

A multigenerational perspective on elephant family ranging in Amboseli, Kenya

Vicki Fishlock^{1}, Harvey Croze¹, Phyllis C Lee^{1,2}, Keith Lindsay¹, Norah Njiraini¹, Catherine Sayialel¹, Cynthia Moss¹*

¹Amboseli Trust for Elephants, PO Box 15135, Langata 00509, Nairobi, Kenya.

²Faculty of Natural Sciences, University of Stirling, Stirling, Scotland.

*Correspondence: vfishlock@elephanttrust.org

Submission date: 20 February 2026 | **Accepted date:** 29 June 2026

Orcid: 0000-0002-9439-0307

Abstract

Throughout their range, elephants have substantial ecological and socio-economic impacts as well as being of high conservation value; and their ranging patterns and habitat use receive significant research and policy attention. Although relatively small, the elephant population of the Amboseli ecosystem is part of an open population of African savannah elephants, that connects multi-use landscapes and protected areas (PAs) in Kenya and Tanzania. The study population for the Amboseli Elephant Research Project (AERP) has steadily increased in size over time, largely due to the traditional tolerance of Maasai communities, which has evolved into successful community-led conservation efforts. In this paper, we investigate the ranging patterns of elephant families over the very long term, using encounter data on individually recognized elephants in the central Amboseli study zone to classify stability and shifts of space use over generations. We restricted data to families known to the monitoring team for over 30 years, and classified family range use as Central, Peripheral or Shifting depending on the frequency with which they used the central study zone. Central and Peripheral families were distinguished by time spent in the central zone, with little long-term change. Shifting families showed significant changes (most often declines) in central zone use; average sightings declined from a mean 27.3% to 14.9% of total observation days. We examine family sizes to demonstrate that there was no relationship between family size and ranging strategy. Finally, we present multigenerational collaring data for one family using each strategy. Using these complementary datasets, we show how community-based protection strategies coupled with conservation efforts in Amboseli have enabled elephants to maintain and adapt their ranges.

Additional Keywords: long-term monitoring, landscape connectivity, behavioural flexibility.

Résumé

Partout où ils sont présents, les éléphants montrent qu'ils ont un fort impact écologique et socio-économique

et qu'ils sont d'une valeur considérable en matière de conservation. Leurs schémas de déplacement et l'usage de leur habitat font l'objet d'une grande attention en termes de recherche et d'élaboration de politiques. Les éléphants de l'écosystème d'Amboseli font partie d'une population ouverte d'éléphants de savane d'Afrique qui, bien que relativement petite, connecte des paysages multifonctionnels et des zones protégées au Kenya et en Tanzanie. La population étudiée dans le cadre du projet de recherche sur les éléphants d'Amboseli (AERP) n'a cessé d'augmenter au fil du temps, en grande partie grâce à la tolérance traditionnelle de la part des communautés masai – une tolérance qui a conduit à des actions de conservation couronnées de succès, menées par les communautés elles-mêmes. Dans cet article, nous étudions les schémas de répartition des familles d'éléphants sur le très long terme, en utilisant des données d'observation portant sur des sujets individuellement identifiés dans la zone d'étude centrale du parc d'Amboseli, afin de classer la stabilité et les variations dans l'usage de l'espace au fil des générations. Nous avons limité les données à recueillir aux familles d'éléphants connues depuis plus de trente ans par l'équipe chargée du suivi, et avons classé l'utilisation de l'aire de répartition dans les catégories «centrale», «périphérique» ou «en alternance», selon la fréquence à laquelle la zone d'étude centrale était parcourue par les éléphants. Les familles montrant une utilisation «centrale» et «périphérique» se distinguaient par leur temps passé dans la zone centrale, sans changement notable à long terme. Les familles se caractérisant par un usage «en alternance» faisaient preuve d'une utilisation très mouvante (et le plus souvent déclinant au fil du temps) dans leur occupation de la zone centrale, avec des éléphants répertoriés en moyenne sur 27,3 % du total des jours d'observation, puis se réduisant à 14,9 % de la période. Nous analysons ici la taille des familles afin de démontrer qu'il n'existait pas de relation entre ce critère et la stratégie de déplacement. Enfin, nous présentons, pour chacune des stratégies, les données de suivi par collier GPS recueillies sur plusieurs générations d'une même famille. Grâce à ces ensembles de données complémentaires, nous montrons combien des stratégies de protection menées par les communautés associées aux actions de conservation au sein du parc d'Amboseli ont permis aux éléphants de préserver et d'adapter leur aire de répartition.

Mots-clés supplémentaires: Suivi à long terme, connectivité paysagère, flexibilité comportementale

Introduction

Where and how elephants move to exploit resources across landscapes has major impacts on those landscapes and the coexisting people, plants and animals. Quantitatively assessed by Leuthold and Sale (1973) and reviewed by Wall et al. (2021), African savannah elephant (*Loxodonta africana*) space use is influenced by environmental conditions (Burton-Roberts et al. 2022; Kuria et al. 2024), sex and life history stages (Fishlock et al. 2023; Kuria et al. 2024; Mandinyenya et al. 2024), habitats, landscape, and human activity (Goldenberg et al. 2018; Wall et al. 2021) and is, above all, highly variable among individuals and family groups. Studies commonly report orders-of-magnitude differences in range size among subjects in the same landscape. Elephant range is also socially learned (McComb et al. 2001; Pinter-Wollman et al. 2008), probably inherited by females (Charif et al. 2005; Fishlock et al. 2016) and flexible

through repopulation and range expansions (Chase et al. 2011).

Elephant ranging decisions therefore reflect a balance of social and ecological opportunities and risks (Goldenberg et al. 2018). The elephant population using Amboseli National Park (NP) in southern Kenya has shown slow but steady growth since the start of the long-term research programme from ~600 in 1972 to 2,200 at present. The small founder population was protected from poaching and escaped later poaching resurgences seen in other parts of Kenya, owing to the efforts of community members and conservation partners (Maingi et al. 2012). Amboseli's multi-use landscape has maintained biodiversity because traditional transhumant land and resource-use practices tolerate wildlife, and this provides the cornerstone of modern conservation practices (Reid 2012). Although challenges in this coexistence landscape have long been flagged (Okello et al. 2009) and are of growing concern, the net result for elephants to date has been a safe, open landscape where elephant movements remain largely unrestricted (Fig. 1).

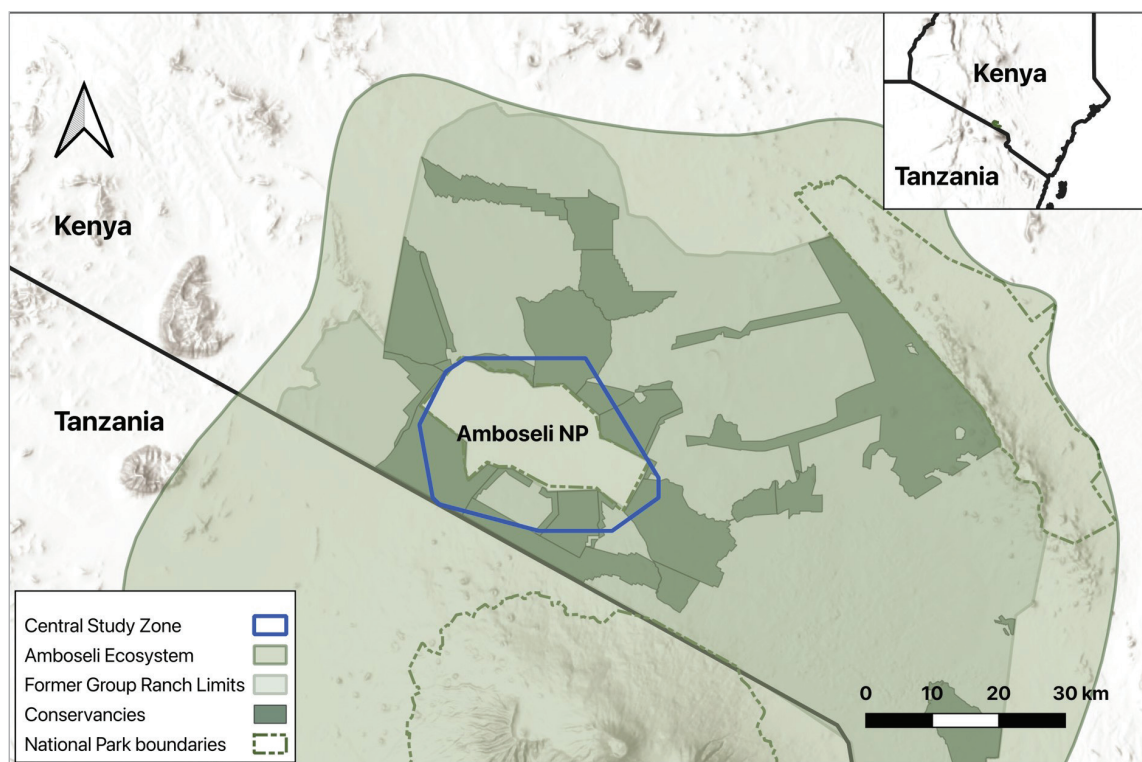


Figure 1. Amboseli ecosystem, PAs and conservancies. The map shows the outline of six former group ranches (Eselengei, Kimana, Kuku-A and Kuku-B, Mbirikani, Olgulului-Olororashi) where pastoralism was the primary land use prior to subdivision which began in 2020. Areas outside conservancies and PAs comprise a mixed-use landscape including pastoralism, tourism, settlement, and expanding agriculture. Greater Amboseli ecosystem is an approximate boundary.

Since 1972, the AERP monitoring team has tracked individual life histories and the social dynamics of elephants born into Amboseli families, and over half a century, we have noted shifts in how some families use the landscape. Here we explore the population-wide occurrence of range shifts over the very long term, extending work by Goldenberg et al. (2018) in Samburu and addressing the suggestion that “no accurate assessment of the lifetime range of a free-ranging elephant has been made” (Osborn 2004). Amboseli’s history as an undisturbed baseline elephant population (Moss et al. 2011) makes these patterns of particular interest for considering the consequences of long-term landscape changes. Amboseli also represents a landscape of coexistence, where elephants and other wildlife range across a mosaic of land use and habitat types. As this coexistence is under increasing pressure, maintaining connectivity will require landscape-scale planning that integrates PAs

with surrounding rangelands and balances wildlife conservation with pastoral livelihoods and other competing land uses.

Previous work in Amboseli mapped family occupancy within the core study area and identified both seasonal and annual patterns of space use by neighbourhoods of families (Croze and Moss 2011). Data from nine collared females, supplemented by opportunistic observations by community scouts, further demonstrated extensive use of habitats outside Amboseli NP. In this paper, we deepen this perspective by combining long-term direct sightings of recognized families in the central study zone with collar data spanning the late 1970s to the present. We classified family ranging strategies as Central, Peripheral or Shifting based on long-term patterns of use of the central study zone, quantified using occupancy and temporal trends in sightings. We then used collar data from representative families to independently corroborate these strategy classifications.

Methods

All data manipulations and statistical analyses were conducted in R (R Core Team 2024) within RStudio (RStudio Team 2022) using standard tidyverse packages (e.g. dplyr, purrr, lme4, ggplot2) unless otherwise stated. Maps were produced from R shapefile manipulations in QGIS version 3.32.0, with the addition of a hillshade layer from ESRI (accessed November 2025). All figures and maps were created by the authors. Elephant groups were monitored following the methods in Moss et al. (2011); field teams selected their observation route based on their experience and likely areas of elephant use, rather than following transects, and preferentially allocate observations to rarely seen groups. Elephants were recorded once per observation day, in the first group sighted. Monitoring was therefore opportunistic rather than systematically effort-standardized, and observer coverage varied spatially and temporally with accessibility and field logistics. Consequently, reported sighting frequency reflects both elephant space use and observation effort. Nonetheless, the dataset spans more than 50 years with broad ecosystem coverage and repeated sampling of known individuals and family groups, providing a robust basis for analysing long-term population patterns. To minimize bias arising from uneven temporal observation effort, analyses were restricted to months with more than 10 observation days.

Occupancy modelling

We calculated the average number of months per year that families were sighted in the central study area for 50 families, known since 1975 for at least 30 years, or that had split from known families prior to 2005. We excluded family units that had recently split to avoid biasing the data towards elephants undergoing shifting social and/or ecological strategies, which is a key driver of family splits (Wittemyer et al. 2005). The central area was defined as the parts of Amboseli NP and its surroundings that were accessible to and therefore regularly monitored by research teams (~800 km²; Fig. 1).

To estimate long-term trends in the use of the central area, we fitted a linear model of monthly occupancy (NMonthsSeen ~ Year) for each

family. The slope values from the model describe temporal trends in occupancy, and mean fitted values represent average use intensity for each year. Families were subsequently allocated strategy categories based on these two metrics. We calculated family visibility as the number of months a family was observed in a given year, irrespective of strategy. We then derived visibility statistics for each family over time by computing the average number of observation days per month, using data from 521 months from 1975 in which we conducted more than 10 survey days (median 17 days per month, range 10–30).

Family and group sizes

Elephant ranging and grouping decisions reflect social and ecological opportunities and risks, so we examined both family and recorded group sizes for each strategy type based on 40,000 sightings from long-term monitoring (Moss et al. 2011). We determined family size from our demographic dataset, as the number of individuals alive and resident in the family (including pre-dispersal males), and calculated the average family size per decade. We used decades as the time unit for analysis, as this appropriately captures medium-term environmental changes such as droughts and recovery; landscape-level changes in livestock grazing, human infrastructure and settlements that affect elephant behaviour; and population dynamics such as family-member maturation, dispersal, births and deaths that might affect ranging decisions. Because socio-ecological strategies were not evenly distributed across decades (with “shifters” represented primarily since the 2000s), we fitted models without any strategy × decade interaction. This approach avoids confounding temporal and sampling effects while allowing us to test for main effects of decade (as a proxy of change) and strategy on family or group size.

Range sizes

To estimate range use over time, we used locations derived from collars deployed on female elephants from three family units (IB, MB, VA) (Table 1). Early collars (1977–79, 1996–89) were VHF¹ models that used aerial searches to determine elephant locations, while later collars (2008–present) were GSM² models that record locations remotely. Because the number

¹VHF = Very High Frequency radio waves

²GSM = Global System for Mobile Communications

Table 1. Details of collars deployed on female elephants since 1977. For GSM collars, we thinned fixes to three per month to match the approximate number of VHF flight-based locations.

ID	Family	Birth year	Collared	Collar type	No. of points used
Virginia	VA	1928	1977	VHF	18
Isis	IB	1936	1979	VHF	18
Maggie	MB	1942	1979	VHF	16
Vicky	VA	1969	1996–98	VHF	19
			2008–09	GSM	54
			2011–12	GSM	63
Maude	MB	1969	1996–98	VHF	19
Ida	IB	1983	2011–13	GSM	69
Maureen	MB	1980	2011–13	GSM	84
Vvork	VA	2001	2021–24	GSM	117

of fixes for VHF collars is inherently low, we determined the median monthly fixes per VHF collar and used this figure to thin our GSM dataset before calculating annual Minimum Convex Polygons (MCPs). Because GSM deployments often spanned multiple years, we constructed MCPs annually. This avoids inflating home-range estimates due to longer collar duration and reduces the risk of conflating interannual environmental variation with movement patterns. We calculated MCPs in R using the *sf* package (Pebesma 2018) and plotted these in QGIS using the AniMove plugin. For overlap statistics, we used the *st_intersection* function from the *sf* package to quantify individual site fidelity for females with collars lasting more than one year, calculating the proportion of each range reused in the subsequent year. To assess longer-term range overlaps (same family, different decades), we used a symmetric overlap index to capture overall spatial consistency across sequential periods, calculated as the mean proportion of ranges that overlapped across sequential periods.

Results

Occupancy modelling

For families tracked for more than five years, elephant families spent a median of 7.4 months using the central area per year (*n* = 64 families, range 3–11 months, mean 7.36 ± 2.93 SD). Trends in monthly occupancy for 50 families known for

at least 30 years showed a mix of ranging strategies (Table 2). Families with stable occupancy patterns (low slope changes) were divided into Central or Peripheral groups based on an occupancy threshold of eight months per year. For 13 families exhibiting obvious changes in central area occupancy, we calculated absolute slopes and used the median as the threshold for slope change that designated families as Shifting (Table 2, Fig. 2). Average visibility of families who shifted range dropped from a mean of 27.3% to 15.0% of observation days, whereas Central families were consistently visible for 20–24% of observation days across all decades.

Family and group sizes

Amboseli families showed a general increase in size across the course of the study. A mixed-effects model including family identity as a random effect indicated that decade strongly influenced family size as expected ($\chi^2_{(5)} = 2985.5$, *p* < 0.001). However, family size did not differ by ranging strategy ($\chi^2_{(2)} = 4.0$, *p* = 0.13; Fig. 3A), indicating that strategy was independent of family size. Encountered group sizes showed a downward trend across the study (Fig. 3B), but this trend was similarly influenced by decade effects, not family ranging strategy (decade: $\chi^2_{(5)} = 2829.2$, *p* < 0.001; strategy: $\chi^2_{(2)} = 2.33$, *p* = 0.069).

Range sizes

Annual MCP sizes were highly variable among collared females and across years, as reported in most

Table 2. Strategy classification for Amboseli families based on monthly occupancy of the central study zone.

Strategy	Criterion		No. of families	Mean fitted occupancy (mo/yr)
	Absolute slope	Mean fitted occupancy (mo)		
Central	<0.16	≥ 8	20	9.59
Peripheral	<0.16	< 8	17	5.88
Shifting	≥ 0.16		13	7.28

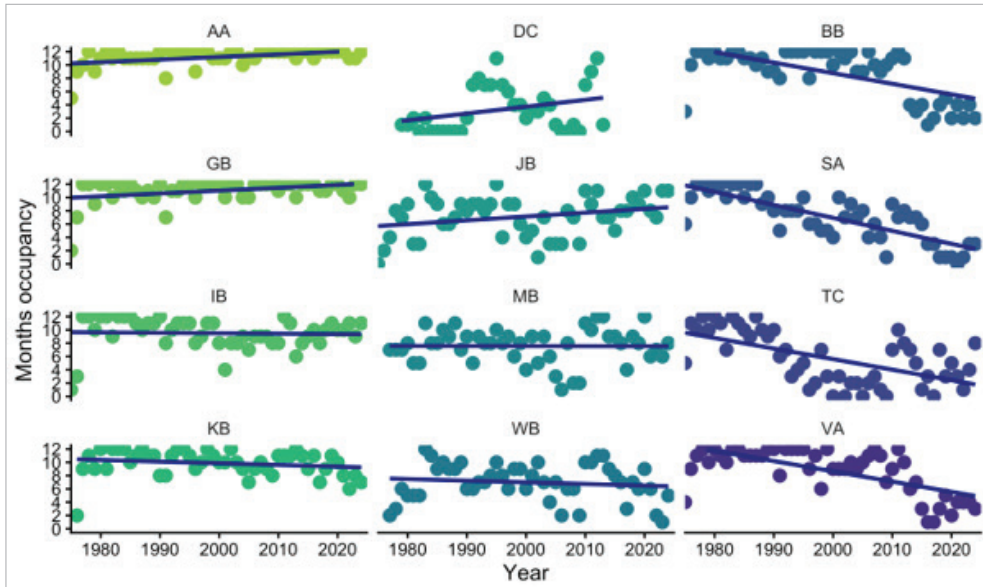


Figure 2. Occupancy patterns for example families showing Central (left), Peripheral (centre) and Shifting (right) ranging strategies over five decades. Labels above the graphs indicate family ID codes.

previous studies, including previous work from Amboseli (range 34–1,158 km²: Fig. 4A). Despite this variation, family range sizes were consistent between the earliest and most recent collaring periods, especially for the Shifting family, VA, for which we had the most comprehensive dataset. Annual site fidelity, measured as the proportion of the annual range reused each subsequent year, was also variable (Fig. 4B) and slightly lower than reported from elsewhere (Kuria et al. 2024; Gathuku and Wittemyer 2025), although this may partly reflect the influence of a drought in 2022–23 on data for one collared individual (Vvork). Estimates may also be conservative because we used MCP rather than kernel density methods to include data from early VHF collars, which is why we don't directly compare this analysis with

previous estimates of range size for our ecosystem. Long-term comparisons of annual MCP overlap (Fig. 4B, Fig. 5) supported the ranging strategies identified from family sightings. Central and Peripheral families showed substantial spatial overlap between collaring periods, indicating stable long-term range use, whereas the Shifting family showed reduced overlap and a clear shift in range location through time.

Discussion

We present results that highlight elephants' flexibility and capacity for change. Amboseli's elephant population is undoubtedly thriving. Over the long term, or an elephant's lifetime, while some families have remained small or gone extinct, we show that many have grown in size and also changed how

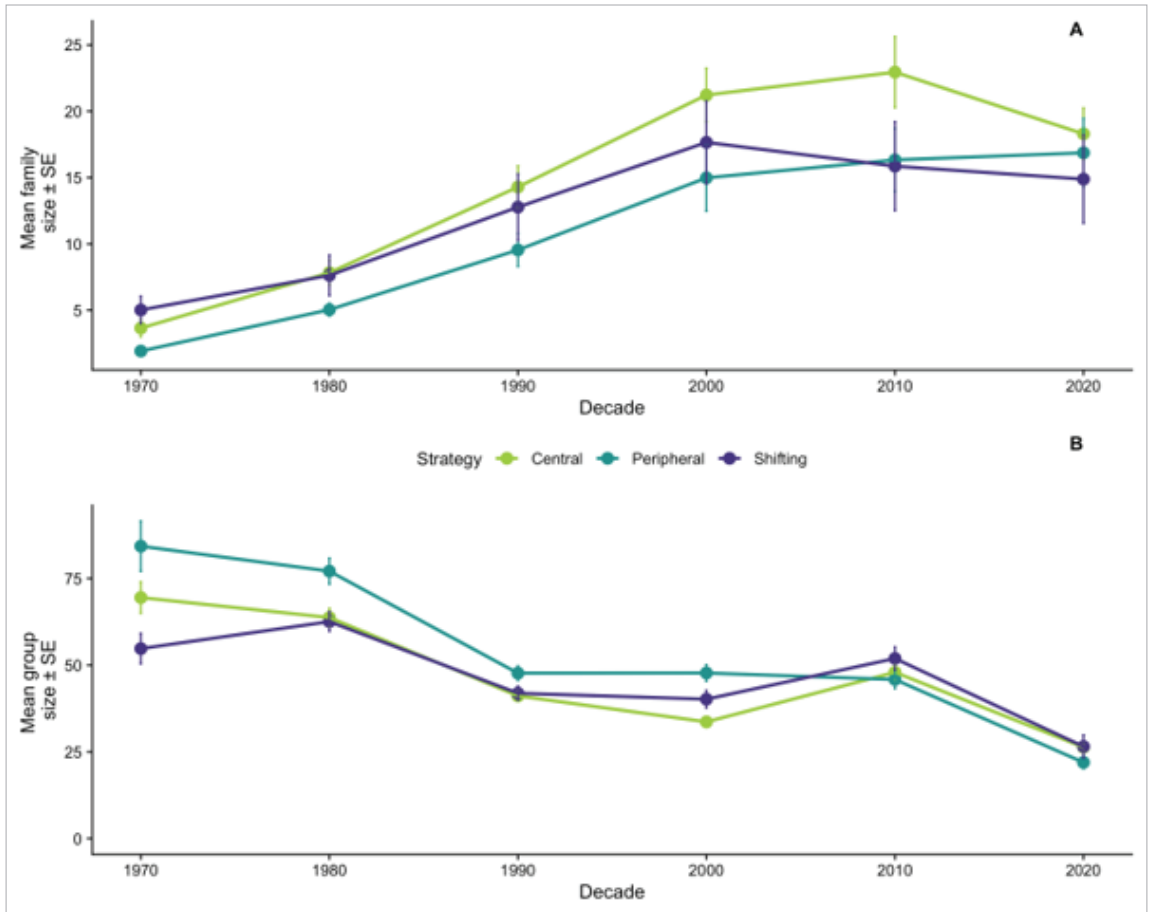


Figure 3. Long-term changes in family and group sizes in relation to ranging strategy. Relatively large group sizes in the 1970s and 1980s were attributed to elephants seeking refuge in Amboseli NP, which allowed them to avoid livestock and people after the Park's gazettement took effect in 1976. Since the 1990s, increased community tolerance and improved security have allowed elephants to disperse more widely across the landscape resulting in smaller group sizes being encountered. Sample periods and numbers of families: 1975–79 50/families, 1980 and 1990/55 families; 2000/63 families; 2010/66 families; 2020-year range 2020–2025/68 families.

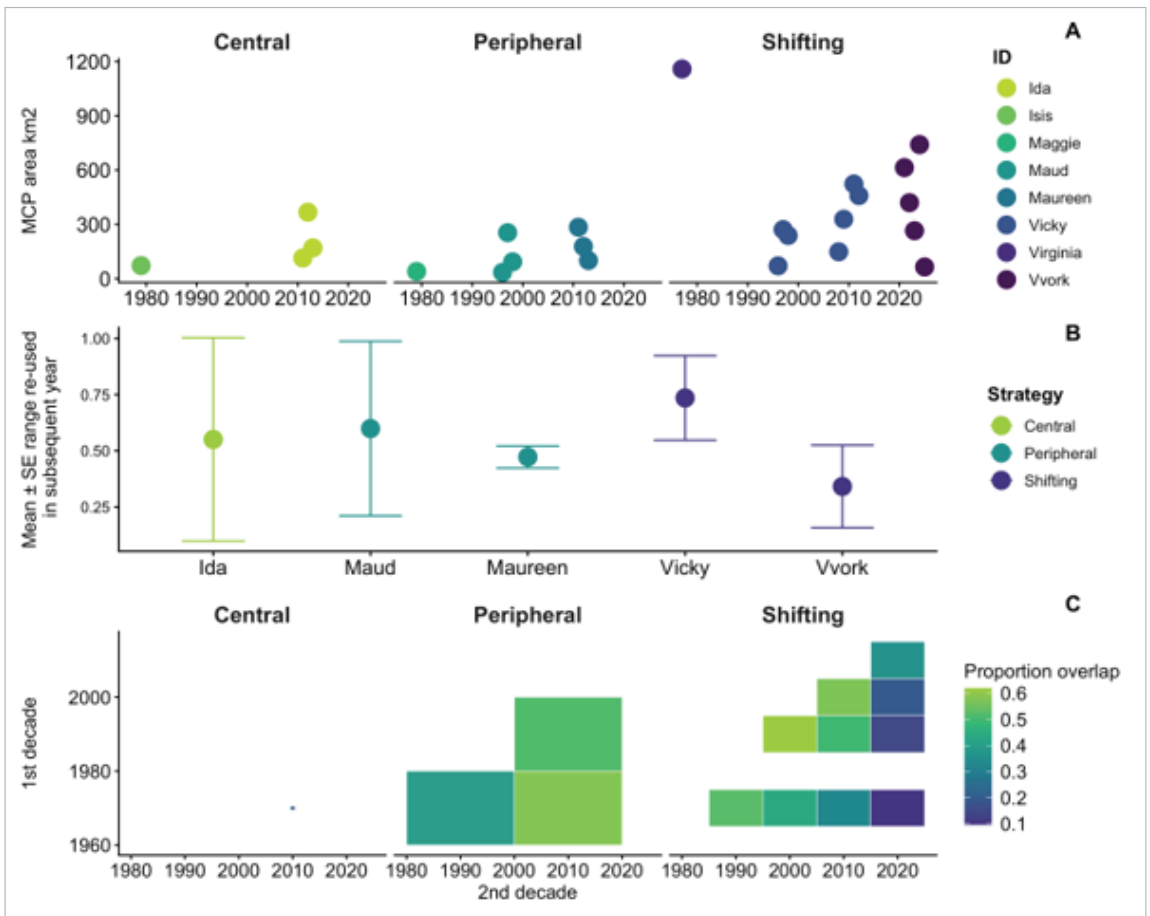


Figure 4. Collar data metrics for Central (IB), Peripheral (MB) and Shifting family (VA) over decades: (A) annual MCP area ranges; (B) annual range re-use (fidelity) as a proportion of previous years' range; (C) symmetrical overlap in ranges between sequential decades for each strategy type.

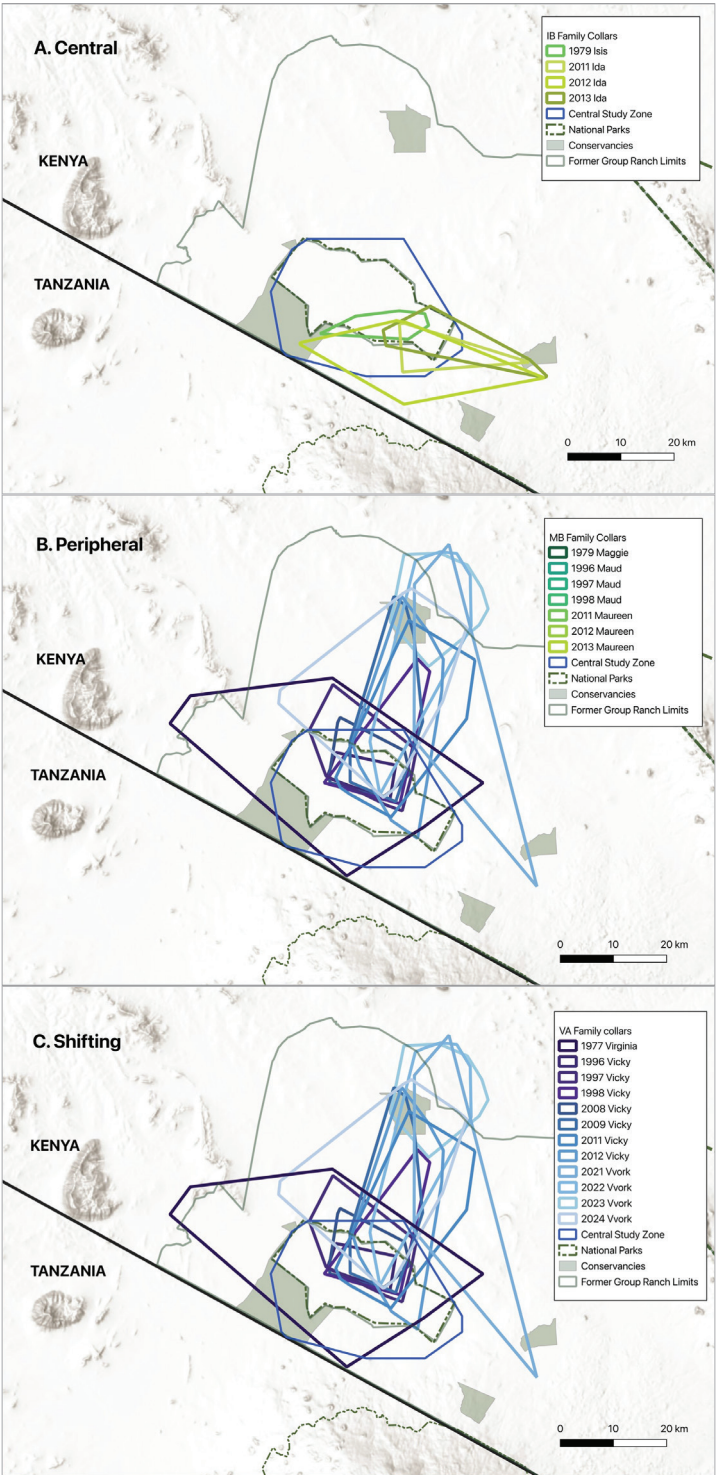


Figure 5. Annual MCP ranges for 10 females collared over 14 years for (A) Central family, (B) Peripheral family; and (C) Shifting family MCPs are shown to illustrate spatial overlap between collaring periods and long-term range stability; differences in polygon area are not intended as a comparison of annual range size among families.

they use the landscape and its resources. Some ranging strategies are stable over generations, despite membership changes affecting leadership and family size, yet a significant proportion of families have opportunistically shifted their range use. Although these shifts are mostly captured through encounters, rather than tracking data, the long-term stability of our study methods and the size of the families involved make us confident that these conclusions represent true spatial shifts.

Range shifts may reflect responses to local environmental pressures, such as water availability or grazing competition, but may also represent new movement strategies that develop over generations, as an undisturbed population is free to explore a landscape. These changes, therefore, reflect success: elephants exploiting available habitat and resources and accruing reproductive success as a result. In Amboseli, these are also human successes: the establishment of community conservancies and strong community-led conservation support across a multi-use landscape have rendered Amboseli a stronghold for wildlife and created landscape security for elephants that allows them to explore and adapt. Results from the Samburu ecosystem (Goldenberg et al. 2016) showed that stable matriarchal units exhibit long-term fidelity to core ranges, while peripheral (disturbed) families tracked resources opportunistically across a human-dominated landscape. Amboseli provides a contrasting example, where high tolerance and strong coexistence allow both stable and shifting ranging strategies to persist in a connected system, with population links to the greater Tsavo ecosystem, northern Tanzania and the Southern Rift.

Shifting ranging strategies may not be the norm for elephants, as indicated by high site fidelity shown in some long-term tracking analyses (Gathuku and Wittemyer 2025), but they are not rare either, and this flexibility in home ranges warrants attention in conservation planning. Designing PAs or corridors based on past use may be no guide to future elephant needs or movements, especially in the light of land-use changes and climate change. Permanent shifts in range use can also be precipitated by conservation decisions, such as the provision of

water or shifts in livestock management, which reduce competitive pressures. We suggest that thinking of elephant ranging as static or fixed is a mistake. Instead, elephants' capacity for flexibility should be incorporated in conservation planning frameworks as a design tool to mediate interactions between human and elephant communities. This is particularly important in landscapes where coexistence paradigms are rapidly shifting in response to land use changes and human population growth (Tiller and Williams 2021).

Success in conservation planning requires that Kenya's nascent land use policies and plans are well-resourced and properly enforced and integrated with local and national-level conservation planning frameworks. While elephant flexibility enables persistence amid change, it also relies on maintaining permeable coexistence landscapes, in which human tolerance is well-supported. Behavioural flexibility on both sides requires that humans and elephants are able to exercise behavioural and livelihood flexibility, which in turn depends on protecting the ecological and social conditions, including perceived safety, that enable such adaptive responses. Land use policies and conservation practices cannot rely too heavily on the goodwill of rights holders without addressing the challenges of sharing space with wildlife in the face of climate change and economic shifts. Amboseli's elephants demonstrate that conservation success is measured not only in numbers but also in the space and choices available to wildlife over its use. Recognizing and accommodating this dynamism is crucial to sustaining coexistence in the future.

Acknowledgements

We thank Amboseli's Maasai landowners for their tolerance of Amboseli Trust for Elephants' research and the elephants. We also thank our ecosystem partners, Big Life, Amboseli Ecosystem Trust, Kenya Wildlife Service and Wildlife Research and Training Institute. All research was carried out in full compliance with permitting and ethical requirements from the Office of the President. Current NACOSTI licence 850117.

References

Burton-Roberts R, Cordes LS, Slotow R, Vanak AT, Thaker M, Govender N, Shannon G. 2022. Seasonal

range fidelity of a megaherbivore in response to environmental change. *Scientific Reports* 12 (1): 22008.

Calabrese JM, Fleming CH. 2016. ctmm: An R package for analysing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution* 7 (9): 1124–1132.

Charif RA, Ramey RR, Langbauer Jr WR, Payne KB, Martin RB, Brown LM. 2005. Spatial relationships and matrilineal kinship in African savannah elephant (*Loxodonta africana*) clans. *Behavioural Ecology and Sociobiology* 57 (4): 327–338.

Chase MJ, Griffin CR. 2011. Elephants of south-east Angola in war and peace: their decline, re-colonization and recent status. *African Journal of Ecology* 49 (3): 353–361.

Croze H, Moss CJ. 2011. Patterns of occupancy in time and space. In: Moss CJ, Croze H, Lee PC (Eds.). *The Amboseli Elephants: a long-term perspective on a long-lived mammal*. University of Chicago Press. Chicago, pp. 89–105.

Fishlock V, Caldwell C, Lee PC. 2016. Elephant resource-use traditions. *Animal Cognition* 19 (2): 429–433.

Fishlock V, Tiller L, Njiraini N, Sayialel C, Lee P, Moss C, Mukenka J, Ngene S, Omondi P. 2023. Bridging the Rift: demonstrating large mammal landscape connectivity from Amboseli National Park to the greater Maasai Mara. *Pachyderm* 64: 107–111.

Gathuku NM, Wittemyer G. 2025. Identification of key landscape drivers of range size and range shifts in African savannah elephants in northern Kenya. *Landscape Ecology* 40 (11): 212.

Goldenberg SZ, Douglas-Hamilton I, Wittemyer G. 2018. Inter-generational change in African elephant range use is associated with poaching risk, primary productivity and adult mortality. *Proceedings of the Royal Society B: Biological Sciences* 285 (1879): 20180286.

Kuria LW, Kimuyu DM, Kinyanjui MJ, Wittemyer G, Ihwagi FW. 2024. Seasonal variation in the ranging behaviour of elephants in the Laikipia–Samburu ecosystem. *Ecology and Evolution* 14 (8): 70198.

Leuthold W, Sale JB. 1973. Movements and patterns of habitat utilization of elephants in Tsavo National Park, Kenya. *African Journal of Ecology* 11 (3–4): 369–384.

Maingi JK, Mukenka JM, Kyale DM, Muasya RM. 2012. Spatiotemporal patterns of elephant poaching in south-eastern Kenya. *Wildlife Research* 39 (3): 234–249.

Mandinyanya B, Mingione M, Traill LW, Malatesta L, Attorre F. 2024. Sex differences in home range and habitat use by savannah elephants in Gonarezhou National Park, Zimbabwe. *Pachyderm* 65: 104–118.

Moss CJ, Croze H, Lee PC. (Eds.), 2011. *The Amboseli elephants: a long-term perspective on a long-lived mammal*. University of Chicago Press, Chicago.

McComb K, Moss C, Durant SM, Baker L, Sayialel S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science* 292 (5516): 491–494.

Okello MM, Njumbi SJ, Kiringe JW, Isiche, J. 2015. Habitat use and preference by the African elephant outside of the protected area, and management implications in the Amboseli Landscape, Kenya. *International Journal of Biodiversity and Conservation* 7 (3): 211–226.

Osborn F. 2004. The concept of home range in relation to elephants in Africa. *Pachyderm* 37: 37–44.

Pebesma E. 2018. Simple features for R: standardized support for spatial vector data. *The R Journal* 10 (1): 439–446.

Pinter-Wollman N, Isbell LA, Hart LA. 2008. The relationship between social behaviour and habitat familiarity in African elephants (*Loxodonta africana*). *Proceedings of the Royal Society B: Biological Sciences* 276 (1659): 1009–1014.

R Core Team. 2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL: <https://www.R-project.org/>

RStudio Team. 2022. RStudio: integrated development environment for R. RStudio, PBC, Boston. URL: <https://www.rstudio.com/>

Reid R. 2012. *Savannahs of our birth: people, wildlife, and change in East Africa*. University of California Press, Berkeley.

Tiller LN, Williams HF. 2021. The elephant in the farm: long-term solutions are the key to coexistence. *Animal Conservation* 24: 733–734.

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. *Current Biology* 31 (11): 2437–2445.

Wittemyer G, Douglas-Hamilton I, Getz WM. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour* 69: 1357–1371.