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71 1 Abstract

The African savannah elephant, a critical keystone species, plays an essential role in 72 biodiversity, impacting habitat creation and nutrient dispersal. This study aimed to 73 examine the movement ecology of 10 adult male African savannah elephants, and 74 their habitat use in both protected and unprotected lands and even traversing 75 international boundaries in Botswana and Zimbabwe, home to the largest remaining 76 elephant population. The analyses focused on their habitat use and environmental 77 and physiological impact on movement. The data was collected using GPS and VHF 78 transmitters on August 22 and 23, 2022 and were analysed through Kernel Density 79 Estimation (KDE) and compositional analysis using R and QGIS, showing the 80 importance of variations in habitat preferences and spatial use. Important 81 observations into daily patterns, hourly variations, monthly trends, temperature 82 influences, individual preferences, feeding and resting patterns, ecological insights 83 and musth's influence on all these factors were obtained. The findings reveal the 84 complexity of elephant behaviour and habitat interaction and use, offering a better 85 understanding of their spatial behaviour, movement patterns and responses to 86 environmental factors. Unexpected preferences and avoidance of particular 87 environments were observed, indicating the need for more research on this 88 important population for a better understanding of how elephants are using this 89 region, in this important area for elephant conservation, to make effective long-term 90 management decisions. The findings of the study provide a foundation for future 91 study and conservation efforts by highlighting the necessity of a thorough 92 understanding of elephant interactions with their surroundings, including complex 93 behaviours like crop raiding and different physiological states such as musth. 94

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- 96 **Keywords:** adult male African savannah elephant; movement; speed; musth; Kernel
- 97 Density Estimation; Spatial use/selection, habitat selection

99 2 Scientific Background and Rationale

The African savannah elephant (Loxodonta africana), one of the two recognised 100 species of African elephants, is a fundamental keystone species that plays a pivotal 101 role in upholding biodiversity (de Knegt et al., 2011). These majestic creatures are 102 the largest terrestrial animals on Earth and are sometimes referred to as "landscape 103 architects" because of their capacity to mould and sustain the ecosystems they 104 inhabit. Elephants have been a subject of extensive scientific interest due to their 105 remarkable size and ecological significance. Over time, a combination of genetic. 106 morphological and behavioural research established that there are in fact two African 107 elephant species-the forest elephant (Loxodonta cyclotis) and the savannah (or 108 bush) elephant (Loxodonta africana) (Comstock et al., 2002). This finding extends 109 beyond taxonomical significance and also influences further conservation efforts. 110 This has resulted in the development of targeted strategies, preservation of genetic 111 diversity, more efficient allocation of resources and enhanced public engagement, 112 ensuring that both species receive the attention and protection they require. As the 113 largest land mammal, it has significant influence on its habitat, as they play an active 114 role in the functioning of ecosystems through its contributions to habitat creation and 115 maintenance, as well as its role in seed and nutrient dispersal. These activities are 116 crucial for the survival and well-being of various other species within the ecosystems 117 elephants inhibit (Poulsen et al., 2018). 118

There are significant distinctions in the social structures, behaviour and responses to 119 environmental stressors between male and female African Savannah elephants. 120 Female elephants typically establish matriarchal herds, while males engage in 121 complex social dynamics characterized by fission-fusion relationships-where the 122 composition and size of the group evolve over time and with environmental 123 movement—as well as age-dependent social networks that exhibit hierarchical 124 gueuing behaviour in high-stakes situations (O'Connell-Rodwell et al., 2011). The 125 study by Lee et al. (2022) examines the varying impacts of environmental and social 126 difficulties on male and female elephants. While the impact of family disturbance 127 appears to have a greater effect on females, possibly due to their involvement in 128 matriarchal social systems, males are more significantly affected by drought, 129 especially at critical periods of their development. The variations in behaviour and 130 response to external influences highlight the intricate interaction between gender, 131 age, and surroundings within the social ecology of African savannah elephants. 132

Understanding the behaviour and ecology of male African savannah elephants is 133 crucial for effective conservation and mitigation of human-elephant conflict. Studies 134 have shown that male forest elephants exhibit unique movement ecology and 135 behaviour when selecting habitats, operating at a different spatial scale than females 136 (Beirne et al., 2021; de Knegt et al., 2011). Male African savannah elephants use 137 chemical information to monitor female movements, which may be crucial for mate 138 selection and reproduction (Poole, 1987). Older males also play a leadership role in 139 all-male elephant groups, facilitating cooperation and guiding group movements 140 (Allen et al., 2020). However, male elephants' long-distance movements in search of 141 mates and resources can make them more vulnerable to human-wildlife conflict, 142 particularly in fragmented habitats (Gara et al., 2021). Male elephants have been 143 found to modify their behaviour in response to human threats and can discriminate 144 between different levels of danger (Wittemyer et al., 2008). Additionally, crop-raiding 145 behaviour in male African savannah elephants is influenced by their social networks 146

and life history milestones (Chiyo et al., 2012). Therefore, understanding male
 elephant movement patterns and behaviour at different spatial scales and in different

contexts is essential for effective conservation management and mitigating human-

150 elephant conflict.

Crop raiding by male African elephants is a multifaceted issue with various 151 influences and implications. According to Osborn (2004) findings, there is a seasonal 152 variation in the feeding patterns of elephants that engage in crop-raiding activities in 153 Zimbabwe. This indicates that the timing of these raids has a crucial role in shaping 154 the behaviour of these elephants. Further research expanded upon previous 155 findings by showing a connection between lunar cycles and the likelihood of 156 elephants to engage in risk avoidance behaviour while utilising crops grown by 157 humans (Gunn et al., 2014). 158

In Botswana the extent to which farmers in the Okavango Delta region embraced 159 deterrent innovations, revealed a notable inclination towards the adoption of novel 160 practises especially the use of chilli pepper (Noga et al., 2015). Another kind 161 of olfactory repellent was introduced in Uganda and Kenya which was very 162 successful and deterred 82% of all the crop raiding attempt during the study (Tiller et 163 al., 2022). More traditional methods approaches were also taken into account, 164 including the implementation of beehive fences in the northern region of Kenya (King 165 et al., 2011). This method was not preferred by farmers in the Okavango 166 Delta region in Botswana as it was perceived as a low deterrent (Noga et al., 2015). 167 Ahlering et al. (2011) found that crop raiding has a significant correlation with 168 heightened stress levels in male elephants, indicating potential physiological 169 consequences. Troup et al. (2020) further found that elephants exhibit complex 170 movement patterns during crop-raiding, with variations in speed possibly reflecting a 171 valuation of risks and rewards. The observed navigation patterns of elephants could 172 potentially be linked to their awareness of human activities, physical barriers, and the 173 spatial arrangement of crops within the area. Collectively, these studies provide a 174 comprehensive perspective on crop raiding, highlighting the significance of 175 individualised techniques. 176

Alongside crop raiding, the role of protected areas in the conservation and behaviour 177 of African elephants emerges as a key factor. Elephants are moving out of their 178 protected areas in southern Kenya. This could be a sign of natural growth patterns 179 and human-elephant conflicts (Ahlering et al., 2012). A study conducted in the 180 Marsabit protected region reveals the apparent seasonal movement patterns of 181 elephants, which are influenced by several factors such as accessibility to forage 182 and water, as well as human activities, ultimately determining their migratory 183 behaviour (Ngene et al., 2010). Another study demonstrated that protected areas 184 have an important impact on the home and habitat use ranges of elephants, 185 highlighting the role these areas play in providing safety for elephants while also 186 potentially constraining their habitat (Wall et al., 2021). The present distribution of 187 elephants comprises just 17% of their potential habitat, while a significant 57.4% 188 occurs outside of protected regions (Wall et al., 2021). It is further hypothesised that 189 elephants also increase their speed outside of protected areas (Douglas-Hamilton et 190 al., 2005). To secure the future of elephants, one important management strategy is 191 to find areas of high use outside protected areas that could be potentially become 192 future protected areas could serve as a corridor to connect two protected areas. 193

Corridors are essential for species conservation and protected area planning, 194 particularly for species, to enhance gene flow, population viability, and conservation 195 of critical processes (Jachowski et al., 2013). The present efforts to determine, 196 organise and give importance to corridors for the protection of species concentrate 197 on how individual species move in reaction to habitat preservation and management 198 along these corridors (Sawyer et al., 2011). Recently, African savannah elephants 199 have been observed to be restricted to protected areas due to disturbed or broken 200 wildlife corridors and display streaking behaviour, a behaviour where they rapidly run 201 through an area without stopping or browsing (Douglas-Hamilton et al., 2005). 202 Streaking has further been hypothesised to be the response to environmental factors 203 such as nutrient availability, reproductive tactics (Taylor et al., 2020) and water 204 sources (Yussuf A. Wato et al., 2018). However, Douglas-Hamilton et al. (2005) and 205 206 Jones et al. (2012) found that human disturbance in corridors caused a decrease in corridor usage and an increase in streaking behaviour. Jachowski et al. (2013) 207 examined the relationship between the physiological state of African savannah 208 elephants and their use of corridors and streaking behaviour and discovered that 209 elephants in poor physiological condition were more likely to use corridors and 210 exhibit streaking behaviour, which highlighted the importance of considering the 211 physiological state of elephants. So even though this behaviour has been studied the 212 ecological significance is not yet fully understood. 213

Another behaviour that is poorly understood is why predominantly male African 214 savannah elephants are found in the Makgadikgadi Pans National Park, a low 215 nutrient and water area. According to a study by Douglas-Hamilton et al. (2005) the 216 Makgadikgadi Pans in Botswana are an essential ecosystem for African savannah 217 elephants as it provides a critical source of nutrients during the dry season when 218 food is scarce, and elephants rely on this area for survival. Despite this importance, 219 there is a lack of knowledge about how elephants search for nutrients and the factors 220 that influence their movement patterns within this region, which may be due to the 221 vastness of the Makgadikgadi Pans making it difficult to track individual elephants 222 and monitor their movements and habitat use. However, advancements in tracking 223 technology and analysis methods have enabled researchers to study elephant 224 movement patterns in more detail; GPS collars and remote sensing data are now 225 used to track their movements over large areas and analyse the factors that affect 226 their decisions (Owen-Smith et al., 2020). 227

The broadened understanding of spatial use and habitat selection by elephants 228 extends to other regions, offering critical insights into their complex ecology, 229 behaviour and interactions with human-dominated areas. Habitat selections by 230 elephants is multifaceted, affected by various natural and anthropogenic factors. One 231 study found that a functional response was observed in the selection of habitats in 232 relation to tree cover, both spatially and temporally (Roever et al., 2012). During the 233 rainy season, it was shown that tree cover did not significantly influence habitat 234 selection in the mesic, eastern populations, but there was further increased 235 variability in selection during this period; meanwhile, selection for low slopes, high 236 tree cover and greater distance from anthropogenic factors was consistent across 237 populations, yet the variability in selection coefficients changed as a function of the 238 abundance of a given resource within the home range (Roever et al., 2012). De Boer 239 et al. (2000) discovered similar findings of preference of dense forest patches among 240 males (de Knegt et al., 2011) and have adjusted their habits and diet in response to 241 factors such as water salinity, seasonal changes, poaching, and the vital presence of 242

forest patches. Bastille-Rousseau et al. (2020) found that there were seasonal 243 changes in habitat selection and noted that elephants clustered around permanent 244 water sources and human settlements during the dry season and moved to seasonal 245 waters during the rainy season. Elephants demonstrate the ability to adapt their 246 spatial behaviours in response to human presence and various risk factors, such as 247 poaching (Graham et al., 2009). These adaptations are observed in both dry and 248 rainy seasons, as well as in unfenced ecosystems where human-induced pressures 249 are prevalent. A case study conducted in Gorongosa National Park in Mozambigue 250 exemplifies how elephants strategically modify their movements and exhibit a 251 preference for engaging in risky activities during the night while seeking refuge 252 during the day (Gaynor et al., 2018). 253

The life stage of an animal significantly influences movement patterns; for instance, 254 migratory patterns of adolescent birds can differ markedly from mature individuals 255 (Newton, 2007), and the roaming behaviours of sub-adult lions stand apart from 256 those of territorial adults (Davidson et al., 2013). In male African savannah 257 elephants, musth, a period of heightened sexual activity characterised by 258 physiological and behavioural changes (Poole, 1987), illustrates another influential 259 life stage. During musth, elephants secrete temporin from their temporal glands 260 located behind their eyes, a fluid rich in chemical compounds that convey an 261 elephant's age, health, reproductive status, and dominance, facilitating peer 262 assessments for mating or social decisions (Poole, 1987). As the condition develops, 263 behavioural shifts make elephants more aggressive and unpredictable, pushing them 264 into scent-marking activities like urine dribbling and dung dropping, emblematic of 265 their dominance (Poole, 1987). Musth is thought to be triggered by hormonal 266 changes and is more commonly observed in older males, who may experience 267 longer periods of musth and exhibit more extreme behaviours than younger males 268 (Ganswindt et al., 2003, 2005). This comprehension of male elephants' chemical 269 signals during musth is pivotal for conservation and management, serving as tools to 270 observe elephant populations and guide decisions on their mobility and habitat 271 preference. 272

In summary, the African savannah elephant is a keystone species that plays an 273 essential role in maintaining biodiversity in the ecosystems they inhabit. 274 Understanding the movement patterns and behaviour, impacted by various 275 276 environmental stressors, social structures, of male elephants is crucial for effective conservation management and mitigating human-elephant conflict. The complexity of 277 male elephant behaviour extends to unique habitat selection, responses to human 278 threats and musth. Crop raiding is a complex problem that involves variations in 279 feeding patterns. In response to this issue, different deterrents are utilised (King et 280 al., 2011; Noga et al., 2015; Tiller et al., 2022). Additionally, the impact of protected 281 areas, wildlife corridors and the disturbances caused by human activities present 282 new challenges and opportunities for understanding this behaviour. The 283 Makgadikgadi Pans National Park (MPNP) is a unique environment that is critical to 284 the survival of the largest remaining elephant population in the world and is a key 285 component of the Kavango Zambezi Transfrontier Conservation Area, about which 286 little is known about in terms of its importance to elephant movement across this 287 288 landscape. Finally, musth, with its profound impact on movement patterns and habitat requirements, plays a crucial role in male elephant conservation and 289 management. Understanding how musth affects male elephant spatial needs will 290 ensure key habitats are conserved to ensure future populations. Overall, continued 291

- research and conservation efforts are necessary to ensure the survival of this iconic species and the ecosystems they inhabit.
- 294

295 2.1 Aim and Research Objectives

The aim of this study is to analyse the initial movement data of 10 adult male African savannah elephants. These elephants were fitted with satellite radio collars in MPNP in August 2022 by the Botswana-based NGO, Elephants for Africa (EfA). The study seeks to identify potential wildlife corridors. Additionally, it aims to offer a comprehensive preliminary analysis, which can lead to recommendations for subsequent conservation efforts based on the results.

- 302 This data was used to investigate the following objectives;
- 1. To determine home ranges of 10 male African savannah elephants
- To assess the impact of environmental factors such as water sources and
 human activity on the movement behaviour of male African savannah
 elephants.
- 307 3. To compare the movement patterns and behaviour of male African savannah 308 elephants during different times of day, month, and temperatures.
- To identify areas of high conservation value based on the movement patterns
 of male African savannah elephants and devise recommendations for these
 areas, future research and monitoring efforts based on the findings of the
 study.

314 3 Methods

315 3.1 Study Site and Study Species

Ten male African savannah elephants were darted and collared in the Makgadikgadi 316 Pans National Park (MPNP), a partially fenced protected area, thus the elephants 317 where not restricted to this location and the study site includes areas of Botswana 318 and Zimbabwe, as dictated by the elephants' movements. The elephants were 319 collared by the NGO, Elephants for Africa (EfA, as part of a larger research project 320 investigating the male elephants of this region and the potential nutritional 321 deficiencies driving range expansion in this region. EfA operates out of a research 322 camp, located in the village of Khumaga on the banks of the Boteti River, bordering 323 MPNP (Figure 1.). 324

325 To mitigate the potential risk of drowning after being darted, the 10 adult male

African savannah elephants (assessed to be adults from the air by their size, tusk

size and other features by two very experienced personnel) were deliberately not

collared in close proximity to the Boteti River, to ensure their safety during the

darting process. During the study, one of the elephants, identified as IR SAT 6214,

entered the state of musth. For data on the elephants refer to Appendix 1.



331

Figure 1. Map of area near the Boteti River in Botswana where 10 adult male African savannah elephants (*Loxodonta africana*) were fitted with Iridium Satellite and UHF collars (AFRICA WILDLIFE TRACKING, n.d.).

335 3.2 Data collection

The author did not collect the data used in this study. Instead, a collaboration was established between the author and Elephants for Africa, a registered charity in England and Wales and NGO in Botswana dedicated to protecting the endangered African savannah elephant through research and education. Elephants for Africa focuses on understanding the ecological and social needs of male African savannah
elephants and aims to mitigate human-wildlife conflicts (Elephants for Africa, 2023).
They work collaboratively with researchers to disseminate scientific information to
local authorities and raise community awareness. In alignment with the
organisation's research objectives, the data collection method employed in this study
was adapted from established techniques previously used by Elephants for Africa
and resembles the methodology outlined by Evans (2006).

10 adult male elephants were selected randomly in MPNP by flying a small spotter 347 plane to locate the elephants, once spotted a helicopter was radioed in, from which 348 the veterinarian and an experienced elephant biologist assessed the age of the 349 elephant(s), if a suitably aged elephant was present, they were darted by the 350 veterinarian. The elephants were darted with etorphine hydrochloride (M99) by a 351 veterinarian using gun-propelled syringes. Seven elephants were darted on August 352 22, 2022, while the remaining three were darted on August 23, 2022. Once sedated, 353 the elephants were measured and fitted with GPS (Global Positioning System) 354 collars. The GPS collars are the IR-SAT Tag (Iridium Satellite and UHF Tag) which 355 provide wildlife tracking and telemetry by utilising a low-power UHF Transceiver and 356 an IR-SAT module (AFRICA WILDLIFE TRACKING, n.d.). In three cases, a vehicle 357 crew assisted in the process. The collars were programmed to collect and transmit 358 the date, time, geographical coordinates, and temperature every hour. Additionally, 359 each collar had a VHF (Very High Frequency) transmitter with a unique frequency, 360 enabling tracking from the air and ground. 361

362 3.3 Analyses Using R and QGIS for each objective

The analyses of the dataset consisting of the tracking data collected from 10 adult male African savannah elephants was done using RStudio (Version 2023.06.0 Build 421), R version 4.3.0 (2023-04-21 ucrt) (R Core Team, 2023) and QGIS version 3.24.1-Tisler (QGIS.org, 2023).

The dataset spans from August 22nd, 2022, to June 1st, 2023, with GPS points recorded at hourly intervals. First to ensure data quality and reliability the data was cleaned and the timestamps were reformatted. The timestamps were then manipulated. The aim of this manipulation was to isolate the month and time components for analytical purposes (Wickham, 2017).

372 3.3.1 Objective 1 analyses

For the first objective of this study, raw coordinates were extracted from the dataset 373 in QGIS. The "adehabitat" package (Calenge, 2006) was used to perform kernel 374 density estimation (KDE) find the habitat use (at 95% confidence interval) and the 375 core home ranges (at 50% confidence interval) of each elephant and of all the data 376 together. This study utilised the ad hoc smoothing parameter, 'href,' which 377 dynamically adjusts the bandwidth based on the distribution of the data. This data-378 driven approach mitigates over-smoothing or under-smoothing issues, leading to 379 more accurate KDE outcomes (Schuler et al., 2014). The KDE polygons were turned 380 into 'sf' (simple features) objects with EPSG:32735 (WGS 84 / UTM zone 35S) 381 coordinate reference systems. 382

383 3.3.2 Objective 2 analyses

A multifaceted approach was employed for the second objective of this study. The following data were added onto the map; habitat landuse data set, which is a 10m raster with global landuse but only one section was downloaded that covers the study area (Esri & Microsoft, 2022), waterways for both Zimbabwe and Botswana (OpenStreetMap contributors, 2020; rcmrd., 2015), roads for both countries (AICD., 2017; OpenStreetMap contributors, 2023) and protected areas for both countries (UNEP-WCMC & IUCN, 2023).

The linear features on the layers were buffered to 20m. This buffer allowed elephants to be detected using the road and waterways within these 20m. All the layers were merged and dissolved into a comprehensive land use layer displaying all the available habitat for analyses. The Kernel Density Estimation (KDE) polygons were used to cut areas from the land use layer to determine the habitat selection preferences of each elephant.

397 **3.3.3 Objective 3 analyses**

To assess objective 3, the habitat use was calculated using compositional analysis. 398 The protected areas were unionised with the dissolved land-use map. The KDE 399 shapefiles were clipped to the dissolved land-use layer. The areas found within these 400 clipped layers were then saved into two CSV files; one file with the 50% confidence 401 interval called "all50" and another with the 95% confidence interval called "all95". 402 The landuse layer's areas were also saved as a CSV file. The available area, and 403 used areas at 95% and 50% confidence intervals, were extracted, and the mean 404 composition within each area were calculated and visually represented through pie 405 charts. Compositional analysis was conducted using the 'compana' function on both 406 95% and 50% confidence interval data, and the resulting ranking matrices were 407 interpreted further. 408

409 **3.3.4 Objective 4 analyses**

To achieve the fourth objective of this study, analyses were done on how elephant speed varies during different hours, months, temperatures and day and night.

412 Speed between consecutive points were computed.

Day and night were distinguished in RStudio. Four boxplots were generated to
visualise the distribution of elephant speeds at different hours; nighttime and
daytime; months and temperature. A Wilcoxon rank sum test showed the significant
difference in speed between day and night and a spearman's rank correlation test
was calculated to show the correlation for the rest.

Lastly, the speed within and without protected areas was considered for tagged
African savannah elephants. Using QGIS software, GPS coordinates were
transformed to delineate locations falling inside and outside designated protected
zones. Timestamps across these segmented areas were harmonised and speed
calculations were subsequently performed based on the GPS coordinates. A boxplot
depicted the results and Wilcoxon rank sum test calculated the significance.

4 Results

425 4.1 Kernel Density Estimations

In Table 1., Kernel Density Estimation reveals striking variability in the spatial usage patterns among 10 individual adult male African Savannah elephants. KDE was employed with the ad hoc smoothing parameter (href) to analyse the home ranges and spatial use. The analyses are presented at two distinct confidence levels: 50% and 95%, measured in meters², presented on Figure 2.. The 50% confidence interval represents the core home range, reflecting the primary area where an individual elephant is most likely to be found. The 95% confidence interval defines the broader habitat use, encompassing the wider areas frequented by the elephant. It was found that the broader habitat use and home-range for IR SAT 6208 (2922587.0m2 and 576297.9m2, respectively) is a lot larger than the other elephants. IR SAT 6209 has the smallest home range (21120.7 m2) and smallest total habitat use (191008.4 m2).





Table 1. Kernel density estimation (KDE) of each individual 10 adult male African
 savannah elephants at 50% and 95% confidence intervals using the ad hoc
 smoothing parameter (href). The areas are calculated in m².

Individual	Kernel Density Estimation at 50%	Kernel Density Estimation at 95%
	(m²)	(m²)
IR SAT 6207	67712.0	441867.5
IR SAT 6208	576297.9	2922587.0
IR SAT 6209	21120.7	191008.4
IR SAT 6210	33935.3	238710.9
IR SAT 6211	46826.5	256529.1
IR SAT 6212	123024.2	751151.6
IR SAT 6213	32090.9	402591.8
IR SAT 6214	56780.1	469369.4
IR SAT 6215	61338.5	645400.3
IR SAT 6216	152075.5	923998.1
All Individuals	160890.1	1501758.0

448

449

450 **4.2 Habitat Selection and Compositional Analysis**

The compositional analysis and habitat selection matrices presented in Table 2. offer 451 key insights into the preferences of African Savannah elephants for different types of 452 land cover. Figure 3. provides a visualisation of habitat utilisation, indicating that the 453 elephants' actual habitat use at both 50% and 95% confidence intervals diverges 454 markedly from the available land composition within the study area. When the 455 available habitat is compared to the habitat the elephants utilised, there is a clear 456 and similar selection of habitat by the elephants at both the 95% and 50% 457 confidence interval for home range (Figure 3.). Table 2. shows avoidance/selection 458 ranking for each of the habitats. The selection was the same for both the 95% and 459 50% confidence intervals. The three habitats that was most selected for were, 460 Shrub/Scrub in PA, Roads in PA and Roads. The three habitats that were most 461 avoided were Crops in PA, Crops and Bare Ground. 462



Figure 3 (a-c). a) Pie chart of land composition available within the study area
 utilised by all 10 collared adult male African savannah elephants, land type is divided
 into nine habitat types within and without protected areas (PA), b) and c) pie charts
 showing actual habitat utilised by the 10 collared adult male African savannah
 elephants at 50% and 95% confidence intervals

Table 2. habitat selection ranking matrices for two distinct compositional analyses (a and b). The presence of the "+" or "-" symbol indicates whether the row habitat was ranked higher (+) or lower (-) than the column habitat, indicating a greater or lesser degree of habitat selection. The plus or minus sign is tripled (+++) in cases where the pairwise difference was found to be statistically significant (p < 0.05). The ranking of row habitats is determined based on the frequency of higher rank places, denoted as either "+" or "++". A rank of 1 indicates the highest level of selection, while a rank of 18 indicates the highest level of avoidance.

Table 2.								(Colur	nn Ha	bitate	5							
Row Habitats	w	WPA	т	ТРА	FV	FVPA	С	СРА	BA	BAP A	BG	BGP A	S	SPA	Wa	WaP A	R	RPA	RAN K
(a) Full habitat us	e (95%	confi	dence	interva	l) with	in													
Water (W)	0					+	+++	+++	+	+++	+++	+				-			11
Water in PA (WPA)	+++	0	+	-	+	+++	+++	+++	+++	+++	+++	+++	-		+	+++	-		6
Trees (T)	+++	-	0		+	+++	+++	+++	+++	+++	+++	+++			-	+			8
Trees in PA (TPA)	+++	+	+++	0	+++	+++	+++	+++	+++	+++	+++	+++	+		+	+++	-		5
Flooded Vegetation (FV)	+++	-	-		0	+	+++	+++	+++	+++	+++	+				+			9
Flooded Vegetation in PA (FVPA)	-				-	0	+	+++	+	+++	+++	+				-			12
Crops (C)						-	0	+	-	-	-	-							17
Crops in PA (CPA)							-	0			-	-							18
Built Area (BA)	-					-	+	+++	0	+++	+	+							13
Built Area in PA (BAPA)							+	+++		0	+	-							14
Bare Ground (BG)							+	+	-	-	0	-							16
Bare Ground in PA (BGPA)	-				-	-	+	+	-	+	+	0			-	-			15
Scrub/Shrub (S)	+++	+	+++	-	+++	+++	+++	+++	+++	+++	+++	+++	0		+	+++			5
Scrub/Shrub in PA (SPA)	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	0	+++	+++	+++	+++	1
Waterways (Wa)	+++	-	+	-	+++	+++	+++	+++	+++	+++	+++	+	-		0	+++	-		7
Waterways in PA (WaPA)	+		-		-	+	+++	+++	+++	+++	+++	+				0			10
Roads (R)	+++	+	+++	+	+++	+++	+++	+++	+++	+++	+++	+++	+++		+	+++	0		3
Roads in PA (RPA)	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++		+++	+++	+++	0	2
(b) Core home -	range	e (50%	∕₀ con	fiden	ce int	erval)	with	in											
Water (W)	0					+	+++	+++	+	+++	+++	+				-			11

Water in PA (WPA)	+++	0	+	-	+	+++	+++	+++	+++	+++	+++	+++	-		+	+++	-		6
Trees (T)	+++	-	0		+	+++	+++	+++	+++	+++	+++	+++			-	+++			8
Trees in PA (TPA)	+++	+	+++	0	+++	+++	+++	+++	+++	+++	+++	+++	+++		+	+++	-		4
Flooded Vegetation (FV)	+++		-		0	+	+++	+++	+++	+++	+++	+				+			9
Flooded Vegetation in PA (FVPA)	-				-	0	+	+++	+	+++	+++	+				-			12
Crops (C)						-	0	+		-	-	-							17
Crops in PA (CPA)							-	0			-	-							18
Built Area (BA)	-					-	+++	+++	0	+++	+	+							13
Built Area in PA (BAPA)							+	+++		0	+	-							14
Bare Ground (BG)							+	+	-	-	0	-							16
Bare Ground in PA (BGPA)	-				-	-	+	+	-	+	+	0				-			15
Scrub/Shrub (S)	+++	+	+++		+++	+++	+++	+++	+++	+++	+++	+++	0		+	+++			5
Scrub/Shrub in PA (SPA)	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	0	+++	+++	+++	+++	1
Waterways (Wa)	+++	-	+	-	+++	+++	+++	+++	+++	+++	+++	+++	-		0	+++	-		7
Waterways in PA (WaPA)	+				-	+	+++	+++	+++	+++	+++	+				0			10
Roads (R)	+++	+	+++	+	+++	+++	+++	+++	+++	+++	+++	+++	+++		+	+++	0		3
Roads in PA (RPA)	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++		+++	+++	+++	0	2

487 4.3 Speed of Movement Within and Without Protected Areas

A slight difference in the median speeds exhibited by the 10 adult male African
 savannah elephants in both protected and unprotected areas is visualised (Figure 4).
 This observation implies that there are modest behavioural adjustments made by the
 elephants in response to varying degrees of human activity and environmental
 security.





493

Figure 4. Comparative analysis of speed (m/s) of 10 adult male African savannah elephants inside and outside of protected areas.

The median speeds in Figure 4 were found to be 0.056 m/s and 0.057 m/s for protected and unprotected areas, respectively, indicating a slight increase in speed in unprotected areas. The interquartile range also exhibited a difference between protected (0.13) and unprotected (0.16) areas. The Wilcoxon rank sum test with continuity correction revealed a statistically significant difference in speed between the protected and unprotected areas (W = 412263539, p-value < 0), supporting the alternative hypothesis that the true location shift is not equal to 0.

503 4.4 Speed During Day and Night

504 There were distinct fluctuations in the speed of the elephants throughout the day 505 (figure 6), with subtle but statistically meaningful differences between daytime and 506 nighttime activities.





507

Figure 5. Comparison of combined speed (m/s) of 10 adult male African savannah
 elephants during day (between 6am and 6pm) and night (between 6pm and 6am)
 periods.

Figure 5 illustrates the distribution of combined speed measurements across day and night periods of 10 adult African savannah elephants. The mean for the day was 0.14m/s and the mean for the night was 0.12m/s. However, the median speeds of day and night were 0.07m/s and 0.05m/s, respectively. The interquartile range was 0.13 for the night and 0.17 for the day. The Wilcoxon rank sum test reported a statistically significant difference in speed between day and night (W = 459,526,416, p-value > 0)

519 4.5 Speed During Different Hours of Day

Figure 6 highlights distinct fluctuations in speed throughout the day, possibly
 reflecting the elephants' adaptive behavioural rhythms in response to environmental
 conditions and activity levels.



523

Figure 6. Variation in combined speed (m/s) of 10 adult male African savannah elephants across different hours of the day.

The boxplot Figure 6 shows a clear pattern of fluctuation in combined speed of the 526 10 elephants in relation to the time of day. The median speeds exhibit a noticeable 527 increase starting from the early morning at 0.04m/s at hour 4, then reaching a peak 528 at 0.09m/s at hour 8, then a slight dip at hour 12tot 0.03m/s, another peak is reached 529 at 0.11m/s at hour 16, after that the speed is gradually decreasing towards the night 530 (hour 23 at 0.05m/s). The interguartile ranges, representing the spread of the data, 531 follow a similar trend with the highest values observed during the late afternoon 532 hours 16 to 18 with ranges at 0.21, 0.22 and 0.20, respectively. The shortest IQR 533 found was at hour 3 with a range of 0.06. The Spearman's rank correlation test 534 showed a statistically significant, but weak, positive correlation between speed and 535 hour (rho = 0.144 and a p-value < 0). 536

537 4.6 Speed During Different Months

538 The following results investigate the speed variations among 10 adult male African 539 savannah elephants over different months.





Figure 7. Combined speed (m/s) of 10 adult male African savannah elephants compared to different months of the year.

The boxplot in Figure 7 visualises the distribution of combined speed (m/s) of 10 543 adult African savannah elephants over 10 months (August 2022 to May 2023), June 544 was removed as there was only one day of data. The median values show that the 545 speed is higher during the beginning of the year, specifically in January, month 1 546 (0.09 m/s), and shows a decreasing trend towards the middle of the year, reaching 547 its lowest point in August, month 8 (0.05 m/s). Additionally, the interguartile range 548 (IQR) reveals the spread of the data around the median, with the highest IQR 549 observed in January (0.23) and the lowest in August (0.11). The results of the 550 Spearman's rank correlation test indicate a statistically significant negative 551 correlation between speed and month (rho = -0.07045441, p-value < 0). This 552 suggests that there is an inverse relationship between the two variables, though this 553 relationship is weak. 554

555 4.7 Speed During Different Temperatures

The following section investigates how varying temperature conditions (ranging from 14°C to 49°C) influence the speed of 10 adult male African savannah elephants,

⁵⁵⁸ highlighting both median speeds and variations within interquartile ranges.



559

Figure 8. Variation in combined speed (m/s) of 10 adult male African savannah elephants across different temperature ranges (14°C to 49°C).

The median speed shows a complex pattern across the studied temperature range 562 (14°C to 54°C) in Figure 8. The median speed declines from 14°C to 17°C with 563 speeds form 0.10m/s at 14°C down to 0.03m/s at 17°C, the speed then stabilises 564 and gradually increases until 35°C with 0.09m/s, this is followed by a decrease until 565 46°C with 0.05m/s, the speed then spikes at 47°C (0.06m/s) and decreases 566 dramatically at 48°C and 49°C (0.03m/s for both temperatures). The interguartile 567 range generally exhibited fluctuations within a relatively confined range from 0.08 to 568 0.23 across the majority of temperatures. Notable exceptions include a considerable 569 increase in range at 14°C and 15°C with ranges of 0.12 and 0.25, respectively and 570 then another increase between 46°C and 47°C with a range of 0.19 and 0.23, 571 respectively, and followed by a sudden decrease at 48°C to 49°C (0.14 and 0.11, 572 respectively). The Spearman's rank correlation test indicated a statistically 573 significant, but weak, positive correlation between speed and temperature (rho = 574 0.0439, p-value < 0). 575

576 **5 Discussion**

This study provides insights into the intricate relationship among spatial use, habitat 577 selection and movement dynamics in adult male African Savannah elephants. The 578 analysis of KDE demonstrates a significant variation in the size of core home ranges 579 and broader habitat utilisation across individual elephants. This highlights the 580 necessity for adaptable conservation strategies that take into account the unique 581 characteristics of each elephant's mobility patterns. The difference seen between the 582 composition of available land and the actual use of habitats, underscores the 583 discerning behaviour of elephants with regards to their selection of habitat types. 584 This choice is consistent with specific habitat types, particularly Shrub/Scrub in 585 Protected Areas and Roads, while avoiding others such as Crops and Bare Ground. 586 As a result, this has significant implications for land management and the reduction 587 of human-elephant conflict. Moreover, our research outcomes validate slight yet 588

statistically noteworthy differences in the speeds of elephants both within and 589 outside designated prtotected areas. These distinctions perhaps indicate adaptive 590 behavioural changes in reaction to human presence and the level of environmental 591 protection. Diurnal and seasonal variations in movement speed are also evident. 592 indicating that elephants are not solely responding to human-altered environments, 593 but are also adjusting their behaviours in a multifaceted manner in response to 594 natural environmental factors, such as temperature and diurnal cycles. Therefore, 595 the findings support the need for a comprehensive understanding of elephant 596 ecology, which is crucial for the development of more efficient conservation 597 approaches. 598

The spatial use and home ranges of African savannah elephants have long been 599 subjects of interest, especially with the increased application of KDE to wildlife 600 studies. KDE provides a nuanced lens through which animal movement and habitat 601 utilisation can be assessed, particularly in relation to available resources. The use of 602 KDE in this study demonstrates the considerable variation in spatial use patterns 603 among 10 individual adult male African Savannah elephants (refer to Appendix 2. for 604 the individual visualisations). The huge home range of IR SAT 6208, especially when 605 contrasted against the comparatively small range of IR SAT 6209, may suggest 606 changes in resource distribution, according to our analysis of these KDE values. 607 Disparities in spatial utilisation can be attributed to changes in water availability, 608 specifically during the dry season as opposed to the rainy season (Bastille-Rousseau 609 et al., 2020). The observed patterns of movement are consistent with the existing 610 knowledge that animals, including elephants, tend to travel greater distances to 611 locate water sources during seasons of low rainfall (Bastille-Rousseau et al., 2020). 612 Furthermore, it is evident that elephants' actual habitat use at both confidence 613 intervals differs significantly from the available land composition within the study 614 area, highlighting the selective nature of their spatial behaviour. The divergence 615 seen could potentially be attributed to the regional and temporal variability of 616 resources, as well (Ngene et al., 2010). For example, it was observed that 617 shrub/scrub habitats within protected areas (PA) and roads within PAs were the most 618 favoured environments. Conversely, crops within PAs, crops, and bare ground were 619 found to be mostly unpreferred by the subject of study. These decisions could be 620 influenced by factors such as the availability of food, the presence of potential 621 threats and ease of movement (Ngene et al., 2010). However, as the data was 622 collected during the same time this difference of some individuals greater range 623 could also be explained by the fact the individuals with the smaller ranges were 624 mostly in protected areas thus limited by the constraint of the protected area (De 625 Boer et al., 2000). The KDE analysis showed significant differences in the spatial 626 behaviour of individual male elephants. For instance, IR SAT 6208 exhibited a 627 notably larger home range compared to others. This extensive range may imply that 628 IR SAT 6208 travelled great distances, possibly in search of another protected area, 629 eventually reaching Hwange National Park in Zimbabwe. Additionally, the elephant's 630 larger and more diverse habitat use could make it more likely to engage in crop-631 raiding activities. 632

The relationship between crop-raiding by elephants and the role of protected areas in elephant conservation presents a complex relation influenced by various human and environmental factors. The movement patterns of adult male African savannah elephants further reveal intriguing insights into their adaptive behaviours in response to human activities and environmental conditions (Graham et al., 2009). For

instance, in this study there is a significant difference in the elephants' speed of 638 movement within and outside of protected areas, suggesting that elephants adjust 639 their behaviour depending on the level of human activity and environmental security 640 they encounter. The individual calculations (appendix 5) show that certain individuals 641 have a more significant difference, this may be due to these individuals spending a 642 greater amount of time in unprotected areas. The significance of protected areas in 643 the conservation of elephants should not be ignored. Elephants find a degree of 644 security in these regions, while a significant portion of their habitat is situated beyond 645 the boundaries of these protected areas (Wall et al., 2021). These results support 646 past studies that show male elephants can recognise different levels of threat and 647 adjust their behaviour in accordance with those perceptions (Wittemyer et al., 2008). 648 The understanding of this concept holds significant importance in the development of 649 effective conservation strategies and the reduction of human-elephant conflict. Such 650 conflicts frequently arise when male elephants wander beyond designated protected 651 zones in pursuit of mates and resources (Gara et al., 2021). The issue of crop-652 raiding by elephants is a significant source of conflict between human populations 653 and wildlife. In response, a range of efforts have been implemented to deter this 654 behaviour. A few examples of deterrents are chilli pepper as an olfactory deterrent 655 (Noga et al., 2015) and beehive fences, which have demonstrated diverse levels of 656 effectiveness (King et al., 2011; Noga et al., 2015). Further research has indicated 657 that the occurrence of crop raiding by male elephants is impacted by their social 658 networks and life history milestones (Chiyo et al., 2012). 659

One possible hypothesis that has been proposed how elephants are mitigating the 660 effects of habitat fragmentation is to utilise human-constructed roads as a means of 661 facilitating more efficient migration between fragmented areas. The theory is 662 supported by the compositional analysis. It appears that their preference lies towards 663 Shrub/Scrub vegetation in protected areas (PAs), as well as roads within PAs and 664 roads in general (as seen in Table 2). This observation is consistent with recent 665 academic findings indicating that elephants, particularly those inhabiting 666 densely forested areas, have a preference for utilising man-made and unpaved 667 roads for movement, predominantly during nighttime hours (Scalbert et al., 2023). 668 One plausible rationale for this choice may be attributed to the fact that roads 669 provide easier and more energy-efficient travel pathways, particularly when moving 670 large distances within their vast home ranges. Contrarily to what was expected, the 671 elephants did not prefer tree habitat, although trees are the most abundant habitats 672 available. Nevertheless, the lack of a preference for trees could suggest an 673 alternative adaptive approach adopted by elephants in this area, potentially to the 674 comparatively low poaching rates and therefore lower necessity to seek canopy 675 shelter (Graham et al., 2009). Although the overall patterns provide a comprehensive 676 understanding of habitat selection and spatial utilisation, it is imperative to 677 acknowledge the presence of individual variations among the elephants (see 678 Appendix 3 and 4). As an example, it is observed that elephant 6216 exhibits a 679 pronounced inclination towards tree environments, which deviates from the 680 prevailing pattern in this study. However, when looking at the individual habitat use 681 most elephants do have a preference to trees habitats outside of protected areas, 682 which may suggest that the elephants do use trees as cover in areas which they may 683 feel threatened (see Appendix 3). The observed variance in habitat and road usage 684 choices may potentially be attributed to factors such as age, social standing or past 685 686 experiences.

The African savannah elephant is one of many animals whose conservation efforts 687 are greatly aided by the existence of corridors. According to Jachowski et al. (2013), 688 the presence of these narrow strips of land have an important function in allowing the 689 movement of animals between habitats that are fragmented. As there is a distinct 690 selection of habitats, it is implied that not all available areas are suitable for 691 elephants, highlighting the need for carefully built corridors that connect these 692 favoured habitats. The behaviour of elephants is significantly influenced by human 693 activities and the consequent disturbances in corridors. The findings of Douglas-694 Hamilton et al. (2005) and Jones et al. (2012) indicate that these disruptions have 695 resulted in a reduction in the utilisation of corridors and an increase in the 696 occurrence of "streaking" behaviour. The term "streaking" describes an elephant's 697 inclination to pass through an area quickly and unabated, possibly as an adaptive 698 reaction to increased human activity or unfavourable environmental conditions. It is 699 interesting to note that an elephant's tendency to use corridors or engage in 700 streaking behaviour is correlated with its physiological state (Jachowski et al., 701 2013). The necessity of corridors is further supported by the elephants' speed of 702 703 movement, which is dependent upon the conservation condition of the region and many environmental elements. For example, the observed differences in speed 704 between regions with protective measures in place and those without, as well as 705 fluctuations during different time periods, suggest that elephants exhibit adaptive 706 behaviour in response to human presence and environmental factors. The presence 707 of these subtle behaviours suggests that the design of corridors should include not 708 only the spatial aspects, but also the time patterns of elephant movement. 709

This paper's findings illustrate subtle fluctuations in the speeds of adult male African 710 savannah elephants, particularly within the context of the rainy and dry seasons. The 711 data suggests that there is a tendency for speeds to be higher in the month of 712 January, which could be linked to an increased level of activity to move (see for 713 individual differences refer to Appendix 5,6 and 8). The variations in speed may be 714 associated with the availability of resources such as temporary waterholes and fresh 715 vegetation, which are more abundant during periods of rainfall, therefore increasing 716 movement (Ngene et al., 2010). During periods of low precipitation, elephants have 717 been observed to decrease their range and stay closer to permanent water sources 718 (Ngene et al., 2010). This discovery provides additional support for the statement 719 made by Douglas-Hamilton et al. (2005) on the significance of Makgadikgadi Pans in 720 Botswana as a crucial ecosystem for these elephants, specifically in terms of nutrient 721 accessibility during the dry season. In Individuals where this trend was not observed, 722 could have been observed to expand their range and travel at higher velocities in 723 order to locate essential resources, during the dry season (Osborn, 2004); or stayed 724 within a smaller area during the rainy season due to the availability of and 725 abundance of resources. Individuals with a larger range could be evidence to 726 suggest that some elephants may be more vulnerable to climatic fluctuations due to 727 their more extensive and varied areas of movement (see Appendix 2). Elephants 728 also exhibit strong and consistent preferences for certain land cover types, avoiding 729 areas like "Crops" and "Bare Ground," which might particularly have occurred during 730 resource-scarce dry periods. 731

The influence of temperature on the movement speed of adult male African
savannah elephants was examined, revealing a nuanced pattern of speed variations
across a temperature range of 14°C to 49°C (Appendix 9.). It is important to
acknowledge that the reported association between speed and temperature may be

influenced by other underlying causes. Elephants may exhibit decreased speed at 736 high temperatures because of energy conservation or to minimise the potential risks 737 of overheating. This observation is supported by the data presented Appendix 7, 738 where a decrease in elephant movement during the peak noon hours, when 739 temperatures reach their highest, is seen. Likewise, the observed decrease in speed 740 at lower temperatures may suggest sleep during lower temperatures, specifically 741 around the second hour (Figure 6, Appendix 7). Therefore, the complex pattern 742 implies that despite a slight correlation, temperature is one of many variables 743 exerting influence on the speed of these elephants. These results correlate with prior 744 studies that have demonstrated the multifaceted nature of elephant movement, 745 which is influenced by a combination of environmental and anthropogenic influences 746 (Owen-Smith et al., 2020; Roever et al., 2012; Bastille-Rousseau et al., 2020). 747

Musth in male African savannah elephants, which is defined by heightened sexual 748 activity and increased aggression, was observed Elephant 6214. The elephant was 749 captured on a camp trap deployed by Elephants for Africa, with obvious signs of 750 musth (wet back legs and heavy discharge from his temporal glands). Using the 751 satellite data, it be could seen that he then left the MPNP and ended up north of his 752 location. The collar data showed a clear increase in speed (see Appendix 8), 753 together with a noticeable change in patterns of range and spatial use changes in 754 locomotion and speed, and thus it can be concluded that Elephant 6214 was in 755 musth from the beginning of January 2023 until approximately mid-March 2023. His 756 homerange at the 95% confidence interval illustrated two distinct and large areas, 757 indicating that the elephant exhibited more movement while in musth (see Appendix 758 2). The behaviour of "streaking" observed during musth likely represents a search for 759 mates, a theory that is further supported by the elephant's travel towards the north. 760 This direction is less frequently chosen by other males in the study, who 761 predominantly moved towards the east, northeast, or slightly northwest. 762

The distinctive directional preference seen in Elephant 6214 suggests that it was
actively seeking female, as there are few females in the MPNP (Evans, 2019).
Furthermore, this particular individual had much greater speeds in areas without
protection (see Appendix 5) and maintained an average speed that was noticeably
higher compared to the other collared elephants (see Appendices 6-9).

While the study offers comprehensive insights into the spatial use, movement 768 dynamics, and habitat selection of adult male African Savannah elephants, several 769 limitations should be acknowledged in the discussion. Firstly, the study relies heavily 770 on KDE for analysis, which, although nuanced, may not fully capture all factors 771 influencing elephant movement. Another limitation within the KDE analysis may be 772 the ad hoc smoothing parameter, href. The smoothing value for href is determined 773 based on the distribution of points. However, it has been shown that this parameter 774 may over smooth multimodal distributions that arise from clustered sites, leading to 775 an overestimation of home range sizes (Gimenez et al., 2005). The study's sample 776 size is also guite small so the findings must be interpreted with care as this may not 777 be a good representative for the entire population within the MPNP. Additionally, 778 individual variations among elephants, such as Elephant 6214 showing unique 779 behaviours during musth, suggest that the results may not be universally applicable 780 across all individuals. The study took into account seasonal factors like as rainfall 781 and temperature, but other environmental variables may also impact elephant 782 movement. The collected temperatures revealed anomalies, reaching a maximum 783

value of 54°C, (Appendix 9). It was evident after speaking with the manufacturer that
these may be caused by either equipment failure or the elephant itself becoming
very hot. Furthermore, temperatures within MPNP rarely exceed 45°C. The study
suggests that adaptive behavioural changes are influenced by the presence of
humans and protected areas. However, it is important to acknowledge that there
may be more elements that have not been thoroughly investigated, which could also
play a role in determining these behaviours.

791 6 Conclusion

In conclusion, this study provides significant observations on the intricate relationship 792 of spatial use, habitat preference, and movement behaviours in adult male African 793 Savannah elephants. The use of Kernel Density Estimation (KDE) revealed 794 significant differences in the core home ranges, usage of habitats, and speed of 795 elephants. These findings indicate that the movement patterns of individual 796 elephants are distinct and impacted by a multitude of biological, environmental, and 797 anthropogenic factors. The elephants exhibited selective behaviour when choosing 798 their habitats. These findings hold significant implications for the development of 799 800 conservation strategies and land management practises aimed at mitigating humanelephant conflict. 801

802

The investigation also exposed subtle adaptive behaviours in elephants, as indicated by the small but statistically significant variations in their movement speeds both inside and outside designated protected areas, as well as in response to natural environmental conditions. These findings hold significant value in the development of more efficient and sophisticated conservation methods, particularly in relation to the establishment of wildlife corridors and the mitigation of human-elephant conflict.

809

Additionally, the study highlighted the significance of individual variability observed among elephants, emphasising the necessity for adaptable and localised conservation strategies. As an example, the behaviour exhibited by Elephant 6214 during its musth period exhibited higher speeds and larger territories, potentially

driven by the pursuit of potential mates. This illustrates the intricate influence of behavioural states such as musth on spatial dynamics.

816

In conclusion, this study enhances our comprehension of elephant ecology and 817 shows the importance of adaptable conservation policies grounded in evidence. 818 These strategies should consider the intricate relationships between spatial 819 utilisation, habitat preference, and migratory patterns exhibited by these magnificent 820 creatures. It further stresses the need for a comprehensive and flexible strategy 821 towards elephant conservation, which acknowledges the delicate relationship 822 between elephants and their surrounding ecosystems, the need for wildlife to have 823 access to unprotected lands and thus the continued need for viable human-elephant 824 825 mitigation strategies to enable human-elephant coexistence.

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Appendices

Appendix 1. Collaring data of all 10 adult male African savannah elephants (Loxodonta africana). Elephants for Africa unpublished data.

	1	2	3	4	5	6	7	8	9	10
Date of collaring	22/08/22	22/08/22	22/08/22	22/08/22	22/08/22	22/08/22	22/08/22	23/08/22	23/08/22	23/08/22
Time darted	09:16:00	10:03:00	11:49:00	12:44:00	13:34:00	15:06:00	15:43:00	08:54:00	09:55:00	10:55:00
Collar number	IR SAT 6210	IR SAT 6209	IR SAT 6214	IR SAT 6208	IR SAT 6213	IR SAT 6215	IR SAT 6211	IR SAT 6216	IR SAT 6212	IR SAT 6207
GPS S	-20.45458	-20.46482	-20.46266	-20.47514	-20.48219	-20.346	-20.35393	-20.34684	-20.32219	-20.31218
GPS E	24.59488	24.60646	24.58967	24.567203	24.5669	24.50847	24.49653	24.5713	24.60062	24.61863
Estmated age	36yr+	36yr+	36yr+	36+yr	36+yr	36+yr	36yr+	26-35yr	36 yr+	26-35yr
Sex	М	М	Μ	М	М	М	М	М	М	М

Appendix 2. visualisation of the KDE for each of the 10 individual adult male African savannah elephants at 50% and 95% confidence intervals.







Appendix 3 (a-j). Pie charts showing actual habitat utilised by each individual
 collared adult male African savannah elephant within the study at 50% confidence
 interval, land type is divided into nine habitat types within and without protected
 areas (PA)



Appendix 4 (a-j). Pie charts showing actual habitat utilised by each individual
 collared adult male African savannah elephant within the study at 95% confidence
 interval, land type is divided into nine habitat types within and without protected
 areas (PA)



Appendix 5 (a-j). Movement speeds (m/s) in protected areas (PA) and unprotected areas for 10 different adult individual African savannah elephants (6207 to 6216). Elephants 6208, 6209 and 6210 exhibited higher median speeds in protected areas, while all others moved significantly faster in unprotected areas. The interquartile ranges also showed variations, such as the largest value of 0.32 in unprotected areas for Elephant 6214 and the smallest value of 0.07 in unprotected areas for Elephant 6209.





Appendix 6 (a-j). Speed (m/s) in 10 different adult individual African savannah
 elephants (6207-6212) compared to day and night periods. The median speeds
 consistently showed higher values during the day for the majority of the elephants,
 except for Elephant 6209 where the difference was minimal. Interquartile range
 (IQR), representing the dispersion of speed, also varied among the elephants, often
 showing a broader spread during the day



Appendix 7 (a-j). Analysis of speed (m/s) in 10 different adult individual African
 savannah elephants (6207-6212). The median speeds are typically lowest during the
 early hours of the night and increased in speed during early morning and late
 afternoon.





1092

Appendix 8 (a-j). Speed (m/s) in 10 different adult individual African savannah elephants (6207-6212) compared to different months. The median speeds showed values ranging from 0.02 m/s to 0.17 m/s, with variations between the individuals.
 The interquartile range, displayed a wide difference across datasets.



Appendix 9 (a-j). Temperature-dependent analysis of speed (m/s) variations in 10
 different adult individual African savannah elephants (6207 to 6216). A complex
 relationship between temperature and speed is demonstrated among all 10
 individuals. There are individualised and intricate patterns of variations across
 temperatures, fluctuations and unique trends in median speeds across temperatures,
 with inconsistencies and missing data points at certain temperatures.



(a) Elephant 6207

1104

17C

14C

20C

23C

26C

32C

350

Temperature (°C)

380

41C

44C

47C

50C

29C

53C

