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Elephants' habitat use and behaviour when outside of Gonarezhou National Park

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Elephant conservation in Africa occurs within and beyond gazetted protected areas. We collared and tracked 19 male and seven female savanna elephants (*Loxodonta africana*) in Gonarezhou National Park (GNP), Zimbabwe, between 2016 and 2022. We investigated the extent of elephant activity outside the park and the role that season and diel played in this. We further documented habitat use, including the use of human-dominated landscapes. Our results showed that male elephants were more likely to move outside the GNP than females, dispersing at greater distances than females. Male elephants moved as far as 60 km from Gonarezhou, while females typically did not disperse farther than 15 km. Most movement outside protected area boundaries were during the cool-dry season (April–July). Male and female elephants returned to the GNP during the hot-wet season (December to March). When outside the GNP, male elephants preferred forested land cover types, while females remained in shrublands. Collared elephants avoided areas adjacent to GNP where human population densities were high. Surface water may also play a role in elephant movement outside of Gonarezhou, but we did not have reliable data to validate this. Our results indicate some use of areas neighbouring GNP by elephants, particularly in Mozambique, but not widespread dispersal.

Conservation implications: To achieve a stable elephant population growth rate in GNP, conservation planning in the region should consider immediate interventions for addressing barriers to the movement of elephants to Zinave and Banhine National Parks in Mozambique to avoid the risk of escalating fragmentation of the landscape. In addition, the communal area linking Gonarezhou to Kruger National Park should be prioritised for conservation efforts and pilot projects to test the functionality of the Sengwe corridor.

Keywords: protected areas; Savanna elephants; transfrontier conservation; Gonarezhou; habitat use; dispersal.

Introduction

One of the greatest conservation success stories has been the increase in protected land globally in this era of massive loss in biodiversity (Jones et al. 2018), with more than 260 000 protected areas (PAs) now covering over 15.3% of the world's terrestrial area (UNEP-WCMC & IUCN 2024). Conservation of biodiversity is also conducted through Transfrontier Parks that encompass areas that overlap political boundaries between sovereign states, including one or more PAs (Sandwith et al. 2001). The principle of creating Transfrontier Conservation Areas (TFCAs) focuses on dissolving political and economic borders to re-establish traditional migratory routes for wildlife (Barquet 2015). Most of these PAs represent conservation 'fortresses' that keep wildlife in and humans out (Huang et al. 2024). However, extensive human activity, including grazing, logging, and poaching, poses threats to protected areas, undermining their role as primary defence against biodiversity loss (Rai et al. 2021).

Maintaining connectivity between PAs is important for the long-term viability of wildlife populations. Conservation corridors are widely acknowledged as effective links between habitats at a large scale (Riggio & Caro 2017). African savanna elephants (*Loxodonta africana*) play a significant role in shaping the conservation management objectives of protected areas (Ferreira, Greaver & Simms 2017). However, human pressures from communities living near PAs represent just one aspect of the broader anthropogenic impact on endangered wildlife at the landscape scale. Multiple threats, such as habitat loss, poaching, unsustainable extraction of natural resources, and the degradation of natural habitats (including corridors) between PAs, detrimentally affect species populations (Neelakantan, DeFries & Krishnamurthy 2019). The use of non-protected wildlife corridors by humans often diminishes connectivity between PAs, subsequently

Note: Additional supporting information may be found in the online version of this article as Online Appendix 1.

threatening endangered species (Tscharntke et al. 2012). Several of these species risk genetic inbreeding if barriers to dispersal persist (Natesh et al. 2017). Ecological corridors remain a viable management tool to maintain biodiversity at large scales and to allow species and ecological processes to track climate change (Gregory et al. 2021).

Elephants leaving protected areas threaten the lives and livelihoods of rural people living alongside these areas (Osborn & Parker 2003). Human populations bordering PAs or living in wildlife migratory corridors interact with wild animals. These interactions are mostly negative because wild animals are killed, or humans lose their lives, crops, and infrastructure (Hariohay & Røskaft 2015). Elephants avoid densely populated areas (Douglas-Hamilton, Krink &Vollrath 2005; Graham et al. 2009). Among the major conflicts associated with human landscapes is the destruction of crops.

Protected areas contain approximately 48% of southern Africa's elephants, with well-protected and connected areas providing the best solutions for the conservation of savanna elephants and their landscapes (Huang et al. 2024). The rest of the southern Africa's elephants are in landscapes outside of protected areas, some of which are occupied by humans. Protected area managers typically seek to conserve biodiversity, and elephants act as ecological engineers that alter several aspects of biological diversity, including microhabitat availability (Valeix et al. 2011). To ensure long-term stability of Africa's elephants, conservation activities must recognise the importance of connectivity and availability of space for these animals (Van Aarde & Jackson 2007). Savanna elephants across the continent are listed as endangered, given the variety of threats they face (Gobush et al. 2021); however, elephants in southern Africa have shown a stable growth rate for the past quarter century (Huang et al. 2024).

Where dispersal is limited, the density of elephants may exacerbate the effects they have on biodiversity. The way elephants use landscapes depends on the distribution of water (Chamaillé-Jammes, Valeix & Fritz 2007; Loarie, Van Aarde & Pimm 2009), availability of forage (Codron et al. 2006), shade (Kinahan, Pimm & Van Aarde 2007), and resources that elephants select for at different intensities during different seasons (Young, Ferreira & Van Aarde 2009).

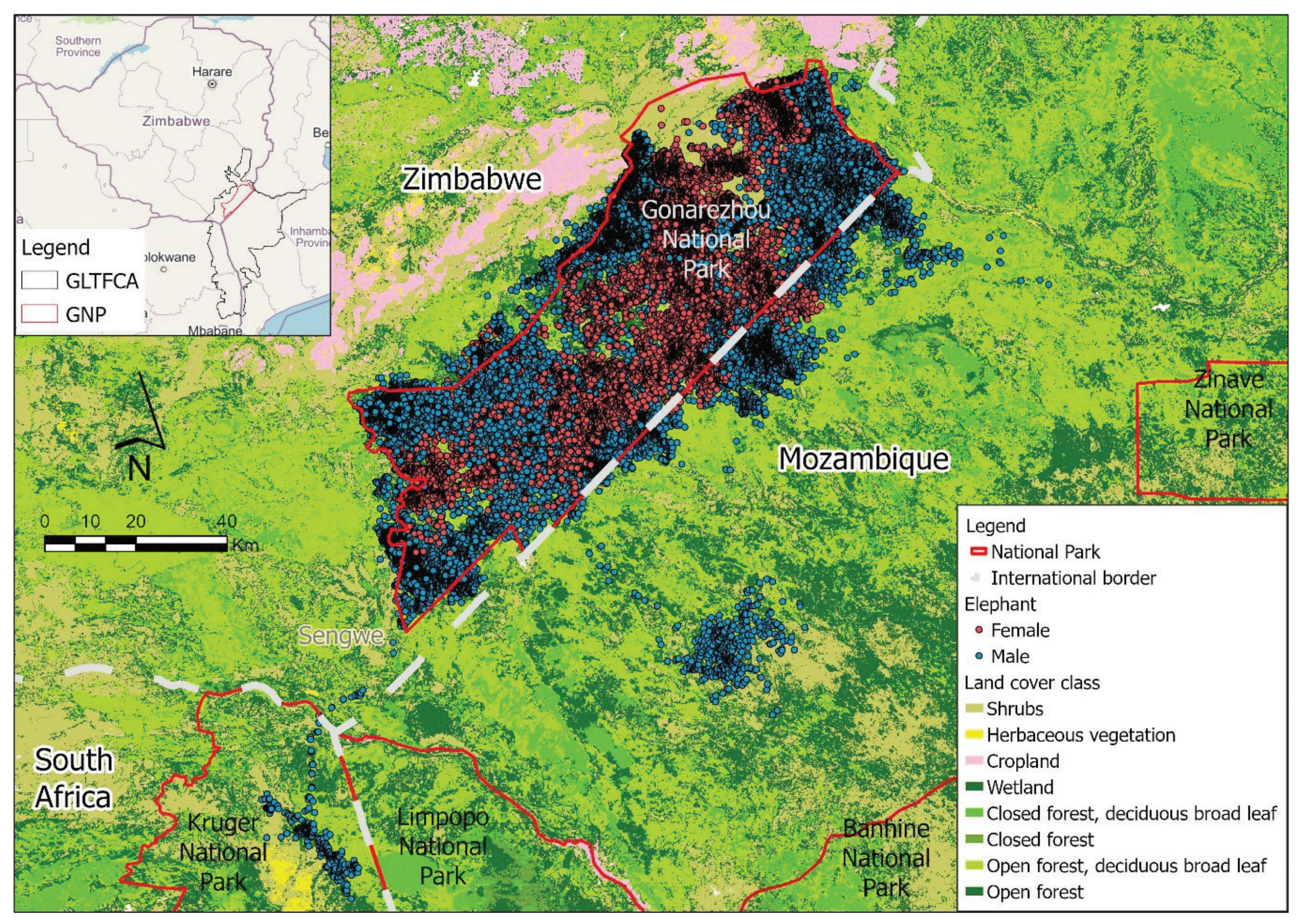
In southern Africa, seasonal rainfall and surface water availability strongly influence elephant movement behaviour (Bohrer et al. 2014; Loarie et al. 2009). At a landscape scale, movement beyond PA boundaries may further be influenced by corridor linkages (Douglas-Hamilton et al. 2005), avoidance of direct and indirect conflict with humans (Graham et al. 2009), and age and sex differences (Stokke & Du Toit 2002). Home ranges of bull elephants may be larger and more overlapping than breeding herds, and the movement rules for adult males may be dictated by water availability, male-to-male competition, and searching for receptive females (Smit, Grant & Whyte 2007). Vegetation parameters may also drive localised movement. In Kruger National Park, for example, Ferguson (2017) found a seasonal peak in elephant 'excursions' that was caused by the marula (*Sclerocarya birrea*) fruiting season.

Gonarezhou National Park (GNP) is surrounded by local communities within Zimbabwe and borders private properties on the eastern border with Mozambique. It is separated from Kruger National Park by a landscape settled with people and interspersed patches of wilderness areas that are woodlands undisturbed by humans. Most of the northern and western boundaries of GNP have an electrified fixed knot fence, erected primarily to control the spread of foot and mouth disease. This leaves the eastern boundary and part of the southern boundary accessible for migrations by elephants. The influence of elephants on the decline of tree species and the degradation of vegetation types in GNP has been recorded (Gandiwa et al. 2012; Kupika et al. 2014; O'Connor et al. 2024; Tafangenyasha 2001). The dispersal of elephants from GNP to neighbouring PAs such as Zinave and Banhine in Mozambique is important to avoid further habitat degradation. Currently, the elephant population in GNP has a growth rate of about 6% per annum (Dunham 2022). Considering the global conservation status of African savanna elephants, dispersal of these elephants to other less populated areas would be ideal and the best option for managing this elephant population. This study investigated the extent to which male and female elephants used landscapes outside GNP, focusing on the effects of season and land cover types on the likelihood of dispersal outside the protected area. It also examined the impact of time of day on elephant activity and landscape use in Mozambique and Sengwe communal lands that form the landscape between GNP and Kruger National Park. In addition, the study evaluated behavioural differences among elephants when ranging in non-protected areas with varying human densities.

Research methods and design

Study site

Gonarezhou National Park is part of the Great Limpopo Transfrontier Conservation Area (GLTFCA) (Figure 1), which includes Kruger National Park (KNP) in South Africa and Limpopo, Banhine, and Zinave National Parks in Mozambique. The GLTFCA was set up to promote sustainable land use and biodiversity conservation (Munthali 2007). The Sengwe-Tshipise Wilderness Corridor (STWC) joins GNP and KNP, but local communities are living in this region (Chirozva, Black & Higgins 2017). Gonarezhou National Park also borders local communal lands, as well as a private reserve and a community conservancy in the north. The land use systems within the STWC include human settlements, subsistence agriculture, and trophy hunting. There are approximately 3488 homesteads and 13 527 people living in this area (ZIMSTAT 2022). These areas are in the southeast lowveld of Zimbabwe and receive an annual mean rainfall of 500 mm per annum. Dominant vegetation types include



Note: The circled dots represent the elephant locations between 2016 and 2022 (blue colour = male, purple colour = female).

FIGURE 1: Map of the study area showing the protected areas in the Great Limpopo Transfrontier Conservation Area (Gonarezhou, Kruger, Limpopo, Banhine, and Zinave. The coloured background represents different land cover types.

woodland savanna, deciduous forested broad-leaved woodlands with a mixture of shrublands and grasslands, and *Colophospermum mopane*, dominated by dry deciduous savanna woodlands. The vegetation within GNP comprises physiognomic types of 59% woodland savanna, 40% scrubland, and 1% savanna grassland (Martini et al. 2016). The mean annual rainfall for GNP is 552 mm with three climatic seasons that include the hot-wet (HW) season (November to March) when 90% of annual rain falls; the cool-dry (CD) season (April–August); and the hot-dry (HD) season (September–October) (Gandiwa 2014; Republic of Zimbabwe 2016). Data from a local weather station at Chipinda Pools show that maximum monthly mean temperatures range between 26 °C in July and 36 °C in January, while the minimum monthly mean temperatures range between 9 °C in June and 24 °C in January.

The eastern boundary of GNP borders the Gaza province of Mozambique. The land use systems within this area include private game farms conducting consumptive utilisation (hunting), photographic tourism, and communal areas that conduct subsistence farming. Banhine and Zinave National Parks are separated from GNP by landscapes of the Chicualacuala and Massangena districts of Mozambique. Chicualacuala and Massangena districts had a population of about 27 456 and 21 965 people, respectively, in 2017, with densities of residents per square kilometre being lower than the average of the rest of Gaza Province (Bondarenko et al. 2020). In the north, GNP is fenced with a 2.1 m fence that is electrified. This fence was primarily erected to control further human encroachment into the GNP. All of the western and part of the southern boundary of the GNP is also fenced with 2.1 m and 1.2 m tall fences erected by the Veterinary Services Department of Zimbabwe to stop the potential spread of diseases from wildlife to livestock (Matope et al. 2023). There is no fence on the eastern boundary with Mozambique, and approximately one-third of the southern boundary is unfenced.

Elephant location data

Adult elephants (n = 26) were immobilised and collared with iridium satellite collars (model SM 2000E, https://awt.co.za) between 2016 (February) and 2022 (November). Each collar records its position every 4 h. All handling procedures were performed by personnel licensed to immobilise and tag elephants in the wild following professional and humane guidelines (Dublin 2023). A research permit and animal ethics clearance certificate were secured from ZPWMA [23(1)(C)(II)09/2023]. Of the 26 study elephants, seven were adult cows in mixed herds and 19 were adult bulls (see Online Appendix 1, Table A1-1). These elephants were all collared within GNP and were free to utilise unfenced areas within and outside the boundaries of GNP (Figure 1). Global Positioning System (GPS) data points for when the elephants under study were outside the borders of GNP were extracted using the selection feature in ArcGIS Pro (ESRI 2022) and split into three seasons and combined across years. The HW season was defined as December to March inclusive, the CD season as April to July inclusive, and the HD season as August to November inclusive (Gandiwa 2014).

Land cover classification

The Copernicus Global Land Service data (CGLS 2019) was used to define the land cover types within the GNP landscape. The CGLS delivers an annual dynamic global land cover (CGLS-LC100) product at 100-m spatial resolution (Buchhorn et al. 2020). The CGLS-LC100 product (V3.0) was used as a downloaded GeoTIFF that contained one discrete land cover map and fractional cover maps for eight classes that include shrubs, herbaceous vegetation, cropland, wetland, closed forest, closed forest with deciduous broadleaf, open forest, and open forest with deciduous broad leaf (see Online Appendix, Table A1-2). The classes were defined according to the United Nations Land Cover Classification System – UN LCCS (Tsendbazar et al. 2021). Processing of the land cover data was conducted in ArcGIS Pro (ESRI 2022), matching each elephant location data point to land cover classes using the Extract Values to Points tool. Each value referred to a land cover class, and these data were used to define the land cover classes used by elephants when inside and outside the GNP. To determine the distance of each elephant location data point from the GNP boundary, the Euclidean spatial analyst tool was used to create a Euclidean distance GeoTIFF with the GNP boundary being the input vector file. Distance values were then extracted to the elephant location data point file, associating each point with a distance value which was then used in the analysis for distances from the GNP boundary.

Analysis

All analyses were conducted using the R environment for statistical computing (R Core Team 2021) and were considered significant at an alpha level of 95% (i.e. with a *p*-value < 0.05). A two-way ANOVA was used to test if there were any significant differences in the presence of individual elephants in Mozambique or Sengwe based on the time of the day (day or night), using a Poisson regression with log link. A log-linear regression model was used to test whether the differences in minimum Euclidean distance from the GNP boundary, based on sex and season, were significant. Chi-squared tests were used to determine whether there were significant differences between the land cover types used by elephants when they were inside and outside the GNP. Multinomial regression was used to further evaluate differences based on sex, location, and the joint effect of sex and location on the use of land cover types by elephants.

Ethical considerations

Ethical clearance to conduct this study was obtained from the Zimbabwe Parks and Wildlife Management Authority (No. 151/43/P/REND).

Results

Dispersal of study elephants out of the GNP boundary was limited during the first 3 years of the study period (Figure 2) but increased post-2020, with most movement being across the eastern boundary of GNP, into Mozambique. Results indicated increased elephant presence in the Mozambique landscape adjacent to GNP compared to the Sengwe communal area. Elephant activity outside GNP was higher in the adjacent Mozambique landscape (68.17%) than in the Sengwe communal area (31.83%). The ANOVA, using Poisson regression with a log link, showed that time of day ($F_{1,384} = 9750$, $p < 0.05$), landscape type ($F_{1,1456} = 8293$, $p < 0.05$), and the combined effect of both time of day and location ($F_{1,162} = 8132$, $p < 0.05$) (Table 1) significantly influenced the use of the Mozambique and Sengwe landscapes by the study individuals. Chi-squared tests showed that there were significant differences in the land cover types that were utilised by elephants when they were inside versus outside the Gonarezhou ($\chi^2 = 5712$, $df = 7$, $p < 0.05$). The multinomial regression established that, outside of GNP, males predominantly used Open Forest (deciduous broadleaf) habitats and reduced their use of shrublands (Table 2), whereas females continued to utilise shrub-dominated areas similar to those they favoured inside of GNP (Figure 3). The log-linear regression model showed that distances travelled by the elephants were significantly different ($F_{5,10770} = 133.1$, $p < 0.05$) between all seasons for both males and females. Males travelled significantly longer distances than females during all three seasons ($F_{5,10770} = 133.1$, $p < 0.05$) (Table 3), with females remaining within a 15 km radius of the GNP boundary and males travelling up to 60 km (Figure 4). Female elephants travelled significantly farther outside the GNP during the CD season (mean distance 1299.70 m, range: 1147.86 m – 1471.64 m), less during the HD season (mean distance 791.40 m, range: 564.07 m – 1110.33 m), and the least during the HW season (mean distance 502.23 m, range: 355.96 m – 708.59 m). Male elephants instead travelled approximately the same amount during the CD season (mean distance 2795.26 m, range: 2157.42 m – 3621.70 m) and the HD season (mean distance 2930.53 m, range: 1455.91 m–5898.73 m) but showed more variability during the latter. During the HW season, males travelled the least away from the GNP (mean distance 1763.37 m, range: 864.81 m – 3595.52 m).

Discussion

Within the GLTFCA, GNP represents a formally protected (core) area surrounded by land use systems offering varying degrees of protection. These land use systems pose various threats to wildlife dispersal, such as poaching, with some offering no opportunities for movement because of linear infrastructure such as fences. This isolates the GNP elephant population, likely contributing to the consistently high growth rate (Huang et al. 2024).

HW, hot-wet season; CD, cool-dry season; HD, hot-dry season.

FIGURE 2: Layout of seasonal movement patterns of all collared elephants from 2016 to 2022, with empty layouts indicating a period when there were no collared elephants in Gonarezhou National Park.

TABLE 1: *p*-values from the ANOVA (Poisson regression with log link) showing significant differences in the expected number of observations of elephants by time of day (Day or Night) and location (Sengwe or Mozambique).

Source of variation	Estimate	s.e.	*Z* value	*p*
(Intercept)	7.40	0.02	424.03	< 2e-16 *
Daytime-Night	0.21	0.02	9.13	< 2e-16 *
Location-Sengwe	-1.10	0.03	-31.48	< 2e-16 *
Daytime-Night: Location-Sengwe	0.55	0.04	12.54	< 2e-16 *

*, $p < 0.05$.
s.e., standard error; ANOVA, analysis of variance.

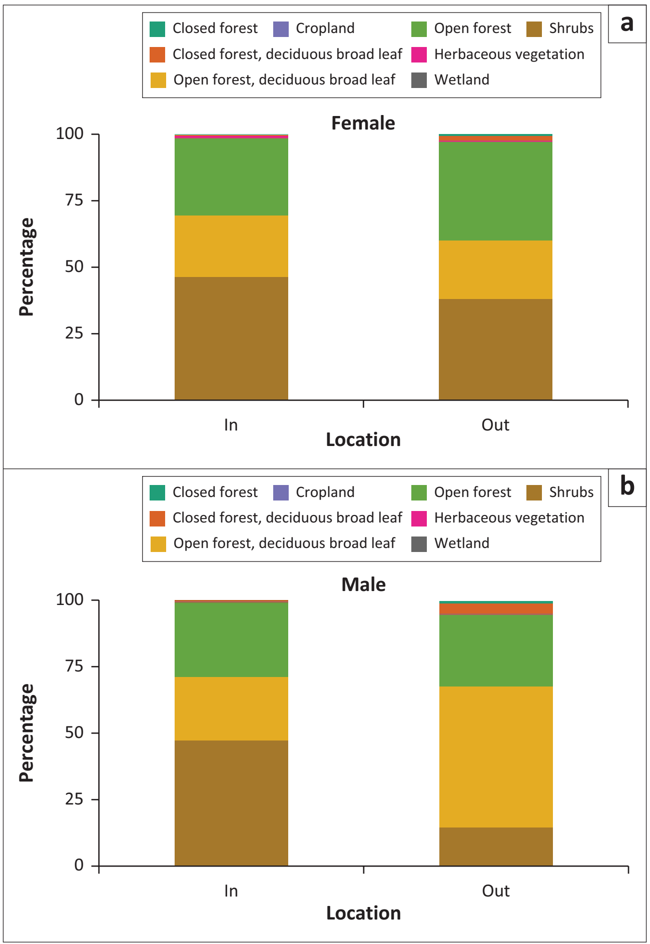
TABLE 2: *p*-values for differences between sex, location, and their joint effect resulting from a multinomial logistic regression having Sex = 'Female' and Location = 'Closed Forest' as the reference category.

Landcover type	Intercept	sexMale	locationOut	sexMale:locationOut
Closed forest, deciduous broad leaf	0.00	0.03	0.59*	0.14*
Cropland	0.57*	0.00	0.70*	0.76*
Herbaceous vegetation	0.00	0.00	0.01	0.00
Open forest	0.00	0.03	0.00	0.20*
Open forest, deciduous broad leaf	0.00	0.09*	0.00	0.19*
Shrubs	0.00	0.07*	0.00	0.00
Wetland	0.00	0.00	0.45*	0.01

*, $p > 0.05$.

The increased use of Mozambique by elephants post-2020 could have been influenced by the provision of artificial water (Tshipa et al. 2017), increased law enforcement activities (Demeke 2003) in some private concessions in Mozambique, and a reduction in trophy hunting during the coronavirus disease 2019 (COVID-19) pandemic (Tucker et al. 2023). Elephants spent more time in Mozambique than in the Sengwe region, based on location data across all years and seasons combined (Figure 2). The study elephants mostly dispersed to Mozambique through wildlife concessions. Some of these elephants ranged farther into the Massangena and Chicualacuala districts, both having a human population density of approximately 2 persons per square kilometre (see Online Appendix, Table A1-3). Use of the Sengwe area by elephants was proportionally lower (31.83%), possibly because of human presence in the region. In the Sebungwe region, Hoare and Du Toit (1999) found that elephant density was unrelated to human density until a threshold of human density of about 15.6 persons per km^2 was reached, after which resident elephants effectively disappeared from the area. The Sengwe communal area is part of the wildlife corridor that connects Gonarezhou NP and Kruger NP, and the movement of elephants between these two protected areas was also recorded by Henley et al. (2023). Our results suggest that the elephants under study avoid areas inhabited by subsistence farmers, and the majority of elephant location data in Sengwe were recorded at night (Figure 5). However, when elephants do move into communal lands (typically at night), it suggests the possibility of crop-raiding behaviour.

Graham et al. (2009) found that elephants had a preference for communal areas with croplands at night, rather than during the day. Past studies show that savanna elephants



Note: Shown are proportional habitat use values (percent) by sex for comparison.

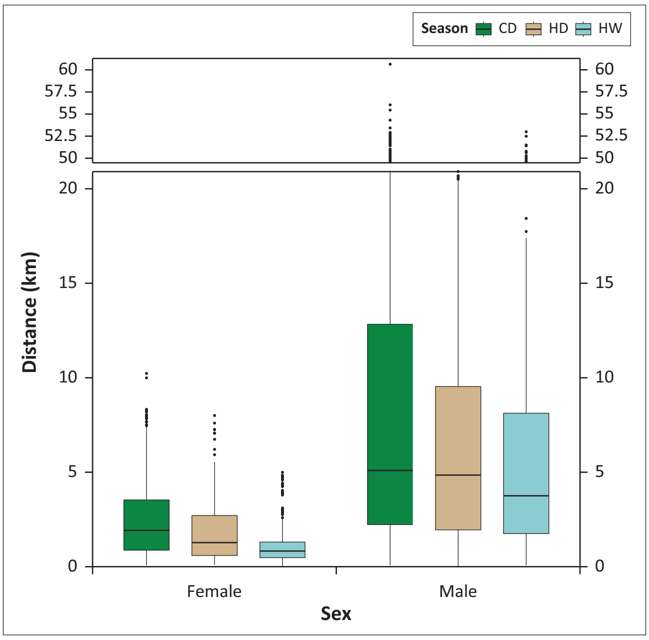
FIGURE 3: A comparison for use of different land cover types by male and female elephants when inside versus outside of Gonarezhou National Park. (a) Female elephants land cover types; (b) Male elephants land cover types.

TABLE 3: *p*-values from the ANOVA (log-linear regression model), showing that the likelihood of travelling far from the GNP (given that the elephant went outside) varied significantly (*p*-value < 0.05) by sex (male or female) and season.

Source of variation	Estimate	s.e.	*T* value	*p*
Intercept	7.17	0.06	116.14	< 2e-16*
Sex-Male	0.77	0.07	11.43	< 2e-16*
Season-HD	-0.50	0.11	-4.66	3.25e-06*
Season-HW	-0.95	0.11	-8.70	< 2e-16*
Sex-Male: Season-HD	0.47	0.11	4.15	3.32e-05*
Sex-Male: Season-HW	0.53	0.12	4.60	4.29e-06*

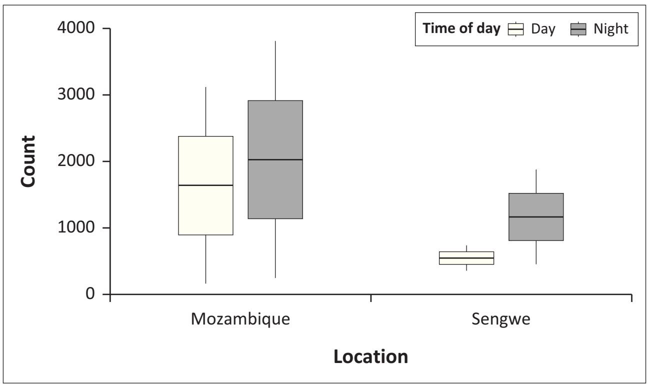
Note: 'Intercept' represents the reference categories that were Sex = 'Female' and Season = 'CD'.
s.e., standard error; HD, hot-dry; HW, hot-wet; CD, cool-dry.
*, $p < 0.05$.
Estimate is the calculated value of the regression coefficient.

use the cover of the night to move onto cropland where they raid crops (Bell 1984; Hoare 1995). We were unable to demonstrate this during our study, as the elephants spent relatively little time in areas dominated by crop fields (Figure 5). Nevertheless, the risk-avoidance strategy of preferred nocturnal movement by elephants in the Sengwe communal areas (Figure 5) appears to be consistent with other research carried out on temporal patterns of elephant movement relative to unprotected and protected areas (Ihwagi et al. 2018; Wittemyer et al. 2007).



CD, cool-dry season; HD, hot-dry season; HW, hot-wet season.

FIGURE 4: Box plots showing the distances travelled outside of the Gonarezhou National Park (from the boundary) by male and female elephants during different seasons.



Note: Count, number of elephant data points in each location.

FIGURE 5: Box plots showing distribution of count data for elephant locations in Mozambique and Sengwe landscapes during night and day.

Our results showed that males had a higher probability of dispersing outside the protected area and travelled farther than females (Ngene et al. 2010). This suggests that there may be an opportunity for elephant dispersal between large PAs in the region because the long-distance movements can show potential migration routes (Huang et al. 2022). The GNP has several linear barriers, which include fences and roads that surround the park that could be limiting female elephants because they travel in breeding herds with calves that may be unable to cross barriers (Naidoo et al. 2022). Male elephants in other parts of Africa are known to break fences more frequently than females (Slotow 2011), suggesting that their movements are less limited by any form of barrier. Movement outside the GNP by study elephants was in areas with no fences, including the 100 km long border with Mozambique and a small section of the south-eastern corner of the GNP.

The distribution patterns of elephants can be influenced by fear landscapes as they avoid areas with threats to their safety (Cook & Henely 2019; Cromsigt et al. 2013). They facultatively alter their behaviour to avoid risk in areas dominated by humans, and that helps them to maintain connectivity in fragmented land use systems, possibly lessening some of the potential negative impacts of fragmentation (Graham et al. 2009). Evidence shows that female elephants, in family units, take fewer risks and do not travel far from PAs (Wall et al. 2021), which suggests that elephants perceive areas farther from core protected zones as increasingly risky because human activity is a major cause of mortality and injury in adult elephants (Obanda et al. 2008). This was not demonstrated in our study. Females that remained close to the PA demonstrated possible risk avoidance behaviour (Mortimer et al. 2021) and considering how complex and dynamic anthropogenic mortality risk is in human-dominated landscapes, varying distances from PAs are perceived differently as the ability to quickly escape into a safe zone diminishes with increasing distance from a PA (Chiyo et al. 2014).

Our results showed that elephants preferred to be in the park during the HD and HW seasons, and as the seasons progressed from CD to HD to HW (cool to hot), the probability of elephants dispersing outside the park significantly decreased, indicating how the PA was used as refugia during the hot months. A study of elephants from northern Kruger also found that elephants moved to communal areas in Mozambique and Zimbabwe more during the dry season than the wet season (Cook, Henely & Parrini 2015). The findings of our study suggest some habitat drivers; however, overall movement outside the GNP appears to be driven by the need to access forage, water, and potential mates (for bulls) (Bohrer et al. 2014; Owen-Smith et al. 2020). Our study found that, outside the GNP, male elephants preferred forested areas with deciduous broadleaf vegetation, likely as a strategy to access forage and possibly for concealment (Graham et al. 2009).

Elephants are sensitive to seasonal variation in potential anthropogenic mortality risk, as hostile human-elephant interactions tend to be more frequent in the dry season compared to the wet season (Kangwana, Moss & Croze 2011). Contrary to these findings, elephants in our study were unlikely responding to increased potential anthropogenic mortality risk in the dry season, as it is the season when they utilised areas outside the GNP the most. It may also be that surface water was less available in GNP during the dry season, as there was no artificial water provision in GNP. The probability of our study elephants leaving the GNP was lowest during the wet season, likely because the benefits of using areas with livestock and human activity are minimal when water and forage are abundant within the PA (Chiyo et al. 2014).

Study elephants moved into wildlife concessions in Mozambique to access forage and provisioned water, and anecdotal reports from personnel managing the wildlife concessions in Mozambique neighbouring GNP indicated increased use of their water points by elephants from GNP during the dry season (Werno Drinkwater, pers. comm). Alternatively, they may have been responding to dry season resource distribution, which is likely to consist of a few discrete foraging patches, for example, around swamps, water sources, and patchily distributed *Senegalia* and *Vachellia* browse (Stokke & Du Toit 2002). This explanation is consistent with the behaviour of an elephant bull that travelled about 60 km to the same patch of land in Mozambique close to Banhine National Park for three consecutive years, returning to GNP at the beginning of the HD season. This elephant bull might have been attracted by marula fruits, as similar seasonal movements were recorded in the GLTFCA during the marula (*Sclerocarya birrea*) fruiting season (Ferguson 2017).

The diurnal and nocturnal behaviour of the study elephants in Sengwe demonstrated risk-avoidance behaviour that moderates connectivity by limiting the movement of elephants in the area to mostly at night. Ensuring that the corridor between Gonarezhou and Kruger NP is functional could enhance the persistence of elephants in the Sengwe landscape, but our data suggest that most elephants will avoid this area until a corridor allows for movement. Disturbance of wildlife associated with human population density remains relatively high across much of the Sengwe landscape, although not as high on the Mozambique side. Intensification of agriculture in the southern regions outside of GNP is leading to fragmentation and associated isolation effects; however, two collared elephant bulls did travel from GNP to Kruger National Park and then returned, but such movements may represent a small proportion of the elephant population resident in GNP. Moreover, those elephants that dispersed into Mozambique did not manage to connect with either Zinave or Banhine National Parks. Consequently, the identification and conservation of appropriate wildlife corridors between GNP and KNP should be a priority for the GLTFCA. Our results aid with the understanding of corridor uses by elephants that could influence elephant persistence in both the protected and non-protected areas within the GLTFCA landscape.

Conclusion

This study illustrated how elephants from GNP interact with landscapes outside of the PA. The only remaining open areas that allow the movement of elephants from GNP into the GLTFCA landscape are to the east, where the GNP shares the 100-km boundary with Mozambique and a section of the south-eastern corner of the GNP, which gives elephants access to the Sengwe Tshipise Wildlife Corridor. Some of the study elephants travelled into Kruger NP, but most of the observed movement was into Mozambique, although none of these connected with any of the PAs there. Conservation planning for functional connectivity within this region of the GLTFCA should consider ways of encouraging the movement of elephants from GNP to Zinave and Banhine National Parks in Mozambique if this landscape is to remain connected. A section of the communal areas adjacent to the GNP that is being cleared of land mines could offer a potential functional corridor through the Sengwe. To improve connectivity, there is a need to consider practical steps that include non-lethal deterrent strategies for mitigating human–wildlife conflict (in consultation with local communities) and also addressing socio-political barriers such as fences and settlement patterns that limit the movement of wildlife. The landscape could benefit from further studies that explore the long-term impact of creating corridors, the role of artificial water provision within non-protected areas, and strategies to reduce fear landscapes.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

B.R.M. contributed to the conceptualisation, design of method, formal analysis, investigation, writing, visualisation, data curation and writing of the article. M.M. contributed to the design of method, formal analysis, visualisation, data curation and writing of the article. L.W.T. and F.A. contributed to the conceptualisation, design of method, formal analysis, validation, supervision, and writing of the article.

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