

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

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African Wild Dog Connectivity under Climate Change

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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 has been studied repeatedly, little is known about the consequences of environmental change on 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 environmental scenarios; one assuming a maximum flood, one assuming a minimum flood. These scenarios serve to approximate environmental conditions under amplified climatic variability, as it is expected under continued climate change.

During maximum flood, the Okavango Delta poses an important dispersal barrier that reduces dispersal prospects between distinct areas and increases dispersal durations. At maximum flood, dispersal into the central habitats of the Okavango Delta is reduced by 77% and dispersal durations increased by 19%. Across the entire study area, the differences are less dramatic, with 12% lower dispersal success and 17% longer dispersal durations during maximum flood. We also found that a maximum flood shifted dispersal bottlenecks and areas with a high potential for human-wildlife conflict closer towards densely populated villages. We provide a rich suite of maps to visualize the differences between minimum and maximum flood.

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. Taking into account such differences will be key to designing future proof conservation strategies, particularly in light of ongoing climate change. Our results also have direct applicability for the conservation of the endangered African wild dog as we highlight critical dispersal corridors and human-wildlife conflict zones in two distinct scenarios.

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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; ?). 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. 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 because. 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 km<sup>2</sup> 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 21<sup>st</sup> 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.

## 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 km<sup>2</sup>) and comprises all long distance dispersal events previously recorded in this area (Cozzi et al., 2020; Hofmann et al., 2021). The flood-pulsing rhythm of the OD is mainly dictated by precipitation in the Angolian highlands, which serve as catchment areas from which water is further channelled 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 km<sup>2</sup>, whereas during maximum flood more than 9'000 km<sup>2</sup> 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 50 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 1 a).

## 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 to 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 [that 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). The model presented in [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 ?].

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 ?? 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.  $\beta$ -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 ?. 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 3. Difference maps to visualize the differences between minimum and maximum flood are given in Figure 4. Source-specific maps are presented in the Appendix. As the heatmaps in Figure 3a 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 4a) 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 3b), where several pinchpoints 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 4b). Despite its apparent importance in linking the eastern and western sections of the delta, it is evident from (Figure 3a) 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 3c). 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 4c). 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 4c). Our analysis of inter-patch connectivity further demonstrates notable differences in dispersal prospects and dispersal durations depending on the extent of the flood (Figure 3d and Table 1). While  $4139 \pm 35.95$  simulated dispersers reach another source area during minimum extent, only  $3628 \pm 38.28$  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  $4139 \pm 35.95$  steps to  $3628 \pm 38.28$  steps during maximum flood. These differences are particularly pronounced for individuals dispersing into source area 6. While the area is reached by  $1325 \pm 31.80$  simulated individuals during minimum flood, only  $300 \pm 17.30$ , i.e. 77% less, arrive there during maximum flood. Furthermore, the dispersal duration into source area six from any other source area increases by 19% from  $773 \pm 15.06$  steps to  $919 \pm 30.18$  steps.

## 4 Discussion

According to our simulations, the propensity to move between the eastern and western part of the delta is much lower during maximum extent. This is mainly due to the flood-waters and the city of Maun acting as dispersal barriers. During maximum extent, the floodwaters of the delta close a gap between the delta and Maun that otherwise would serve as dispersal corridor. Anecdotal evidence supports this hypothesis, for the only dispersing individuals recorded to move from the eastern to the western part of the delta moved at times of low flood. In line with this, it appears that a large flood extent pushes dispersing individuals to move closer to human inhabited areas such as the village of Maun.

Predicting how climate change will impact the dispersal ability of AWDs is challenging for multiple reasons. First of all, predicting the flooding patterns of the OD under climate change is merely impossible due to the complex feedbacks between surface-temperature, soil conditions, precipitation patterns and the associated changes in vegetation. Second, the delta is not only prone to changes in environmental conditions, but also to changes in anthropogenic use of the inflowing water. Finally, it is unclear how AWDs, in fact, how any species, will cope with environmental change due to global warming. Even though some studies predict that AWD populations are likely to decline under increasing temperatures, these studies fail to account for the behavioral plasticity of their focal species. AWDs respiratory system, for instance, has evolved as a perfect adaptation to high temperatures and AWDs may, in fact, profit from a comparative advantage (cite an economist) over their competitors and prey under rising temperatures. Although the theory of comparative advantages is a fundamental concept in economics, it has yet to find its way into ecological studies.

Murray-Hudson et al. (2006) predicted that increased temperatures, additional human abstractions, and reduced river flows might lead to a “Delta dying” and that the impact of climate will be much more pronounced than the impact of anthropogenic water use.

Although local rainfalls in Botswana are expected to increase in terms of intensity, simulations show that the length of the rainy season will decline, more than offsetting the incline in precipitation Akinyemi (2019).

Although dispersal is generally believed to be beneficial for the long term viability of species, it can also lead to the net-loss of individuals in areas where edge effects and anthropogenic mortality are high (Leigh et al., 2012).

We studied a population of African wild dogs that resides in a natural environment with little human influence. This is only representative for a small share of the extant wild dog

populations, as most individuals reside in areas that are prone to substantial edge effects. For these populations, the benefit of dispersal is disputed, as dispersal under high anthropogenic mortality may lead to a net-loss of individuals (Leigh et al., 2012).

Dispersal is an important, if not the most important, driver of landscape connectivity and therefore of major interest to conservation authorities. It has also been demonstrated that dispersal may lead to population declines in areas where anthropogenic mortality is high and dispersal prospects low (Leigh et al., 2012).

Efforts aiming at restoring or improving landscape connectivity should consider and take into account changes in landscape characteristics due to climate change.

We assessed the implications of environmental change on the dispersal prospects, yet we did not consider how changing conditions alter dispersal propensity.

According to our simulations, dispersers are able to cover larger distances during periods of low flood. This finding is little surprising, considering that inundated areas act as dispersal barriers and force dispersers to detour and circumvent water-covered areas. However, it still leads to an interesting hypothesis. Previous studies have shown that the euclidean dispersal distance of female coalitions is larger than that of male coalitions. This has led to ... However, demographic analyses have also revealed that female offspring tend to emigrate from their pack at younger ages and earlier in the year, when floodwaters are still at a relatively low level (Behr). It is thus conceivable that the sex-differences in reported dispersal distances is mainly a consequence of environmental conditions during dispersal, rather than owed to physiological differences between sexes.

While our analysis marks an important step into incorporating environmental change into studies of connectivity, there are several critical additions that should be considered in the future. We studied dispersal and connectivity under two different environmental scenarios, yet our movement model assumed that dispersers had identical habitat and movement preferences in both scenarios. In reality, however, it can be expected that movement and habitat kernels of dispersers differ depending on the season considered (examples).

An additional complication arises when species movement is not solely driven by environmental conditions, but also affected by intra- and inter-specific factors. For instance, ... has shown that dispersers... Rendering such conditions alone is challenging, yet rendering the conditions under changing environmental conditions is merely impossible.

Climate change will not only change species distribution but also community composition (Thuiller et al., 2006).

To address such differences, researchers could model habitat and movement preferences

using season-dependent models, or, alternatively, by combining hidden markov models with step-selection functions. (cite papers that fieberg sent)

For the discussion: Through changing environmental conditions, climate change will also impact the distribution of various species with far-reaching consequences on inter- and intra-specific competition (Abrahms). Due to a lack of data, we omitted any inclusion of social factors in our dispersal model, albeit they are known to be important determinants of dispersal (Armansin). Studying how climate change influences species distribution and their interactions, and ultimately how this alters dispersal, will be challenging but necessary to more realistically simulate dispersal.

Akinyemi (2019) predicts fewer rain days in Botswana (may want to look at predictions for Angola though)

Only recently, it has been discovered that AWDs communicate using shared marking sites. The role of such marking sites for dispersing coalitions remains to be investigated, yet it is likely that, akin to resident packs, use SMS as navigation waypoint and demarcation lines. Chemical analyses suggest that the compounds used for communication are highly volatile and may not persist in extreme climate conditions. In result, dispersers may lose their ability to effectively navigate across the landscape and locate potential mates with whom to settle. This would reduce pack-formation prospects and undermine...

Validating predictions from individual-based dispersal models is challenging and requires additional dispersal data, which is inherently scarce anyways. Scitcen science may help to fill this gap by augmenting observed GPS data with occasional sightings of uncollared dispersing coalitions. This is especially critical for species that disperse across borders and beyond confined study areas. The African carnivore wildbook offers ...

While a better understanding of the ODs flooding regime under global change is of major interest, reliable predictions remain challenging due to the complex interplay between climate, anthropogenic water use, animal behavior, and topography of the region.

Although the OD is arguably the main driver of seasonal change across the studied ecosystem, there are several other factors that undergo seasonal change, including vegetation and the abundance and distribution of prey or predators.

The OD is an important driver of species distribution and it has been found that an expanding flood limits available habitat, thus leading to more inter-specific competition, particularly between AWDs and lions.

Although validating the predictions resulting from our dispersal model is challenging, the simulations enable us to generate several interesting hypotheses...

Connectivity analyses that omit dynamism, be it due to seasonality or climate change, not only fail to capture an important aspect of reality, but also forego the ability to gain an understanding of connectivity under “non-average” conditions, such as those expected under climate change.

How climate change will affect the distribution of African wild dogs is not known. Given that the species has occurred across the entire Sub-Saharan continent suggests that this species is highly adaptable and limited mainly by the presence of humans, yet less by the habitat itself.

#### 4.1 Conclusion

Our dispersal simulations across two extreme climatic scenarios reveal striking differences in dispersal prospects and landscape connectivity for dispersing AWDs. This implies that (1) climatic variation, be it due to seasonality or climate change, must be included in analyses dealing with dispersal and (2) that projected climate change is likely to have profound impacts on landscape connectivity.

Nevertheless, a more comprehensive understanding of dispersal under changing environmental conditions is critical for designing effective conservation strategies in the light of climate change. By predicting and modeling dispersal patterns under different scenarios, we can better anticipate the impacts of climate change on species and design effective conservation strategies to protect them. This is especially important for endangered species that are already at the verge of extinction.

### 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.

## **7 Acknowledgements**

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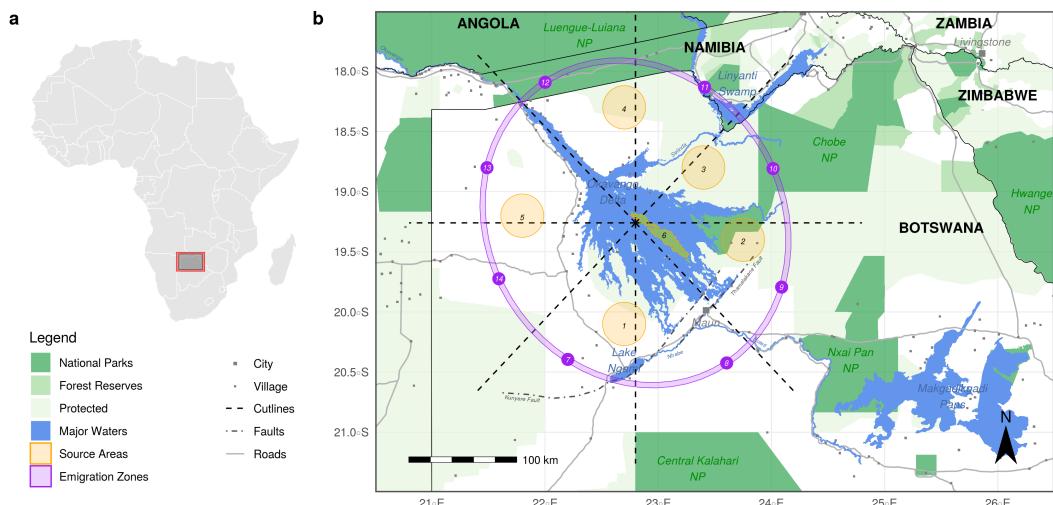
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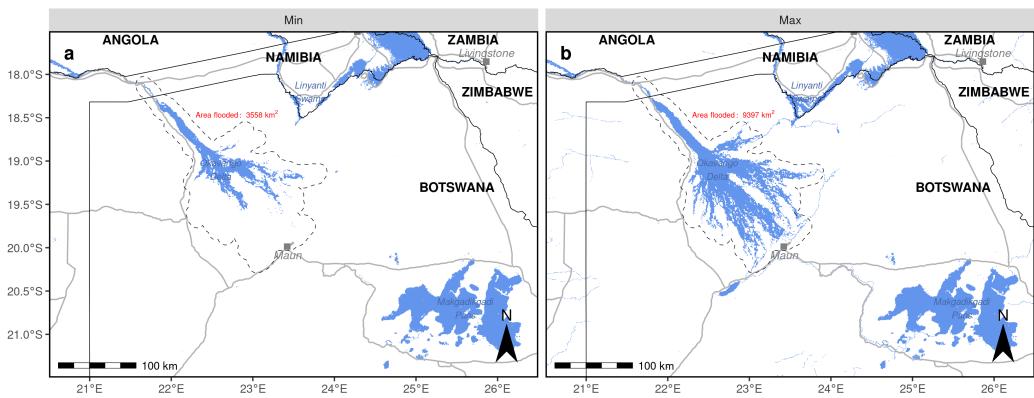
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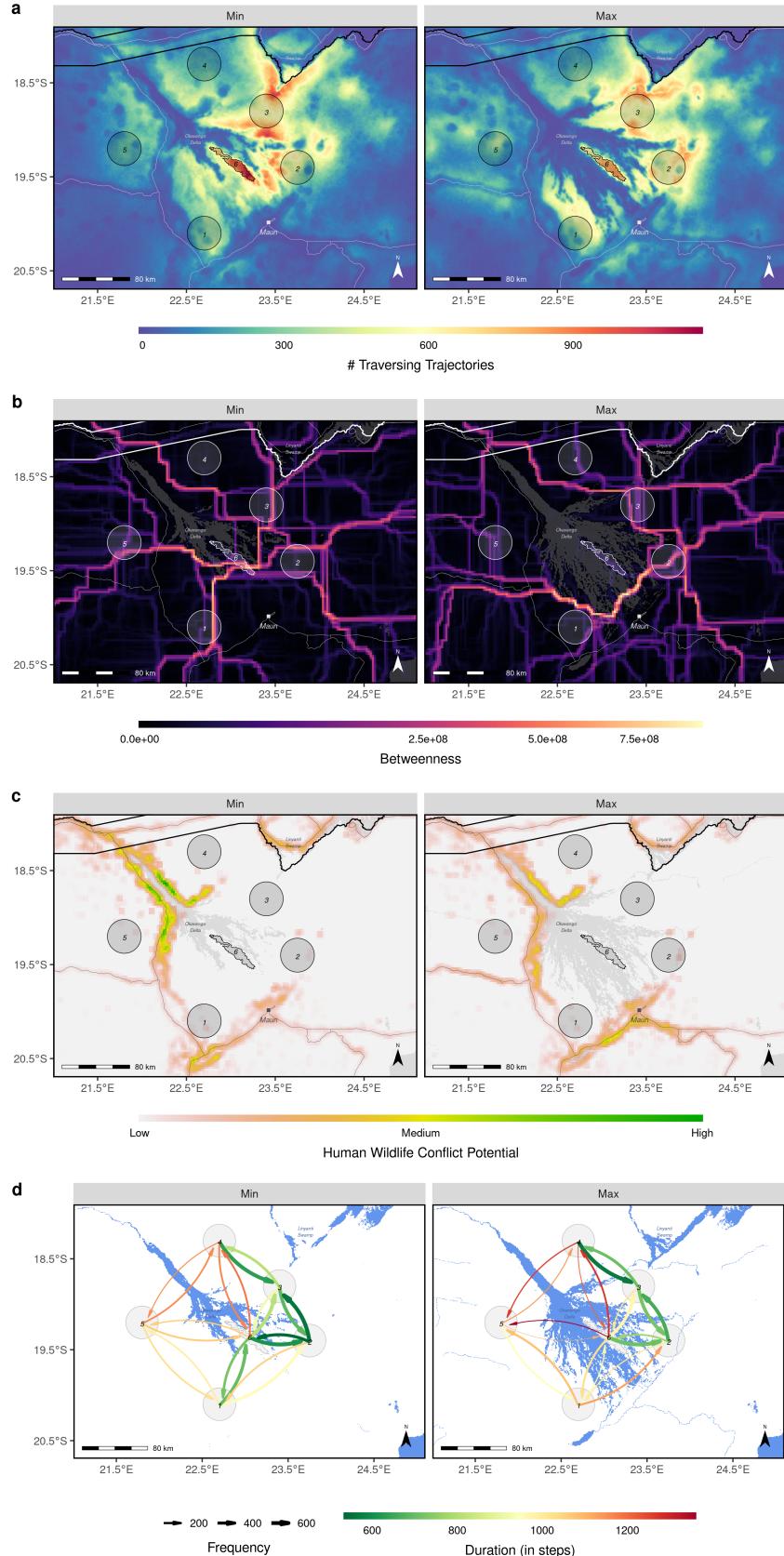
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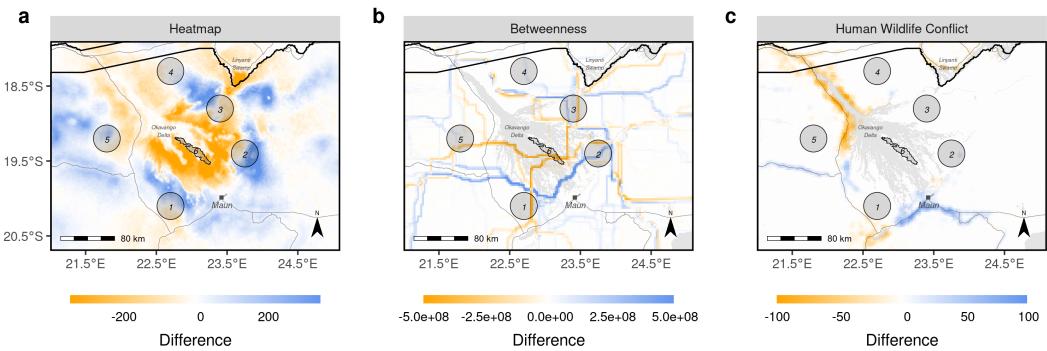
**Figure 1:** (a) Location of the study area in Southern Africa across which we simulated dispersing African wild dogs. To mitigate edge effects, our study area comprised a buffer zone (red polygon) within which we randomized covariate values of the habitat layers. (b) The study area was centered on 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 km<sup>2</sup>, whereas during maximum flood (b) it covered 9'397 km<sup>2</sup>. The two maps were generated using 700 remote sensed MODIS MCD43A4 satellite images spanning the years 2000 to 2019.



**Figure 3:** (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.) 23



**Figure 4:** Difference maps generated for (a) heatmaps, (b) betweenness maps, and (c) maps of human wildlife conflict. 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	1	2	3	4	5	6		
To	1	Min	1000 ± 0	129 ± 10.13	56 ± 7.02	30 ± 5.4	131 ± 10.37	284 ± 14.54	1	Min	1 ± 0	1055 ± 45.68	1122 ± 62.33	1471 ± 57.13	1025 ± 45.95	721 ± 27.23
	1	Max	1000 ± 0	64 ± 7.54	27 ± 5.05	7 ± 2.6	137 ± 10.84	174 ± 12.13	1	Max	1 ± 0.45	1003 ± 60.72	1332 ± 81.53	1401 ± 128.82	950 ± 44.82	1026 ± 33.55
2	2	Min	329 ± 14.67	1000 ± 0	518 ± 15.42	319 ± 14.37	92 ± 8.99	637 ± 15.33	2	Min	959 ± 28.17	1 ± 0.01	688 ± 23.57	1121 ± 27.2	1378 ± 42.62	611 ± 19.32
	2	Max	160 ± 11.56	1000 ± 0	515 ± 15.57	276 ± 13.71	18 ± 4.05	631 ± 15.93	2	Max	1130 ± 38.76	1 ± 0	721 ± 24.19	1086 ± 29.72	1503 ± 104.25	708 ± 18.23
3	3	Min	251 ± 13.8	672 ± 14.69	1000 ± 0	616 ± 15.05	103 ± 9.56	549 ± 16.39	3	Min	1125 ± 31.86	558 ± 19.42	1 ± 0	630 ± 19.02	1320 ± 33.21	814 ± 21.68
	3	Max	61 ± 7.34	545 ± 15.29	1000 ± 0	666 ± 14.71	32 ± 5.3	418 ± 15.26	3	Max	1333 ± 50.98	657 ± 22.44	1 ± 0.41	564 ± 19.47	1260 ± 82.97	971 ± 23.77
4	4	Min	66 ± 7.71	167 ± 11.94	317 ± 14.5	1000 ± 0	126 ± 10.58	139 ± 11.13	4	Min	1367 ± 44.61	1088 ± 37.22	809 ± 32.17	1 ± 0.01	1159 ± 42.5	1189 ± 41.06
	4	Max	15 ± 3.87	136 ± 10.82	368 ± 14.64	1000 ± 0	45 ± 6.51	128 ± 10.67	4	Max	1866 ± 86.69	1153 ± 43.76	704 ± 28.5	1 ± 0	1141 ± 67.52	1276 ± 36.25
5	5	Min	114 ± 10.44	29 ± 5.27	24 ± 4.83	50 ± 6.76	1000 ± 0	78 ± 8.55	5	Min	992 ± 43.38	1463 ± 66.87	1268 ± 104.1	1153 ± 67.73	1 ± 0.09	1060 ± 60.11
	5	Max	190 ± 12.17	7 ± 2.64	10 ± 3.07	64 ± 7.51	1000 ± 0	32 ± 5.56	5	Max	1083 ± 38.32	1524 ± 172.02	1211 ± 164.09	1265 ± 54.3	1 ± 0.01	1361 ± 73.93
6	6	Min	437 ± 15.96	391 ± 15.71	221 ± 13.05	139 ± 10.88	139 ± 10.91	1000 ± 0	6	Min	698 ± 22.63	534 ± 24.5	919 ± 38.5	1166 ± 40.34	1061 ± 43.03	1 ± 0.09
	6	Max	65 ± 7.69	127 ± 11.04	64 ± 7.72	34 ± 5.71	8 ± 2.75	1000 ± 0	6	Max	928 ± 61.33	772 ± 49.47	1023 ± 62.79	1206 ± 86.47	1106 ± 163.4	1 ± 0.05
7	7	Min	413 ± 15.92	38 ± 5.74	20 ± 4.22	10 ± 3.16	105 ± 9.67	130 ± 10.55	7	Min	483 ± 23.49	1286 ± 67.05	1366 ± 93.58	1465 ± 103.83	1010 ± 49.42	995 ± 36.92
	7	Max	369 ± 15.8	36 ± 5.77	10 ± 3.08	4 ± 1.96	124 ± 10.56	68 ± 7.64	7	Max	734 ± 25.64	1182 ± 68.29	1673 ± 83.2	1475 ± 216.38	1044 ± 46.49	1252 ± 50.72
8	8	Min	378 ± 15.48	67 ± 7.9	33 ± 5.72	13 ± 3.53	38 ± 6.3	138 ± 11.11	8	Min	543 ± 25.11	1185 ± 56.28	1324 ± 79.58	1628 ± 80.28	1315 ± 76.69	954 ± 40.21
	8	Max	443 ± 16.08	168 ± 11.45	72 ± 8.41	28 ± 5.26	53 ± 7.22	169 ± 11.81	8	Max	689 ± 24.3	909 ± 41.5	1174 ± 58.57	1355 ± 84.7	1332 ± 60.79	1166 ± 36.17
9	9	Min	177 ± 12.28	552 ± 15.3	346 ± 15.52	175 ± 12.33	40 ± 6.33	344 ± 15.4	9	Min	1143 ± 39.19	461 ± 22.61	804 ± 27.84	1226 ± 33.79	1467 ± 57.83	952 ± 27.35
	9	Max	187 ± 12.44	746 ± 14.04	408 ± 15.33	210 ± 12.29	20 ± 4.36	446 ± 16.37	9	Max	1110 ± 35.85	372 ± 16.02	871 ± 25.22	1180 ± 34.08	1373 ± 91.83	921 ± 21.81
10	10	Min	221 ± 12.74	725 ± 13.86	771 ± 13.03	498 ± 16.23	73 ± 8.16	482 ± 15.88	10	Min	1215 ± 30.84	468 ± 18.43	470 ± 17.32	873 ± 21.86	1489 ± 38.33	947 ± 22.47
	10	Max	105 ± 9.86	768 ± 13.42	758 ± 13.75	490 ± 15.49	21 ± 4.43	473 ± 16.1	10	Max	1295 ± 45.35	413 ± 15.54	467 ± 16.31	887 ± 23.63	1456 ± 93.27	1012 ± 21.72
11	11	Min	126 ± 10.6	374 ± 14.92	618 ± 14.73	625 ± 15.12	75 ± 8.18	276 ± 14.52	11	Min	1344 ± 38.5	958 ± 26.2	593 ± 21.7	493 ± 19.78	1464 ± 44.43	1182 ± 28.29
	11	Max	12 ± 3.49	204 ± 12.65	450 ± 15.39	576 ± 15.68	32 ± 5.56	141 ± 10.82	11	Max	1428 ± 95.5	1109 ± 37.92	680 ± 25.1	572 ± 21.8	1347 ± 87.04	1258 ± 35.32
12	12	Min	50 ± 6.66	92 ± 9.07	192 ± 12.22	502 ± 15.53	256 ± 13.56	83 ± 8.63	12	Min	1352 ± 59.94	1330 ± 41.14	1068 ± 35.35	493 ± 21.6	936 ± 31.04	1381 ± 43.78
	12	Max	14 ± 3.82	62 ± 7.42	214 ± 13.01	543 ± 15.82	99 ± 9.47	51 ± 6.99	12	Max	1540 ± 77.33	1293 ± 48.93	981 ± 36.72	477 ± 22.65	1006 ± 54.61	1449 ± 58.7
13	13	Min	50 ± 6.96	25 ± 4.84	46 ± 6.48	125 ± 10.49	665 ± 14.89	45 ± 6.6	13	Min	1158 ± 66.47	1484 ± 76.32	1304 ± 67.35	928 ± 48.03	399 ± 14.97	1297 ± 60.06
	13	Max	150 ± 11.29	8 ± 2.79	37 ± 6.06	117 ± 10.07	780 ± 13.15	26 ± 4.93	13	Max	1216 ± 39.35	1154 ± 151.4	1289 ± 76.11	975 ± 44.66	318 ± 14.11	1451 ± 75.68
14	14	Min	115 ± 9.99	15 ± 3.93	7 ± 2.69	19 ± 4.26	445 ± 15.73	46 ± 6.44	14	Min	892 ± 49.38	1375 ± 75.81	1668 ± 114.09	1310 ± 108.91	480 ± 22.47	1288 ± 61.95
	14	Max	287 ± 14.11	9 ± 2.93	7 ± 2.52	33 ± 5.52	676 ± 14.72	38 ± 6.14	14	Max	953 ± 29.81	1288 ± 128.49	1570 ± 168.96	1434 ± 71.05	509 ± 18.88	1344 ± 63.92