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The influence of biophysical characteristics on elephant space use in an African savanna

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ABSTRACT

Understanding the influence of biophysical variables on spatial distribution and seasonal locations of elephants is valuable inter alia in understanding their movement patterns, and the carrying capacity to optimise the conservation of their habitats. Furthermore, understanding elephant distribution in time and space is beneficial for predicting locations for tourist viewing and determining potential areas of human–wildlife conflicts. In this study, we examined the environmental drivers of seasonal variations in elephant ranges and movement using telemetry data. Using the elephant tracking data and biophysical characteristics, the Adaptive-Local Convex Hull (a-LoCoH) and the Maximum Entropy Modelling (MaxEnt) algorithm were adopted to determine their potential locations and distribution in a protected area. The jackknife approach was used to assess the environmental factors influencing seasonal elephant movements based on collar data from ten individual elephants tracked between December 2015 and April 2018. The performance of the elephant distribution models for the two seasons was assessed using the area under the curve from the receiver operating characteristic based on a 30% test holdout data. Results showed that the core a-LoCoH home of elephants was larger in the dry than wet season (Wilcoxon signed-rank test; $W = 3$, $Z = 2.4973$, $p < 0.012$). However, no noticeable differences were observed (Wilcoxon signed-rank test; $W = 10$, $Z = 1.7838$, $p < 0.07$) between the dry and wet season for the total (90%) a-LoCoH ranges. The MaxEnt modelling results showed that distance to the artificial water holes was the most influential variable in predicting the potential elephant spatial distribution in both wet and dry seasons, while the normalised difference vegetation index, a proxy for forage availability, was more influential in the dry season in predicting elephant distribution. The study concludes that seasonal elephant space use is mostly influenced by water availability in both seasons, while forage availability and variability influence elephant distribution more strongly in the dry than wet season. The study provides valuable insight into the biophysical characteristics of elephant home ranges. This is useful for the sustainable management of elephants and their habitats.

1. Introduction

The African elephant, the biggest mammal on Earth, is found in 37 of the 54 African countries (WWF, 2020). It inhabits a wide range of environments from rainforests (White et al., 1993) to deserts (Viljoen and Bothma, 1990). However, whereas African elephants are commonly regarded as generalists owing to their ability to adapt to various landscapes (Kerley and Landman, 2006), their movements are dictated by landscape biophysical characteristics and seasonality. Elephants are regarded as keystone species based on their disproportionate influence on ecosystem structure and function across several landscapes (Pratt and Gwynne, 1977; Sorokina et al., 2024; Tafangenyasha, 1997). According to Blake et al. (2009) and Pringle (2008), African elephants are regarded as environmental engineers in recognition of their ecological impacts, including opening up dense forests that allow other smaller animals access to previously unused landscapes. In this regard, understanding the influence of the spatial and physical variables of a landscape on elephant movement is critical for optimising the management and conservation of elephant habitats.

Whereas ivory poaching has been a major threat to elephant numbers for a long time, recently, active and proactive management in some conservation areas in Africa has resulted in growth in elephant numbers

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(Sorokina et al., 2024). This in turn has led to the loss of biodiversity in certain areas (Kerley and Landman, 2006), which has created a paradox for policy and decision-makers since their high numbers are not sustainable. Nevertheless, African elephants are considered an endangered species in the Convention on International Trade in Endangered Species (CITES) such as Botswana, Namibia, South Africa and Zimbabwe and in the rest of the African continent (Cumming et al., 1997). Moreover, in some regions, elephant populations are thought to be too high for the continuity of other species including woodlands. In such cases, managers have adopted measures to artificially reduce their numbers (Whyte et al., 1998).

Various biophysical environmental variables have been shown to affect the spatial dispersal, movement and ranges of elephants (Venter et al., 2015; Xu et al., 2024). These include the availability of water (Charmaille-Jammes et al., 2013; Gara, 2014; Ngene et al., 2009a), topography (Ngene et al., 2009b; Wall et al., 2013) and vegetation (Dzinotizei et al., 2019; Gara, 2014; Loarie et al., 2009b; Ndaimani et al., 2017). Elephants are thought to be water-dependent (especially lactating females with young calves). Studies such as those of Loarie et al. (2009a) and Ndaimani et al. (2017) have found that elephants typically range up to 20 km from the water points during the dry season, but this range is reduced during the wet season when water availability is not a critical factor (Harris et al., 2008). Here we test assumptions about the relationship between seasonal water availability and elephant distributions. Forage availability and variability, as well as preferences, affect the spatial distribution of elephants (Muposhi et al., 2016). Their diet consists mainly of grass and browse (Codron et al., 2006; Laws, 1970). In the African savanna, elephants also use trees as cover from harsh weather conditions including rain and high temperatures (Kinahan et al., 2007). In the savanna ecosystem, the limited availability of forage is an essential covariate in elephant distribution modelling during the dry season (Ndaimani et al., 2017). Topography, represented by elevation and its derivatives such as slope, aspect and Terrain Ruggedness Index (TRI), has also been found to influence elephant spatial distribution (Ochieng, 2015). For instance, in Marsabit in Kenya, elephants were shown to prefer higher elevations and terrain for foraging during the dry season but moved to lower elevations and terrain in the wet season to avoid injuries caused by slipping (Ngene et al., 2009a). Slope (percentage change in elevation) and aspect (the direction to which the slope faces) have been reported to affect vegetation patterns, thereby affecting elephants' spatial distribution (De Knegt et al., 2011).

In southern Africa, to minimise human–wildlife conflicts, regulate elephant populations, manage habitats and optimise tourism, elephants are commonly found in fenced protected areas (Slotow et al., 2005; Whitehouse and Schoeman, 2003) (Clemen et al., 2021; Kioko et al., 2008; Osipova et al., 2018; Vanak et al., 2010; Xu et al., 2024). However, such measures alter elephant movements and have been shown to affect their natural habits (Ngene et al., 2009a). Hence, as a first step towards sustainable management of elephants and their habitat, it is necessary to further understand the implications of biophysical variables on elephant distribution in protected areas. Additionally, understanding seasonal elephant distribution provides a critical knowledge base for sectors such as tourism that depend on elephant sightings.

Species distribution modelling has been used to predict elephant habitats using factors influencing species occurrence and their probabilities. Typically, these models aim to generate species distribution/habitat suitability maps (Austin, 2007; Lombardi et al., 2022). Various species distribution modelling techniques have been developed. These include generalised linear models, spatial interpolators, decision trees, random forests and neural networks (Merow et al., 2013; Phillips et al., 2006). These approaches are grouped as either 'presence-based' or 'absence-based'. Hence, the primary consideration when choosing approaches to determine species distribution is the availability of the presence/absence of species records (Elith et al., 2011; Shekede et al., 2018). Since obtaining absence records for species distribution modelling at a landscape scale is often complicated and costly (Ochieng, 2015), techniques that solely rely on presence records such as Genetic Algorithms for Rule Production and Maximum Entropy model (MaxEnt) have been developed (Baldwin, 2009). Among these, the MaxEnt algorithm has been the most popular owing to its ease of use and ability to effectively incorporate presence-only records; Shekede et al., 2018; Alatawi et al., 2020). Typically, MaxEnt accounts for absence records by generating pseudo-absence points based on the known distribution of presence points.

Hence, the overall aim of this study was to determine the influence of biophysical factors on elephant distribution in a protected area. Specifically, the objective of the study was to determine key environmental variables influencing elephant seasonal space utilisation and distribution within the Hwange National Park (Hwange NP), Zimbabwe. We hypothesise that biophysical factors influencing elephant locations in a protected area vary with seasonality.

2. Materials and methods

2.1. Study area

This study was conducted in Hwange NP, Zimbabwe (between latitudes 18°S and 20°S and longitudes 25°E and 27°E) with an area of approximately 14,651 km^2 and divided into ten management sections (Fig. 1). The altitude of the area falls in the 900 to 1000 m above sea level range (Dudley, 1999). The 2018 Wildlife and Environment Zimbabwe counts estimated the elephant population in the park to be approximately 23,000. Based on these estimates, the mean density of the elephant population within the study area is three animals/km^2 (Charmaille-Jammes et al., 2009). The highest (9/km^2) and lowest (0.5/km^2) concentrations are found in the Shapi Main and Shakwanki camps, respectively (Davies, 1996).

The national park is characterised by a semi-arid climate with a mean annual precipitation of ~600 mm (Charmaille-Jammes et al., 2013). Mean yearly rainfall of 488 mm, 728 mm and 639 mm were estimated from satellite multi-parameter rain rates during the 2016, 2017 and 2018 study period, respectively. April to November is generally dry while November to March is generally wet (Dzinotizei et al., 2019). The mean annual temperature is about 25 °C (Dzinotizei et al., 2019). Water is abundant in rain-fed pools during the wet season and dries after the rainy season, and the park relies on pumped artificial waterholes (Charmaillé-Jammes et al., 2007b). The Kalahari sands soil type dominates the area (Dzinotizei et al., 2019) and supports bushland and woodland vegetation that includes: *Baikiaea plurijuga Ochna pulchra, Terminalia sericea, Combretum spp* and *Colophospermum mopane* (Dzinotizei et al., 2019).

2.2. Data acquisition and pre-processing

2.2.1. Elephant location data

In this study, telemetry-derived elephant data collected between December 2015 and April 2018 was utilised. In total, ten elephants (nine females and one male) of separate matriarch or bachelor herds were randomly chosen in each management domain (one elephant per park management unit) and collared with African Wildlife Tracking GPS units (see Table 1). (See Tables 2 and 3.)

The collaring GPS units (Fig. 2) record elephant locations every four hours. The life expectancy of power packs for these units is two years. In this study all the power packs lasted beyond life expectancy, hence the two-and-a-quarter-year data collection. Elephant immobilisation and collaring were performed in accordance with conditions set by The University of Zimbabwe research board (Grant No. 91048).

2.2.2. Environmental variables

Seven exploratory environmental variables were identified for modelling elephant space utilisation in Hwange NP. These were: distance to artificial water sources, TRI, elevation, slope aspect, slope, and

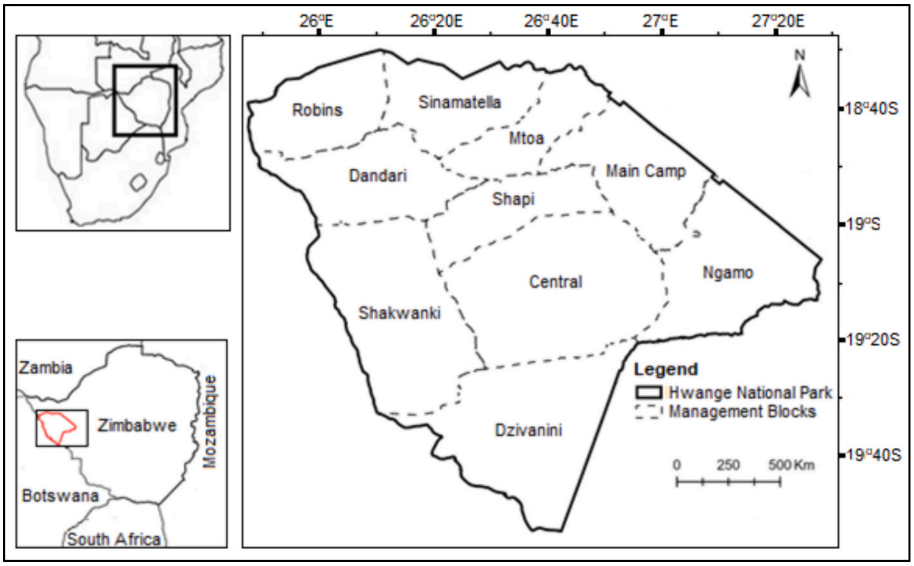

Fig. 1. Hwange National Park and the management units.

Table 1
Elephant collaring details (collaring code, location, date, time and sex).

Collar code	GPS X	GPS Y	Collaring date	Collaring time	Last fix date	Last fix time	Sex
UZ1	481,191	7,903,511	18-Dec – 15	14:34	09-Apr – 18	07:38	Female
UZ2	493,112	7,895,091	18-Dec – 15	18:01	30-Sep – 17	22:17	Male
UZ3	499,376	7,870,332	19-Dec – 15	19:01	09-Apr – 18	07:39	Female
UZ4	543,850	7,890,770	20-Dec – 15	14:41	09-Apr – 18	07:29	Female
UZ5	534,126	7,889,388	20-Dec – 15	18:36	09-Apr – 18	07:33	Female
UZ6	425,233	7,931,360	22-Dec – 15	11:57	09-Apr – 18	07:47	Female
UZ7	394,832	7,939,845	22-Dec – 15	18:40	09-Apr – 18	07:46	Female
UZ8	398,517	7,931,866	23-Dec – 15	12:20	09-Apr – 18	07:47	Female
UZ10	507,680	7,897,763	24-Dec – 15	12:30	09-Apr – 18	07:49	Female
UZ11	507,732	7,894,256	24-Dec – 15	13:30	30-Sep – 17	22:31	Female

Table 2
Variance inflation factors (VIFs) of the predictor variables before and after collinearity diagnostics tests.

	Dry Season VIF		Wet Season VIF	
Variable	Before collinearity diagnostics	After collinearity diagnostics	Before collinearity diagnostics	After collinearity diagnostics
Slope aspect	1.03	1.02	1.03	1.02
DEM	1.47	1.47	1.62	1.66
Distance to water	1.15	1.14	1.1	1.12
Terrain Ruggedness Index	7.36		5.5	
Slope	7.21	1.19	5.43	1.25
Mean NDVI	2.7	2.65	1.42	1.44
Stddev NDVI	2.96	2.9	1.4	1.44

the normalised difference vegetation index (NDVI) derivatives (i.e., NDVI seasonal mean and NDVI seasonal standard deviation). The predictor variables were converted to raster layers and resampled to the same spatial resolution (500 m) covering the same spatial extent. For compatibility with the MaxEnt model, the predictor variable layers were transformed to an ASCII file with the Universal Transverse Mercator Zone 36 South coordinate system using ArcGIS model builder.

2.2.3. Normalised difference vegetation index

Availability and variability of forage in African savannas during the dry season is a critical driver of habitat suitability and elephant space use (Fullman et al., 2017; Gara, 2014). Previous studies have demonstrated that NDVI is a reliable representation of feed richness for elephants (Charmaillé-Jammes et al., 2007a; Loarie et al., 2009b; Muposhi et al., 2016; Wall et al., 2013). NDVI is a popular index for estimation of vegetation vigour derived from near-infrared and red bands of satellite imagery strongly reflected and absorbed by vegetation, respectively (Fitzgerald et al., 2018; Pittiglio et al., 2013; Walsh et al., 1997).

$$NDVI = \frac{(NIR - R)}{(NIR + R)} \tag{1}$$

MODIS Terra (MOD13A1), freely available at the 500 m spatial resolution, was used to extract NDVI seasonal mean and standard deviation data of the study area between 1 December 2015 and 30 April 2018. MOD13A1 data are provided already pre-processed for atmospheric attenuation (Ndaimani et al., 2017; Olofsson et al., 2007).

2.2.4. Terrain ruggedness index, elevation, slope aspect and slope degree

The freely available Shuttle Radar Topography Mission Digital Elevation Model (DEM) with 90 m resolution (Farr and Kobrick, 2000) was adopted to derive the DEM data and its derivatives. DEM derivatives i.e. slope angle (slope), slope aspect (aspect) and TRI of the focal area

Table 3
a-LoCoH 90%-total and 50%-core home ranges.

	50% a-LoCoH (km^2)		90% a-LoCoH (km^2)	
Elephant ID	Dry season	Wet season	Dry season	Wet season
UZ1	149.94	266.87	561.37	944.68
UZ2	115.36	63.20	1066.32	393.16
UZ3	40.37	98.38	192.21	500.35
UZ4	28.83	157.56	146.03	614.77
UZ5	39.77	98.21	130.33	359.61
UZ6	35.63	37.72	190.19	170.56
UZ7	99.03	218.08	397.79	793.85
UZ8	133.16	706.38	718.84	2411.03
UZ10	176.65	359.49	886.16	1087.87
UZ11	14.38	59.45	102.59	234.88
Pooled mean	**83.31**	**206.61**	**439.18**	**751.08**
Stddev	**58.35**	**203.66**	**350.48**	**656.12**
Median	**69.70**	**127.97**	**295.00**	**557.56**
Minimum	**14.38**	**37.72**	**102.59**	**170.56**
Maximum	**176.65**	**706.38**	**1066.32**	**2411.03**
Range	**162.27**	**668.65**	**963.73**	**2240.47**

were derived using Google Earth Engine. The TRI (which approximates the overall elevation difference of a particular cell on a grid) was considered; since it is more robust than the vector ruggedness measure in calculating the unevenness of terrain for wildlife applications (Sappington et al., 2007).

2.2.5. Distance to water (surface water)

Water availability is an essential driver of space utilisation by elephants, particularly in semi-arid savannas (Charmaille-Jammes et al., 2013). Throughout the elephant tracking period, the mean yearly rainfall was estimated at 488 mm, 728 mm, and 639 mm for the years 2016, 2017, and 2018, respectively, using satellite data from the Tropical Rainfall Measuring Mission multi-parameter rain rates. In this study, the dry season was from April to October, while the wet season was from November to March. In the study area, in the rainy season, water is prevalent through rain-fed pools (Charmaillé-Jammes et al., 2007b). However, in the dry season, the pools dry up and the park reverts to using pumped waterholes. A study conducted in Kruger National Park, South Africa, found distinct distribution patterns among various herbivores around rivers and waterholes. The study revealed that the majority of grazer species tended to congregate around artificial waterholes, while browsers and mixed feeders showed indifference to waterholes and instead preferred association with the main rivers (Smit et al., 2007). Therefore, following Gara (2014), this study assumed that artificially pumped waterholes are vital drivers of elephants' use of space within the park. Hence, the distance to the water map was created using the artificial water hole data (Fig. 3) acquired from the Zimbabwe Parks and Wildlife Authority (ZimParks). The map utilised the Euclidean distance algorithm in ArcGIS with 500 m spatial resolution from the midpoint of every 500 m cell to the nearest artificial water point (Asner and Levick, 2012).

2.2.6. Pre-processing of elephant movement data

To determine elephant locations (Wall et al., 2014), the movement data were transformed to Universal Transverse Mercator Zone 35 South based on the World Geodetic System (WGS-84) ellipsoid. As per Gara (2014) and Ngene (2010) who noted that seasons determine elephant behaviour, the movement data were categorised into the dry and wet seasons. All subsequent analyses were executed using these pre-processed and classified datasets (Fig. 4). The Adaptive-Local Convex Hull (a-LoCoH) was utilised to determine the movement metrics and home range. (See Fig. 5.)

3. Data analysis

3.1. Modelling spatial distribution of elephants

The MaxEnt algorithm (Phillips et al., 2006) was used to determine the potential distribution of elephants in Hwange NP. The environmental factors that influence seasonal elephant movements were determined using the jackknife approach (Shekede et al., 2018). MaxEnt is a popular machine learning algorithm used in species distribution modelling based on presence-only records (Elith and Graham, 2009). Elephant tracking data described above was used as the response variable, while the seven environmental variables discussed earlier were selected as predictor variables. Their choice was motivated by existing literature (Charmaille-Jammes et al., 2013; Chibeya, 2019; Gara, 2014; Ndaimani et al., 2017; Ngene et al., 2009b; Ochieng, 2015; Wall et al., 2013) owing to their potential influence on elephants space utilisation and popularity in elephant distribution models (Charmaille-Jammes

Fig. 2. Installation of the tracking collar system. The collar weight and installation are approximately 10 kg and 10 min, respectively.

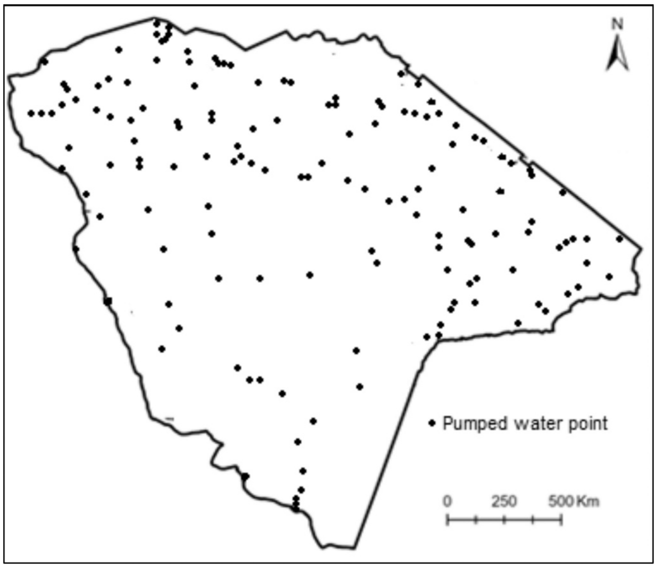

Fig. 3. Hwange National Park boundary, roads and waterpoints within the park.

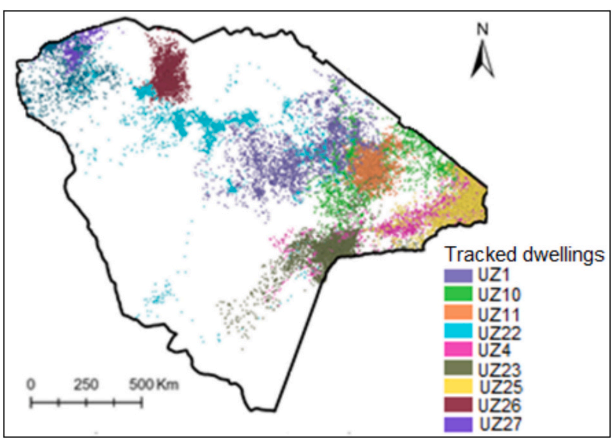

Fig. 4. Filtered GPS movement data.

et al., 2013; Chibeya, 2019; Gara, 2014; Ndaimani et al., 2017; Ngene et al., 2009b; Ochieng, 2015; Wall et al., 2013).

3.2. Testing for multi-collinearity

Environmental variables utilised in this study for habitat modelling were first tested for collinearity before use in MaxEnt. Collinearity tests measure the degree to which the predictor variables are related to each other using variance inflation factors (VIFs) (Akinwande et al., 2015). In statistical species distribution modelling, high collinearity among the predictor variables often causes model over-fitting (Pradhan, 2016). Following Shekede et al. (2018), the Uncertainty Analysis for Species Distribution Models (USDM) package in R (Naimi et al., 2014) was set to iteratively detect multi-collinearity among predictor variables by calculating VIFs of each set of predictor variables. Table 1 summarises the VIFs of the predictor variables before and after collinearity diagnostics. Slope and TRI were highly correlated in the wet season ($R^2 = 0.74$) and in the dry season ($R^2 = 0.90$). TRI was eliminated from further consideration using stepwise correlation tests in USDM for both models. Following the removal of collinear variables, using MaxEnt the remaining exploratory variables were included in the model of the potential distribution of elephants in the park for the two seasons.

3.3. Model evaluation

The performance of the two seasons elephant distribution models was assessed using the area under the curve (AUC) from the receiver operating characteristic using the 30% test holdout data. The AUC evaluates the performance of the MaxEnt species distribution. Baldwin (2009) recommends classifying the performance of models as not-better-than random, fair-model and good-model, which translates to an AUC range below 0.5, between 0.5 and 0.7 and 0.7 to 0.9, respectively. The two species distribution models employed in this study had an AUC between 0.613 and 0.644, translating to fair models capable of indicating the environmental factors that most influenced elephant space usage in the park (Shekede et al., 2018).

3.4. Assessing the importance of environmental factors in predicting space use by elephants

The exploratory variables' percentage contribution in determining spatial elephant distribution in the park was assessed using the jackknife approach. This approach compares the model prediction accuracy iteratively when each predictor variable is excluded from the model (Elith et al., 2011; Phillips et al., 2006; Shekede et al., 2018). The bootstrapping option in MaxEnt was employed in both models whereby ten replicate models were automatically run for each season, then averaged to find their mean performance. During each run, MaxEnt randomly split

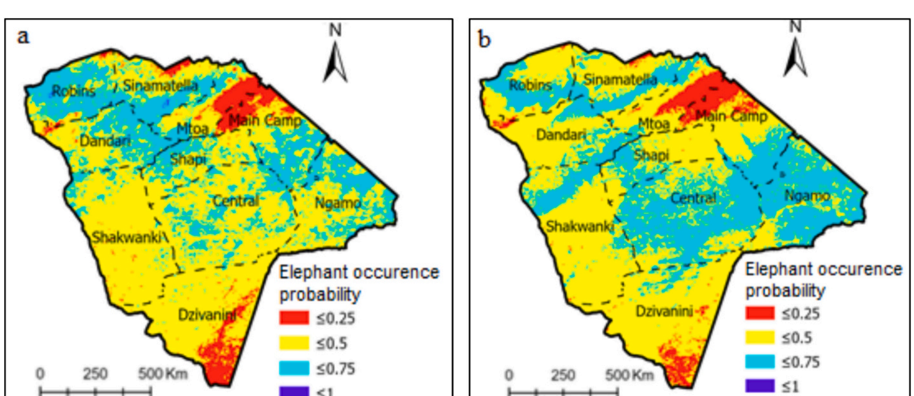

Fig. 5. Spatial distribution of elephants (a) dry season (b) wet season.

into 30% test and 70% training sets without replacement of the elephant occurrence data (Beans et al., 2012; Phillips et al., 2006; Shekede et al., 2018). The MaxEnt model was trained, and the accuracy of predictions was tested using the two datasets, respectively (Beans et al., 2012).

4. Results

4.1. Seasonal comparison of space utilisation distributions

Variations in elephant home ranges were observed between core a-LoCoH home range in the wet season and dry seasons (Wilcoxon signed-rank test; $W = 3$, $Z = 2.50$, $p < 0.01$). However, no significant differences (Wilcoxon signed-rank test; $W = 10$, $Z = 1.78$, $p < 0.07$) between the two seasons were found for the total (90%) a-LoCoH ranges. Table provides a summary of the 90% and 50% a-LoCoH home ranges. The 50% a-LoCoH home ranges varied from 37,722 to 706,376 km^2 for the wet season and from 14,376 to 76,649 km^2 for the dry season. Ninety per cent of a-LoCoH areas showed that the elephants ranged in areas between 170,559 and 2411,032 km^2 and from 102,594 to 1066,323 km^2 for the wet and dry seasons, respectively.

Figure shows the results of the predicted spatial distribution of elephants modelled using MaxEnt for the dry season (a) and wet season (b). The figure, based on the a-LoCoH home ranges, shows that 50% of areas with all elephants are mainly dis-aggregated into smaller areas with a higher number of watering holes in both the dry and wet seasons. The figure also shows that the park is generally suitable for elephant habitation, with >43.6% of the area (Central, Ngamo, Shapi and Main camp) modelled as potentially suitable (i.e., >50% suitable in the wet season). However, the area predicted to be suitable declines sharply (by 19.5%), especially in the central parts of the park. Results also show that the southern management blocks (Shakwanki and Dzivanini) are generally marginally suitable for elephant habitation.

4.2. Environmental variables influencing elephant distribution

Results in Table 4 show that several predictor environmental variables explain the spatial distribution of elephants in the park in both seasons.

In both seasons, distance to water was the most significant predictor in the MaxEnt models. Distance to water explained 75.8% (wet season) and 52.7% (dry season) of the variation in elephant distribution. In the wet season, slope and elevation explain 11.1% and 8.6% of the variation in elephant spatial distribution. Surprisingly, NDVI and aspect were not particularly valuable in explaining elephant habitat in the park but NDVI and elevation became more important during the dry season (Fig. 6).

5. Discussion

This study showed that in the wet season, distance to water points, slope and elevation explained ~96% of the variation in elephant distribution in the Hwange NP. This observation can be explained by the fact that in the wet season, forage resources are abundant within the park; hence NDVI has minimal influence on elephant distribution. However, NDVI as an indicator of forage resource abundance becomes more critical during the dry season.

In both seasons, distance to water was found to significantly influence the elephant's spatial distribution. This result can be attributed to the fact that Hwange NP is in a semi-arid region that receives <650 mm of rain per annum. The park has no naturally occurring perennial water points; therefore, during the dry season, the availability of water is limited to the artificial waterholes (Charmaillé-Jammes et al., 2007b). The relative influence of these water points declines in the wet season owing to the availability of other rain-fed pools accessible to elephants (Charmaillé-Jammes et al., 2007b; Dzinotizei et al., 2019; Tshipa et al., 2017). Temperatures are generally lower in the wet season than in the dry season; which reduces elephants' use of water holes for cooling (Ochieng, 2015).

The concentration of elephants around water sources during the dry season is a well-documented behaviour observed across various ecosystems; being inside a 20 km radius of water sources enables the elephants to drink habitually (De Beer et al., 2006; Loarie et al., 2009b; Ndaimani et al., 2017). These findings also corroborate studies by Ndaimani et al. (2017) in Gonarezhou National Park, Zimbabwe, where the availability of water was a key predictor of elephant distribution. Ochieng (2015) also noted the influence of distance to dams as a significant environmental variable in the dry season in Mpala, Kenya. In the Hwange NP, Charmaillé-Jammes et al. (2007b) reported that distance to water is a critical variable that influences elephant densities, noting an over-abundance of elephants near water holes in the dry season. These findings point to water resources as a critical variable in elephant spatial distribution and, hence can be used as a management tool in avoiding the destruction of vegetation by elephants through strategic placement of artificial waterholes (Charmaillé-Jammes et al., 2007b; Davies et al., 2018; Ochieng, 2015).

However, it is essential to approach the interpretation of this behaviour with caution. This is particularly important when drawing conclusions about elephant movement patterns based on limited sample sizes; these may raise concerns about the representativeness and reliability of the findings. Such a small sample size may not adequately capture the full breadth of elephant movement dynamics and could introduce biases or inaccuracies into the analysis. Despite these limitations, it is worth noting that the observed clustering of elephants near waterholes during the dry season still holds significance by offering valuable insights into the usage density of waterholes by elephants during periods of water scarcity. This information can be particularly useful for park management and conservation efforts, highlighting areas of high elephant activity and potential resource competition (Smit et al., 2007).

Results also show the relatively high importance of NDVI in predicting elephant's spatial distribution in the dry season compared to the wet season. This observation suggests that apart from water requirements, both the quality and quantity of forage increase in importance during the dry season when vegetation quality is affected by moisture deficiency. However, in the wet season, the abundant vegetation within the park leads to better elephant distribution by other factors (Loarie et al., 2009a). Ochieng (2015) found that NDVI proxies for forage quality and quantity influenced space utilisation by elephants. A previous study in the Hwange NP by Charmaillé-Jammes et al. (2007b) also found that during the dry season, elephant densities increased with vegetation availability. These findings further reinforce the centrality of vegetation productivity in sustaining the vast dietary requirements of elephants. However, previous research has shown that as the elephant population size increases, they tend to move into areas characterised by lower NDVI, and thus lower forage quality (Clemen et al., 2021). Nonetheless, the spatial and temporal resolution of NDVI data used in this study may not align with the scales relevant to elephant movement, and may overlook localised vegetation dynamics that influence elephant

Table 4
Contributions of the percentages of predictor variables across seasons.

	Distance to water	Slope	Elevation	NDVI stddev	NDVI mean	Slope aspect
Wet season	75.8%	11.1%	8.6%	2.4%	1.4%	0.6%
Dry season	52.7%	4.6%	10.3%	10.1%	13.1%	9.2%

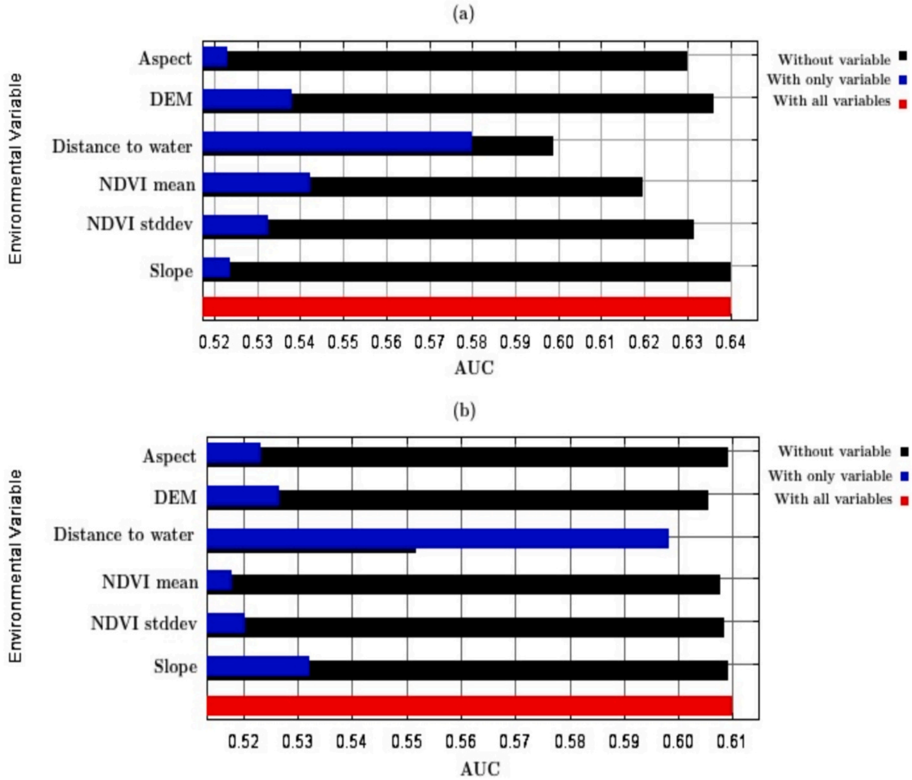

Fig. 6. Jackknife variable importance comparisons of (a) dry season and (b) wet season.

mobility. Utilising higher-resolution satellite imagery or ground-based monitoring methods could provide a more detailed understanding of vegetation-elephant interactions.

This study found that in the wet season, slope was more influential in predicting elephant spatial distribution (11%) than in the dry season (5%). This finding suggests that in the dry season, forage quality and quantity decline, resulting in elephants descending to the lower slopes to access artificial water holes and higher-quality vegetation. A similar study in Mpala, Kenya by Ochieng (2015) suggested that in the wet season, elephants use steeper slopes based on the abundance of forage and water, while in the dry season, lower slopes act as forage reserves since they require less energy to be accessed. Ngene et al. (2009a) showed that elephants could pass through steeper slopes by using zig-zag tracks. In Hwange NP, it is therefore plausible that elephants employ this movement pattern to avoid slipping and falling when moving up steeper slopes.

Aspect, i.e., slope direction, had little influence on space used by elephants in the wet season, explaining only 0.6% of the variation in elephant spread within the park. However, in the dry season, the influence of aspect became significant (9.2%). The influence of slope aspect on elephant spatial distribution is indirect through the interaction of the slope aspect and vegetation. In the wet season, vegetation is abundant in the park, hence slope aspect's influence is minimal. In the dry season, vegetation vigour varies in the slope aspect. This is because the slope aspect influences the amount of sunlight received. This, in turn, impacts the soil temperature and wetness, thereby influencing vegetation diversity (Chibeya, 2019; Hirzel and Le Lay, 2008). This finding improves the available knowledge on the interaction of elephant spatial distribution and vegetation diversity in the study area.

In both seasons, results show that elevation is essential in predicting elephants' spatial movement as indicated by the relative importance of 8.6% and 10.3% in the wet and dry seasons, respectively. The elevation in Hwange NP ranges from 839 to 1137 m. This finding indicates that regardless of other seasonal factors, elephants in the study area prefer elevation ranges that facilitate roaming. This observation is consistent with findings by Chibeya (2019) who found that elephants prefer elevation in the range of 990–1020 m in the savanna ecosystem of Zambia. Wall et al. (2006) also found that elephants prefer relatively low elevations. The avoidance of high elevation could also be due to the lack of diverse forage (West et al., 2016). Vegetation diversity is affected by elevation through soil wetness, soil stability and temperature differences owing to high altitude (Chibeya, 2019; Hirzel and Le Lay, 2008). These findings advance available knowledge of how elevation and its derivatives affect elephant distribution and are a starting point for future studies delineating areas in elevation ranges where elephants are least likely to be found.

This study's strength lies in its assessment of environmental variables influencing space use, as well as modelling their potential habitat. This study for the first time used the a-LoCoH approach to determine elephant locations in the study area, while the majority of previous elephant studies determined ranges using the minimum convex hull (MCP) or kernel density estimator approaches that are not sensitive to outliers in animal site data (Shadrack et al., 2017; Tshipa et al., 2017). Hence, our study offers new information on the key environmental variables that influence seasonal elephant movement. Furthermore, as aforementioned, findings in this study are valuable in informing elephant management strategies by providing the specific seasons during which some factors are critical in influencing elephant distribution.

6. Conclusion

The determination of environmental variables governing elephant locations in protected areas is useful for park management and conservation efforts, highlighting areas of high elephant activity and potential resource competition. By classifying elephant range metrics in this study, we sought to determine how they use space in the Hwange NP in the wet versus the dry seasons. Factors that influence their seasonal spatial distribution were also investigated. The study findings show that the movement metrics were significantly different, with elephants moving faster in the wet than in the dry season. Also, the findings show that their core range was significantly different in the two seasons. These findings further demonstrate the existing assertions that elephants in the savanna utilise smaller ranges in the dry season as determined by water and forage availability. The study findings further illustrate the need to understand elephant–landscape interaction as a means towards their sustainable management and protection. Such knowledge is also valuable for (among others) management of human–wildlife conflicts and tourism in that these activities rely on animal sighting.

CRediT authorship contribution statement

Liberty Mlambo: Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Elhadi Adam:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Conceptualization. **Munyaradzi Davis Shekede:** Writing – review & editing, Project administration, Methodology. **John Odindi:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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