Sex differences in home range and habitat use by savannah elephants in Gonarezhou National Park, Zimbabwe

Robert Mandinyenya[1,2], Marco Mingione[3], Lochrane W Traill[4], Luca Malatesta[2], Fabio Attorre[2]*

[1]Scientific Services, Gonarezhou Conservation Trust, Gonarezhou National Park, Chiredzi, Private Bag, 7003 Zimbabwe
[2]Department of Environmental Biology, Sapienza University of Rome, Italy
[3]Department of Political Sciences, University of Roma, Tre, Italy
[4]School of Biology, University of Leeds, LS2 9JT, United Kingdom

*corresponding author: bob@gonarezhou.org

Abstract
Protected areas (PAs) in southern Africa provide refuge to important megafauna such as the savannah elephant (*Loxodonta africana*). Sections of these protected areas are often transfrontier conservation complexes, whose objective is to facilitate historic patterns of animal dispersal. Knowledge of megafauna home ranges, habitat use, and dispersal in key PAs can inform vital decision-making for elephant conservation. Location data were derived from satellite collars fitted on 26 savannah elephants from 2016 to 2022 in Gonarezhou National Park, Zimbabwe to investigate seasonal and sex differences in elephants' home range sizes, home range overlap, and their interaction with environmental variables. Differences in the size of home ranges between sexes in all seasons were not significant. Both male and female elephants had high site fidelity, retaining 60% of their home ranges between consecutive seasons. Only females, possibly tracking forage quality, showed reduced overlap of home ranges between the hot dry and hot wet seasons. Male elephants preferred vegetation types dominated by *Colophospermum mopane*, whereas females used more diverse upland vegetation types, showing a preference for higher elevations than males over all seasons. In areas where elephant movement is restricted by fences and human settlements, continuous monitoring of elephant space use is recommended, and research dynamics should be taken into account when developing site-specific management plans.

Résumé
Les zones protégées en Afrique australe représentent des refuges pour une importante mégafaune telle que l'éléphant de savane (*Loxodonta africana*). Il est fréquent que des sections de ces zones protégées soient des complexes de conservation transfrontaliers, dont l'objectif est de faciliter les schémas de dispersion historiques des animaux. La connaissance des domaines vitaux de la mégafaune, de l'utilisation de leur habitat et de leur dispersion dans des zones protégées clés peut contribuer à des prises de décision essentielles pour la conservation des éléphants. Des données de localisation ont été extraites de colliers émetteurs installés sur 26 éléphants de savane entre 2016 et 2022 dans le parc national de Gonarezhou au Zimbabwe, afin d'étudier les variations éventuelles, selon la saison et le sexe des animaux, sur la surface et le chevauchement de leurs domaines vitaux ainsi que sur leur interaction avec les variables environnementales. Les dimensions des domaines vitaux chez les mâles et les femelles n'ont pas montré de différences significatives, toutes saisons confondues. Tous ont fait preuve d'une grande fidélité au site en conservant 60% de leur domaine vital sur les saisons consécutives. Seules les femelles, probablement en recherche d'une certaine qualité de fourrage, ont présenté un chevauchement plus faible de leurs domaines vitaux entre la saison sèche et la saison humide en période chaude. Les éléphants mâles ont affiché un goût plus prononcé pour un type de

végétation dominée par *Colophospermum mopane*, contrairement aux femelles qui se tournaient vers une végétation d'altitude plus variée, indiquant une préférence pour les hauteurs sur toutes les saisons. Dans les zones où les déplacements des éléphants sont contraints par des clôtures et des installations humaines, nous recommandons une surveillance continue de l'utilisation de l'espace par les éléphants et une prise en compte des résultats lors du développement de plans de gestion de site spécifiques.

Introduction

African savannah elephants (*Loxodonta africana*) are relatively more abundant in southern Africa than in eastern and central Africa (Henley et al. 2023). 70 to 80% of the current elephant range is located outside Protected Areas (PAs), and this distribution outside of PAs accounts for 17% of the potential elephant range areas in Africa (Ihwagi 2019; Wall et al. 2021). The range of African savannah elephants is increasingly being reduced and they are gradually becoming dependent on PAs (Stoldt et al. 2020). Therefore, it is critical to have effectively managed PAs to protect the future of African savannah elephants and also to improve the capacity of unprotected areas to host elephant populations co-existing with humans.

This study contributes to effective management of elephant ranges in PAs in southern Africa and elsewhere by investigating seasonal and sex differences in elephants' home range sizes, home range overlap, and their interaction with environmental variables, in Gonarezhou National Park (GNP), Zimbabwe. Movement is essential to animal biology, and the decisions made by animals have profound consequences at individual and ecosystem levels (Beirne et al. 2021). African savannah elephants use their home ranges in different ways, with some dispersing seasonally and others favouring the same core area throughout the year (Leggett 2006). Home ranges of male elephants that are sexually mature are different from those of females (mature and immature) and immature male elephants. Males in musth have significantly larger home ranges than females (Whitehouse and Schoeman 2003), due to the nutritional and hormonal requirements of breeding males (Wilkie and Douglas-Hamilton 2018). Seasonal movements and variation in habitat use are associated with the availability of rainfall and forage preference (Babaasa 2000). The distribution of food resources for large herbivores in natural environments is not consistent (Leggett 2006) and it is postulated that the impact of elephants on vegetation is reduced by seasonal space use (Babaasa 2000).

The distribution of African savannah elephants is influenced by a combination of factors such as soil type, topography, elevation, rainfall, and latterly interference by humans (Bailey and Provenza 2008; Bohrer et. al 2014; Williams et. al 2018; MacFadyen et. al 2019; Benitez et. al 2022). Seasonal change in the distribution of forage influences the use of space and movement patterns of elephants (Wittemyer et al. 2007). Elephants migrate from one area to another within the landscape to maximize food intake (Prins and Van Langevelde 2008). These movement are considered to arise from (1) natural selection acting over generations (Regan et al. 2020); and/or (2) new behaviours that are learned by animals during their lifespan (Laca 2008). Like other large herbivores who are generalists, savannah elephants employ mixed feeding strategies (on herbaceous and woody vegetation) (Staver et al. 2021; Troup 2021).

The interaction of elephants and humans results in serious conflicts, mostly in areas adjacent to PAs (Hoare 1999; Buchholtz et. al 2019; Adams et. al 2021). When such conflicts occur, fencing elephants out of human-dominated landscapes is a common solution, but this can accelerate the destruction of natural habitats as elephant populations are compressed into PAs (Douglas-Hamilton et al. 2005). Furthermore, savannah elephant ranges are declining due to habitat fragmentation resulting from the increase in human population and associated land-use changes (Ipavec et al. 2007). The mosaic of bushland and woodlands in and around GNP is no exception. The designation of conservation landscapes and their spatial arrangement determine the fate of both elephants and their habitats (Huang et al. 2024).

Movement behaviour and home-range use of savannah elephants is relatively well documented (Presotto et. al 2019; Sach et. al 2020; Grogan et. al 2020; Mlambo et. al 2021). Savannah elephants in ecosystems such as the Samburu–Laikipia ecosystem in Kenya have home ranges of about 10–80 km^2 in fenced areas and about 90–800 km^2 in open areas (Dolmia et al. 2007; Douglas-Hamilton et al. 2005; Leggett 2006). Elephants have been documented travelling very long distances, including migrations of over 400 km by elephants in Mali (Blake and Douglas-Hamilton 2003), and long migrations by desert elephants in Namibia between their dry and wet season ranges (Leggett 2006).

There are no previous studies of the home ranges, site fidelity, and relationships between environmental variables and home range sizes of elephants in the GNP. Previous research used GPS tracking data to understand elephant occurrence away from water sources (Ndaimani et al. 2017), but sampling was only done for the northern section of the GNP and during the dry season. Mukomberawa et al. (2023) report on vegetation types used by elephants but do not consider differences by sex or season. This study filled this gap by monitoring and analysing the ranging patterns of elephants in the GNP landscape, and comparing differences between sexes and seasons

For most mammals, water is required for osmo- and thermoregulation. In hot areas where water is also scarce, elephants use evaporative cooling for thermoregulation resulting in a high daily water debt; therefore, elephants' movement patterns reflect the need for regular access to water sources (Dunkin et al. 2013). However, their maximum distance from water follows a distinct seasonal pattern (Chamaillé-Jammes et al. 2013). Thaker et al. (2019) found that elephants in Kruger NP were rarely more than 1.5 km from water and spent about 22% of their time close to water sources, dwelling adjacent to water for longer periods during the dry season than in the wet season. The objectives of this study were to: i) investigate the variation in home range sizes between male and female elephants across seasons; ii) determine the overlap of the home ranges between consecutive seasons as a measure of spatial use intensity; and iii) establish how environmental variables (distance from water, and vegetation productivity) influence home range sizes of elephants.

Materials and Methods

Study area

Gonarezhou National Park (Fig. 1) is located in the low-veld south-east of Zimbabwe, between 21°00′–22°15′ S and 30°15′–32°30′ E. It was established in the early 1930s as a game reserve and was upgraded to a national park, covering an area of 5,053 km^2, under the Parks and Wildlife Act of 1975 (Jakarasi et al. 2014). GNP borders a privately owned reserve to the northwest, communal lands of the Chiredzi district to the north, south, and west, and communal lands of the Chipinge district to the northeast, and shares a border of more than 100 km with Mozambique to the east. The GNP is part of the Greater Limpopo Transfrontier Conservation Area (GLTFCA) (Gandiwa et al. 2013). The altitude ranges between 160 and 560 m above sea level. Three climatic seasons can be recognised in the Gonarezhou landscape, the hot wet (HW) season (November to March, when 90% of annual rain falls); the cool dry (CD) season (April to August); and the hot dry (HD) season (September to October) (Gandiwa 2014; Republic of Zimbabwe 2016). Data from a local weather station show that long-term mean monthly maximum temperatures range between 26°C in July and 36°C in January, while mean monthly minimum temperatures range between 9°C in June and 24°C in January. The mean annual rainfall is 552 mm. The two principal vegetation types are woodland savannah and scrubland, covering 59% and 40% of GNP, respectively. Woodland savannah comprises dry deciduous vegetation, characteristic species being *Colophospermum mopane* and woodlands of *Julbernadia globiflora*, *Brachystegia glaucescens* and *Guiborrtia conjugata*. Scrublands are dominated by mixed shrubs and herbaceous vegetation. (Gandiwa et al. 2011; Martini et al. 2016). The Park contains a wide variety of large mammalian herbivore species, including common eland (*Taurotragus oryx*), South African giraffe (*Giraffa camelopardalis giraffa*), nyala (*Tragelaphus angasii*), and blue wildebeest (*Connochaetes taurinus*), as well as savannah elephant (Dunham 2012). The elephant population density was 2.22 individuals per km^2 in 2022 and has been increasing in the recent years (Dunham 2022). Elephant poaching in the GNP is not well documented, but the number of elephants poached has declined, from 58 poached elephants recorded in 2015 to only two in 2023 (R Mandinyenya, pers. obs. 2022).

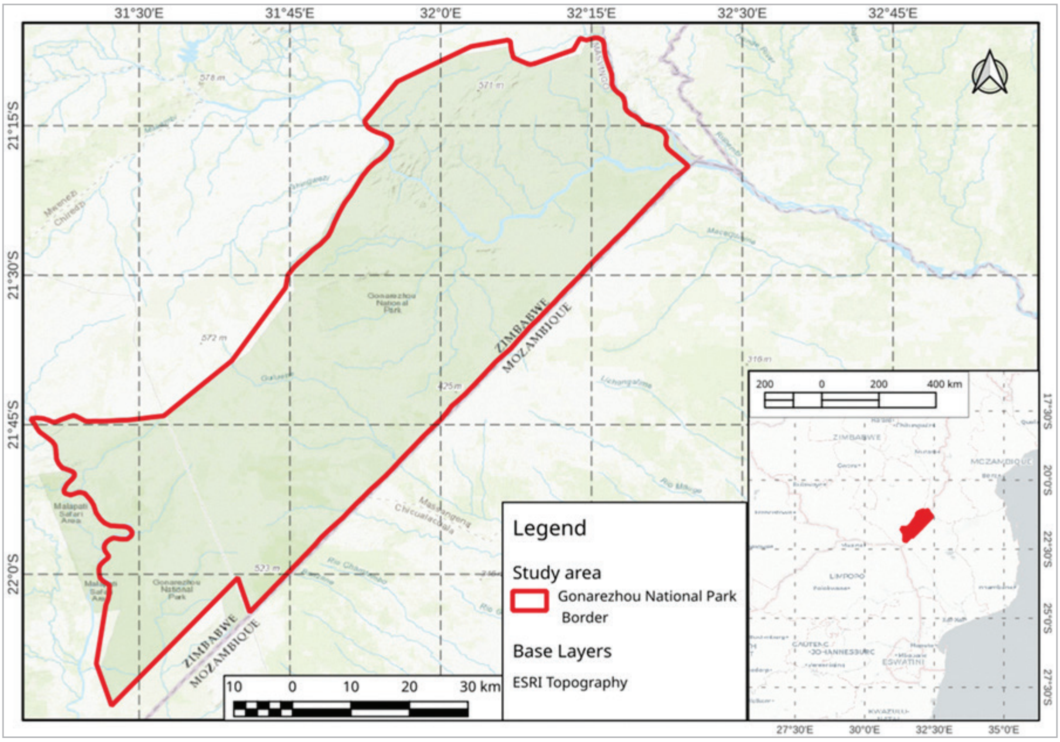

Figure 1. The study site: Gonarezhou National Park in southeast Zimbabwe.

Elephant movement

A total of 26 African savannah elephants were immobilized and collared with Africa Wildlife Tracking GPS collars (model SM 2000E; https://awt.co.za) between February 2016 and November 2022. Collars were programmed to take a GPS coordinate at 4-hour intervals. In this study, seven adult females from different herds and 19 solitary adult bull elephants were tracked during two distinct periods: 2016–2018 and 2020–2022. The gap in data collection coincided with the Covid-19 pandemic.

The average period an individual was tracked was 503 days (minimum: 36 days; maximum: 849 days). The number of GPS fixes per individual elephant ranged from 335 to 5,015 with a median value of 2,914 points, corresponding to 486 days. Data from the first day collar tracking was eliminated from each data set to remove the typical movement behaviour caused by collaring (Northrup et al. 2014). Telemetry locations were classified into three seasons and combined across years. The HW season was defined as December–March; the CD season as April–July, and the HD season as August–November (Gandiwa 2014b).

Environmental variables

Data related to environmental variables were obtained from globally available Earth Observation (EO) datasets in raster format. All environmental variable data sets were resampled at a 0.25 × 0.25 km spatial resolution, for the entire study area and a 10-km buffer area surrounding the square that contains all GPS locations. All datasets were obtained and pre-processed using the Google Earth Engine Code Editor, a web-based IDE for the Earth Engine JavaScript API (https://code.earthengine.google.com/) (Fig. 2).

Normalised Vegetation Index (NDVI)

As a proxy for vegetation productivity, we used the Normalized Difference Vegetation Index (NDVI), obtained from a transformation of the reflectance values in spectral bands closely related to photosynthetic activity. The NDVI ranges in value from –1.0 to +1.0 and index values were computed using Landsat 8 composites from reflectance values for red and near-infrared (NIR) bands as (NIR – red) / (NIR + red).

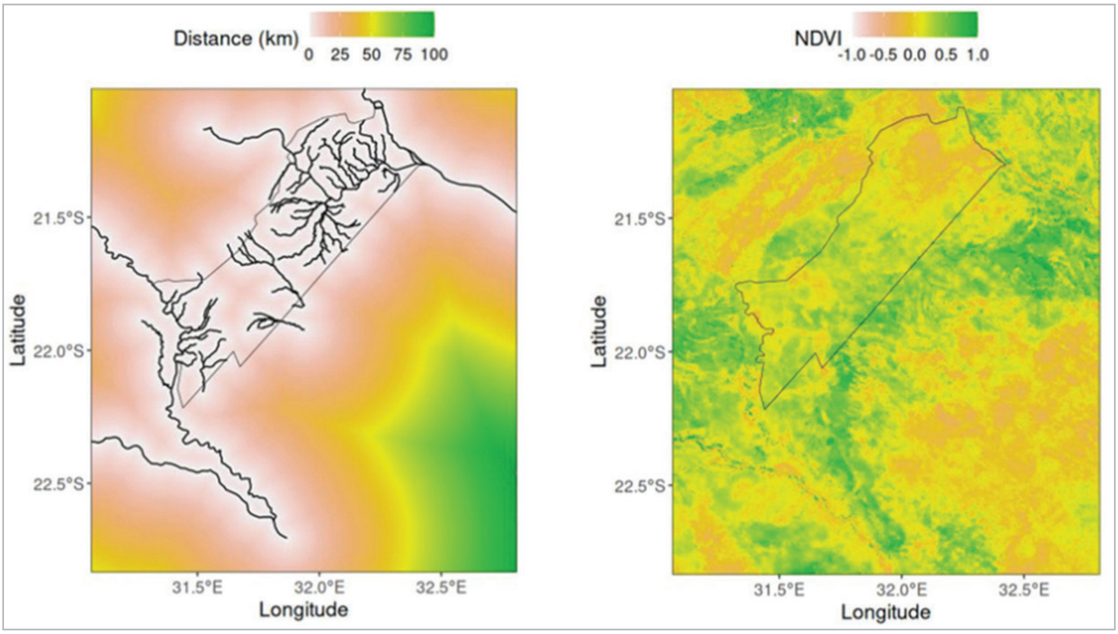

Figure 2. Representation of the environmental variables used in our analyses: (left) distance from water (in km), and (right) Normalized Difference Vegetation Index (NDVI) values.

For this study, NDVI values were obtained from Landsat 8 Collection 1 Tier 1 monthly composites, made from Tier 1 orthorectified scenes, using the calibrated top-of-atmosphere (TOA) reflectance (Landsat 8 courtesy of the U.S. Geological Survey: https://www.usgs.gov/landsat-missions/landsat-collection-1). Composites were created from all images once every 32 days beginning from the first day of the year and continuing to Day 352. The last composite of the year, beginning on Day 353, overlaps with the first composite of the following year by 20 days. All images available for the 32 days are included in the monthly composite. We computed NDVI values for the whole study period, from 2016 to 2021 inclusive. The seasonal averages were obtained by computing the median NDVI values of each raster pixel over the entire time series for every season. Values for the closest raster cell, were assigned to individual elephants for each time point, based on distance from the elephant's GPS location to the centroid of the raster cell.

Vegetation

The vegetation classes were defined following the classification of GNP vegetation by Cunliffe et al. (2012) and reclassified into five categories by joining classes that occur on similar geology and those with the same dominant woody plant species. The five categories, in order of spatial cover-age, were: *C. mopane* (2025 km^2), *Upland sandveld* (1774 km^2), *Upland igneous* (824 km^2), *Androstachys johnsonii* (168 km^2), and *Alluvium* (115 km^2).

Distance from water sources

The distance from the closest permanent water source required some additional preprocessing. Starting from a shapefile that was created by digitizing a basemap in ArcGIS Pro (ESRI 2022) and then including the location of all major rivers and water sources in the area, we created a raster of the same spatial resolution as the one of NDVI, and we calculated the minimum distance of each raster cell to a perennial water source. Afterwards, we assigned these values to elephants' GPS locations, once again using the closest raster cell centroid.

Data analysis

All analyses were conducted in the R environment for statistical computing (R Studio Team 2020). Estimation of home ranges categorized by season (HW, HD, CD) and sex was done with the 'adehabitatHR' package for utilization distribution, using kernel density estimators (KDE) at 95% (Fleming and Calabrese 2017). The utilization distribution is the bivariate function giving the probability density that an animal is found at a point according to its geographical coordinates. This model defines the home range as the minimum area in which an animal has some specified probability of being located (Worton 1995). A 2-way ANOVA was used to determine whether there were significant differences between the sizes of the home range by sex and season. A kernel home range overlap method (Fieberg and Kochanny 2005) was used to assess the spatial interaction of seasonal home ranges for both sexes. We estimated the extent of overlap using the Bhattacharyya Affinity (BA; Bhattacharyya 1943) method, whereby BA index values measure the similarity between the utilization distribution. This method was chosen because home ranges were not utilized evenly, hence shared use of space is best measured as overlap in terms of activity rather than in terms of extent (Millspaugh et al. 2004; Fieberg and Kochanny 2005). The BA index provides a practical way to compute the overlap between the utilization distributions of two seasons A and B.

Once all data from environmental variables were collated, statistical analysis was straightforward as the elephant's location is known for each time point, as well as the corresponding features of the surrounding environment. Chi-square analysis was used to determine whether there were significant differences between the vegetation types used by male and female elephants and whether there were significant differences in the vegetation types used by elephants between seasons. A multinomial logistic regression with pairwise comparison was used to determine whether male and female elephants used vegetation types differently during different seasons.

Results

Mean home range sizes for both sexes across all seasons were less than 500 km^2. Comparison of home ranges in the three seasons showed no significant differences in home range sizes of male and female elephants ($F_{2,128} = 0.996$, $p = 0.372$). The effect of sex on home range sizes (in km^2) was not significant ($p = 0.206$) and season also did not have a significant effect on the size of home ranges ($p = 0.184$) (Fig. 3; Table 1).

Both male and female elephants showed high site fidelity, retaining an average of 59.31% of their home ranges throughout consecutive seasons (Fig. 4; Table 2).

For female elephants, there was a noticeable difference in their home ranges between the HD and HW seasons (BA = 0.42096, SD = 0.218795). Outliers in data for male elephants are cases where there was little to no overlap of home ranges during consecutive seasons, probably representing animals that travelled long distances in and out of the NP.

Our results show that both male and female elephants remained relatively close to rivers (Table 3), with females remaining closer (mean = 1.82 km, SE = 0.023) during the HD season.

There was a significant difference ($\chi^2 = 6344$, df = 4, $p < 0.001$) in use of vegetation types by male and female elephants during different seasons. The females used mainly Mopane (33%), Upland igneous (32.5%), and Upland sandveld (27.9%) vegetation types, while males mostly used the *C. mopane* (62.9%) vegetation type (Fig. 5; Table 4).

There were minor differences that were observed by season ($\chi^2 = 609.2$, df = 8, $p < 0.05$), and by sex and season combined (Table 5), but not for all types of vegetation. Both male and female elephants selected areas with similar NDVI values across all seasons. Seasonal mean NDVI values for females were: HW = 0.397, CD = 0.383 and HD = 0.380; and for males: HW= 0.395, CD = 0.401 and HD = 0.389 (Fig. 6).

Discussion

To understand elephant range patterns, this study examined how collared elephants in the GNP used their space. It quantifies the use of space by savannah elephants in GNP and determines the variation in the use of space across seasons and between sexes. The results showed that most of the space that the study elephants used was within the boundaries of the PA and there were no significant differences between the home ranges of male and female elephants during different seasons. This is similar to the findings by Mlambo et al. (2021) who found no significant differences in the home ranges of elephants in Hwange NP between the

Table 1. Effect of sex, season, and interaction between sex and season on the size of elephant home ranges using a 2-way ANOVA. (df = degrees of freedom)

Source of variation	df	Sum of squares	Mean square	*F*-value	p-value
Sex	1	108,388	108,388	1.619	0.206
Season	2	229,592	114,796	1.714	0.184
Sex:Season	2	133,330	66,665	0.996	0.372
Residuals	128	8,571,235	66,963		

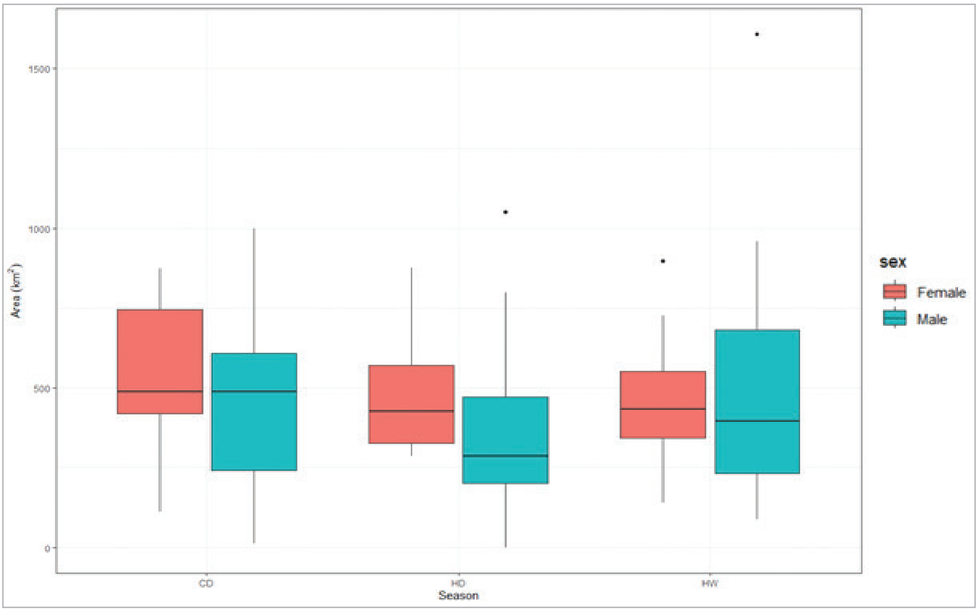

Figure 3. Home range area (KDE 95%) for male and female elephants in the GNP for all years (2016–2018 and 2020–2022) disaggregated by season. In the box-and-whisker plots, horizontal bars indicate means, the boxes show the interquartile ranges, and the whiskers show 95% confidence limits. Black points are outliers. CD = cool dry, HD = hot dry, HW = hot wet.

Table 2. Seasonal overlap of elephant home ranges by sex and based on the Bhattacharyya Affinity (BA) index. Seasons are: CD = cool dry, HD = hot dry, HW = hot wet. N = Number of combinations within the data for when there is a transition from one season to another, SD = Standard Deviation from the mean BA index, SE = Standard Error, CI = Confidence Interval.

Seasonal transitions	Sex	N	BA index value	SD	SE	CI
CD to HD	Female	10	0.630	0.165	0.052	0.118
CD to HD	Male	20	0.589	0.248	0.055	0.116
HD to HW	Female	11	0.421	0.219	0.066	0.147
HD to HW	Male	32	0.583	0.219	0.039	0.079
HW to CD	Female	11	0.712	0.128	0.039	0.086
HW to CD	Male	25	0.623	0.179	0.036	0.074

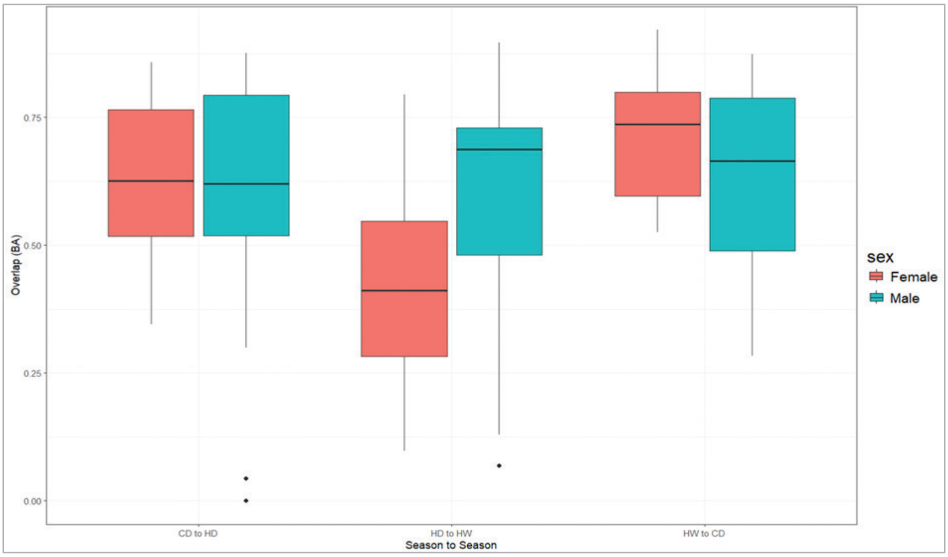

Figure 4. Overlap of home ranges for female and male elephants in GNP, and between consecutive seasons. Data here are across years. The overlap is measured using the Bhattacharyya Affinity (BA) index, where zero and one indicate no similarity and complete similarity, respectively. For explanations of box-and-whisker plots and abbreviations, see the Figure 3 legend.

Table 3. Mean distance (km) of male and female elephants from major river systems in different seasons, based on composite data for 2016–2018 and 2020–2022. N = Number of elephant data points, SD = Standard Deviation, SE = Standard Error, CI = Confidence Interval.

Season	Sex	N	Mean (km)	SD	SE	CI
HW	Female	5,253	2.558	2.274	0.031	0.062
	Male	14,127	2.003	2.146	0.018	0.035
CD	Female	7,401	2.272	2.158	0.025	0.049
	Male	14,602	2.832	6.454	0.053	0.105
HD	Female	6,992	1.824	1.890	0.023	0.044
	Male	18,627	3.730	3.729	0.027	0.054

wet and dry seasons. However, male elephants are known to utilize larger spaces than females, mostly when they are in musth and seeking females in oestrus far outside their non-musth ranges (Whitehouse and Schoeman 2003; Leggett 2006). Wall et al. (2021) found that human activities overwhelmingly determine overall elephant ranges within a PA, while environmental conditions, mainly vegetation productivity and water availability, are the principal factors affecting short-term changes in the use of space. Other studies report similar movements in response to the spatial distribution of resources, with elephants in unfenced PAs utilizing lands outside PAs as corridors between core areas in different PAs (Douglas-Hamilton et al. 2005; Tshipa et al. 2017). In this study, three bulls travelled long distances to Kruger NP and into Mozambique towards Banhine NP, but returned to GNP after about three months (unpublished data).

Our results showed that the studied elephants retained at least 60% of their home range between consecutive seasons. GNP is fenced along the northern and western boundaries where it borders communities of the Chiredzi rural district, which likely contributes to high fidelity to the Park by elephants in these areas. Linear infrastructure such as fences may act as barriers to seasonal movements, forcing elephants to use the same landscape across consecutive seasons.

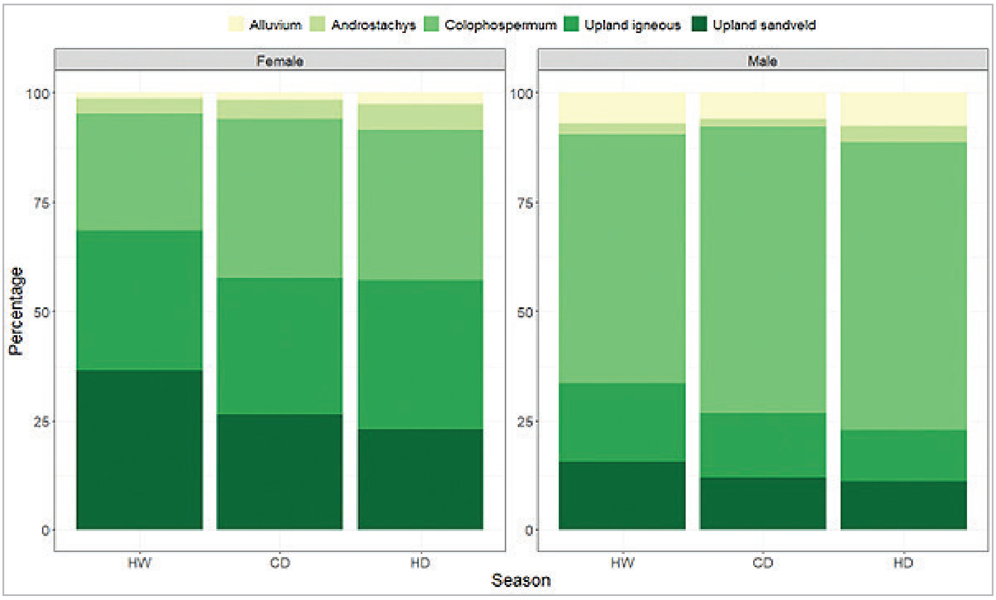

Figure 5. Vegetation use (%) by male and female elephants in different seasons, based on composite data for 2016–2018 and 2020–2022.

Table 4. Total utilization (%) of different vegetation types by female and male elephants over the entire study period.

	Vegetation Type				
	Alluvium	***Androstachys***	***Colophospermum***	**Upland igneous**	**Upland sandveld**
Female	1.97	4.61	33.1	32.5	27.9
Male	6.99	2.8	62.9	14.6	12.7

Table 5. p-values for differences between sex, season, and their joint effect resulting from a multinomial logistic regression having Alluvium as the reference category.

Vegetation type	**(Intercept)**	**Sex male**	**Season CD**	**Season HD**	**Sex male:season CD**	**Sex male:season HD**
Androstachys	0	0	0.982	0.547	0.798	0.019
Colophospermum	0	0	0.571	0.005	0.186	0.002
Upland igneous	0	0	0.113	0	0.197	0.538
Upland sandveld	0	0	0	0	0.009	0

This can interfere with elephant access to preferred foods by concentrating them in certain areas, likely increasing their impact on certain vegetation communities (Grant et al. 2007). The spaces used by the elephants tracked for this study overlapped significantly over consecutive seasons, indicating high site fidelity. There was a significant difference in the areas occupied by female elephants between HD and HW seasons, although the sizes of home ranges remained similar. The decrease in the proportion of repeated visits (overlap) from the HD to the HW season might reflect changes in female elephants' seasonal preferences and movements from dry season woody food sources to grasslands during the wet season (O'Connor et al. 2007). However, the high degree of overall site fidelity shown by elephants in GNP raises some concerns. Repeat visits by elephants to the same areas during

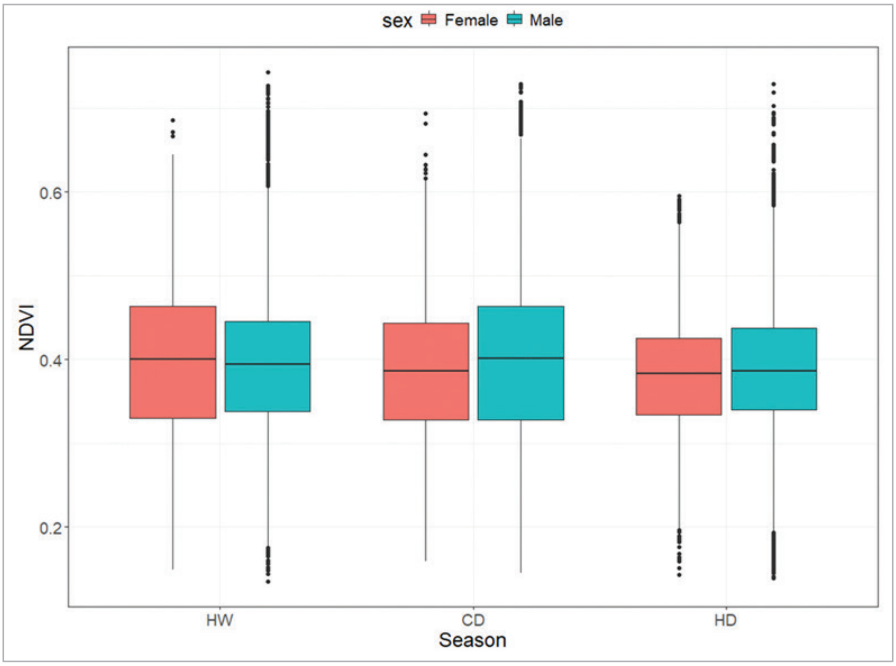

Figure 6. Seasonal selections of vegetation productivity (NDVI) of different areas by male and female elephants. For explanations of the box-and-whisker plots and abbreviations, see the Figure 3 legend.

consecutive seasons and years can have negative impacts on vegetation (Owen-Smith et al. 2006; O'Connor et al. 2007; Owen-Smith et al. 2019), particularly woody vegetation (Guldemond and van Aarde 2008). Furthermore, elephant foraging on woody seedlings and saplings can depress the regeneration of woodland areas (Baxter and Getz 2005). These impacts of elephants on vegetation in Gonarezhou NP are not yet fully understood and more work in the field is required to address this knowledge gap.

Both male and female elephants remained close to water during this study, with females staying closer to water, particularly during the HD season. Adult males can roam farther from water; while females, whose movements are constrained by their offspring, gather in areas close to permanent surface water (Stokke et al. 2002). During the HW season, elephant breeding herds are less dependent on the distribution of permanent surface water sources. Therefore they may range farther and wider than during dry seasons, when they typically remain near surface water to provide for the needs of neonate and young elephants (Stokke and du Toit, 2002; Wittemyer et al. 2007; Young et al. 2009). Mlambo et al. (2021) found that elephants in Hwange NP roam over larger areas during the wet season than in dry season. Surface water is more widely available during the wet season allowing elephants to occupy more extensive ranges, while the shift to a smaller core seasonal range during the dry season is probably a way of optimizing energy expenditure by reducing the distance travelled to water points. Consequently, surface water availability defines key resource areas and shapes the seasonal restriction of the foraging range (Chamaillé-Jammes et al. 2007). In GNP, there are fewer rainfall events during the CD season than during the preceding HW season, but surface water sources may still contain water that is accessible to elephants. However, our study, based on elephant tracking data, did not provide information on this possibility.

Although most male elephants in GNP remained close to surface water, some of the study males spent more time farther from water, especially when travelling long distances. In Chobe NP, Stokke and du Toit (2002) found that male elephants roam widely in the dry season between widely scattered patches of high quality resources, to which they have exclusive access. These include drainage sumps, ephemeral pans, and watercourses that no longer contain surface water but where the water table is close enough to the soil surface to sustain green grass and forbs well into the dry season. In our study, the results relate only to available data on main drainage and river systems. Smit et al. (2007) identified the presence of large areas in Kruger NP that were used exclusively by bulls and suggests that these bulls live in smaller groups with lower collective feeding requirements and a wider habitat tolerance. This also enables them to avoid conflict with other bulls in musth, which occurs in areas with mixed herds. Resource and spatial segregation between male and female elephants results in differential impacts on vegetation due to differences in the size between male and female elephants and in feeding behaviour between the groups of bulls and females in mixed herds (Stokke and du Toit 2002). Male elephants with larger bodies are known to be less selective feeders than females (Stokke 1999). Our results showed that male elephants preferred vegetation types dominated by Colophospermum mopane, while females preferred upland vegetation types that have a diverse composition of woody plant species, possibly roaming these areas in search of high-quality forage. In northern Botswana, Stokke and du Toit (2000) found that bulls have lower dietary diversity, in terms of woody plant species, than female elephants and use vegetation patches with lower woody plant species richness.

On average, both males and females utilized areas with moderately green vegetation across all seasons and both sexes used the Upland sandveld less during the dry seasons than during the wet season. Loarie et al. (2009) found that elephants consistently seek out greener vegetation throughout the year and manage to do so by utilizing vegetation with different phenologies and by selecting landscapes greener than their surroundings. The results suggest a correlation between vegetation productivity/greenness (NDVI) and space use by savannah elephants that does not vary depending on seasonal resource constraints, since both elephant sexes selected areas with similar NDVI values across seasons, most likely due to forage preferences. While the link between NDVI and vegetation quality is complex, there are several reasons to suspect that green vegetation has higher nutritional quality because vegetation stands that are green are likely to contain more standing biomass and higher nitrogen content (Thoma et al. 2002). Our results suggest that even at low NDVI values, female elephants were able to obtain their nutritional requirements. This difference in the distribution, stability, and quantity of vegetation productivity as a coarse measure of food availability (Murwira and Skidmore 2005; Chamaille´-Jammes et al. 2007a; Wittemyer et al. 2007b), explains differences in the spatial patterns of use of different areas by savannah elephants between wet and dry seasons.

Conclusion

Understanding elephant preferences in spatial and temporal dimensions is critical in the management of PAs for the sustainability of both elephant populations and biodiversity. This study increases our understanding of the seasonal use of male and female elephant ranges in GNP. Repeat visits to the same study sites within consecutive seasons and over three years highlighted the potential impact of elephants on vegetation in some areas of the Park, and there is a need for further field studies to determine these impacts. One factor we were unable to consider was the possible influence of elephant densities on the relationship between elephants' use of space and vegetation productivity. Taking density into account may yield additional insights into how the use of space by elephants relates to the availability of water and food resources. There is a need for continuous monitoring of elephant use of space, especially in range areas where elephant movement is restricted by changing land use practices and fences. Therefore, differences in patterns of elephant spatial use between sexes and across seasons should be considered when developing site-specific objectives and PA management strategies, to ensure the long-term sustainability of a healthy elephant population in Gonarezhou National Park and elsewhere in African range States.

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