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RESEARCH ARTICLE

Identification of key landscape drivers of range size and range shifts in African savanna elephants in northern Kenya

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Abstract

Context Drivers of animal ranging behavior are diverse and often dynamic in changing landscapes. Understanding correlates of home range sizes and shifts can reveal factors influencing wildlife populations and offer insights into responses to environmental change.

Objectives We investigated drivers of African savanna elephant multi-year, annual, and seasonal range sizes and shifts.

Methods We estimated annual and seasonal range sizes, range shifts, and their correlates using a 20-year tracking dataset (110 elephants) in northern Kenya, allowing diagnosis of drivers of range use and change.

Results Home range sizes varied widely across sampled individuals (average AKDE core area = 839.62 km^2, SD = 1483.09 km^2, and home range = 3567.37 km^2, SD = 6066.05 km^2). Individuals' annual and overall seasonal ranges overlapped strongly, with the greatest shifts between dry and wet seasons. Smaller annual home ranges were associated with higher mean rainfall and water availability, whereas larger ranges were correlated with rainfall variability. Seasonal core areas were smaller with higher productivity (normalized difference vegetation index, NDVI), surface and permanent water, elevation, but larger with increasing terrain ruggedness (TRI), human modification, and NDVI variability. Individuals' annual and seasonal overlap increased with TRI; seasonal shifts were greater with high human modification. Dry-to-wet overlap increased with seasonal water, wet-to-dry overlap increased with rainfall variability but decreased with mean rainfall.

Conclusions Water, terrain, and human impacts were key factors shaping elephant space use. This longitudinal study highlights the influence of human land-use changes on elephant behavior and underscores the need for effective resource management, particularly water management, for elephant conservation.

Keywords Home range · Range overlap · Utilization distribution · Tracking data · African savanna elephants

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Introduction

An animal’s home range (Hansteen et al. 1997; Powell and Mitchell 2012) is the area traversed by animals to look for food and mating opportunities and to meet the needs of offspring (Burt 1943). In other words, it is the fundamental unit of an animal’s space use (Burt 1943; Börger et al. 2008). Home range size and location are dynamic and influenced by various intrinsic and extrinsic factors, with the spatial distribution, quality, and quantity of extrinsic factors driving movement across the landscape (Burt 1943; Powell and Mitchell 2012; Walton et al. 2017). For example, home range size differs in relation to a species’ foraging ecology, body mass/life history, and social structure (Burt 1943; Powell and Mitchell 2012; Ofstad et al. 2016; Walton et al. 2017), as well as in relation to ecological variables such as productivity, water resources, and predator–prey interactions (Laundre et al. 2010; Snider et al. 2021; Dulude-de Broin et al. 2023; Broekman et al. 2024; Lassiter et al. 2024). Fluctuations in environmental variables can cause the expansion or contraction of home ranges (Burt 1943; Goldenberg et al. 2018; Donnell 2020). Understanding drivers of seasonal and annual changes in home range size can provide insight into key factors influencing a population and offer insights into how populations may respond to environmental changes (South 1999; Powell and Mitchell 2012).

Identifying factors that influence home range “philopatry”, or the tendency to stay in the same area, can further reveal fundamental processes affecting ranging behavior (Switzer 1997; Gerber et al. 2019). Inter-annual home range philopatry (or fidelity) is widespread in terrestrial and aquatic species, enabling individuals to exploit seasonal resources and avoid threats, thereby increasing their fitness (Faille et al. 2010; Morrison and Bolger 2012; Tambling et al. 2015; Northrup et al. 2016; Guttridge et al. 2017; Shakeri et al. 2021). For instance, female philopatry to nursery areas in scalloped hammerhead sharks in the Mexican Pacific may increase reproductive success (Rangel-Morales et al. 2022). Additionally, differences in range philopatry between males and females in Svalbard polar bears, where subadult females showed the least fidelity, were thought to be driven by roaming behavior in their sub-adulthood and later natal site fidelity in their adult stages (Lone et al. 2013). Individuals in a population might show differences in philopatry driven by opportunistic search for scarce resources or due to resource tracking based on environmental cues and/or memory (Edwards et al. 2009; Passadore et al. 2018; Purdon et al. 2018; Abrahms et al. 2021; Morrison et al. 2021). However, strong differences in philopatry are rare among individuals within a population if resources are abundant and/or predictable (Knip et al. 2012; Habel et al. 2016). In such cases, identifying the drivers of philopatry, or lack thereof, can provide insights into key spatial aspects that structure different strategies that species use to adapt to changes in their habitats.

These range-use patterns align with the principles of various resource use theories, which provide valuable frameworks for understanding animal interactions with their environment, particularly in large herbivores like elephants that inhabit heterogeneous and seasonally dynamic landscapes (Burton-Roberts et al. 2022). For instance, optimal foraging theory (OFT) and the marginal value theorem (MVT) suggest that animals make movement decisions that maximize energetic gain while minimizing the associated costs, leading to space use patterns that reflect both resource availability and predictability (Charnov 1976; Stephens and Krebs 1986). When resources (water, forage) are stable and plentiful, animals tend to exhibit higher home range philopatry and have smaller, more consistent home ranges (Van Moorter et al. 2013; Benhamou 2014). This resource-use efficiency aligns particularly well with the exploitation efficiency hypothesis, a concept closely related to and often incorporated into OFT, which posits that higher efficiency in resource utilization is associated with reduced spatial use (Dickie et al. 2022). Conversely, in environments where resources are scarce or fluctuate seasonally, individuals may expand their ranges and reduce fidelity, consistent with risk-spreading strategies in which individuals lessen the potential impacts of unpredictable resources by distributing risk across time, space, or resources. An example of this is elk alternating between habitats when exposed to predation or food scarcity (Orians and Wittenberger 1991; Wolf et al. 2009; Hebblewhite and Merrill 2011). Additionally, *the landscape of fear* concept posits that when animals perceive risks, such as human presence or disturbance, they will adjust their resource selection and space use accordingly to avoid those risks (Laundre et al. 2010). These behaviors are further influenced by individual traits (e.g., sex, age), social factors, and landscape complexity, resulting in nuanced, context- and scale-dependent patterns of space use (Goldenberg et al. 2018).

In this study, we explore range dynamics with the African savanna elephant as our model species. Elephants have significant spatial requirements, high water and forage demands, low predation risks, and play a key role as ecosystem engineers (Owen-Smith 1988; Fritz et al. 2002; Scholes and Mennell 2008; Shannon et al. 2011). Moving forward, we also acknowledge that the same ecological drivers we examine here (e.g., productivity/NDVI, water, rainfall, human modification, terrain) may behave differently for mesoherbivores or other species sharing these landscapes with the elephants, given variations in energy budgets, predation risk, inter-guild competition, and behavioral differences (Jarman 1974; du Toit and Owen-Smith 1989; Laundre et al. 2010; Ofstad et al. 2016). Thus, while our focus is elephant-centered, the patterns we investigate are relevant to broader studies of how ecological and anthropogenic drivers shape animal movements across body sizes and trophic levels. Applying the theoretical approaches outlined above to empirical studies of home range dynamics across taxa and ecosystems will enable researchers to infer behavioral strategies and anticipate animal responses to anthropogenic changes, such as habitat fragmentation and climatic shifts.

While free-ranging populations of African savanna elephants generally have been declining across Africa due to ivory poaching and habitat loss from agricultural expansion (Wittemyer et al. 2014; Cerling et al. 2016; Schlossberg et al. 2020; Wall et al. 2021b), recent expansions have been recorded in some ecosystems (Thouless et al. 2016), which can result in expanding conflicts (Hahn et al. 2022). Within this context, it is crucial to identify the drivers of range size and range shifts for practical conservation planning efforts, particularly given the species' extensive spatial requirements. A continental-scale assessment of elephant range use across Africa found that the sizes of annual home ranges were overall decreasing with the increase in human footprint index (HFI) and protected area intersection (PAI), but shorter-term (16-day) ranges were structured by available resources, increasing with increases in vegetation (NDVI) and permanent water availability (Wall et al. 2021b). Similarly, another study across 13 African study sites found that elephant displacement decreased with increased rainfall; in Uganda, elephant home range sizes were negatively correlated with precipitation and with net primary productivity (Young and Van Aarde 2010; Grogan et al. 2020). More variation in human modification was also associated with increased elephant home range sizes in Namibia (Benitez et al. 2022). Seasonality drove shifts in home range sizes in Mozambique, with increased space use in the early dry season relative to late dry season in Mozambique, while in Uganda, wet season home ranges were larger than dry season ranges, locally influenced by water, where elephants moved further from water in the wet season (Grogan et al. 2020; Macandza and Mamugy 2022). In northern Kenya, dry-season home ranges tended to be smaller and closer to permanent water sources compared to wet-season ranges, and home ranges were strongly influenced by social dominance factors, with higher-ranking groups residing within preferred areas like protected reserves near permanent water sources (Wittemyer et al. 2007). While multiple studies on elephant home range dynamics have explored the drivers of home range size (Grainger et al. 2005; de Beer and van Aarde 2008; Shadrack et al. 2017; Wall et al. 2021b), few have used extensive longitudinal datasets to investigate how home ranges change in size over multiple decades and the ecological correlates of those long-term changes (Wall et al. 2021b).

In addition to changes in African elephant range sizes, it is essential to understand the drivers of shifts in the location of elephant home ranges. A study in South Africa documented high vegetation quality and increased rainfall as key drivers of elephant range consistency (Burton-Roberts et al. 2022). Rainfall and water were also identified as important factors influencing inter-seasonal range shifts in northern Kenya, with northward movements associated with increased rainfall, and southward shifts driven by a reduction in temporary water (Thouless 1995), whereas another study highlighted the importance of productivity and poaching risk to inter-annual changes in ranging behavior, with shifts toward areas of greater productivity and away from areas where poaching had occurred (Goldenberg et al. 2018). Multiscale, long-term shifts in home range locations have rarely been investigated (but see Goldenberg et al. 2018) additionally, few studies have looked at similarities in utilization distributions across different time scales in African elephants (but see Burton-Roberts et al. 2022). A comprehensive investigation to elucidate the drivers of individuals' home range shifts can enhance our understanding of elephant-ranging behavior at a time when human land use expansion and climatic change demand an urgent understanding of this behavior.

This study aimed to investigate the landscape factors influencing the home range dynamics of African elephants in northern Kenya. Specifically, our objectives were to determine: (1) annual and seasonal home range sizes and the variability in range size across individuals, seasons and years; (2) landscape characteristics influencing the variations in annual and seasonal home range sizes; (3) annual and seasonal fidelity (consistency) of space use within individuals; and (4) key environmental variables driving range fidelity (or shifts). We assessed differences between males and females for each of these objectives. Based on foraging theory, we predicted that annual rainfall, primary productivity, and water availability would have a negative correlation with range size (smaller ranges in areas with more resources) and positive correlation with philopatry (stable ranges over time and with more resources). In contrast, we predicted that increased human presence would correspond with increased home range size and reduced philopatry (Goldenberg et al. 2018; Burton-Roberts et al. 2022), in relation to the lower predictability of range access and quality in the face of human activities. We also anticipated larger home range sizes and reduced fidelity among males, given their broader ranging behavior related to mate searching (Wall et al. 2021a). Based on previous work on elephants, we predicted that the wet season home range would be larger and overlap more than dry season ranges (Orrick 2018; Grogan et al. 2020; Kuria et al. 2024). Finally, we predicted that elephants would avoid higher elevation, steep slopes, and rugged terrain, especially in the wet season when resources are plentiful and there is no need to explore these energetically expensive areas (Wall et al. 2006; Berti et al. 2025). We discuss the implications of our results in the context of the changing landscapes impacting elephant populations across Africa.

Materials and methods

Study area

The Laikipia-Samburu ecosystem (0.4°S to 2.0°N, 36.2°E to 38.3°E, Fig. 1) is home to the second-largest wild elephant population in Kenya (Ministry of Tourism and Wildlife 2017). The 33,800 km^2 area has diverse land use and land-cover types comprised of government-protected areas like national parks, reserves, and national forests; private ranches; community conservancies; pastoralist community rangelands; and agricultural settlements (Ihwagi et al. 2015; Goldenberg et al. 2018). The region is characterized by agro-pastoralist land use, but areas of extensive agriculture also exist, particularly in the more mesic uplands. The region varies in elevation between 355 m and 2,277 m. The Samburu section of the study area (Fig. 1a) is prone to drought and is primarily characterized by semi-arid grassland and shrubland, with *Vachellia tortilis* and *Commiphora* shrubs as the dominant vegetation (Ihwagi et al. 2010; Kahindi et al. 2010). Rainfall also varies across this system, averaging 400–600 mm per year in the highlands and 200–400 mm in the arid lowlands (Kimuyu et al. 2017). Rainfall occurs primarily in two distinct seasons: the long rains from April to May and the short rains from November to December (Wittemyer et al. 2007; Ouko et al. 2020). Given the general arid nature of the ecosystem, water distribution is a key factor influencing land use and wildlife space utilization. The key water source in the ecosystem is the semi-permanent Ewaso-Nyiro River.

Elephant movement data

We analyzed GPS tracking data collected from 2001 to 2021 from 110 tracked elephants (Fig. 1). The data were collected from both male (n = 48) and female (n = 62) elephants; data from a single female elephant represented the movements of a family herd numbering approximately 6–24 individuals, while males represented socially independent individuals. The unique individual identification/name (ID), age, and sex of each tracked elephant were recorded on immobilization forms when the elephants were fitted with collars. All immobilizations were conducted per the Kenya Wildlife Service immobilization and translocation protocol (Kenya Wildlife Service 2019).

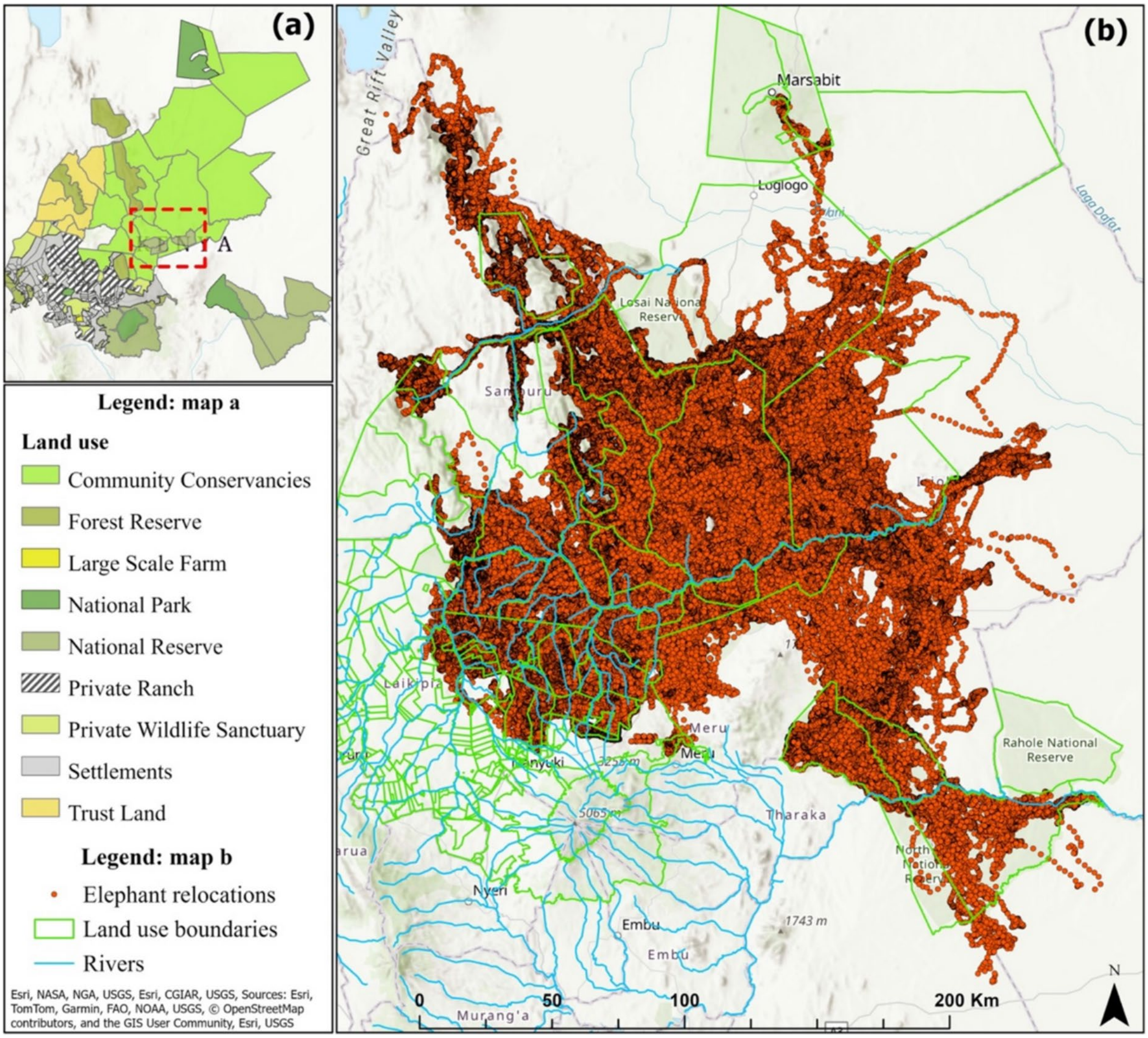

Fig. 1 Map of the study area **a** the Samburu section (dotted red rectangle) within the study area. **b** GPS relocations collected from 2001 to 2021 (from ~ 110 tagged individuals) overlayed with land use boundaries and major water courses (perennial and permanent rivers)

To clean the data, we first filtered out erroneous fixes by applying a latitude and longitude filter corresponding to the extent of the study area; secondly, we used a 7 km/h speed filter to remove biologically unrealistic speeds, i.e., fixes that fell above this threshold (see Wall et al. 2013). We then removed fixes that were collected before deployment and after the collar's termination using the deployment and removal or fall-off dates (when a collar fails mechanically or breaks due to wear and tear). The final dataset for analysis consisted of 3,850,840 locations from the 110 individuals.

Before home range analysis, we created annual and seasonal subsets of the data. Annual datasets were bound between 1st October and 30th September, which generally corresponds to the end of the long dry season and the beginning of the long wet season; this separation has been used to demarcate annual data in several studies within the same elephant population (Wittemyer et al. 2013, 2021; Parker et al. 2021). Annual datasets that did not have at least 80% of the expected fixes for the 365 days from October 1st to September 30th were excluded from annual home range estimates. In the final dataset, we excluded 174 elephant-years out of 426 due to these criteria. Most collars in the final dataset recorded locations at 1-h intervals (180 annual datasets), with a minority collecting at 30-min (38 annual datasets) and 2-h intervals (34 annual datasets) in some years.

To define seasons for the seasonal datasets, we clustered Normalized Difference Vegetation Index (NDVI) values extracted for the annually defined ecosystem-wide minimum convex polygon (MCP) home range (Mohr 1947) as calculated using the adehabiatHR package (Calenge 2006). The 16-day NDVI values extracted from Google Earth Engine (GEE) were grouped into 2 clusters using the R package mclust (Scrucca et al. 2023), which were then used to assign the raw data to either wet or dry seasons depending on a cutoff value of the 2 clusters, data below this cutoff was classified as dry and vice versa for the wet season (Bastille-Rousseau et al. 2020; Wall et al. 2024). Further, post-hoc exclusion of seasonal datasets was performed by assessing individuals whose seasonal semi-variance did not asymptote (see sect. “Home range size and shift estimation” below) (Fleming et al. 2014) and/or had less than 1.5 months of data per season.

Home range size and shift estimation

Using the ctmm package (Calabrese et al. 2016) in R, we calculated the semi-variance function (SVF) to assess the autocorrelation of the movement data for each individual (Fleming et al. 2014; Péron et al. 2016). Asymptotic properties in the variograms were used to denote if an individual’s movements in a given study period (i.e., annual or seasonal) demonstrated range residency (Supplementary File 1: Fig. S1). Individuals whose semi-variance reached an asymptote were considered range residents and were included in the final analysis, and data from individuals who did not reach an asymptote were excluded.

We fit home range estimation models to annual and seasonal movement data that demonstrated range residency via perturbative Hybrid restricted maximum likelihood (pHREML). This estimator was chosen over maximum likelihood (ML) and restricted maximum likelihood (REML) due to its low computational cost and because it performs as well or better than these other estimators (Fleming et al. 2019). The models were ranked using Akaike’s Information Criterion adjusted for small sample sizes (AICc), and the top model was used to estimate 95% and 50% home ranges through the fitting of autocorrelated kernel density estimators (AKDE) (Akaike 1973; Anderson et al. 1994; Fleming et al. 2015). This method of home range estimation was used because it accounts for autocorrelation in the data and is robust to changes in sampling schedules (Calabrese et al. 2016). Due to the exclusion of annual and seasonal datasets that did not meet the residency criteria, we also estimated MCP home ranges using the full dataset, regardless of range residency, for size comparisons (Calenge 2006).

Two criteria for a good overlap estimator are that it should not depend on ad-hoc rules, such as 50% or 95% isopleths, thereby providing the actual home range overlap, and it should be robust to small sample sizes (Winner et al. 2018; Tilberg and Dixon 2022). This is satisfied by the utilization distribution overlap index (UDOI). We quantified intra-individual (site fidelity) home range overlap using UDOI, where pairwise values closer to 1 indicate high overlap (site fidelity) and values closer to 0 represent low overlap (home range shift) (Tilberg and Dixon 2022). We also estimated the non-distributional geometric home range shift metrics of GPS centroid shifts to investigate whether our findings using UDOI were consistent and to provide options for similar studies (see Supplementary File 2: Sects. 1.3 and 1.4). For each individual, we calculated consecutive annual (e.g., 2020–2021 and 2021–2022) and seasonal (e.g., 2020–2021_dry and 2020–2021_wet, or 2020–2021_wet and 2020–2021_wet) UDOI overlaps and shifts. Seasonal shifts were assessed for all possible consecutive season combinations, i.e., wet-wet, dry-dry, dry–wet, and wet-dry.

Environmental data

For each home range polygon (annual and seasonal), we extracted and processed three landscape covariates from Google Earth Engine (GEE) using the R package rgee (Aybar et al. 2020). GEE extracted covariates included 250 m-resolution NDVI from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite (Justice et al.

1998), daily precipitation from the Climate Hazards Group InfraRed Precipitation (CHIPRS) with 0.05° and 0.25° spatial resolutions (Funk et al. 2015) which captured seasonal and nonseasonal rainfall, and surface water availability indices from the Joint Research Centre (JRC) global surface water 30 m-resolution maps (Pekel et al. 2016). We used the long-term water history (1984–2021) assets from JRC, which capture the temporal distribution of water documented per pixel, per year, and month. The annual dataset has bands for both permanent and seasonal water, while the monthly history provides data on whether water was detected or not (Pekel et al. 2016). From these datasets, we extracted the total number of pixels of each water type for each polygon. Additionally, we used a static surface water layer from spatial data manually collected in the field by Save the Elephants (STE) that included damns, boreholes and other human water sources.

Two variables reflecting human activity were used in this analysis: the static Human Modification Index (gHM), and the temporally dynamic global record of annual terrestrial Human Footprint (HF). gHM is a cumulative measure of terrestrial land modification from global datasets (Kennedy et al. 2019), while HF provides annual datasets of buildings, population density, lights, crops, pasture, and transportation structures (Mu et al. 2022). Given that the majority of the study area consists of rural rangelands, we assumed these layers represent different human impacts on the landscape. Finally, we extracted elevation values from digital elevation models produced by the National Aeronautics and Space Administration (NASA) Shuttle Radar Topography Mission Global (Farr et al. 2003). From the elevation, we also calculated slope and terrain ruggedness index (TRI) as additional topographical covariates.

We evaluated all covariates extracted for each polygon for correlation using a variance inflation factor (VIF) analysis. Additionally, we examined bivariate relationships between the explanatory variables and the response variable. Variables that had the least significant bivariate relationships with the response variable and high variance inflation factor (VIF) were excluded from further analysis (Supplementary File 1: Table S1). This resulted in models at each scale having different covariates assessed.

Statistical analyses

Home range size

To understand the landscape and individual properties related to variation in home range size at both annual and seasonal scales, we employed Bayesian linear regression models with home range size as the response variable. We accounted for repeated measures of individuals and years by assigning individual (ID) and year (annual ID) as random effects, while environmental variables were assigned as fixed effects. Ecological covariates were summarized within each 95% AKDE and 50% AKDE annual and seasonal home range polygon and included the following (see sect. "Home range size and shift estimation" for more details on derivation): NDVI mean, NDVI standard deviation, rainfall mean, rainfall standard deviation, slope, TRI, elevation, annual human footprint, global Human Modification Index (gHM), surface water density, monthly water detection, permanent and seasonal water density. Water density per polygon was calculated by dividing the totals of JRC pixel counts of water detection and the total length of streams (from the Save the Elephants (STE) spatial database) by the area (km^2) of each AKDE polygon. For seasonal analyses, we also included a fixed categorical variable of season (dry = 0, wet = 1) and a fixed variable to control for sampling effort (GPS months per season, i.e., total fixes per season divided by 30 days/month worth of fixes depending on reporting interval). The sex (male = 0; female = 1) of each elephant was included as a fixed effect, but we did not include elephant age in our models because the age of collared females did not represent the age of the oldest female in a family group; we target younger females for collaring so as not to risk the life of the oldest females who generally lead their group (McComb et al. 2001; Moss 2001; Wittemyer et al. 2005).

The home range size was log-transformed to fit assumptions of normality. All continuous covariates were standardized by subtracting the mean and dividing by the standard deviation $\left(\frac{x-\bar{x}}{\sigma}\right)$. We implemented our analysis with the rjags package version 4.13, using a Markov-Chain Monte Carlo (MCMC) algorithm with 100,000 iterations, discarding the first 20% of iterations as burn-in (Plummer 2023). We assessed model convergence by visually inspecting trace plots generated using the MCMCvis package (Youngflesh 2018) and by ensuring Rhat values were below 1.02, indicating the chains were well-mixed (Gelman and Rubin 1992). To evaluate model fit, we calculated Bayesian p-values, i.e., the proportion of simulated data sets according to the model that are more extreme than the actual data. All p-values were close to the ideal value of 0.50, and overlayed graphs of simulated versus actual data indicated good model fits (see Supplementary File 1: Sect. 1.2).

Home range shifts

Because UDOI home range overlap values were bound between 0 and 1, we fit a beta regression to the response variable using the package brms version 2.20.4 (Bürkner 2017), we decided to use brms instead of rjags to reduce the computational time. Covariates in models of UDOI overlap were calculated as the differences in environmental variables (see description in sect. "Materials and methods") assessed over each contrast, i.e., former values subtracted from later values, with positive values indicating higher values in the later utilization distributions (UD). In seasonal models, we included a categorical fixed effect that identified four contrasts: wet-wet, dry-dry, wet-dry, and dry–wet, where these contrasts were always temporally sequential. We used models with interacting annual-seasonal dyads (e.g., 2011–2012_wet vs. 2011–2012_dry, 2012–2013_wet vs. 2012–2013_dry, etc.) as random effects to account for repeated measures within each unique seasonal combination. We also included individual identity (ID) as a random effect for all models.

We then ran MCMC sampling with 20,000 iterations, discarding the first 50% of iterations as burn-in. We assessed model convergence as described above (see section). Finally, we assessed model fit using posterior predictive checks, which indicated an exceptional model fit (see Supplementary File 1: Sect. 1.4). For all relationships between the response and predictor variables, we assessed support for directional effects using the posterior probability of direction, calculated as the proportion of posterior samples that are greater than or less than zero. For parameters with strong support, i.e., none of the credible intervals overlap 0, and posterior probability (*P* from here on) = 0.95, we report the posterior probabilities in the supplementary materials (Supplementary File 2: Tables S2–S7).

Most data cleaning and all mapping were performed in ArcGIS Pro 3.2 (ESRI 2023); additional data cleaning and all other analyses were conducted using R version 4.2.1 (R Core Team 2022).

Results

Overall home range size and sex differences

We had 88 individuals, with over 80% of the expected number of fix/relocations, in at least one year. After visual inspections of variograms, 72 of the 88 possible individuals demonstrated range residency at the annual scale (47 females, 25 males). Overall, the mean annual 50% and 95% AKDE home range estimates for these 72 individuals were 839.62 km^2 (SD = 1,483.09 km^2) and 3,567.37 km^2 (SD = 6,066.05 km^2), respectively. Males had slightly larger annual 50% and 95% AKDE home ranges than females, but both credible intervals (CIs) of this difference overlapped 0, as shown by the posterior probabilities in sect. "Predictors for home range size variations" (Fig. 2b). Mean male 50% AKDE range size was 850.76 km^2 (SD = 1653.07 km^2), mean female 50% AKDE was 834.4 km^2 (SD = 1401.86 km^2); mean male 95% AKDE home range was 3687.62 km^2 (SD = 6849.63 km^2), mean female 95% AKDE was 3510.25 km^2 (SD = 5678.41 km^2). Using the same set of individuals (72), annual MCP estimates were smaller than AKDE estimates; the mean 50% MCP was 691.46 km^2 (SD = 1112.86), and the 95% MCP was 1888.92 km^2 (SD = 2118.057). However, we also estimated MCP home ranges for all annual datasets, including datasets that did not satisfy the range residency criteria (Supplementary File 2: Table S1).

At the seasonal scale, 108 individuals had over 1.5 months of data for at least one season, and 99 demonstrated range residency over at least one season (58 females, 41 males). Their average 50% and 95% AKDE home range sizes were 1,178.98 km^2 (SD = 2,910.20 km^2) and 4,933.53 km^2 (SD = 12,172.81 km^2), respectively. Notably, AKDE seasonal ranges were larger than annual ranges, which is an effect of the differences in individuals included in the analyses, 99 individuals compared to 72 that had clear asymptotes. Including all 99 individuals,

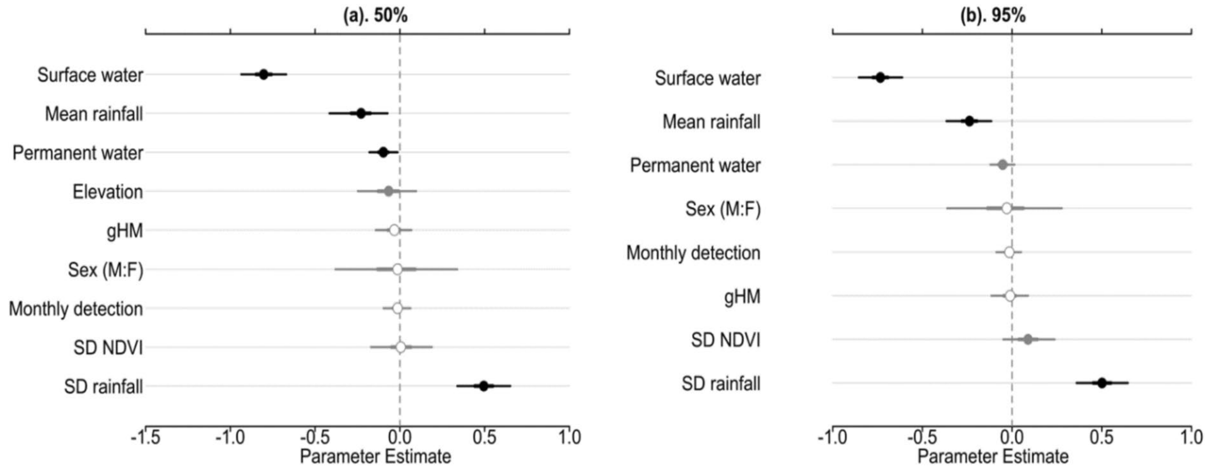

Fig. 2 Ordered results in order of positive to negative correlations from annual home range size models for **a** 50% isopleth range, **b** 95% isopleth range. Grey bars indicate parameter estimates for which the 95% (open circles) and 50% (closed circles) credible intervals (CI) overlap zero

female overall seasonal ranges were generally bigger than those of males: 50% home range averaged 1387.60 km^2 (SD = 3397.66 km^2) for females compared to 745.03 km^2 (SD = 1350.11 km^2) for males, and 95% home range sizes averaged 5787.63 km^2 (SD = 14,262.09 km^2) for females compared to 3161.88 km^2 (SD = 5426.52 km^2) for males. We also provide size estimates using the same 72 individuals for which annual range sizes were analyzed, along with overall seasonal results for comparison in the supplementary materials (Supplementary File 2: Sects. 1.1 and 1.2). Seasonal MCP estimates (99 individuals) were also smaller than AKDE estimates, with mean 50% and 95% MCP estimates of 429.72 km^2 (SD = 794.55) and 1202.63 km^2 (SD = 1611.73), respectively. Similar to annual estimates, we also estimated seasonal MCP home ranges for datasets that did not satisfy the range residency criteria (Supplementary File 2: Table S1).

Predictors for home range size variations

Annually, the landscape features that were correlated with home range size were generally consistent across both isopleths. Both the 50% AKDE and 95% AKDE home range size decreased with increased surface water density, permanent water density, and mean rainfall (Fig. 2). Rainfall variation had a strong and positive correlation with both 50% AKDE and 95% AKDE home ranges, i.e., more variable rainfall was associated with larger annual home ranges (Fig. 2). There was no clear evidence for positive or negative effects of standard deviation of NDVI (P = 0.53), monthly water detection (P = −0.51) or sex (P = −0.53) on 50% AKDE home range sizes, however there was moderate evidence of negative correlations with elevation (P = −0.78) and global human modification index (P = −0.74). 95% of AKDE home range sizes showed moderate-to-weak negative correlations with global human modification index (P = −0.69) and sex (P = −0.60), indicating that males had larger home range sizes than females. Additionally, the standard deviation of NDVI showed a moderate-to-strong positive correlation with 95% AKDE home range size (P = 0.90) (Fig. 2b).

The tested landscape variables had a greater influence on seasonal range sizes than on annual range sizes. As with annual ranges, greater density of permanent water and higher average NDVI values were correlated with smaller wet and dry season 50% AKDE ranges, but the relationship with permanent water was moderate in the dry season ($P = -0.77$) (Fig. 3a and b). This relationship was opposite for the wet and dry season 95% range isopleths, which were larger with greater permanent water density. All 50% and 95% seasonal home ranges were smaller with greater surface water density (see discussion below on differences in these two metrics). Dry season 50%

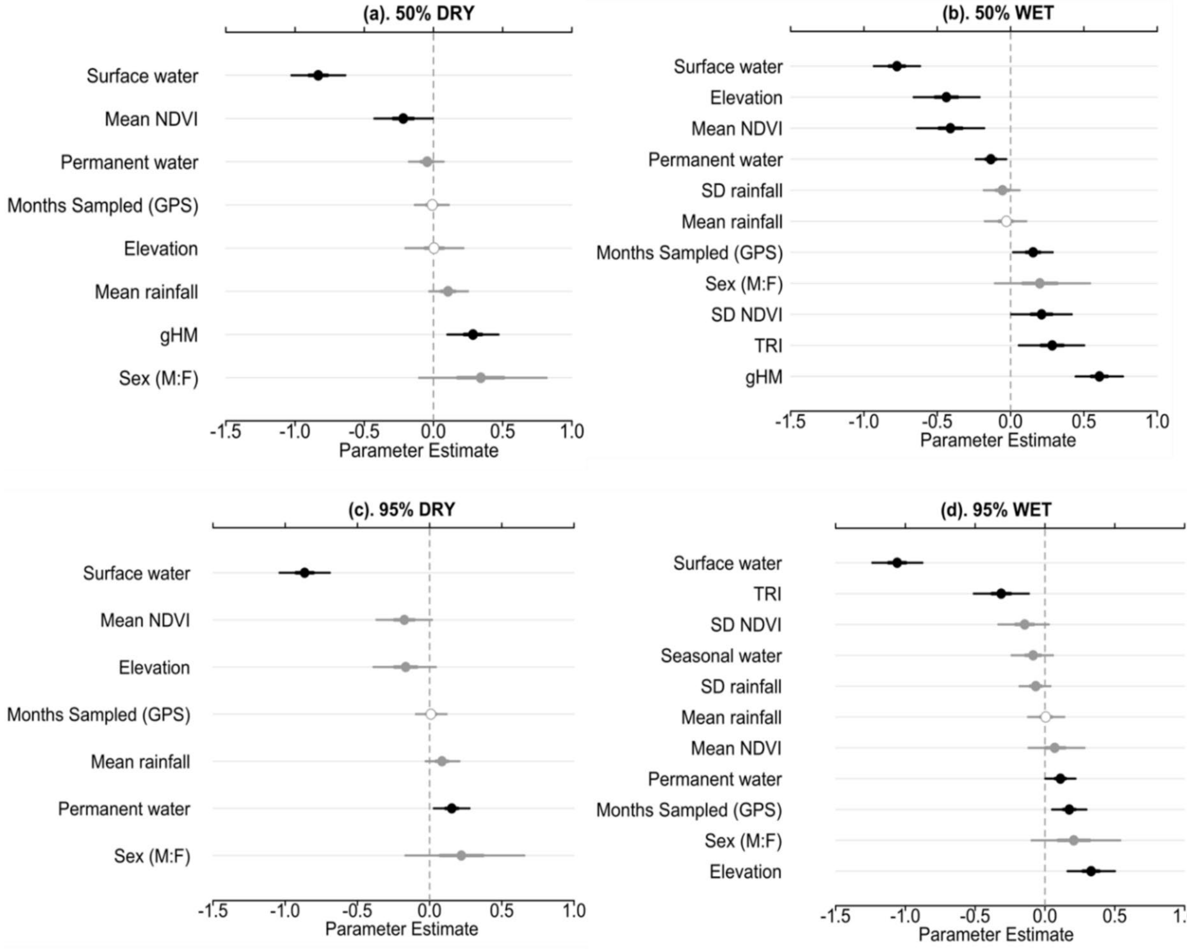

Fig. 3 Ordered results from within-season home range size models for **a** 50% isopleth dry season range, **b** 50% isopleth wet season range, **c** 95% isopleth dry season range, **d** 95% isopleth wet season range. Grey bars indicate parameter estimates for which the 95% (open circles) and 50% (closed circles) credible intervals (CI) overlap zero

AKDE ranges increased with greater gHM values (Fig. 3a). Similarly, the 50% AKDE ranges during the wet season generally increased with greater gHM but decreased with higher mean NDVI (Fig. 3b). The Terrain Ruggedness Index (TRI) was influential in determining the size of the wet season range, with larger range sizes in more rugged areas for the 50% AKDE areas and smaller range sizes in more rugged regions for the 95% isopleth home range. Results were also opposite for elevation: wet season 50% AKDE ranges and dry season 95% ranges were smaller with increased elevation while wet season 95% AKDE ranges were larger with increased elevation (Fig. 3). Range sizes tended to increase with greater sampling in the wet season (Fig. 3b, d), but sampling effort had no effect in the dry season range estimation, 50% AKDE dry ($P = -0.57$) and 95% AKDE dry ($P = -0.58$), (Fig. 3a, c). Sex effects on 50% AKDE dry season range sizes were strong and positive, but moderate for 50% AKDE wet ($P = 0.89$), 95% AKDE dry ($P = 0.86$) and 95% AKDE wet ($P = 0.90$), suggesting females have slightly larger seasonal ranges relative to males (Fig. 3).

Home range shifts and sex differences.

On average, similarity in utilization distributions (UDs) was high across both seasonal and annual ranges. The most substantial overlap was found in interannual home ranges of individuals, with a mean

UDOI of 0.92 (range: 0.52–0.99). Seasonal overlaps were slightly lower, with mean UDOI = 0.86 (range: 0.1–0.99) (Fig. 4a). There was lower overlap across seasons (dry–wet and wet-dry), while within seasons overlaps were slightly higher (dry-dry and wet-wet) especially wet-wet season overlaps (Fig. 5). Females exhibited higher annual overlaps than males, but there was no strong support for sex differences in fidelity at the seasonal scale (P = 0.57) (Figs. 4b and 6). Of note, females seemed to show more overlap than males

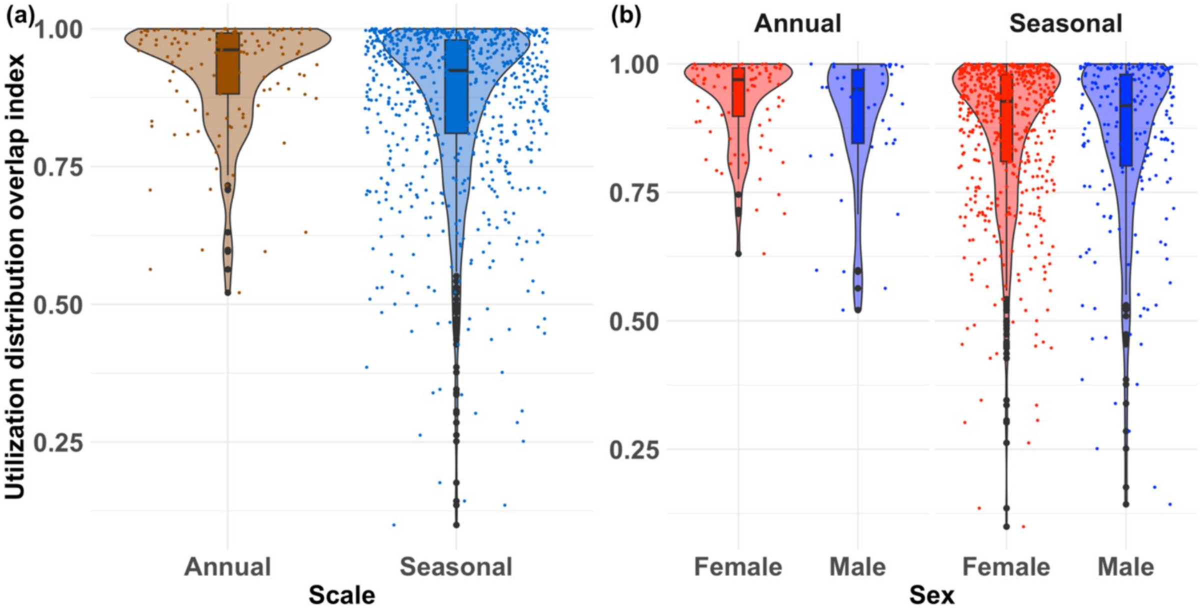

Fig. 4 Utilization distribution overlap index (UDOI – higher values show greater overlap) shows that **a** annual overlap tended to be stronger than seasonal overlap, and **b** Females tended to have greater overlap than males both annually and seasonally

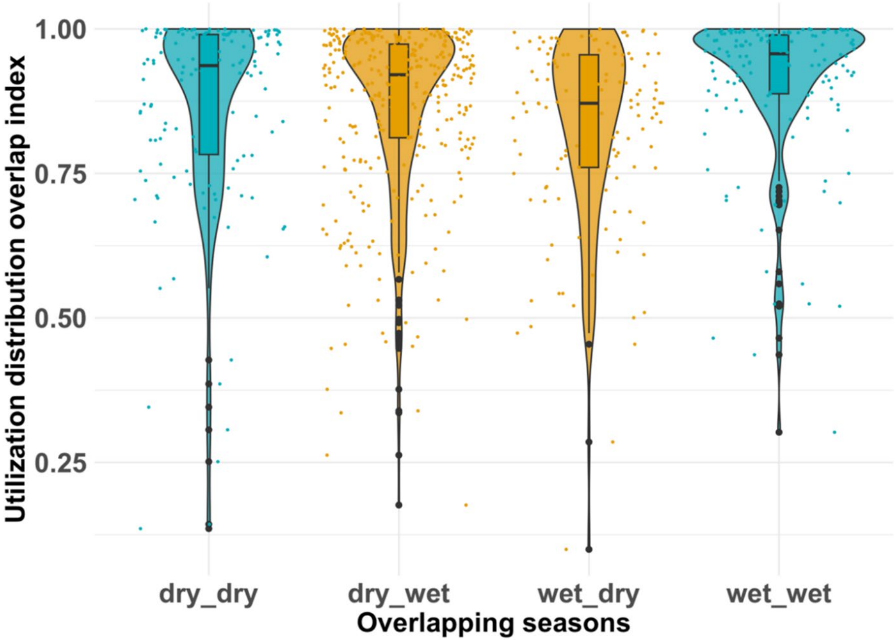

Fig. 5 Seasonal overlaps were contrasted between consecutive dry or wet seasons, as well as in relation to seasonal transitions from dry to wet or wet to dry. UDOI values were lowest, showed the most divergence, when transitioning from the wet to dry season, and were generally more similar between consecutive dry or wet seasons

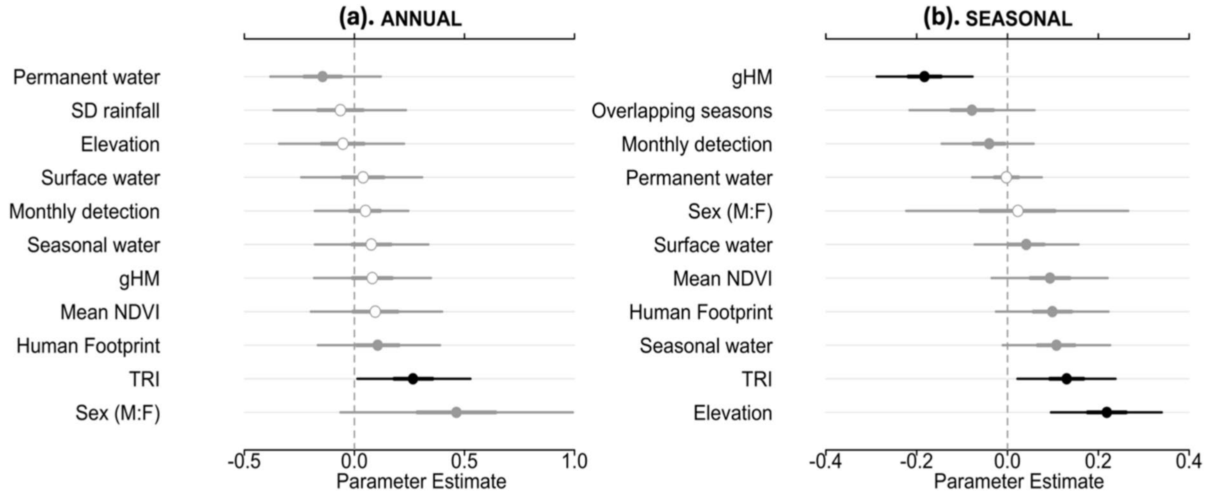

Fig. 6 Ordered results from home range overlaps models with UDOI as the response variable. Grey bars indicate parameter estimates for which the 95% (open circles) and 50% (closed circles) credible intervals (CI) overlap zero

when seasons transitioned from wet-to-dry ($P=0.89$) and wet-to-wet ($P=0.85$) (Fig. 7c, d).

Environmental predictors for home range overlap

Annual and seasonal home ranges overlapped more with increased terrain ruggedness (TRI) (Fig. 6). Similarly, overlap was greater during transitions from dry-to-wet and dry-to-dry with increasing ruggedness (Fig. 7a, b), but home ranges overlapped less with increasing TRI in wet-to-dry transitions (Fig. 7c). Overall seasonal overlaps, dry-to-wet, wet-to-dry, and wet-to-wet overlaps increased with increasing elevation (Figs. 6b and 7a, c, d, respectively).

Higher gHM was correlated with less overlap seasonally (Fig. 6b), and the same was observed during transitions, but the effects were moderate from wet-to-dry ($P=-0.86$) and wet-to-wet ($P=-0.80$) transitions (Fig. 7c, d). Similarly, overlap increased with increasing human footprint seasonally, dry-to-dry, dry-to-wet, and moderately annually ($P=0.77$). The opposite correlation was observed during the wet-to-dry transition ($P=-0.86$) (Fig. 7c), possibly indicating that elephant movements were not constrained by human presence when conditions transitioned from favorable to unfavorable.

Home ranges overlapped less with increasing mean rainfall and more with higher rainfall variability for wet-to-dry and wet-to-wet transitions. The latter finding suggests elephants did not shift their ranges when precipitation was unpredictable, especially after a wet season (Fig. 7c, d). In terms of productivity, overall seasonal and wet-to-dry overlaps increased with increasing mean NDVI, but this effect was moderate at the annual scale ($P=0.74$). NDVI variability was positively influential on fidelity during similar transitions, i.e., wet-to-wet ($P=0.82$) and dry-to-dry ($P=0.82$) (Fig. 7b, d), suggesting that the patchier the vegetation, the higher the fidelity when conditions are constant. The effect was opposite during dry-to-wet transition ($P=-0.87$), implying elephants moved to track these resources when conditions improved, i.e., from dry to wet season.

Finally, there was higher overlap with increasing seasonal water density seasonally (Fig. 6b), during the dry-to-wet transition, but less overlap during the wet-to-dry transition (Fig. 7a, c). There was no strong support of seasonal water effects on annual overlaps ($P=-0.72$) (Fig. 6a) or during similar season transitions, wet-to-wet ($P=-0.64$) and dry-to-dry ($P=-0.55$) (Fig. 7b, d). For posterior distributions for the other covariates, see supplementary information (Supplementary File 2: Tables S8–S13).

Discussion

The dynamics of African elephant space use, such as range size and shifts over time, are driven by a complex interplay of social, environmental, and

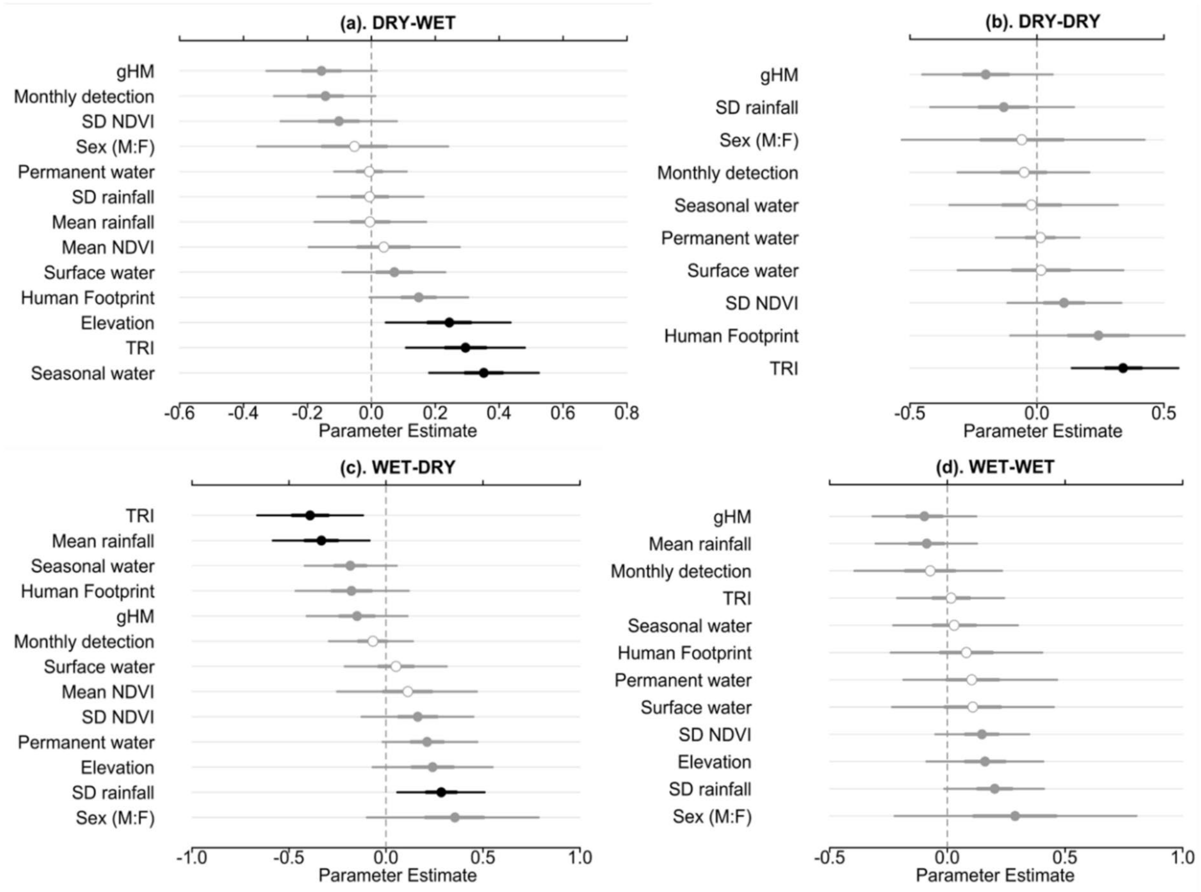

Fig. 7 Ordered results from home range overlaps models with UDOI as the response variable for each seasonal dyad. Grey bars indicate parameter estimates for which the 95% (open circles) and 50% (closed circles) credible intervals (CI) overlap zero

anthropogenic factors (Goldenberg et al. 2018; Purdon et al. 2018; Bastille-Rousseau et al. 2020; Sach et al. 2020; Du Plessis et al. 2021). In this study, we utilized GPS tracking data collected over a two-decade period to identify factors influencing elephant space use and shifts in ranges over time within the Laikipia-Samburu ecosystem. Our results indicated no significant differences in annual home range sizes between males and females, although seasonal home ranges were larger for females than males, and considerable individual variability was observed. Water availability emerged as a key factor influencing range size, with higher densities of surface and permanent water correlating with smaller annual and seasonal core home ranges. Similarly, rainfall was influential at the annual scale, with home range sizes decreasing with increasing mean rainfall and increasing with increasing rainfall variability. Factors such as surface and permanent water, vegetation productivity, terrain ruggedness, elevation, and human modification also influenced range sizes.

Home range overlap was high both annually and seasonally, highlighting the relative stability in range use by elephants over time, particularly in females, and suggesting African savanna elephants in the study ecosystem display site fidelity. Environmental predictors such as terrain ruggedness, elevation, rainfall variability, vegetation productivity, water availability, and human modification significantly affected home range overlaps. Overall, our study provides insights into the environmental and anthropogenic factors that influence elephant spatial behavior, highlighting the significance of rainfall, water resources, and human activities, with implications for conservation and management strategies in arid and semi-arid ecosystems.

Home range size correlates

Multiple studies have found differences in the home ranges of males and females (De Villiers and Kok 1997; Whitehouse and Schoeman 2003; Wall et al. 2013; Taylor et al. 2020; Benitez et al. 2022). In contrast, our study found no significant differences in annual home range size between males and females. Interestingly, contrary to our expectations, females exhibited larger seasonal home ranges than males. Despite this, our findings align with broader patterns reported in studies of sex-specific ranging behavior (Ofstad et al. 2019; Cavazza et al. 2024). In the study ecosystem, we observed a high degree of variability in range sizes across individuals of both sexes. Some individuals utilized extensive areas while others remained relatively localized. This, in part, may be related to the diverse habitat mosaics across the ecosystems, from semi-arid lowlands to mesic montane forests in higher elevation areas. However, even among individuals using similar areas, we found strong differentiation. Such individual variability appears to be a characteristic of elephant spatial behavior and may be related to personality-environment interactions rather than simply ecological differences (Bastille-Rousseau and Wittemyer 2019). Individual variation in space use is common in some species that inhabit diverse ecosystems; for instance, Eurasian Curlew (*Numenius arquata*) showed strong individual variation in home range sizes (Dall et al. 2004; Sih et al. 2004; Mander 2022). However, in many ungulates, range sizes are similar within the same ecosystem (Lesage et al. 2000; Saïd et al. 2005). This high degree of heterogeneity suggests that diverse, individual-specific strategies make generalities regarding elephant space use difficult.

Water was the dominant feature structuring annual and seasonal range sizes in the semi-arid study ecosystem, demonstrating the strongest effect sizes in our models. Generally, as predicted, we found that home range sizes were smaller in areas with more water, including both surface and permanent water sources. Notably, while surface water showed consistent negative correlations with range size, the effect of permanent water was more complex, associated with smaller 50% dry and wet ranges but larger 95% dry and wet AKDE ranges (sect. "Predictors for home range size variations"). This suggests that elephants may travel further away from static water sources, increasing the total area used but not necessarily expanding core use areas. Similarly, rainfall patterns also influenced range size, with greater rainfall variability associated with larger annual ranges, while greater mean rainfall was associated with smaller annual ranges (sect. "Predictors for home range size variations").

On the whole, these results indicate elephants did not move as much when water resources were abundant. This finding is consistent with previous studies in other ecosystems, underscoring the importance of water availability, particularly in arid and semi-arid environments (de Beer and van Aarde 2008; Benitez et al. 2022). Consistent with studies in other systems, we also found that high variability in rainfall was associated with larger home ranges, suggesting that elephants expand their ranges where rainfall is unpredictable (Bohrer et al. 2014; Benitez et al. 2022). Similar dynamics have been observed in ungulates, such as the oryx (*Oryx gazella)* and wildebeest *(Connochaetes taurinus)* which increased their movements, core area and general movements respectively when water access became uncertain (Corp et al. 1998; Boyers et al. 2019).

The seasonal dynamics we observed reinforce the previously found relationship between water distribution and movement in elephants. For example, in South Africa, range sizes decreased exponentially with an increase in water point density during both the dry and wet seasons (de Beer and van Aarde 2008). However, our study also found that, after controlling for surface water coverage, the 95% AKDE home ranges of wet and dry seasons were larger with increasing permanent water density. This effect is likely related to the annual variability in the remotely sensed JRC water layer, in contrast to the permanent water layer of digitized, static surface water features. This contrast may indicate that while ranges are generally smaller with more water in semi-arid systems, good rainy seasons that increase the surface water availability led to range expansions, such that elephants could access areas far from permanent water sources. Similarly, African buffalo (*Syncerus caffer*) showed adaptive strategies that depended on various social and ecological factors (Naidoo et al. 2012).

Our results also revealed the importance of vegetation productivity at the seasonal scale that was not apparent at the annual scale. Variability in productivity (as measured by NDVI standard deviation) drove elephants to increase their 50% wet season and 95% annual AKDE ranges, likely to track better vegetation quality or social opportunities, such as seeking mates or strengthening bonds (Fishlock and Lee 2013; Bastille-Rousseau et al. 2020). This relationship is consistent with theoretical expectations that animals will range more widely under uncertainty to buffer against unpredictable resources (Orians and Wittenberger 1991). Such movement responses to variability in forage have been observed across taxa. For example, migratory caribou (*Rangifer tarandus*) and plains bison (*Bison bison*) exhibit larger or more dynamic ranges in years with patchy or inconsistent vegetation productivity (Merkle et al. 2014; Bastille-Rousseau et al. 2018).

Conversely, we observed that increases in mean NDVI were associated with reduced 50% AKDE range sizes in both wet and dry seasons, indicating a tendency for elephants to stay in more productive areas when forage is abundant (Grogan et al. 2020). This finding is supported by another study in South Africa, where researchers found that wet-season home ranges decreased with increasing seasonal productivity (Young et al. 2009). This aligns with predictions from optimal foraging and exploitation theory, that animals will conserve energy when possible, and has parallels in species such as elk (*Cervus canadensis*), which reduce movement when local forage quality is high (Morales et al. 2004; Hebblewhite and Merrill 2011).

The global human modification index exhibited scale-dependent effects, with gHM being correlated with core area (50% AKDE) and seasonal and annual ranges, but in opposite directions. Elephants expanded their seasonal core ranges in areas with greater human modification. Conversely, annual 50% AKDE ranges were smaller, with greater human modification, possibly to access undisturbed patches within the human-dominated matrix (Orrick 2018). Taken together, these findings are consistent with the *landscape of fear* framework, which predicts that animals alter their movement patterns to avoid perceived risk, even at the cost of suboptimal resource access (Laundre et al. 2010; Bleicher 2017). Examples of altered space use in response to risk have also been recorded in leopards (*Panthera pardus*) and coyotes (*Canis latrans*), which show increased range size and plasticity in response to human disturbance (Gehrt et al. 2009; McKaughan et al. 2024). Relatedly, an earlier study in the same ecosystem revealed that elephant families had smaller ranges within the protected area, particularly away from human settlements. In contrast, subordinate individuals relied on areas outside the more preferred protected areas and had larger ranges (Wittemyer et al. 2007). This suggests that social status may mediate responses to humans, further highlighting the complexity of individual movement decisions in human-dominated landscapes.

Home range shifts correlates

Understanding drivers of shifts in space use can provide insight into how elephants respond to changing landscapes and identify factors that may lead to reduced use or even range abandonment. Perhaps because most of our study area is rangeland and therefore was not undergoing the same degree of agricultural development as other areas, we found high annual overlap, indicating strong site fidelity in the study elephants. Such fidelity is beneficial in various species through the benefits of exploiting known resources and more effectively avoiding threats (Tambling et al. 2015; Northrup et al. 2016). While the elephants generally demonstrated strong fidelity, we found evidence of range shifting across seasons (dry-to-wet and wet-to-dry), reflecting the elephants' adaptive response to seasonal changes in resource availability (Burton-Roberts et al. 2022). This aligns with the dynamics of seasonal range shifts, as previously observed in northern Kenya (Thouless 1995). Interestingly, sex was not a correlate of overall seasonal home range overlaps; however, females had higher annual, wet-to-dry, and wet-to-wet overlaps than males, which may be due to the more stable social structures and habitat use patterns of female-led groups. Further, male elephants have been found to exhibit more shifts when in musth and with age (Taylor et al. 2020). Females having higher fidelity has been documented in other species as well, for example, older female caribou exhibited more philopatry (Schaefer et al. 2000), and there is a general trend in mammals of male dispersal and philopatric females (Greenwood 1980; Stephen Dobson 1982; Rangel-Morales et al. 2022).

Annual, seasonal, dry-to-wet, and dry-to-dry overlaps were influenced by terrain, with stronger fidelity associated with more rugged areas, possibly due to constraints on adjusting ranges in such areas (Huang et al. 2022). Similarly, elephants maintained high site fidelity across the same seasons (wet-wet and dry-dry) with higher terrain ruggedness but shifted more with increased elevation in the wet-wet transition. The effects of terrain in the contrasting season transitions were opposite, i.e., decreased wet-to-dry fidelity with increased ruggedness, indicating that the type of seasonal transition influenced how site fidelity was structured. We hypothesize that rugged terrain offers better forage when it is getting drier; this has been documented in Botswana, where authors reported higher shrub density and stem breakage by elephants in rugged terrain during the dry season (Nellemann et al. 2002). This is further supported by studies in other species like the gemsbok (*Oryx g. gazella*) in Namibia, which also moved from low to high sites and hillsides during drought events (Lehmann 2015).

Our work on home range shifts builds upon the study by Goldenberg et al. (2018), which assessed the intergenerational shifts of African elephant home ranges in relation to demographic, human, and ecological variables, and found intergenerational shifts according to resource availability and away from areas where significant poaching events had occurred. Our work did not examine lineage-specific range shifts; instead, we utilized all available tracking data and compared various measures of range shifts for individuals across consecutive intervals (seasons or years); however, we predicted human activity would affect individual range shifts similar to how it affected intergenerational shifts. As predicted, we observed that seasonally and across all transition types, home ranges shifted more with increasing human modification (gHM), implying that elephants have to adjust their movements and space use more in areas with greater human activity, and, conversely, can maintain higher site fidelity in areas with less human activity. As with previous continental-scale analyses, this highlights the importance of human presence on elephants' spatial behavior (Wall et al. 2021a; Benitez et al. 2022). This is also consistent with the *landscape of fear* framework, discussed above (Laundre et al. 2010). Large carnivores and ungulates responded similarly to risk, with persistent human activity resulting in reduced site fidelity and more frequent restructuring of space use (Faille et al. 2010; Smith et al. 2015).

The lack of strong effects regarding temporal human footprint density, i.e., annual human presence compared to the human modification index (cumulative human activities), on both home range sizes and shifts might imply that the level of disturbance/modification variably affects elephant ranging behaviors in northern Kenya. Additionally, human factors, such as poaching, have been documented to drive directional home range shifts across generations in northern Kenya (Goldenberg et al. 2018). Other studies have found that some species change their space use depending on the type of human presence. For example, wild boars (*Sus scrofa*) avoided beaches but selected for sites near infrastructure, especially when the disturbances were low, which the authors attributed to the availability of anthropogenic food in these areas (Brogi et al. 2023). Similarly, large predators avoided human presence temporally by increasing nocturnality with more human presence when human activity was temporally predictable (Nickel et al. 2020; Brogi et al. 2023).

Similar to previous findings on elephant site fidelity, we found an evident but moderate influence of vegetative productivity on fidelity. Elephants moved more (less overlap) with more variable vegetation, especially during transitions into the dry season (Fig. 7b, d) (Goldenberg et al. 2018; Burton-Roberts et al. 2022). This aligns with theoretical models that predict animals will reduce site fidelity when resource predictability declines (Switzer 1993; Spencer 2012). The opposite, i.e., high fidelity when resources are predictable, has been demonstrated in mountain goats (*Oreamnos americanus*) and elk (*Cervus elaphus),* which revisited sites where forage quality was higher (Wolf et al. 2009; Shakeri et al. 2021).

The role of water as the dominant resource driver of elephant home range locations, as documented in multiple studies (Roever et al. 2013; Bohrer et al. 2014; Burton-Roberts et al. 2022), however, may outweigh the effects of fluctuating productivity. There was high site fidelity, especially when transitioning from wet-to-dry seasons, with more variability in rainfall and increasing permanent water, implying that water uncertainty and scarcity during this transition drove elephants to stay in areas with predictable water. Additionally, and contrary to our prediction, during the transition from wet to dry seasons, elephants shifted their ranges more with increased mean rainfall and seasonal water, likely because they could more freely track resources when water was readily available across the landscape. Similar resource-tracking behaviors similar to those described here also occur across diverse taxa such as in mule deer (*Odocoileus hemionus*), mountain goats (*Oreamnos americanus*) and many migratory birds (Aikens et al. 2017; Thorup et al. 2017; Abrahms et al. 2021; Shakeri et al. 2021). This finding underscores the importance of flexible movement strategies across different taxa in response to changing resource availability.

Limitations and further studies

We lacked enough data on elephant demography and sociality to analyze differences in home range dynamics according to social context or age. Future research with similar analyses, including covariates that reflect family group size and demographic composition, would provide deeper insights into how demographic and social factors influence site fidelity (or philopatry) and home range size (sensu Wittemyer et al. 2007). Additionally, while AKDE is robust to small sample sizes and variable sampling schedules, and accounts for autocorrelation in the data, it led to the omission of key individuals who did not meet the range residency criteria (see sect. "Materials and methods") (Calabrese et al. 2016). Our 50% and 95% annual and seasonal MCP estimates were also smaller than AKDE estimates irrespective of s in the analysis (Figs. 8, 9 and 10 & Supplementary File 2: Table S1), as is typical of the AKDE method (Noonan et al. 2019; Signer and Fieberg 2021). The generally large size of the AKDE range estimates relative to the distribution of the observed data likely results in some landscape covariates being misaligned with the observed GPS data. This has the potential to impact inferences drawn from modeling range size in relation to range-specific landscape conditions. However, in this study, we found results from analysis of the 50% AKDE range, which adhered more closely to the observed data, and the 95% AKDE ranges were largely similar, suggesting that results were robust to any misalignment. In future analyses, it may be useful to compare results derived using AKDE with those from a home range estimate that is more closely aligned with observed data distribution.

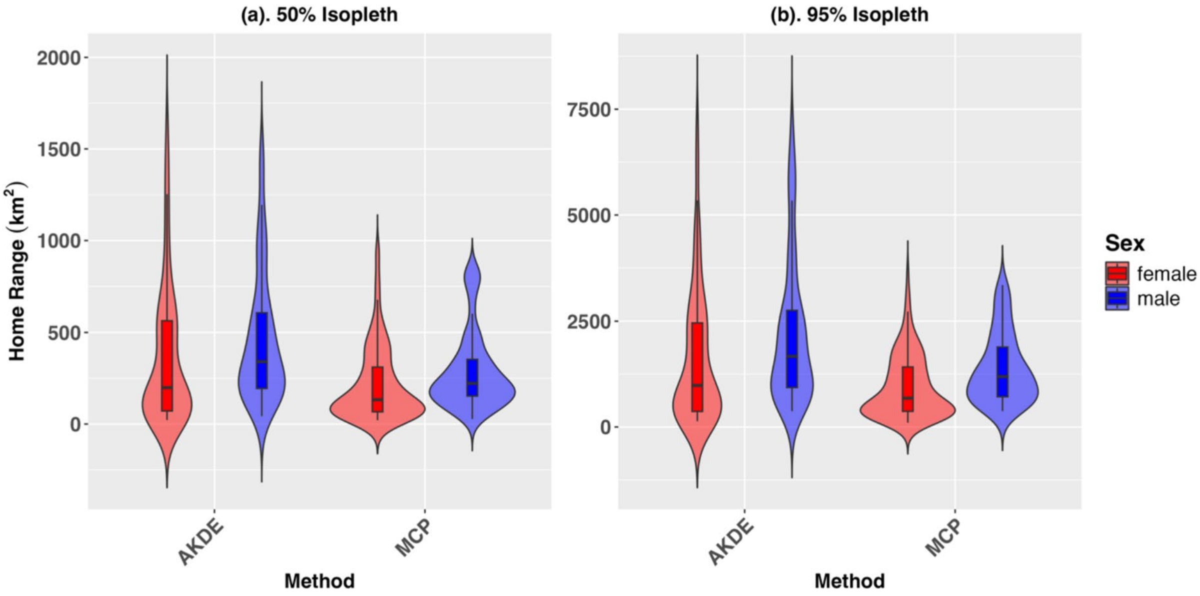

Fig. 8 Comparative analysis of annual home range estimates across sex and methods

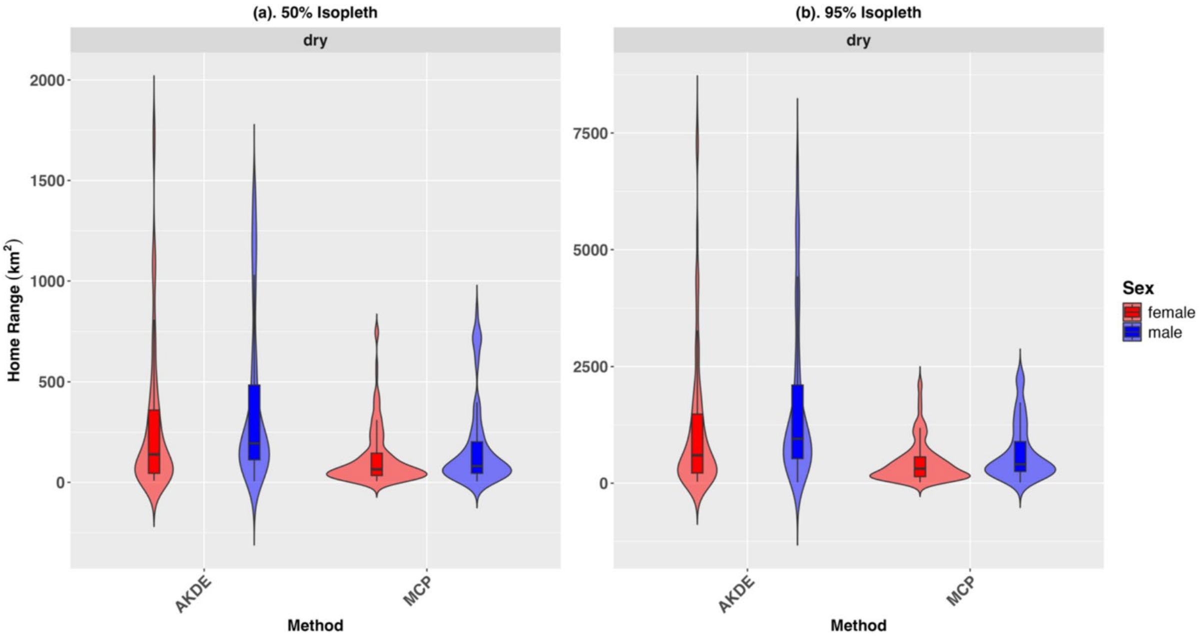

Fig. 9 Comparative analysis of dry season home range estimates across sex and methods

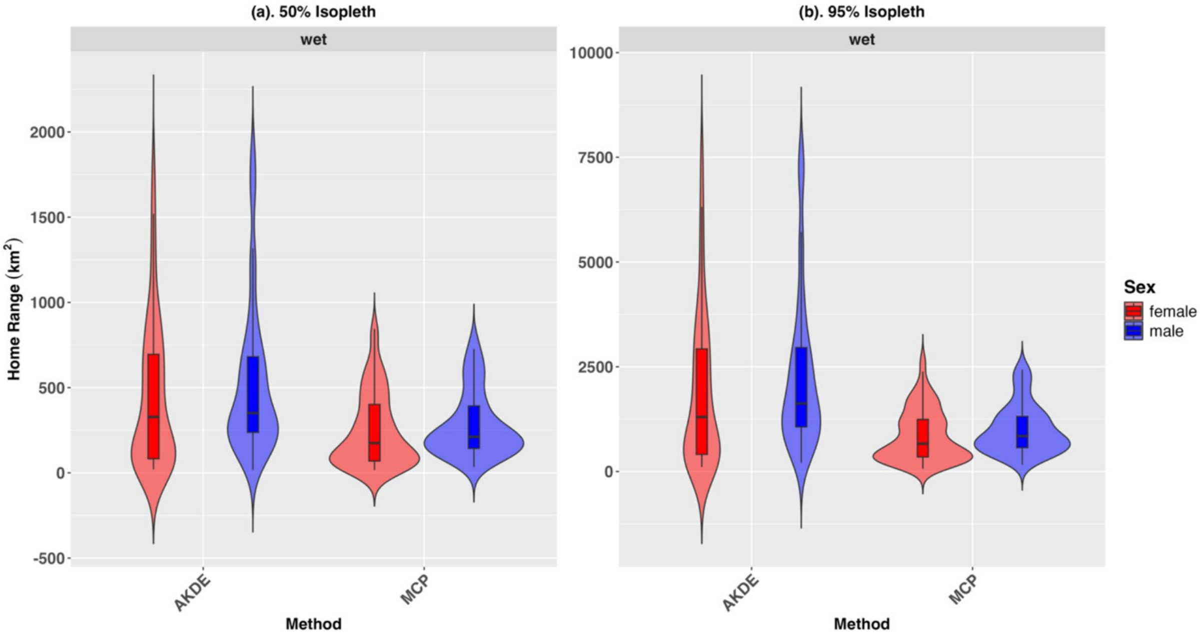

Fig. 10 Comparative analysis of wet season home range estimates across sex and methods

Conclusion

Our research offers comprehensive, multiscale insights into the relationships between range size and range shifts of African elephants in a changing landscape, utilizing 20 years of tracking data. We highlight the nuanced influences of various environmental factors on elephant space use over multiple spatial and temporal scales. Our results suggest that water, human modification, topography, and vegetation productivity influence the ranging behaviors of elephants at these different scales. Our results, especially, underscore the importance of water in structuring elephant space use, with implications for conservation actions during dry seasons or severe droughts, when human-elephant conflicts are particularly high (Moses et al. 2016; Munyao et al. 2020). Ensuring water access for elephants away from human settlements during these periods can reduce negative interactions between elephants and humans.

More broadly, our findings offer broader insights into how elephants respond to changing landscapes, with direct relevance for managing elephant populations across Africa. As elephant habitats continue to be altered by expanding agriculture, infrastructure development, human settlement, climate change, and other factors that cause unpredictability in resources (Chase et al. 2016; IUCN 2020), understanding the drivers of elephant space use and range fidelity becomes increasingly urgent. The patterns observed in the Laikipia-Samburu ecosystem reflect the challenges facing elephant populations across the continent, namely, navigating increasingly fragmented and unpredictable environments while balancing ecological needs with anthropogenic pressures (Wall et al. 2021a). Overall, our findings identify the drivers of elephant space use behavior, which can be harnessed to inform management decisions regarding this endangered keystone species, with potential applications to other species.

Our findings align with theoretical predictions regarding resource tracking, exploitation efficiency, and optimal foraging theory and demonstrate how elephants respond to the landscape of fear. Elephant space-use strategies are shaped by trade-offs between resource acquisition (vegetation and water), conserving energy, and risk avoidance (human presence and the level of human modification). By linking our results to these theories and frameworks, we provide a framework for anticipating elephant, and potentially other species with large spatial requirements, responses to changing environmental, topographical, and anthropogenic conditions. In this way, elephants serve as a valuable model species for investigating predictions of animal space use relative to landscape characteristics, offering insights into how fundamental drivers of ranging behavior are influenced by body size, ecological role, and human pressures. Similar investigations of smaller-bodied herbivores could provide insight into how body size influences ranging behavior within the herbivore guild.

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Author contributions N.M.G. developed the methods, performed all analyses, and drafted the manuscript with assistance from G.W. G.W. provided valuable input on the final methods, datasets, manuscript and edited the manuscript. Both authors read and approved the final manuscript.

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Data availability All tracking data used in this study are the property of Save the Elephants (http://info@savetheelephants.org). Due to the sensitive nature of elephant tracking data and the protected status of African elephants, the data will be made available upon request to the corresponding author and Save the Elephants. The code and example data used for reproducing these analyses in the study will be available once this manuscript is accepted for publication.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval All protocols adhered the Kenya Wildlife Service (KWS) and Colorado State University standards.

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