Research Article

African Wild Dog Dispersal and Implications for Management

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ABSTRACT Successful conservation of species that roam and disperse over large areas requires detailed understanding of their movement patterns and connectivity between subpopulations. But empirical information on movement, space use, and connectivity is lacking for many species, and data acquisition is often hindered when study animals cross international borders. The African wild dog (*Lycaon pictus*) exemplifies such species that require vast undisturbed areas to support viable, self-sustaining populations. To study wild dog dispersal and investigate potential barriers to movements and causes of mortality during dispersal, between 2016 and 2019 we followed the fate of 16 dispersing coalitions (i.e., same-sex group of ≥1 dispersing African wild dogs) in northern Botswana through global positioning system (GPS)-satellite telemetry. Dispersing wild dogs covered ≤54 km in 24 hours and traveled 150 km to Namibia and 360 km to Zimbabwe within 10 days. Wild dogs were little hindered in their movements by natural landscape features, whereas medium to densely human-populated landscapes represented obstacles to dispersal. Human-caused mortality was responsible for >90% of the recorded deaths. Our results suggest that a holistic approach to the management and conservation of highly mobile species is necessary to develop effective research and evidence-based conservation programs across transfrontier protected areas, including the need for coordinated research efforts through collaboration between national and international conservation authorities.

KEY WORDS Botswana, conservation management, dispersal, Kavango-Zambesi Transfrontier Conservation Area, movement, Okavango Delta, transfrontier protected areas.

Many threatened species, particularly those prone to conflict with humans, are confined within relatively small and increasingly isolated protected areas surrounded by human-dominated landscapes (Graham et al. 2009, Bauer et al. 2015). The small and scattered nature of these protected areas is of particular concern for the management and conservation of species that naturally move, migrate, or disperse over large areas (Durant et al. 2017, Tshipa et al. 2017). Therefore, efforts have been made to protect contiguous natural areas to preserve vital connections between protected areas. But empirical information on movement patterns, dispersal, and connectivity is lacking for many of the wide-ranging species for which these larger protected areas have been created (Tshipa et al. 2017). This lack of information prevents a thorough assessment of the effectiveness of protected areas for species persistence and potentially limits their development. One such area is the Kavango-Zambesi Transfrontier Conservation Area (KAZA-TFCA) in southern Africa, which forms the largest transfrontier conservation area in the world spanning 500,000 km^2 and 5 countries (Fig. S1, available online in Supporting Information).

Dispersal of individuals is an important process governing the population dynamics of socially and spatially structured populations (Bowler and Benton 2005). It promotes gene flow, facilitates the rescuing of small subpopulations (which may be susceptible to local extirpation), and enables the recolonization of unoccupied territories. Through immigration and emigration, dispersal is one of the major

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processes changing the structure of existing social groups and leading to the formation of new reproductive groups. Information on dispersal such as distance covered, dispersal trajectories, survival rates, and reproductive success is thus important for a spatially explicit understanding of population dynamics (Bowler and Benton 2005). In addition to direct demographic consequences, dispersal also influences disease transmission and increases human–wildlife conflict when dispersing individuals encounter human activities or domestic animals (Woodroffe et al. 2005, Hassell et al. 2017). Therefore, a better understanding of where, when, and how dispersers move is important for improving landscape-scale management and conservation in and around protected areas (Zeller et al. 2012, Cushman et al. 2013, Tesson and Edelaar 2013).

The African wild dog (*Lycaon pictus*) exemplifies species characterized by the need for vast areas of natural or semi-natural habitat and is recognized as a flagship species within the KAZA-TFCA. The African wild dog is among Africa's most endangered large carnivores and about 6,000 free-ranging individuals remain in a few isolated subpopulations, few of which are large enough to be buffered from stochastic events (Woodroffe and Sillero-Zubiri 2012). Therefore, understanding dispersal-mediated connectivity between subpopulations is fundamental for the management and conservation of the species.

African wild dogs disperse in same-sex dispersing coalitions (i.e., same-sex group of ≥1 dispersing African wild dogs; McNutt 1996) and can travel several hundred kilometers from natal ranges (Davies-Mostert et al. 2012, Masenga et al. 2016). Owing mainly to technological limitations, however, very little systematic information has been available concerning the details of such dispersal events, and knowledge of African wild dog dispersal has been largely limited to individual age, coalition size at emigration, and straight-line distance covered (Frame and Frame 1976, McNutt 1996, Somers et al. 2008, Davies-Mostert et al. 2012). Only very recently has detailed global positioning system (GPS) information been collected on a few dispersing African wild dogs (Masenga et al. 2016, Abrahms et al. 2017, Woodroffe et al. 2019). Consequently, our understanding of African wild dog population connectivity suffers from this shortage of information and is often inferred from data collected on resident individuals (Jackson et al. 2016). Mortality during dispersal is thought to be high (Courchamp and Macdonald 2001), but empirical information is limited. We present empirical data on the dispersal trajectories of African wild dogs across the KAZA-TFCA landscape and describe movement metrics during dispersal, the effect of landscape features on dispersal trajectories, and the associated causes of mortality.

STUDY AREA

We conducted this study between 2016 and 2019 in northern Botswana and surrounding areas of the KAZA-TFCA, including the Namibian border and western Zimbabwe. The area (−17.8°S and −20.5°S to 22.2°E and 27.0°E) encompassed roughly 60,000 km^2, is mostly flat and at an elevation of 900–1,000 m above sea level. This large study area contained the historical core study site of the Botswana Predator Conservation Trust (BPCT) that spans approximately 3,000 km^2 (McNutt 1996, Cozzi et al. 2013), where each dispersal event started (Fig. 1). The region is characterized by a dynamic mosaic of swamps within the Okavango Delta and the Chobe-Linyanti systems, and by the adjacent semi-arid wooded savannas (Mendelson et al. 2010; Fig. 1). Rainfall is seasonal (Nov–Mar) and out of phase with the annual flood that comes from the catchment area of the Okavango River basin in Angola and reaches the BPCT core study site around June (Mendelson et al. 2010). The area is unfenced, with the exclusion of a few veterinary cordon fences that do not represent any barrier to African wild dog movements (Cozzi et al. 2013). All major large carnivores and herbivores typical of African savannas are common throughout the large study area (Cozzi et al. 2013, Bennitt et al. 2019). Human populations and activities are concentrated along the major roads at the southern and western distal ends of the Okavango Delta (Mendelson et al. 2010; Fig. 1).

METHODS

Fieldwork

We immobilized candidate dispersing individuals of both sexes for the purpose of deploying GPS-collars (Vertex Lite, Vectronic Aerospace GmbH, Berlin, Germany) while they were still within their natal pack. We identified candidate dispersers based on their age, number of same-sex siblings, pack size, and presence of unrelated individuals of the opposite sex in the pack (McNutt 1996). Collared dispersers originated from 9 resident packs regularly followed by the BPCT in the core study site. The majority of the immobilizations occurred during October and November to anticipate peak dispersal season between December and February (McNutt 1996). Following Osofsky et al. (1996), we darted candidate dispersers at a distance of 10–15 m using a CO_2-powered dart gun with a 3-ml dart (Dan-Inject ApS, Denmark) and a combination of ketmine, xylazine, and atropine, which we reversed with yohimbine. Anaesthetics quantity changed slightly according to individual size and conditions but averaged 0.45 mg, 0.55 mg, and 1.25 mg, respectively (Osofsky et al. 1996). A Botswana-registered wildlife veterinarian was responsible for all immobilization procedures, as specified under Research Permit EWT 8/36/4 XXXVI (33) issued by the Botswana Ministry of Environment, which regulates animal care and use. We obtained location data from 16 African wild dogs in as many dispersing coalitions. Data from this study is available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.tqjq2bvvc).

We programmed the GPS-collars to record positions at 4-hour intervals during dispersal and to daily send locations to a base station through the Iridium satellite network. This allowed remote tracking of collared individuals across international borders and where field conditions were prohibitive for direct observation. We also programmed the collars to send a mortality signal following 24 hours of

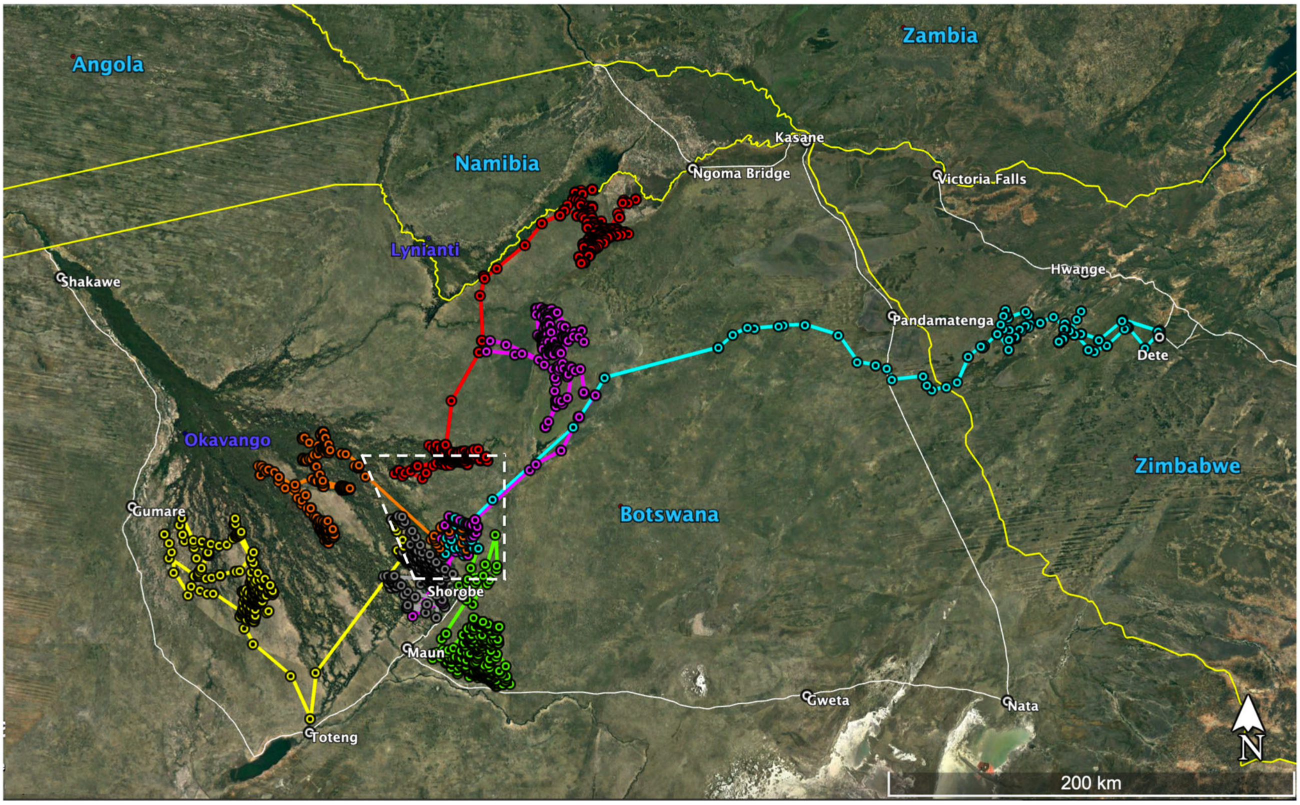

Figure 1. Example of African wild dog dispersal trajectories (colored lines) across part of the Kavango-Zambesi Transfrontier Conservation Area. Dots represent single global positioning system locations. The Okavango Delta and the Linyanti Swamp are visible in darker shades of green. The surrounding landscape is composed of semi arid-wooded savannahs. Yellow thin lines represent international boundaries, and white thin lines represent major roads. Major villages and cities are represented by the white dots. The white dotted polygon represents the main study area of the Botswana Predator Conservation Trust (~3,000 km^2), where each dispersal event started. Underlying map: Google Earth.

inactivity, which allowed us to locate the carcass and investigate the cause of mortality on the same day. Particularly, we differentiated between natural and human-related causes of mortality. Lions (*Panthera leo*) and other large carnivores are the main cause of natural mortality in African wild dogs and bite marks and open wounds can be identified on African wild dog carcasses, which are typically not consumed. Additional causes of natural mortality may include injuries, such as limb fractures. Human-related causes of mortality may include shooting, poisoning, snaring, and vehicle collisions (Woodroffe and Sillero-Zubiri 2012). In the absence of contradictory evidence, individuals that died within national parks were assumed to have died of natural causes.

Analysis

We used GPS tracking to describe African wild dog movement metrics and dispersal trajectories in northern Botswana and reveal this study population's potential connectivity with the rest of KAZA-TFCA. We investigated rates and causes of mortality during dispersal, and assessed differences in movement patterns between resident and dispersing individuals.

For each collared individual, we calculated and plotted the net squared displacement (NSD) statistics. The NSD is calculated as the square of the Euclidean distance from the start of a path (the collaring site in our case) to a given GPS location along the same path (Börger and Fryxell 2012). Inflection points in NSD over time can be used to infer time of emigration and time of settlement (Börger and Fryxell 2012). Prior to emigration and after settlement, the NSD resembles that of a resident pack (i.e., it fluctuates around a constant value); NSD increases over time between emigration and settlement (Börger and Fryxell 2012): the transient phase of dispersal. Given the sudden displacement away from the territory of the natal pack following emigration (Fig. S2, available online in Supporting Information), we deemed visual investigation of the NSD was appropriate to assess the precise emigration date (Cozzi et al. 2016). We corroborated this information with field observations. Following emigration of the collared individual, we visited its natal pack within a few days to know how many and which siblings of the same sex had dispersed with it (we assumed that no dogs had died or dispersed independently in such a short time). Depending on terrain accessibility, we also visited dispersing coalitions after emigration to confirm coalition size and investigate any association with individuals of the opposite sex. Similarly to emigration, we used field observations and inflection point in NSD plots to visually assess settlement date (Fig. S2). Because, from a demographic perspective and realized connectivity, dispersal is only meaningful if it leads to reproduction (or at least its attempt), we considered first reproduction after the date of settlement as part of the settlement phase of dispersal.

For each coalition, we further calculated descriptive statistics including maximum Euclidean distance covered in 4-hour and 24-hour windows, Euclidean distance between the last location before emigration and the first locations after settlement, cumulative distance between the last location before emigration and the first location after settlement, time to settlement, and Euclidean distance to the farthest location reached during the entire tracking period trajectory. We used 1-way analysis of variance to investigate differences between male and female coalitions for all movement metrics calculated; to test for differences between pre-emigration, transience, and settlement; and to test for the effect of coalition size.

To assess the influence of human presence and activity along the major roads on African wild dog movements, we investigated their movement behavior within 1 km of villages, cattle posts, or crop fields, which we defined as contact with humans. Specifically, we investigated whether there was a directional change >90° (i.e., retreating) within 24 hours following contact with humans. We investigated angle change in relation to the direction showed by African wild dogs 24 hours prior to contact with humans. As per chance alone, on 50% of occasions dispersers may have retreated irrespective of human presence; therefore, we considered a result value >75% as indicative of a negative effect of human presence and activity on movement. We digitized locations of villages, cattle posts, and field crops from Google Earth (Google, Mountain View, CA, USA) images (Fig. S3, available online in Supporting Information).

Because of the highly variable extent of the Okavango Delta's flooded surface that contracts and expands across months and years (Mendelson et al. 2010, Cozzi et al. 2013) and the unavailability of satellite imagery at the desired spatial and temporal resolution, we qualitatively assessed only the effect of water on the movement behavior of dispersing African wild dogs. We differentiated between coalitions that dispersed through permanent swamp, coalitions that passed through seasonally flooded areas, and coalitions that dispersed away from any water body (Fig. S4, available online in Supporting Information). We inferred permanent and seasonal swamps from Google Earth images and from over 10 years of knowledge of the area by the leading author. We summarize some major features linked to the effect of water on dispersal, and provide GPS data of dispersing African wild dogs in the Dryad Digital Repository for reference (https://doi.org/10.5061/dryad.tqjq2bvvc).

RESULTS

Dispersal Movement Metrics

Averaged across all of the individual's maxima, maximum distances covered during dispersal were 17 km (range = 8–35 km) over 4 hours and 35 km (range = 11–54 km) over 24 hours (Table 1). The daily maximum distance covered was larger ($t = 3.8$, $P < 0.01$) during the transient phase of dispersal ($\bar{x} = 35 \pm 7$ [SE] km) compared to the pre-emigration phase (20 ± 3 km), and the latter was not significantly different ($t = 0.9$, $P = 0.3$) from the settlement phase (24 ± 7 km). Mean cumulative daily distance (summed over the fixes collected 4 hr apart) was 13.4 km and 9.4 km during transience and after settlement, respectively (Table S1, available online in Supporting Information). Mean cumulative distance to settlement was 548 km (range = 111–1,242 km; Table 1). Long-distance dispersal events that resulted in settlement outside the historical BPCT core study site had a mean Euclidean distance to settlement of 110 km (Table 1), lasted on average 32 days (Table S1, available online in Supporting Information), and were substantially shorter in duration ($t = 1.8$, $P = 0.08$) than dispersal trajectories that settled within the historical BPCT core study site (estimated at 52 days). Two remarkable dispersal events included a 345-km journey covered in 9 days that ended in Zimbabwe, and a 154-km journey over 5 days that ended on the Namibian border. On average females covered greater distances than males for all movement statistics calculated (Table 1), although these differences were not statistically significant (all $P > 0.05$).

Coalitions that dispersed to areas outside the historical BPCT core study site were on average smaller ($\bar{x} \pm 1$ SD = 2.7 ± 0.9 individuals) than coalitions that dispersed within the larger study area (3.9 ± 2.0 individuals) at the onset of dispersal; however, this difference was also not significant ($t = 1.4$, $P = 0.18$). Coalition size showed a marginally significant negative relationship with maximum distance covered over 4 hours in the transient phase ($t = -1.8$, $P = 0.09$), and a marginally significant positive relationship in the settlement phase ($t = 2.0$, $P = 0.07$); it had no effect on the other movement metrics.

Effect of Landscape Features on Dispersal Trajectories

Five coalitions dispersed through the permanent swamp, 10 traveled in the vicinity or along seasonally flooded areas, and 1 never passed close to the Okavango Delta (Fig. S4). Across all 5 coalitions, average time spent traveling through the permanent swamp was 15 days (4–35). Two of the 5 coalitions covered 84 km and 90 km through the swamp in 6 days (Fig. 1). Of the 10 coalitions, 5 never crossed water, whereas the other 5 crossed between 1 and 12 times. Given the distance covered by dispersing African wild dogs in a few hours, dispersers in some of these suspected crossing events may have circumnavigated the distal dry end of the Okavango Delta.

In contrast, our data suggest that human villages and human activities strongly obstruct movement during dispersal. On 27 occasions, 10 dispersing coalitions moved within 1 km of villages, cattle posts, or crop fields and in 89% of these cases they retreated in the opposite direction within 24 hours (Figs. 1 and S3; Table 1). No dispersing coalitions ever crossed the main road Nata – Maun – Toteng – Gumare, along which are located various villages and human activities (Figs. 1 and S3).

Mortality During Dispersal

We recorded 4 mortality incidents in which 12 African wild dogs died; 3 of these incidents were due to human causes,

Table 1. Overview of African wild dog dispersal events across the the Kavango-Zambesi Transfrontier Conservation Area in southern Africa between 2016 and 2019. Euclidean distances are calculated from the date of emigration. All distances are given in kilometers.

Sex	Coalition size[a]	Euclidean distance to settlement	Max. Euclidean distance reached	Cumulative distance to settlement	Max. distance covered in 4 hr in transience	Max. distance covered in 4 hr in settlement	Max. distance covered in 24 hr pre-emigration	Max. distance covered in 24 hr in transience	Max. distance covered in 24 hr in settlement	Main study area[b]	Number of occasions <1 km from villages	Number of occasions retreated from villages
Female	4	311	345	614	18.3	14.1	10.9	54	22.9	Outside	1	1
Male	2	133	154	613	26.6	14	18.2	52.4	24.2	Outside	3	3
Female	2	100	115	487	35.4	14.5	14.7	48.7	30.3	Outside	1	1
Male	2	69	116	493	13.7	10.7	12.6	45	19.5	Outside	2	2
Female	2	62	72	535	11.6	9.3	16.6	25.8	18.6	Outside	[c]	[c]
Male	4	53	91	405	10.9	16.7	11.5	42.8	29.5	Outside	0	0
Male	3	45	67	111	NA	8.6	12.8	31.8	18.3	Outside	0	0
Female	2	25	73	542	15.4	9.6	47.5	50.9	23.2	Inside	2	2
Female	1	21	43	311	NA[d]	NA	6.5	17.7	21.8	Inside	5	5
Male	3	21	48	640	22.6	15.4	20.1	44.2	32.9	Inside	0	0
Female	6	21	70	1,242	14.3	20	26.2	39.7	31.1	Inside	5	5
Male	5	6	41	585	13.4	12.6	28	25.1	26.5	Inside	1	1
Male	7	NA	NA	NA	NA[d]	NA	NA	12.3	24.3	Inside	0	0
Male	5	NA	NA	NA	8	11.5	NA	10.6	8.9	Inside	5	3
Female	2	NA	NA	NA	17.9	NA	19.4	32	NA	Inside	2	1
Female	4	NA	NA	NA	11.8	NA	28.8	24.4	NA	Inside	0	0
$\bar{x}$		72	103	548	17	13	20	35	24			
Min.		6	41	111	8	8.6	6.5	10.6	8.9			
Max.		311	345	1,242	35.4	20	47.5	54	32.9			
$\bar{x}$ (female)		90	120	621	18	14	21	37	25			
$\bar{x}$ (male)		55	86	474	16	13	17	33	23			

[a] At time of emigration.
[b] Includes coalitions that reached or settled outside the main study area during the time they were monitored.
[c] We did not attempt to investigate retreat from cattle posts and crop fields because, given their abundance, it was not clear which segment of the dispersal trajectory may have been influenced by which cattle posts and crop fields.
[d] Collars failed to change to 1 fix/4-hour schedule.

accounting for 11 out of 12 African wild dogs killed (Table S2, available online in Supporting Information). One coalition of 2 dispersing females died of poisoning during the transient phase of dispersal, and 2 other incidents involved newly formed packs immediately after settlement. One pack was shot (we found 2 of 4 dispersing African wild dogs) and 1 pack was poisoned at the den (we found 3 of 5 adults and their 4 pups). The only African wild dog that died of natural causes died during the transient phase of dispersal (Table S2). We did not detect any effect of maximum Euclidean distance reached on mortality ($t = -0.6$, $P = 0.55$). Our data showed that 33% of the coalitions ($n = 9$) that dispersed through human-dominated landscapes (2–176 days) did not survive.

DISCUSSION

With this study, we systematically followed dispersing African wild dogs across a large area of the KAZA-TFCA and highlighted their ability to reach locations hundreds of kilometers apart within a few days, thus securing potential connectivity between distant subpopulations. Natural features appear to present little challenge to connectivity, but we showed that human presence and activity can limit connectivity by hindering dispersal movements and by increasing dispersal mortality outside protected areas. This could substantially reduce connectivity between even closely neighboring populations. One example is the lack of observed dispersal event between the Okavango Delta and the >50,000 km^2 Central Kalahari Game Reserve and Makgadikgadi National Park ecosystems, only about 120 km to the south but separated by the Nata – Maun – Toteng – Gumare road and its associated villages and human activities. Our results thus call for the need to quantitatively assess realized connectivity (i.e., effective gene flow that is dependent on successful reproduction at the settlement site) with this information being of particular utility in future conservation and management plans.

Our continuous data collection allowed us to re-evaluate and correct some earlier interpretations of African wild dog dispersal, which were biased by limits in our historical capacity to keep track of dispersing individuals. To conform to common practice imposed by logistic and technological constraints, we differentiated between local (i.e., remaining within the historical BPCT core study site) and long-distance (i.e., moving outside the historical BPCT core study site) dispersers. Local dispersers are likely to be re-sighted within their original study site, and our understanding of dispersal has previously been biased towards such local re-encounters. On the other hand, long-distance dispersers are unlikely to be re-observed and have often been excluded from further analysis (McNutt 1996, Woodroffe 2011). In our case, 44% of the dispersing coalitions that we followed, which represented 35% of observed dispersing individuals, dispersed outside the historical BPCT core study site. Their fate would have been unknown, had we not been able to track them using GPS-satellite technology. Given the importance of long-distance dispersal for connectivity and gene flow, these long-distance dispersers have a particularly high conservation value and should not be ignored (Barton et al. 2019).

We still do not fully understand why some coalitions travel farther distances than others. The female coalitions traveled farther for all calculated movement statistics, although similar numbers of male and female coalitions dispersed locally and over long distances. Researchers have suggested male philopatry in eastern Africa (Frame and Frame 1976), and female philopatry for the Okavango ecosystem in Botswana (McNutt 1996). Apparent contrasting results between our study and the study by McNutt (1996), who researched the same population of African wild dogs and showed that females covered shorter distances than males, may be because McNutt (1996) focused on successful dispersers that settled within the BPCT core study site. When settling locally near home, it may be beneficial for females to be as close as possible to the natal, and thus familiar, territory. Such familiarity may be beneficial in the location of suitable denning sites. The effect of coalition size on dispersal patterns and distance covered remains to be understood and further investigated.

How far dispersers travel before they settle may be explained by 3 mutually non-exclusive hypotheses. Unless they travel and settle in human-dominated landscapes where mortality is high (as shown in this study) and hence occupancy low, dispersers are likely to have to settle between resident packs and slowly carve out their exclusive territory. In this case, smaller coalitions may need to travel farther (which we observed in this study) because of their limited competitiveness against resident groups. Second, smaller coalitions may be less attractive to potential mates and thus need to travel farther to find suitable partners. Finally, dispersers continue in their fast and highly directional movements until they locate potential mates, in which case longer dispersal movements may be indicative of low occupancy rates, yielding fewer opportunities for the formation of new packs. Information on local population density and the distribution of resident individuals is important to fully understand dispersal processes and confirm or reject these hypotheses (Cozzi et al. 2018, Maag et al. 2018). Given the large spatial scale at which dispersal takes place, such information may only be collected through a well-coordinated effort between national and international researcher institutions and government authorities (Kark et al. 2015).

Our data reveal noteworthy differences between dispersing coalitions and resident packs in the same population in the Okavango Delta, in terms of distances covered and in the effect of landscape features on those movements, and such differences are important for our understanding of connectivity across larger landscapes. Distances covered during transience were greater than during the pre-emigration and settlement phases, the latter 2 being more similar to typical resident-like movement patterns. Similarly, Pomilia et al. (2015) reported a maximum distance traveled of 42 km in 24 hours and tracked across 4 consecutive locations. Our observed maximum daily distance traveled between 2 locations 24 hours apart (hence biased low compared to the method by Pomilia et al. [2015]) was 54 km; we observed a distance of 35 km covered in just 4 hours. Our recorded average cumulative daily distance traveled during transience of 13.4 km was also considerably larger than the 8.5 km reported by Pomilia et al. (2015) for resident packs.

Furthermore, although the effect of water bodies needs further investigation based on more precise information of the flood extent at a more refined temporal and spatial scale, our observations suggest that dispersers may perceive water bodies differently than resident packs. Although resident packs in the Okavango Delta were substantially restricted by water (Cozzi et al. 2013), dispersers show a marked willingness to cross water (10 of the 15 dispersing coalitions that contacted water crossed it). Such differences between residents and dispersers may be due to the use of water by resident packs as easy-to-defend territory boundaries and the need and motivation of dispersing individuals to cross into the territory of unrelated packs. Whichever the ultimate cause may be, the use of information collected on resident packs may result in an overestimation of the obstructing effect of water on dispersal. Based on the above differences, and in line with Jackson et al. (2016) and Abrahms et al. (2017), we caution against the use of information collected on resident individuals to create resistance maps and assess population connectivity.

We also showed that human presence and activity represent an important barrier to African wild dog movements and these results are in line with findings from eastern Africa (Masenga et al. 2016). One can speculate that dispersing coalitions may be able to navigate around a few scattered cattle posts, but high human density may pose a more impenetrable barrier (Fig. S3). We recommend that additional movement data should be collected on more dispersing African wild dogs, along with precise information on human presence and activities, to rigorously assess the dispersal permeability of such regions. Human density and activities, land use practices, vehicle traffic, active persecution, and other forms of human disturbance may all result in African wild dogs avoiding these areas; collection of these data may be best coordinated with governmental agencies such as Department of Home Affairs and Statistics.

Over 90% of mortality events amongst our dispersing African wild dogs were human-caused, suggesting that human activity represents a significant limiting factor on African wild dog dispersal success, which may be best understood as a move from the natal patch to a new patch and successful reproduction in the new patch (realized connectivity). Our results also suggest that the settlement phase of dispersal, rather than the transient phase, is when wild dogs are most susceptible to human-related mortality. During transience, when African wild dogs move up to 50 km/day, dispersers are unlikely to spend several days within a given location thus reducing the likelihood of active persecution by humans as a result of persistent livestock losses. Accordingly, we think that the 2 African wild dogs that were poisoned during transience were not the intended victims, for they had not been in the region before. The high mobility of dispersers may, however, expose them to a higher encounter rate with snares or road crossings, and these causes of mortality should be thoroughly assessed in the future. Dispersing African wild dogs that settle in human-dominated landscapes may be at highest risk, facing extermination through shooting or poisoning. Additionally, the denning period, when African wild dogs are most easily located, appears to expose individuals and packs to greater mortality risk. For instance, 1 pack was poisoned by placing poisoned water at the entrance of the den. Our data thus shows the importance of considering human acceptance when assessing large carnivore movements and recolonization processes across human-dominated landscapes (Behr et al. 2017) and highlights the need to work alongside local communities to mitigate conflicts and increase acceptance beyond the boundaries of protected areas.

MANAGEMENT IMPLICATIONS

Our study highlights how the conservation of highly mobile species such as African wild dogs necessitates a paradigm shift toward a more holistic approach that incentivizes protection outside protected areas, across wider landscapes and international boundaries. The spatial extent of our study (60,000 km^2 vs. 3,000 km^2 regularly monitored by the BPCT) also shows the need for increased collaboration between national and international researcher institutions, government authorities, and private operators. Although the GPS-satellite technology embedded in the collars allows us to remotely follow the movements of wide-ranging individuals, key information such as survival rate, causes of mortality, reproductive success, and regional population density can only be collected through intensive fieldwork that needs be coordinated internationally. Such international collaborations will be crucial for the successful improvement of research, management, and conservation efforts across larger natural areas such as the KAZA-TFCA.

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