ANNUAL REPORT

2022

AMBOSELI TRUST FOR ELEPHANTS

www.elephanttrust.org

TABLE OF CONTENTS

I. Introduction

Misson Statement

The Amboseli Elephant Research Project is the world's longest continuous elephant research programme. ATE contributes trailblazing knowledge of large mammal socioecology, provides a basis for public understanding and concern for elephants and their ecosystems, and communicates information enhancing conservation in the Amboseli ecosystem and for regional and global elephant populations.

Famous male elephant Craig, born the same year the project began

LC matriarch Libby, born the same year as our study began, and now 50 years old

Introduction

In September 2022, the Amboseli Trust for Elephants celebrated 50 years of continuous observation of the elephants in the Amboseli ecosystem. We use this report to highlight some of the most interesting findings from the research by the Amboseli Elephant Research Team on elephants, their movements and use of the ecosystem, and their behaviour and social dynamics. Most members of the research team have been with us for over 10 years, and some for more than 40 years. We have also had many excellent collaborators joining the team, again some for most of the project's timespan.

We would like to thank those people in the ecosystem who have made the project possible over 50 years. Firstly we thank the Maasai landowners and individuals that have enabled coexistence with elephants, and secondly our ecosystem partners: the Wildlife Training and Research Institute (WRTI), the Kenya Wildlife Service (KWS), the Group Ranches and Community Conservancies, Amboseli Ecosystem Trust and Big Life Foundation. We also thank our collaborators, our Trustees and all our donors for their sustained interest in our research results and for their support in protecting the elephants and ecosystem of the Amboseli ecosystem.

Several notable events occurred in 2022 in addition to our 50th anniversary. We entered a sustained La Niña dry period, which has negatively impacted all ecosystem residents human, livestock and wildlife.

The elephant population numbered over 1900 at the end of 2022, and we have been able to track almost 4000 elephants from birth to death. Although the Amboseli population at ~2000 is small by comparison to other Kenyan regions (Tsavo, ~16,000; Laikipia / Samburu, ~8,000 from KWS reports) and tiny by reference to the 130,000 found in southern African countries, our detailed individually based knowledge of reproductive dynamics and population parameters for both males and females contributes to a greater understanding of the resilience of elephants in Kenya and across Africa as well as the threats facing their populations.

ATE team present on the occasion of the 50th Anniversary

II. Long-Term Monitoring

A) Environmental dynamics in a changing climate

Long-term studies are increasingly important for modelling the future of animal populations, given uncertain and fluctuating climate regimes. While still a brief study in some contexts, such as an elephant's potential lifespan of longer than 75 years, the 50 years of our study allows us to model ecological and landscape responses to any changes over a period of increasingly unpredictable climate dynamics.

By climate monitoring standards, 50 years is momentary! However, the fact that we can link local patterns of total rainfall and rainfall variability to seasonal responses to grass, herb and shrub biomass over the long-term (40 years of vegetation plots and water-table measurements) allows us to present trends (Figures 1 & 2). Variability in rainfall, temperature and vegetation growth is likely to be one of the major underlying issues associated with ongoing climate change. When rain and biomass production are shifted from the norm by highly variable patterns of rain and temperature, rangeland management becomes unpredictable and difficult. More erratic rainfall may increase variability in elephant movements and make the overlap between livestock and elephants more complex to manage.

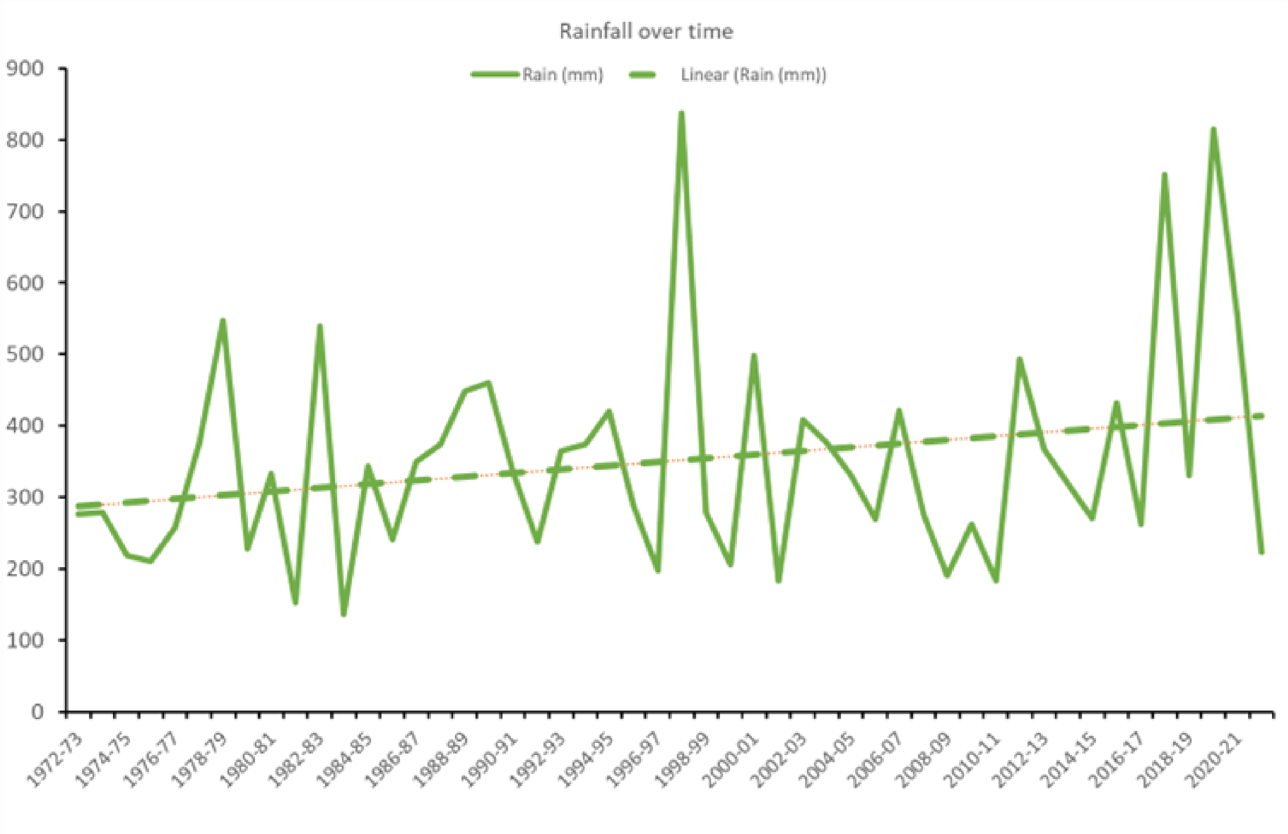

Figure 1: Total rainfall in mm for annual rain years (Oct-Sept) 1972-2022

Has rainfall increased overall? The trendline in Figure 1 suggests a slight increase over time, but the graphical trend in Figure 2a suggests only a few months fall outside the 10% increase line comparing monthly means prior to 1980 and those after 1980 (1980 chosen as the year detectable influences of climate change became apparent [1]). What is evident is that the variance around monthly rainfall has increased since 1980 in all months but Feb and Oct (Figure 2b). Again it is the unpredictability in timing as well as the amount of rainfall that has been changing over time.

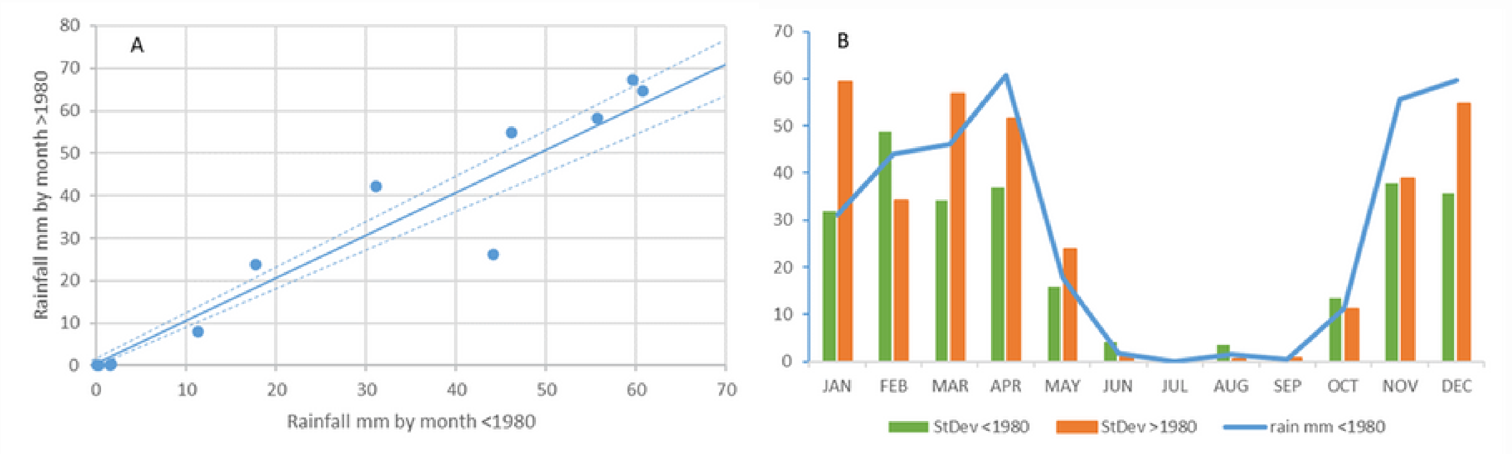

Figure 2: (A) graphical comparison of mean rainfall in any month pre and post 1980; (B) Standard deviation in monthly rainfall pre and post 1980. Mean monthly rainfall shown as blue line.

The question of what elephants are eating was first examined in Amboseli by Keith Lindsay using direct observations in the 1980s [2] and is currently being investigated by a KWS collaborator and MSc student Peter Kimani with Professor Robert Chira, University of Nairobi. The excitement of having a project last for 50 years is being able to apply entirely new methods, in this case, looking at the DNA from plants that is found in the dung of elephants. These results should be ready for publication in the next year. We now have both baseline, “historical” data and current diets for comparison in the face of dramatically changing ranging, vegetation and habitat distributions [3] (Figure 3). In addition Peter’s project will assess the role of elephant consumption on species of conservation concern (sandalwood, *Santalum spp*. and invasive species e.g. *Opuntia*).

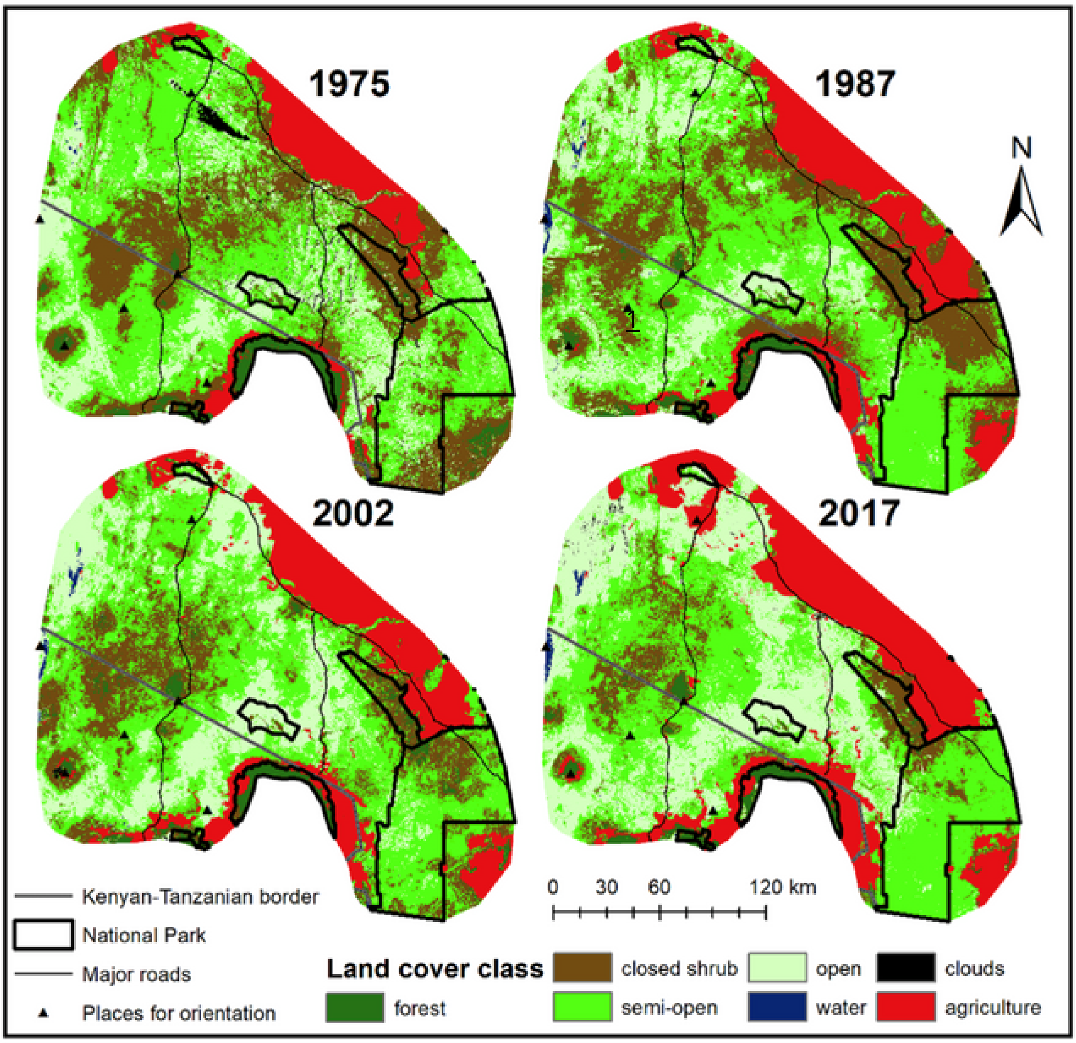

Figure 3: Land use cover changes from 1975 to 2017 in the Amboseli ecosystem. From Schüßler et al. 2018.

B) Elephant monitoring database

In 2022, we launched a new database that was designed by Dr Fran Root and Dr Vicki Fishlock. This database now holds all our sightings of elephants (group size, group composition, location and habitats), censuses of presence and absence of members of families, new births, deaths and disappearances, and events such as oestrus, musth, mating and male dispersal. Ecological monitoring information (rainfall, vegetation biomass, water table) is now linked to the sightings of elephants (Figure 4).

The aim of the database, which was over three years in construction, was to make our data accessible and of use to the global elephant community. We have moved beyond a simple relational database into a data management system that allows users to add, map, query, edit and inspect data. In a recent paper in Pachyderm [4] we share some of the key concepts that drove this process and outline our hopes for making elements of the structure available to other projects that may benefit from similar capacities. As we note in the article, we are open to collaborations to help field elephant researchers refine and simplify this database to suit their needs for exploratory analysis.

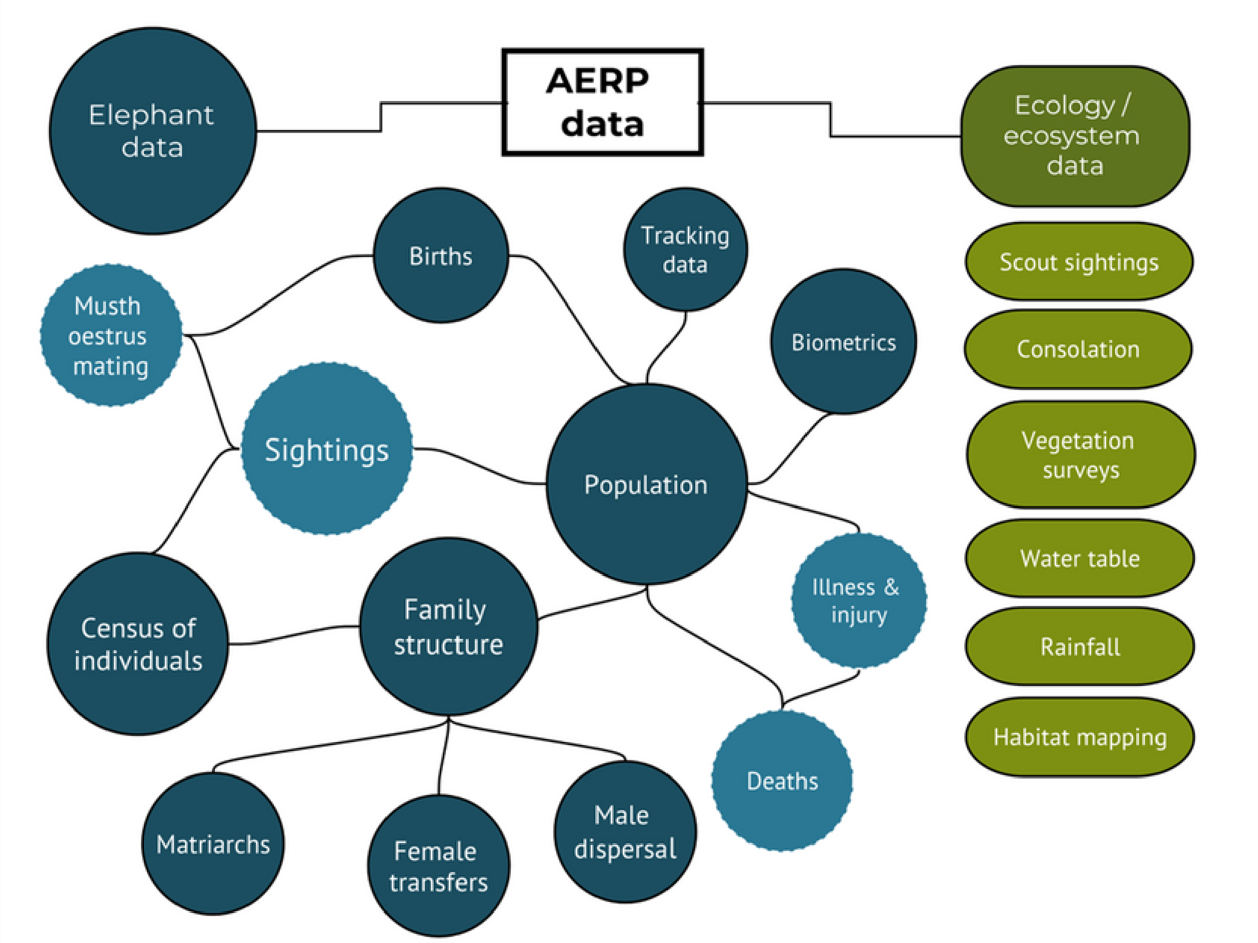

Figure 4: Schematic of the parameters in Amboseli dataset, from Fishlock et al. 2022.

C) Elephant movement dynamics

Between 1995 and 1997, in collaboration with Save the Elephants and Dr Iain Douglas-Hamilton, we investigated the movements of four adult males via VHF radio and then GPS satellite collars [5]. In 2016, the 47-year-old male Tim was collared to examine his movements around farmers' fields [6]. This small sample (relative to the now huge samples on elephants elsewhere) provided us with some insights into how the adult males move within their established "bull areas", but we remain in ignorance of how young males, newly dispersed from their families, find safe foraging areas for semi-permanent residence. To try to answer this question in 2019 and 2020, we collared eight males aged between 11-13 years old who had either just left their natal families or were in the process of leaving. In the three years of monitoring, we have yet to see a male firmly establish a "bull area". These young males appear to be in the process of exploring the entire extent of the greater Amboseli ecosystem (Figure 5), and have ranged south and east into Tsavo West National Park, into areas next to Mkomazi in Tanzania, as far west as Lake Natron, and well south of Kilimanjaro (beyond Longido in Tanzania). Males have also ranged into the Chuylu Hills and as far as the Mombasa Road. The movements of these young males are currently being analysed and written-up for publication with our collaborators in WRTI. We see that for at least two years post-dispersal, males continue to significantly shift areas and range widely, even during tough ecological conditions (Figure 6).


Two young males playing

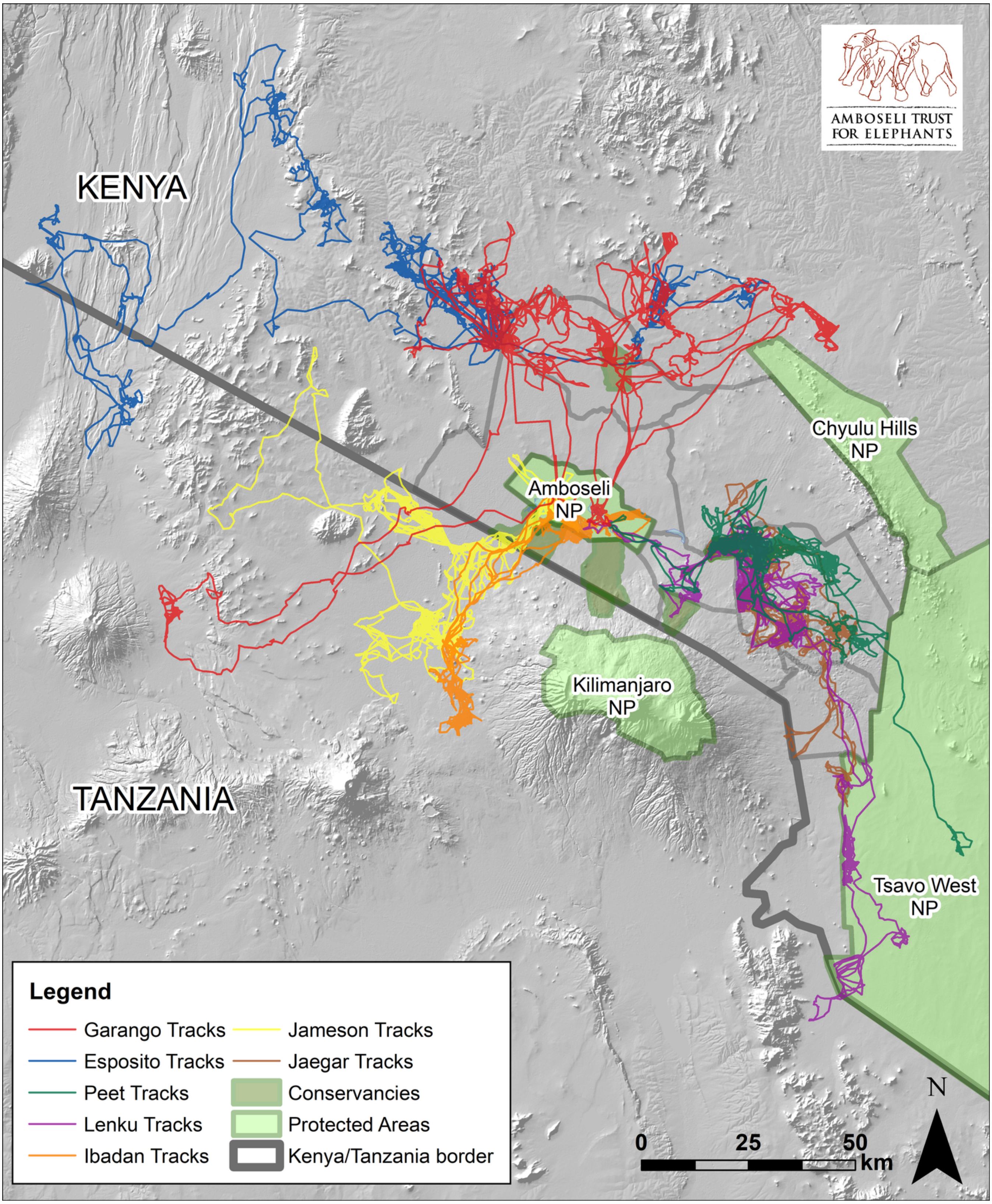

Figure 5: 2022 all tracks of dispersal age males, hourly fixes. Note the long-distance movements of males to Tsavo, Tanzania, far west and north towards the Mombasa Road.

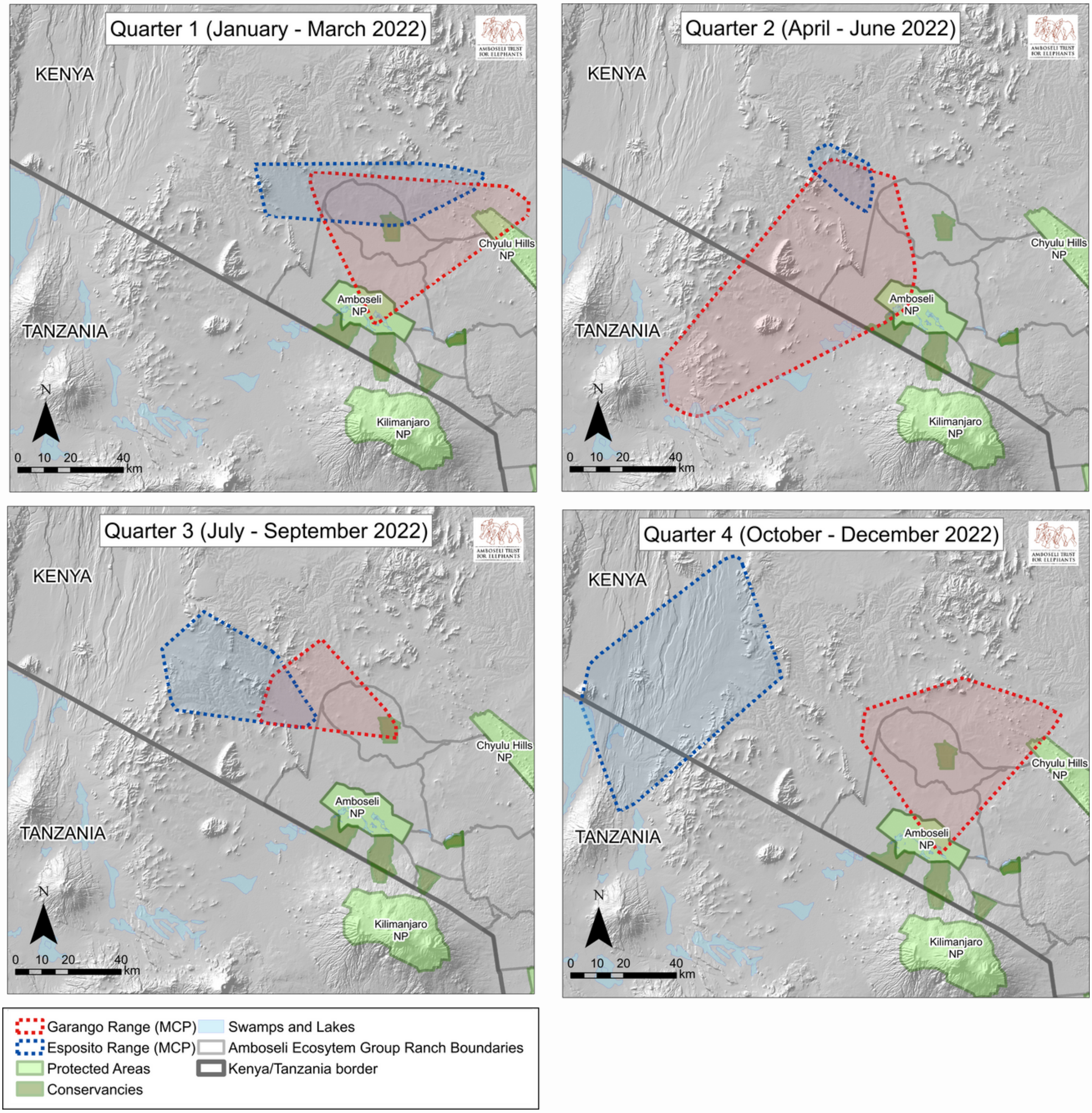

Figure 6: Garango and Esposito exhibited major range shifts during 2022. Ranges based on 100% MCP (Maximum Convex Polygon) using hourly tracking points shown in Figure 5.

Females from six families (BA, EB, IB, MB, SA, VA) were initially VHF collared and tracked in the 1970s and two more families (HA, KA) plus two repeats (MB, VA) were added in the 1990s [6]. Between 2011-2013, satellite collars were placed on females from five families known to use areas far from the central swamps (LB, IB, MB, VA, WA). These repeated studies have enabled exploration of long-term shifts in family ranging: for example the VA family is now firmly resident in Selenkay and only an occasional visitor to the protected area of Amboseli National Park (Figure 7).

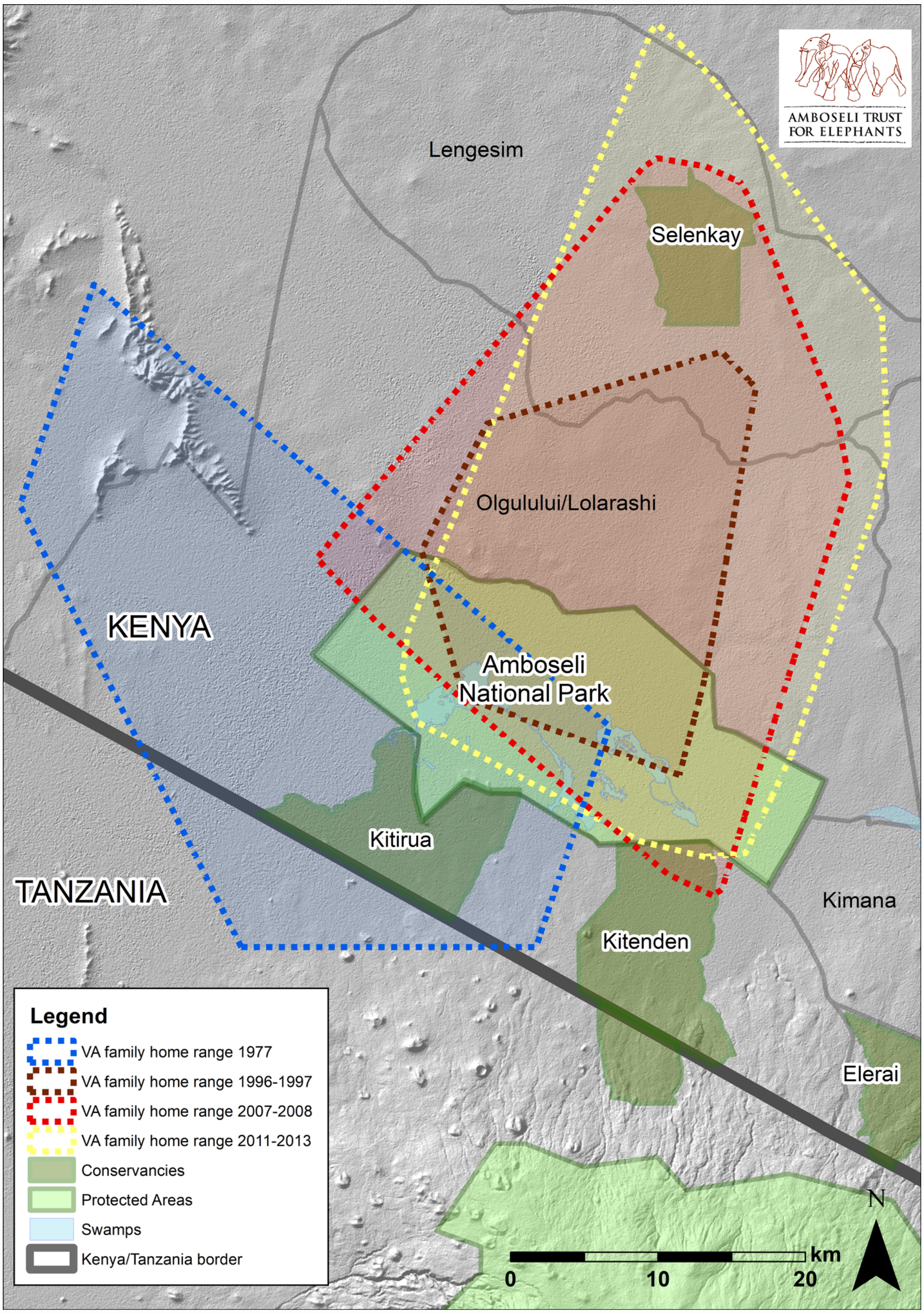

Figure 7: Range shifts for a single Amboseli family since the late 1970s. The areas represent 100% MCP from hourly tracking on collars or daily fixed for older collars.

D) Population dynamics in response to environmental unpredictability

How do elephant populations vary over time and what are the consequences of this variation for population persistence? This is one of the key questions that our 50-year study has been able to explore. We have shown the following major effects:
Starvation, disease, and death. Droughts, which reduce standing food biomass for grazers and browsers and increase disease and parasite burdens, cause major mortality among un-weaned calves and the oldest individuals [7]. This kind and level of mortality is expected and is consistent with results from a number of populations across Africa (Samburu, Tsavo, Tarangire, Kruger) [8]. What we have been able to add to this perspective is how these “one-off” events have consequences for the population structure which affects reproductive rates and population growth in the longer term [9]. Effective elimination of an age class produces both a gap in the number of reproductive-aged females 10 years later and therefore in calf production, and opportunities for increased reproductive rates when competition is lifted. This knowledge over 50 years will allow us to model how drastic mortality can lead to population instability (ongoing demographic modelling).
Consequences for individuals. Droughts leave traces in survivors; as is seen in other very long-term mammal studies (e.g. Amboseli baboons, mountain gorillas, Gombe and Kibale chimpanzees, Samburu elephants [10]). Experiences of adversity through growth faltering in early life, loss of mother, loss of matriarch, and family disruption make for increased susceptibility to threats over the lifespan [11]. Such individuals have shorter lives, reproduce at later ages, and may ultimately be less successful competitors and thus have fewer offspring. Fewer family members, inexperienced matriarchs and reduced opportunities for social networking may directly reduce calf survival.
Boom years and overall trends. When there are fewer competitors, both elephants and other species including livestock, elephants can reproduce at the highest possible rates. We have reported a maximum of 16.8% rate of population increase for one year (following a two-year drought with net decline), while the long-term average rate of population increase was 2.7%, and the minimum was a 9.7% decline[7].

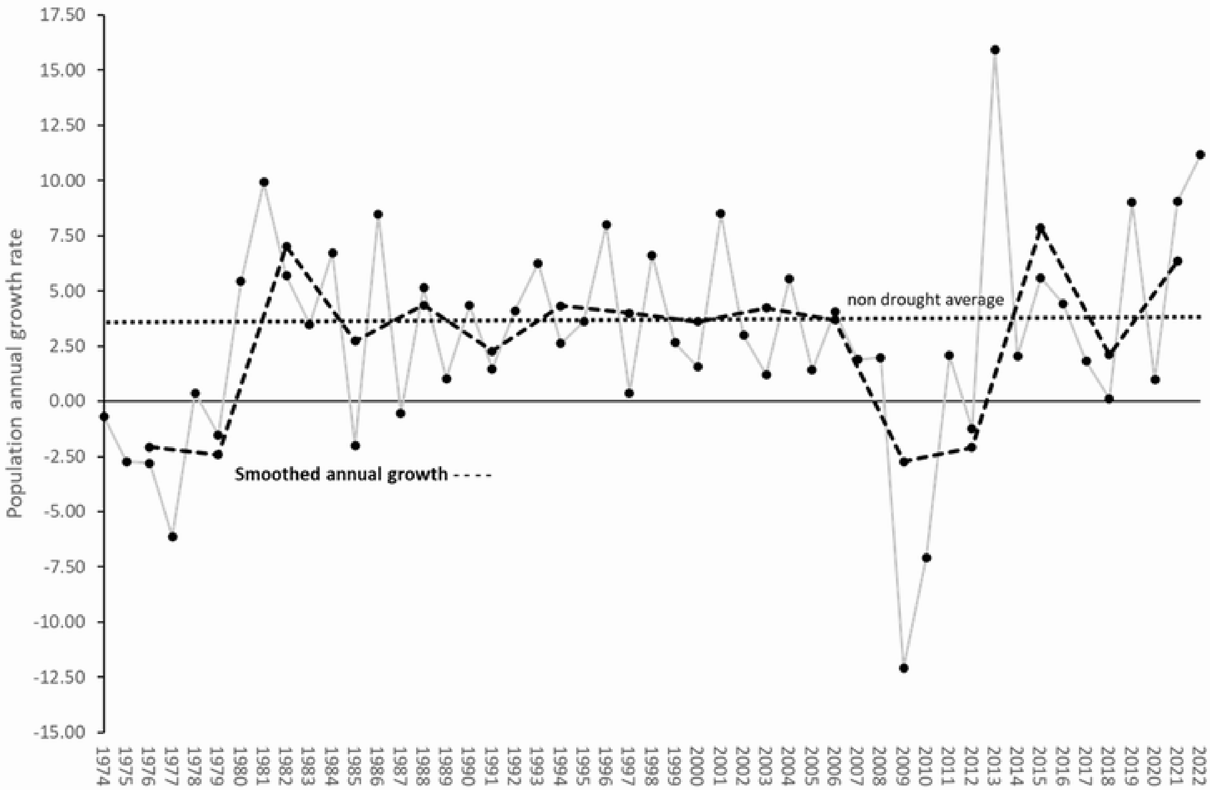

Figure 8: Population trends over fifty years expressed as percentage annual rate of increase (annual and smoothed). The Amboseli elephant population represents one of the best protected and consistently naturally increasing in Kenya.

III. Elephant Behaviour and Social Dynamics

While AERP has built on the results of early researchers, and benefited greatly from the findings of other studies on elephants throughout Africa, our enduring and unique contributions to understanding elephant behaviour have been:

(a) the first confirmation of the phenomenon of musth in African elephants in 1981 [12], which has changed the way we view male behaviour and lifespan;
(b) the first description of oestrus behaviour in 1983 [13], allowing for predictions of female reproductive onset and paternity [14];
(c) charting for the first time how elephants grow up within their families [15], and for males, how and when they decide to leave families [16], debunking the myth that males are driven out of families;
(d) an understanding of growth patterns and the differences between males and females in growth costs [17], reflected in mortality, in dispersal from the natal family, and foraging energetics including crop foraging [18];
(e) detailed studies of communication and cognition [19], which have enabled perspectives on elephant social relationships, wild welfare and human-elephant relationships and which are of significance in the management of human-elephant coexistence [20].
(f) monitoring individual patterns of sociality, reproduction and death over the lifespan for both males and females [11].

Combining basic observations with genetics [21], audio techniques [22] and film/video [23], and as technologies have improved, have allowed the project to capture new dimensions to add to our early findings. In addition, collaborations with community members and local scouts has contributed to our greater understanding of elephants and their ecosystem.

Social turnover in family units:

Our ongoing studies of family dynamics under conditions of mortality and leadership change have been able to suggest why some populations of elephants are resistant to disruption, while others, that lack strong, experienced females to replace females at death, show long-term problems such as fragmented families led by traumatised orphans and low reproductive success. Despite the death of at least one and generally two or three leaders within each family over the 50 years of the study, the population has been robust in rebounding from negative effects (see Figure 8 above). In part, this long-term success in the face of threats may be due to our observations that females tend to become matriarchs at around 30 years of age and thus have had many years of environmental and social experiences before they lead their families. Large, growing families such as we see in Amboseli, where family size has gone from an average of 3 adult females in the 1970s to as many as 34 adult females over the course of the study (median = 8.5 females over the age of 9 years in 2022), are the result of successes in leadership.

How family size affects grouping:

As families have grown in size over the study, average group size has become smaller than that of the family, especially in the dry season when finding food is difficult for a large group. Dry seasons result in smaller elephant groups, especially during drought years (Figure 9). During these times, families become less able to all be together and females also spend less time with females from other families.

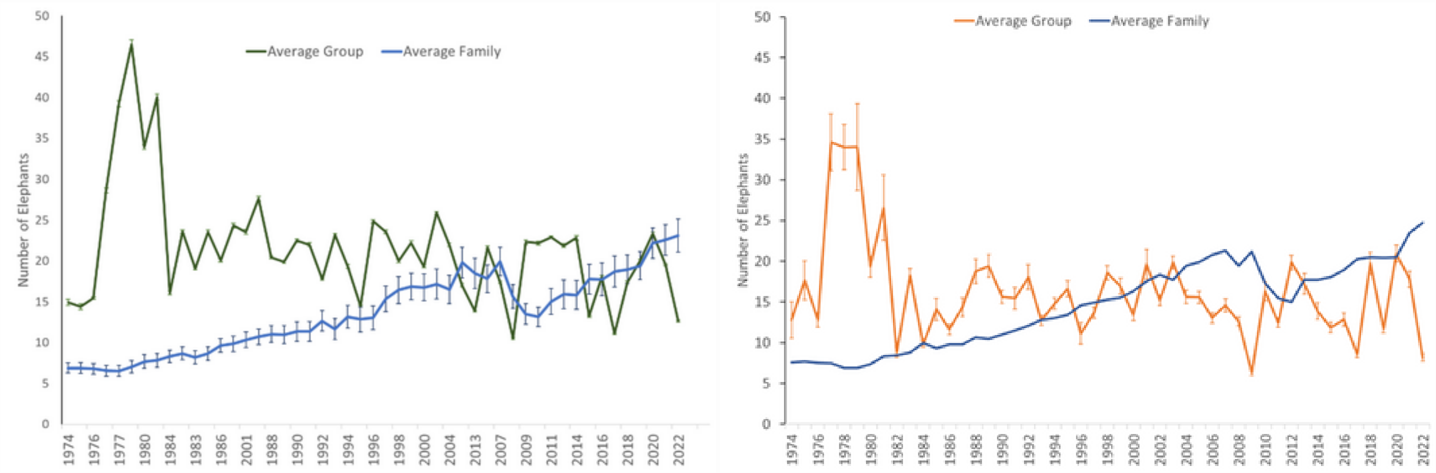

Figure 9: Comparison of (A) mean (±SE) Family size (total numbers) with Average Group size (±SE) overall and (B) Group size (±SE) during the Dry Season. Dry Season groups are smaller, more variable and less likely to contain an entire family. Drought years (1984, 1996, 2009, 2022) show this effect most clearly.

These very long-term trends in sociability, both within the family (cohesion) and between other families (gregariousness: Figure 10), demonstrate the amazing flexibility of elephants in their grouping dynamics. Social dynamics are driven by both food availability and by individual preferences to group with other elephants [24], which makes simplistic conclusions about the nature of elephant groups difficult.

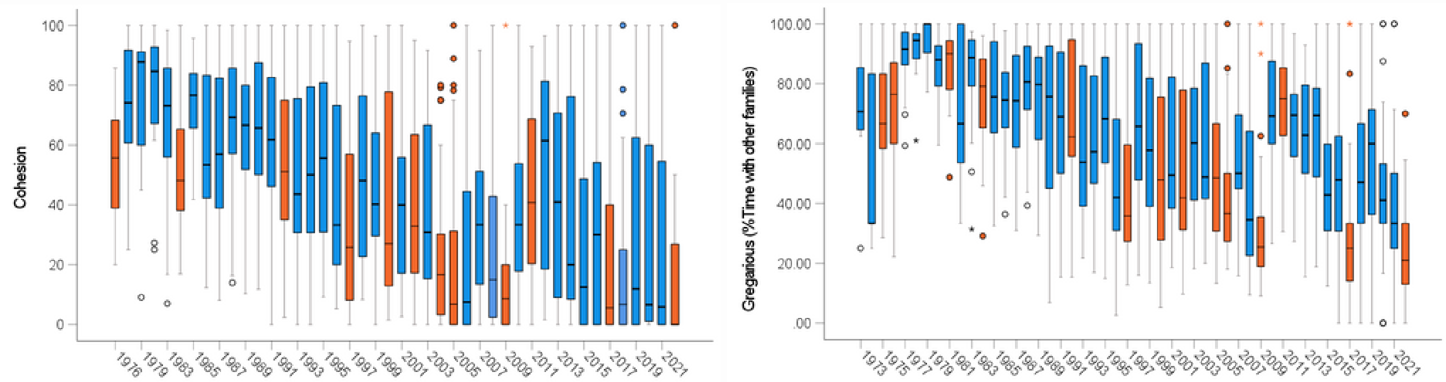

Figure 10: Box plots of annual percentages of Cohesion - time spent with all family members together and Gregariousness (time spent with other families). Error bars represent 95% confidence intervals, drought years are indicated in red.

IV. Collaborations and Dissemination

A) Overview of collaborative research

Over the 50 years of the project, we have collaborated with global scientists, filmmakers, painters and sculptors, writers and poets. Although our research collaborations may be better known, knowledge from all these different perspectives, about the lives of the Amboseli elephants and their ecosystem, has enriched our perspectives on and understanding of elephants generally.

Ongoing collaborations:

- ATE, KWS and University of Nairobi, Professor Robert Chira. Peter Kimani MSc student: Environmental DNA used to assess elephant diets in a rapidly transforming landscape. ATE Mentor, Dr Vicki Fishlock.
- ATE, Wildlife Research and Training Institute: Joseph Mukeka, Dr Shadrack Ngene, Dr Patrick Omondi: Explorer males: the dispersal and movements of young male elephants at independence. ATE Mentors, Dr Vicki Fishlock & Dr Lydia Tiller.
- ATE, York University UK (remote collaboration) Prof Colin Beale & Helen Mylne PhD student, modelling social networks for male elephants from 50 years of data. ATE Mentors, Prof Phyllis Lee and Dr Vicki Fishlock.

Planned collaborations:

- ATE, Southern Tanzania Elephant Project & TAWIRI: investigating the use of the ATE database for other researchers. ATE Mentor, Dr Vicki Fishlock
- ATE & WRTI, University of Nairobi Population genetics and connectivity (in development)
- ATE & WRTI Sospeter Kiambi Using long-term demographics and mortality records to assess bias in population monitoring indicators.
- ATE, KWS veterinarian, Dr Edward Kariuki, elephant disease and causes of mortality

Historical collaborators with ongoing projects:

- ATE, Elephant Voices (Joyce Poole): Elephant communication
- ATE, University of Sussex (Lucy Bates): Comparative cognition
- ATE, University of Aarhus (David Lusseau): Demographic modelling over the long term
- ATE (Keith Lindsay): Captive elephants and implications for wild populations

B) Dissemination

Our research findings have been widely disseminated; we have published 100+ articles in over 45 different peer-reviewed journals, 30+ book chapters, 10+ MSc and PhD theses, and seven books. We aim to continue to disseminate our findings in both peer-reviewed and popular media, as well as reports for other elephant biologists, so that our unique knowledge from these individuals will continue to act as a baseline for understanding elephant behaviour. Our studies contribute to elephant genetics, reproduction, development, communication and cognition, responses to landscapes and climate change as well as potentially enabling comparative models of population dynamics across Africa. The two most recent years of ATE and collaborator publications are listed below.

2022

Fishlock, V.F., Michelmore-Root, F. Njiraini, N, Sayialel, K., Moss, C.J. & Lee, P.C. (2022). Developing a user-centred system for long-term elephant monitoring. Pachyderm, 63, 183-189.
Poole, J.H. & Granli, P. (2022) The Gorongosa elephants through war and recovery. Pachyderm, 63, 38-54.
Sanare, J. E., Valli, D., Leweri, C., Glatzer, G., Fishlock, V., & Treydte, A. C. (2022). A socio-ecological approach to understanding how land use challenges human-elephant coexistence in northern Tanzania. Diversity, 14(7), 513.
Shannon, G., Cordes, L. S., Slotow, R., Moss, C., & McComb, K. (2022). Social disruption impairs predatory threat assessment in African elephants. Animals, 12(4), 495.
Smit, J. B., Searle, C. E., Buchanan-Smith, H. M., Strampelli, P., Mkuburo, L., Kakengi, V. A., ... & Lee, P. C. (2022). Anthropogenic risk increases night-time activities and associations in African elephants (Loxodonta africana) in the Ruaha-Rungwa ecosystem, Tanzania. African Journal of Ecology.
Wiśniewska, M., Puga-Gonzalez, I., Lee, P., Moss, C., Russell, G., Garnier, S., & Sueur, C. (2022). Simulated poaching affects global connectivity and efficiency in social networks of African savanna elephants—An exemplar of how human disturbance impacts group-living species. PLOS Computational Biology, 18(1), e1009792.

2021

Brakes, P., Carroll, E.L., Dall, S.R., Keith, S.A., McGregor, P.K., Mesnick, S.L., Noad, M.J., Rendell, L., Robbins, M.M., Rutz, C. and Thornton, A. (2021). A deepening understanding of animal culture suggests lessons for conservation. Proceedings of the Royal Society B, 288(1949), p.20202718.

Campbell-Staton, S.C., Arnold, B.J., Gonçalves, D., Granli, P., Poole, J., Long, R.A. and Pringle, R.M., 2021. Ivory poaching and the rapid evolution of tusklessness in African elephants. Science, 374(6566), pp.483-487.

Hartmann, W. L., Fishlock, V., & Leslie, A. (2021). First guidelines and suggested best protocol for surveying African elephants (Loxodonta africana) using a drone. Koedoe, 63(1), 1-9.

Hedwig, D., Poole, J., & Granli, P. (2021). Does Social Complexity Drive Vocal Complexity? Insights from the Two African Elephant Species. Animals, 11(11), 3071.

Lee, P. C., Moss, C. J., Njiraini, N., Poole, J. H., Sayialel, K., & Fishlock, V. L. (2021). Cohort consequences of drought and family disruption for male and female African elephants. Behavioral Ecology.

Poole, J., & Granli, P. (2021). The Elephant Ethogram: a library of African elephant behaviour. Pachyderm, 62, 105-111.

V. Activities with Stakeholders and Communities

A) Stakeholder engagement

ATE continues to play an active role as a technical advisor to the Amboseli Ecosystem Trust (AET), and especially in collaboration with KWS and Big Life Foundation who are the principal agencies managing the human-wildlife interface in the Amboseli ecosystem. We seconded one member of staff to the Amboseli Ecosystem Trust for their community work (Moses Saruni), and we have taken on a new research assistant from the community after a period of training as an intern (Issack Letunka).
The importance of changing landscape dynamics, and the impacts on humans and elephants cannot be understated for the future of the ecosystem. To that end, in our 50th year ATE concluded we must formally expand our research capacity in this area, and we recruited Dr Lydia Tiller as a dedicated Coexistence & Connectivity specialist. Dr Tiller's role is to: 1) support ATE's ongoing ecosystem connectivity research 2) develop a coexistence research programme in collaboration with Big Life Foundation exploring existing datasets on the human-elephant interface and developing new research ideas to test methods to manage/mitigate coexistence and 3) recruit a research team to conduct the new programme. Ultimately, we intend to recruit research assistants and graduate students in this area and build a research programme that actively supports and is accountable to communities living alongside wildlife and the partners that manage the interface.

B) Training, sensitisation and filming

ATE, through Team members Norah Njiraini and Tal Manor, provides training in elephant behaviour, biology, growth, ageing and sexing to our collaborators in Kenya and for range country biologists and conservation managers from Africa and Asia. While much external training was paused during the Covid-19 pandemic, we aim to re-establish this program in the future. Mentoring in collaborative data science and analysis with WRTI and other science stakeholders are part of the planned activities for Dr Tiller for 2023 and beyond.

Supporting Government of Kenya authorised film-makers

Over the 50 years of the project, ATE's collaboration on many internationally distributed films has enabled a global audience to experience and appreciate the elephants of Amboseli and the wildlife of Kenya. Our collaborations with the Kenyan press and Kenyan filmmakers are equally important in spreading knowledge and enjoyment of the elephants of Amboseli.

- Collaborated with BBC Natural History (viewership of 1 billion), to air in 2023.
- Interviews with ITV (UK) news.
- Local television presentations and collaboration with Citizen TV, SUSO (Peter Moll).
- BBC filmmakers for series "Dynasties" (ongoing from 2020), broadcast in 2022
- Queens" series (Wildstar), wrapped late 2022

C) Consolation Scheme

Our consolation scheme, which addresses the loss of cattle, sheep/goats, and donkeys as a result of interactions with elephants outside the protected area of Amboseli National Park, was called on to support 53 consolation events in 2022 (57 cows, 5 sheep), across the active zone (Figure 11). The high level of consolation, representing almost KSh 1.2million in payments, is a function of the high overlap between livestock and elephants because of the ongoing 2022 drought. Nonetheless our programme continued to encourage successful coexistence between pastoralists and elephants as we did not have to cancel any payments due to community action against elephants.

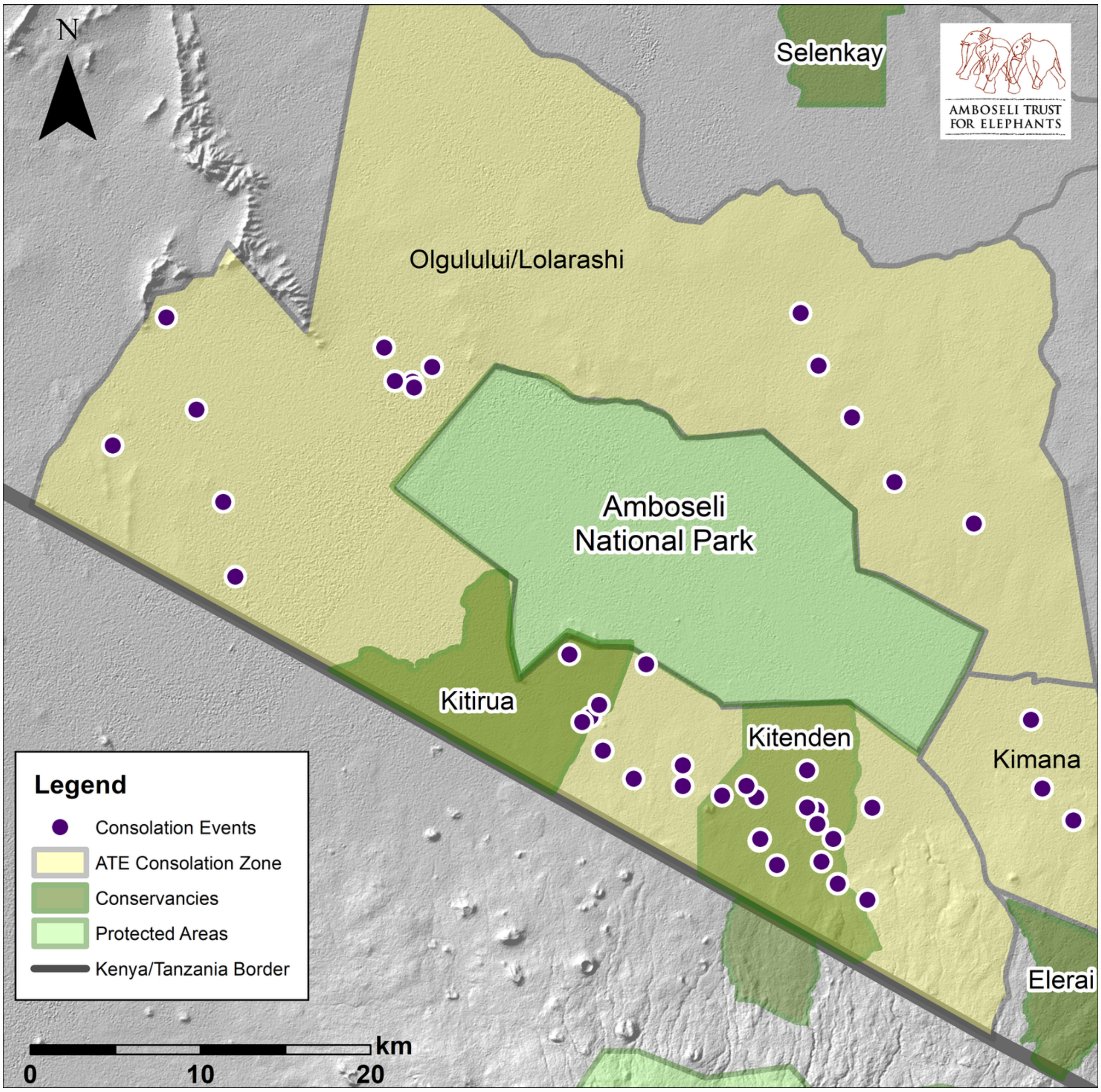

Figure 11: Location of consolation events in 2022

D) Scholarships

ATE fosters livelihood development among young men and women through funding scholarships for primary, secondary and university students from the Group Ranches surrounding Amboseli National Park. In the calendar year 2022 we sponsored 22 students in total (15 girls and 7 boys). For our secondary school scholarships, we concentrate on girls but in 2022, we took on more male students due to the drought situation. In addition, we have one male student who has almost completed his MSc. As always, we look forward to seeing him succeed in his future endeavours. ATE's scholarships build capacity and develop livelihoods in many areas of learning and professional training for young community members who share their lives with elephants, and our ecosystem partners.

Miriam Nampaso with her father and Mrs Sylvi Nyambura (ATE)

Miriam Nampaso pictured here with her father and Mrs Sylvi Nyambura (ATE). Miriam has just completed her Secondary school education. She has been one of our most disadvantaged students, becoming a mother in Form 1 and having to leave her child so she can go back to school. Seeing her complete her Secondary education is a major achievement and we celebrate her success.

Cynthia Moss, Director
Phyllis Lee, Director of Science
February 2022

Reference noted in text

[1] international Panel on Climate Change (1989): United Nations
[2] Lindsay, W.K. (2011) Chapter 5 In Moss, C.J., Croze, H. & Lee P.C. (eds). The Amboseli Elephants, University of Chicago Press
[3] Schüßler, D., Lee, P.C., & Stadtmann, R. (2018). Analyzing land use change to identify migration corridors of African elephants (Loxodonta africana) in the Kenyan-Tanzanian borderlands. Landscape ecology, 33, 2121-2136.
[4] Fishlock, V., Michelmore-Root, F., Njiraini, N., Sayialel, C., Moss,1C., & Lee, P. (2022). Developing a user-centred system for long-term elephant monitoring. Pachyderm, 63, 183-189.
[5] Croze, H. & Moss, C.J. (2011) Chapter 7 in Moss, Croze & Lee, The Amboseli Elephants.
[6] Wilkie, R., & Douglas-Hamilton, I. (2018). High-resolution tracking technology reveals distinct patterns in nocturnal crop raiding behaviour of an African elephant (Loxodonta africana) in Amboseli, Kenya. Pachyderm, 59, 41-48.
[7] Lee, P.C., Moss, C.J., Njiraini, N., Poole, J.H., Sayialel, K., & Fishlock, V.L. (2022). Cohort consequences of drought and family disruption for male and female African elephants. Behavioral Ecology, 33(2), 408-418.
[8] See Okello, M. M., Kenana, L., Maliti, H., Kiringe, J. W., Kanga, E., Warinwa, F., ... & Mwangi, P. (2016). Population density of elephants and other key large herbivores in the Amboseli ecosystem of Kenya in relation to droughts. Journal of Arid Environments, 135, 64-74; Wato, Y. A., Heitkönig, I. M., van Wieren, S. E., Wahungu, G., Prins, H. H., & van Langevelde, F. (2016). Prolonged drought results in starvation of African elephant (Loxodonta africana). Biological Conservation, 203, 89-96.; Foley, C., Pettorelli, N., & Foley, L. (2008). Severe drought and calf survival in elephants. Biology letters, 4, 541-544.; Woolley, L. A., Mackey, R. L., Page, B. R., & Slotow, R. (2008). Modelling the effect of age-specific mortality on elephant Loxodonta africana populations: can natural mortality provide regulation?. Oryx, 42, 49-57. Wittemyer, G., Daballen, D., & Douglas-Hamilton, I. (2013). Comparative demography of an at-risk African elephant population. PloS one, 8(1), e53726.
[9] Moss, C. J. (2001). The demography of an African elephant (Loxodonta africana) population in Amboseli, Kenya. Journal of Zoology, 255(2), 145-156. Lusseau, D., & Lee, P. C. (2016). Can we sustainably harvest ivory?. Current Biology, 26(21), 2951-2956.; Lee, Lindsay & Moss (2011) Chapter 6 in Moss, Croze & Lee, The Amboseli Elephants; Lee, P. C., Moss, C. J., Njiraini, N., Poole, J. H., Sayialel, K., & Fishlock, V. L. (2022). Cohort consequences of drought and family disruption for male and female African elephants. Behavioral Ecology, 33(2), 408-418.; Lee, P. C., Bussière, L. F., Webber, C. E., Poole, J. H., & Moss, C. J. (2013). Enduring consequences of early experiences: 40 year effects on survival and success among African elephants (Loxodonta africana). Biology letters, 9(2), 20130011.
[10] See Tung, J., Archie, E. A., Altmann, J., & Alberts, S. C. (2016). Cumulative early life adversity predicts longevity in wild baboons. Nature communications, 7(1), 11181. Morrison, R. E., Eckardt, W., Colchero, F., Vecellio, V., & Stoinski, T. S. (2021). Social groups buffer maternal loss in mountain gorillas. Elife, 10, e62939. Stanton, M. A., Lonsdorf, E. V., Murray, C. M., & Pusey, A. E. (2020). Consequences of maternal loss before and after weaning in male and female wild chimpanzees. Behavioral Ecology and Sociobiology, 74, 1-11. Goldenberg, S. Z., & Wittemyer, G. (2017). Orphaned female elephant social bonds reflect lack of access to mature adults. Scientific Reports, 7(1), 1-7.
[11] McComb, K., Shannon, G., Durant, S. M., Sayialel, K., Slotow, R., Poole, J., & Moss, C. (2011). Leadership in elephants: the adaptive value of age. Proceedings of the Royal Society B: Biological Sciences, 278(1722), 3270-3276.; Lee, P. C., Fishlock, V., Webber, C. E., & Moss, C. J. (2016). The reproductive advantages of a long life: longevity and senescence in wild female African elephants. Behavioral Ecology and Sociobiology, 70, 337-345.
[12] Poole, J. H., & Moss, C. J. (1981). Musth in the African elephant, Loxodonta africana. Nature, 292, 830-831.
[13]Moss, C. J. (1983). Oestrous behaviour and female choice in the African elephant. Behaviour, 86(3-4), 167-195.; Bates, L. A., Handford, R., Lee, P. C., Njiraini, N., Poole, J. H., Sayialel, K., ... & Byrne, R. W. (2010). Why do African elephants (Loxodonta africana) simulate oestrus? An analysis of longitudinal data. PLoS One, 5(4), e10052.

Reference noted in text

[14] Hollister-Smith, J. A., Poole, J. H., Archie, E. A., Vance, E. A., Georgiadis, N. J., Moss, C. J., & Alberts, S. C. (2007). Age, musth and paternity success in wild male African elephants, Loxodonta africana. Animal Behaviour, 74(2), 287-296.
[15] Lee, P. C., & Moss, C. J. (1986). Early maternal investment in male and female African elephant calves. Behavioral Ecology and Sociobiology, 18, 353-361. Lee, P. C. (1986). Early social development among African elephant calves. National Geographic Research, 2(3), 388-401. [1]
[16] Lee, P. C., & Moss, C. J. (1999). The social context for learning and behavioural development among wild African elephants. Mammalian social learning: comparative and ecological perspectives, 102-125.
[17] Lee, P. C., & Moss, C. J. (1995). Statural growth in known-age African elephants (Loxodonta africana). Journal of Zoology, 236(1), 29-41.; Lee, P. C., Sayialel, S., Lindsay, W. K., & Moss, C. J. (2012). African elephant age determination from teeth: validation from known individuals. African Journal of Ecology, 50(1), 9-20. Chiyo, P. I., Lee, P. C., Moss, C. J., Archie, E. A., Hollister-Smith, J. A., & Alberts, S. C. (2011). No risk, no gain: effects of crop raiding and genetic diversity on body size in male elephants. Behavioral Ecology, 22(3), 552-558.
[18] Chiyo, P. I., Archie, E. A., Hollister-Smith, J. A., Lee, P. C., Poole, J. H., Moss, C. J., & Alberts, S. C. (2011). Association patterns of African elephants in all-male groups: the role of age and genetic relatedness. Animal Behaviour, 81(6), 1093-1099.; Chiyo, P. I., Wilson, J. W., Archie, E. A., Lee, P. C., Moss, C. J., & Alberts, S. C. (2014). The influence of forage, protected areas, and mating prospects on grouping patterns of male elephants. Behavioral Ecology, 25(6), 1494-1504.
[19] McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. Science, 292(5516), 491-494. McComb, K., Shannon, G., Sayialel, K. N., & Moss, C. (2014). Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. Proceedings of the National Academy of Sciences, 111(14), 5433-5438.
[20] Kangwana (2011) Chapter 20; Browne-Nuñez (2011) Chapter 19. In Moss, Croze & Lee, The Amboseli Elephants.
[21] Archie, E. A., Moss, C. J., & Alberts, S. C. (2003). Characterization of tetranucleotide microsatellite loci in the African savannah elephant (Loxodonta africana africana). Molecular Ecology Notes, 3(2), 244-246.; Archie, E. A., Moss, C. J., & Alberts, S. C. (2006). The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. Proceedings of the Royal Society B: Biological Sciences, 273(1586), 513-522.
[22] McComb, K., Moss, C., Sayialel, S., & Baker, L. (2000). Unusually extensive networks of vocal recognition in African elephants. Animal behaviour, 59(6), 1103-1109. Byrne, R. W., Bates, L. A., & Moss, C. J. (2009). Elephant cognition in primate perspective. Comparative Cognition & Behavior Reviews.; Bates, L. A., Poole, J. H., & Byrne, R. W. (2008). Elephant cognition. Current Biology, 18(13), R544-R546.; Bates, L. A., Sayialel, K. N., Njiraini, N. W., Poole, J. H., Moss, C. J., & Byrne, R. W. (2008). African elephants have expectations about the locations of out-of-sight family members. Biology Letters, 4(1), 34-36.
[23] See https://www.elephantvoices.org/
[24] Boult, V. L., Sibly, R. M., Quaife, T., Fishlock, V., Moss, C., & Lee, P. C. (2019). Modelling large herbivore movement decisions: Beyond food availability as a predictor of ranging patterns. African Journal of Ecology, 57, 10-19.raphical trend in Figure 2a suggests only a few months fall outside the 10% increase line comparing monthly means prior to 1980 and those after 1980 (1980 chosen as the year detectable influences of climate change became apparent). What is evident is that the variance around monthly rainfall has increased since 1980 in all months but Feb and Oct (Figure 2b). Again it is the unpredictability in timing as well as the amount of rainfall that has been changing over time.