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Partial migration links local surface-water management to large-scale elephant conservation in the world's largest transfrontier conservation area. *Biological Conservation*, 215, 46-50.

Partial migration links local surface-water management to large-scale elephant conservation in the world's largest transfrontier conservation area

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Abstract

Successful conservation of large mammals requires vast areas to maintain viable populations. This often requires to embrace large-scale approaches that extend beyond the borders of formally protected areas. However, the quality of the scientific knowledge about animal movement across large conservation areas vary, and could limit the effectiveness of conservation efforts. Here we used GPS tracking to conduct the first study of large-scale movements of African elephants (*Loxodonta africana*) in Hwange NP (Zimbabwe), which is an unfenced park part of the Kavango-Zambezi Transfrontier Conservation Area, the world's largest terrestrial conservation area. We show that some, but not all, elephants migrate seasonally, with wet- to dry-season movements linked to the provision of water in Hwange NP. The distance between the most distant locations of individual elephants reaches 260 km. In this partial migration system influenced by management practices, over 20% of the elephants have wet-season ranges established in Botswana, outside of protected areas in private or communal wildlife management areas. Our results call for the urgent drafting of a regional action plan, involving all stakeholders identified by our study and their neighbours, to predict and react to what would happen if water provision in Hwange NP was to suddenly change because of management practices or extreme climate change. Beyond this critical conservation issue for the world's largest elephant meta-population, our results also highlight the relevance of large-scale conservation areas combined with integrative planning involving national wildlife management institutions and the private and communal sector.

Keywords. Connectivity; Land sharing; Management; Migration; Protected area; Water.

Highlights.

- A partial migration by African elephants is revealed in western Zimbabwe.
- Wet- to dry-season movements are linked to the provision of water in Hwange NP.
- Some wet-season ranges are established in Botswana, outside of protected areas.
- Conservation of large-mammal migrations is facilitated by large conservation areas.
- However, management plans beyond land use and country borders are critically needed.

1. Introduction

The conservation of large mammals requires the protection of vast areas to maintain viable populations (Macdonald et al., 2013). This is often neither feasible, nor desirable, given trade-offs between land sparing and other factors, particularly the livelihoods of human populations (Fischer et al., 2011). As a result, large mammal conservation needs to embrace an integrative view that extends beyond the borders of protected areas and includes all stakeholders (Cumming et al., 2015).

The recent development of Transfrontier Conservation Areas (hereafter TFCA) attempts to overcome this challenge. For instance, the Kavango-Zambezi (KAZA) TFCA, covering five countries in southern Africa and now the world's largest terrestrial conservation area (520,000 km²)(Fig. A1), was legally established in 2011. It currently hosts over 50% of all African savannah elephants (*Loxodonta africana*)(Chase et al., 2016), and elephant conservation and management, and the maintenance of connectivity between protected areas, is at the heart of this project (see www.kavangozambezi.org).

To be successful, such approach requires understanding the spatio-temporal dynamics of the populations of target species. Additionally, grasping the extent to which management actions can affect populations locally, but also beyond the border of the management area, is critical. Information about the patterns and drivers of animal movement is therefore particularly valuable, especially when focusing on long-ranging migratory species (Bolger et al., 2008).

The amount and quality of the scientific knowledge about animal movement across large-scale conservation areas vary however. This is understandable because monitoring animal movement across large areas remains logistically challenging and expensive. In some cases, movements are obvious, such as the simultaneous migration of hundreds of thousands of animals (e.g. the Serengeti wildebeest *Connochaetes taurinus*). In others, local knowledge, sometimes supported by census data,

could be suggestive of some animal redistribution in the landscape (Bruce et al., 2014). However, in many cases, movement data could improve the effectiveness of conservation efforts. For instance, it may help in supporting or revising the current limits of conservation areas or in designing corridors within these. By clearly identifying linkages between areas, studies could also reveal which stakeholders influence and/or manage the same animals. Finally, improved knowledge could generate acceptance of a common view of the functioning of the system by stakeholders, thus facilitating the integrative management approach.

We conducted our study in Hwange National Park, Zimbabwe. This large unfenced park borders Botswana and is part of the KAZA TFCA (Fig. A1). Artificial water provisioning within the north-eastern section of Hwange NP (Fig. A1) has allowed the increase of the Hwange elephant population from less than 1000 individuals in the 1930's (Davison, 1967) to an estimated 45000 individuals in the 2014 dry season (Chase et al., 2016). Recent road censuses conducted within the area of the Park where artificial waterholes are maintained show strong a seasonal increase in elephant numbers during the dry seasons (Chamaillé-Jammes et al. 2009). This seasonal increase is more important during dry years when more of the natural pans of the rest of the Park dry up (Chamaillé-Jammes et al. 2007a, b). Because demographic processes cannot explain these increases, nor any of the other factors considered (e.g. human disturbance outside the Park), we parsimoniously assumed that access to surface water is a key driver of large scale seasonal movements of elephants inside, and possibly outside, the Park. Here, we used GPS tracking to conduct the first study of large scale elephant movements in Hwange NP and explored the links to other areas of KAZA. We discuss how our results highlight the relevance of TFCAs and provide clear directions to improve the conservation and management of the world's largest elephant population.

2. Methods

2.1 Study area

Hwange NP covers ~15000km² of semi-arid wooded savannas. Mean annual rainfall is ~ 600mm and most of the rain falls between November and April, during which natural pans fill up. Most of these pan dry up during the course of the dry season (Chamaillé-Jammes et al., 2007b). As there is no permanent river in the Park, during the dry season water is mostly available at the artificial waterholes in which groundwater is continuously pumped (Fig. A1). In the dry season, elephant breeding herds do not forage more than 15 km away from water (Chamaillé-Jammes et al., 2013). The limited distribution of water, combined with one of the highest densities in the world (~3 elephants per km²; Chase et al., 2016), regulate the dynamics of the population (Chamaillé-Jammes et al., 2008).

2.2. Elephant movement data

Thirty-three GPS collars were deployed on adult females in different breeding herds. All elephants were captured in the eastern section of Hwange NP (Fig. A1). Collars were deployed in August 2009 (n=10), November 2012 (n=13), November 2014 (n=8) and February 2015 (n=2). See Fig. A2 for an overview of monitoring periods. The frequency of location acquisition varied between between collars, and for this study focusing on large-scale movements we retained only one location per day. The data have been archived, and can be visualized, on movebank.org (study name: African elephant (Migration) Chamaillé-Jammes Hwange NP).

2.3 Analysis of seasonal range overlaps

We used a location-based kernel approach (Worton, 1989) to estimate, for each individual, the ranges

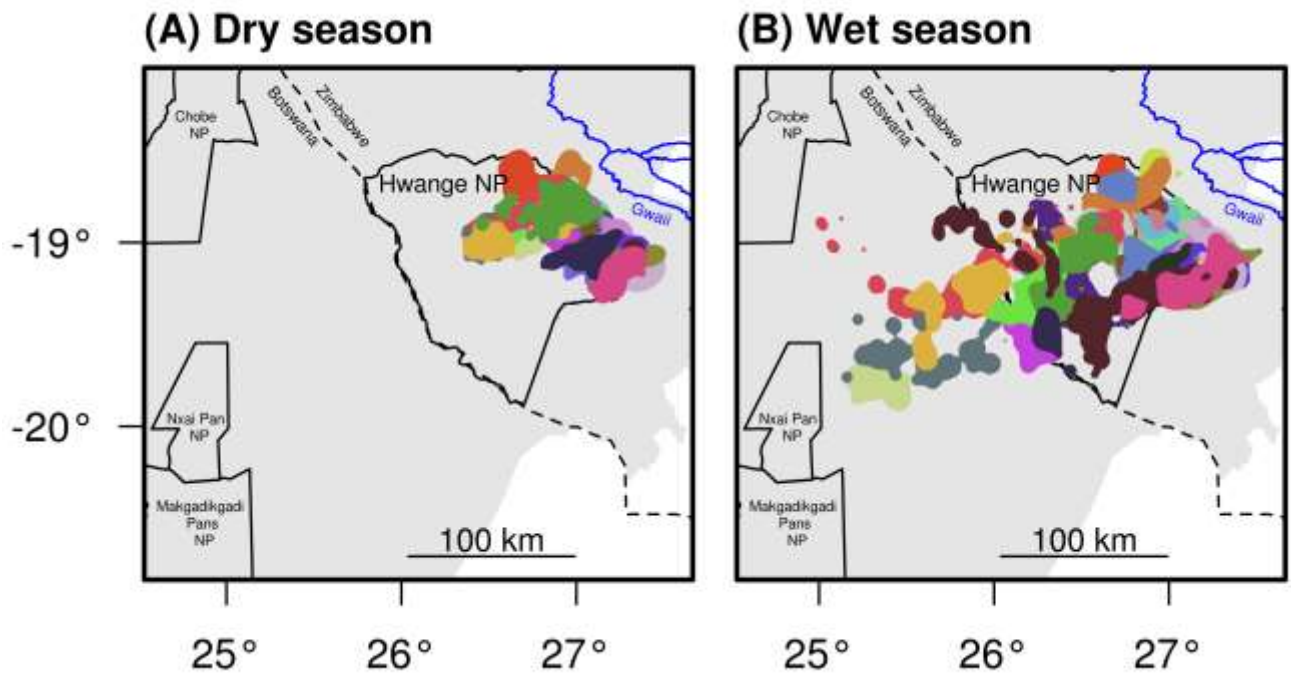
(90% utilization distribution) of elephants during the core of the wet and dry seasons. We selected the core of the seasons to avoid confounding effects of transit that would artificially inflate the overlap between ranges. Based on seasonal rainfall patterns (Chamaillé-Jammes et al., 2006), the core wet season was defined as the February/March period, and the core dry season as the September/October period. We then estimated the amount of range overlap using the Bhattacharyya's coefficient (Benhamou et al., 2014). We also measured the distance between range centroids to inform on range separation when overlap was nil.

3. Results

3.1 Seasonal range overlaps

Dry-season ranges of the monitored elephants were always located in the eastern section of Hwange NP (Fig. 1A). In contrast, their wet-season ranges were spread out along a north-east / south-west gradient extending into Botswana (Fig. 1B). Accordingly, the range overlap and the distance between dry- and wet-season ranges were very variable (Fig. A3), indicating the presence of both resident and migrant individuals. Nine (28 %) elephants migrated more than 50 km between seasons (up to 172 km)(Fig. A3). For these, the distance between their most distant locations varied between 108 and 260 km. Across years, elephants were generally faithful to their wet- and dry-season ranges, as revealed by the large overlaps and the short distances between consecutive dry- or wet-season ranges (Fig. A3). See Fig. A4 and A5 for displays of the temporal dynamics of elephant movements in relation to wet season ranges.

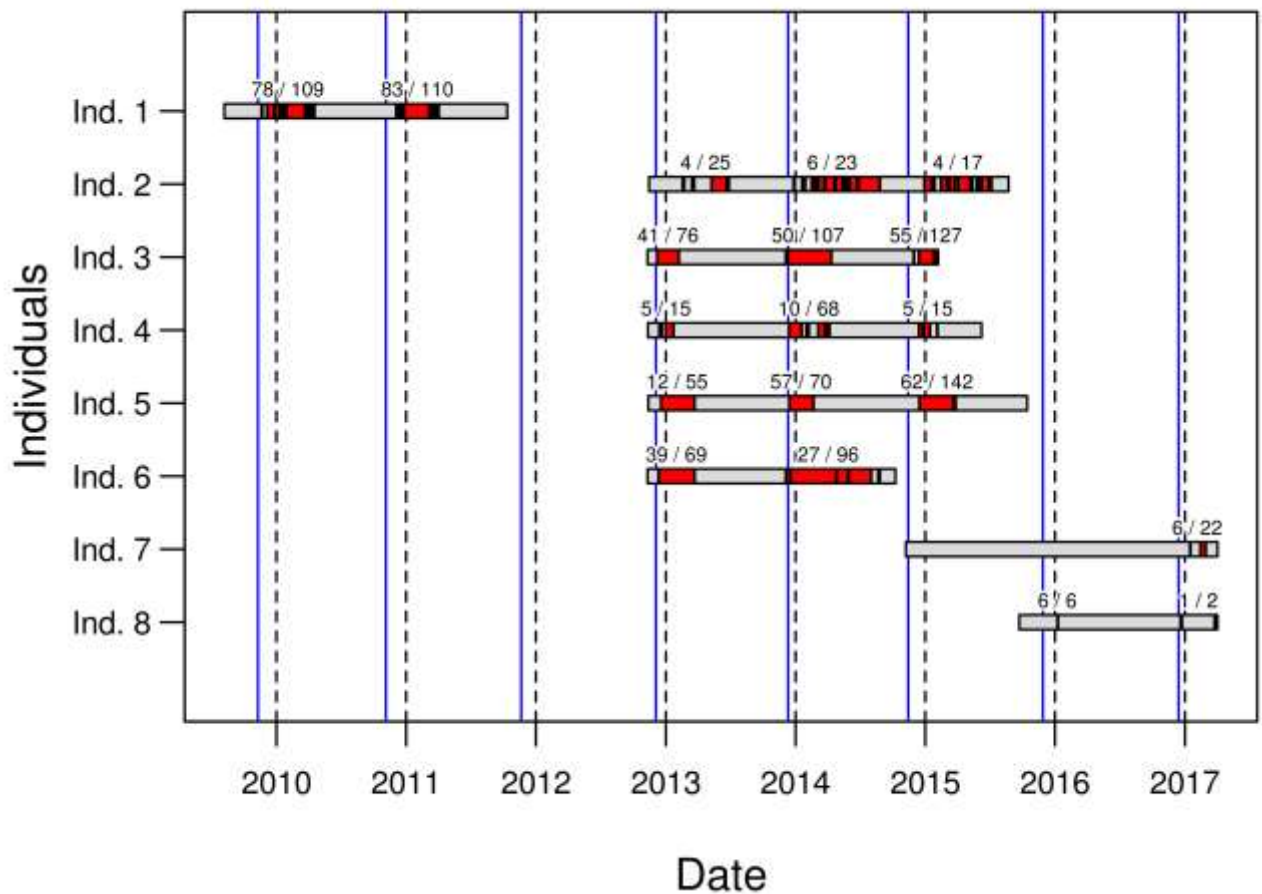
Figure 1. (A) Dry-season and (B) wet-season ranges of elephants collared in Hwange NP. Each individual is associated with a different color. The area in grey is within the boundary of the Kavango-Zambezi Transfrontier Conservation Area. Limits of Hwange, Chobe, Nxai and Makgadikgadi Pans National Parks are shown.



3.2 Transboundary movements

Eight (24 %) elephants crossed the border with Botswana. This generally occurred soon after the first heavy rains in their dry season range (Fig. 2). The time spent in Botswana varied between elephants and years (Fig. 2, Fig. A4). The distance at which elephants ventured into Botswana also varied, with several elephants using areas located 100km away or more from the border (Fig. 1B, 2). Nxai Pan National Park was visited during only one season, by two elephants, only 3 times in total and for less than 3 days each time (not shown). Other protected areas were not visited.

Figure 2. Timeline of the periods spent in Botswana, for the 8 elephants that crossed the border. The overall monitoring period is shown in grey. Periods spent in Botswana are shown in red. Short periods appear as thick dark lines. Numbers indicate the median / maximum distance to the border when in Botswana, for each wet season. The dotted vertical line shows the first day of the year. The blue vertical line shows, for each wet season, the date of the first day with > 20 mm of rainfall. Rainfall data were obtained from Little Makalolo camp, located in the eastern section of Hwange NP. The date of first rainfall > 20 mm in 2010 is approximate due to a lack of accurate records. Individual ID numbers are the same as those used in Fig. A4, which displays temporal displacement from wet season range.



4. Discussion

Our study revealed that some elephants of the Hwange NP population undertakes large-scale seasonal migration, with dry- and wet-season ranges separated by distances that fall within the first quartile of large herbivore migration distances (Berger, 2004; Teitelbaum et al., 2015). These seasonal movements are likely to be driven by the absence of surface water throughout much of the area during the dry season. Migratory elephants move back to their wet-season range soon after the first rains replenish seasonal water pans. Water-driven seasonal movements are well-known in elephants, albeit rarely at the scale observed here (e.g. Loarie et al., 2009; Young et al., 2009; Wittemyer et al., 2007).

4.1 *The origin of the partial migration*

Surface water is also driving migrations in other African herbivores: for instance, Plains zebra (*Equus quagga*) migrate from the Nxai pan area (wet-season range, Botswana) to the Chobe river (Botswana & Namibia, Naidoo et al., 2014); in Tanzania, blue wildebeest and Plains zebra migrate from grassy plains surrounding Tarangire NP to the permanent river that crosses the park (Morrison et al., 2016).

The originality of the Hwange elephant migration is that it depends on man-made waterholes in an area where no permanent water sources could be found prior to human intervention (Davison, 1967). The first permanent waterholes were created after 1935 (Davison 1967), and their numbers increased until the 80s (Anonymous, 1999).

The closest permanent water source is the Gwaii river located 50 km east of Hwange NP (Fig. 1) and elephants might have migrated to this river in the past (Williamson, 1975; Cumming, 1981). The creation of artificial waterholes would have allowed elephants to shorten their migration or even become resident. By remaining in Hwange NP, elephants would also have avoided the dangers of

crossing communal areas occupied by small-scale farmers or trophy hunting concessions that were established along the park boundary. It is however not clear if elephants would have emigrated from as far as Botswana. In 1969, a study conducted along the Botswana border did not support the hypothesis of a directional flux (Williamson, 1975).

Another scenario is that artificial waterholes were discovered by elephants that came from elsewhere but used the same wet-season range in the western section of the Park or Botswana. Rather than returning to their original dry-season range, these elephants would have started migrating to the east of Hwange NP or even became resident in this area where water is found throughout the year. In such case, this would be one of the first management-induced migrations ever recorded.

The seasonal movement of elephants in Hwange NP can be qualified as a partial migration, where some animals migrate but others don't (Chapman et al., 2011). The reasons underlying inter-individual differences are however unclear. All elephants used the same general area in the dry season, and we therefore cannot argue that differences in the quality of their ranges forced some to migrate and not others (as argued by Naidoo et al. (2012) to explain buffalo partial migration in Botswana and Namibia). Partial migration is usually explained by inter-individual differences in needs, sensitivity to predation, or ability to compete (Chapman et al., 2011). We believe the later is more likely to apply here, as by definition competition-based partial migration are more likely to emerge at high density when competition gets more intense, a situation certainly faced by elephants in Hwange NP (Chamaille-Jammes et al., 2008). Dominance hierarchies between elephant family herds have been well documented and can influence their movement patterns (Wittemyer et al., 2007). Therefore, it is possible that dominance between herds is driving the observed migration. The question as to which of the dominant or sudominant herds are migrating remains to be answered however.

4.2. Conservation and management implications of the migration

Migration is usually considered a globally threatened phenomenon, particularly for large mammals (Harris et al., 2009). Yet, we know very little about how migrations are established, evolve, and persist over time (Dingle, 2014). This makes restoring historic migration that no longer occur, challenging although possible (Bartlam-Brooks et al., 2011). What is often overlooked is that this lack of knowledge limits our understanding as to whether recent management practices can lead to the emergence of novel migrations or migration routes. For instance, do animals explore beyond their home range to discover better places? How much better should the newly discovered places be to overcome the risks of using an unfamiliar place? Answers to these questions are required to understand the evolution of migrations in the Anthropocene, with human activities changing the resource dynamics and disrupting climate patterns.

Over twenty percent of the monitored elephants migrated across an international boundary. The actual proportion of elephants migrating between the two countries is unknown. However, a number of collars were deployed after the first rains when migrants had left the capture area (Fig. A2), suggesting the actual proportion of migrants may be higher than in our sample. Several potential migration routes linking Hwange NP to other protected areas had been identified in the KAZA TFCA documents (Anonymous, 2015), and conserving or restoring migrations between protected areas was expected to allow for natural elephant meta-population dynamics (van Aarde & Jackson, 2007). Few elephant migration routes are however actually supported by empirical and indisputable movement data. A few elephants collared in Chobe NP (Fig. 1) were indeed relocated in Hwange NP (Chamaillé-Jammes, pers. obs.). Such observation demonstrates the existence of routes linking protected areas together, but without ascertaining their numerical importance. In our study, visits of elephants to protected areas of Botswana were extremely rare and short. Elephants that migrated to Botswana

mostly moved into Wildlife Management Areas (e.g. photographic safari concessions), outside of formally protected areas. This confirms the importance of conservation strategies that include areas outside protected areas (Cumming et al., 2015), and specifically underlines the importance of the private sector and communities to effectively protect elephants.

Our results also support the establishment of region-wide elephant management policies. A regional water management policy, or at least an integration of a regional water management perspective, is currently lacking from elephant management within KAZA. Water provisioning in Hwange NP comes under pressure during dry years and the long-term sustainability of pumping, i.e. the proportion of renewable vs. fossil aquifers being exploited, is unknown. Changes in water provision practices (voluntary or not), or more severe droughts (a phenomenon already observed: Chamailé-Jammes et al., 2007c) could have a dramatic effect on elephant distribution. Yet, there is no national or regional plan on what would happen if water provision in Hwange NP was to suddenly change. Drafting such a plan is urgently required to ensure the long-term persistence of this stronghold elephant population. Additionally, our study reveals that nation-level attribution of elephant numbers, which drives many international conservation efforts and policies, may be strongly biased by the timing of censuses.

4.3. Conclusion

Large conservation areas including various land use types can play a key-role in preserving large-mammal and their migrations, although these can be influenced, and possibly emerged, from local management practices. In this context, establishing the existence of these (sometimes partial) migrations, describing their routes and endpoints, and understanding their causes, is essential. Also, ultimately, this large-scale form of land-sharing, which will require in-depth discussions among stakeholders to be successful, is critical to design conservation plans that are relevant with regard to the

scales of climate and socio-economic changes.

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Supplementary Appendix

Figure A1. Map of southern Africa. The solid red line shows the boundary of the Kavango-Zambezi Transfrontier Conservation Area. The study elephants were collared in Hwange National Park (black polygon). In the inset, elephant captures sites are shown (crosses), along with the locations of the artificial waterholes that provide water during the dry season in Hwange NP (blue dots).

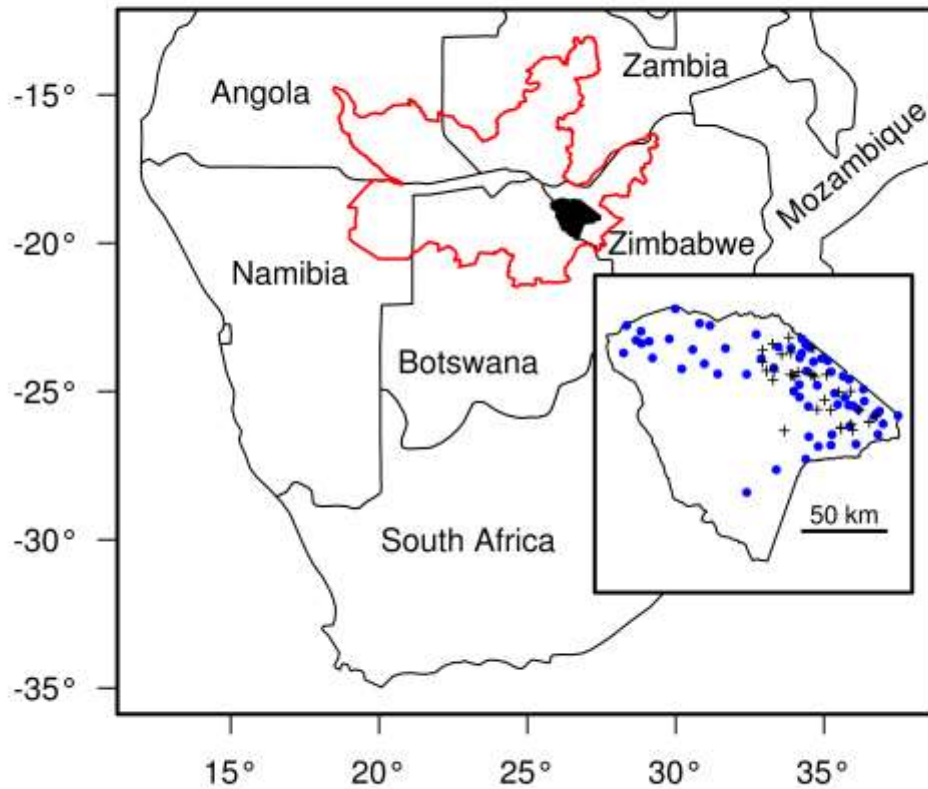


Figure A2. Timeline of the elephant monitoring. For each elephant, the monitoring period is shown in grey. The dotted vertical line shows the first day of the year. The solid vertical line shows, for each wet season, the date of the first day with > 20 mm of rainfall. Rainfall data were obtained from Little Makalolo camp, located in the eastern section of Hwange NP (19.0688°E / 27.2515°S). The date of first rainfall > 20 mm in 2010 is approximate due to a lack of accurate records.

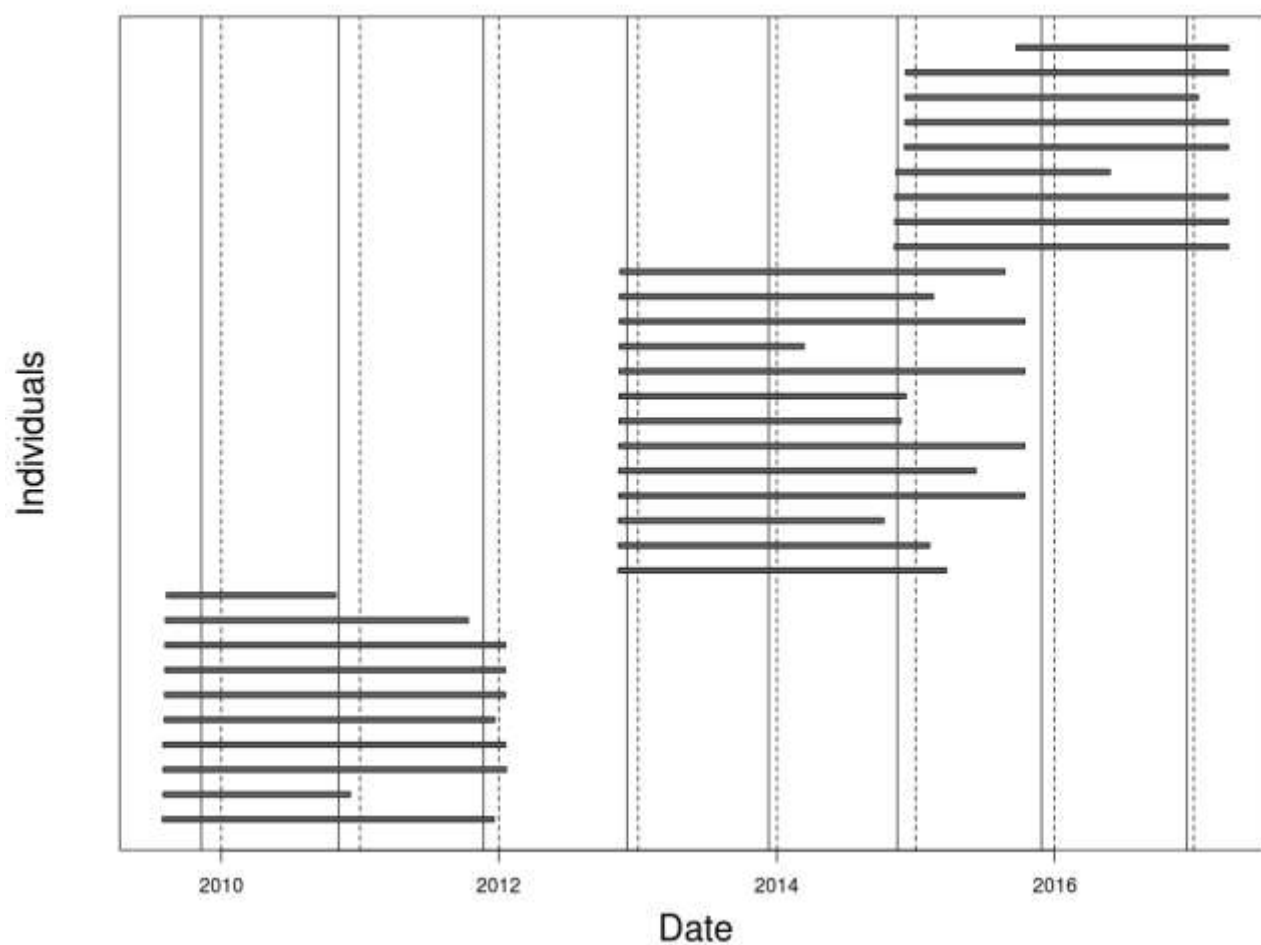


Figure A3. Tukey boxplots showing (A) the overlap between consecutive seasonal ranges and (B) the distance between range centroids. For some individuals tracked during a long period of time, several data points were available for comparisons of the same type (e.g. overlap between wet and dry seasons). To avoid unbalanced pseudo-replication, for each elephant only the first comparison available was used displayed. Choosing the comparisons used randomly within elephants did not change the results qualitatively.

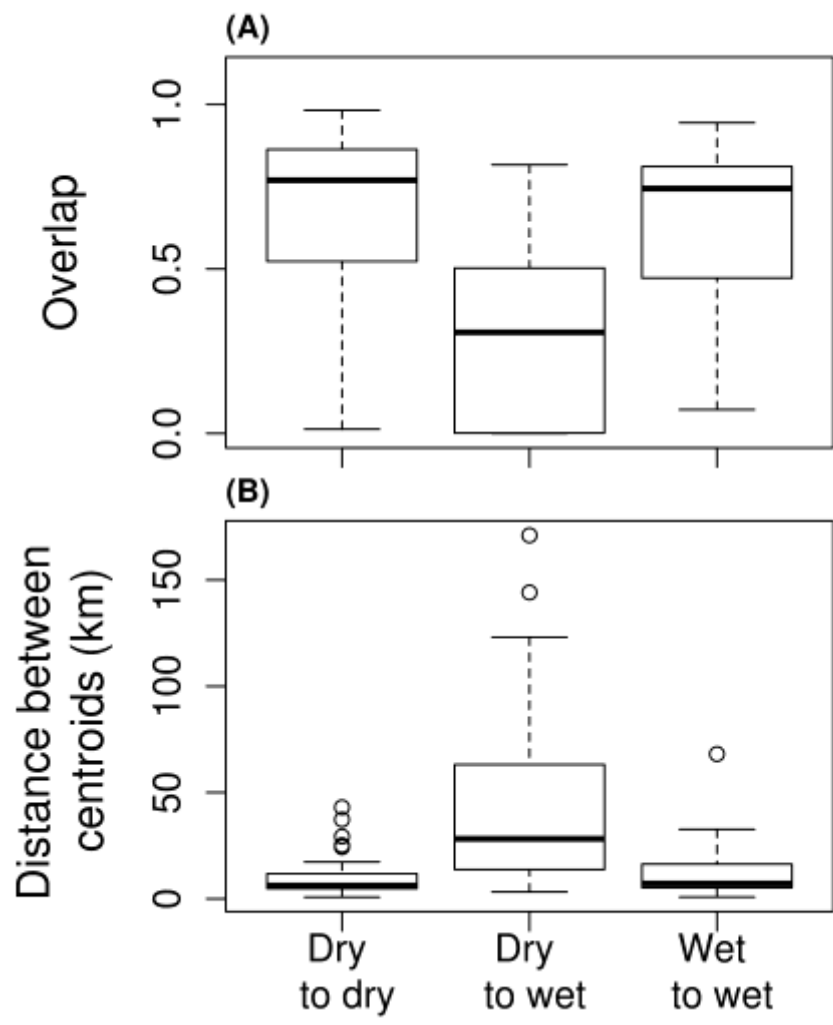


Figure A4. Temporal dynamics of the distance to the centroid of the first wet season of monitoring, for the 8 individuals that went to Botswana. Periods spent in Botswana are indicated in blue. Core wet and dry seasons are indicated in red and green respectively. See Fig. 2 in the main text for distance to the Botswana borders.

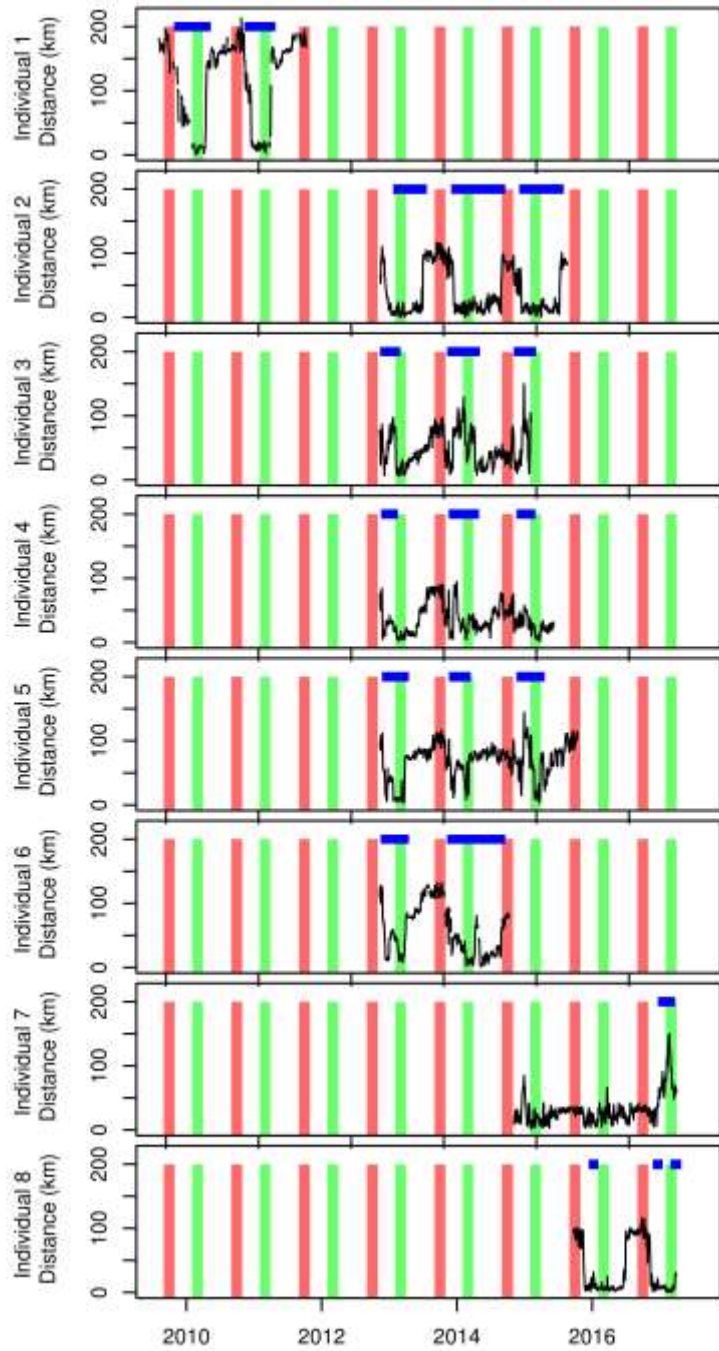


Figure A5. Temporal dynamics of the distance to the centroid of the first wet season of monitoring, for the individuals that did not go to Botswana. Core wet and dry seasons are indicated in red and green respectively.

