

African Wild Dog Dispersal and Connectivity under Climate Change - Lessons Learned from Seasonal Flood Extremes

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Abstract

Climate change is expected to profoundly impact the life history of wild-living animal populations. While the impacts of climate change on the demographics of local subpopulations have been studied repeatedly, little is known about the consequences for dispersal and connectivity.

We capitalize on a “natural experimental setup”, the flood-pulse driven change in surface-water across the Okavango Delta in northern Botswana, to investigate the impact of changing environmental conditions on dispersal patterns and connectivity of the endangered African wild dog (*Lycaon pictus*). For this, we simulate dispersal trajectories across the Okavango Delta under two extreme scenarios that serve to represent environmental conditions akin to those expected under continued climate change; one assuming a maximum flood, one assuming a minimum flood.

During maximum flood, the Okavango Delta poses an important dispersal barrier that reduces dispersal prospects in increases dispersal durations between distinct areas. Across the entire study area, we observe 12% lower dispersal success and 17% longer dispersal durations during maximum flood. Most notably, dispersal into the central habitats of the Okavango Delta is reduced by 78% with an accompanied increase in dispersal durations of 19%. Depending on the flood, dispersal corridors traversed different areas and dispersers moved into proximity of different human-dominated areas.

Whilst the exact impacts of climate change on the flooding regime of the Okavango Delta remain unknown, our results suggest that connectivity will vastly differ depending on future flood conditions. Acknowledging such differences will be key to design effective conservation strategies, especially in light of ongoing climate change. Since we highlight critical dispersal corridors and human-wildlife conflict zones for two distinct future scenarios, our results will facilitate the evidence-based conservation of the endangered African wild dog.

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1 Introduction

1.1 Climate Change and Dispersal

Climate change is expected to profoundly impact ecosystems across the globe with far-reaching consequences for the species living therein (Ozgul et al., 2010; Radchuk et al., 2019; IPCC, 2022). By altering environmental conditions, climate change affects animal behavior (Fuller et al., 2016), resource availability (Durant et al., 2007), population dynamics (Paniw et al., 2021), and the distribution of wild living animal populations (Thomas et al., 2004; Thuiller et al., 2006). An important life-history pathway through which species may mediate the negative consequences of climate change is dispersal (Anderson et al., 2012), i.e. the movement of individuals away from their natal location to the site of first reproduction (Clobert et al., 2012). Through dispersal, species may adapt to climate change by tracking favorable habitat conditions (Raia et al., 2012) and by shifting into a different region of their fundamental niche (Kokko, 2006). Dispersal also facilitates the colonization empty habitats (Gustafson and Gardner, 1996; Hanski, 1999; MacArthur and Wilson, 2001), promotes the reinforcement of weakened and small subpopulations (Brown and Kodric-Brown, 1977), and safeguards genetic diversity (Frankham et al., 2002; Leigh et al., 2012; Baguette et al., 2013), thus providing additional resilience against changing environmental conditions (Kokko, 2006; Fahrig, 2003).

1.2 Connectivity

While dispersal offers a means to offset the negative demographic consequences of climate change (Kokko, 2006; Hodgson et al., 2009; Travis et al., 2013), it itself is a function of climatic and environmental conditions (e.g. Elliot et al., 2014; Behr, 2020). The link between dispersal and the environment can either be indirect, for example if the propensity of individuals to disperse depends on environmental conditions, or direct, when the biophysical environment through which dispersers move affects dispersal prospects (Travis et al., 2013). The latter highlights that dispersal is also inextricably linked to the concept landscape connectivity (Baguette et al., 2013), which is understood as the degree to which the landscape facilitates or impedes movements (Taylor et al., 1993). A sufficient degree of landscape connectivity is thus a critical prerequisite for successful dispersal (Fahrig, 2003), yet the continued degradation and destruction habitats worldwide continues to imperil the dispersal prospects of many species (Melbourne and Hastings, 2008; Sawyer et al., 2011). Conservation strategies that aim at facilitating dispersal by improving landscape connectiv-

ity are therefore often viewed as pinnacle of all conservation strategies (Heller and Zavaleta, 2009). Despite this, our understanding of dispersal and its implications for connectivity is limited, especially in light of changing environmental conditions.

1.3 Modeling Connectivity

To study dispersal and connectivity, various modeling techniques have emerged (see e.g. Etherington, 2016 and Diniz et al., 2019 for overviews). Initially, the techniques were limited to examining structural aspects of connectivity by focusing on the composition and configuration of habitat patches, while ignoring species' responses to the landscape matrix (Tischendorf and Fahrig, 2000; Doerr et al., 2011). With the increasing availability of telemetry data and methods to study species' habitat and movement preferences (Boyce et al., 2002; Fortin et al., 2009; Cushman and Lewis, 2010; Avgar et al., 2016), preferably during dispersal (Elliot et al., 2014), however, the focus has shifted towards a more functional view on connectivity, which also takes into account how species interact with their surroundings (Tischendorf and Fahrig, 2000; Doerr et al., 2011). Currently, the most prominent *functional* connectivity models are based on least-cost path analysis (LCPA, Adriaensen et al., 2003) and circuit theory (CT, McRae et al., 2008), two graph-based methods that estimate conductance of the landscape by means of a resistance (or inversely permeability) surface (Zeller et al., 2012). Such a surface is meant to reflect the ease or willingness at which the focal species traverses a specific area and is generated by consolidating multiple habitat layers into a single layer of resistance (Zeller et al., 2012). Since both LCPA and CT approaches make assumptions that are rarely met by dispersing individuals, individual-based movement models (IBMMs), in which dispersal movements are simulated explicitly, have also gained some momentum (Kanagaraj et al., 2013; Allen et al., 2016; Hauenstein et al., 2019; Diniz et al., 2019; Zeller et al., 2020; Unnithan Kumar et al., 2022a,b; Hofmann et al., 2023). IBMMs provide great modeling flexibility and are thus considered powerful tools for examining connectivity under different landscape configurations (Littlefield et al., 2019; Unnithan Kumar et al., 2022b). However, most connectivity studies focus on a snapshot in time and fail to account for changing environmental conditions, such as those akin to climate change. Moreover, the challenges associated with studying dispersing animals further impairs the collection of data during dispersal at the appropriate temporal and spatial scale (Graves et al., 2014; Vasudev et al., 2015) and weakens our ability to project dispersal prospects under changing environmental conditions into the future.

1.4 Climate Change and Seasonality

Predicting the impacts of climate change on dispersal and connectivity is non-trivial and typically requires spatial information about future climatic or environmental conditions over the area of interest (Littlefield et al., 2019). This information can then be used in various ways. Ashrafzadeh et al. (2019), for example, combined climatic predictions until 2070 with a species-distribution model for mountain newts (*Neurergus kaiseri*) in Iran to demonstrate a decrease in connectivity due to increased habitat fragmentation. Similarly, Luo et al. (2021) mapped the future distribution of the giant spiny frog (*Quasipaa spinosa*) under different representative climate pathways and reported a reduction in connectivity for the species across South-East Asia. In these studies, the focus lies on the impacts of climate change on species distribution and subsequent changes in connectivity due to the configuration of habitat patches, yet less on the habitat matrix and its implications for dispersal. For martens, (*Martes americana*), Wasserman et al. (2012) developed several resistance layers emerging under different climate scenarios and find that already low warmings will result in increased isolation of remaining subpopulations. While not primarily focused on climate change, another body of literature captures environmental variability by generating resistance surfaces for different scenarios. Mui et al. (2017), for instance, developed seasonal resistance maps for Blanding's turtle *Emydoidea blandingii* showing that connectivity was substantially lower in late summer compared to spring. Similarly, Osipova et al. (2019) studied connectivity for African elephants (*Loxodonta africana*) during wet and dry season and found that ignoring seasonality resulted in an underestimation of connectivity during the wet season and an overestimation during the dry season. For the same species, Kaszta et al. (2021) provide monthly updated connectivity maps revealing that connectivity varies strongly across a typical year. Finally, Zeller et al. (2020) use dynamic resistance surfaces showing differences in connectivity for black bears *Ursus americanus*. Altogether, the studies exemplify that connectivity should not be regarded as static in time, but dynamic across and within years.

In many cases, anticipating environmental conditions under climate change is not viable as relevant data is not available or entails major uncertainty (Collins et al., 2012). This is particularly true for complex ecosystems with intricate feedback loops and in cases where one is interested in landscape characteristics, rather than climatic conditions. In general, it is accepted that aside from increasing temperatures, climate change will also amplify the frequency and magnitude of extreme events, such as severe droughts, heavy precipitation, floods, and storms (Stott, 2016; Ummenhofer and Meehl, 2017; IPCC, 2022). Thus, instead

of attempting to study the impacts of climate change directly, one may capitalize on naturally occurring fluctuations of the environment to gauge the likely consequences of shifting the system towards what is currently considered an extreme.

1.5 Okavango Delta

The Okavango Delta (OD) in Southern Africa poses a unique opportunity to study the impacts of extreme environmental change on species dispersal ability and connectivity in a large scale natural experiment setup. The OD is the world's largest inland delta and characterized by substantial seasonal differences in surface-water cover. Throughout the course of a year, the area covered by the OD's floodwaters can fluctuate between 3'000 and 10'000 km² with striking variability within and between years (Gumbrecht et al., 2004; Wolski et al., 2017). Importantly, the region is among the most vulnerable to climate change, as a temperature increase of 4 to 6°C above pre-industrial levels is expected within the 21st century (Engelbrecht et al., 2015; Akinyemi, 2019), which is far beyond the global average (IPCC, 2022). A keystone predator in this ecosystem and an umbrella species for conservation efforts is the African wild dog (AWD, *Lycaon pictus*). While the species was once widespread across entire Sub-Saharan Africa, it has disappeared from a vast majority of its historic range, mainly due to human persecution, deadly diseases, and continued destruction and degradation of its habitats (Woodroffe and Sillero-Zubiri, 2012). AWDs are characterized by an unsurpassed dispersal ability, as young individuals that leave their natal pack can cover several hundred kilometers within a few days (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020). Dispersal typically happens in dispersal coalitions of same-sex siblings (McNutt, 1996). Previous research has shown that the ODs floodwaters pose a major dispersal barrier, yet the analysis was centered around an average flooding scenario (Hofmann et al., 2021).

1.6 What We Did

Here, we utilize a previously parameterized and validated dispersal model as IBMM to simulate dispersal and assess dispersal success and connectivity patterns for African wild dogs under two extreme scenarios: one assuming maximum flooding of the Okavango delta and one assuming minimum flooding of the Okavango delta. The IBMM was trained using GPS data collected during dispersal and frequently updated environmental data, thus providing a high degree of realism (Hofmann et al., 2021). Given that dispersers avoid crossing through water (albeit we do occasionally observe it in the field), we anticipated that dispersal

prospects and connectivity during maximum flood would be low. Moreover, when the flood extent of the OD is at its maximum, the water extends almost into the densely populated village of Maun. Since both the flood and humans are avoided by dispersing wild dogs, we anticipated that a fully flooded Delta would result in a total halt of movement between the Western and Eastern side of the OD. Information on habitat selection or connectivity is also suitable for predicting areas with an elevated potential for human wildlife conflict (Buchholtz et al., 2020). Hence, also quantified areas with high potential for human wildlife conflict.

2 Materials and Methods

We conducted all data preparation and analyses using the programming language R (R Core Team, 2022). For any spatial data manipulation, we used the packages `terra` (Hijmans, 2022) and `spatstat` (Baddeley et al., 2015). Several helper functions for the dispersal simulation algorithm were written in C++ and imported to R using the `Rcpp` package (Eddelbuettel and François, 2011). Network analysis was achieved in `igraph` (Csardi and Nepusz, 2006) and figures were generated using `ggplot2` (Wickham, 2016) and `ggnetwork` (Briatte, 2021). All R-scripts required to replicate our analyses are provided through an online repository.

2.1 Study Area

The study area for this analysis was focused on the Okavango delta (OD) and its surroundings in Southern Africa, comprising parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia (Figure 1). While our primary focus lied on the immediate surroundings of the Okavango Delta, we considered an extended rectangular extent stretching from 20°30' E to 26°E. This encompasses a total of 300'000 km²) and comprises all long distance dispersal events previously recorded in this area (Cozzi et al., 2020; Hofmann et al., 2021). The annual flood-pulsing rhythm of the OD is mainly dictated by precipitation in the Angolan highlands, which serve as catchment areas from which water is further channeled into the Okavango River and transported into the OD (Wolski et al., 2017). Although precipitation reaches its maximum between December and March, the collected water only slowly descends through the Okavango River and its distributaries, reaching the distal ends of the delta only towards July or August. In result, peak flooding is out of sync with local precipitation, such that the flood usually arrives in the OD during the peak dry season. Once the water reaches the OD's distal ends, it percolates at the Thamalakane and Kunyere Faults, two natural faultlines at which the waterflow is hindered. During minimum extent, the flood covers an

area of only 3'600 km², whereas during maximum flood more than 9'000 km² are flooded. Vegetation in this study area is dominated by mopane forest, mixed acacia woodland, and grassland. Human influence is low and mainly concentrated around small villages at the western periphery of the OD as well as the city of Maun at the south-eastern tip of the OD. Large portions of land are dedicated national parks, game reserves or forest reserves. The study area is also part of the world's largest transboundary conservation initiative, the Kavango-Zambezi Transfrontier Conservation Area. Previous studies have attributed a high potential of this initiative for improving connectivity for various species (Brennan et al., 2020; Lines et al., 2021; Hofmann et al., 2021).

2.2 Spatial Habitat Layers

We represented the physical landscape through which dispersers could move by a set of spatially referenced habitat layers, each with a resolution of 250 m. The set of layers included water-cover, distance-to-water, tree-cover, shrub/grassland-cover, and a human influence layer depicting anthropogenic influences through villages, roads, and agriculture. A detailed description of the different habitat layers is provided in (Hofmann et al., 2021). Importantly, the water-cover and derived distance-to water layers were generated using MODIS Terra MCD43A4 satellite imagery that was classified into binary water-cover maps using a “floodmapping” algorithm developed by (Wolski et al., 2017). This allowed us to generate almost weekly updated “floodmaps”, thus providing detailed information about the flood-extent at any given point in time. In total, we generated 700 floodmaps between the years 2000 and 2019, based on which we generated a minimal and maximum flood scenario. To create the minimum (maximum) flood scenario, we averaged the 100 floodmaps with the smallest (highest) flood extent and generated a binary layer by masking all pixels that were inundated in less than 50% of the maps. The resulting maps are presented in Figure 2. Ultimately, we combined the habitat layers into two stacks, one representing the minimum flood scenario, one representing the maximum flood scenario. To mitigate edge effects during the dispersal simulation, we followed Koen et al. (2010) and expanded the spatial extent of the stacked layers by 20% and randomized habitat values within the so created buffer zone (red rectangle in Figure 1a).

2.3 Source Areas and Emigration Zones

We simulated dispersing AWDs originating from six distinct source areas located in the vicinity of the OD (Figure 1). We placed source areas in regions that remained dry during

both the minimum and maximum flooding scenario and are known to host viable wild living wild dog populations. While source areas one to five were located across the delta's periphery, source area six laid in the OD's center. The selection of distinct source areas served to facilitate the identification and quantification of the number of successful dispersal events between different regions of the OD. Besides source areas, we also generated "emigration zones" that we used as checkpoints to determine if and where simulated individuals left the delta's immediate surroundings (Figure 1). We generated these zones by first overlaying the OD with an elliptic that we dissected into roughly equally sized polygons in accordance with cardinal points (Figure 1).

2.4 Dispersal Simulation

We used a previously parameterized and validated dispersal model to simulate dispersal of AWDs. The dispersal model was trained using GPS data of 16 wild dog coalitions dispersing across northern Botswana (Hofmann et al., 2023) which was fed into an integrated step-selection function (iSSF, Avgar et al., 2016). In iSSFs, consecutive GPS locations are converted into steps (the straight-line traveled between two GPS recordings (Turchin, 1998)) and compared to a set of *random* steps in a conditional logistic regression framework (Fortin et al., 2005; Thurfjell et al., 2014; Muff et al., 2020; Fieberg et al., 2021). Because iSSFs capitalize on the autocorrelated nature of the collected data, they provide better estimates of connectivity than traditional resource selection approaches (Zeller et al., 2016). The model presented in Hofmann et al. (2023) comprised of a movement kernel, describing how dispersers move across the landscape in the absence of habitat selection, a habitat kernel, indicating preferred or avoided habitat features, and interactions among the two, i.e. how movement behavior changes depending on habitat conditions. According to this model, the main characteristics of AWD dispersal movements are avoidance of water, avoidance of areas influenced by humans, and a preference for directional and fast movements. The model parameters are provided in Appendix SX and explained in Hofmann et al., 2023.

Originating from each of the six source areas, we simulated 2'000 individuals dispersing for a total of 2'000 steps. 1'000 individuals were simulated assuming a minimum flood, the remaining 1'000 assuming a maximum flood. This resulted in the simulation of a total of 12'000 individuals. The simulation procedure was based on the algorithm described in Hofmann et al. (2023) and works as follows. A random location within the source area is defined as starting point. Originating from the starting point, a set of 25 random steps is generated by sampling step lengths from a gamma distribution fitted to observed steps (shape

$= 0.37$, scale = $6'316$) and turning angles from a uniform distribution $(-\pi, +\pi)$. Along each random step the underlying spatial covariates are extracted, and relevant movement metrics are computed. β -estimates from the fitted model are used to predict the probability of each step for being chosen, given the steps associated covariates. Among the 25 proposed steps, one is chosen at random based on assigned probabilities. The location of the animal is updated, and the procedure is repeated until the desired number of steps is realized. Here, we simulated each individual for 2'000 steps, corresponding to a dispersal duration of 400 days and the longest dispersal duration recorded in this study area (Cozzi et al., 2020; Hofmann et al., 2021). The simulated trajectories can be understood as correlated random walks.

2.5 Derived Metrics

Based on simulated dispersal trajectories we quantified connectivity and identified areas of elevated potential for human wildlife conflict. Our assessment of connectivity was based on the three complementary connectivity metrics for IBMMs discussed in Hofmann et al. (2023). The set of metrics comprised of *heatmaps*, depicting areas of intense use, *betweenness maps*, highlighting dispersal corridors and bottlenecks and *maps of inter-patch connectivity*, visualizing dispersal success, and duration into distinct habitat patches. We generated heatmaps by superimposing the study area with a grid with a spatial resolution of 1 km and quantifying the frequency of simulated trajectories traversing each grid cell. To compute spatially mapped betweenness scores, we overlaid the study area with a grid that had a resolution of 2.5 km and determined 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 emphasis on regions where individuals moved in circles. This 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 and Wittemyer, 2021). Betweenness was computed using the igraph R-package (Csardi and Nepusz, 2006). Because the computations associated with calculating betweenness scores are computationally more demanding, we deemed the grid size of 2.5 km a sensible compromise between efficiency and resolution. As a final connectivity metric, we computed the number of successful dispersal events between each of the six distinct source areas. We coin this type of connectivity “inter-patch connectivity”. Dispersal

between two areas was said to be successful whenever the trajectory of an individual leaving one area intersected with the polygon of another area. We also estimated the number of individuals that left the OD's vicinity and moved into an emigration zone. To quantify the dispersal durations required to move between source areas or into emigration zones, we recorded the minimum number of steps that individuals moved before arriving at the respective destination. Besides connectivity, we also identified zones with a high potential for human wildlife conflict. For this, we isolated all simulated locations where simulated individuals moved within 500 meters of the nearest human-influenced grid-cell. Based on the so isolated coordinates we generated density maps. To highlight differences between derived metrics during maximum and minimum flooding, we computed difference maps for the heatmap, betweenness map, and human wildlife conflict maps.

3 Results

Figures depicting the derived connectivity and human-wildlife conflict maps are provided in Figure 5. Difference maps to visualize the differences between minimum and maximum flood are given in Figure 6. For brevity, we will here focus on system-wide connectivity patterns and only selectively point to regional results. Local connectivity maps derived for each source-area separately are presented in the Appendix. As the heatmaps in Figure 5a reveal, the OD acts as major dispersal barrier during maximum flood yet reveals vital dispersal habitat during minimum flood. Differences between maximum and minimum flood (Figure 6a) are particularly pronounced for the region between source areas 1 and 2, where few dispersers occur during times of maximum flood. In fact, because the floodwaters of the OD reach almost into Maun, the OD creates a line of separation between its eastern and western sections. The separation is further amplified as the city of Maun is avoided by dispersers in both scenarios. Similar patterns are observed on the betweenness maps (Figure 5b), where several pinch-points and bottlenecks linking source area 6 to the surrounding source areas exist during minimum flood. During maximum flood, however, these links vanish and instead a single corridor at the south-eastern tip of the OD emerges (Figure 6b). Despite its apparent importance in linking the eastern and western sections of the delta, it is evident from (Figure 5a) that this corridor is only rarely used, especially during the maximum flood scenario. As for the potential for human wildlife conflict, two clusters emerge (Figure 5c). The first cluster lies at the inflow of the Okavango Delta between source areas 4 and 5 and is most pronounced during minimum flood (Figure 6c). Another, albeit visually less distinct, cluster covers the area at the distal end of the OD, stretching from lake Ngami to

Maun. This area appears particularly relevant at maximum flood (Figure 6c). Our analysis of inter-patch connectivity further demonstrates notable differences in dispersal prospects and dispersal durations depending on the extent of the flood (Figure 5d and Table 1). While $4'137 \pm 34.60$ simulated dispersers reach another source area during minimum extent, only $3'627 \pm 39.09$ do so during maximum extent, thus indicating an overall decrease in dispersal success of 12 % during maximum flood. Concomitantly, the average minimum dispersal durations increases by 17 %, i.e. from 612 ± 7.24 steps to 717 ± 8.56 steps during maximum flood. These differences are particularly pronounced for individuals dispersing into source area 6 on Chief's Island. While the area is reached by $1'325 \pm 31.49$ simulated individuals during minimum flood, only 298 ± 16.47 , i.e. 78 % less, arrive there during maximum flood. Furthermore, the dispersal duration into source area six from any other source area increases by 19 % from 772 ± 15.20 steps to 920 ± 30.23 steps. In few occasions, connectivity between some areas increased during maximum flooding, for instance. Temporary emigration increased from $5'458 \pm 21.68$ to $5'551 \pm 20.06$ trajectories (i.e. by 2 %). Permanent emigration increased from $4'202 \pm 35.79$ to $4'405 \pm 35.74$ trajectories (i.e. by 5 %).

4 Discussion

4.1 Brief Summary

In this study, we used a previously parameterized and validated movement model to simulate dispersal trajectories of AWDs across the OD under two extreme environmental scenarios: one representing minimal flooding and one representing maximum flooding. This approach allowed us to investigate connectivity patterns that emerge under extreme environmental conditions, similar to those projected under climate change. Predictions of flood conditions across the OD under climate change remain ambiguous, yet it is generally agreed that climate change will amplify climatic variability and result in either exacerbated or attenuated flood events. Our two reference scenarios served to approximate these conditions. By providing a comprehensive set of connectivity maps for both scenarios, we highlighted how dispersal routes and prospects of the endangered AWD changed depending on flood conditions. Our simulations revealed that the propensity to move between the eastern and western sections of the OD decreased significantly during maximum flood. This effect likely resulted from the combined influence of floodwaters and anthropogenic pressures, which together formed a dispersal barrier that limited connectivity. When flooding was at a minimum, on the other hand, the retracted floodwaters revealed vital dispersal habitats that facilitated movement

between the western and eastern regions of the OD. Anecdotal evidence supports the notion that vital dispersal habitats are only available during periods of low flood, for the only dispersal coalition recorded to successfully move between the eastern and western delta using GPS data was observed at a time of minimal flooding (Cozzi et al., 2020). The lack of dispersal habitat during maximum flood also resulted in an almost complete isolation of Chief's Island, the OD's central peninsular (source area 6 in Figure 1b). The peninsular itself remains dry in both scenarios, yet becomes entirely surrounded by water during times of maximum flood. This limits pathways to emigrate or immigrate and results in low dispersal prospects for individuals moving towards this area. Despite the general reduction of connectivity and increased dispersal durations during maximum flood, the number of dispersers moving between some of the source areas increased during maximum flood. This was, for instance, the case for movements between sour areas 1 and 4 and likely resulted from individuals that were deflected by the expanded flood and redirected into more accessible habitats. The deflection of individuals by the flood also had direct implications for the spatial arrangement of dispersal corridors as movement routes that traverse the central parts of the OD disappeared and more individuals were funneled through a corridor running along the southern fringes of the OD.

4.2 Validating Predictions

Although the movement model underlying our simulations was validated using independent dispersal data (see Hofmann et al., 2023), assessing the reliability of our predictions for the two extreme flooding scenarios remains challenging. Firstly, because collecting data of dispersing individuals is difficult *per se* (Fattebert et al., 2015; Cozzi et al., 2020) and, secondly, because flood-conditions akin to those studied here only occur rarely (Wolski et al., 2017). Dispersers typically only make up for a small proportion of the entire population and predicting the timing of dispersal is often non-trivial. Coupled with the limited battery-lifetime of most conventional GPS collars, it is logistically unfeasible to collected large amounts of GPS data during dispersal. However, as an alternative to GPS data, genetic or observational data could also yield insight into functional connectivity. Genetic data is often viewed as ultimate measure of functional connectivity (Baguette et al., 2013) and thus often serves as validation of connectivity maps (e.g. Cushman and Lewis, 2010 or Spear et al., 2010). Genetic analysis across southern Africa revealed moderate levels of dispersal and identified a genetically particularly diverse population cluster located near northern Botswana (Tensen et al., 2022). While such analyses provide valuable insights into long-term dispersal patterns,

they are unlikely to yield insights on short-term connectivity patterns such as those studied here. Observational data, on the other hand, readily delivers information on seasonally changing dispersal patterns. Such data may not only be collected by trained field assistants, but could also be obtained through photographic evidence from tourists in a citizen's science approach. AWDs, as well as most other large carnivores, are individually identifiable, either by their coat pattern or other unique features. Given a set of georeferenced images, individuals can thus be traced through space and time. Cozzi (2013) provide first evidence on the usefulness of this approach. As of today, however, the moderate amount of data collected and spatially biased sampling effort prohibits using such data for validation purposes. Finally, our representation of the flood was, by design, focused on rare extreme events. Since the beginning of our dataset. Consequently, the amount of data suitable for validation is limited.

4.3 Climate Change in the Okavango Delta

Despite the importance of the OD as a driver of ecosystem functioning, species distribution, and dispersal corridors, predicting flood patterns under future conditions has proven notoriously difficult (Wolski and Murray-Hudson, 2008). This is owed to the intricate interplay between climatic conditions, anthropogenic water usage, and the topographic peculiarities of the region. In regard to climatic conditions, Southern Africa is projected to face temperature rises above the global average (Engelbrecht et al., 2015). According to predictions, this will cause a more intense but shorter rainy season in Botswana (Akinyemi, 2019). Precipitation across the ODs catchment areas in Angola is expected to increase but it remains unclear whether elevated precipitation levels will be offset by increased temperatures and accelerated evapotranspiration (Wolski and Murray-Hudson, 2008; Moses and Hambira, 2018). In a recent study, Wolski and Murray-Hudson (2008) used three competing climate models and predicted that conditions across the delta may range from "much wetter" to "much drier". Accurate predictions of future conditions across the OD are further hindered by multi-decadal oscillations in precipitation patterns in Angola that cause shifts between wet and dry periods and may offset or amplify long term trends over short periods (Wolski and Murray-Hudson, 2008; Wolski et al., 2012). Besides climatic uncertainties, the OD's future is plagued by socio-economic uncertainties. The OD and its tributaries represent important water-sources for adjacent communities and are subject to intense developmental debates about future abstractions. These result from an ever-growing human population, increasing socio-economic needs, and resettlement in Angola following peace (Kgathi et al.,

2006) and have culminated in large uncertainties regarding the dimensions of future water abstractions (Hughes et al., 2011). Although upstream abstractions along the Okavango River are thought to have relatively little impact on the flooding pattern of the OD, the combined effects of climate change and anthropogenic abstractions could result in significant “delta-drying” (Murray-Hudson et al., 2006). A final complicating factor is the OD’s shallow gradient (1:3300, Gumbrecht et al., 2004) in result to which water only slowly descends through the OD. Hippos dredge many of the slow-moving waterways and thereby ensure a steady flow of water, yet their behavior can also lead to the creation of new waterways and thus to a spatial redistribution of floodwater across the delta (McCarthy et al., 1998). In summary, the significant uncertainties regarding future flood conditions preclude clear predictions of connectivity and complicate the protection and preservation of important movement corridors, especially in light of climate change. Thus, instead of anticipating and preparing for a single, clearly defined scenario, conservation authorities must maintain flexibility and develop a multitude of strategies that can be applied to each case.

4.4 Social Resistance

Here, we focused on the influence of environmental resistance on dispersal but disregarded the impact of social resistance. That is, while our simulation rendered how environmental features affect dispersal behavior, it neglected potential interactions between dispersing AWDs and their conspecifics, predators, or prey. This was a simplifying assumption and owed to a lack of data on sympatric species at the appropriate temporal and spatial scale. According to the social resistance hypothesis, however, dispersers’ movement patterns are likely to be driven not only by environmental features, but by a combination of environmental-, intra-, and interspecific conditions (Armansin et al., 2019). Together, intra- and inter-specific factors are sometimes referred to the *social landscape* through which dispersers move and are thought to be important drivers of dispersal behavior (Wey et al., 2015). Previously, this has been demonstrated for dispersing meerkats (*Suricata suricatta*), a species surprisingly similar to the AWD in terms of its social organization and dispersal behavior (Cozzi et al., 2018). Similarly, it has been discovered that AWDs rely on shared marking sites to advocate presence and reproductive status (Apps et al., 2022; Claase et al., 2022). Although the sites are primarily used by resident AWDs, even dispersers or competing species use them occasionally to obtain information on the presence of local packs. In fact, dispersers may use the marking sites to more effectively navigate the social landscape and avoid competitors or locate other-sex dispersal coalitions. Besides such intra-specific factors,

also the distribution and abundance of prey can be expected to have direct consequences on dispersal routes, as dispersers are usually in search of suitable, i.e. prey-rich, territory to settle. This goes to show that accounting for the social landscape will not only add another level of realism, but also additional complications. Interacting species cannot be considered as independent of each other, meaning that the impact of climate change on one species will result in trophic cascades affecting several species at once with substantial alterations in the community composition (Thuiller et al., 2006).

AWDs primarily prey on species that are either restricted by access to water or by the forage growing in its close proximity. Attraction of prey to water is particularly evident during the dry season, when pans and puddles dry up and forage becomes scarce across the landscape. During these periods, floodplains serve as fallback habitat and attract large herds of ungulates that forage near rivers and streams filled by floodwater (Bonyongo, 2005; Bennett et al., 2014). We previously reported that dispersing AWDs also prefer moving near water sources, likely in an attempt to track their prey (Hofmann et al., 2021). However, a reduction in the spatial extent of flood and associated losses in floodplain habitats could lead to increased concentration of prey and intensified competition among large carnivores. Within this carnivore community, AWDs are inferior predators and face challenges in competition with lions, spotted hyenas. Resident or dispersing AWDs that avoid superior competitors in space or time may get forced into areas of moderate prey-availability (Dröge et al., 2017). An increased flood-level, on the other hand, will likely limit the amount of suitable habitat across the OD's landscape. Recent research on lions has demonstrated that flooding reduces the carrying capacity of the system for lions, resulting in a crowding within remaining habitats and increased competition. It is, however, unclear how an increased flood level will affect inter-specific competition and whether AWDs will persist under elevated levels of intra-guild competition.

4.5 Anthropogenic Resistance

To this day, the social acceptance of AWDs among the local population of northern Botswana has not been investigated. This prohibits a deeper understanding of the anthropogenic resistance experienced by dispersing individuals (Ghoddousi et al., 2021). Talk a bit about anthropogenic resistance. While our dispersal model rendered dispersers' behavior with regards to the presence of humans, it did not take human behavior into account. This is generally referred to as anthropogenic resistance. The employed dispersal model rendered how biophysical elements and anthropogenic presence influence dispersal movements. It did

not, however, account for social or anthropogenic resistance. Corridors that are estimated based on landscape features only may over- or under-estimate true connectivity. Overestimate in areas where there is strong anthropogenic resistance (e.g. hunting, trapping) - Underestimate in areas where humans facilitate movements (e.g. through supplementary food supplies). The flood might funnel individuals into unsafe areas with high risk of human-caused mortality (Northrup et al., 2012) (i.e. ecological traps). Depending on the flood, individuals get funneled towards different regions of high anthropogenic influence, suggesting that climate change may induce spatial shifts in regions with a high potential for human-wildlife conflict. Depending on the level of anthropogenic resistance that dispersing wild dogs experience in the different areas, these regions may act as ecological traps into which individuals get funneled due to external conditions.

4.6 Human Wildlife Conflict

It is well documented that a close proximity between humans and wildlife increases the likelihood of human-wildlife conflict (e.g. Michalski et al., 2006 or Chapman and McPhee, 2016). It can thus be expected that areas where dispersers move into proximity of human-dominated landscapes hold an increased potential for human-wildlife-conflict (HWC). It has been suggested that climate change will increase competition between humans and wildlife for scarce resources and thereby exacerbate HWC globally Abrahms (2021). Our simulations suggest that dispersers may indeed utilize different routes depending on flood conditions. In our case, this did not result in an overall increase in HWC, but we observed a regional shift of where dispersers come into the vicinity of human-dominated areas. During minimum flood, these areas were most prominent along the OD's panhandle, where the Okavango River enters the alluvial fan of the OD. The panhandle is inhabited comparably densely (13 inh. / km²) and used for both agricultural farming (11% covered by agricultural fields) and livestock farming (9 cattle / km²). It has previously received attention as a hotspot for human-wildlife conflict due to livestock depredation by carnivores (LeFlore et al., 2019) and repeated elephant raids (Buchholtz et al., 2020). During maximum flood, in contrast, a larger number of dispersers moved into proximity of Maun and the adjacent region of Lake Ngami at the southern fringes of the OD. Maun is the biggest and most densely populated city in the study area (31 inh. / km²) and serves as hub for touristic excursions into the OD. Its surrounding area is agriculturally less intensively used (1% covered by agricultural fields) but the livestock density is comparably high (13 cattle / km²). Despite this and the fact less than 3% of livestock depredations can be linked to

AWDs, there have been numerous occasions where AWDs were harmed or killed within the city's proximity (Gusset et al., 2009; Cozzi et al., 2020). While the panhandle and the city of Maun themselves are unprotected, they are located near formally protected areas and may thus serve as ecological traps for wildlife leaving the surrounding protected areas (Woodroffe and Ginsberg, 1998; Northrup et al., 2012). Dispersing individuals appear to be particularly at risk, as they readily venture outside protected areas into hostile landscapes (Elliot et al., 2014; Cozzi et al., 2020). In Zambia, dispersal and the associated mortality have caused deterioration of genetic diversity and resulted in the net loss of individuals (Leigh et al., 2012). Recent genetic analyses across southern Africa, in contrast, identified a genetically diverse population cluster near northern Botswana, suggesting moderate levels of dispersal (Tensen et al., 2022). Nevertheless, anticipating how climate change and the associated changes in the biophysical landscape through which dispersers move will impact hWC will be paramount to prioritize efforts and more efficiently conserve and sustain dispersal pathways.

4.7 Conclusion

Our dispersal simulations across two extreme environmental scenarios revealed striking differences in dispersal prospects and landscape connectivity for dispersing AWDs. We thereby showed that extreme environmental conditions, akin to those projected under climate change, will have important impacts on functional connectivity and may alter areas of HWC. Given the complexity of the studied ecosystem and its associated intricate feedback loops, predictions of future conditions remain challenging and plagued by uncertainty. Wildlife managers and conservation bodies therefore need to move beyond focusing on single scenarios and consider multiple possibilities to adequately respond to changes in the environment due to climate change, while also coping with the socio-economic needs of an ever-expanding human population. This will require the development of protection strategies that can accommodate both more extreme pronounced, or less intense flood. Successful conservation strategies will be of particular relevance for wide-ranging, endangered species that are already at the verge of extinction, such as the African wild dog.

5 Authors' Contributions

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

for publication.

6 Data Availability

Access to R-scripts to replicate our analysis will be provided through an online repository at the time of publication.

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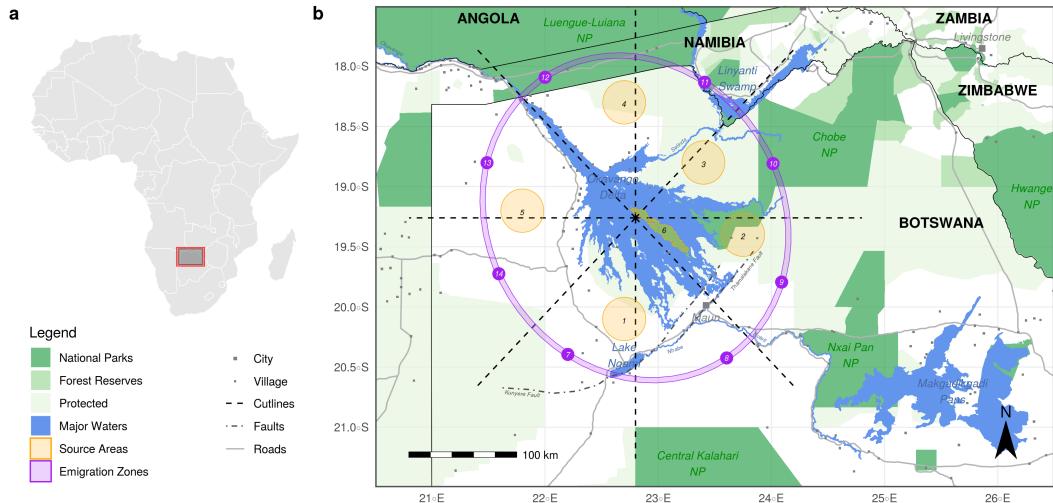


Figure 1: (a) Location of the study area in Southern Africa across which we simulated dispersing African wild dogs. To mitigate edge effects, our study area comprised a buffer zone (red polygon) within which we randomized covariate values of the habitat layers. (b) The study area was centered on the Okavango Delta and encompassed its immediate surroundings. We initiated simulated dispersers at random locations within one of the six source areas (orange polygons) that we distributed across the delta. Emigration zones (purple polygons) served as checkpoints to identify if and where simulated dispersers left the close surroundings of the Okavango delta. These zones were generated using a set of cutlines (black 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 the cardinal directions.

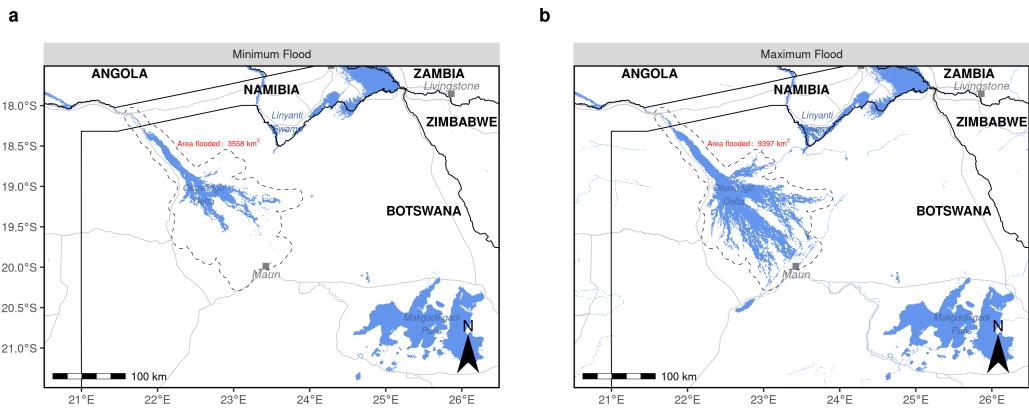


Figure 2: Flood extent in the minimum (a) and maximum (b) flood scenarios. In the minimum flood scenario (a), water stretched across 3'558 km², whereas during maximum flood (b) it covered 9'397 km². The two maps were generated using 700 remote sensed MODIS MCD43A4 satellite images spanning the years 2000 to 2019.

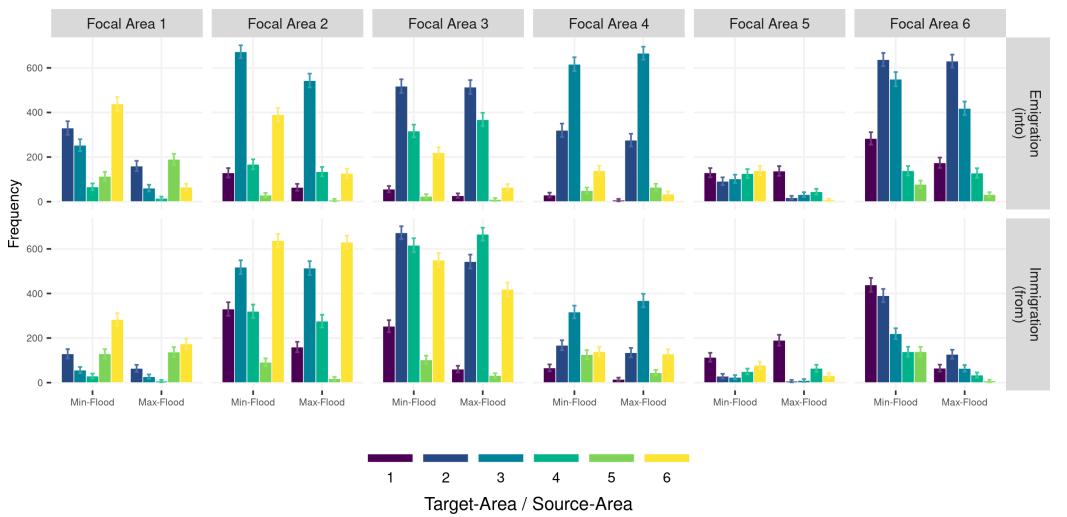


Figure 3: Number of individuals emigrating from, or immigrating into a specific source area (focal area). Colors indicate into which other areas emigrants moved or from which other areas immigrants originate. For instance, the most left plot in the upper panel shows the number of individuals moving from source area 1 into the six other source areas during minimum and maximum flood, respectively.

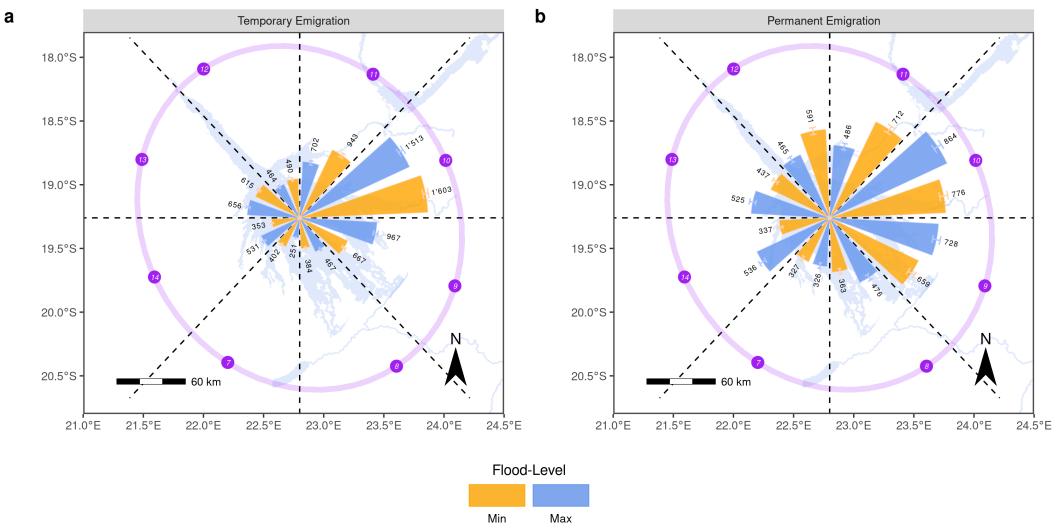


Figure 4: Absolute number of simulated trajectories running into each of the designated emigration zones (purple) during minimum and maximum flood. Subfigure (a) depicts the total number of emigrating trajectories, including temporary emigrants that eventually returned into the OD's vicinity. Subfigure (b) only depicts permanent emigration events.

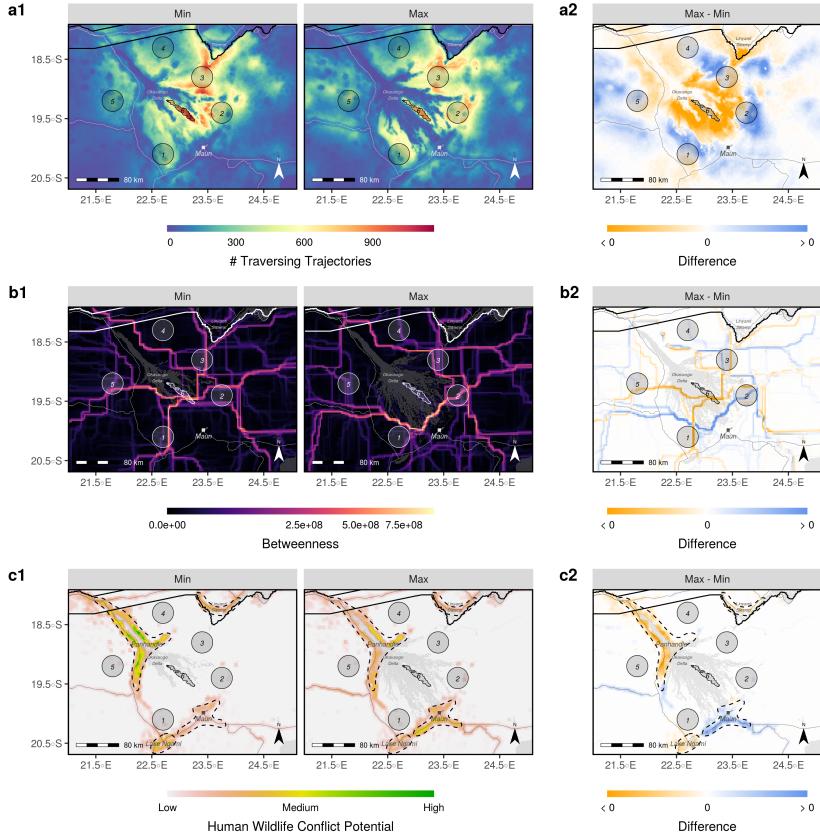


Figure 5: (a) Heatmaps, (b) betweenness maps, (c) maps of human wildlife conflict, and (d) maps of inter-patch connectivity, derived from simulated dispersal events. Left panels were derived from the minimum flood scenario, right panels from the maximum flood scenario. Source areas from which dispersers 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. Note that for clarity in (d) we only present links between adjacent source areas. Additional, source-specific maps for each of the four metrics are provided in the appendix.)



99_Difference.png

Figure 6: Difference maps generated from the (a) heatmaps, (b) betweenness maps, and (c) maps of human wildlife conflict in Figure 5. The maps depict the difference between maximum and minimum flood for each metric (i.e. $Metric_{flood:max} - Metric_{flood:min}$). Orange regions indicate that the respective metric was higher during minimum flood, blue regions that the metric was higher during maximum flood.

Table 1: (a) Dispersal frequency and (b) duration (in steps) between source areas (labeled 1 to 6) and emigration zones (labeled 7 to 14) during minimum and maximum flood.

		From													
		1	2	3	4	5	6	From	2	3	4	5	6		
To	1	Min	1000 ± 0	129 ± 10.73	56 ± 7.22	30 ± 5.5	130 ± 10.64	284 ± 14.27	Min	1 ± 0	1052 ± 45.57	1123 ± 62.35	1475 ± 59.49	1024 ± 44.65	721 ± 28.59
	14	Max	1000 ± 0	64 ± 7.93	27 ± 5.12	7 ± 2.59	138 ± 11.19	174 ± 11.88	Max	1 ± 0.47	1010 ± 59.36	1329 ± 79.1	1411 ± 124.88	949 ± 44.16	1027 ± 33.84
1	Min	330 ± 15.45	1000 ± 0	518 ± 15.65	320 ± 15.28	92 ± 8.9	637 ± 15.16	Min	960 ± 28.44	1 ± 0.01	688 ± 22.56	1120 ± 26.52	1378 ± 43.1	611 ± 19.05	
2	Max	160 ± 11.87	1000 ± 0	514 ± 15.91	276 ± 14.62	18 ± 4.12	631 ± 14.81	Max	1128 ± 39.12	1 ± 0	723 ± 23.68	1089 ± 30.07	1509 ± 101.35	709 ± 19.28	
3	Min	253 ± 13.73	673 ± 14.74	1000 ± 0	616 ± 15.93	102 ± 9.59	550 ± 16.19	Min	1125 ± 32.17	558 ± 19.47	1 ± 0	629 ± 18.99	1318 ± 35.16	814 ± 22.05	
4	Max	61 ± 7.57	543 ± 15.86	1000 ± 0	666 ± 14.84	32 ± 5.31	419 ± 15.55	Max	1330 ± 51.15	658 ± 21.34	1 ± 0.4	564 ± 19.18	1263 ± 86.09	972 ± 24.72	
5	Min	66 ± 7.86	168 ± 11.36	317 ± 14.51	1000 ± 0	126 ± 10.18	139 ± 10.83	Min	1369 ± 45.6	1085 ± 38	807 ± 31.14	1 ± 0.01	1161 ± 42.09	1188 ± 40.24	
6	Max	15 ± 3.78	135 ± 10.77	368 ± 15.33	1000 ± 0	45 ± 6.49	128 ± 10.92	Max	1568 ± 68.27	1151 ± 43.04	704 ± 29.7	1 ± 0	1140 ± 66.77	1275 ± 37.76	
7	Min	114 ± 10.22	29 ± 5.28	24 ± 4.8	50 ± 6.73	1000 ± 0	78 ± 8.52	Min	991 ± 45.9	1465 ± 69.63	1262 ± 106.51	1152 ± 70.15	1 ± 0.09	1065 ± 57.26	
8	Max	190 ± 12.44	7 ± 2.72	10 ± 3.21	65 ± 8.03	1000 ± 0	32 ± 5.32	Max	1083 ± 38.26	1526 ± 169.88	1216 ± 160.94	1269 ± 50.48	1 ± 0.01	1359 ± 71.28	
9	Min	439 ± 15.91	391 ± 15.24	220 ± 12.38	139 ± 11.22	139 ± 10.98	1000 ± 0	Min	696 ± 23.21	535 ± 25.03	921 ± 39.88	1165 ± 41.97	1064 ± 42	1 ± 0.09	
10	Max	65 ± 8	127 ± 10.37	64 ± 7.48	34 ± 5.86	8 ± 2.77	1000 ± 0	Max	928 ± 59.98	777 ± 50.21	1022 ± 62.82	1204 ± 83.77	1113 ± 162.42	1 ± 0.04	
11	Min	412 ± 15.82	38 ± 5.95	20 ± 4.46	10 ± 3.09	105 ± 9.62	130 ± 10.82	Min	483 ± 23.02	1290 ± 65.55	1361 ± 93.87	1462 ± 106.88	1011 ± 50.72	995 ± 37.14	
12	Max	369 ± 14.47	36 ± 5.91	10 ± 3.01	4 ± 1.9	124 ± 10.61	68 ± 7.71	Max	734 ± 26.74	1180 ± 68.81	1671 ± 84.1	1486 ± 216.02	1046 ± 49.97	1253 ± 49.81	
13	Min	377 ± 15.51	67 ± 7.93	33 ± 5.77	13 ± 3.54	38 ± 6.03	137 ± 10.95	Min	543 ± 24.93	1188 ± 58.61	1326 ± 76.33	1627 ± 80.53	1312 ± 76.45	953 ± 41.08	
14	Max	443 ± 14.85	168 ± 11.46	72 ± 8.18	28 ± 4.97	53 ± 6.95	168 ± 11.98	Max	688 ± 23.74	908 ± 41.43	1177 ± 56.84	1352 ± 79.76	1329 ± 55.66	1167 ± 37.35	
1	Min	178 ± 12.01	551 ± 15.69	347 ± 14.53	175 ± 12.2	40 ± 6.1	344 ± 14.92	Min	1145 ± 38.84	462 ± 21.34	805 ± 27.76	1225 ± 35.91	1462 ± 59.73	950 ± 25.88	
2	Max	188 ± 12.15	746 ± 13.74	407 ± 15.29	211 ± 12.9	20 ± 4.28	445 ± 15.88	Max	1109 ± 34.28	372 ± 16.47	872 ± 24.91	1179 ± 34.64	1376 ± 89.62	921 ± 22.52	
3	Min	223 ± 12.82	725 ± 13.84	771 ± 12.85	498 ± 16.02	73 ± 8.42	482 ± 16.08	Min	1214 ± 30.66	468 ± 17.95	471 ± 17.71	872 ± 22.31	1489 ± 40	946 ± 22.06	
4	Max	105 ± 9.81	768 ± 12.91	757 ± 13.58	490 ± 15.87	21 ± 4.43	472 ± 15.82	Max	1294 ± 45.11	413 ± 15.31	467 ± 16.58	886 ± 22.69	1456 ± 92.16	1014 ± 22.45	
5	Min	128 ± 10.95	374 ± 15.26	619 ± 15.17	625 ± 14.95	75 ± 8.34	278 ± 13.25	Min	1345 ± 39.71	959 ± 27.15	592 ± 21.91	493 ± 19.92	1463 ± 43.67	1181 ± 28.88	
6	Max	12 ± 3.47	204 ± 12.69	456 ± 15.99	576 ± 15.97	32 ± 5.77	141 ± 11.26	Max	1425 ± 102.1	1109 ± 36.18	681 ± 25.66	572 ± 21.75	1346 ± 85.45	1255 ± 35.65	
7	Min	50 ± 8.83	92 ± 9.32	192 ± 12.27	502 ± 16.21	256 ± 13.75	83 ± 8.77	Min	1359 ± 61.03	1327 ± 41.72	1068 ± 34.4	493 ± 20.75	937 ± 30.63	1382 ± 42.85	
8	Max	14 ± 3.68	62 ± 7.61	214 ± 13.55	542 ± 16.28	99 ± 9.46	51 ± 6.93	Max	1534 ± 78.37	1292 ± 51.25	981 ± 34.48	478 ± 22.21	1005 ± 56.52	1445 ± 57.51	
9	Min	50 ± 6.81	25 ± 4.9	46 ± 6.45	125 ± 10.38	665 ± 14.98	45 ± 6.21	Min	1160 ± 62.27	1479 ± 76.43	1300 ± 66.24	927 ± 49.65	399 ± 15.63	1302 ± 59.59	
10	Max	150 ± 10.81	8 ± 2.85	37 ± 5.84	117 ± 10	781 ± 13.64	26 ± 4.9	Max	1219 ± 40.97	1148 ± 149.5	1289 ± 80.28	975 ± 49.38	319 ± 14.14	1453 ± 73.18	
11	Min	114 ± 10.14	15 ± 3.85	7 ± 2.65	19 ± 4.37	446 ± 15.43	46 ± 6.57	Min	893 ± 50.08	1376 ± 78.19	1684 ± 112.78	1304 ± 115.43	480 ± 22.25	1293 ± 60.16	
12	Max	287 ± 14.32	9 ± 3.02	7 ± 2.7	33 ± 5.72	675 ± 15.04	38 ± 5.86	Max	954 ± 30.69	1287 ± 132.1	1569 ± 175.42	1435 ± 71.93	509 ± 19.21	1342 ± 60.78	

Frequency

Step Number