (Bonyongo, 2005; Bennitt et al., 2014), and dispersal corridors (Hofmann et al., 2021; Hofmann et al., 2023), forecasting its flooding regime under climate change has proven notoriously difficult. Predictions of the flood extent under climate change range from “much drier” to “much wetter” depending on the employed model and climate scenario (Murray-Hudson et al., 2006; Wolski & Murray-Hudson, 2008).

Within this ecosystem a keystone predator and an umbrella species for conservation efforts is the African wild dog (*Lycaon pictus*), a large carnivore that is characterized by a

69 remarkable dispersal ability (McNutt, 1996; Davies–Mostert et al., 2012; Masenga et al.,
70 2016; Cozzi et al., 2020; Sandoval-Seres et al., 2022). Under favorable conditions, young
71 individuals that leave their natal pack can cover up to several hundred kilometers within
72 a few days, crossing a vast diversity of habitat-conditions (e.g., Cozzi et al., 2020). While
73 historically observed Euclidean dispersal distances are limited to 5-500 km (Davies–Mostert
74 et al., 2012; Cozzi et al., 2020; Sandoval-Seres et al., 2022), cumulative dispersal distances
75 of over 5,000 km have been recorded (Masenga et al., 2016). Previous research on dispersing
76 individuals revealed that the Delta’s floodwater represents a major barrier to dispersal (Hof-
77 mann et al., 2021; Hofmann et al., 2023) and it can be hypothesized that wild dog dispersal
78 and connectivity will be profoundly influenced by future changes in the flood regime, as
79 expected under the influence of climate change.

80 Utilizing a previously validated individual-based movement model parametrized with em-
81 pirical GPS data collected on dispersing wild dogs, we simulated 12,000 individual dispersal
82 trajectories under two extreme environmental scenarios: one assuming a maximum flood
83 extent, representing above-average wet climatic conditions, and one assuming a minimum
84 flood extent, representing acute dry conditions. Both scenarios reflect possible outcomes
85 under the effect of climate change. For each scenario, we assessed dispersal success and dis-
86 persal durations of simulated trajectories between distinct regions, mapped the emergence
87 of alternative dispersal corridors and bottlenecks, and investigated how differing corridor
88 arrangements influenced the potential for HWC (Figure 1). We anticipated lower dispersal
89 success and connectivity, as well as an increased propensity to disperse outside the main
90 study area during maximum flood. Furthermore, we anticipated major dispersal corridors
91 to differ between minimum and maximum flood, thus resulting in alternative hotspots for
92 HWC. Ultimately, our goal was to highlight that altered climatic conditions and associ-
93 ated changes in landscape characteristics can substantially affect the spatial arrangement of
94 movement corridors and, subsequently, the potential for HWC.

95 **2 Materials and Methods**

96 **2.1 Study Area**

97 To investigate the effects of flood extremes on dispersal and connectivity, we focused on a
98 *core study area* of 70,000 km² that comprised the Delta and its surroundings (Figure 2b;
99 purple circle). To accommodate for the long-distance dispersal events observed in this
100 ecosystem (Cozzi et al., 2020; Hofmann et al., 2021; Cozzi et al., 2023), we also considered

101 an *extended study area* of 300,000 km² spanning from 21°30' S to 17°30' S to and 20°30' E
 102 to 26°E and comprising the Delta and parts of Angola, Namibia, Botswana, Zimbabwe, and
 103 Zambia (Figure 2a). Rainfall in this area averages at 450 mm and is mainly concentrated to
 104 the wet season between November and April (Mendelsohn & El Obeid, 2004). Even though
 105 local rains and ground table levels resulting from floods of previous years may impact annual
 106 flood levels (McCarthy, 2006), the Delta's flood extent is primarily driven by precipitation
 107 patterns in its catchment areas in the Angolan highlands, from where water is channeled
 108 into the Cubango and Cuito rivers and subsequently discharged into the Okavango Delta
 109 (McCarthy et al., 1997; McCarthy et al., 2003). Since water only slowly descends from the
 110 catchment areas into the Delta and across its shallow alluvial fan (gradient $\sim 1/3,400$, Mc-
 111 Carthy et al., 1997), the flood usually reaches its maximum extent long after the local rains
 112 have ceased, during the peak dry season in July or August. Once the floodwater reaches the
 113 Delta's distal ends, it percolates at the Thamalakane and Kunyere Faults, two natural fault
 114 lines at which the water-flow is hindered (Figure 2b). After reaching its maximum extent,
 115 water evaporates or percolates and the flood steadily retracts over subsequent months. Such
 116 inner-annual dynamics are further amplified or buffered by multi-annual cycles in precipi-
 117 tation patterns across Angola (Wolski et al., 2012). Due to the intricate interplay between
 118 precipitation patterns in Angola, local ground-table levels, evapotranspiration, and anthro-
 119 pogenic water abstractions, predictions of the flood extent under climate change have proven
 120 challenging and range from "much drier" to "much wetter" depending on employed climate
 121 scenarios (Kgathi et al., 2006; Wolski & Murray-Hudson, 2008; Hughes et al., 2011; Wolski
 122 et al., 2012; Moses & Hambira, 2018). In the core study area, the vegetation is dominated
 123 by mopane forest (*Colophospermum mopane*), mixed woodland acacia-dominated (*Acacia*
 124 *spp.*), and grassland (Mendelsohn et al., 2010). Human influence is relatively low and mainly
 125 concentrated around small villages at the western and southern periphery of the Delta. The
 126 largest urban center is Maun, a spread-out settlement at the south-eastern tip of the Delta.
 127 Large portions of the core study area are designated as national parks, game reserves, or
 128 wildlife management areas. Some remaining sections of land are used for cattle farming
 129 and suffer from moderate levels livestock depredation and associated human-wildlife conflict
 130 (Gusset et al., 2009; McNutt et al., 2017). The core study area and its extended surroundings
 131 are part of the world's largest transboundary conservation initiative, the Kavango-Zambezi
 132 Transfrontier Conservation Area (KAZA-TFCA, Figure 2a), which attempts to re-establish
 133 connectivity among several core habitats. Previous studies have indicated that this initia-
 134 tive has high potential for improving connectivity among subpopulations of various species

135 (Brennan et al., 2020; Lines et al., 2021), including African wild dogs (Hofmann et al., 2021).
136 However, a better understanding of connectivity within this ecosystem under climate change
137 is lacking.

138 2.2 Spatial Habitat Layers

139 We represented the physical landscape through which dispersers could move by a set of
140 spatially referenced habitat layers, each with a resolution of 250 m x 250 m. The set
141 of layers included water-cover, distance-to-water, tree-cover, shrub/grassland-cover, and a
142 composite human influence layer representing settlements, roads, and agricultural areas. A
143 detailed description of these layers is provided by Hofmann et al. (2021). However, unlike
144 Hofmann and colleagues, who used a single, static flood map, we employed composite flood
145 maps to study connectivity. Specifically, we generated water-cover layers using MODIS
146 Terra MCD43A4 satellite imagery that we classified into binary water-cover maps using an
147 algorithm developed by Wolski et al. (2017) and implemented in R ([https://github.com/
148 DavidDHofmann/floodmapr](https://github.com/DavidDHofmann/floodmapr)). This algorithm allowed us to generate weekly updated “flood
149 extent maps”, thus providing detailed information about the flood at any given point in
150 time. In total, we generated 700 flood extent maps, covering the years 2000 to 2019. We
151 used these maps to produce minimum and maximum flood scenarios, representative of dry
152 and wet climatic conditions, assuming that climate change will shift the system towards
153 one of these extremes in the long run. To create the baseline minimum (and respectively,
154 maximum) flood scenario, we averaged the 100 flood extent maps with the smallest (highest)
155 flood extent and generated a binary layer by masking all pixels that were inundated in less
156 than 50% of the maps (see also Figure 1). By averaging across 100 flood extent maps, we
157 followed a conservative approach and mitigated chances of misrepresenting minimum and
158 maximum flood extent due to inaccuracies or artifacts in single remote sensed flood extent
159 maps. The final minimum and maximum flood extent maps (Figure 3) show that the flood
160 in the two scenarios covers 3,500 km² and 9,500 km², respectively. Finally, we combined
161 the two flood extent maps with the set of above-mentioned habitat layers into two spatial
162 stacks, each representative of one scenario (Figure 1). To prevent edge effects during the
163 dispersal simulation, we followed Koen et al. (2010) and expanded the stacks to an extent
164 that was 20% wider and taller than the original, filling the so created buffer zone (gray
165 buffer in Figure 2b) with randomized values from the respective layers. This would allow
166 simulated dispersers to leave and re-enter the main study area via randomized buffer zones.

2.3 Source Areas and Egression Zones

We simulated dispersing wild dogs originating from six distinct *source areas* located within the main study area (Figure 2b). Defining these source areas was necessary to enable identification and quantification of the number of successful dispersal events between different regions of the core study area across the two flood scenarios. We selected source areas in regions that remained dry during both scenarios and are known to host viable African wild dog subpopulations. Nevertheless, these areas are not exhaustive and viable wild dog populations are known to reside outside of them. The study area comprises mostly of continuous habitat, yet natural and anthropogenic landscape features allow the subdivision of the core study area into several sub-regions. The Delta’s hydrography and human settlements at its southern fringes result in a natural latitudinal split between the eastern (areas 1, 2, and 3) and western (areas 4 and 5) Delta (Figure 2b). Areas 1 and 2 are separated longitudinally by the Selinda Spillway, a waterway that connects the Delta with the Linyanti Swamp, while areas 2 and 3 are separated by the Khwai River, which inundates the Mababe Depression east of the Delta (Figure 2b). On the western side of the Delta, areas 4 and 5 are longitudinally separated by the Thaoga River drainage at Nokaneng (Figure 2b). Finally, the Delta hosts a central island, known as Chief’s Island, which we defined as source area 6 (Figure 2b). The shape of this area was determined by its borders towards water during the maximum flood scenario, whereas all other source areas were defined using circular polygons with radii of 20 km at somewhat equal distances to each other. We deliberately selected equally sized areas to facilitate comparability between them and to minimize variability in simulated connectivity due to target-effects. We also avoided source areas that directly bordered each other, as simulated individuals initiated close to a shared border would immediately result in connectivity and obscure differences between the two scenarios. Besides source areas 1 to 6, we also generated *egression zones* (Figure 2b). These zones enabled us to determine through which regions simulated individuals left the core study area, as well as to identify after how many simulated steps they did so. We generated these zones by overlaying the Delta with an ellipse that we dissected into equally sized polygons in accordance with cardinal directions (Figure 2b). Overall, the selection of source areas and egression zones was based on a mixture between biological and computational considerations.

2.4 Dispersal Simulation

We used a previously parameterized and validated dispersal model to simulate dispersal of African wild dogs. This dispersal model was trained using GPS data obtained from 16

200 wild dog coalitions dispersing across northern Botswana (Hofmann et al., 2023). These data
 201 were collected at a sampling rate of four hours, with the exception of one GPS location in
 202 the afternoon being skipped in order to accommodate the species tendency to be less active
 203 during this period (details in Cozzi et al., 2020; Hofmann et al., 2021). As such, a total of five
 204 GPS locations were collected per day. The collected data were then fed into an integrated
 205 step-selection function (iSSF, Avgar et al., 2016), where consecutive GPS locations were
 206 converted into *observed steps* (the straight-line connecting two consecutive GPS recordings;
 207 Turchin, 1998) and compared to a set of *random steps* using (mixed effects) conditional
 208 logistic regression (Fortin et al., 2005; Thurfjell et al., 2014; Muff et al., 2020; Fieberg et al.,
 209 2021; but see Michelot et al., 2024 for alternative approaches). iSSFs provide less biased
 210 estimates of habitat-selection than traditional resource-selection functions (Forester et al.,
 211 2009; Zeller et al., 2016) and bear the benefit that random steps are drawn from parametric
 212 step-length and turning-angle distributions, such that a model parametrized using iSSFs
 213 resembles a fully mechanistic model from which movement can be simulated (Signer et al.,
 214 2017; Potts & Börger, 2023; Signer et al., 2023). In contrast to graph-based connectivity
 215 models (e.g., least-cost path analysis or circuit-theory), simulations from iSSFs alleviate
 216 the need for resistance surfaces, which are often subjective (Simpkins et al., 2017; Marrec
 217 et al., 2020) and overestimate conductance in difficult to reach habitat (Signer et al., 2017;
 218 Hofmann et al., 2023). The dispersal model presented by Hofmann et al. (2023) comprised
 219 a habitat-selection function (describing habitat selection), a movement kernel (describing
 220 dispersers' movement capacities), and potential interactions between the two. According
 221 to the parametrized model, the main characteristics of wild dog dispersal movements are
 222 avoidance of water, avoidance of areas influenced by humans, and a preference for directional
 223 and fast movements. The associated model parameters (provided in Figure S1) can be used
 224 to predict probabilities of a step being chosen among a set of random steps (details in
 225 Supporting Information S1), which allows to simulate movements in discrete time.

226 Originating from each of the six source areas (Figure 2b), we simulated 2,000 individual
 227 dispersing trajectories, each composed of 2,000 steps. Two thousand steps corresponded to
 228 a dispersal duration of ~ 400 days, which marks the longest dispersal duration recorded
 229 in the study area (Cozzi et al., 2020; Hofmann et al., 2021). By simulating 2,000 steps,
 230 we generated the maximum amount of information possible and did not limit connectivity
 231 by defining a dispersal cap. Note that we assumed that individuals would not disperse for
 232 longer than 2,000 steps, but did not model settlement explicitly. This is because only little
 233 is known about how dispersing wild dogs locate potential mates and a suitable territory

to settle. Olfactory cues at shared scent-marking sites appear to play a crucial role, yet these are extremely difficult to find and monitor (Apps et al., 2022; Claase et al., 2022). We simulated 1,000 trajectories under the minimum flood extent, the remaining 1,000 under the maximum flood extent. Across the six source areas, this resulted in the simulation of a total of 12,000 individual dispersal trajectories, which sufficed to achieve convergence in relevant connectivity metrics (Hofmann et al., 2023). The simulation procedure was based on the algorithm described by (Signer et al., 2017) and Hofmann et al. (2023) and works as follows. A random location within the source area is defined as the starting point. Originating from the starting point, a set of 25 random steps is generated by sampling step lengths (sl) from a gamma distribution fitted to observed steps (shape = 0.37, scale = 6,316) and turning angles (ta) from a uniform distribution ($-\pi, +\pi$). Along each random step, the underlying spatial covariates are extracted, and relevant movement metrics computed ($\log(sl)$ and $\cos(ta)$). β -estimates from the fitted dispersal model are then used to predict the probability of each step being chosen, given the step's associated covariates and movement metrics, as well as characteristics of all other proposed steps. Among the 25 proposed steps, one is chosen at random based on assigned probabilities. The procedure is then repeated until a total of 2,000 steps is simulated.

2.5 Derived Metrics

Based on simulated dispersal trajectories, we quantified connectivity, identified the emergence of alternative dispersal corridors, and highlighted areas with elevated potential for HWC. Our approach drew upon the set of complementary connectivity metrics for individual-based movement models discussed by Hofmann et al. (2023), and was expanded to include a map highlighting areas with elevated HWC potential. The set of connectivity metrics comprised *inter-patch connectivity* metrics, summarizing dispersal success and duration into distinct habitat patches, *heatmaps*, depicting areas of intense use by dispersers, and *betweenness maps*, highlighting dispersal corridors and bottlenecks. Finally, the *HWC maps* served to reveal areas where simulated dispersers moved into the vicinity of human-dominated landscapes. To illustrate differences between metrics during maximum and minimum flooding, we computed difference maps for the heatmaps, betweenness maps, and HWC maps.

2.5.1 Inter-Patch Connectivity

To measure inter-patch connectivity, we tallied the number of trajectories successfully moving from one source-area to another and computed the average minimum dispersal duration

(in number of steps) required to make those connections. Dispersal between two areas was said to be successful whenever a trajectory originating from one area intersected with the polygon of another area. If a trajectory moved through multiple areas, a connection into each of them from the original source was recorded. We also estimated the number of individual trajectories that left the core study area and moved into one of the egression zones. To quantify variability in our estimates, we generated bootstrap samples by randomly drawing 1,000 simulated trajectories per source area 1,000 times with replacement and computing 95%-percentile intervals.

2.5.2 Intensity of Use

To quantify intensity of use of different areas, we generated heatmaps (also known as *utilization distributions* or *flow-maps*) by superimposing the study area with a grid with a spatial resolution of 1 km x 1 km and determining the number of simulated trajectories traversing each grid cell. Such maps are essentially movement-restricted permeability surfaces, thus highlighting areas of intense use (Signer et al., 2017; Hofmann et al., 2023; Potts & Börger, 2023). Heatmaps are relatively insensitive towards the chosen resolution and a 1 km x 1 km grid appeared to provide a good balance between detail and computational feasibility.

2.5.3 Betweenness

To compute spatially mapped betweenness scores, we overlaid the study area with a grid that had a resolution of 2.5 km x 2.5 km and computed the frequency at which simulated individuals transitioned from one grid-cell to another. A cell-transition was said to occur whenever a simulated step crossed from one grid-cell across or into another. In case the same individual repeatedly realized the same cell-transition, we only counted a single transition to avoid overemphasizing regions where individuals moved in circles. This procedure resulted in a weighted edge-list that we used to compute weighted betweenness scores for each grid-cell, i.e. the importance of the respective grid-cell in facilitating movement into adjacent areas (Bastille-Rousseau et al., 2018; Bastille-Rousseau & Wittemyer, 2021). We computed betweenness using the **igraph** R-package (Csardi & Nepusz, 2006). Calculations of betweenness scores are computationally demanding and result in discrete and narrow dispersal corridors (Hofmann et al., 2023). A higher map resolution thus results in increased computation time and narrower corridors. In our case, a grid size of 2.5 km x 2.5 km provided a sensible compromise between computational efficiency and biological relevance of emerging corridors (see also the appendix of Hofmann et al., 2023).

2.5.4 Human-Wildlife Conflict

To pinpoint potential hotspots for HWC, we identified regions where simulated trajectories moved into the vicinity of human-dominated landscapes. For this, we isolated locations along simulated trajectories that ranged ≤ 500 meters to the nearest grid-cell with human influence > 0 . Based on the so isolated coordinates, we generated density maps highlighting likely hotspots for HWC. While this approach of mapping potential HWC ignores human population density, we also generated a compound metric by multiplying the generated heatmaps with a continuous human-influence map (Supporting Information S10). Notably, not every animal in the vicinity of human-dominated landscapes implies conflict, hence we chose to use the term *potential* hotspots for HWC. We prepared these maps at a resolution of 1 km x 1 km.

2.6 Software

We conducted all data preparation and analyses using the programming language **R** (R Core Team, 2023). For any spatial data manipulation, we used the **R**-packages **terra** (Hijmans et al., 2023) and **spatstat** (Baddeley et al., 2015). Several helper functions for the dispersal simulation algorithm were written in **C++** and imported into **R** using the **Rcpp** package (Edelbuettel & François, 2011). Network analysis was achieved in **igraph** (Csardi & Nepusz, 2006) and figures were generated using **ggplot2** (Wickham et al., 2023) and **ggnetwork** (Briatte et al., 2023). Notably, a similar simulation procedure as employed in our analysis has recently been added to the **amt** **R**-package (Signer et al., 2023).

3 Results

3.1 Inter-Patch Connectivity

Our analysis of inter-patch connectivity revealed significant differences in dispersal success and duration depending on the flood scenario (Figure 4, Figure 5, Figure S2). Of the 6,000 simulated dispersal trajectories for each flood scenario, $4,137 \pm 35$ trajectories reached another source area during minimum flood, whereas $3,625 \pm 32$ trajectories did so during maximum flood, indicating a 12% lower dispersal success during maximum flood (Figure 4a1). Concurrently, the average dispersal duration of trajectories moving from one source area to another was 17% lower during maximum flood, with 122 ± 1 days compared to 143 ± 2 days (Figure 4b1) during minimum flood. The disparities were most pronounced for trajectories dispersing into source area 6 (the Delta's center), with $1,327 \pm 30$ simulated trajectories

reaching area 6 during minimum flood compared to 297 ± 17 trajectories (i.e., 78% lower) during maximum flood (Figure 4a1). Source area 6 therefore appeared to be particularly vulnerable to isolation in the maximum flood scenario. Interestingly, connectivity between some source areas was higher during maximum flood. For instance, the number of trajectories running from area 5 into area 4 was 67% higher, with 114 ± 10 trajectories during minimum flood compared to 190 ± 12 trajectories during maximum flood (Figure 4a1). Simulated individuals therefore responded to unfavorable habitat conditions by dispersing into another region of the landscape. Contrary to our expectations, movement into egression zones (areas 7 - 14) was only marginally higher during maximum flood, with the number of trajectories rising by 2%, from $5,457 \pm 22$ to $5,553 \pm 20$ (Figure 4a2 and Figure S5).

3.2 Intensity of Use

Heatmaps revealed that the Delta acted as a major dispersal barrier during maximum flood, but became permeable during minimum flood (Figure 6a). During maximum flood, the floodwater extended from the Delta's inflow until the densely inhabited regions at its southern fringes (the town of Maun and its surroundings), such that the negative impacts of water on dispersal were further aggravated by the negative effects of anthropogenic presence. Consequently, there was a substantial decrease in the dispersal frequency across the southern fringes of the Delta during maximum flood (Figure 6a). During minimum flood, however, the retracting flood revealed vast dispersal areas that individuals used to move across the otherwise inundated regions (Figure 6a).

3.3 Betweenness

Findings from the betweenness maps, which display corridors and pinch-points between neighboring areas, reinforced patterns observed on the heatmaps (Figure 6b). Multiple corridors linking source area 6 to the surrounding source areas existed during minimum flood, but many of them vanished during maximum flood (Figure 6b). Instead, a single corridor at the south-eastern tip of the Delta emerged (Figure 6b). Despite the corridor's high betweenness score, its apparent ability to link the eastern and western sections of the Delta was limited, as evidenced by a low traversal frequency on the heatmap (Figure 6a).

3.4 Human-Wildlife Conflict

The HWC maps highlighted two potential hotspots for HWC that depended on climatic extremes (Figure 6c). The first hotspot was located at the Delta's inflow between source

360 areas 3 and 4 and was most prominent during minimum flood. During maximum flood, by
 361 contrast, the density of simulated locations in the vicinity of humans decreased by 41% in
 362 this area (Figure 6c and Figure S9). Another hotspot, albeit visually less distinct, covered
 363 the region at the distal end of the Delta, extending across the town of Maun (Figure 6c).
 364 This area was particularly relevant during maximum flood, with a density that was 126%
 365 higher than during minimum flood (Figure 6c and Figure S9). The diversion of individuals
 366 from one area to another depending on flood conditions therefore drives the emergence of
 367 potential hotspots for HWC.

368 4 Discussion

369 4.1 Impacts of Extreme Environmental Conditions on Dispersal

370 We investigated the impacts of extreme environmental conditions, as anticipated under the
 371 influence of climate change, on dispersal and connectivity. For this, we employed a previously
 372 parameterized and validated movement model and simulated dispersal trajectories of African
 373 wild dogs in the Okavango Delta under extreme conditions. Our findings indicate that an
 374 amplified flood can significantly reduce dispersal success, prolong dispersal durations, and
 375 alter the spatial structure of major dispersal corridors, thereby creating or shifting hotspots
 376 of potential human-wildlife conflict (HWC).

377 Wetter-than-usual climatic conditions, a likely scenario for this study area (Wolski &
 378 Murray-Hudson, 2008; IPCC, 2022), resulted in significant barriers to dispersal and con-
 379 nectivity, and in an overall increase in dispersal durations. This was largely a result of
 380 simulated individuals avoiding large water bodies, thus detouring through more suitable
 381 habitats (Cozzi et al., 2013; Cozzi et al., 2020; Hofmann et al., 2021; Hofmann et al.,
 382 2023). Movement constraints due to changes in environmental conditions can thus lead to
 383 subpopulation isolation (up to > 75% in our case), thereby jeopardizing recolonization ef-
 384 forts following local extinctions, and impacting population dynamics, gene flow, and genetic
 385 diversity (Hanski, 1999; Frankham et al., 2002; Leigh et al., 2012; Baguette et al., 2013).

386 The African wild dog exhibits a remarkable dispersal ability, sometimes dispersing sev-
 387 eral hundred kilometers across international borders (McNutt, 1996; Davies–Mostert et al.,
 388 2012; Masenga et al., 2016; Cozzi et al., 2020; Sandoval-Seres et al., 2022; Cozzi et al., 2023).
 389 This ability likely evolved as an adaptation to the relatively low density at which the species
 390 occurs (Creel & Creel, 2002; Masenga et al., 2016) and may have been sustained by a his-
 391 torically well-connected landscape that imposed low mortality (sensu Fahrig, 2007). Today,

392 however, the need for vast dispersal habitats makes this species vulnerable to habitat loss
 393 and fragmentation (Woodroffe & Sillero-Zubiri, 2012; 2020). When dispersing animals are
 394 forced to alter their dispersal routes due to changing environmental conditions, this could
 395 result in non-optimal dispersal behavior in human-altered landscapes (Fahrig, 2007). This
 396 is particularly problematic when dispersers are channeled through areas with high anthro-
 397 pogenic resistance and elevated risk of mortality (Fahrig, 2007; Van Der Meer et al., 2014;
 398 Ghoddousi et al., 2021). For a population of African wild dogs in Zambia, Leigh et al. (2012)
 399 revealed that dispersal and the associated mortality indeed led to a decline in genetic diver-
 400 sity and, subsequently, to a net-loss of individuals. At present, our own study population
 401 appears to benefit from moderate levels of dispersal, as an analysis across Southern Africa
 402 revealed a genetically healthy cluster in the Kavango-Zambezi Transfrontier Conservation
 403 Area (Tensen et al., 2022). This cluster may, however, be at risk depending on future flood
 404 conditions.

405 As dispersal is a key process influencing population dynamics (Hanski, 1999; Clobert et
 406 al., 2012), any climatic-induced alteration will have cascading effects that amplify or buffer
 407 the effect of climatic changes on population persistence and viability. Lower connectivity and
 408 prolonged dispersal durations due to adverse environmental conditions will inevitably result
 409 in increased energetic expenditures and exposure to various threats such as predation, com-
 410 petition, human encounters, and diseases (Alberts & Altmann, 1995; Yoder, 2004; Stamps
 411 et al., 2005; Bonte et al., 2012), thus further jeopardizing dispersal success and its effect on
 412 population dynamics. Higher ambient temperatures have previously been associated with
 413 negative effects on wild dog reproductive success (Woodroffe et al., 2017; Abrahms et al.,
 414 2022), survival (Rabaiotti et al., 2021), and, consequently, population persistence (Rabaiotti
 415 et al., 2023). The negative effect of hotter climatic conditions on local population survival
 416 and recruitment may be further exacerbated by reduced dispersal success and connectivity
 417 in case of amplified flooding regimes.

418 Even though our finding that an increased flood extent reduces connectivity seems unsur-
 419 prising, it is non-trivial to quantify such impacts and to predict the spatial rearrangements
 420 of movement corridors they entail. Wild dogs avoid crossing water bodies, yet are capa-
 421 ble of doing so if they really need to, especially during dispersal (McNutt, 1996; Cozzi et
 422 al., 2013; Cozzi et al., 2020; Hofmann et al., 2023). By simply assuming such obstacles
 423 to be impenetrable, one may miss important corridors that lead across narrow sections of
 424 unsuitable habitat (Marrec et al., 2020). Using simulations from integrated step-selection
 425 functions (iSSFs), however, one can realistically render that an animals' decision to dis-

perse across a specific habitat is conditional on what's available at alternative steps. A disperser surrounded by a hostile matrix may readily cross water, whereas an individual dispersing through favorable habitat can choose to avoid water entirely. Another challenge when predicting the impacts of climate change on connectivity is that future on-the-ground conditions are rarely known (e.g., Wolski and Murray-Hudson, 2008). To overcome this, we leveraged historic data on seasonal variation of the flood extent and assumed that climate change would shift the ecosystem towards conditions that currently mark extremes. A similar approach can be applied in systems where the relationships between changing conditions and functional connectivity are less evident.

While wet extremes appear to hinder dispersal and connectivity, the opposite applies for amplified dry conditions, because areas that are inundated under normal circumstances become free of water and therefore passable. Predictions suggest that climate change will result in elevated precipitation across the Delta's catchment areas in Angola (Wolski & Murray-Hudson, 2008; IPCC, 2022), thus resulting in above-average flooded regions. Concomitantly, however, hotter temperatures and increased levels of evapotranspiration are anticipated for the Delta's basin in Botswana, suggesting that dry periods may be experienced too (Wolski & Murray-Hudson, 2008; Moses & Hambira, 2018; Akinyemi & Abiodun, 2019; IPCC, 2022). The Delta's expanse is also affected by multi-decadal oscillations in precipitation patterns, which may periodically offset or amplify long-term trends (Wolski et al., 2012). The overall impact of climate change on flood patterns therefore remains unknown (Wolski & Murray-Hudson, 2008; Wolski et al., 2012) and this lack of knowledge is aggravated by uncertainties regarding future anthropogenic water abstractions along the Okavango River (Kgathi et al., 2006; Murray-Hudson et al., 2006; Hughes et al., 2011). It is nonetheless worth noting that our maximum flood extent map, which was prepared based on 100 maximum flood extents observed on over 700 weekly-updated floodmaps, is conservative compared to historically observed flood extents in the Delta. While the flood in our map encompasses an area of 9,500 km², the Delta may inundate an area of up to 14,000 km² in exceptional cases (McCarthy et al., 2003; Gumbricht et al., 2004). Changes in dispersal behavior and connectivity due to climate change may therefore be more pronounced than reported here.

4.2 Human-Wildlife Conflict

Our analysis revealed that dispersers utilize different movement corridors depending on flood conditions, leading to the emergence and shifting of potential hotspots for HWC. An increased proximity between humans and carnivores is typically associated with a higher

459 potential for conflict (e.g., Michalski et al., 2006; Chapman and McPhee, 2016). Especially
 460 dispersers, which often venture outside protected areas, expose themselves to anthropogenic
 461 hostility (Elliot et al., 2014; Cozzi et al., 2020; Vasudev et al., 2023). In our case, the fun-
 462 neling of individuals through alternative dispersal corridors resulted in the shift of potential
 463 HWC hotspots, potentially increasing HWC and retaliatory killing. One example is the area
 464 surrounding Maun, where HWC is expected to rise during wet periods, exacerbating existing
 465 human-wildlife conflict (Gusset et al., 2009; McNutt et al., 2017; Cozzi et al., 2020). Iden-
 466 tifying and mapping the conflict-connectivity interface (i.e., areas prone to HWC) in light
 467 of climate change can improve our understanding of connectivity (Vasudev et al., 2023) and
 468 could aid in prioritizing mitigation and prevention measures that have the highest impact
 469 (Treves et al., 2011; Buchholtz et al., 2020) or to develop appropriate compensation schemes
 470 (McNutt et al., 2017). However, it is important to note that encounters between animals and
 471 humans do not imperatively imply HWC, and that the severity of conflict and its impact on
 472 connectivity likely depends on humans' perception and attitude towards wildlife (Ghoddousi
 473 et al., 2021). Besides the risks associated with direct mortality through human persecution,
 474 a higher proximity to humans also increases the risk of indirect mortality through disease
 475 transmissions from domestic animals (Cleaveland et al., 2000; Van De Bildt, 2002). Previous
 476 outbreaks of distemper and rabies have caused the local extermination of African wild dogs
 477 in several African countries (Woodroffe et al., 2004). As infected dispersing individuals may
 478 further spread diseases within protected areas, a better understanding of points of interac-
 479 tion between humans and wildlife will facilitate the implementation of targeted vaccination
 480 programs in the face of climatic change (Vial et al., 2006).

481 **4.3 Methodological Limitations and Future Research Directions**

482 In the present study, we ignored mortality during dispersal and assumed all simulated dis-
 483 persers to survive for 2,000 steps (~ 400 days). This likely resulted in an overestimation of
 484 connectivity, especially between distant source areas (Kramer-Schadt et al., 2004; Diniz et
 485 al., 2019; Fletcher Jr. et al., 2019; Day et al., 2020). The inclusion of mortality in individual-
 486 based simulations is relatively straight forward (Fletcher Jr. et al., 2019; Fletcher Jr. et al.,
 487 2023), yet its estimation for dispersing individuals has proven difficult (Behr et al., 2023).
 488 During the course of our study, we recorded and confirmed only two mortality events during
 489 dispersal, thus precluding a detailed investigation. Notably, unless the risk of mortality
 490 is included in simulations in a spatially explicit manner, its inclusion will merely shorten
 491 the length of simulated trajectories and its impact on inferred connectivity patterns will be

492 relative in nature.

493 Even though we assumed vegetation to remain unchanged in both extreme scenarios,
494 we acknowledge that vegetation cover and phenology may shift in response to climate
495 change, potentially influencing dispersal indirectly through prey availability (Bonyongo,
496 2005). While flooding represents the primary barrier to dispersing individuals (Cozzi et
497 al., 2020; Hofmann et al., 2021; Hofmann et al., 2023), refining and capturing the role of
498 vegetation dynamics on prey distribution and dispersal will therefore be crucial. However,
499 predicting the impacts of climate change on vegetation cover and its effect on the distribution
500 of prey will be challenging and is an area for continued research.

501 Our dispersal model was validated using independent dispersal data (see Hofmann et
502 al., 2023), yet validating predictions of connectivity and HWC under the two presented
503 scenarios remains challenging. This is mainly owed to the difficulty of monitoring dispersing
504 individuals *per se*, coupled with the low likelihood of observing dispersal during periods of
505 extreme flooding. Genetic data could serve to validate predictions of historical connectivity
506 patterns (Cushman & Lewis, 2010; Spear et al., 2010), yet is equally difficult to collect
507 and does not provide a means of validating predicted connectivity patterns in the short
508 run. Observational data, including photographic evidence from citizen scientists, however,
509 could serve to fill this gap (Marnewick et al., 2014; Cozzi et al., 2023). Most carnivores are
510 individually identifiable, either by their coat pattern or other unique morphological features
511 (e.g., Pennycuik and Rudnai, 1970 and Kelly, 2001). Automatic recognition of individuals
512 from photographic evidence using artificial intelligence will therefore open up new avenues to
513 track individuals through space and time (Cozzi et al., 2023). The so collected data provides
514 a means to monitor dispersal across unprecedented temporal and validate predicted patterns
515 of landscape connectivity.

516 4.4 Conclusion and Implications

517 In conclusion, our dispersal simulation across two extreme environmental scenarios revealed
518 striking differences in dispersal prospects and landscape connectivity for dispersing animals.
519 We thereby showed that extreme environmental conditions, akin to those projected under
520 climate change, will have important impacts on functional connectivity and may alter ar-
521 eas susceptible to human-wildlife conflict. Gaining insights into the dispersal patterns of
522 various wide-ranging species under changing conditions will be critical for designing and
523 preserving movement corridors (Vasudev et al., 2015). Wildlife managers and conserva-
524 tion bodies would also benefit from moving beyond a static assessment of connectivity and

525 considering multiple, potentially extreme, projections of environmental conditions to help
526 gauge the impacts of climate change on dispersal and connectivity. Successful conservation
527 strategies will be of particular relevance for wide-ranging and dispersal-dependent species
528 that are already threatened with extinction, such as the African wild dog. Ultimately, our
529 study provides valuable insights into the potential effects of climate change on dispersal,
530 connectivity, and human-wildlife-conflict dynamics, emphasizing the relevance of proactive
531 conservation measures and targeted mitigation strategies that incorporate predictions of
532 environmental change.

533 **5 Authors' Contributions**

534 D.D.H., G.C., D.M.B., A.O. and conceived the study, D.D.H. and G.C. designed method-
535 ology; D.D.H., G.C., D.M.B., and J.W.M. collected the data; D.D.H. analysed the data;
536 D.D.H. and G.C. wrote the first draft of the manuscript and all authors contributed to the
537 drafts at several stages and gave final approval for publication.

538 **6 Data Availability**

539 The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.z34tmpgnm> (Hofmann et al., 2024). R-codes required to repro-
540 duce all analyses are accessible through GitHub at <https://github.com/DavidDHofmann/FloodDispersal>. Additional information on the preparation of covariate layers are provided
541 by Hofmann et al. (2021) and a detailed description of the dispersal model is given by
542 Hofmann et al. (2023).

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Figure 1: Conceptual illustration of the employed analytical framework to investigate connectivity for dispersing African wild dogs under a minimum and maximum flood extent in the Okavango Delta. (a) Based on a series of 700 floodmaps, obtained between the years 2000 and 2019, we derived extreme scenarios for a minimum and maximum flood, using the minimum 100 and maximum 100 historically observed flood extremes. These layers were then joined with a static set of covariates and fed into a dispersal simulation. (b) The dispersal simulation was based on a previously parametrized integrated step-selection function for dispersing wild dogs and allowed simulating dispersal trajectories in the two extreme scenarios. (c) From simulated dispersal trajectories we generated four summary maps, highlighting connectivity patterns and areas potentially prone to human-wildlife conflict.

Figure 2: (a) Location of the study area, which forms part of the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA, red polygon) in Southern Africa. (b) The division of the core study area (enclosed by the purple ellipse) into sub-areas (1 to 6) was based on the hydrographic structure of the Okavango Delta and its tributaries. We simulated dispersal trajectories starting at random locations within each of the six source areas (orange circles). Purple zones (7 to 14) represent zones that we used to identify if and where simulated dispersers left the close surroundings of the Okavango Delta (thus called egression zones). These zones were generated using a set of cutlines (purple dotted lines) originating from the center of the Delta that dissected an elliptical buffer surrounding the Delta into sections of equal size and in accordance with cardinal directions. The yellow lines represent GPS trajectories of dispersing wild dogs that were observed using GPS collars. While not all of these individuals were used to parametrize the dispersal model presented by Hofmann et al. (2023), they serve to highlight the spatial scale at which the species disperses. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Figure 3: (a) Minimum and (b) maximum flood extent. The two maps were generated based on 100 minimum and 100 maximum flood extent maps from a series of 700 almost weekly updated remote sensed MODIS MCD43A4 satellite images spanning the years 2000 to 2019.

Figure 4: (a) Dispersal frequency (measured as the number of dispersal trajectories) and (b) dispersal duration (in days) between (a1, b1) source areas (labeled 1 to 6) and (a2, b2) egression zones (labeled 7 to 14) during minimum and maximum flood. Final rows and columns of each subplot represent summary statistics across all areas. For instance, the bottom row in a1 highlights for each source area the total number of trajectories successfully dispersing into a target area. The last column, in contrast, indicates the total number of trajectories immigrating into each target area. Values indicate mean \pm SD. The colors are mapped in a non-linear fashion to avoid over-emphasis on final rows and columns.

Figure 5: Dispersal frequency and duration between source areas 1 to 6 in the core study area during the minimum (left panel) and maximum (right panel) flood scenario. The dispersal frequency shows the number of trajectories that emigrated from a specific source area and successfully immigrated into another one. The dispersal duration indicates the mean dispersal duration (in days) required before trajectories arrived at the respective area. Although links between non-neighboring source areas occurred in the simulation, we here only present links between adjacent source areas for brevity. Detailed plots about source-specific inter-patch connectivity are provided in Figures S3 and S4.

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Figure 6: (a) Heatmaps, (b) betweenness maps, and (c) maps of potential for HWC derived from simulated dispersal trajectories. Left panels were derived from the minimum flood scenario, right panels from the maximum flood scenario. Source areas from which dispersers were released are numbered 1-6. The color scale for betweenness scores in (b) was square-rooted to improve visibility of corridors with lower values. Source-specific heatmaps, betweenness maps, and HWC maps are provided in Figures S6-S8.