Flooding of the Okavango Delta influences Connectivity for Dispersing African Wild Dogs

David D. Hofmann[1,2,§] Gabriele Cozzi[1,2] John W. McNutt[2]
Arpat Ozgul[1] Dominik M. Behr[1,2]

September 11, 2022

[1] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstarsse 190, 8057 Zurich, Switzerland.

[2] Botswana Predator Conservation Program, Private Bag 13, Maun, Botswana.

[§] Corresponding author (david.hofmann2@uzh.ch)

Running Title: None

Keywords: Seasonal Flooding of the Okavango Delta and its Consequences for African Wild Dog Connectivity

Abstract

Climate change is expected to profoundly impact vital rates of wild living animal populations. While the impact 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 between such subpopulations.

Here, we capitalize on natural, flood-pulse driven environmental change across the Okavando Deltas in northern Botswana to investigate the impact of changing environmental conditions on the dispersal ability of the endangered African wild dog. For this, we utilize a previously parametrized dispersal model and apply it to simulate dispersal under two extreme environmental scenarios; one assuming minimal flood extent, one assuming maximum flood extent.

In genral, our results suggest only a marginal impact of the flood extent on dispersal prospects. Even during maximum flood, dispersal between neighboring patches remained high. Between a few selected patches, however, dispersal was substantially restricted during times of high flood. That is the Okavango delta posed a substantial dispersal barrier that reduced connectivity between patches during maximum flood, but revealed vital dispersal corridors that facilitated dispersal into neighboring areas during minimum flood. Besides a better understanding of the conservation needs for the African wild dog, our study also presents a first step towards incorporating environmental change due to seasonality or climate change. It also emphasizes the usefulness of individual-based dispersal simulations as a conservation tool to study impacts of environmental change in a spatially realistic way.

Contents

1 Introduction

1.1 Climate Change

Despite the importance of climate change in determining species viability, predicting the way and extent to which it will affect species remains challenging. One exciting avenue to gain insights into the implications of environmental change is to utilize seasonal variation in the environment.

Cite IPCC, Planetary boundaries, Tucker (step length). Phenological shifts. Cite Robynne, Arpat, Megan, Dominik, Rabaiotti etc.

1.2 Vital Rates

Several studies investigating the impacts of climate change on life-history traits have revealed that population persistence may critically depends on climate conditions (**?**). While many studies examine climate impacts on survival and reproductive rates, the influence of global change or climatic extreme events on dispersal prospects has received little attention.

Ecosystems that undergoe seasonal environmental variation, in particular arid regions that experience extreme climatic conditions, are among the most vulnerable to climate change.

1.3 Dispersal

1.4 Connectivity

Dispersal is an important, if not the important, driver of landscape connectivity and therefore of major interest to conservation authorities.

1.5 Okavango Delta and African Wild Dogs

The Okavango delta in Southern Africa poses a unique opportunity to study the impacts of environmetal change on species dispersal ability and connectivity in large scale natural experiment setup. According to projections by the IPCC, Botswana and its surroundings are among the most vulnerable to climate change.

2 Methods

We conducted all analyses using the programming language R.

2.1 Study Area

The study area for this analysis was focused on the Okavango delta and its surroundings in Southern Africa, comprising parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia (Figure 1). To accommodate for the long distance dispersal events commonly observed in African wild dogs (e.g. (**???**)), we considered a large rectangular extent stretching from 20°30' E to 26°E. totaling to an area of 300'000 km^2. The dominant geographical feature in this region is the Okavango delta (OD), the world's largest inland delta and the main driver of seasonal environmental change in the region. The flood-pulsing rhythm of the OD is mainly dictated by precipitation in the Angolian highlands, where rainfalls are channeled into the OD through the Okavango River. Although precipitation in Angola peaks in ..., water only slowly descends through the Okavango river and its tributaries, reaching the distal ends (i.e. the faults) of the delta in July or August. At minimum extent, the flood covers an area of 3'600 km^2, whereas during maximum flood it covers more than 9'000 km^2. Vegetation in the study area is dominated by dense mopane forest, mixed acacia woodland, and plain grassland. Human influence in the study area is low and mainly concentrated around small villages at the western periphery of the delta and to the city of Maun at the southern tip of the delta. 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.

2.2 Spatial Habitat Layers

We represented the physical landscape through which dispersers could move by a set of spatially referenced habitat layers each resolve at 250m x 250m. 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 layers is provided in **??**. Importantly, the water-cover and the derived distance-to water layers were generated using MODIS Terra satellite imagery, which enabled us to generate weekly updated layers that provided detailed information about the flood-extent at any given point in time. We had a total of 8xx remote sensed floodmaps at our disposal and used them to generate two extreme scenarios; a minimal and maximum flood scenario. To create the minimum flood scenario, we tallied the 50 floodmaps with smallest flood extent into an average image. Finally, we created a binary map... Similarly, we created an average image for high flood using the 50 most flooded maps. The resulting maps are depicted in Figure 2. For completeness we also generated an "average" floodmap by averaging across all 800 floodmaps available to us. The results based upond this layer are presented in the Appendix.

2.3 Dispersal Model

Our dispersal model was based on a previously parametrized and validated *integrated step-selection function (iSSF)* applied to the dispersal data of 16 dispersing African wild dogs inhabiting the surroundings of the Moremi National Park in the Okavango delta (**?**). The iSSF model consists of two complementary "kernels" plus their interactions. The first kernel is a movement kernel and describes general movement behavior of dispersing AWDs, irrespective of habitat conditions. The second kernel is a habitat kernel and describes preferences of AWDs with regards to environmental conditions. Finally, the model also includes interactions among the two kernels and therefore allows to render how movement behavior changes depending on habitat conditions.

2.4 Source Areas

We simulated dispersing AWDs originating from nine distinct source patches located in the vicinity of the Okavango delta. The source areas were generated as follows. First, we overlayed the OD with an oval that was bound by geographical landmarks; in the north, the oval was bound by the Inflow of the Okavango river into the "pan-handle" of the OD, north-east the oval was bound by the Selinda-Spillway and the Linyanty swamp, towards South-East it was bound by the Boteti river, and towards South-West by Lake Ngami. We then dissected the polygon into five distinct patches using the same natural landmarks (Figure 1). Patch one was given by the area south of the Boteti river and area two by the area north of it up until the panhandle. Area three stretched from the region easf of Maun towards north until the Selinda-spillway, whereas area four stretched north of the spillway until west towards the panhandle. Finally, a fifrth source area marked the peninsuale in the center of the OD. In addition to these five source patches, we also distributed small peripheral patches that we used to simulate individuals immigrating *into* system and to keep track of individuals leaving it.

2.5 Dispersal Simulation

For both environmental scenarios we simulated 1'000 individuals dispersing from each of the nine source area depicted in Figure 1. The simulation algorithm was based on the algorithm described in **??** and works as follows. A random location within the source area is chosen as a starting point. Originating from the starting point, a set of 25 random steps are generated by sampling step lengths from a gamma distribution fitted to observed steps (what is a step?) (shape = , scale =) and turning angles from a uniform distibution on $(-\pi, +\pi)$. Along each random step the underlying spatial covariates are extracted and relevant movement metrics are computed (i.e. log(sl), cos(ta), ta). The parametrized dispersal model is used to predict the probability of each step for being chosen given the steps covariate values. One of the steps is sampled based on assigned probabilities and the location of the animal is updated. The procedure is then repated until the desired number of steps (in our case 2000) is realized. Resulting trajectories resemble correlated random walks. As the original model was trained using 4-hourly steps, a simulated step also resembled straight line movements within four hours.

2.6 Connectivity

Based on simulated dispersal trajectories in the two scenarios we quantified connectivity in three complementary ways. First, we generated heatmaps depicting the frequency at which different areas in the landscape were visited by simulated dispersers. Such heatmaps serve to detect dispersal hotspots but are less suitable to detect pinchpoints and bottlenecks. Hence, we also computed spatially explicit betweenness scores which are useful to highlight such pinchpoints (Bastille). To compute betweenness, we overlayed the study area with a regular grid with 2.5 km x 2.5 km grid cells and determined how often simulated individuals transitioned from one grid-cell to another. In cases where the same individual repeatedly realized the same cell-transition, we only counted a single transition to avoid emphasizing regions regions in which individuals moved in circles. Finally, we calculated the number of successful dispersal events between the different source areas. We coin this type of connectivity "inter-patch connectivity". Dispersal between two areas was said to be successful whenever a trajectory leaving one area intersected with the target area. To gauge the dispersal duration needed to move between patches (be consistent with "patches", "source-areas" etc.), we also recorded the minimum number of steps that individuals had to move to move between areas.

3 Results

Heatmaps produced from simulated dispersal trajectories reveal that the OD acts as a major dispersal barrier during periods of high flood, but reveals viable dispersal corridors during periods of low flood. In particular, our analysis reveals that the area north-west of Maun is frequently visited by dispersers at in the minimum-flood scenario, yet that an extended flood, coupled with high human influence around the city of Maun, enforces simulated individuals to either detour around Maun, or to slip through the narrow window between village and flood. Similarly, the betweenness map indicates the presence of a dispersal corridor extending from the western section of the delta leading across the delta's center into its western part, yet only during low-flood. During maximum flood, the same corridor is pushed south and enforces dispersers to move closer to the city of Maun. In general, connectivity during maxium flood is lower compared to the minimum flood scenario (number links vs. number liks). Most notably, source area 5 is almost inaccessible during maximum flood.

Most notably, the area north-west of Maun acts as dispersal habitat during phases of low flood, yet is almost inaccessible during phases of maxium flood. This is reflected in the heatmap, where connectivity across the western part of the delta is low during maximum flood, but also in the betweenness map, where an important movement corridors through the delta is only visible during minimum flood. Although connectivity across large parts of the landscape remains unchanged across environmental scenarios, one critical movement corridor shifts in response to an expanding flood. Most notably, a corridor that links the western and eastern part of the delta during minimum flood gets redirected further south, thus leading more closely to the city of Maun. Unsurprisingly, the differences are more pronounced for areas directly affected by the flood, yet it is worth noting that even some areas not directly affected by the flood.

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.

? 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 **?**.

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 itra- 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.

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)

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 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. Sciticen science may help to fill this gap by augmenting observed GPS data with occasional sightings of uncollared dispersing coalitions. This is especially ciritical for species that disperse across borders and beyond confined study areas. The African carnivore wildbook offers ...

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.

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 anlayses dealing with dispersal and (2) that projected climate change is likely to have profound impacts on landscape connectivity.

5 Authors' Contributions

D.D.H., D.M.B., A.O. and G.C. conceived the study and designed methodology; D.M.B., G.C., and J.W.M. collected the data; D.D.H. and D.M.B. analysed the data; G.C. and A.O. assisted with modeling; D.D.H., D.M.B., and G.C. 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

GPS movement data of dispersing wild dogs is available on dryad (?). Access to R-scripts that exemplify the application of the proposed approach using simulated data are provided through Github (`https://github.com/DavidDHofmann/DispersalSimulation`). In addition, all codes required to reproduce the African wild dog case study will be made available through an online repository at the time of publication.

7 Acknowledgements

We thank the Ministry of Environment and Tourism of Botswana for granting permission to conduct this research. We thank C. Botes, I. Clavadetscher, and G. Camenisch for assisting with wild dog immobilizations. We also thank B. Abrahms for sharing her data of three dispersing wild dogs. Furthermore, we would like to thank Johannes Signer for assisting with the simulation algorithm. This study was funded by Albert-Heim Foundation, Basler Stiftung für Biologische Forschung, Claraz Foundation, Idea Wild, Jacot Foundation, National Geographic Society, Parrotia Stiftung, Stiftung Temperatio, Wilderness Wildlife Trust Foundation, Forschungkredit der Universität Zürich, and a Swiss National Science Foundation Grant (31003A_182286) to A. Ozgul.

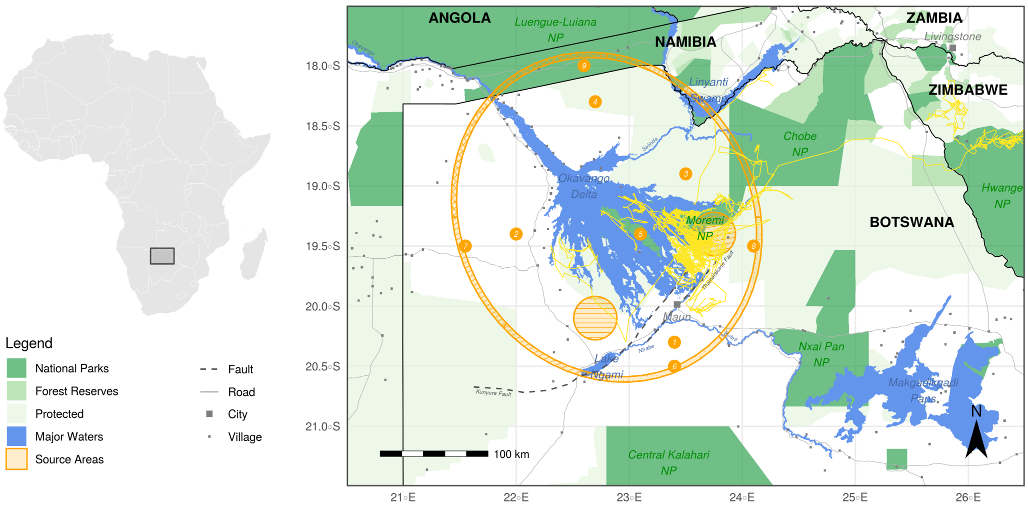

Figure 1: Study area across which we simulated dispersal events. Virtual dispersers were released at random locations within the orange source areas.

99_FloodExtent.png

Figure 2

99_Heatmaps.png

Figure 3

99_DifferenceMap.png

Figure 4

99_Betweenness.png

Figure 5

Table 1: Frequency

From / To	1	2
1	- -	129 ± 10.80 64 ± 7.76
2	329 ± 14.75 160 ± 11.62	- -
3	412 ± 15.94 370 ± 14.44	38 ± 6.19 36 ± 5.72
4	115 ± 10.36 287 ± 14.54	15 ± 3.78 9 ± 2.97
5	50 ± 7.05 150 ± 11.96	25 ± 4.82 8 ± 2.81
6	50 ± 6.97 14 ± 3.86	93 ± 9.04 62 ± 7.61
7	128 ± 10.66 12 ± 3.47	374 ± 15.24 204 ± 12.66
8	222 ± 13.25 105 ± 9.74	725 ± 14.03 768 ± 13.18
9	177 ± 11.76 188 ± 12.25	552 ± 16.32 746 ± 13.63
	377 ± 15.56	67 ± 7.99

Table 2: Duration

From To	1	2
1	- -	1054 ± 44.56 1007 ± 60.63
2	959 ± 27.42 1130 ± 38.83	- -
3	483 ± 23.49 733 ± 26.53	1289 ± 67.45 1181 ± 70.65
4	893 ± 46.14 953 ± 29.33	1376 ± 77.58 1289 ± 132.78
5	1157 ± 71.11 1217 ± 39.49	1481 ± 75.38 1145 ± 142.17
6	1361 ± 61.99 1533 ± 77.33	1325 ± 42.11 1290 ± 52.01
7	1343 ± 38.13 1428 ± 93.59	960 ± 26.80 1107 ± 38.67
8	1212 ± 31.27 1296 ± 44.33	468 ± 17.45 412 ± 15.50
9	1143 ± 37.39 1111 ± 34.65	461 ± 22.23 372 ± 16.39
10	542 ± 25.66 689 ± 23.83	1184 ± 58.39 909 ± 41.20