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RESEARCH ARTICLE

Identification of landscape features structuring movement connectivity for Namibian elephants

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Abstract
Context Human modification of landscapes poses a significant threat to wildlife, particularly in Africa where population growth and land conversion are expected to increase. Habitat loss and fragmentation have led to declines in wildlife populations, highlighting the need to identify and preserve critical habitats, including core use areas and connectivity between them. Most recently, the identification of habitat corridors has become a key objective.
Objectives Our study objectives are to (1) empirically quantify connectivity across the Kunene—Etosha landscape in Northwestern Namibia using GPS tracking data on wild African elephants, and (2) assess the landscape features (i.e., geologic, biotic, and human-made) influencing connectivity and corridor types (e.g., fast movement corridors versus slow multi-use movement corridors).
Methods We used GPS telemetry data from 66 elephants collared in Northwestern Namibia to empirically quantify connectivity using a graph theoretic approach and assess landscape features influencing connectivity. Based on the 'movescape' approach, we identify different types of corridors and examined how landscape features differed across these corridors using multiple regression models on locations classified into different types of use categories by machine learning algorithms.
Results Our results revealed strong variation in connectivity across the landscape, with paths of high connectivity near water sources between the study areas. We found that factors related to water sources and human presence primarily influenced connectivity. Water holes serve as hubs across the ecosystem for both male and female elephants with lower use areas peripheral to areas with water. Connectivity between Kunene and Etosha National Park was relatively rare among the collared elephants, but we highlight the key areas used to move between the two regions.
Conclusion Water was the key feature structuring space use, and human presence influenced

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connectivity between water points, highlighting the importance of landscape planning in relation to limited water sources and human activities. Our results suggest that focusing management efforts on areas where water is limited for both elephants and humans will be important to reduce conflict and maintain ecosystem connectivity.

Keywords African elephant · *Loxodonta africana* · Landscape ecology · Movescape · Network theory · Landscape conservation

Introduction

Human modification of landscapes is a primary threat to wildlife (Kennedy et al. 2019). With global human population projected to reach 9.7 billion by 2050 (United Nations 2022), increased landscape modification is expected. Across Africa and Asia alone, for instance, global cropland is expected to increase by 26% (Williams et al. 2021a). The associated land conversion and habitat loss are likely to exacerbate ongoing declines in wildlife populations and will be detrimental to the long-term persistence of species (Brook et al. 2008). Thus, identifying and preserving critical wildlife habitats is crucial for ensuring the persistence of species, particularly in the face of rapid landscape changes (Hanski 1999; Fahrig 2003).

Small populations are especially at risk of extinction due to increased vulnerability to inbreeding depression, demographic stochasticity, environmental catastrophes, and genetic drift (Caughley 1994). Connectivity between populations has been identified as the critical mechanism to alleviate such demographic stressors and reduce the risk of extirpation (Caughley 1994; Hanski 1999). Ensuring connectivity is an important mechanism for the long-term persistence of populations as it enables demographic rescue, genetic exchange between different populations, and mobility across landscapes to avoid or minimize negative consequences in the face of climate dynamics. In recognition of the importance of connectivity, the identification of corridors has become a core objective in wildlife conservation and management globally (Osipova et al. 2019; Jennings et al. 2020; Kaszta et al. 2020).

Numerous methods have been developed to identify and predict areas with high levels of connectivity. Among the most widely used approaches are resistance surface modeling based on circuit theory or least-cost path analysis (McRae et al. 2008; Etherington 2016). In the case of the least-cost path, model misspecification or the animal not using the least-cost path in the environment can result in inaccurate prediction (Kumar et al. 2022). Some researchers advocate for alternative but related approaches, such as instituting correlated random walks on a resistance surface with the inclusion of mortality layers (Fletcher et al. 2019). However, obtaining mortality risk information may be challenging and misspecification issues remain. More recently, empirical-based approaches have been developed to identify and quantify connectivity from GPS tracking data without modeling (Bastille-Rousseau and Wittemyer 2021). Namely, the application of graph theoretic approaches allows straightforward calculation of the importance of a given GPS position or path to the broader landscape connectivity, i.e., derivation of betweenness values for every GPS position (Bastille-Rousseau et al. 2018b). Since graph theoretic approaches rely on empirical data, they need large sample sizes to appropriately capture and characterize connectivity across the landscape. Nonetheless, due to their empirical basis, these approaches provide an accurate representation of the observed animal movement on the landscape (Bastille-Rousseau et al. 2018b; Bastille-Rousseau and Wittemyer 2021). More recently, approaches to integrate numerous metrics derived from tracking data have attempted to provide a more holistic definition of how the movement of a species of interest is structured across the landscape—defining the ‘movescape’ (Bastille-Rousseau and Wittemyer 2021). Importantly, the movescape approach can be used to define different types of connectivity or corridors, such as high connectivity areas where animals walk in a fast, directed manner versus areas where animals meander and spend an increased amount of time (Bastille-Rousseau and Wittemyer 2021). Such information can be crucial in directing management interventions for landscape planning initiatives.

The African elephant (*Loxodonta africana*) is the largest extant terrestrial mammalian species and is listed as endangered by the IUCN (Gobush et al. 2022). The remaining populations of African elephants face several primary threats, including illegal killing, human-elephant conflict, and changes in land use that result in habitat loss and fragmentation (Wittemyer et al. 2014; Tucker et al. 2018; Gobush et al. 2022). Due to its significant body size, elephants require more space compared to other species on the landscape (Peters 1986). As a result of increased human encroachment, the elephant range is increasingly restricted, with many historically viable areas no longer able to support the species (Wall et al. 2021). Land conversion for agriculture (Williams et al. 2021a) and accelerated human population growth around protected area edges (Wittemyer et al. 2008) combine to threaten both core populations and their connectivity. To address these common challenges, continent-wide efforts have been undertaken to track African elephants across their range to better understand the spatial needs of the species (Wall et al. 2021).

The arid lands of northwestern Namibia harbor important elephant habitats that contain both nationally protected areas and community lands that support elephant populations (Leggett 2006). A key objective for elephant management in this area is to maintain connectivity between Etosha National Park and the surrounding community conservation areas in the Kunene region located in the south and west of the national park. Maintaining landscape connectivity for elephants plays a crucial role in promoting resilience of elephant populations in the event of disease outbreak, such as anthrax (Huang et al. 2022, 2023). To fulfill this goal, it is important to identify key connectivity areas and the factors predictive of connectivity. We used GPS telemetry data from elephants across the Kunene region and Etosha National Park to address the following objectives: (1) empirically quantify connectivity across the Kunene—Etosha landscape in northwestern Namibia using GPS tracking data on wild African elephants, and (2) assess the landscape features (i.e., geologic, biotic, and human-made) influencing connectivity and corridor types (e.g., fast movement corridors versus slow multi-use movement corridors).

Methods

Study area

The study area is in northwestern Namibia, encompassing both the Kunene community-owned lands and Etosha National Park (ETS; Fig. 1). This semi-arid region exhibits a strong rainfall gradient receiving up to 500 mm in the eastern section of Etosha to less than 150 mm in the western portion of Kunene (Funk et al. 2015). Etosha National Park is a 22,270 km^2 largely fenced protected area, with porous sections in the northwest near Kunene. The estimated elephant population is approximately 2900 animals (Kilian 2015). The Kunene area consists of a patchwork of community conservancies and hunting concessions that support approximately 1100 elephants (Craig and Gibson 2016), with low human population density. Elephants are known to disperse between the two areas (Kilian 2015). Land cover types in the area include semi-arid savannah and arid desert.

Data collection

We analyzed GPS relocation data collected from 66 African elephants (37 females, 29 males) across our study area (37 from ETS; 29 from Kunene) collected between 2008 and 2015. All capture and collaring procedures were performed by veterinarians from the Namibian Ministry of Environment and Tourism, following South African National Standards for Animal Welfare and Care (SABS 2000). The GPS collection schedule varied between collars—41 individuals were fitted with collars collecting a 30 min fix interval, 15 individuals with a 20 min interval, and 10 individuals with a 15 min interval. To remove spatial errors in the dataset, we applied a filter excluding any consecutive relocation points greater than or equal to 10 km/h. We used 'adehabitatLT' to create the type II trajectory objects from relocation data and used the cleaned trajectory when calculating movement metrics (Calenge 2015).

Movement metrics and types

To empirically quantify connectivity across the landscape derived from the tracking data (Objective 1), we employed graph theoretic approaches to calculate attributes of connectivity defined by elephant movements across the ecosystem (Bastille-Rousseau and Wittemyer 2021). Graph metrics were calculated on a 150 m × 150 m grid overlaying the study area, where the 150 m spatial resolution was chosen because it was the average 30 min inter-step distance traveled by the study elephants. In our application of the graph

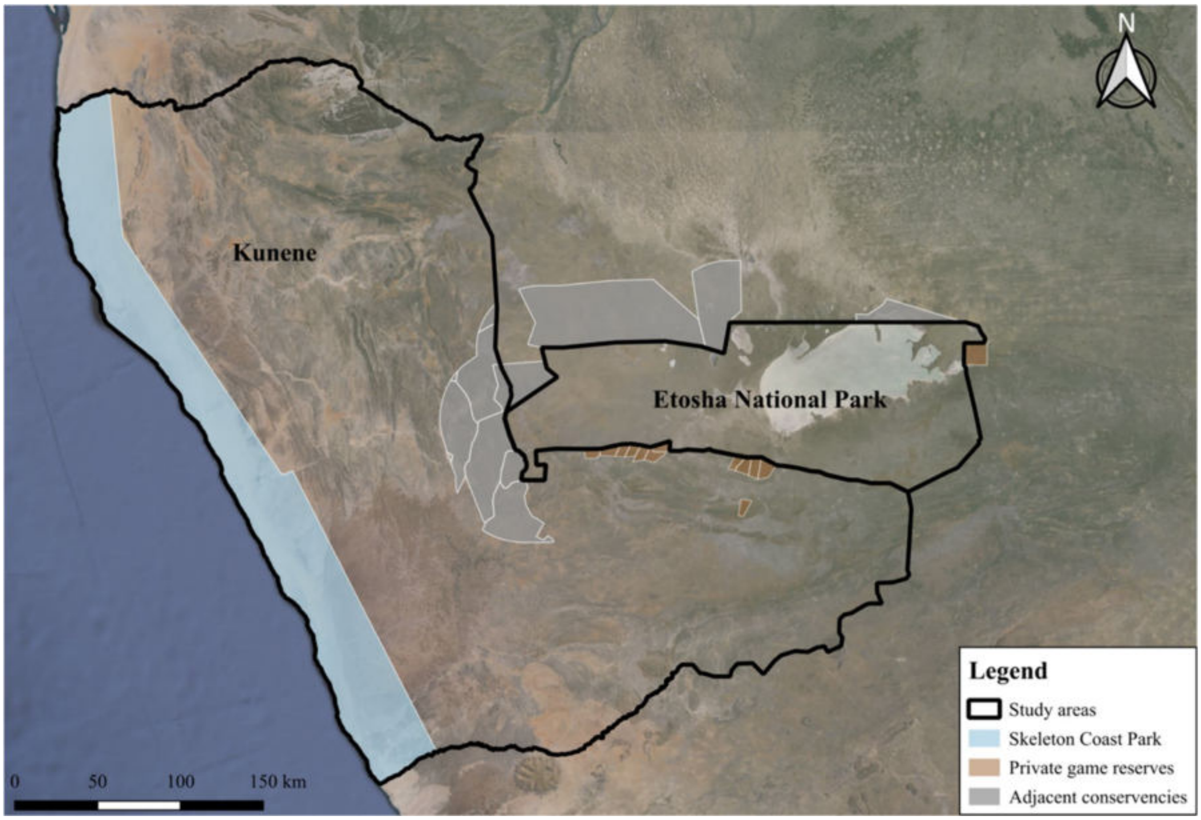

Fig. 1 The study areas include Etosha National Park (ENP) and Kunene Region. Conservancies and private game reserves adjacent to ENP are also depicted in the figure. The background is a satellite imagery provided by Google Satellites

theoretic approach, nodes were pixels in the grid that contained relocation (GPS) points from the study elephants' trajectory. Edges were the pixels that lie on the straight line connecting consecutive relocation points of the same individual located in different pixels (Bastille-Rousseau et al. 2018a). We calculated three metrics from this graph (i.e., betweenness, degree, and weight). Betweenness is the measure of the number of shortest paths connecting all nodes on a graph that pass through a given node. Degree is the measure of the number of connections each node has in the network. Weight is the number of GPS points falling in a given pixel (i.e., the intensity of use by the elephant). Connectivity was defined using betweenness (Objective 1). We used the 'movescape' framework to delineate spatial structuring in areas with high connectivity that can serve to define the type of corridors (Objective 2) (Bastille-Rousseau and Wittemyer 2021). To do this, we analyzed the relationships between the three metrics from the network characterization of the elephant movements, and two metrics from the animal trajectory (i.e., speed and the dot product of the turning angle). Specifically, we performed an unsupervised classification technique (i.e., two-step Gaussian mixture modeling) on the five metrics by setting the maximum number of clusters to be 8 following the methodology outlined by Bastille-Rousseau and Wittemyer 2021. We then evaluated the optimal number of clusters (from 1 through 8) using the Bayesian Information Criterion (BIC) to achieve a more conservative evaluation given the large dataset (number of relocations = 2,437,675; (Aho et al. 2014). The defined clusters represented the most substantive types of movements observed and were used in further analyses.

Environmental variables and modeling approach

To address our second objective to characterize landscape features associated with connectivity, we built candidate models to evaluate factors influencing the global centrality measure (betweenness) of any given pixel in our study area. We log-transformed the response variable (betweenness) and applied individual as a random-effect in our linear regression to quantify factors influencing the connectivity of a given pixel on the landscape. Our model included an auto-covariate term based on an inverse weighting scheme, a symmetric neighborhood metric, and a search radius that was defined dynamically for each elephant to select the lowest value at which all points have neighbors to account for spatial autocorrelation (Bardos et al. 2015). Environmental covariates explored were elevation, slope, terrain roughness index, global human modification index, distance from waterholes, distance from perennial rivers, distance from seasonal rivers, distance from roads, distance from towns and settlements, distance from wetlands, and normalized difference vegetation index (NDVI) (Table 1). We considered elevation, slope, terrain roughness index, distance from roads, towns and settlements, and global human modification index given these features have been found to influence elephant space use and movement (Bastille-Rousseau and Wittemyer 2019; Wall et al. 2024). Distance from waterholes layer was calculated from recorded man-made waterholes points within the system. Given the importance of water to elephants in arid ecosystems, we included perennial and seasonal rivers and wetlands (Polansky et al. 2015). Lastly, we included various measures of NDVI to account for differences in vegetation productivity across space and time (i.e., seasonality).

Elevation and global human modification index were directly downloaded from Google Earth Engine (Jarvis et al. 2008; Gorelick et al. 2017; Kennedy et al. 2019). The roughness index was calculated in QGIS (Wilson et al. 2007; QGIS Development Team 2019). We computed the yearly maximum and coefficient of variation (i.e., standard deviation/mean) of the normalized difference vegetation index (NDVI) for every pixel in our study area across our study period (2008–2015) using Landsat 7 and 8 imagery in Google Earth Engine. All covariates were down sampled to 150 × 150 m to align with the scale of the movement network grid. We developed five candidate models, to assess the influence of geologic, environmental, anthropogenic, and combined landscape features on betweenness values. Our candidate model set includes the geologic model (slope, distance from waterholes, distance from perennial rivers, distance from wetlands), anthropogenic model (global human modification index, distance from roads, distance from settlements), environmental model (maxNDVI, cvNDVI, distance from waterholes, distance from perennial rivers, and distance from wetlands), water model (distance from waterholes, distance from perennial rivers, distance from wetlands), and global model (combination of all the variables in the models above) (Supplementary Material Table S1).

To address our second objective of determining landscape conditions related to different types of corridors, we used a similar spatial regression structure, including the incorporation of an auto-covariate term and contrasting different covariate sets in each model. We used generalized linear models with a

Table 1 Covariate layers used in the modeling framework and associated data sources

Layer names	Source
Elevation and slope	SRTM image collection in Google Earth Engine (Jarvis et al. 2008)
Roughness index	Calculated using roughness algorithm in QGIS using elevation layer as an input
Global human modification index	gHM layer in Google Earth Engine (Kennedy et al. 2019)
Percent settlement	Derived from (Sirko et al. 2021)
Distance from water holes	Etosha ecological institute
Distance from perennial rivers	Etosha ecological institute
Distance from roads	Etosha ecological institute
Distance from towns and settlements	Etosha ecological institute
Distance from wetlands	Etosha ecological institute
Normalized difference vegetation index	Derived from Landsat 7 and 8 image collection from Google Earth Engine
Cattle abundance	Etosha ecological institute

logit-link function to assess landscape features associated with the different movement clusters related to high connectivity areas. Additional covariates explored included percent settlement within an average step (150 m) moving window and cattle abundance in addition to all the environmental covariates described above. Both variables were included in the human model and global model while the rest of the models remain the same in the candidate model set. We applied this spatial logistic regression to quantify landscape differences between high connectivity areas with fast and slow speeds (fast and slow corridors) according to mean speed values of a particular cluster (Table 2) and differences between the corridor and non-corridor pixels, and separately for males and females. We only included pixels with greater than or equal to 95% confidence assigned to a particular movement cluster for this analysis.

Before including variables in the models, we checked for multicollinearity by examining the variance inflation factor (VIF). VIF values for all the variables were < 2, well below the recommended criteria to be included in the same model (Dormann et al. 2013). We evaluated the models in the candidate model sets using BIC and made inferences from the best-performing model (i.e., the model with the lowest BIC score). To visualize the connectivity of our study area, we applied linear interpolation of the maximum betweenness values onto the steps in between (Bastille-Rousseau and Wittemyer 2021) (Fig. 5). All covariates were centered to their mean and scaled by dividing by their standard deviation (Gelman and Hill 2006). All analyses were conducted in R version 4.1.2 (R Core Team 2020). We used the ‘car’, ‘dplyr’, ‘ggplot2’, and ‘lubridate’ packages to clean, format, and visualize our data (Grolemund and Wickham 2011; Wickham 2016; Wickham et al. 2020). We used ‘moveNT’ to calculate relevant network theory-based metrics (Bastille-Rousseau 2023). Lastly, we used the ‘spdep’ package to calculate a spatial autoregressive term (Roger Bivand 2022), and ‘lme4’ and ‘ROCR’ for regression analyses (Sing et al. 2005; Zwitser et al. 2011). Model selection tables for regression analysis can be found in the accompanied Supplementary Material. Additionally, we included a comparison between different intensities of use in the Supplementary Material.

Results

We found connectivity (measured as betweenness values) varied strongly across the landscape, with well-defined paths of high connectivity near natural water sources, such as rivers and wetlands, in the area between Kunene region and Etosha National Park (Objective 1; Fig. 2). We also found that all the covariates assessed contributed to the explanatory power of the most parsimonious model of betweenness values (i.e., connectivity) (Objective 1). Maximum and coefficient of variation of NDVI (productivity) values of a given year, distance from waterholes, and distance from roads and settlements were positively correlated with betweenness (i.e., higher values, higher connectivity). Covariates of natural water sources, such as distance from rivers and distance from wetlands, and

Table 2 Summary of the unsupervised classification applied to 5 movement metrics of 66 African elephants inhabiting Etosha National Park and the Kunene multi-use conservancies area in Northwestern Namibia

Metrics	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Cluster 7
Weight	1.9658	1.1028	− 0.2394	− 0.2762	− 0.374	0.0761	19.3168
Degree	2.0242	0.9491	− 0.2309	− 0.2301	− 0.5927	0.3681	2.4292
Betweenness	1.304	− 0.1948	1.9268	− 0.1969	− 0.0745	1.2165	5.7943
Speed	− 0.3027	− 0.4018	2.3684	− 0.0986	0.6917	0.0987	1.9898
DotP	− 0.2971	− 0.3189	0.0424	− 0.0274	0.5599	0.1499	0.0069
Proportion of pixels	0.1529	0.1804	0.1345	0.1886	0.0705	0.256	0.0172
Proportion of individuals	0.8636	0.9697	0.7576	0.9848	0.5455	1	0.1364
Intensity of use	High-use	High-use	Low-use	Low-use	Low-use	Medium-use	Highest-use
Corridor type	Slow	NC	Fast	NC	NC	Slow	Fast
	NC	Non-corridor pixels with average negative betweenness values					

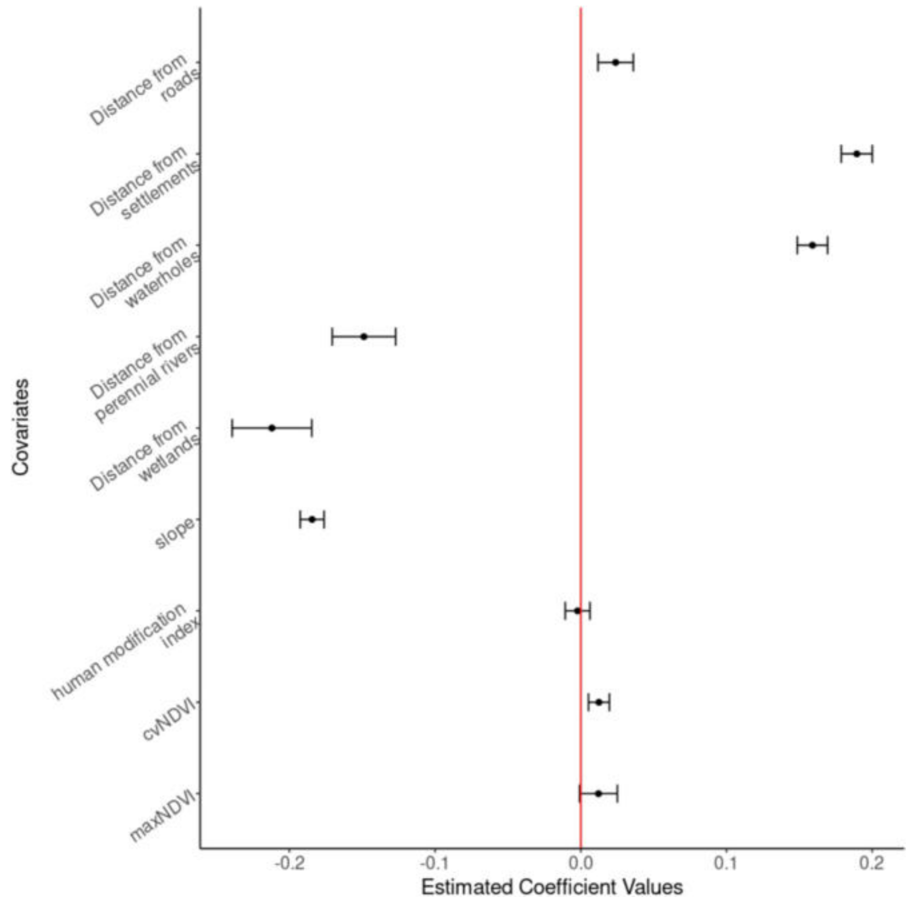

Fig. 2 Coefficient estimates from the most parsimonious model explain the variation in betweenness (connectivity) on the landscape. The covariates with the highest coefficient values tended to be related to water on the landscape

slope were negatively correlated with betweenness (i.e., closer to water and less slope had higher connectivity; Fig. 2).

We identified 7 unique population-level movement types (clusters) with different levels of use intensity, directionality, betweenness, and movement speed following the 'movescape' analytical approach (Objective 2; Table 2). No individual was found to have more than 7 clusters indicating that the chosen maximum number of clusters (8) was sufficient for this dataset. Four of these clusters were related to areas of high connectivity (i.e., clusters 1, 3, 6, and 7). However, clusters 1 and 6 were associated with low and medium speed (extended use), whereas clusters 3 and 7 were associated with faster speed (Table 2).

We found that the global model was the most parsimonious model for both males and females with AUC values of 0.781 and 0.683, respectively (Objective 2). Cattle abundance, distance from wetlands, distance from perennial rivers, and slope were negatively correlated with corridor pixels, indicating corridors were near water, in flatter areas, and away from livestock. These results were consistent for males and females. Distance from towns and global human modification index were positively correlated with corridor pixels, indicating corridors were further from towns but in areas of higher human modification. Interestingly, corridor pixels are positively correlated with distance from waterholes for males while they are negatively correlated for females. Our measure of productivity had a positive effect on corridors for females only (Fig. 3).

The top model of differences between highly directional, fast-corridor (cluster 3), and slow-corridor (cluster 6) was the global (AUC = 0.8954) and water (AUC = 0.8667) models for males and females, respectively. However, it was clear that water proximity was key for structuring the location of these two types of corridors for both sexes (Table 2). For females, fast corridors tended to be away from

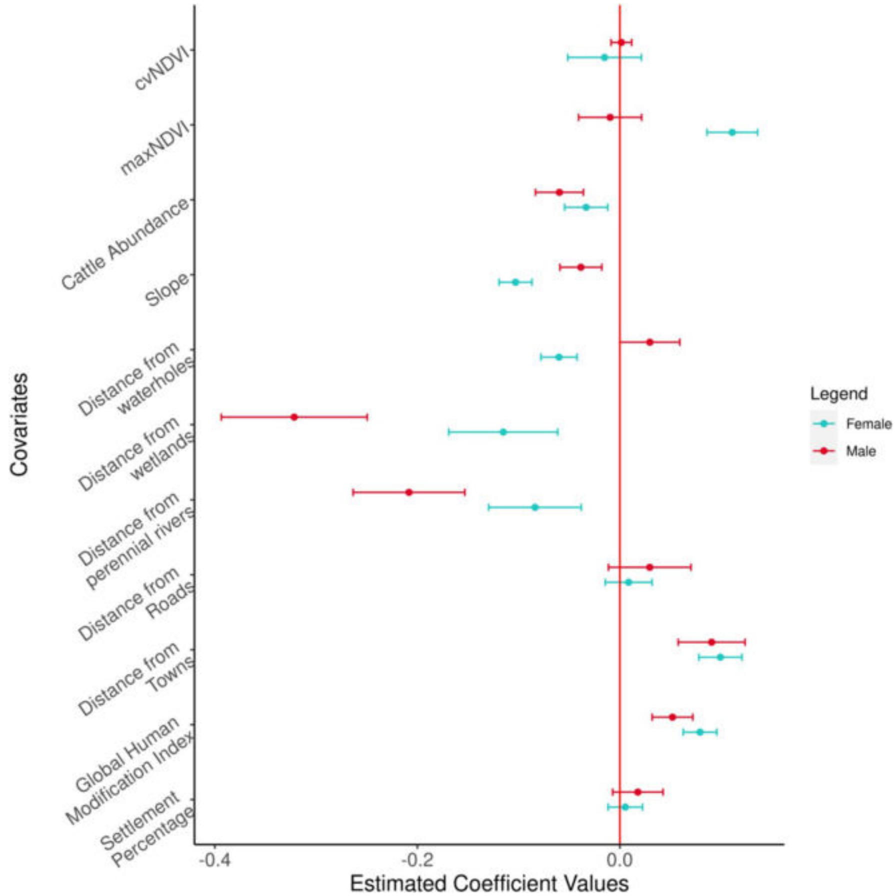

Fig. 3 The subset of coefficient estimates and associated confidence intervals included in the most parsimonious model for males (red) and females (females) evaluating differences between the corridor and non-corridor. Landscape features related to water distribution and human modification were the strongest predictors of differentiation between the corridor and non-corridor areas for both sexes

water resources, while males displayed the opposite (Table 2). Both males and females were using locations on the landscape near waterholes with much slower speeds and higher weight (Table 2; Fig. 4).

Discussion

As human population and landscape modification accelerate, proactive conservation of key areas for landscape connectivity is critical to the long-term protection of wildlife populations. This study provides insight into important corridors and associated environmental features within and between two regions of conservation importance for African elephant conservation in Namibia using 8 years of GPS tracking data. We found areas of high connectivity were relatively ubiquitous, highlighting that the landscape remains open to elephant movements within each region (Fig. 5). Connectivity within our study site was primarily influenced by proximity to natural water sources and anthropogenic features, similar to many other African elephant populations and large ungulates across the continent (Bastille-Rousseau et al. 2018b; Osipova et al. 2019; Crego et al. 2021).

We identified 4 different corridor types in the ecosystem, whereby each was identified by differing levels of use intensity, speed, and directionality. Although the majority of individuals (at least 75%) contributed to the classification of 3 corridor types (high-use slow, low-use fast, and medium-use slow corridors as defined in Table 2), only 13.6% of individuals in our sample exhibited high-use fast corridor movements (Table 2). This illustrates that individuals differed in their movement behaviors and responses to landscape features as documented in other elephant movement studies (Bastille-Rousseau and Wittemyer 2019; Chan et al. 2022). Such diversity in movement and space use strategies is important to take into consideration when making management decisions.

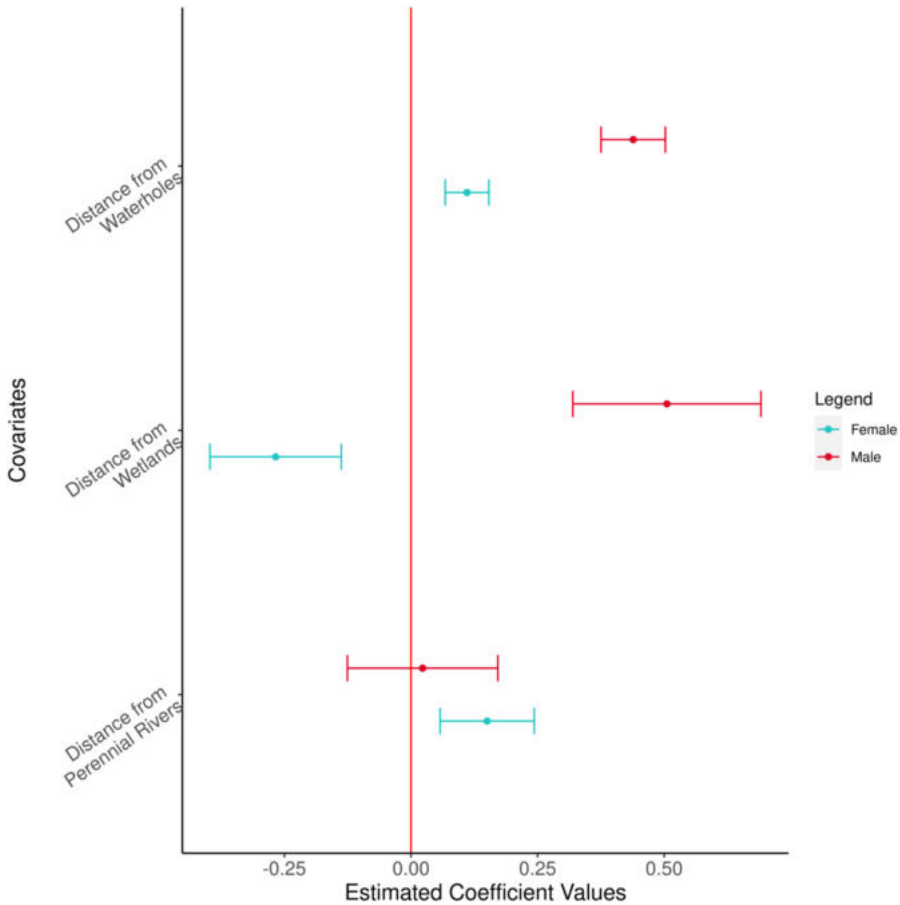

Fig. 4 Coefficient estimates and associated confidence intervals are included in the most parsimonious model for both males and females evaluating differences between fast and slow corridors

Water structured the landscape connectivity in our study system (Fig. 2), similar to what has been found in Samburu, Kenya (Bastille-Rousseau and Wittemyer 2021), another water-limited system. In this semi-arid environment, where water access is critical, perhaps it was not surprising elephant connectivity was strongly structured with respect to this resource. When we mapped the resulting 7 different movement clusters spatially (Supplementary Material: Fig. S4), we found that elephants in Etosha National Park use high-speed, directed walks when approaching waterholes. This aligned with the results of Polansky et al. (2015), who identified such behavior using behavioral change point analysis (Polansky et al. 2015). This high-speed directed movement corresponded to cluster 7 in this analysis (Table 2). Furthermore, Polansky et al. documented a switch in movement types near waterholes (Polansky et al. 2015). Similarly, the movescape approach identified a shift to slower more stationary use at water holes, identified as clusters 1 and 6 (slow, high/medium intensity of use) (Supplementary Material: Fig. S4). With a reduction in precipitation projected in the region due to climate change (Bucchignani et al. 2018), the importance of access to water for meeting the survival and reproductive needs of these elephants will only increase. These model outputs could be invaluable in identifying and conserving critical areas and corridors to help meet those needs.

Notably, we found that elephants avoided using areas with high cattle abundance that were close to human settlements and towns, passing through such areas using higher-speed corridors as defined by the movescape technique. Other studies have also reported that covariates related to human presence affect the connectivity of African elephants (Epps et al. 2011; Songhurst et al. 2016; Osipova et al. 2019; Bastille-Rousseau and Wittemyer 2021). Furthermore, the movements of other large herbivores, such as reticulated giraffes and plains zebra, were

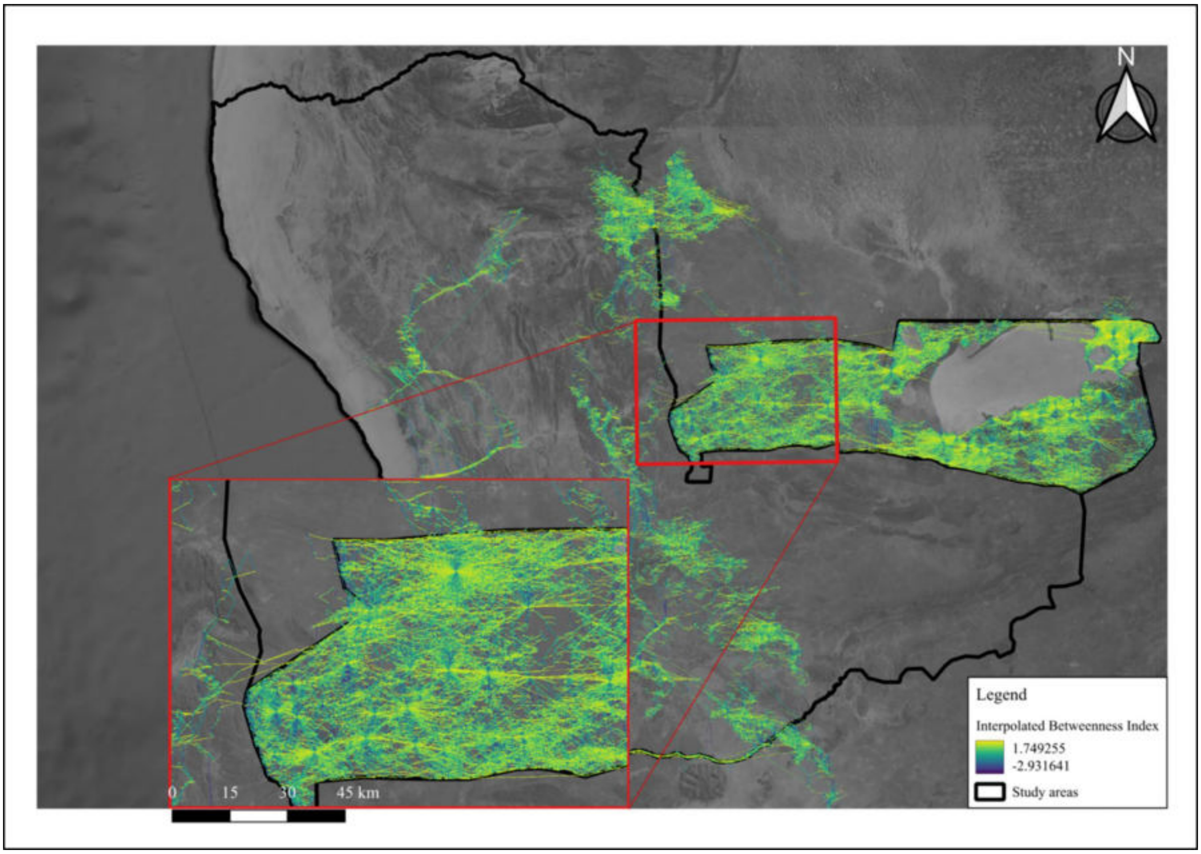

Fig. 5 Highlighting three connective routes used by African elephants between Etosha National Park and an adjacent Kunene region. The layer used in this figure is a linear interpolated betweenness index derived from GPS collars of 66 African elephants in the region. The higher the betweenness index value, the more central (i.e., more connected) the pixel is to the rest of the network

impeded by high cattle ranching intensity on the landscape (Crego et al. 2021). Previous work has identified the importance of elephant defined corridors for other species (Epps et al. 2011; Riggio et al. 2022), highlighting that the relationships identified here may be general to the wildlife community. Balancing the livelihood needs of local people with the connectivity required by large wild herbivores remains challenging (Rudnick et al. 2012; Donaldson et al. 2017).

Across several representations of connectivity, we found that human-related features were highly influential, as documented across numerous mammalian species (Morrison and Bolger 2014; Stabach et al. 2016; Tucker et al. 2018). Given the limited connectivity found between Kunene and Etosha National Park, it is important to protect the identified areas of connectivity in this area. The mobility of the remaining populations of African elephants is threatened by human presence (Bastille-Rousseau and Wittemyer 2021; Lohay et al. 2022), and projected population growth and associated economic development (Williams et al. 2021a; United Nations 2022) are a threat to the integrity of African elephant populations and other highly mobile species across Africa. With the reported disproportionate growth around the protected areas where most elephant populations find refuge (Wittemyer et al. 2008), carefully managing incoming infrastructure development will be one of the key components to ensure remaining corridors.

Differences in movement behaviors and factors structuring the locations of different corridors were found between males and females, which also has been documented in other populations (Roever et al. 2013; Vogel et al. 2020; Beirne et al. 2021). When evaluating environmental features associated with different corridor types (i.e., fast v. slow) between the sexes, covariates related to water sources primarily structured the different corridor usage types for females while both water and human-related covariates determined different corridor types for males (Supplementary Material Tables S1 and S2; Fig. 4). Similarly, in Samburu, Kenya, water sources were one of the important variables in explaining corridor type, but human presence and productivity-related variables played an important role for both sexes (Bastille-Rousseau and Wittemyer 2021).

Connective movements between the Kunene community-managed area and Etosha National Park were relatively rare. About 4 individuals in our sample of 66 used the corridors between the western part of Etosha National Park and an adjacent Kunene multi-use community area (Fig. 5). The relatively low connectivity may be due to our low sampling in areas with lower density (lack of individuals using both areas). Ensuring the connectivity between the two can benefit both elephant populations (Caughley 1994; Hanski 1999; Bulman et al. 2007) and likely other species (Epps et al. 2011). Our analysis suggested the key connectivity areas between Kunene and ENP are limited and should be prioritized in conservation efforts going forward. The bottleneck in this connective movement could have negative impacts similar to those documented for wildebeest (Morrison and Bolger 2014) and other large mammals with similar space requirements (Crego et al. 2021; Lohay et al. 2022). Areas with higher wildlife protection efforts and lower anthropogenic impacts, such as Etosha National Park, could act as a source population on the landscape (Lee and Bolger 2017). Finally, identifying wildlife corridors and infrastructure crossings (Bastille-Rousseau et al. 2018b) can facilitate protection and land use planning efforts to promote connectivity and ensure long-term population persistence (Morrison and Bolger 2014; Lohay et al. 2022).

This study highlights how the structure of the landscape can influence connectivity adding valuable pieces of information to understanding the movement behavior of this species (Wittemyer et al. 2019). Given the reproductive biology and relatively low population size, ensuring the connectivity between protected areas, such as Etosha National Park, and surrounding buffer areas (Kunene region) could be key in ensuring long-term population persistence for the elephant populations in the region and could be a case study for other areas across Africa amidst the threats facing the species over the next century (Buchignani et al. 2018; Williams et al. 2021b; Gobush et al. 2022).

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Author contribution AC, PL, and GW conceptualize the study. AC wrote the main manuscript, conducted the analyses, and prepared all figures and tables. PL, GW, JS, and KW edited the manuscript. KW collected the data. All authors reviewed the manuscript.

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Data availability Given poaching concerns, the datasets generated or analyzed during the current study are not publicly available but can be made available upon reasonable request via Movebank (ID: 1807299477).

Declarations

Competing interests The authors declare no competing interests.

Ethical approval Animal captures were carried out by veterinarians from the Namibian Ministry of Environment and Tourism following the South African National Standards for Animal Welfare and Care (SABS 2000).

Consent for publication All authors have agreed to publish this manuscript.

References

Aho K, Derryberry D, Peterson T (2014) Model selection for ecologists: the worldviews of AIC and BIC. Ecology 95:631

Bardos DC, Guillera-Arroita G, Wintle BA (2015) Valid automodels for spatially autocorrelated occupancy and abundance data. Methods Ecol Evol 6:1137–1149

Bastille-Rousseau G (2023) moveNT: an R package for the analysis of movement data using network theory

Bastille-Rousseau G, Wittemyer G (2019) Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals. Ecol Lett 22:1417–1427

Bastille-Rousseau G, Wittemyer G (2021) Characterizing the landscape of movement to identify critical wildlife habitat and corridors. Conserv Biol 35:346–359

Bastille-Rousseau G, Douglas-Hamilton I, Blake S, Northrup JM, Wittemyer G (2018a) Applying network theory to animal movements to identify properties of landscape space use. Ecol Appl 28:854–864

Bastille-Rousseau G, Wall J, Douglas-Hamilton I, Wittemyer G (2018b) Optimizing the positioning of wildlife crossing structures using GPS telemetry. J Appl Ecol. https://doi.org/10.1111/1365-2664.13117

Beirne C, Houslay TM, Morkel P, Clark CJ, Fay M, Okouyi J, White LJ, Poulsen JR (2021) African forest elephant movements depend on time scale and individual behavior. Sci Rep. https://doi.org/10.1038/s41598-021-91627-z

Bivand R (2022) R packages for analyzing spatial data: a comparative case study with areal data. Geogr Anal 54:488–518

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. Trends Ecol Evol 23:453–460

Bucchignani E, Mercogliano P, Panitz HJ, Montesarchio M (2018) Climate change projections for the Middle East-North Africa domain with COSMO-CLM at different spatial resolutions. Adv Clim Chang Res 9:66–80

Bulman CR, Wilson RJ, Holt AR, Bravo LG, Early RI, Warren MS, Thomas CD (2007) Minimum viable metapopulation size, extinction debt, and the conservation of a declining species. Ecol Appl 17:1460–1473

Calenge C (2015) Analysis of animal movements in R: the adehabitatLT package. R Foundation for Statistical Computing, Vienna, pp 1–82

Caughley G (1994) Directions in conservation biology. J Anim Ecol 63:215–244

Chan AN, Wittemyer G, McEvoy J, Williams AC, Cox N, Soe P, Grindley M, Shwe NM, Chit AM, Oo ZM, Leimgruber P (2022) Landscape characteristics influence ranging behavior of Asian elephants at the human-wildlands interface in Myanmar. Mov Ecol 10:1–15

Craig GC, Gibson DSC (2016) Aerial survey of elephants and other animals in Northwest Namibia. Ministry of Environment and Tourism & Africa Elephant Fund, UNEP

Crego RD, Wells HB, Ndung'u KS, Evans L, Njeri Nduguta R, Chege MA, Brown MB, Ogutu JO, Ojwang GO, Fennessy J, O'Connor D (2021) Moving through the mosaic: identifying critical linkage zones for large herbivores across a multiple-use African landscape. Landsc Ecol 36:1325–1340

De Boeck P, Bakker M, Zwitser R, Nivard M, Hofman A, Tuerlinckx F, Partchev I (2011) The estimation of item response models with the lmer function from the lme4 package in R. J Stat Softw 39:1–28

Donaldson L, Wilson RJ, Maclean IMD (2017) Old concepts, new challenges: adapting landscape-scale conservation to the twenty-first century. Biodivers Conserv 26:527–552

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

Epps CW, Mutayoba BM, Gwin L, Brashares JS (2011) An empirical evaluation of the African elephant as a focal species for connectivity planning in East Africa. Divers Distrib 17:603–612

Etherington TR (2016) Least-cost modelling and landscape ecology: concepts, applications, and opportunities. Curr Landsc Ecol Rep 1:40–53

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fletcher RJ Jr, Sefair JA, Wang C, Poli CL, Smith TA, Bruna EM, Holt RD, Barfield M, Marx AJ, Acevedo MA (2019) Towards a unified framework for connectivity that disentangles movement and mortality in space and time. Ecol Lett 22:1680–1689

Funk C, Peterson P, Landsfeld M, Pedreros D, Verdin J, Shukla S, Husak G, Rowland J, Harrison L, Hoell A, Michaelsen J (2015) The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes. Sci Data 2:150066

Gelman A, Hill J (2006) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press

Gobush KS, Edwards CTT, Balfour D (2022) THE IUCN RED LIST OF THREATENED SPECIES™

Gorelick N, Hancher M, Dixon M, Simon I, Thau D, Moore R (2017) Google earth engine planetary-scale geospatial analysis for everyone. Remote Sens Environ 2017:18–27

Grolemund G, Wickham H (2011) Dates and times made easy with lubridate. J Stat Software 40:1–25

Hanski I (1999) Metapopulation ecology. Oxford University Press

Huang YH, Kausrud K, Hassim A, Ochai SO, van Schalkwyk OL, Dekker EH, Buyantuev A, Cloete CC, Kilian JW, Mfune JK, Kamath PL (2022) Environmental drivers of biseasonal anthrax outbreak dynamics in two multihost savanna systems. Ecol Monogr. https://doi.org/10.1002/ecm.1526

Huang YH, Owen-Smith N, Henley MD, Kilian JW, Kamath PL, Ochai SO, van Heerden H, Mfune JK, Getz WM, Turner WC (2023) Variation in herbivore space use: comparing two savanna ecosystems with different anthrax outbreak patterns in southern Africa. Mov Ecol. https://doi.org/10.1186/s40462-023-00385-2

Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m database. https://srtmcsi.cgiar.org

Jennings MK, Zeller KA, Lewison RL (2020) Supporting adaptive connectivity in dynamic landscapes. Land 9:295

Kaszta Ż, Cushman SA, Macdonald DW (2020) Prioritizing habitat core areas and corridors for a large carnivore across its range. Anim Conserv 23:607–616

Kennedy CM, Oakleaf JR, Theobald DM, Baruch-Mordo S, Kiesecker J (2019) Managing the middle: a shift in conservation priorities based on the global human modification gradient. Glob Chang Biol. https://doi.org/10.1111/gcb.14549

Kilian JW (2015) Aerial survey of Etosha National Park. Internal Report to the Ministry of Environment and Tourism

Kumar SU, Turnbull J, Hartman Davies O, Hodgetts T, Cushman SA (2022) Moving beyond landscape resistance: considerations for the future of connectivity modelling and conservation science. Landsc Ecol 37:2465–2480

Lee DE, Bolger DT (2017) Movements and source–sink dynamics of a Masai giraffe metapopulation. Popul Ecol 59:157–168

Leggett KEA (2006) Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. Afr Zool 41:17–36

Lohay GG, Riggio J, Lobora AL, Kissui BM, Morrison TA (2022) Wildlife movements and landscape connectivity in the tarangire ecosystem. In: Christian K, Bond ML, Lee DE (eds) Tarangire human-wildlife coexistence in a fragmented ecosystem. Springer International Publishing, Cham, pp 255–276

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724

Morrison TA, Bolger DT (2014) Connectivity and bottlenecks in a migratory wildebeest *Connochaetes taurinus* population. Oryx 48:613–621

Osipova L, Okello MM, Njumbi SJ, Ngene S, Western D, Hayward MW, Balkenhol N (2019) Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. Anim Conserv 22:35–48

Peters RH (1986) The ecological implications of body size. Cambridge University Press

Polansky L, Kilian W, Wittemyer G (2015) Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. Proce R Soc B Biol Sci 282:20143042–20143042

QGIS Development Team (2019) QGIS geographic information system

R Core Team (2020) R: A Language and Environment for Statistical Computing

Riggio J, Foreman K, Freedman E, Gottlieb B, Hendler D, Radomille D, Rodriguez R, Yamashita T, Kioko J, Kiffner C (2022) Predicting wildlife corridors for multiple species in an East African ungulate community. PLoS ONE. https://doi.org/10.1371/journal.pone.0265136

Roever CL, van Aarde RJ, Leggett K (2013) Functional connectivity within conservation networks: delineating corridors for African elephants. Biol Conserv 157:128–135

Rudnick DA, Ryan SJ, Beier P, Cushman SA, Dieffenbach F, Epps CW, Gerber LR, Hartter J, Jenness JS, Kintsch J, Merenlender AM (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues Ecol 16:1–23

SABS (2000) South African standard: translocation of certain species of wild herbivore (1st ed.)

Sing T, Sander O, Beerenwinkel N, Lengauer T (2005) ROCR: visualizing classifier performance in R. Bioinformatics 21:7881

Sirko W, Kashubin S, Ritter M et al (2021) Continental-Scale Building Detection from High Resolution Satellite Imagery. CoRR. https://arxiv.org/abs/2107.12283

Songhurst A, McCulloch G, Coulson T (2016) Finding pathways to human-elephant coexistence: a risky business. Oryx 50:713–720

Stabach JA, Wittemyer G, Boone RB, Reid RS, Worden JS (2016) Variation in habitat selection by white-bearded wildebeest across different degrees of human disturbance. Ecosphere. https://doi.org/10.1002/ecs2.1428

Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, Ali AH, Allen AM, Attias N, Avgar T, Bartlam-Brooks H (2018) Moving in the anthropocene: global reductions in terrestrial mammalian movements. Science 359:466–469

United Nations (2022) Population. In: World population prospects. https://www.un.org/en/global-issues/population. Accessed 20 May 2023

Vogel SM, Lambert B, Songhurst AC, McCulloch GP, Stronza AL, Coulson T (2020) Exploring movement decisions: can Bayesian movement-state models explain crop consumption behaviour in elephants (*Loxodonta africana*)? J Anim Ecol 89:1055–1068

Wall J, Wittemyer G, Klinkenberg B, LeMay V, Blake S, Strindberg S, Henley M, Vollrath F, Maisels F, Ferwerda J, Douglas-Hamilton I (2021) Human footprint and protected areas shape elephant range across Africa. Curr Biol 31(11):2437–2445

Wall J, Hahn N, Carroll S, Mwiu S, Goss M, Sairowua W, Tiedeman K, Kiambi S, Omondi P, Douglas-Hamilton I, Wittemyer G (2024) Land use drives differential resource selection by African elephants in the Greater Mara Ecosystem, Kenya. Mov Ecol 12:11

Wickham H (2016) ggplot2: elegant graphics for data analysis

Wickham H, François R, Henry L, Müller K (2020) dplyr: a grammar of data manipulation. Cran

Williams DR, Clark M, Buchanan GM, Ficetola GF, Rondinini C, Tilman D (2021a) Proactive conservation to prevent habitat losses to agricultural expansion. Nat Sustain 4(4):314–322

Williams JW, Ordonez A, Svenning JC (2021b) A unifying framework for studying and managing climate-driven rates of ecological change. Nat Ecol Evol 5:17–26

Wilson MFJ, O'Connell B, Brown C, Guinan JC, Grehan AJ (2007) Multiscale terrain analysis of multibeam

bathymetry data for habitat mapping on the continental slope. Mar Geodesy 30:3
Wittemyer G, Elsen P, Bean WT, Burton ACO, Brashares JS (2008) Accelerated human population growth at protected area edges. Science 321:123–126
Wittemyer G, Northrup JM, Blanc J, Douglas-Hamilton I, Omondi P, Burnham KP (2014) Illegal killing for ivory drives global decline in African elephants. Proc Natl Acad Sci USA 111:13117–13121
Wittemyer G, Northrup JM, Bastille-Rousseau G (2019) Behavioural valuation of landscapes using movement data. Phil Trans R Soc B 374:46