WILD NATURE INSTITUTE

1 Jan 2026

Director General
Tanzania Wildlife Research Institute
P.O. Box 661
Arusha, Tanzania

Dear TAWIRI Director General,
I am submitting the attached progress report summarizing the research project "Ungulate Ecology, Health, and Conservation in Tanzania including Giraffe Population Genetics and Demography."
I am requesting an extension to continue these studies for an additional year for foreign researchers:

- Derek E. Lee
- Monica L. Bond

Tanzanian researchers:

- George Gwaltu Lohay
- James Martin Madeli

And Driver/Field Assistants:

- Emmanuel Andrew Kimaro

Pursuant to continuation of our research, I request that TAWIRI send an introduction letter to:

- **TANAPA** for the following National Parks:
    - Tarangire
    - Serengeti
    - Lake Manyara
    - Ruaha
    - Nyerere
    - Arusha
- **NCAA** for:
    - Ngorongoro Conservation Area
- **TAWA** for:
    - Manyara Ranch Conservancy
    - Grumeti Game Reserve
    - Ikorongo Game Reserve
    - Lolkisale Game Controlled Area
    - Mtowambu Game Controlled Area
    - Lake Natron Game Controlled Area
    - Burungi WMA, Randilen WMA, and Ikona WMA

Thank you for your consideration.
Sincerely yours,

Derek E. Lee
Derek E. Lee

Attachments List:

1. TAWIRI cover letter
2. Progress Report including 2 published papers
3. Lee TAWIRI extension form
4. Bond TAWIRI extension form
5. Lohay TAWIRI extension form
6. Madeli TAWIRI extension form
7. Lohay collaboration letter
8. COSTECH cover letter
9. Lee COSTECH extension form
10. Bond COSTECH extension form
11. Lohay COSTECH extension form
12. Madeli COSTECH extension form
13. Research extension form (new)
14. Lee CV
15. Bond CV
16. Lohay CV
17. Madeli CV

Ungulate Ecology, Health, and Conservation in Tanzania including Giraffe Population Genetics and Demography

Annual Progress Report 2025 & Permit Renewal Proposal 2026

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EXECUTIVE SUMMARY

- This project continues to provide data and analyses to inform priority research areas as described in Tanzania Wildlife Research Agenda 2021-2031 (TAWIRI 2021) including: **Wildlife ecology and ecological interactions** [priority areas i.Behavioural and nutrition ecology, ii.Population, distribution and reproductive ecology, vi.Range ecology/management, vii.Population genetics, xiii.Migratory routes, corridors, buffer zones and dispersal areas, xvi.Ecological monitoring methods]; **Wildlife population monitoring** [priority areas i.Population monitoring of large mammals, ii.Population monitoring of rare, endemic and endangered species, iv.Ecological monitoring methods and applications, vii.Social, environmental and ecological drivers of population dynamics, viii.Wildlife population monitoring methods]; **Habitat and biodiversity conservation** [priority areas ii.Composition, distribution and abundance of wildlife in protected areas and non-protected areas, vii.Conservation policy analysis]; **Wildlife diseases** [priority areas ii.Ecology, epidemiology and control of wildlife diseases]; **Wildlife conservation policies** [priority areas iv.Land use planning for supporting livelihoods and conservation goals, viii.Community-based natural resource management (CBNRM) in conservation].

- This project also provides data and analyses to answer research targets in TAWIRI's Giraffe Conservation Research Framework 2020, namely research on: 2.1 giraffes' habitat use and foraging preference, 2.2 giraffe health and impact on survival, 2.3 population size, distribution and connectivity, 2.4 human dimensions and giraffe conservation.

- During the past permit period, we completed 3 giraffe photo capture-mark-recapture surveys in Tarangire Ecosystem, 3 surveys in Serengeti Ecosystem.

- We published two manuscripts in scientific journals regarding giraffes and other ungulates (attached). Three manuscripts are in progress.

- We ask to continue giraffe photographic surveys to obtain robust estimates of population size, trend, and demographic rates for giraffes in northern Tanzania.

- We will conduct giraffe photo surveys in the coming year in Tarangire National Park, Serengeti National Park, Lake Manyara National Park, Arusha National Park, Ruaha National Park, Nyerere National Park, Ngorongoro Conservation Area, Manyara Ranch, Burunge WMA, Randilen WMA, Ikona WMA, Grumeti Game Reserve, Ikorongo Game Reserve, Mtowambu GCA, Lake Natron GCA, and Lolkisale GCA.

- We ask permission to be allowed free entry to the areas listed above. While working in the parks, conservation area, and WMAs, we also request continued permission to camp while collecting data and to drive off-road when necessary because these data cannot be collected only from the roads.

INTRODUCTION

Populations of giraffe (*Giraffa camelopardalis*) have declined throughout the species' range in recent years, leaving remaining populations increasingly isolated. We seek to better understand the metapopulation dynamics and genetic structure of giraffes across a large region of Tanzania. We are continuing demographic studies based upon photographic capture-recapture data in the Tarangire Ecosystem (Tarangire NP, Randilen and Burunge WMAs, Manyara Ranch, Mtowambu GCA, Lolkisale GCA, and Lake Natron GCA, and Lake Manyara NP), Serengeti Ecosystem (Serengeti National Park, Ngorongoro Conservation Area, Ikona WMA, Grumeti GR, and Ikorongo GR), and Arusha National Park. These photo capture-recapture data build upon our long-term database that can be used to estimate population sizes, survival, and reproduction rates at each site. We completed all giraffe DNA sampling collected under previous permits, and these are being processed and analyzed. We have no plans for additional DNA sampling at this time.

Objectives and Conservation Implications

This project objective is to provide data and analyses to inform priority research areas as described in Tanzania Wildlife Research Agenda 2021-2031 (TAWIRI 2021) including: Wildlife ecology and ecological interactions [priority areas i.Behavioural and nutrition ecology, ii.Population, distribution and reproductive ecology, vi.Range ecology/management, vii.Population genetics, xiii.Migratory routes, corridors, buffer zones and dispersal areas, xvi.Ecological monitoring methods]; Wildlife population monitoring [priority areas i.Population monitoring of large mammals, ii.Population monitoring of rare, endemic and endangered species, iv.Ecological monitoring methods and applications, vii.Social, environmental and ecological drivers of population dynamics, viii.Wildlife population monitoring methods]; Habitat and biodiversity conservation [priority areas ii.Composition, distribution and abundance of wildlife in protected areas and non-protected areas, vii.Conservation policy analysis]; Wildlife diseases [priority areas ii.Ecology, epidemiology and control of wildlife diseases]; Wildlife conservation policies [priority areas iv.Land use planning for supporting livelihoods and conservation goals, viii.Community-based natural resource management (CBNRM) in conservation].

This project also provides data and analyses to answer research targets in TAWIRI's Giraffe Conservation Research Framework 2020, namely research on: 2.1 giraffes' habitat use and foraging preference, 2.2 giraffe health and impact on survival, 2.3

population size, distribution and connectivity, 2.4 human dimensions and giraffe conservation.

METHODS

Study Areas

Field research takes place in Tarangire National Park, Lake Manyara National Park, Ruaha National Park, Nyerere National Park, Arusha National Park, Serengeti National Park, Ngorongoro Conservation Area, Manyara Ranch, Lolkisale Game Controlled Area, Mtowambu Game Controlled Area, Lake Natron Game Controlled Area, Burunge WMA, Randilen WMA, Ikona WMA, Grumeti Game Reserve, and Ikorongo Game Reserve.

Road Surveys

We conduct daytime vehicle road surveys for photo capture-recapture. Driving speed is between 15 and 20 kph on all transects. Sampling design is a robust design with 2 sampling events at each site during each sampling occasion. A sampling event consists of 1 round of driving all fixed-route road transects within a site. Study design calls for sampling occasions 3 times per year near the end of each precipitation season (vuli, masika, and kiangazi). Thus, sampling is scheduled from mid Jan-mid Feb, mid May-mid Jun, and mid Sep-mid Oct each year.

During sampling events we attempt to photograph every individual giraffe encountered. Each photographic image constitutes the application of a new mark, or the recapture of an existing mark. We employ Wild-ID pattern recognition software to identify individuals by their unique coat patterns (Bolger et al. 2012). Photographed animals are considered ‘marked’ when their first photograph is taken, while animals already in the photo database are photographically ‘recaptured’. Every individual giraffe encountered is classified to age class (calf, subadult, adult) and sex (male, female), photographed for individual identification and size quantification, location recorded as GPS coordinates and site designation. Distance (in meters) to each giraffe is measured using a laser range finder. These data are analyzed using open, robust design models in program MARK to estimate population size, survival probability, and recapture probability.

We also collect Distance sampling data in NCA for all giraffes visible along both sides of the track out to 500 m in order to estimate population size and distribution of giraffes in NCA. Distance data record the group size and perpendicular distance from the transect to each group of animals when first detected. When a group or singleton is sighted (groups for giraffes were defined as < 500 m between individuals), we halt the vehicle and record the perpendicular distance from the track to the animal(s) measured with a laser rangefinder (Bushnell Arc 1000; Bushnell Outdoor Products, Overland Park, Kansas), the total number of individuals by sex and age class, and the GPS position of the vehicle. If the sighting is a cluster of animals, distance is measured as the perpendicular distance from the track to the middle of the group.

We also collect covariate data relevant to estimates of giraffe density, population size, survival and reproduction. These include vegetation type, species composition, and density. DNA samples were collected under previous permits, these samples are being processed and analyzed. No new samples are required.

RESULTS

Previous findings:

We documented spatial variation in demographic rates of giraffes among the 5 sites in the Tarangire Ecosystem (**Lee et al. 2016a**). The Tarangire giraffe metapopulation is still interconnected by a few movements among sites, but LMNP and MGCA are nearly isolated from the rest of the ecosystem (**Lee & Bolger 2017**). The Tarangire National Park and Manyara Ranch subpopulations are the engines of metapopulation growth and health, but anthropogenic impacts outside protected areas have a negative effect on overall metapopulation growth resulting in an overall declining metapopulation (**Lee & Bolger 2017**). Presence of migratory herds of wildebeest and zebras increased local giraffe calf survival (**Lee et al. 2016b**). Giraffe calf survival varied by season of birth, with highest survival found in calves born during the dry season (**Lee et al. 2017**). Giraffe Skin Disease prevalence varied significantly among sites and appeared to vary according to soil fertility. There is no mortality due to GSD disease (**Lee & Bond 2016, Bond et al. 2016**). In **Lee et al. (2018)** we demonstrated that some characteristics of giraffe coat spot shape were heritable, and that variation in neonatal survival was associated with spot size and shape covariates. A habitat model and corridor detection algorithm delineated the Tarangire Ecosystem wildebeest migration habitat between Tarangire NP and Lake Natron (**Bond et al. 2017**). We documented the ecological success of CBNRM in Wildlife Management Areas (WMAs) for wildlife conservation (**Lee & Bond 2018, Lee 2018**). We published the first account of a wild giraffe nursing multiple calves (**Bond & Lee 2019**). We quantified giraffe home range sizes in the Tarangire Ecosystem and found home range sizes across Africa were correlated with rainfall (**Knüsel et al. 2019**). In **Bond et al. (2019)**, we found food availability rather than predation risk mediated grouping dynamics of adult giraffes, while predation risk was the most important factor influencing congregations with calves. Two papers, Giraffe translocations: A review and discussion of considerations **(Muller et al. 2020)** and Giraffe translocation population viability analysis **(Lee et al. 2020)** provide strong guidance to biologists and managers planning translocations of giraffe. Using one of the largest-scale metapopulation networks ever studied in a wild mammal, in **Bond et al. (2020)** we reveal that social communities of giraffes living closer to human settlements exhibit weaker relationship strengths and more exclusive social associations. In **Bond et al. (2021)** Sociability increases survival in adult female giraffes, we found that females that grouped with more other females leads to higher survival. Benefits of female grouping may include cooperative care of young, more efficient foraging, and reduced stress in general. Effect of sociability on survival was more than that of the natural surrounding or proximity to people, although living closer to towns also lowered survival. Female Masai giraffes live in distinct social communities of up to 90 other friends, and although areas used by these communities often overlap, they have very different rates of reproduction and calf survival, we showed in **Bond et al (2021)** Socially defined subpopulations reveal demographic variation in a giraffe metapopulation. This means that population structure can arise from social behavior rather than discrete space use. Calf survival and reproductive rates were higher in the social communities that spent more time outside of the national parks. Dispersal, the process where animals reaching sexual maturity move away from family, is important for maintaining genetic diversity and is key to the long-term persistence of natural populations. For most animals, this involves having to make risky journeys into the unknown in the hope of finding new communities in which to settle and reproduce. However, many animal societies—including those of humans—have structured social communities that overlap in space with one-another. These potentially provide opportunities for maturing individuals to disperse socially without having to make large physical displacements. **Bond et al (2021)** Leaving by staying: Social dispersal in giraffes, shows that this strategy is employed by young dispersing giraffes. We studied social relationships of more than 1000 giraffes in the Tarangire Ecosystem over 5 years. In **LaVista-Ferres et al (2021)** Social connectedness and movements among communities of giraffes vary by sex and age class, we found that males were more socially connected than females to all the other giraffes. Adult males wander long distances looking for mating opportunities. Young males visit many different groups as they explore their social environment before moving permanently away from their mothers and sisters. Females had stronger and enduring social relationships over the years than males. In the end, female giraffes have closer 'friends' than male giraffes, while males have more 'acquaintances' than females. This information is important for understanding population dynamics, spread of information, and even how diseases move through a population and is therefore important for conservation. A native bush-encroaching shrub species called Sickle Bush (*Dichrostachys cinerea*) is disliked by livestock keepers and rangeland managers, but loved as forage by wild giraffes, according to Forage selection by Masai giraffes (*Giraffa camelopardalis tippelskirchi*) at multiple spatial scales (**Levi et al. 2022**). The findings showed that giraffe significantly preferred foraging on bush-encroaching species such as the native Sickle Bush at local and landscape spatial scales and in both the wet and dry seasons. The results of this study suggest that browsing wildlife such as giraffes could be adversely affected by the removal of Sickle Bush from rangelands. In Trophic processes constrain seasonal ungulate distributions at two scales in an East African savanna (**James et al. 2022**), we found giraffe distribution in the Tarangire Ecosystem was less constrained by water (they were not closer to rivers and waterholes during the dry season than the wet seasons) but more constrained by the seasonal presence of preferred food such as *Vachellia drepanolobium* in the long rains. These results provide important information for effective conservation strategies for giraffes and other ungulates in the Tarangire Ecosystem. Animal coat patterns may have several functions, one of which might be to help individuals to recognize each other. In Phenotypic matching by spot pattern potentially mediates female giraffe social associations (**Morandi et al. 2022**), we revealed that spot traits were individually variable among adult female giraffes in the Tarangire Ecosystem, and that females showed stronger associations with other females that had similar spot shapes. Spot patterns of giraffes could be a visual cue for communicating and for recognizing related family members. In Masai giraffe population change over 40 years in Arusha National Park **(Lee et al. 2023)**, we enumerated individual giraffes to see how well they were doing compared to 40 years ago and collected DNA from dung samples to assess the genetic connectivity of the park's giraffes with other giraffe populations in the region. We documented a 49% population decline and changes in the age distribution, adult sex ratio, reproductive rate, and movement patterns relative to the previous study. In Effects of local climate anomalies on giraffe survival **(Bond et al. 2023)**, we found that in an East African savanna, higher temperatures positively affected adult giraffe survival, indicating this mega-herbivore is adapted to hot conditions, but adult and juvenile giraffe survival was reduced during rainier wet seasons, possibly due to parasites and disease and/or increased stalking cover for predators. Higher vegetation greenness also reduced adult giraffe survival, potentially because faster leaf growth reduces nutrient quality. Climate effects were most pronounced for giraffes living closer to the edge of the protected areas during the short rains, possibly because of higher livestock-mediated disease risk and/or muddier conditions that prevent effective anti-poaching patrols. Projected climate changes in East Africa, including heavier rainfall during the short rains, will likely threaten persistence of giraffes in one of Earth's most important landscapes for large terrestrial mammals, pointing to the need for effective land-use planning and law enforcement to provide giraffes more resilience to the coming changes. In Genetic evidence of population subdivision among Masai giraffes separated by the Gregory Rift Valley in Tanzania **(Lohay et al. 2023)**, we showed that populations of Masai giraffes separated geographically by the Great Rift Escarpment have not interbred — or exchanged genetic material — in more than a thousand years, and in some cases hundreds of thousands of years. We recommend that the two populations be considered separately for conservation purposes, with separate but coordinated conservation efforts to manage each population. In Extinction risks and mititgation for a megaherbivoe, the giraffe, in a human-influenced landscape under climate change **(Bond et al. 2023)**, we combined the information learned from previous studies of giraffes to create an individual-based model that simulated realistic population dynamics and extinction risk under different scenarios of environmental change over 50 years. Results showed that the greatest risk of population declines and extinction for giraffes is caused by a reduction in wildlife law enforcement leading to more poaching. The study highlights the great utility of law enforcement as a nature conservation tool. In Sexual dimorphisms in body proportions of Masai giraffes and the evolution of the giraffe's neck **(Cavener et al. 2024)**, we measured differences in body proportions between male and female giraffes, both captive and wild, and found females have a proportionally longer neck and torso, whereas males have proportionally longer forelegs and more massive necks. We speculate the initial evolution of the long neck and legs was driven by female nutritional demands (reaching deep into bushes and higher into trees) and mating (males with longer legs can mount females) and later the neck mass was increased in males as a result of neck sparring. In Anthropogenic and climatic drivers of population densities in an African savanna ungulate community **(Bierhoff et al. 2024)**, we quantified population trends, determined the primary environmental correlates of densities, and identified covariation in densities among species. Large fluctuations in climatic factors mediated highly synchronous temporal density variation among all species. We documented more spatial than temporal variation in four of the five species, suggesting that spatial heterogeneity may provide some buffer against temporal variation in the environment. Protection of sufficient habitats and water sources should allow ungulates to respond to a temporally changing world by moving across space. Further, among-species covariation patterns identified two potential ungulate guilds (impala—dik–dik—waterbuck; eland—Grant's gazelle) that should aid in developing efficient and coordinated management actions.

New findings:

In **"Does the chain of Eastern Arc Mountains impede gene flow? Genetic evidence from the African savanna elephant and the Masai giraffe in Tanzania"**

(Lohay et al. 2025), we found that there is high genetic differentiation between populations found east and west of the Eastern Arc Mountains for both elephants and giraffes, and there is no female-mediated gene flow between these populations. Populations found west of the Eastern Arc Mountains show high genetic connectivity suggesting historical gene flow between them. Our study reveals that the Eastern Arc Mountains play a significant role in blocking the gene flow of these species.

In **"Demographic drivers of population dynamics reveal subpopulation-specific conservation needs for giraffes in the Serengeti Ecosystem" (Bond et al. 2025)**, we found significant differences in adult and subadult survival probabilities among 4 Serengeti subpopulations, with lower adult survival associated with declining subpopulations. Retrospective population analysis for the Seronera subpopulation reiterated that adult survival is a critical demographic driver of population dynamics for giraffes. The 2 subpopulations adjacent to the protected area boundary declined over 48 years, whereas the Seronera subpopulation stabilized since 2008. Only one individual moved between subpopulations, providing evidence for subpopulation insularity and potential genetic structuring of the overall population. These factors underscore the need for subpopulation-specific conservation strategies aimed at raising adult survival within the western and northeastern parts of the Serengeti Ecosystem. Our findings highlight the importance of understanding subpopulation dynamics and their demographic drivers for evidence-based conservation and management to recover endangered giraffe populations.

See attached papers for more details.

DISCUSSION AND CONSERVATION RECOMMENDATIONS

Our data benefit managers and policymakers by providing information on status and trends for economically important endangered wildlife species such as giraffe and other ungulates.

The population management actions with highest expected effectiveness are those aimed at increasing adult female survival, such as increasing wildlife law enforcement and reducing tarmac road speed limits with signs, police presence, and speed bumps on roads near protected areas to prevent vehicle collisions. We also suggest efforts be made to protect habitats outside National Parks for the migratory wildebeest and zebra populations, particularly between Tarangire NP and the Lake Natron-Gelai Plains breeding grounds. Protecting the long-distance migration and breeding grounds directly benefits Tarangire NP tourism revenues and indirectly benefits giraffe calf survival. Conserving connectivity habitat between protected areas will help ensure natural movements of giraffes and other species can continue.

We strive to assist wildlife and land management authorities by collecting data to answer management-related questions, so utility can be maximized during surveys. If there are any ancillary data or results desired by wildlife researchers, authorities, or managers that we can collect during our surveys, we will do our best to provide them. Any stakeholder with interest in these data or the ongoing surveys should contact the author of this report at Derek@WildNatureInstitute.org or +14157630348.

CONTINUATION OF CURRENT RESEARCH ACTIVITIES IN 2026

Due to the nature of population studies, more data, particularly longer time spans of data, increase the utility and power to make strong inferences. In 2026 we are asking to continue this project to add to the long-term data already collected.

We will conduct activities in the coming year in Tarangire National Park, Lake Manyara National Park, Ruaha National Park, Nyerere National Park, Arusha National Park, Serengeti National Park, Ngorongoro Conservation Area, Manyara Ranch, Lolkisale Game Controlled Area, Mtowambu Game Controlled Area, Lake Natron Game Controlled Area, Burunge WMA, Randilen WMA, Ikona WMA, Grumeti Game Reserve, and Ikorongo Game Reserve.

We ask to continue giraffe photographic surveys to: obtain robust estimates of population size, trend, and demographic rates for giraffes in northern Tanzania.

We ask permission to be allowed free entry to the areas listed above. While working in the parks, conservation area, and WMAs, we also request continued permission to camp while collecting data and to drive off-road when necessary because these data cannot be collected only from the roads.

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RESEARCH ARTICLE

Demographic drivers of population dynamics reveal subpopulation-specific conservation needs for giraffes in the Serengeti Ecosystem

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Abstract

Survival, reproduction, and movement are the key demographic parameters that drive population dynamics. Factors affecting these demographic parameters in large, long-lived, extinction-threatened mammals are diverse and may differentially affect subpopulations in disparate parts of an ecosystem. We conducted annual photographic surveys to uniquely identify 1,520 giraffes at 4 subpopulations around the Serengeti Ecosystem in Tanzania to estimate demographic parameters of age- and sex-specific survival probabilities, reproduction, population densities, group sizes, and long-distance movements. In the Seronera (central) subpopulation, we combined 15 years of data from 3 independent survey schemes, developed a Bayesian hidden Markov model to estimate demographic parameters, and conducted a retrospective population analysis to elucidate the demographic drivers of temporal changes in population growth rate. We collected data over 4–5 years for 3 other subpopulations, and used frequentist methods to estimate demographic parameters. We compared our results with historical estimates from the 1970s and 2000s to examine long-term population trends and demographic drivers. We found significant differences in adult and subadult survival probabilities among subpopulations, with

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lower adult survival associated with declining subpopulations. Retrospective population analysis for the Seronera subpopulation reiterated that adult survival is a critical demographic driver of population dynamics for giraffes. The 2 subpopulations adjacent to the protected area boundary declined over 48 years, whereas the Seronera subpopulation stabilized since 2008. Only one individual moved between subpopulations, providing evidence for subpopulation insularity and potential genetic structuring of the overall population. These factors underscore the need for subpopulation-specific conservation strategies aimed at raising adult survival within the western and northeastern parts of the Serengeti Ecosystem. Community-based conservation efforts adjacent to protected areas have been effective in raising adult survival and density elsewhere. Our findings highlight the importance of understanding subpopulation dynamics and their demographic drivers for evidence-based conservation and management to recover endangered giraffe populations.

KEYWORDS

Bayesian hidden Markov model, demography, *Giraffa camelopardalis*, *Giraffa tippelskirchi*, multistate mark-recapture analysis, robust design

Estimating key demographic parameters like survival, reproduction, and movement is fundamental to wildlife population biology because demographic parameters mediate population dynamics and the evolution of life-history strategies (Mills 2013, Murray and Sandercock 2020). Quantifying demographic parameters over time and space is essential for management of wildlife because specific demographic drivers of population growth or decline can then be identified. This becomes particularly important for long-lived, slow-reproducing species with complex life histories (Bond et al. 2023*a*) that are highly vulnerable to population declines (Cardillo et al. 2005) and face significant conservation challenges (Muller et al. 2018). Especially useful for estimating demographic parameters are longitudinal live-encounter data from identifiable individuals and methods to account for imperfect detection, which provide parameter estimates that are relatively unbiased and precise compared to methods that do not account for imperfect detection (Lebreton et al. 1992, Nichols 1992). Long-term and individual-based demographic studies on multiple subpopulations are rare yet invaluable for pinpointing factors that mediate population dynamics, thus informing successful conservation and management of extinction-threatened species (Ripple et al. 2015, Lee et al. 2022).

The giraffe (*Giraffa* ssp.) is one of the world's few megaherbivore species—plant-eating mammals that can reach an adult mass >1,000 kg (Owen-Smith 1988). Giraffes live up to 30 years, produce a single calf after a 15-month gestation period (Bercovitch and Berry 2017), and have a 20-month interbirth interval (Lee et al. 2017). The slow life history of giraffes combined with their large space-use requirements (Knüsel et al. 2019) makes populations especially vulnerable to declines in adult survival and local extirpation (Carmona et al. 2021, Bond et al. 2023*a*). The Masai giraffe (*G. tippelskirchi*), the species found in southern Kenya and throughout Tanzania, declined by 40% over 3 decades to an estimated 35,000 individuals, was listed as endangered on the International Union for Conservation of Nature (IUCN) Red List in 2019 (Bolger et al. 2019), and was considered warranted for listing as threatened under the United States Endangered Species Act in 2024 (U.S. Fish and Wildlife Service 2024). Recent findings by Lohay et al. (2023) revealed that Masai giraffes east and west of the Gregory Rift Escarpments are genetically distinct, and there is significant population genetic structure and low gene flow among subpopulations in northern Tanzania (Brown et al. 2007, Lohay et al. 2023). This suggests that Masai giraffe subpopulations may be more at risk than previously believed and underscores the need for knowledge about subpopulation conservation status and the demographic drivers of their population dynamics.

The Serengeti Ecosystem of western Tanzania (Figure 1A) supports the largest population of Masai giraffes on Earth, hosting more than twice as many individuals as any other ecosystem throughout the species' range (Bolger et al. 2019). Two previous studies estimated population size and structure of 3 subpopulations of giraffes, Seronera (central), Kirawira (west), and Bologonja (northeast; Figure 1A, B), based on aerial counts and ground-based surveys (Pellow 1983, Strauss et al. 2015) and demographic parameters using photographic capture-mark-recapture (CMR) methods in Seronera (Pellew 1983, Strauss et al. 2015) and Kirawira (Strauss et al. 2015).

In the 1970s, herbivore populations—including giraffes, buffaloes (*Syncerus caffer*), and wildebeests (*Connochaetes taurinus*)—had recovered from the devastating rinderpest epidemics that began in the late 1800s and ended in the early 1960s. The increase in grazing herbivore numbers after release from rinderpest resulted in less late-season grass biomass, which reduced the annual area burned and led to tree and shrub regeneration that ultimately increased food supply for giraffes (Norton-Griffiths 1979, Sinclair 1979). Pellew (1983) considered the giraffe population of the 1970s to be expanding. Strauss et al. (2015) documented a 67–86% decline in giraffe densities in 2010 compared to 1975, a decrease in the proportion of younger individuals, a drop in adult and subadult survival probabilities in Seronera, and smaller group sizes. These demographic changes were attributed to poaching by humans and limited preferred forage from changes in woody vegetation communities, suggesting both top-down and bottom-up influences on population dynamics in giraffes (Strauss et al. 2015).

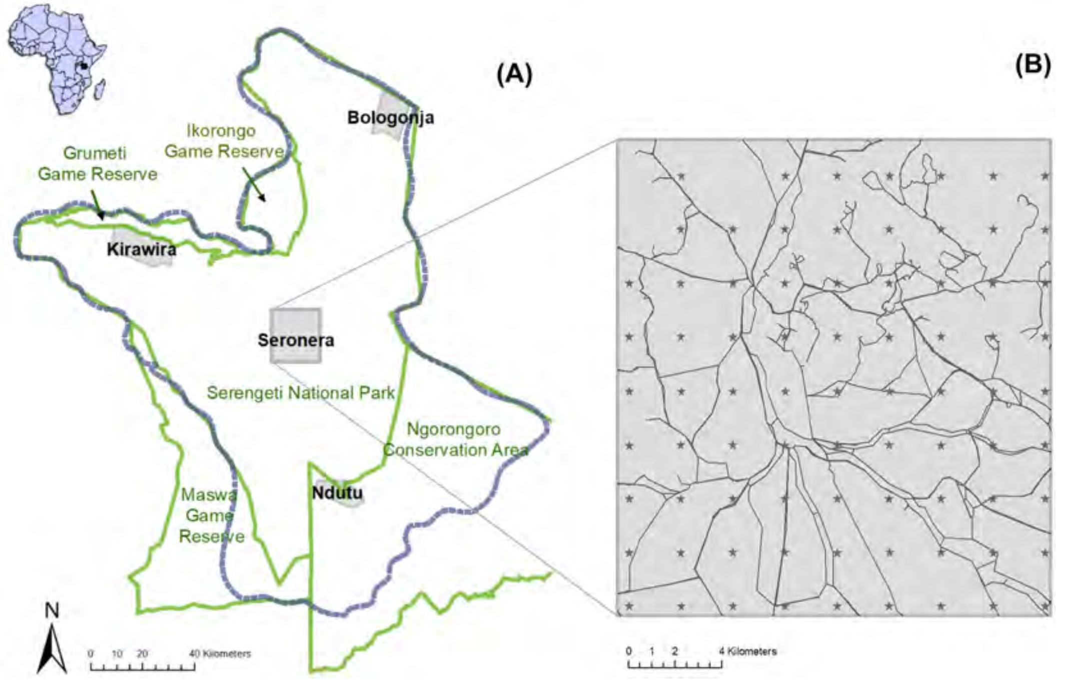

FIGURE 1 Western Masai giraffe study area in the Serengeti Ecosystem, Tanzania (blue dashed line); inset is location within Africa. Green polygons are protected areas. A) Four giraffe demography study sites in Seronera (central), Kirawira (west), Bologonja (northeast), and Ndutu (south). B) Seronera study site with active encounter survey roads (gray lines) and camera trap locations (gray stars).

Since 2010, the landscape of the Serengeti Ecosystem has continued to be transformed by human activities. A large expansion in the number of lodges and visitors (Larsen et al. 2020) and concomitant increases in roads have occurred, with associated impacts on water sources and vegetation. Increases in the human population along the protected area boundaries have also been observed (Larsen et al. 2020). Illegal hunting and poaching for bushmeat markets have been documented in the Serengeti (Masolele 2018), while wildlife law enforcement efforts in Tanzania have fluctuated because of broad-scale events such as global recessions, the COVID-19 pandemic, and government policy transitions (Kideghesho et al. 2021). Thus, human activities dynamically affect wildlife populations (Veldhuis et al. 2019) in addition to natural processes such as predation, climatic variation, and density dependence (*sensu* Lee et al. 2016*a*, *b*; Bond et al. 2021*a*, 2023*a*, *b*).

We analyzed a longitudinal, individual-based photographic CMR dataset (Foster 1966, Lee et al. 2022) to estimate current giraffe densities, demographic parameters, and group sizes in subpopulations in the western (Kirawira), northeastern (Bologonja), southern (Ndutu), and central (Seronera) areas of the Serengeti Ecosystem (Figure 1A), and examined 48-year trends using historical data from Pellew (1983) and Strauss et al. (2015). We quantified 15-year dynamics (2008–2023) and demographic parameters of the giraffe subpopulation in the central Serengeti (Seronera) and used retrospective population analysis that quantifies the temporal correlation between annual demographic rates and the annual subpopulation growth rate to identify the demographic drivers of observed population dynamics (Schaub et al. 2013, Schaub and Kéry 2022). We also determined geographic isolation of subpopulations by quantifying individual long-distance movements among the central, western, northeastern, and southern Serengeti subpopulations, all separated by >40 km.

STUDY AREA

Three study sites (Seronera, Kirawira, and Bologonja) were selected by Pellew (1983) to include vegetation types representative of Sinclair's (1972) woodland strata, and we added a fourth site (Ndutu) in the south (Figure 1A). Seronera (240 km^2) in the central Serengeti National Park is a woodland-grassland savanna dominated by umbrella thorn (*Vachellia tortilis*) and glossy-leaved corkwood (*Commiphora trothae*), with grassland plains in the southern portion of the site. Kirawira (210 km^2) is largely open grasslands with blackthorn (*Senegalia mellifera*) and woodland scrub thicket dominated by gum acacia (*S. senegal*) and splendid thorn (*V. robusta*) in the western corridor of the park, along the southern border of the Grumeti Game Reserve. Bologonja (175 km^2) in northeastern Serengeti is composed of grasslands and woodlands dominated by red thorn (*V. gerrardii*) and whistling thorn (*V. drepanolobium*) adjacent to the Masai Mara National Reserve in southern Kenya. Ndutu (113 km^2) is composed of umbrella thorn woodlands, marshes, short grasslands, and soda lakes in the southern Serengeti National Park and western Ngorongoro Conservation Area. Tourist presence is generally high year-round in Seronera (except for April, the rainiest month), seasonally high in Ndutu (December–March) during the birthing period for the populations of wildebeests, gazelles (*Nanger granti* and *Eudorcas thomsonii*), and plains zebras (*Equus quagga*), and seasonally high in Kirawira and Bologonja (July–November) corresponding to when the wildebeests are in those areas. Soil types underlying the woodlands differed in each of the 4 study sites (Figure S2, World Agroforestry Centre Geoscience Lab downloaded from http://landscapesportal.org/layers/geonode:tanzania_soil).

METHODS

In Seronera, we obtained data from active encounter surveys and from camera traps (Swanson et al. 2015) during 3 distinct but continuous time periods over 15 years (2008–2023; Table 1). We used a Bayesian approach in Seronera, as this enabled estimation of survival, reproduction, population density, and population growth rate while incorporating and accounting for multiple sources of variability and uncertainty inherent in jointly analyzing

TABLE 1 Study site and years of collection of photographic capture-mark-recapture (CMR) data for Masai giraffes in the Serengeti Ecosystem, Tanzania. The X indicates the number of surveys; x is a single survey and xx or xxx means 2 or 3 surveys conducted for robust design.

	Year of data collection														
	Active encounter surveys + aerial surveys with ground counts			Camera trapping surveys						Active encounter surveys					
Study site	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2018**	**2019**	**2020**	**2021**	**2022**	**2023**
Seronera (center)	xx	xx	xxx	xx	xx	xx	xx	xx	xx	xxx	xx	xx	xx	x	xx
Kirawira (west)	xxx	xxx	xxx								x		x		x
Bologonja (northeast)	x	x	x								x		x		x
Ndutu (south)										x	x		x		

datasets based on differing data collection methodologies, and propagating parameter uncertainty to the derived parameters (Kéry and Schaub 2012, Schaub and Kéry 2022). In Kirawira, Bologonja, and Ndutu, we collected data using active encounter surveys from 2018 to 2023 (Table 1) and compared derived parameters to those reported in previous studies. To replicate and facilitate comparisons with previous work reported in Pellew (1983) and Strauss et al. (2015), we used a frequentist approach (Cooch and White 2019) to generate subpopulation-specific demographic estimates of survival, reproduction, population density, and population growth rate.

Individual-based capture-mark-recapture data collection

The 4 study sites (Figure 1A) represented common Serengeti vegetation types from woodlands to grassland savannas. We collected giraffe identification photographs annually in October (the end of the annual dry season) using active encounter road transect surveys (2008–2010, 2018–2023) and camera traps (2011–2016), with consistent protocols for image quality and animal identification (Table 1). We used photographs of coat spot patterns for identification of giraffes because their patterns are individually unique and unchanging so their marks cannot be lost (Foster 1966). During active encounter surveys (2008–2010 and 2018–2023), we drove road transects and when giraffes were seen we slowly approached and photographed each animal's right side. For camera trap data (2011–2016), we used all sufficient-quality right-side images of giraffes.

In 2008, we initiated active encounter road transect surveys for giraffes within the same Seronera study site as Pellew (1983; Figure 1B) and conducted a full survey of the study site bi-weekly every October for the first 2 years, with a third survey conducted in the third year. Some roads were occasionally surveyed more than once, and we added those photographic data to the bi-weekly survey. In 2010, researchers from Snapshot Serengeti (Swanson et al. 2015) constructed an array of camera traps in the Seronera woodlands that overlapped the Pellew study site boundary (Figure 1B); Snapshot Serengeti provided us with giraffe photographs taken between 2011 until 2016 by cameras within the boundary, from which we sub-sampled the right-side October images and categorized them into either the first or last 2 weeks of the month. Starting in 2018 until 2023, we conducted 2 (but 2018 = 3 and 2022 = 1) consecutive active encounter road transect surveys of the Pellew study site every October, and drove all roads once per survey. No photographic data were available for 2017. From 2019–2023, we collected giraffe photographs approximately every other year within Kirawira and Bologonja, and in 2018, 2019, and 2021 in Ndutu.

For all photographs, we recorded sex (male, female) and age class (calf [<1 year old], subadult [1–2 years old], or adult [≥3 years old]) based on a suite of physical characteristics (Strauss et al. 2015). We recorded the global positioning system (GPS) location of each individual or center of the herd during active surveys, and the GPS location of the camera trap for the camera grid data, which we then used to calculate each giraffe's mean distance to edge of the survey boundary as a spatial individual covariate for detection (Royle et al. 2014). We matched giraffe identification images using WildID, a computer program that matches large datasets of giraffe images collected using our protocols with low error rates (Bolger et al. 2012). After matching, we created an encounter history for every identified individual, recording whether (1) or not (0) the animal was seen during each secondary sampling occasion within a primary sampling event in our robust design methodology for Seronera, or during each single annual survey for Kirawira, Bologonja, and Ndutu.

Data analysis

We used the encounter-history data to estimate age class- and sex-specific annual apparent survival probabilities, annual recruitment, annual immigration, annual abundance, annual density, population growth rate, and mean and maximum group sizes for each of the subpopulations. Research on eastern Masai giraffes from the Tarangire Ecosystem, situated 200 km southeast of the Serengeti, revealed that male and female calves and subadults exhibited similar survival probabilities (Lee and Bond 2022). However, starting at age 3, female giraffes showed significantly higher survival probabilities than males. These findings formed the basis of our 3-stage birth-flow life-cycle graphs for western Masai giraffes in Serengeti (Figure 2). Because Tarangire and Serengeti share similar ecological conditions, the insights from Tarangire provide valuable guidance for understanding giraffe populations and conservation strategies in the Serengeti.

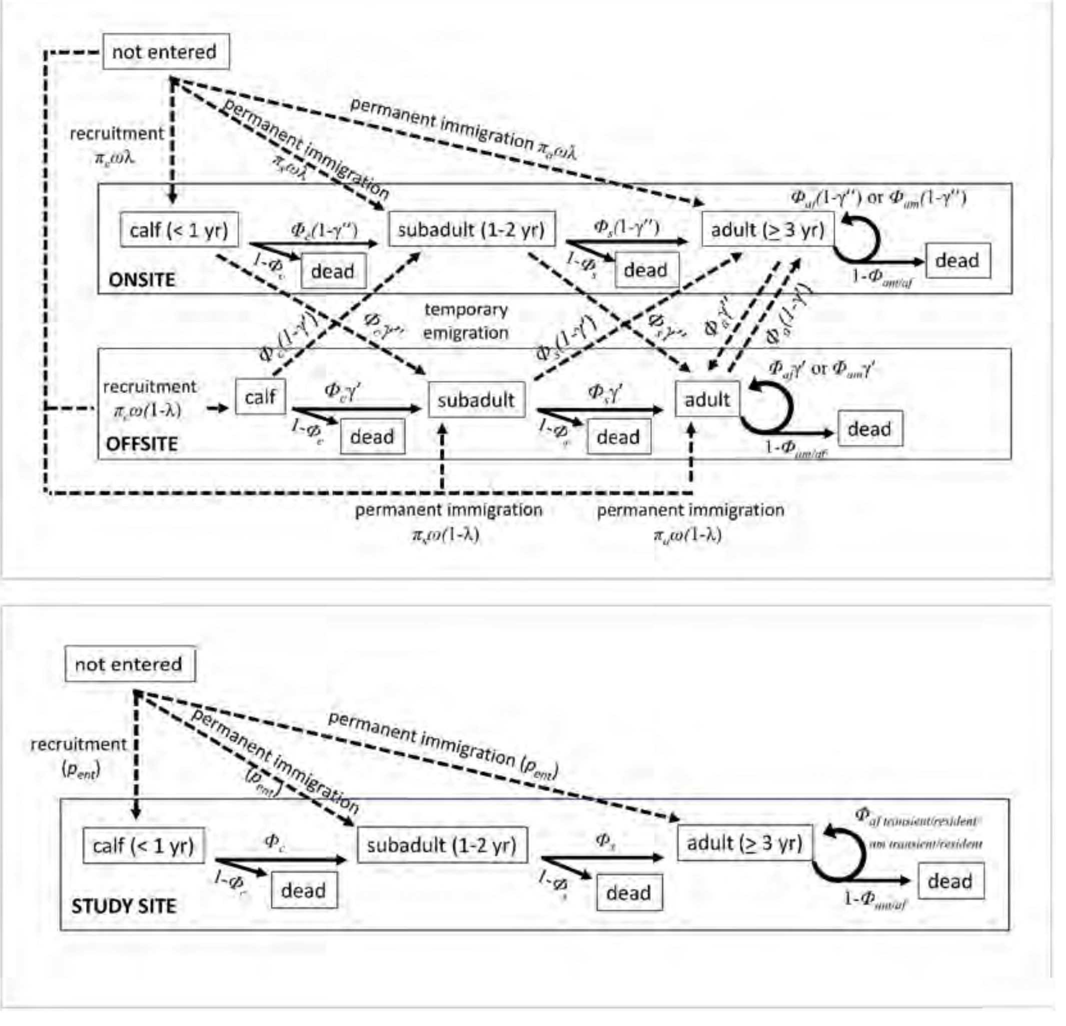

FIGURE 2 Birth flow life-cycle graphs for western Masai giraffes in the Serengeti Ecosystem for subpopulations in Seronera (top) and Kirawira, Bologonja, and Ndutu (bottom). Transitions among life-cycle stages are on an annual basis. Recruitment is birth, and permanent immigration is movement into the subpopulation. In robust design (top), temporary emigration out of and into the Seronera subpopulation occurs in the intervals between primary events. Demographic parameters included survival (Φ), probability of detection (p), probability of staying offsite (γ'), temporary emigration (γ''), proportion of recruits and immigrants entering onsite (λ), removal entry probability (ω), and new recruits (π). Age-sex groups included calf (c), subadult (s), adult males (am), and adult females (af). In the bottom graph, p_{ent} is probability of entry into the subpopulation.

Demography and population dynamics over 15 years in Seronera

For Seronera, we used a robust design for our data collection and analysis, which involved >1 sampling occasions (secondary surveys) within a given event (primary survey). We conducted the primary survey once per year. This design assumed a closed population—meaning no births, deaths, immigration, or emigration—within a primary sampling event but an open population between primary events. The time frame for data collection within each primary survey event was <1 month, so we assumed we met the closure assumption for robust design CMR analyses while still ensuring that every survey was independent. Robust design improves the precision and identifiability of parameters in the CMR framework (Pollock 1982) and enables the estimation of temporary emigration (Kendall et al. 1995) and entry probabilities into the study site (Kendall and Nichols 2002). The maximum number of secondary survey occasions within a primary survey event in our study was 3.

We estimated sex- and age-class-specific detection and demographic parameters for Seronera (Table S1) using a Bayesian hidden Markov model (HMM) of the closed robust design (Rankin et al. 2016, Gibson et al. 2018, Riecke et al. 2018). We fit a model that portrayed the life-cycle graph of giraffes (Figure 2, top). We used the multistate formulation of the Jolly-Seber model with state transitions, and employed data augmentation to account for animals that likely entered the subpopulation and were never detected (Kéry and Schaub 2012, Royle and Dorazio 2012). The multistate formulation has the flexibility to include sex, age classes, and location of individuals (onsite vs. offsite; Kéry and Schaub 2012). The state transitions permitted the estimation of the entry process into the subpopulation, temporary emigration out of the study site between primary events, and apparent annual probability of surviving and transitioning to the next age class. Apparent survival (Φ) is the probability of an animal surviving and not permanently emigrating from the study site between times t and $t + 1$. We incorporated individual spatial heterogeneity in detection probabilities in a spatial CMR context (Royle et al. 2014, Bond et al. 2023*b*) because it is likely that portions of some animal's home ranges were partly or largely outside the surveyed area (thus less available for observation) versus completely within the surveyed area (thus more available for observation). We used each giraffe's mean observed location distance to the edge of the survey area as an index of how much time they likely spent in the surveyed area. We also allowed detection probabilities to differ for the 3 data collection methods, and fixed detection probabilities to zero for a year in which no surveys were conducted (Supplemental Data Analysis 1).

To assess the goodness of fit of our model, we conducted posterior predictive checks by comparing replicated data, simulated under our model, to the actual data that we analyzed using the same model (Gelman et al. 2014). Specifically, we compared the number of individuals detected during each primary event between the replicated and observed data and calculated Bayesian *P*-values for each primary event. Bayesian *P*-values represent the probability that the replicated data could be more extreme than the observed data, with values close to 0.5 indicating a good fit (Gelman et al. 2014).

To accommodate heterogeneity in detection, and in survival probabilities for the adult age class, we incorporated covariates for capture and survival probabilities. We treated age-class-specific detection probabilities as a function of period of data collection, mean distance of all sightings for an individual to the edge of the study site boundary, and sex (for adults), and included a random effect of year. We assigned sex for both the unsexed observed individuals and the augmented pseudo-individuals as a Bernoulli trial based on the empirically observed proportion of females (0.57) in the Seronera subpopulation. For camera traps, we modeled an additional detection parameter with a covariate of number of trap days the grid of cameras was working within each secondary sampling occasion. No data were available for the number of working trap days during the last camera trapping primary sampling event (2016), so we drew trap days from a normal distribution with the mean and standard deviation based on the number of photos obtained during the 2 secondary occasions of that year. Age-class-specific survival probabilities included a random effect of year and a linear effect of sex on the logit of adult survival (we only modeled the effect of sex on adult survival; for mathematical description see Supplemental Data Analysis 1).

For our derived subpopulation parameters, we estimated, per year (i.e., primary event), the following: the number of male and female giraffes alive within the study site (abundance $\hat{N}$), which is the sum of onsite (within the study site and observable) + offsite individuals (either temporarily outside the study site or within the study site but unobservable because they cannot be detected; e.g., they are outside the observable survey area covered by our road transects); the number of male and female giraffes immigrating into the study site (permanent immigrants; adult and subadult recruits); and the number of male and female births (calf recruits). We calculated the subpopulation growth rate as the number alive at time *t* divided by the number alive at time *t* – 1. Similarly, we calculated per capita immigration rates as the number of immigrants at time *t* divided by the abundance $\hat{N}$ at time *t* – 1.

Finally, to explore the demographic drivers of subpopulation dynamics, we correlated the contribution of the variability of each demographic parameter to the variability in the population growth rate in a retrospective population analysis (Schaub et al. 2013, Schaub and Kéry 2022). The magnitude of the correlation coefficient (*r*) represented how much the temporal variation of that demographic parameter contributed to the temporal variation of subpopulation growth rate during the study period. We computed the correlation coefficients in each posterior sample to derive the posterior distributions and reported the mean and 95% credible intervals (Schaub et al. 2013).

We used NIMBLE (version 1.1.0) to implement the Bayesian HMM. We used non-informative priors for all parameters and ran the Markov chain Monte Carlo (MCMC) for 5 chains of 100,000 iterations each with a burn-in phase of 50,000 iterations and a thinning of 5. To confirm that the MCMC chains had converged, we visually examined trace plots and computed the Gelman-Rubin convergence statistic, $\hat{R}$ (Gelman and Rubin 1992; Tables S3 and S4).

Demography and density in Kirawira, Bologonja, and Ndutu

For the Kirawira, Bologonja, and Ndutu sites, we used a frequentist approach to estimate giraffe survival probabilities, reproduction, and abundance. We chose this method to facilitate comparison with frequentist estimates provided by Strauss et al. (2015). We conducted 3 October photographic identification surveys, with missing years between some surveys (Table 1). We did not survey these sites using a robust design. We used the R 4.4.0 (R Core Team 2023) package RMark (Laake 2013) to construct and run open-population Jolly-Seber models using program MARK (White and Burnham 1999). For each site we fit a model that portrayed the life-cycle graph of giraffes (Figure 2, bottom). Derived parameters were the total estimated abundance of all animals alive within the study site in each sex and age class per year (abundance $\hat{N}$), accounting for imperfect detection; the number of male and female giraffes immigrating into the study site (permanent adult and subadult immigrants); and the number of male and female recruits (births; further details provided in Supplemental Data Analysis 2). We assessed the goodness of fit for each site's model from the estimated $\hat{c}$, an indication of the level of overdispersion in the data (Cooch and White 2019).

The size of each study site differed, so we calculated annual giraffe density to enable direct comparison among subpopulations. Because of the lack of geographic closure, our abundance estimates may include some animals whose activity centers fell outside the study area bounds (Cooch and White 2019). Our model in Seronera quantified temporary emigration probabilities of 0.08 (SD = 0.02), meaning approximately 8% of individuals identified within the study site were offsite (or not available for capture) during a given survey. Therefore, we presumed 8% of the subpopulation might have activity centers outside but overlapping the edge of our study site boundary. To provide a density estimate that removed these animals, we reduced the estimated abundance in each subpopulation by 8%. We calculated the density of giraffes whose activity centers were within each study site as $\hat{N}$ – ($\hat{N}$ × 0.08)/study site area (km^2).

We tested for differences in demographic parameters among the 4 subpopulations using analysis of variance with Tukey adjustments for pairwise comparisons, with the TukeyHSD function in R (95% family-wise confidence levels). Specifically, for each demographic parameter and subpopulation, we generated random draws from a normal distribution using the means and standard deviations derived from the frequentist analyses, with the number of draws for each site-parameter combination equal to the number of individually identified giraffes in that category (for the Kirawira, Bologonja, and Ndutu subpopulations). For the demographic parameters of the Seronera subpopulation, we generated 845 random draws from the posterior distribution of the Bayesian HMM.

Comparison of group sizes, movements, and density to historical data

We recorded one GPS location for each giraffe group formation (including singletons) during each survey. We then calculated the number of individual giraffes in each group formation based on our CMR data. We used the same definition of a group as Strauss et al. (2015): individuals feeding, socializing, or moving together, with a solitary individual equaling a group size of one. Giraffe group members are typically self-defining but can be dispersed over a large area (Carter et al. 2013). Our protocol was to consider giraffes to be in different groups if the outermost individual of one group was separated by >500 m from the outermost individual of another group as measured with a GPS. We computed mean and standard deviation (SD) of group size by subpopulation. We tested for differences in mean group sizes among the 4 subpopulations using analysis of variance with Tukey adjustments for pairwise comparisons, with the TukeyHSD function in R (95% family-wise confidence levels). We then compared mean and maximum giraffe group sizes from this study with historical group sizes from the 1970s and the 2000s as reported by Strauss et al. (2015).

Strauss et al. (2015) found no evidence of giraffes moving between the central, western, and northeastern subpopulations within a limited period of 3 years; our aim was to test their findings with a longer time frame and larger dataset, and to include the southern subpopulation (Ndutu) in the movement analysis. We used our CMR data to quantify long-distance dispersal events by individual giraffes among the subpopulations. Our encounter history for each giraffe included the site of each detection, similar to Strauss et al. (2015), enabling us to determine whether any of the individuals in our sample ever transitioned between sites during our study.

Giraffe density estimates from Pellew (1983) and Strauss et al. (2015) used aerial survey data, a method that estimates density as the number of giraffes observed in the study sites at a point in time and typically results in lower density estimates than other methods (Caughley 1974; Jachmann 2001, 2002; Fleming and Tracey 2008). For periods and sites for which no CMR data were available, we used a correction factor to enable comparison of our CMR-derived giraffe density estimates with the historical reports that were based on aerial survey data. We calculated the subpopulation densities of Seronera and Kirawira from 2008–2010 with CMR-derived abundance estimates presented in Strauss et al. (2015) and reduced these abundances by 8% (to correct for giraffes detected in our study sites that might reside primarily outside the boundaries, as described above). The CMR-derived densities from Strauss et al. (2015) were 3.4 (Kirawira) to 5.5 times (Seronera) higher than their aerial survey-derived densities. Lee and Bond (2016) reported an aerial survey-to-CMR correction factor of 3 for giraffes in Tarangire National Park, Tanzania, and Greene et al. (2017) calculated an aerial survey-to-distance-sampling correction factor of 3.5 for giraffes in Manyara Ranch, Tanzania. To be conservative, we adjusted each subpopulation density estimate that was derived from aerial surveys by multiplying by 3 to provide a reasonable comparison of the historical aerial survey density estimates with CMR-derived estimates.

RESULTS

From our photographic CMR data, we identified 1,520 individual giraffes across the 4 subpopulations in the Serengeti Ecosystem during our study period. We observed 845 giraffes in Seronera, 210 in Kirawira, 149 in Bologonja, and 316 in Ndutu (Table S2).

Subpopulation dynamics in Seronera

Posterior predictive checks indicated good model fit, evidenced by an average Bayesian *P*-value of 0.58 (range = 0.39–0.73) across all primary survey events (Figure S3). Detection probabilities were affected by several covariates (Table S3). An individual giraffe's mean distance from the edge of the study site boundary had a clear positive relationship with detection probabilities in all age classes, meaning giraffes that were observed closer to the edge of the study site boundary had lower detection probabilities (Table S3). Detection probabilities during camera trap surveys (2011–2016) were lower compared to active encounter surveys 2008–2010 and active encounter surveys 2018–2023 (Figure S4), whereas we did not find evidence that detection probabilities for both active encounter surveys differed (Table S3). Number of days the camera traps were operable had a positive effect on detection probability. Finally, detection probabilities for adult females were higher than for adult males (Table S3; Figure S4). All biological parameters of interest were estimated while accounting for these detection biases.

The adult age class had the highest apparent survival probabilities, followed by subadults, with calves having the lowest survival probabilities, and adult female giraffes having higher mean survival probabilities than adult males (Table 2). Per capita immigration rates of adult males and females into the Seronera subpopulation were 0.00 or 0.01 over the study period, and higher ($\overline{x}$ = 0.06, SD = 0.04) and more variable for subadults (Figures S5 and S6). The mean probability of temporarily leaving Seronera was 0.08 (SD = 0.02), while the mean probability of remaining offsite site after temporary emigration was 0.85 (SD = 0.07).

Our estimated annual abundance of giraffes in the Seronera subpopulation was 447 (SD = 53) from 2008 to 2023, with a low of 362 in 2012 and a high of 534 in 2020 (Figure S7). Mean abundance from the first 3 years of the study (450 individuals, SE = 15.3) was higher but not statistically different than the mean estimate reported by Strauss et al. (2015) of 401 individuals (SE = 12.2). The subpopulation growth rate indicated fluctuation around a stable growth rate of 1.0 over the 15-year study period (Figure 3 and S8). Our retrospective population analysis indicated that annual population growth rates in Seronera were positively associated with adult survival and calf recruitment (births), while survival of the youngest age classes exerted the least effect on population growth rates (Table 3).

Demography of Kirawira, Bologonja, and Ndutu compared to Seronera

The estimated $\hat{c}$ values for Kirawira and Ndutu were <3, indicating adequate model fit. However, for Bologonja the estimated $\hat{c}$ = 11.05, suggesting overdispersion likely due to the relatively low sample size. Tukey honestly significant difference (HSD) results indicated demographic parameters differed between all pairs of sites with the exception of apparent survival of calves, which differed between Bologonja and all other sites (Table 2; Figure 3 and S9). Recruitment rates among sites were similar (Figure 3 and S9), especially Ndutu and Kirawira, but apparent survival probabilities of calves, adult females, and adult males at Bologonja were notably low relative to other sites, and subadult survival probabilities were lower in Kirawira and especially Bologonja (Figure 3 and S9).

Population growth rates were <1 in Kirawira and Bologonja from 2019–2023 but stable in Seronera and Ndutu (Figure 3). The current density of giraffes was highest in Seronera, followed by Ndutu, Kirawira, and Bologonja in descending order (Table 2), and densities declined in Kirawira and Bologonja from 2019–2023 (Figure 4).

Comparison of group sizes, movements, and density to historical data

Mean group sizes of giraffes in Kirawira from 2019–2023 were twice as large as mean group sizes in the other subpopulations, and the maximum group size was more than 56% larger than the next-largest maximum group size, which was in Seronera (Table 4). Tukey multiple comparisons of means showed that group sizes were

TABLE 2 Mean and standard deviation (SD) of the demographic probabilities for Masai giraffes, and mean and SD of densities, estimated from capture-mark-recapture (CMR) data at 4 sites in the Serengeti Ecosystem, Tanzania, from 2008–2023 in Seronera, 2019–2023 in Kirawira and Bologonja, and 2018–2021 in Ndutu. We also show reported mean demographic parameter estimates from late 1970s (Pellew 1983) and late 2000s (Strauss et al. 2015) for comparison.

	Seronera				Kirawira			Bologonja		Ndutu	
Parameter	Mean 2008–2023	SD	1970s	2000s	Mean 2019–2023	SD	2000s	Mean 2019–2023	SD	Mean 2018–2023	SD
Calf survival ϕ_c	0.73	0.05	0.42	0.57	0.76	0.28	0.67	0.51	0.44	0.75	0.32
Subadult survival ϕ_s	0.76	0.03	0.92	0.79	0.54	0.43	0.85	0.24	0.44	0.75	0.66
Adult male survival ϕ_{am}	0.83	0.06			0.75	0.31		0.52	0.64	0.81	0.28
Adult female survival ϕ_{af}	0.88	0.05	0.95[a]	0.84	0.82	0.38	0.89	0.62	0.87	0.85	0.40
Recruitment π_c	0.18	0.09	0.21	0.13	0.17	0.14	0.18	0.25	0.13	0.18	0.06
Population growth rate λ	1.00	0.07			0.86	0.58		0.72	0.42	0.97	
Density	1.58[b]	0.19			0.39[b]	0.13		0.26[b]	0.11	1.27[b]	0.02

[a]Adult survival was not reported by sex in Pellew (1983).

[b]Density estimates from CMR data were calculated by reducing the abundance estimates by 8% to account for offsite individuals detected during our surveys.

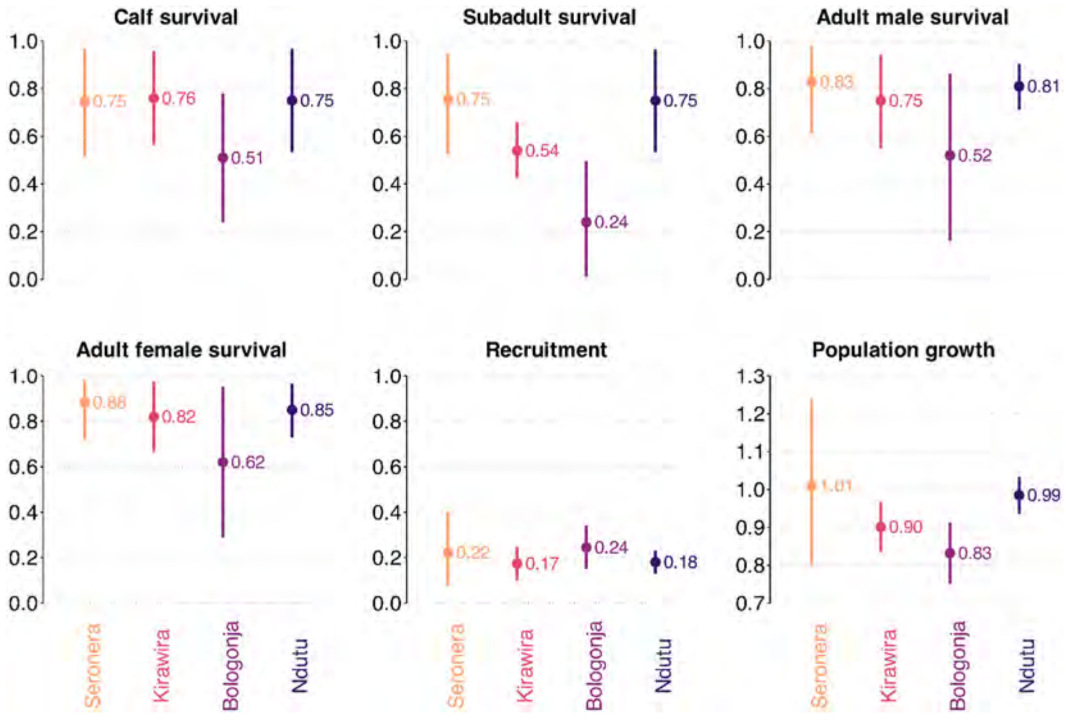

FIGURE 3 Mean estimated demographic probabilities (error bars = 95% CIs) for western Masai giraffes from 2018–2023 in the Seronera study site, 2019–2023 in the Kirawira and Bologonja study sites, and 2018–2021 in the Ndutu study site, Serengeti Ecosystem, Tanzania. Parameters estimated with photographic capture-mark-recapture techniques.

TABLE 3 Mean correlation coefficients (*r*), Bayesian credible intervals, and probability *r* > 0 between variation in a demographic parameter and subpopulation growth rate of Masai giraffes in the Seronera woodlands of the central Serengeti Ecosystem, Tanzania, from 2008–2023. Parameters with an asterisk (*) represent those most correlated with variation in population growth rate, as indicated by a posterior probability of ≥95% that the correlation coefficient *r* does not overlap zero.

Parameter	Mean *r*	2.5%	97.5%	Prob *r* > 0
Calf survival ϕ_c	0.13	−0.40	0.59	0.70
Subadult survival ϕ_s	0.10	−0.44	0.59	0.65
Adult survival ϕ_a	0.66	0.25	0.89	1.00*
Recruitment π_c	0.63	0.21	0.88	1.00*
Subadult immigration π_s	0.49	0.02	0.83	0.98*
Adult male immigration π_{am}	0.27	−0.30	0.75	0.82
Adult female immigration π_{af}	0.29	−0.27	0.76	0.84

similar in Bologonja, Ndutu, and Seronera but larger in Kirawira. These results confirm that giraffe group sizes in the Kirawira region continue to be larger on average than in the other study sites. Comparisons with previous periods (Table 4) suggest that mean group sizes in Bologonja have increased slightly, while maximum group sizes have declined substantially over time. Mean group sizes in Kirawira were slightly larger currently than in the

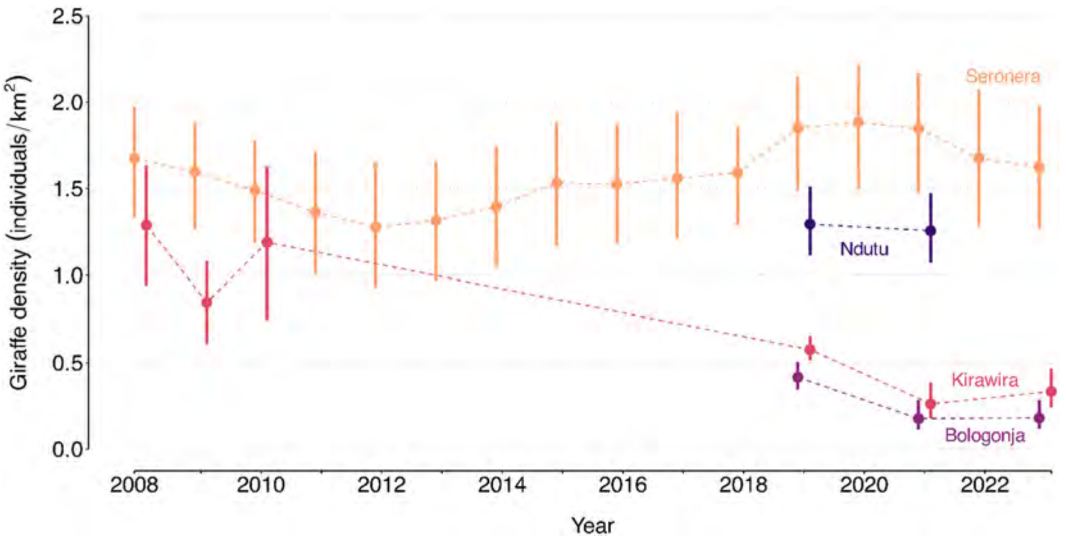

FIGURE 4 Mean estimated densities (individuals/km^2) of western Masai giraffes (error bars = 95% CIs) from 2008–2023 in the Seronera study site, in 2008–2010 and 2019–2023 in the Kirawira study site, in 2019–2023 in the Bologonja study site, and in 2018–2021 in the Ndutu study site, Serengeti Ecosystem, Tanzania. Density estimates derived from capture-mark-recapture data were calculated by reducing the abundance estimates by 8% to account for offsite individuals detected during our surveys.

1970s and nearly twice as large compared to the 2000s, but maximum group size in 2023 was 42% smaller than in the 1970s. In Seronera, contemporary mean and maximum group sizes were markedly similar to those from the 1970s, and were more than twice as large as those recorded in the late 2000s. Group sizes in Ndutu have no historical data for comparison.

Of the 1,520 identified individual giraffes from 2008–2023, only 1 giraffe, a subadult male, transitioned between any of the subpopulations. This male moved 45.3 km from Seronera to Ndutu.

After adjusting estimates derived from aerial data to be comparable with CMR-derived estimates, we observed large declines in giraffe densities between the 1970s and 2000s in all 3 long-term study sites. These declines continued into 2019–2023 in Bologonja and Kirawira (Table 4).

DISCUSSION

Our key results indicate declining Masai giraffe subpopulations in the western corridor (Kirawira) and northeastern woodlands (Bologonja) of the Serengeti Ecosystem since 2008, in contrast with a stable subpopulation in the central Serengeti (Seronera) since 2008 and a relatively stable subpopulation in the southern woodlands (Ndutu) from 2018 to 2021. Kirawira and Bologonja showed similar birth rates as Seronera and Ndutu but had comparatively lower survival of adults and subadults, especially in Bologonja. Fifteen years of stability in the Seronera subpopulation in recent years followed a steep decline in density from the 1970s to the late 2000s (Table 4). This pattern of a roughly 50% population decline between 1970 and the late 1990s with subsequent stabilization in the recent 15 years echoes a broader pattern observed in large mammals in east Africa's protected areas (Craigie et al. 2010). The giraffe subpopulations in Kirawira and Bologonja also steeply declined from the 1970s to the late 2000s but, in contrast to Seronera, continued to decline through 2023.

TABLE 4 Comparison of mean and maximum group sizes and densities of giraffes during the dry season in 4 subpopulations in the Serengeti Ecosystem, Tanzania, over 3 periods: 1975–1977, 2008–2010, and 2018–2023 (Seronera), 2019–2023 (Kirawira and Bologonja), and 2018–2021 (Ndutu).

	Seronera			Kirawira			Bologonja			Ndutu
	1970s	2000s	2018–2023	1970s	2000s	2019–2023	1970s	2000s	2019–2023	2018–2021
Mean group size	9	4.3	9.6	17	12.7	20.3	7	9	10.8	10.0
Max. group size	77	38	78	239	61	138	62	51	29	51
Density (giraffes/km^2)	5.13[a]	1.59[b]	1.75[b]	7.71[a]	1.11[b]	0.39[b]	4.02[a]	0.72[a]	0.26[b]	1.27[b]

[a]Density estimates derived from aerial surveys were multiplied by correction factor 3.0 to account for unobserved individuals and enable comparison with capture-mark-recapture (CMR)-derived densities.

[b]Density estimates derived from CMR data were calculated by reducing the abundance estimates by 8% to account for offsite individuals detected during our surveys.

We found that even with reduced subpopulation densities compared to previous decades, regional patterns of giraffe social grouping remain unchanged over 48 years, with the largest mean and maximum group sizes still found in Kirawira. We recorded only a single long-distance movement (>40 km) among our 4 studied subpopulations, with annual adult immigration rates into Seronera being nearly zero, and subadult immigration low, indicating that these giraffe subpopulations appear quite insular. This observed insularity suggests social structuring within the ecosystem-wide population similar to that documented in the Tarangire Ecosystem (Lavista Ferres et al. 2021, Bond et al. 2021*a*), with genetic structuring documented in both Serengeti and Tarangire (Brown et al. 2007, Lohay et al. 2023). Our findings highlight the need for targeted conservation efforts that address the low survival rates of subadults and especially adults in Kirawira and Bologonja to ensure the long-term viability of this species throughout the Serengeti Ecosystem.

Subpopulation demographic trends

Our estimates of giraffe demographic parameters in Seronera and Ndutu were similar to estimates from populations in protected areas across Africa (Lee et al. 2016, Lee and Strauss 2016). Our long-term, continuous dataset of giraffes in Seronera, in the heart of the Serengeti Ecosystem, revealed the abundance of giraffes in this subpopulation was relatively stable over the past 15 years, with annual fluctuations in population growth rates driven largely by variation in calf recruitment and adult survival, and with minor contributions from subadult immigration. In contrast, data from Kirawira in the western part of the ecosystem indicated that this subpopulation has likely decreased >65% since 2010 and continued to decrease from 2019 to 2021. The Bologonja subpopulation in the northeast part of Serengeti National Park also decreased from 2019 to 2021. Both Kirawira and Bologonja had similar recruitment rates as Ndutu and Seronera but comparatively low survival probabilities. Seronera and Ndutu are located far from the boundaries of the protected areas in the Serengeti Ecosystem, whereas Kirawira and Bologonja are near the boundaries (Figure 1), pointing to potential anthropogenic factors affecting the outlying subpopulations.

In the 1970s the reported density of giraffes in Kirawira was higher than in Seronera, and among the highest densities reported in Africa (Pellew 1983). Conversely, contemporary giraffe density in Kirawira was the second lowest of our 4 study sites and lower than densities reported in the Tarangire Ecosystem (Lee and Bond 2016, Green et al. 2017, Lee and Bond 2022). Considering the 50-year trends, the numbers of giraffes in Kirawira and

Bologonja appear to have plummeted by 85% since the late 1970s and continue to decline, which is reason for concern as the trend for other large mammals indicated declines since 1970 followed by stabilization in recent decades (Craigie et al. 2010).

We also provided the first demographic estimate for giraffes in the woodlands around Lake Ndutu as a baseline for future monitoring, and discovered a higher density of giraffes residing there compared to Bologonja and Kirawira (Figure 4). Overall, the highest density of the 4 subpopulations was in Seronera, both in 2008–2010 and in 2018–2023. This suggests that the woodlands in mollic solonetz soils occurring in the northeastern section of the Seronera study site—where most of the giraffes were detected over our 15-year study period—and extending westwards towards the edges of Serengeti National Park (Figure S2), are high-quality habitats capable of supporting a high density of giraffes. Mollisols are soils that are relatively abundant in organic matter, base rich, and quite fertile and are considered among the most important and productive agricultural soils in the world (Labaz et al. 2024).

The high giraffe population densities in Serengeti during the late 1970s might have been the result of population overshoot of giraffes following their recovery after the end of the rinderpest epidemics. Population overshoot could have caused Pellew (1983) to report densities that were above carrying capacity of the ecosystem, with the downward trend since the 1970s being an adjustment commensurate with the capability of the available habitat to support giraffes, similar to that which occurred with the Serengeti wildebeests after release from rinderpest (Holdo et al. 2009). However, the wildebeest overshoot was approximately 25%, while giraffe populations have fallen 85% since Pellew (1983). If the ecosystem can indeed support giraffe numbers documented by Pellew (1983), we must be careful not to fall into the shifting baseline syndrome (Prins and de Jong 2022).

Demographic drivers of giraffe population dynamics in Serengeti

The results of our demographic and retrospective population analyses agreed generally with expectations for a large, long-lived, slow-reproducing species with delayed maturity (Caswell 2006, Nilsen et al. 2009, Sæther et al. 2013, Paniw et al. 2019, Bond et al. 2023*a*), namely that adult survival was higher than calf and subadult survival, and variation in adult survival and calf recruitment had the strongest correlations with variation in subpopulation growth rate. In large mammalian herbivores, adult survival is usually high and constant while reproduction is typically more variable over time, and therefore reproduction often contributes much to the variance in population growth rates for these species despite the lower sensitivity of population growth to reproductive rate (Charnov 1986, Gaillard et al. 2000, Eberhardt 2002, Sæther et al. 2013, Lee et al. 2016*a*). Adult survival in species with slow life histories should be relatively buffered against environmental variation while reproduction should be more influenced by environmental conditions over space and time (Gaillard et al. 1998, 2000; Paniw et al. 2018). Indeed, within well-protected areas of Tanzania's Tarangire Ecosystem and across Africa, adult female giraffe survival was high and constant across space and time (Lee et al. 2016, Bond et al. 2021*a*) while reproduction varied as a function of soil type (Bond et al. 2021*a*). However, outside Tarangire's protected areas, adult female survival was significantly reduced (Lee et al. 2016*a*), and this lower survival contributed the most to subpopulation extinction risk (Bond et al. 2023*a*).

The likeliest causes of lower adult giraffe survival outside of protected areas are the presence of dense human populations, habitat fragmentation from urbanization and agriculture, and illegal poaching for bushmeat markets or trophies (Muller et al. 2018, Bolger et al. 2019). We agree with the conclusion by Strauss et al. (2015) that illegal hunting is probably the most important factor affecting the spatial variation in apparent survival probabilities of adult giraffes within the Serengeti Ecosystem. The human population is much sparser and there is no agricultural conversion of natural habitats in the central and southern portions of the ecosystem (Seronera and Ndutu) where adult giraffe survival probabilities were highest. Conversely, at Kirawira and Bologonja along the boundaries, adult giraffe survival was lower, and wildlife poaching is a recognized problem in the western corridor (Loibooki et al. 2002, Kaltenborn et al. 2005, Denninger Snyder et al. 2019). Despite a low-density human population adjacent to Bologonja, illegal hunting is the probable culprit affecting giraffe survival there as well. Killing of adult giraffes was suggested as the strongest cause of reduced adult female survival probabilities and the biggest threat to the persistence of giraffes outside protected areas in the Tarangire Ecosystem (Lee et al. 2016*a*, *b*; Bond et al. 2023*a*), indicating the problem extends across the country.

One caveat is that in population modeling based on capture-mark-recapture methods, we can only estimate apparent survival because true mortality and permanent emigration cannot be distinguished (Lebreton et al. 1992). Therefore, it is also possible that adult giraffes are emigrating away from the border subpopulations rather than experiencing higher *in situ* mortality. Human population density is highest in the western part of the Serengeti Ecosystem near Kirawira (where the greatest giraffe decline has been documented), and most of the area along the western border of the park is used for agriculture (Veldhuis et al. 2019). This leads to a large number of illegal incursions by people into the park (Kaltenborn et al. 2005), which could disturb giraffes. It is therefore also plausible that the decline in giraffes documented from the 1970s until the present day is due not to poaching or other factors influencing survival but to anthropogenic disturbances pushing giraffes to other areas outside of our study site boundaries with higher levels of protection, such as the Grumeti Game Reserve adjacent to Kirawira, or more interior areas south of Bologonja. However, our documented low rates of permanent immigration into Seronera and lack of long-distance movements among the 4 sites provide evidence for reduced true survival probabilities as the most likely cause for observed density declines.

In animals with slow life histories, the combination of long life spans, relatively high adult survival, and low rates of immigration makes populations particularly vulnerable to declines from adult mortality that are difficult to ameliorate (Cardillo et al. 2005, Ripple et al. 2015, Carmona et al. 2021). Whether the reductions in the Kirawira and Bologonja giraffe subpopulations were due to persistently high *in situ* mortality—especially of adult females—or to permanent emigration, the subpopulations would likely require a long time to be rescued from extirpation due to low immigration rates. Giraffe survival probabilities and densities were effectively raised in community-based conservation areas adjacent to national parks in the Tarangire Ecosystem through increased law enforcement and more money from ecotourism flowing into the communities (Lee 2018; Lee and Bond 2018*a*, *b*); this could prove effective in the Serengeti system as well. Additional population research at Kirawira and Bologonja is warranted to confirm our observations and determine causes for low apparent survival.

Largest giraffe group sizes in western Serengeti

Estimates of mean group size were larger in all 4 study sites relative to other areas across Africa, where average groups comprised 5 to 6 individuals (Leuthold 1979, Bond et al. 2019). In the 1970s Kirawira, rather than Seronera, supported the highest density of giraffes (Pellew 1983). Further, mean and maximum group sizes of giraffes in the Kirawira site were significantly larger than other sites (Pellew 1983, Strauss et al. 2015) and remained so through the end of the study in 2023. Kirawira includes some woodlands on mollic solonetz soils like in Seronera but also woodlands on eutri-pellic vertisols (Figure S2), which are colloquially called black cotton soils and known for high fertility. The soil type and vegetation composition in Kirawira likely attract large congregations of giraffes, similar to the western part of Manyara Ranch in the Tarangire Ecosystem, where 5 of the 6 largest giraffe groups were recorded during the rainy seasons in extensive patches of sickle bush (*Dichrostachys cinerea*) growing on fertile black cotton soils (Bond et al. 2019). The persistently large group sizes in Kirawira might be due to especially high-quality habitat in the western part of the park, but it is also possible that grouping dynamics in Kirawira compared to other sites are mediated by behavioral differences rather than habitat. We suspect that the western corridor habitat remains capable of supporting a substantially higher density of giraffes—as demonstrated by Pellew (1983)—but their current numbers may be suppressed by external factors such as poaching or disturbances along the edge of the park.

Low rates of long-distance movements

With the exception of one subadult male, we found that individual giraffes in our sample did not undertake long-distance movements among the study sites, a distance of >40 km. There are no geographic or anthropogenic barriers that would inhibit movements, and continuous woodlands occur between all sites except where grassland predominates between Seronera and Ndutu. Giraffes, especially males, have the capacity to travel over long distances (Fennessey 2009, Brown and Bolger 2020, Bond et al. 2021*b*, this study). Several giraffes in Seronera were observed traveling straight-line distances of >40 km over a period of 4 years, as documented by camera trap photos within the larger Seronera grid (P. E. Campbell, Wild Nature Institute, unpublished data), suggesting that individuals within the grid were members of the same super-community (Lavista Ferres et al. 2021). Overall, however, giraffe subpopulations in the Serengeti Ecosystem appear to be largely insular. In addition to documenting essentially no long-distance movements among the subpopulations, we documented extremely low per capita immigration rates of adults and subadults into the Seronera subpopulation over 15 years, despite large areas of continuous suitable woodland habitat that supports giraffes just outside the Seronera study site boundary. This accords with previous evidence about the relatively sedentary nature of these megaherbivores despite their size and large space-use requirements (Knüsel et al. 2019, Bond et al. 2021*b*).

Population genetics showed a surprisingly high genetic differentiation among giraffe subpopulations in the Serengeti and Tarangire Ecosystems, indicating relatively low levels of gene flow (Brown et al. 2007, Lohay et al. 2023). Such insularity of subpopulations suggests likely social and genetic structuring of the giraffe population in the Serengeti that merits further study. Social structuring among giraffes was evident in the Tarangire Ecosystem, with female-based social communities (Bond et al. 2021*a*, *c*) embedded within mixed-sex and age-based super-communities (Lavista Ferres et al. 2021) with few movements among the communities or super-communities and high rates of fidelity. Dagg (2014) noted that despite the mobile lifestyle of giraffes, constantly on the move while browsing, they actually cover a relatively small area and have a low rate of gene flow similar to that of a highly sedentary species. The sedentary nature of giraffes reduces the likelihood of extirpated subpopulations being rescued and increases the amount of time it would take for recolonization.

Uncertainty arising from using multiple datasets

The ability to combine datasets from different sources allowed us to enhance and expand inference, which is especially helpful for long-lived, slow-reproducing animals such as giraffes because many years of longitudinal data are necessary to detect trends. In our Seronera subpopulation, we obtained photographs of giraffes based on different data collection methods over 3 periods, and although we lacked empirical information about some covariate effects on detection and survival, our Bayesian HMM allowed for these covariates to be inferred. Failure to properly address these sources of error could have produced substantial uncertainty in the estimates of key demographic parameters. Bayesian modeling is a powerful tool in the analytical toolbox to deal with missing data and multiple sources of variation. The retrospective population analysis from our combined datasets then allowed us to disentangle the demographic correlates of annual population growth rate with our longer-term time frame. This analytical framework facilitated more reliable inferences about the drivers of long-term demographic and population trends, supporting effective evidence-based conservation and management.

CONSERVATION IMPLICATIONS

Our study revealed biologically significant demographic differences in apparent survival probabilities of adult and subadult giraffes among subpopulations within the Serengeti Ecosystem, along with insularity of the subpopulations. These factors, combined with observed declines over 48 years for 2 subpopulations, underscore the need for subpopulation-specific conservation strategies aimed at raising adult survival within the western and northeastern parts of the Serengeti Ecosystem. Retrospective population analysis reiterated that adult survival is a critical demographic driver of population dynamics for giraffes. Community conservation efforts such as the well-managed Wildlife Management Areas in the Tarangire Ecosystem have been shown to be effective methods of raising adult giraffe survival and density (Lee 2018; Lee and Bond 2018*a*, *b*).

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

ETHICS STATEMENT

The study adhered to relevant regulations and guidelines regarding the ethics of animal welfare.

DATA AVAILABILITY STATEMENT

Data and code are available at: https://doi.org/10.6084/m9.figshare.27118788.

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Does the chain of Eastern Arc Mountains impede gene flow? Genetic evidence from the African savanna elephant and the Masai giraffe in Tanzania

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Abstract

An increase in the human population in recent years poses threats to the conservation of wildlife species. The expansion of human settlement and agricultural activities has led to the loss of wildlife corridors. Apart from the influence of humans on the gene flow of species between protected areas, natural features such as mountains, rivers, and hills can act as a barrier to gene flow. The African savanna elephant (*Loxodonta africana*) and the Masai giraffe (*Giraffa tippelskirchi*) are widely distributed in Tanzania. However, the Eastern Arc Mountains (EAM) and the Gregory Rift Valley (GRV) systems influence gene flow for some species. We conducted a study in southeastern Tanzania covering three major ecosystems: Ruaha–Rungwa, Katavi–Rukwa, and Selous–Mikumi to determine whether there is genetic differentiation between these ecosystems for giraffes and elephants. We analysed the mitochondrial DNA of 450 elephants and 100 giraffes. Our results show that (1) there is high genetic differentiation between populations found east and west of the EAM for both elephants and giraffes, (2) there is no female-mediated gene flow between these populations, (3) Populations found west of the EAM show high genetic connectivity suggesting historical gene flow between them, and (4) elephant populations from Ruaha share haplotypes with both Tarangire and Serengeti ecosystems suggesting historical connectivity between them. Our study reveals that the EAM plays a significant role in the gene flow of these species. However, the recent loss of miombo forests between Ruaha and Katavi, owing to anthropogenic activities, may reduce gene flow in the long run.

Keywords: Eastern Arc Mountains, genetic connectivity, mitochondrial DNA, conservation genetics, Masai giraffe, African savanna elephants.

Introduction

Habitat loss and fragmentation due to land conversion pose significant threats to biodiversity (Fahrig, 2013). To ensure successful conservation efforts, it is essential to maintain genetic connectivity through wildlife corridors (Noss *et al.*, 2012; Taylor, Fahrig & Merriam, 1993). While human activities are a primary driver of fragmentation (Newmark, 2008; Riggio, Jacobson, Hijmans & Caro, 2019), natural barriers such as rivers and mountains can also impede gene flow (Evans, Bliss, Mendel & Tinsley, 2011; Lohay, Weathers, Estes, McGrath & Cavener, 2020; Lohay *et al.*, 2023). Increased isolation can lead to genetic drift, inbreeding, and a higher risk of extinction. Conversely, maintaining connectivity can enhance population viability (Allendorf, Hohenlohe & Luikart, 2010).

In Tanzania, the Ruaha–Rungwa and Selous–Mikumi ecosystems are home to the country's largest elephant (*Loxodonta africana*) populations (Jones *et al.*, 2018; Mkuburo, Nahonyo, Smit, Jones & Kohi, 2020). Genetic studies reveal that habitat fragmentation has limited gene flow, particularly among younger elephants in the Ruaha–Rungwa ecosystems (Lobora *et al.*, 2018). The Eastern Arc Mountains (EAM) also restrict move-

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ment for species like lions (*Panthera leo*) and sable antelope (*Hippotragus niger*) (Pitra, Hansen, Lieckfeldt & Arctander, 2002; Smitz *et al*., 2018). Moreover, the movement of giraffes between Selous and Ruaha is affected by the terrain slope (Crowhurst, Mullins, Mutayoba & Epps, 2013), and the patterns of elephant connectivity have shifted from being terrain-driven to being influenced by human settlements (Epps, Mutayoba, Gwin & Brashares, 2011).

This study investigates the genetic connectivity of African savanna elephants and Masai giraffes (*Giraffa tippelskirchi*) to evaluate how the EAM impact gene flow and genetic differentiation among the Selous–Nyerere, Ruaha–Rungwa, and Katavi–Rukwa ecosystems. We hypothesize that the EAM acts as a barrier, resulting in significant genetic differentiation between populations in these ecosystems. However, we also consider the possibility that some levels of genetic connectivity may still exist, indicating either historical or contemporary movement across the landscape.

We predict that genetic differentiation (F_{ST} values) will be higher among populations separated by the EAM compared to those within the same ecosystem. Furthermore, we expect mitochondrial DNA analyses to reveal distinct population clusters corresponding to geographic regions, reflecting limited gene flow. Conversely, if connectivity is present, individuals from different populations may share mitochondrial DNA haplotypes and exhibit lower genetic differentiation, suggesting ongoing movement between ecosystems despite potential barriers.

Methods

This study explores genetic connectivity in three Tanzanian ecosystems: Nyerere–Selous, Ruaha–Rungwa, and Katavi–Rukwa. The EAM may restrict species movement between Nyerere–Selous and Ruaha–Rungwa. The Ruaha–Rungwa ecosystem, which includes Ruaha National Park and Rungwa Game Reserve, is linked to Katavi–Rukwa through open areas that are not legally protected. The Rufiji River acts as a barrier for Masai giraffes, while increasing human activity and miombo woodland loss threaten wildlife movement (Lobora *et al*., 2018).

The research utilizes mtDNA analysis to complement previous microsatellite studies (Crowhurst *et al*., 2013; Lohay *et al*., 2020). Elephant faecal samples were collected from 2015 to 2017 and preserved in a buffer solution (Ahlering, Hailer, Roberts & Foley, 2011). Blood samples from the Tanzania Wildlife Research Institute (TAWIRI) were stored at –80°C, with DNA extraction performed using the Monarch Nucleic Acid Purification Kit (New England Biolabs). Giraffe faecal samples from Nyerere and Ruaha National Parks were collected between 2020 and 2022, following Lohay *et al*. (2023). DNA extraction was performed using established protocols for elephants (Lobora *et al*., 2018; Lohay *et al*., 2020) and (Lohay *et al*., 2023) for the Masai giraffes. PCR amplification and Sanger sequencing was done using established protocols (Lohay *et al*., 2020, 2023). To assess significant genetic differentiation between populations, we used *F*-statistics implemented in Arlequin version 3.5 (Excoffier & Lischer, 2010), with a significance threshold of $P \leq 0.05$. F_{ST} values closer to 1 indicate greater genetic divergence and less interbreeding.

The mitochondrial DNA (mtDNA) haplotypes obtained in this study were compared with previously published haplotypes, all of which clustered into three subclades: East-Central, Savanna-Wide, and Southeast Savanna (Lohay *et al*., 2020). These subclades were identified through the construction of a neighbour-joining phylogenetic tree using MEGA software (Kumar, Nei, Dudley & Tamura, 2008).

Results

We analysed 450 elephant and 100 giraffe mtDNA samples. We identified 22 elephant haplotypes and five Masai giraffe haplotypes. Only one haplotype was shared between elephant populations on either side of the EAM. Nyerere elephants had Southeast. No haplotypes were shared between the Nyerere and Ruaha Masai giraffe populations (Fig. 1).

Most elephants in the Eastern Arc Mountains (EAM) carry haplotypes common in Tanzania, including Serengeti and Tarangire. Rungwa elephants share haplotypes with those in Serengeti. Elephants from Nyerere and Selous exclusively carry haplotypes of the Southeast-savanna (SS) subclade, while nearly 50% of those in Katavi National Park (KNP) also have SS-related haplotypes. F_{ST} values between Selous (SGR)/Nyerere (NNP) and populations west of the EAM indicated limited female-mediated gene flow, with the highest value between Selous and Lukwati (*e.g.* RNP and PGR, $F_{ST} = 0.845$). In contrast, Ruaha (RNP) had the lowest F_{ST} values with Lukwati and Pigi (Fig. 2, $F_{ST} = 0.010$).

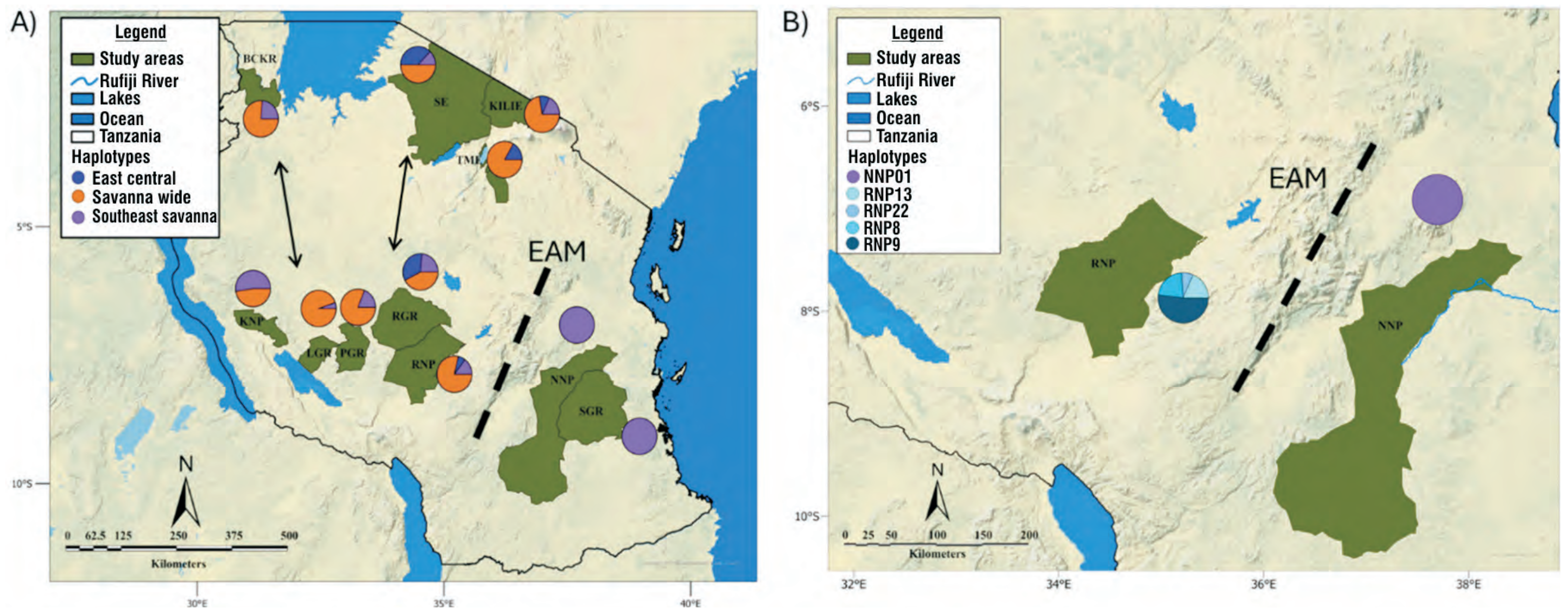

Fig. 1. Maps showing mitochondrial DNA (mtDNA) haplotype distribution in savanna elephants and Masai giraffes. (**A**) Elephants from Selous and Nyerere carried only Southeast-savanna (SS) subclade haplotypes, while those from Ruaha–Rungwa and Katavi–Rukwa had East-Central and Savanna-wide subclade haplotypes. (**B**) Masai giraffes in Nyerere had no shared haplotypes and belonged to two distinct subclades. (National Parks: KNP = Katavi, RNP = Ruaha, NNP = Nyerere, BCKR = Burigi Chato, Game Reserves: PGR = Pigi, LGR = Lukwati, RGR = Rungwa, SGR = Selous, Ecosystems: S.E. = Serengeti, KILIE = Kilimanjaro–Longido, TME = Tarangire Manyara)

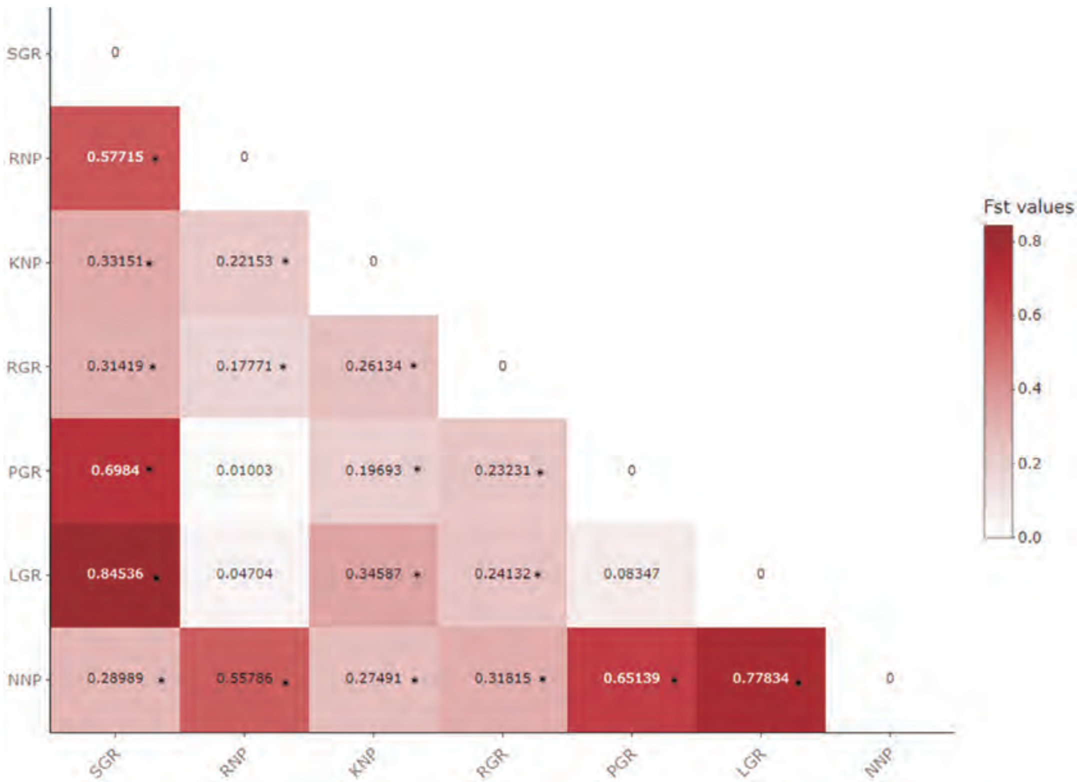

Fig. 2. Pairwise comparison of elephant mtDNA F_{ST} values, illustrating genetic differentiation, with darker shades representing higher F_{ST} values. Pairwise F_{ST} values that are statistically significant ($P \leq 0.05$) are indicated with an asterisk (*).

Most elephants in the EAM carry haplotypes that are widely distributed across Tanzania, including the Serengeti and Tarangire ecosystems. Our results also indicate that Rungwa (RGR) elephants share haplotypes with those in the Serengeti (Fig. 1A). Additionally, all elephants from Nyerere and Selous (Fig. 1A) exclusively carried haplotypes belonging to the Southeast-savanna (SS) subclade. However, nearly 50% of elephants in Katavi National Park (KNP) also carried haplotypes associated with the SS subclade.

The Masai giraffe population in Nyerere National Park (NNP) exhibited low haplotype diversity, with all individuals carrying a single haplotype, likely due to a low-diversity founder population. Genetic differentiation between Ruaha and Nyerere giraffes was high (F_{ST} = 0.374), with no shared haplotypes (Fig. 1B).

Discussion

Our results confirm that the EAM serves as a significant barrier to gene flow for both African savanna elephants and Masai giraffes, with a more pronounced effect observed in giraffes. This difference is likely due to the species-specific movement capabilities. Elephants can navigate steep terrain (Wall, Douglas-Hamilton & Vollrath, 2006), whereas giraffes are more restricted by slopes, leading to reduced dispersal in mountainous areas (Lohay *et al*., 2023).

Mitochondrial DNA patterns support this distinction. Only one elephant haplotype was found to be shared across the EAM, suggesting some historical gene flow mediated by females (Fig. 1). In contrast, giraffes showed no shared haplotypes between the Nyerere (NNP) and Ruaha (RNP) populations, indicating significant population subdivision (F_{ST} = 0.374). Moreover, giraffe haplotypes were found in distinct subclades, with Ruaha individuals clustering with populations west of the Rift, while Nyerere giraffes grouped with eastern populations (Lohay *et al*., 2023). This east–west genetic split reflects patterns seen in northern Tanzania, where the Gregory Rift Valley has separated giraffe lineages for about 290 000 years (Lohay *et al*., 2023). Elephants located west of the EAM, such as those in Ruaha, Rungwa, and Katavi, exhibited low F_{ST} values and shared haplotypes, indicating historical or ongoing gene flow supported by relatively intact corridors. However, increasing habitat loss, particularly of miombo woodlands, poses a growing threat to this connectivity (Lobora *et al*., 2018).

Giraffes, on the other hand, appear to be more sensitive not only to large barriers like mountains but also to finer-scale landscape features. Even in the absence of obvious physical divisions, genetic subdivision among giraffes is often influenced by slope, habitat type, and historical fragmentation (Brown *et al*., 2007; Crowhurst *et al*., 2013; Epps, Wasser, Keim, Mutayoba & Brashares, 2013). Similar genetic fragmentation has been observed in other species, including lions and sable antelopes (Smitz *et al*., 2018; Pitra *et al*., 2002). Our findings reinforce that giraffe populations can become genetically distinct, even over relatively short distances.

These results highlight the need to consider species-specific traits in habitat connectivity assessments. Elephants can navigate fragmented landscapes (Lohay *et al*., 2020, Ahlering *et al*., 2012), while giraffes face greater restrictions. These differences are crucial for conservation, especially amid ongoing land-use changes and deforestation affecting ecological corridors. To further clarify the timing and extent of divergence among giraffe populations, future research should incorporate nuclear DNA and broader geographic sampling. This will help build a more comprehensive understanding of population history and support targeted conservation strategies across Tanzania's key ecosystems.

Acknowledgements

Thanks to Penn State University and Wild Nature Institute for supporting this project. Special thanks to field assistants James Madeli, Emmanuel Kimaro, and the Tanzania Wildlife Research Institute for providing additional elephant tissue samples for this project. We are grateful to the Grumeti Fund for supporting the SAWMA conference. We gratefully acknowledge the Commission for Science and Technology (COSTECH) for granting research clearances #2020-185-NA-1990-172 and #2019-621-NA-2019-132, and Penn State University for approving our research using protocol IACUC#PROTO 201901219.

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References

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Responsible Editor: L. Minnie

FORM NUMBER IV: TAWIRI APPLICATION FORM FOR EXTENSION/RENEWAL OF RESEARCH CLEARANCE

TANZANIA WILDLIFE RESEARCH INSTITUTE (TAWIRI)
P.O. BOX 661, ARUSHA, TANZANIA.
TEL: +255 27 2549571/2548240
FAX: +255 27 2548240. E-MAIL: tawiri@habari.co.tz

1. Personal particulars of the researcher
   (a) Name: Derek E. Lee
   (b) Nationality: USA
   (c) Institute of Affiliation: Wild Nature Institute & Pennsylvania State University
   (d) Contact addresses (e-mail, telephone, fax etc):
   derek@wildnatureinstitute.org
   +1 4157630348, +255 0769477813
   (e) Highest qualification: Ph.D.

2. Title of the research project:
   Ungulate Ecology, Health, and Conservation in Tanzania
   Including: Giraffe Population Genetics and Demography

3. Study/protected area(s) of the study:

   National Park(s): Tarangire, Serengeti, Arusha, Lake Manyara, Ruaha, Nyerere

   Game reserve(s): **Grumeti, Ikorongo**

   Forest reserve(s):

   Wildlife Management Area(s): Burunge, Randilen, Ikona

   Game controlled areas(s): Mtowambu, Lolkisale, Lake Natron

   Open areas (District, Ward, Village):

   Other: Ngorongoro Conservation Area, Manyara Ranch Conservancy

4. Objectives of the research: to obtain robust estimates of population size, trend, and demographic rates for giraffes in northern Tanzanian protected areas.

5. Data collection methods/ tools: We will collect photographic capture-recapture data for demographic analysis.

6. Summary of the progress report: We published 2 manuscripts in scientific journals in 2025. Three manuscripts are in progress.
We ask to continue giraffe photographic surveys.

7. Extension period requested: 16 March 2026 to 15 March 2027

8. Justification for extension of research: Due to the nature of population studies, more data, particularly longer time spans of data, increase the utility and power to make strong inferences. Therefore, in 2026 we are asking to continue giraffe photographic surveys.

9. Name and address of local contact: Dr. George Lohay, East African Road, Plot 39, Block A, PO Box 447, Nambala, Arusha

10. Name (s) of other applicant (s): Monica L. Bond, James Madeli, George Lohay

11. Signature of applicant: *Derek E. Lee*

Date: 1 Jan 2026

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1. Personal particulars of the researcher
   (a) Name: Monica L. Bond
   (b) Nationality: USA
   (c) Institute of Affiliation: Wild Nature Institute & University of Zurich
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      +1 4157630348, +255 0769477813
   (e) Highest qualification: PhD

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10. Name (s) of other applicant (s): Derek Lee, James Madeli, George Lohay

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   (c) Institute of Affiliation: Wild Nature Institute & Grumeti Fund
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   (e) Highest qualification: PhD

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10. Name (s) of other applicant (s): Derek Lee, James Madeli, Monica Bond, Doug Cavener

11. Signature of applicant: George Lohay

Date: 1 Jan 2026

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2. Title of the research project:
   Ungulate Ecology, Health, and Conservation in Tanzania
   Including: Giraffe Population Genetics and Demography

3. Study/protected area(s) of the study:

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9. Name and address of local contact: Dr. George Lohay, East African Road, Plot 39, Block A, PO Box 447, Nambala, Arusha

10. Name (s) of other applicant (s): Derek Lee, George Lohay, Monica Bond

11. Signature of applicant: *James Madeli*

Date: 1 Jan 2026

GRUMETI
FUND

1/1/2026

Director General
Tanzania Wildlife Research Institute
P.O. Box 661
Arusha, Tanzania

Dear Sir,

<u>Re: Support letter for: Ungulate Ecology, Health, and Conservation in Tanzania Including Giraffe Population Genetics and Demography</u>

I am writing to confirm my collaboration with Dr. Derek Lee, Dr. Monica Bond, and Mr. James Madeli on the research project titled *Ungulate Ecology, Health, and Conservation in Tanzania, Including Giraffe Population Genetics and Demography.* I have been part of this research group for the past seven years, initially as a postdoctoral research scholar at Penn State University and now as Head Scientist at the Grumeti Fund.

I am an experienced ecologist with over 15 years of work in Tanzania's protected areas. My doctoral studies at Penn State University provided extensive training in conservation biology, advanced ecological research methods, and population genetics. Over the years, my collaboration with Dr. Derek Lee and Dr. Monica Bond has greatly contributed to the conservation of giraffes in Tanzania. As a local collaborator, I fully support this project and kindly request the renewal of our research permit for 2026. Should you require any additional information, please do not hesitate to contact me at **georgel@grumetifund.org** or by phone at **+255785058525**.

Thank you for your time and consideration.

Yours sincerely,

Dr. George Lohay

RISE Head Scientist-Grumeti Fund

1 Jan 2026

Director General
Tanzania Commission For Science And Technology (COSTECH)
P.O. BOX 4302
Tanzania

Dear COSTECH Director General,

I am submitting the attached progress report summarizing the research project "Ungulate Ecology, Health, and Conservation in Tanzania including Giraffe Population Genetics and Demography." Enclosed, please find COSTECH extension forms and CVs for all researchers involved with the project.

I am requesting an extension to continue these studies for an additional year for foreign researchers:

- Derek Lee
- Monica Bond

Tanzanian researchers:

- George Lohay
- James Madeli

Thank you for your consideration.

Sincerely yours,

Derek E. Lee

Derek E. Lee

TANZANIA COMMISSION FOR SCIENCE AND TECHNOLOGY (COSTECH)

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APPLICATION FOR RESEARCH CLEARANCE EXTENSION (III)

1. Full Name of Principal Investigator: **Dr. Derek Edward Lee**
   (Title/First name/Middle names/Last name)
2. Nationality: **USA** Country of Residence: **Tanzania**
3. Highest qualification: **PhD**
4. Title of research project: **Ungulate Ecology, Health, and Conservation in Tanzania Including: Giraffe Population Genetics and Demography**
5. Contact address: **PO Box 44, Weaverville NC 28787 USA**.
   Email address **derek@wildnatureinstitute.org**
   Mobile number: **+1 4157630348**
6. Project duration **ongoing**
7. When did the project started: **2015**
8. Extension period from: 16 March 2026 to 15 March 2027
9. Duration of the Project as stated in the original application: **ongoing**

Previous clearance: Permit no. **CST00000218-2023-2024-000588**

Date issued: 16 March 2025 Date expired: 15 March 2026

10. Budget: **$15000/yr** Name of Sponsor: **Wild Nature Institute**
11. Objectives of the research: to obtain robust estimates of population size, trend, and demographic rates for giraffes in northern Tanzanian protected areas.
12. Data collection methods/ tools: We will collect photographic capture-recapture data for demographic analysis.
13. Original location of research: Arusha, Manyara, Mara, & Shinyanga, Tabora & Iringa Regions
14. Extension research location: Arusha, Manyara, Mara, & Shinyanga, Tabora & Iringa Regions
15. Summary of progress report (not more than 300 words) What has been accomplished from previous Research Permit: **This project continues to provide data and analyses to inform priority research areas as described in Tanzania Wildlife Research Agenda 2021-2031 (TAWIRI 2021) including: Wildlife ecology and ecological interactions [priority areas i.Behavioural and nutrition ecology, ii.Population, distribution and reproductive ecology, vi.Range ecology/management, vii.Population genetics, xiii.Migratory routes, corridors, buffer zones and dispersal areas, xvi.Ecological monitoring methods]; Wildlife population monitoring [priority areas i.Population monitoring of large mammals, ii.Population monitoring of rare, endemic and endangered species, iv.Ecological monitoring methods and applications, vii.Social, environmental**

and ecological drivers of population dynamics, viii.Wildlife population monitoring methods]; Habitat and biodiversity conservation [priority areas ii.Composition, distribution and abundance of wildlife in protected areas and non-protected areas, vii.Conservation policy analysis]; Wildlife diseases [priority areas ii.Ecology, epidemiology and control of wildlife diseases]; Wildlife conservation policies [priority areas iv.Land use planning for supporting livelihoods and conservation goals, viii.Community-based natural resource management (CBNRM) in conservation]. This project also provides data and analyses to answer research targets in TAWIRI's Giraffe Conservation Research Framework 2020, namely research on: 2.1 giraffes' habitat use and foraging preference, 2.2 giraffe health and impact on survival, 2.3 population size, distribution and connectivity, 2.4 human dimensions and giraffe conservation. During the past 12 months, we completed 3 giraffe photo capture-mark-recapture surveys in Tarangire Ecosystem, 3 surveys in Serengeti Ecosystem. We published 2 manuscripts in scientific journals regarding giraffes and other ungulates. Three manuscripts are in progress.

16. Reasons for extension: **Due to the nature of population studies, more data, particularly longer time spans of data, increase the utility and power to make strong inferences. Therefore, we are asking to continue giraffe photographic surveys.**
17. Co-Principal Investigators: Monica L. Bond, James Madeli, George Lohay
18. Names and address of local collaborator: Dr. George Lohay, East African Road, Plot 39, Block A, PO Box 447, Nambala, Arusha
19. Applicant signature: *Derek E. Lee*

NOTES

This application form must be submitted together with the following:

a) A progress report on research
b) Letter of recommendation of local contact
C) A passport-size photograph (4x5cm) with blue back ground taken at least 3 months

TANZANIA COMMISSION FOR SCIENCE AND TECHNOLOGY
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Tanzania

APPLICATION FOR RESEARCH CLEARANCE EXTENSION (III)

1. Full Name of Principal Investigator: **Dr. Monica Louise Bond**
   (Title/First name/Middle names/Last name)
2. Nationality: **USA** Country of Residence: **Tanzania**
3. Highest qualification: **PhD**
4. Title of research project: **Ungulate Ecology, Health, and Conservation in Tanzania Including: Giraffe Population Genetics and Demography**
5. Contact address: **PO Box 44, Weaverville NC 28787 USA**.
   Email address **monica@wildnatureinstitute.org**
   Mobile number: **+1 4157630348**
6. Project duration **ongoing**
7. When did the project started: **2015**
8. Extension period from: 16 March 2026 to 15 March 2027
9. Duration of the Project as stated in the original application: **ongoing**

Previous clearance: Permit no. **CST00000218-2023-2025-00589**

Date issued: 16 March 2025 Date expired: 15 March 2026

10. Budget: **$15000/yr** Name of Sponsor: **Wild Nature Institute**
11. Objectives of the research: **to obtain robust estimates of population size, trend, and demographic rates for giraffes in northern Tanzanian protected areas.**
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iv.Ecological monitoring methods and applications, vii.Social, environmental and ecological drivers of population dynamics, viii.Wildlife population monitoring methods]; Habitat and biodiversity conservation [priority areas ii.Composition, distribution and abundance of wildlife in protected areas and non-protected areas, vii.Conservation policy analysis]; Wildlife diseases [priority areas ii.Ecology, epidemiology and control of wildlife diseases]; Wildlife conservation policies [priority areas iv.Land use planning for supporting livelihoods and conservation goals, viii.Community-based natural resource management (CBNRM) in conservation]. This project also provides data and analyses to answer research targets in TAWIRI's Giraffe Conservation Research Framework 2020, namely research on: 2.1 giraffes' habitat use and foraging preference, 2.2 giraffe health and impact on survival, 2.3 population size, distribution and connectivity, 2.4 human dimensions and giraffe conservation. During the past 12 months, we completed 3 giraffe photo capture-mark-recapture surveys in Tarangire Ecosystem, 3 surveys in Serengeti Ecosystem. We published 2 manuscripts in scientific journals regarding giraffes and other ungulates. Three manuscripts are in progress.

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Tanzania

APPLICATION FOR RESEARCH CLEARANCE EXTENSION (III)

1. Full Name of Principal Investigator: **Dr. George Lohay**
   (Title/First name/Middle names/Last name)
2. Nationality: **Tanzania** Country of Residence: **USA**
3. Highest qualification: **PhD**
4. Title of research project: **Ungulate Ecology, Health, and Conservation in Tanzania Including: Giraffe Population Genetics and Demography**
5. Contact address: **PO Box 44, Weaverville NC 28787 USA**.
   Email address **gml166@psu.edu**
   Mobile number: **+1 4157630348**
6. Project duration **ongoing**
7. When did the project started: **2015**
8. Extension period from: 16 March 2026 Date expired: 15 March 2027
9. Duration of the Project as stated in the original application: **ongoing**

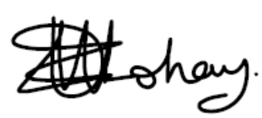
Previous clearance: Permit no. **CST00000096-2023-2025-00083**

Date issued: **16 Mar 2025** Date expired: **15 Mar 2026**

10. Budget: **$15000/yr** Name of Sponsor: **Wild Nature Institute**
11. Objectives of the research: **to obtain robust estimates of population size, trend, and demographic rates for giraffes in northern Tanzanian protected areas.**
12. Data collection methods/ tools: **We will collect photographic capture-recapture data for demographic analysis.**
13. Original location of research: **Arusha, Manyara, Mara, & Shinyanga, Tabora & Iringa Regions**
14. Extension research location: **Arusha, Manyara, Mara, & Shinyanga, Tabora & Iringa Regions**
15. Summary of progress report (not more than 300 words) What has been accomplished from previous Research Permit: **This project continues to provide data and analyses to inform priority research areas as described in Tanzania Wildlife Research Agenda 2021-2031 (TAWIRI 2021) including: Wildlife ecology and ecological interactions [priority areas i.Behavioural and nutrition ecology, ii.Population, distribution and reproductive ecology, vi.Range ecology/management, vii.Population genetics, xiii.Migratory routes, corridors, buffer zones and dispersal areas, xvi.Ecological monitoring methods]; Wildlife population monitoring [priority areas i.Population monitoring of large mammals, ii.Population monitoring of rare, endemic and endangered species,**

iv.Ecological monitoring methods and applications, vii.Social, environmental and ecological drivers of population dynamics, viii.Wildlife population monitoring methods]; Habitat and biodiversity conservation [priority areas ii.Composition, distribution and abundance of wildlife in protected areas and non-protected areas, vii.Conservation policy analysis]; Wildlife diseases [priority areas ii.Ecology, epidemiology and control of wildlife diseases]; Wildlife conservation policies [priority areas iv.Land use planning for supporting livelihoods and conservation goals, viii.Community-based natural resource management (CBNRM) in conservation]. This project also provides data and analyses to answer research targets in TAWIRI's Giraffe Conservation Research Framework 2020, namely research on: 2.1 giraffes' habitat use and foraging preference, 2.2 giraffe health and impact on survival, 2.3 population size, distribution and connectivity, 2.4 human dimensions and giraffe conservation. During the past 12 months, we completed 3 giraffe photo capture-mark-recapture surveys in Tarangire Ecosystem, 3 surveys in Serengeti Ecosystem. We published 2 manuscripts in scientific journals regarding giraffes and other ungulates. Three manuscripts are in progress.

16. Reasons for extension: **Due to the nature of population studies, more data, particularly longer time spans of data, increase the utility and power to make strong inferences. Therefore, we are asking to continue giraffe photographic surveys.**
17. Co-Principal Investigators: **Derek E. Lee, James Madeli, Monica L. Bond**
18. Names and address of local collaborator: **Dr. George Lohay, East African Road, Plot 39, Block A, PO Box 447, Nambala, Arusha**
19. Applicant signature**:**



NOTES

This application form must be submitted together with the following:

a) A progress report on research

b) Letter of recommendation of local contact

C) A passport-size photograph (4x5cm) with blue back ground taken at least 3 months

TANZANIA COMMISSION FOR SCIENCE AND TECHNOLOGY
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P.O. Box 4302
Dar es Salaam
Tanzania

APPLICATION FOR RESEARCH CLEARANCE EXTENSION (III)

1. Full Name of Principal Investigator: **Mr. James Madeli**
   (Title/First name/Middle names/Last name)
2. Nationality: **Tanzania** Country of Residence: **Tanzania**
3. Highest qualification: **MS**
4. Title of research project: **Ungulate Ecology, Health, and Conservation in Tanzania Including: Giraffe Population Genetics and Demography**
5. Contact address: **PO Box 44, Weaverville NC 28787 USA**.
   Email address **james@wildnatureinstitute.org**
   Mobile number: **+1 4157630348**
6. Project duration **ongoing**
7. When did the project started: **2015**
8. Extension period from: 16 March 2026 to 15 March 2027
9. Duration of the Project as stated in the original application: **ongoing**

Previous clearance: Permit no. **CST00000218-2023-2025-00590**

Date issued: 16 March 2025 Date expired: 15 March 2026

10. Budget: **$15000/yr** Name of Sponsor: **Wild Nature Institute**
11. Objectives of the research: **to obtain robust estimates of population size, trend, and demographic rates for giraffes in northern Tanzanian protected areas.**
12. Data collection methods/ tools: **We will collect photographic capture-recapture data for demographic analysis.**
13. Original location of research: **Arusha, Manyara, Mara, & Shinyanga, Tabora & Iringa Regions**
14. Extension research location: **Arusha, Manyara, Mara, & Shinyanga, Tabora & Iringa Regions**
15. Summary of progress report (not more than 300 words) What has been accomplished from previous Research Permit: **This project continues to provide data and analyses to inform priority research areas as described in Tanzania Wildlife Research Agenda 2021-2031 (TAWIRI 2021) including: Wildlife ecology and ecological interactions [priority areas i.Behavioural and nutrition ecology, ii.Population, distribution and reproductive ecology, vi.Range ecology/management, vii.Population genetics, xiii.Migratory routes, corridors, buffer zones and dispersal areas, xvi.Ecological monitoring methods]; Wildlife population monitoring [priority areas i.Population monitoring of large mammals, ii.Population monitoring of rare, endemic and endangered species,**

iv.Ecological monitoring methods and applications, vii.Social, environmental and ecological drivers of population dynamics, viii.Wildlife population monitoring methods]; Habitat and biodiversity conservation [priority areas ii.Composition, distribution and abundance of wildlife in protected areas and non-protected areas, vii.Conservation policy analysis]; Wildlife diseases [priority areas ii.Ecology, epidemiology and control of wildlife diseases]; Wildlife conservation policies [priority areas iv.Land use planning for supporting livelihoods and conservation goals, viii.Community-based natural resource management (CBNRM) in conservation]. This project also provides data and analyses to answer research targets in TAWIRI's Giraffe Conservation Research Framework 2020, namely research on: 2.1 giraffes' habitat use and foraging preference, 2.2 giraffe health and impact on survival, 2.3 population size, distribution and connectivity, 2.4 human dimensions and giraffe conservation. During the past 12 months, we completed 3 giraffe photo capture-mark-recapture surveys in Tarangire Ecosystem, 3 surveys in Serengeti Ecosystem. We published 2 manuscripts in scientific journals regarding giraffes and other ungulates. Three manuscripts are in progress.

16. Reasons for extension: **Due to the nature of population studies, more data, particularly longer time spans of data, increase the utility and power to make strong inferences. Therefore, we are asking to continue giraffe photographic surveys.**
17. Co-Principal Investigators: **Derek E. Lee, George Lohay, Monica L. Bond**
18. Names and address of local collaborator: **Dr. George Lohay, East African Road, Plot 39, Block A, PO Box 447, Nambala, Arusha**
19. Applicant signature**:** *James Madeli*

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This application form must be submitted together with the following:

a) A progress report on research
b) Letter of recommendation of local contact
C) A passport-size photograph (4x5cm) with blue back ground taken at least 3 months

APPLICATION FOR RESEARCH CLEARANCE RENEWAL/EXTENSION

No.	Name	Title	What has been accomplished from Previous Research Permit	Reason for Extension / What is the remaining work	When did Project Started	Duration of the Project
CST00000218-2023-2025-000588	Derek E. Lee	Ungulate Ecology, Health, and Conservation in Tanzania including Giraffe Population Genetics and Demography	During the past year, we completed 6 additional giraffe photo capture-mark-recapture surveys, collected DNA samples for extraction, and published 2 manuscripts in scientific journals.	To continue demographic monitoring of giraffe in Tarangire, Serengeti, Ngorongoro, Arusha, Ruaha, and Nyerere.	2015	indefinite
CST00000218-2023-2024-000589	Monica L. Bond	Ungulate Ecology, Health, and Conservation in Tanzania including Giraffe Population Genetics and Demography	During the past year, we completed 6 additional giraffe photo capture-mark-recapture surveys, collected DNA samples for extraction, and published 2 manuscripts in scientific journals.	To continue demographic monitoring of giraffe in Tarangire, Serengeti, Ngorongoro, Arusha, Ruaha, and Nyerere.	2018	indefinite
CST00000096-2023-2025-000083	George Lohay	Ungulate Ecology, Health, and Conservation in Tanzania including Giraffe Population Genetics and Demography	During the past year, we completed 6 additional giraffe photo capture-mark-recapture surveys, collected DNA samples for extraction, and published 2 manuscripts in scientific journals.	To continue demographic monitoring of giraffe in Tarangire, Serengeti, Ngorongoro, Arusha, Ruaha, and Nyerere.	2018	indefinite

CST00000218-2023-2025-000590	James Madeli	Ungulate Ecology, Health, and Conservation in Tanzania including Giraffe Population Genetics and Demography	During the past year, we completed 6 additional giraffe photo capture-mark-recapture surveys, collected DNA samples for extraction, and published 2 manuscripts in scientific journals.	To continue demographic monitoring of giraffe in Tarangire, Serengeti, Ngorongoro, Arusha, Ruaha, and Nyerere.	2018	indefinite

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P.O. Box 4302
Dar es Salaam
Tanzania

CURRICULUM VITAE (II)

1. Surname (Dr): Lee

   Other names: Derek Edward

2. Citizenship: USA Country of origin: USA

3. Date of Birth: 15 Mar 1971

4. Institutional affiliation: Wild Nature Institute

Mailing address (outside Tanzania) PO Box 44
Weaverville NC 28787

E-mail address: derek@wildnatureinstitute.org

5. University Education

(a) Undergraduate: Degree: BA
Year: 1994
Major subject: Cultural Anthropology
University: University of California, Santa Barbara_
Country: USA

(b) Postgraduate: Degree: MS
Year: 2001
Major subject: Wildlife Management
University: Humboldt State University
Country: USA

(c) Postgraduate: Degree: PhD
Year: 2015

Major subject: Biological Sciences

University: Dartmouth College

Country: USA

6. Position held [start with current position]

Position: Principal Scientist

Year: 2010-present

Institution: Wild Nature Institute

Position: Associate Research Professor

Year: 2018-present

Institution: Pennsylvania State University

7. Academic Awards: Award

Year:

Awarding Institution:

8. Research Grants: Project: Scientific Management of Ungulates

Year: 2013

Granting Institution: Fulbright

9. Consultancies: none

10. Refereed papers:

1. Lohay G, Pearce D, Bond ML, Lobora A, Lee DE, & Cavener D. 2025. Does the chain of Eastern Arc Mountains impede gene flow? Genetic evidence from the African savanna elephant and the Masai giraffe in Tanzania. African Journal of Wildlife Research 55:408-413. DOI: 10.3957/056.055.0408
2. Bond ML, Behr DM, Lee DE, Strauss MKL, Campbell PE, Cavener DR, Lohay GG, Madeli JM, Paniw M, Ozgul A. 2025. Demographic drivers of population dynamics reveal subpopulation-specific conservation needs for giraffes in the Serengeti Ecosystem. Journal of Wildlife Management. DOI: 10.1002/jwmg.70037
3. Bond ML, DE Lee, & M Paniw. 2023. Extinction risks and mitigation for a megaherbivore, the giraffe, in a human-influenced landscape under climate change. Global Change Biology DOI:10.1111/gcb.16970.

4. Lohay GG, DE Lee, L Wu-Cavener, DL Pearce, X Hou, ML Bond, & DR Cavener. 2023. Genetic evidence of population subdivision among Masai giraffes separated by the Gregory Rift Valley in Tanzania. Ecology and Evolution DOI: 10.1002/ece3.10160
5. Bond ML, A Ozgul, & DE Lee. 2023. Effect of local climate anomalies on giraffe survival. Biodiversity and Conservation 32:3179–3197. DOI: 10.1007/s10531-023-02645-4
6. Lee DE, Lohay GC, Madeli J, Cavener DR, Bond ML. 2023. Masai giraffe population change over 40 years in Arusha National Park. African Journal of Ecology 61:345-353. DOI: 10.1111/aje.13115
7. Lee DE, Lohay GC, Cavener DR, Bond ML. 2022. Using spot pattern recognition to examine population biology, evolutionary ecology, sociality, and movements of giraffes: a 70-year retrospective. Mammalian Biology. DOI: 10.1007/s42991-022-00261-3
8. Morandi K, Lindholm AK, Lee DE, Bond ML. 2022. Phenotypic matching by spot pattern potentially mediates female giraffe social associations. Journal of Zoology. DOI: 10.1111/jzo.13009
9. Nur N, Berger RW, Lee DE, Warzybok PM, Jahncke J. 2022. Effects of winter storms and oceanographic conditions on survival to weaning: a 37 year study of northern elephant seals on the Farallon Islands. Marine Ecology Progress Series 691:173-189. DOI: 10.3354/meps14066
10. James NL, Bond ML, Ozgul A, Lee DE. 2022. Trophic processes constrain seasonal ungulate distributions at two scales in an East African savanna. Journal of Mammalogy DOI: 10.1093/jmammal/gyac050
11. Levi M, Lee DE, Bond ML, Treydte AC. 2022. Forage selection by Masai giraffes (Giraffa camelopardalis tippelskirchi) at multiple spatial scales. Journal of Mammalogy. DOI: 10.1093/jmammal/gyac007
12. Lavista Ferres JM, Lee DE, Nasir M, Chen Y-C, Bijral AS, Bercovitch FB, Bond ML. 2021. Social connectedness and movements among communities of giraffes vary by sex and age class. Animal Behaviour. DOI: 10.1016/j.anbehav.2021.08.008
13. Bond ML, Lee DE, Ozgul A, Farine DR, König B. 2021. Leaving by staying: Social dispersal in giraffes. Journal of Animal Ecology. DOI: 10.1111/1365-2656.13582
14. Hanson CT, Lee DE, Bond ML. 2021. Disentangling Post-Fire Logging and High-Severity Fire Effects for Spotted Owls. Birds 2:147-157. DOI: 10.3390/birds2020011
15. Bond ML, König B, Ozgul A, Farine DR, Lee DE. 2021. Socially defined subpopulations reveal demographic variation in a giraffe metapopulation. Journal of Wildlife Management 85:920-931. DOI: 10.1002/jwmg.22044
16. Bond ML, Lee DE, Farine DR, Ozgul A, König B. 2021. Sociability increases survival of adult female giraffes. Proceedings of the Royal Society B 28: 20202770. DOI: 10.1098/rspb.2020.2770
17. Nur N, Bradley RW, Lee DE, Warzybok PM, Jahncke J. 2021. Projecting Long-term Impacts of a Mortality Event on Vertebrates: Incorporating Stochasticity in Population Assessment. Ecosphere DOI: 10.1002/ecs2.3293
18. Lee DE. 2020. Spotted Owls and forest fire: Reply. Ecosphere 11:e03310. DOI: 10.1002/ecs2.3310
19. Bond ML, König B, Lee DE, Ozgul A, Farine DR. 2020. Proximity to humans affects local social structure in a giraffe metapopulation. Journal of Animal Ecology DOI: 10.1111/1365-2656.13247
20. Muller Z, Lee DE, Scheijen CPJ, Carter KD, Strauss M, Deacon F. 2020. Giraffe translocations: A review and discussion of considerations. African Journal of Ecology DOI: 10.1111/aje.12727

21. Lee DE, Fienieg E, Van Oosterhout C, Muller Z, Strauss M, Carter KD, Scheijen CPJ, Deacon F. 2020. Giraffe Translocation Population Viability Analysis. Endangered Species Research DOI: 10.3354/esr01022.
22. Bond ML, Lee DE, Ozgul A, König B. 2019. Fission-fusion dynamics of a megaherbivore are driven by ecological, anthropogenic, temporal, and social factors. Oecologia 19:335-347. DOI: 10.1007/s00442-019-04485-y
23. Knüsel MA, Lee DE, König B, Bond ML. 2019. Correlates of home range sizes of giraffes, *Giraffa camelopardalis*. Animal Behaviour 149:143-151
24. Bond ML, Lee DE. 2019. Simultaneous multiple-calf allonursing by a wild Masai giraffe. African Journal of Ecology DOI: 10.1111/aje.12673
25. Buehler P, Carroll B, Bhatia A, Gupta V, Lee DE. 2019. An automated program to find animals and crop photographs for individual recognition. Ecological Informatics 50:191-196
26. Lee DE, Berger RW, Tietz JR, Warzybok P, Bradley RW, Orr AJ, Towell RG, Jahncke J. 2018. Initial growth of northern fur seal (*Callorhinus ursinus*) colonies at the South Farallon, San Miguel, and Bogoslof Islands. Journal of Mammalogy 99:1529-1538. DOI: 10.1093/jmammal/gyy131
27. Lee DE, Cavener DR, Bond ML. 2018. Seeing spots: Quantifying mother-offspring similarity and assessing fitness consequences of coat pattern traits in a wild population of giraffes (*Giraffa camelopardalis*). PeerJ. DOI: 10.7717/peerj.5690
28. Lee DE. 2018. Evaluating Conservation Effectiveness in a Tanzanian Community Wildlife Management Area. Journal of Wildlife Management 82:1767-1774. DOI: 10.1002/jwmg.21549
29. Lee DE. 2018. Spotted owls and forest fire: a systematic review and meta-analysis of the evidence. Ecosphere 9:e02354. DOI: 10.1002/ecs2.2354
30. Lee DE, Bond ML. 2018. Quantifying the ecological success of a community-based wildlife conservation area in Tanzania. Journal of Mammalogy 99:459-464
31. Hanson CT, Bond ML, Lee DE. 2018. Effects of post-fire logging on California spotted owl occupancy. Nature Conservation 24:93-105
32. Bond ML, Bradley CM, Kiffner C, Morrison TA, Lee DE. 2017. A multi-method approach to delineate and validate migratory corridors. Landscape Ecology 32:1705-1721
33. Bercovitch FB, Berry PS, Dagg A, Deacon F, Doherty JB, Lee DE, Mineur F, Muller Z, Ogden R, Seymour R, Shorrocks B. 2017. How many species of giraffe are there? Current Biology 27:R136-R137
34. Lee DE, Bolger DT. 2017. Movements and source-sink dynamics among subpopulations of giraffe. Population Ecology 59:157-168
35. Lee DE, Bond ML, Bolger DT. 2017. Season of birth affects juvenile survival of giraffe. Population Ecology 59:45-54
36. Lee DE, Kissui BM, Kiwango YA, Bond ML. 2016. Migratory herds of wildebeest and zebra indirectly affect juvenile survival of giraffes. Ecology and Evolution 6:8402-8411
37. Lee DE, Strauss MKL. 2016. Giraffe demography and population ecology. Reference Module in Earth Sciences and Environmental Studies. DOI: 10.1016/B978-0-12-409548-9.09721-9
38. Bond ML, Strauss MKL, and Lee DE. 2016. Soil correlates and mortality from giraffe skin disease in Tanzania. Journal of Wildlife Diseases 52:953-958
39. Manugian SC, Greig D, Lee DE, Becker BH, Allen S, Lowry MS, Harvey JT. 2016. Survival probabilities and movements of harbor seals in central California. Marine Mammal Science 33:154-171
40. Lee DE, Bond ML, Kissui BM, Kiwango YA, Bolger DT. 2016. Spatial variation in giraffe demography: a test of 2 paradigms. Journal of Mammalogy 97:1015-1025

41. Lee DE, Bond ML. 2016. Precision, accuracy, and costs of survey methods for giraffe *Giraffa camelopardalis*. Journal of Mammalogy 97:940-948
42. Lee DE, Bond ML. 2016. The occurrence and prevalence of giraffe skin disease in protected areas of northern Tanzania. Journal of Wildlife Diseases 52:753-755
43. Bond ML, Bradley C, Lee DE. 2016. Foraging habitat selection by California spotted owls after fire. Journal of Wildlife Management 80:1290-1300
44. Lee DE, Bond ML. 2015. Occupancy of California Spotted Owl sites following a large fire in the Sierra Nevada, California. Condor 117:228-236
45. Lee DE, Bond ML, Borchert MI, Tanner R. 2013. Influence of fire and salvage logging on site occupancy of Spotted Owls in the San Jacinto Mountains of southern California. Journal of Wildlife Management 77:1327-1341
46. Bond ML, Lee DE, Siegel RB, Tingley MW. 2013. Diet and home range of California Spotted Owls in a burned forest. Western Birds 44:114-126
47. Lee DE, Bond ML, Siegel RB. 2012. Dynamics of California Spotted Owl breeding-season site occupancy in burned forests. Condor 114:792-802
48. Bolger DT, Morrison TA, Vance B, Lee DE, Farid H. 2012. A computer-assisted system for photographic mark-recapture analysis. Methods in Ecology and Evolution 3:813-822
49. Lee DE, Bettaso J, Bond ML, Bradley RW, Tietz J, Warzybok PM. 2012. Growth, age at maturity, and age-specific survival of the Arboreal Salamander (*Aneides lugubris*) on Southeast Farallon Island, California. Journal of Herpetology 46:64-71
50. Lee DE, Bradley RW, Warzybok PM. 2012. Recruitment of Cassin's Auklet (*Ptychoramphus aleuticus*): Individual age and parental age effects. Auk 129:1-9
51. Lee DE. 2011. Effects of environmental variability and breeding experience on Northern Elephant Seal demography. Journal of Mammalogy 92:517-526
52. Black JM, Lee DE, Ward DH. 2010. Foraging home ranges of Black Brant during spring stopover at Humboldt Bay, California, USA. Wildfowl 60:85-94
53. Brown AC, Lee DE, Bradley RW, Anderson S. 2010. Dynamics of White Shark predation on pinnipeds in California: effects of prey abundance. Copeia 2010 No. 2:232-238
54. Bond ML, Lee DE, Siegel RB. 2010. Winter movements by California Spotted Owls in a post-fire landscape. Western Birds 41:174-180
55. Bond ML, Lee DE, Bradley CM, Hansen CT. 2009. Influence of pre-fire tree mortality from insects and drought on burn severity in conifer forests of the San Bernardino Mountains, California Open Forest Science Journal 2009 No. 2:41-47
56. Bond ML, Lee DE, Siegel RB, Ward JP. 2009. Habitat use and selection by California Spotted Owls in a post-fire landscape. Journal of Wildlife Management 73:1116-1124
57. Moore E, Lyday S, Roletto J, Litle K, Parrish JK, Nevins H, Harvey J, Mortenson J, Grieg D, Piazza M, Hermance A, Lee DE, Adams D, Allen S, Kell S. 2009. Entanglements of marine mammals and seabirds in central California and the north-west coast of the United States 2001-2005. Marine Pollution Bulletin 58:1045-1051
58. Lee DE, Sydeman WJ. 2009. North Pacific climate mediates offspring sex ratios in Northern Elephant Seals. Journal of Mammalogy 90:1-8
59. Tietje WD, Lee DE, Vreeland JK. 2008. Survival and abundance of three species of mice in relation to density of shrubs and prescribed fire in understory of an oak woodland in California. Southwestern Naturalist 53:357-369
60. Lee DE, Abraham C, Warzybok PM, Bradley RW, Sydeman WJ. 2008. Age-specific survival, breeding success, and recruitment in Common Murres (*Uria aalge*) of the California Current System. Auk 125:316-325
61. Lee DE, Nur N, Sydeman WJ. 2007. Climate and demography of the planktivorous Cassin's Auklet *Ptychoramphus aleuticus* off northern California: implications for population change. Journal of Animal Ecology 76:337-347

62. Lee DE, Black JM, Moore JE, Sedinger JS. 2007. Age-specific stopover ecology of Black Brant at Humboldt Bay, California. Wilson Journal of Ornithology 119:9-22
63. Lee DE, Tietje WD. 2005. Dusky-footed Woodrat demography and prescribed fire in a California oak woodland. Journal of Wildlife Management 69:1211-1220
64. Lee DE, Black JM, Hammand M. 2004. Grit site selection of Black Brant at Humboldt Bay, California: Particle size or calcium content? Wilson Bulletin 116:304-313
65. Railsback SF, Harvey BC, Lamberson RR, Lee DE, Claasen NJ, Yoshihara S. 2001. Population-level analysis and validation of an individual-based Cutthroat Trout model. Natural Resource Modeling 15:83-110

11. Other papers and or publications: 1. ______________________________

2. ______________________________

12. Society Membership:
1. American Society of Mammalogists
2. Society for Conservation Biology
3. Ecological Society of America
4. Wildlife Society

13. Signature: _____*Derek E. Lee*______________________________

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Tanzania

CURRICULUM VITAE (II)

1. Surname (Mrs): Bond

   Other names: Monica Louise

2. Citizenship: USA Country of origin: USA

3. Date of Birth: 31 December 1970

4. Institutional affiliation: Wild Nature Institute & University of Zurich

Mailing address (outside Tanzania): PO Box 44, Weaverville, NC 28787

E-mail address: monica@wildnatureinstitute.org

5. University Education

(a) Undergraduate: Degree: B.A.
Year: 1992
Major subject: Biology
University: Duke University
Country: USA

(b) Postgraduate: Degree: M.Sc.
Year: 1996
Major subject: Wildlife Science
University: Oregon State University
Country: USA

(c) Postgraduate: Degree: PhD
Year: 2020
Major subject: Ecology
University: University of Zurich
Country: Switzerland

6. Position held [start with current position]

Position: Post Doctoral Researcher
Year: 2020
Institution: University of Zurich, Switzerland

7. Academic Awards: Award: ____________________
Year: ____________________
Awarding Institution: ____________________

8. Research Grants: Project: ____________________
Year: ____________________
Granting Institution: ____________________

9. Consultancies: 1. ____________________
2. ____________________

10. Refereed papers:

1. Lohay G, Pearce D, Bond ML, Lobora A, Lee DE, & Cavener D. 2025. Does the chain of Eastern Arc Mountains impede gene flow? Genetic evidence from the African savanna elephant and the Masai giraffe in Tanzania. African Journal of Wildlife Research 55:408-413. DOI: 10.3957/056.055.0408
2. Bond ML, Behr DM, Lee DE, Strauss MKL, Campbell PE, Cavener DR, Lohay GG, Madeli JM, Paniw M, Ozgul A. 2025. Demographic drivers of population dynamics reveal subpopulation-specific conservation needs for giraffes in the Serengeti Ecosystem. Journal of Wildlife Management. DOI: 10.1002/jwmg.70037
3. Bond ML, DE Lee, & M Paniw. 2023. Extinction risks and mitigation for a megaherbivore, the giraffe, in a human-influenced landscape under climate change. Global Change Biology DOI:10.1111/gcb.16970.

4. Lohay GG, DE Lee, L Wu-Cavener, DL Pearce, X Hou, ML Bond, & DR Cavener. 2023. Genetic evidence of population subdivision among Masai giraffes separated by the Gregory Rift Valley in Tanzania. Ecology and Evolution DOI: 10.1002/ece3.10160
5. Bond ML, A Ozgul, & DE Lee. 2023. Effect of local climate anomalies on giraffe survival. Biodiversity and Conservation 32:3179–3197. DOI: 10.1007/s10531-023-02645-4
6. Lee DE, Lohay GC, Madeli J, Cavener DR, Bond ML. 2023. Masai giraffe population change over 40 years in Arusha National Park. African Journal of Ecology 61:345-353. DOI: 10.1111/aje.13115
7. Lee DE, Lohay GC, Cavener DR, Bond ML. 2022. Using spot pattern recognition to examine population biology, evolutionary ecology, sociality, and movements of giraffes: a 70-year retrospective. Mammalian Biology in press.
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11. Other papers and or publications: 1. ____________
2. ____________
3. ____________
4. ____________

12. Society Membership: 1. ____________
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5. University Education

(a) Undergraduate: Degree: Bachelor of Science (Hons)
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University: University of Dar es Salaam
Country: Tanzania

(b) Postgraduate: Degree: PhD
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Major subject: Biology
University: The Pennsylvania State University
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6. Position held [start with current position]

Position: Head Scientist RISE

Year: 2023 to present

Institution: Grumeti Fund

Position: Post-doctoral Scholar

Year: 2019 to 2023

Institution: The Pennsylvania State University

Position: Graduate Teaching Assistant

Year: 2014-2019

Institute: The Pennsylvania State University

Position: Research Assistant

Year: 2009-2011

Institution: Serengeti Lion Project (University of Minnesota)

7. Academic Awards: Award: Graduate exhibition

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Awarding Institution: The Pennsylvania State University

8. Research Grants: Project: Genetic connectivity of African Savanna elephants

Year: 2015

Granting Institution: Wildlife Conservation Society (WCS)

9. Consultancies: 1. ___________________________-____________________________

2. ___________________________-____________________________

10. Refereed papers:

1. Lohay G, Pearce D, Bond ML, Lobora A, Lee DE, & Cavener D. 2025. Does the chain of Eastern Arc Mountains impede gene flow? Genetic evidence from the African savanna elephant and the Masai giraffe in Tanzania. African Journal of Wildlife Research 55:408-413. DOI: 10.3957/056.055.0408

2. Bond ML, Behr DM, Lee DE, Strauss MKL, Campbell PE, Cavener DR, Lohay GG, Madeli JM, Paniw M, Ozgul A. 2025. Demographic drivers of population dynamics reveal subpopulation-specific conservation needs for giraffes in the Serengeti Ecosystem. Journal of Wildlife Management. DOI: 10.1002/jwmg.70037
3. Lohay GG, DE Lee, L Wu-Cavener, DL Pearce, X Hou, ML Bond, & DR Cavener. 2023. Genetic evidence of population subdivision among Masai giraffes separated by the Gregory Rift Valley in Tanzania. Ecology and Evolution DOI: 10.1002/ece3.10160
4. Lee DE, Lohay GC, Madeli J, Cavener DR, Bond ML. 2023. Masai giraffe population change over 40 years in Arusha National Park. African Journal of Ecology 61:345-353. DOI: 10.1111/aje.13115
5. Lee DE, Lohay GC, Cavener DR, Bond ML. 2022. Using spot pattern recognition to examine population biology, evolutionary ecology, sociality, and movements of giraffes: a 70-year retrospective. Mammalian Biology in press.Lohay, George, M.G, 2019, Elephant without borders: historical and contemporary genetic connectivity, dissertation thesis, The Pennsylvania State University, https://catalog.libraries.psu.edu/catalog/27984072
6. Lohay, George, G. 2019. An accurate molecular method to sex elephants using PCR amplification of Amelogenin gene George Gwaltu Lohay. BioRxiv, https://doi.org/10.1101/856419

11. Other papers and or publications:

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Year: 2025
Major subject: Conservation Management of African ecosystems, Natural sciences
University: University of Glasgow
Country: United Kingdom

6. Position held [start with current position]

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Year: 2018 to present

Institution: Wild Nature Institute

7. Academic Awards: Award: Karimjee Scholarship

Year: 2024

Awarding Institution: University of Glasgow

8. Research Grants: Project: ____________________

Year: ____________________

Granting Institution: ____________________

9. Consultancies: 1. ____________________

2. ____________________

10. Refereed papers:

1. Bond ML, Behr DM, Lee DE, Strauss MKL, Campbell PE, Cavener DR, Lohay GG, Madeli JM, Paniw M, Ozgul A. 2025. Demographic drivers of population dynamics reveal subpopulation-specific conservation needs for giraffes in the Serengeti Ecosystem. Journal of Wildlife Management. DOI: 10.1002/jwmg.70037
2. Lee DE, Lohay GC, Madeli J, Cavener DR, Bond ML. 2023. Masai giraffe population change over 40 years in Arusha National Park. African Journal of Ecology 61:345-353. DOI: 10.1111/aje.13115

11. Other papers and or publications: 1. ____________________

2. ____________________

12. Society Membership: 1. ____________________

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SEMI ANNUAL PROGRESS REPORT TEMPLATE

Principal Investigator	Name	Nationality	Phone # & E-mail
	Derek Lee	USA	+14157630348 derek@wildnatureinstitute.org
Responsible Institution	Wild Nature Institute		
Project title	Ungulate Ecology, Health, and Conservation in Tanzania Including: Giraffe Population Genetics and Demography		
Project Number:	Permit # CST00000218-2023-2025-000588		
Reporting Period	Semi Annual Report (August – December 2025)		

Summary

Our giraffe research is discovering where Masai giraffes are doing well, where they are not, and why. Our research supports communities working to protect and connect areas important to Masai giraffe conservation. Populations of giraffe (*Giraffa camelopardalis*) have declined throughout the species' range in recent years, leaving remaining populations increasingly isolated. We seek to better understand the metapopulation dynamics and population structure of giraffes across a large region of Tanzania. We are continuing demographic studies based upon photographic capture-recapture data in the Tarangire Ecosystem (Tarangire NP, Randilen and Burunge WMAs, and Manyara Ranch), Serengeti National Park, Ngorongoro Conservation Area, Lake Manyara National Park, and Arusha National Park. These photo capture-recapture data build upon our long-term database that can be used to estimate population sizes, survival, and reproduction rates at each site.

This project continues to provide data and analyses to inform priority research areas as described in Tanzania Wildlife Research Agenda 2021-2031 including: **Wildlife ecology and ecological interactions** [priority areas i.Behavioural and nutrition ecology, ii.Population, distribution and reproductive ecology, vi.Range ecology/management, vii.Population genetics, xiii.Migratory routes, corridors, buffer zones and dispersal areas, xvi.Ecological monitoring methods]; **Wildlife population monitoring** [priority areas i.Population monitoring of large mammals, ii.Population monitoring of rare, endemic and endangered species, iv.Ecological monitoring methods and applications, vii.Social, environmental and ecological drivers of population dynamics, viii.Wildlife population monitoring methods]; **Habitat and biodiversity conservation** [priority areas ii.Composition, distribution and abundance of wildlife in protected areas and non-protected areas, vii.Conservation policy analysis]; **Wildlife diseases** [priority areas ii.Ecology, epidemiology and control of wildlife diseases]; **Wildlife conservation policies** [priority areas iv.Land use planning for supporting livelihoods and conservation goals, viii.Community-based natural resource management (CBNRM) in conservation]. This project also provides data and analyses to answer research targets in TAWIRI's Giraffe Conservation Research Framework 2020, namely research on: 2.1 giraffes' habitat use and foraging preference, 2.2 giraffe health and impact on survival (see results), 2.3 population size, distribution and connectivity, 2.4 human dimensions and giraffe conservation.

Activities and Progress

- During the 2025 permit period, we completed 3 giraffe photo capture-mark-recapture surveys in Tarangire Ecosystem, 3 surveys in Serengeti Ecosystem.
- We published 2 manuscripts in scientific journals regarding giraffes and other ungulates. Three manuscripts are in progress.

Past project findings:

We documented spatial variation in demographic rates of giraffes among the 5 sites in the Tarangire Ecosystem (**Lee et al. 2016a**). The Tarangire giraffe metapopulation is still interconnected by a few movements among sites, but LMNP and MGCA are nearly isolated from the rest of the ecosystem (**Lee & Bolger 2017**). The Tarangire National Park and Manyara Ranch subpopulations are the engines of metapopulation growth and health, but anthropogenic impacts outside protected areas have a negative effect on overall metapopulation growth resulting in an overall declining metapopulation (**Lee & Bolger 2017**). Presence of migratory herds of wildebeest and zebras increased local giraffe calf survival (**Lee et al. 2016b**). Giraffe calf survival varied by season of birth, with highest survival found in calves born during the dry season (**Lee et al. 2017**). Giraffe Skin Disease prevalence varied significantly among sites and appeared to vary according to soil fertility. There is no mortality due to GSD disease (**Lee & Bond 2016, Bond et al. 2016**). In **Lee et al. (2018)** we demonstrated that some characteristics of giraffe coat spot shape were heritable, and that variation in neonatal survival was associated with spot size and shape covariates. A habitat model and corridor detection algorithm delineated the Tarangire Ecosystem wildebeest migration habitat between Tarangire NP and Lake Natron (**Bond et al. 2017**). We documented the ecological success of CBNRM in Wildlife Management Areas (WMAs) for wildlife conservation (**Lee & Bond 2018, Lee 2018**). We published the first account of a wild giraffe nursing multiple calves (**Bond & Lee 2019**). We quantified giraffe home range sizes in the Tarangire Ecosystem and found home range sizes across Africa were correlated with rainfall (**Knüsel et al. 2019**). In **Bond et al. (2019)**, we found food availability rather than predation risk mediated grouping dynamics of adult giraffes, while predation risk was the most important factor influencing congregations with calves. Two papers, Giraffe translocations: A review and discussion of considerations **(Muller et al. 2020)** and Giraffe translocation population viability analysis **(Lee et al. 2020)** provide strong guidance to biologists and managers planning translocations of giraffe. Using one of the largest-scale metapopulation networks ever studied in a wild mammal, in **Bond et al. (2020)** we reveal that social communities of giraffes living closer to human settlements exhibit weaker relationship strengths and more exclusive social associations. In **Bond et al. (2021)** Sociability increases survival in adult female giraffes, we found that females that grouped with more other females leads to higher survival. Benefits of female grouping may include cooperative care of young, more efficient foraging, and reduced stress in general. Effect of sociability on survival was more than that of the natural surrounding or proximity to people, although living closer to towns also lowered survival. Female Masai giraffes live in distinct social communities of up to 90 other friends, and although areas used by these communities often overlap, they have very different rates of reproduction and calf survival, we showed in **Bond et al (2021)** Socially defined subpopulations reveal demographic variation in a giraffe metapopulation. This means that population structure can arise from social behavior rather than discrete space use. Calf survival and reproductive rates were higher in the social communities that spent more time outside of the national parks. Dispersal, the process where animals reaching sexual maturity move away from family, is important for maintaining genetic diversity and is key to the long-term persistence of natural populations. For most animals, this involves having to make risky journeys into the unknown in the hope of finding new communities in which to settle and reproduce. However, many animal societies—including those of humans—have structured social communities that overlap in space with one-another. These potentially provide opportunities for maturing individuals to disperse socially without having to make large physical displacements. **Bond et al (2021)** Leaving by staying: Social dispersal in giraffes, shows that this strategy is employed by young dispersing giraffes. We studied social relationships of more than 1000 giraffes in the Tarangire Ecosystem over 5 years. In **LaVista-Ferres et al (2021)** Social connectedness and movements among communities of giraffes vary by sex and age class, we found that males were more socially connected than females to all the other giraffes. Adult males wander long distances looking for mating opportunities. Young males visit many different groups as they explore their social environment before moving permanently away from their mothers and sisters. Females had stronger and enduring social relationships over the years than males. In the end, female giraffes have closer 'friends' than male giraffes, while males have more 'acquaintances' than females. This information is important for understanding population dynamics, spread of information, and even how diseases move through a population and is therefore important for conservation. A native bush-encroaching shrub species called Sickle Bush (*Dichrostachys cinerea*) is disliked by livestock keepers and rangeland managers, but loved as forage by wild giraffes, according to Forage selection by Masai giraffes (*Giraffa camelopardalis tippelskirchi*) at multiple spatial scales (**Levi et al. 2022**). The findings showed that giraffe significantly preferred foraging on bush-encroaching species such as the native Sickle Bush at local and landscape spatial scales and in both the wet and dry seasons. The results of this study suggest that browsing wildlife such as giraffes could be adversely affected by the removal of Sickle Bush from rangelands. In Trophic processes constrain seasonal ungulate distributions at two scales in an East African savanna (**James et al. 2022**), we found giraffe distribution in the Tarangire Ecosystem was less constrained by water (they were not closer to rivers and waterholes during the dry season than the wet seasons) but more constrained by the seasonal presence of preferred food such as *Vachellia drepanolobium* in the long rains. These results provide important information for effective conservation strategies for giraffes and other ungulates in the Tarangire Ecosystem. Animal coat patterns may have several functions, one of which might be to help individuals to recognize each other. In Phenotypic matching by spot pattern potentially mediates female giraffe social associations (**Morandi et al. 2022**), we revealed that spot traits were individually variable among adult female giraffes in the Tarangire Ecosystem, and that females showed stronger associations with other females that had similar spot shapes. Spot patterns of giraffes could be a visual cue for communicating and for recognizing related family members. In **(Lee et al. 2023)**, we enumerated individual giraffes to see how well they were doing compared to 40 years ago and collected DNA from dung samples to assess the genetic connectivity of the park's giraffes with other giraffe populations in the region. We documented a 49% population decline and changes in the age distribution, adult sex ratio, reproductive rate, and movement patterns relative to the previous study. Mitochondrial DNA analysis revealed genetic connectivity between Arusha National Park and other Masai giraffe populations east of the Gregory Rift Escarpment in northern Tanzania and south-eastern Kenya, providing evidence that Masai giraffe once moved widely across the landscape. In **(Bond et al. 2023)**, we found that in an East African savanna, higher temperatures positively affected adult giraffe survival, indicating this mega-herbivore is adapted to hot conditions, but adult and juvenile giraffe survival was reduced during rainier wet seasons, possibly due to parasites and disease and/or increased stalking cover for predators. Higher vegetation greenness also reduced adult giraffe survival, potentially because faster leaf growth reduces nutrient quality. Climate effects were most pronounced for giraffes living closer to the edge of the protected areas during the short rains, possibly because of higher livestock-mediated disease risk and/or muddier conditions that prevent effective anti-poaching patrols. Projected climate changes in East Africa, including heavier rainfall during the short rains, will likely threaten persistence of giraffes in one of Earth's most important landscapes for large terrestrial mammals, pointing to the need for effective land-use planning and law enforcement to provide giraffes more resilience to the coming changes. In **(Lohay et al. 2023)**, we showed that populations of Masai giraffes separated geographically by the Great Rift Escarpment have not interbred — or exchanged genetic material — in more than a thousand years, and in some cases hundreds of thousands of years. We recommend that the two populations be considered separately for conservation purposes, with separate but coordinated conservation efforts to manage each population. In **(Bond et al. 2023)**, we combined the information learned from previous studies of giraffes to create an individual-based model that simulated realistic population dynamics and extinction risk under different scenarios of environmental change over 50 years. Results showed that the greatest risk of population declines and extinction for giraffes is caused by a reduction in wildlife law enforcement leading to more poaching. The study highlights the great utility of law enforcement as a nature conservation tool. In Sexual dimorphisms in body proportions of Masai giraffes and the evolution of the giraffe's neck **(Cavener et al. 2024)**, we measured differences in body proportions between male and female giraffes, both captive and wild, and found females have a proportionally longer neck and torso, whereas males have proportionally longer forelegs and more massive necks. We speculate the initial evolution of the long neck and legs was driven by female nutritional demands (reaching deep into bushes and higher into trees) and mating (males with longer legs can mount females) and later the neck mass was increased in males as a result of neck sparring. In Anthropogenic and climatic drivers of population densities in an African savanna ungulate community **(Bierhoff et al. 2024)**, we quantified population trends, determined the primary environmental correlates of densities, and identified covariation in densities among species. Large fluctuations in climatic factors mediated highly synchronous temporal density variation among all species. We documented more spatial than temporal variation in four of the five species, suggesting that spatial heterogeneity may provide some buffer against temporal variation in the environment. Protection of sufficient habitats and water sources should allow ungulates to respond to a temporally changing world by moving across space. Further, among-species covariation patterns identified two potential ungulate guilds (impala—dik–dik—waterbuck; eland—Grant's gazelle) that should aid in developing efficient and coordinated management actions.

New findings:

In **"Does the chain of Eastern Arc Mountains impede gene flow? Genetic evidence from the African savanna elephant and the Masai giraffe in Tanzania" (Lohay et al. 2025)**, we found that there is high genetic differentiation between populations found east and west of the Eastern Arc Mountains for both elephants and giraffes, and there is no female-mediated gene flow between these populations. Populations found west of the Eastern Arc Mountains show high genetic connectivity suggesting historical gene flow between them. Our study reveals that the Eastern Arc Mountains play a significant role in blocking the gene flow of these species.

In **"Demographic drivers of population dynamics reveal subpopulation-specific conservation needs for giraffes in the Serengeti Ecosystem" (Bond et al. 2025)**, we found significant differences in adult and subadult survival probabilities among 4 Serengeti subpopulations, with lower adult survival associated with declining subpopulations. Retrospective population analysis for the Seronera subpopulation reiterated that adult survival is a critical demographic driver of population dynamics for giraffes. The 2 subpopulations adjacent to the protected area boundary declined over 48 years, whereas the Seronera subpopulation stabilized since 2008. Only one individual moved between subpopulations, providing evidence for subpopulation insularity and potential genetic structuring of the overall population. These factors underscore the need for subpopulation ‐ specific conservation strategies aimed at raising adult survival within the western and northeastern parts of the Serengeti Ecosystem. Our findings highlight the importance of understanding subpopulation dynamics and their demographic drivers for evidence ‐ based conservation and management to recover endangered giraffe populations.

We disseminate the findings of our research results to different stakeholders via scientific publications, conferences, popular science news articles, weblog, & reports to COSTECH, TAWIRI, TANAPA, NCA, TAWA, & WMA leadership.

Resulting Publications, Clinical Trials, Patents, products

RESULTING PUBLICATIONS:

1. Lohay G, Pearce D, Bond ML, Lobora A, Lee DE, & Cavener D. 2025. Does the chain of Eastern Arc Mountains impede gene flow? Genetic evidence from the African savanna elephant and the Masai giraffe in Tanzania. African Journal of Wildlife Research 55:408-413. DOI: 10.3957/056.055.0408
2. Bond ML, Behr DM, Lee DE, Strauss MKL, Campbell PE, Cavener DR, Lohay GG, Madeli JM, Paniw M, Ozgul A. 2025. Demographic drivers of population dynamics reveal subpopulation-specific conservation needs for giraffes in the Serengeti Ecosystem. Journal of Wildlife Management. DOI: 10.1002/jwmg.70037
3. Cavener DR, Bond ML, Wu-Cavener L, Lohay GG, Cavener MW, Hou X, Pearce D, & Lee DE. 2024. Sexual dimorphisms in body proportions of Masai giraffe and the evolution of the giraffe's neck. Mammalian Biology DOI:10.1007/s42991-024-00424-4.
4. Bierhoff L, Bond ML, Ozgul A, & Lee DE. 2024. Anthropogenic and climatic drivers of population densities in an African savanna ungulate community. Population Ecology. DOI:10.1002/1438-390X.12182
5. Bond ML, DE Lee, & M Paniw. 2023. Extinction risks and mitigation for a megaherbivore, the giraffe, in a human-influenced landscape under climate change. Global Change Biology DOI:10.1111/gcb.16970.
6. Lohay GG, DE Lee, L Wu-Cavener, DL Pearce, X Hou, ML Bond, & DR Cavener. 2023. Genetic evidence of population subdivision among Masai giraffes separated by the Gregory Rift Valley in Tanzania. Ecology and Evolution DOI: 10.1002/ece3.10160
7. Bond ML, A Ozgul, & DE Lee. 2023. Effect of local climate anomalies on giraffe survival. Biodiversity and Conservation 32:3179–3197. DOI: 10.1007/s10531-023-02645-4
8. Lee DE, Lohay GC, Madeli J, Cavener DR, Bond ML. 2023. Masai giraffe population change over 40 years in Arusha National Park. African Journal of Ecology 61:345-353. DOI: 10.1111/aje.13115
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10. Morandi K, Lindholm AK, Lee DE, Bond ML. 2022. Phenotypic matching by spot pattern potentially mediates female giraffe social associations. Journal of Zoology. DOI: 10.1111/jzo.13009
11. James NL, Bond ML, Ozgul A, Lee DE. 2022. Trophic processes constrain seasonal ungulate distributions at two scales in an East African savanna. Journal of Mammalogy DOI: 10.1093/jmammal/gyac050
12. Levi M, Lee DE, Bond ML, Treydte AC. 2022. Forage selection by Masai giraffes (Giraffa camelopardalis tippelskirchi) at multiple spatial scales. Journal of Mammalogy. DOI: 10.1093/jmammal/gyac007
13. Lavista Ferres JM, Lee DE, Nasir M, Chen Y-C, Bijral AS, Bercovitch FB, Bond ML. 2021. Social connectedness and movements among communities of giraffes vary by sex and age class. Animal Behaviour. DOI: 10.1016/j.anbehav.2021.08.008
14. Bond ML, Lee DE, Ozgul A, Farine DR, König B. 2021. Leaving by staying: Social dispersal in giraffes. Journal of Animal Ecology. DOI: 10.1111/1365-2656.13582
15. Bond ML, König B, Ozgul A, Farine DR, Lee DE. 2021. Socially defined subpopulations reveal demographic variation in a giraffe metapopulation. Journal of Wildlife Management 85:920-931. DOI: 10.1002/jwmg.22044
16. Bond ML, Lee DE, Farine DR, Ozgul A, König B. 2021. Sociability increases survival of adult female giraffes. Proceedings of the Royal Society B 28: 20202770. DOI: 10.1098/rspb.2020.2770
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22. Bond ML, Lee DE. 2019. Simultaneous multiple-calf allonursing by a wild Masai giraffe. African Journal of Ecology DOI: 10.1111/aje.12673
23. Buehler P, Carroll B, Bhatia A, Gupta V, Lee DE. 2019. An automated program to find animals and crop photographs for individual recognition. Ecological Informatics 50:191-196
24. Lee DE, Cavener DR, Bond ML. 2018. Seeing spots: Quantifying mother-offspring similarity and assessing fitness consequences of coat pattern traits in a wild population of giraffes (*Giraffa camelopardalis*). PeerJ. DOI: 10.7717/peerj.5690
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29. Lee DE, Bolger DT. 2017. Movements and source-sink dynamics among subpopulations of giraffe. Population Ecology 59:157-168
30. Lee DE, Bond ML, Bolger DT. 2017. Season of birth affects juvenile survival of giraffe. Population Ecology 59:45-54
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32. Lee DE, Strauss MKL. 2016. Giraffe demography and population ecology. Reference Module in Earth Sciences and Environmental Studies. DOI: 10.1016/B978-0-12-409548-9.09721-9
33. Bond ML, Strauss MKL, and Lee DE. 2016. Soil correlates and mortality from giraffe skin disease in Tanzania. Journal of Wildlife Diseases 52:953-958
34. Lee DE, Bond ML, Kissui BM, Kiwango YA, Bolger DT. 2016. Spatial variation in giraffe demography: a test of 2 paradigms. Journal of Mammalogy 97:1015-1025
35. Lee DE, Bond ML. 2016. Precision, accuracy, and costs of survey methods for giraffe *Giraffa camelopardalis*. Journal of Mammalogy 97:940-948
36. Lee DE, Bond ML. 2016. The occurrence and prevalence of giraffe skin disease in protected areas of northern Tanzania. Journal of Wildlife Diseases 52:753-755

COMMENTS: Please see 'Findings/Results' above.

Risks, Issues and Challenges

We experienced no issues or problems that have impacted on the development and implementation of the project during the reporting period.

Next Steps	
Please provide a very briefly list the activities planned and/ other information of relevance for the next stage of the project. • We plan to continue giraffe photographic surveys and analyses to obtain robust estimates of population size, trend, and demographic rates for giraffes in northern Tanzania.	
PI Name: Derek Lee	**Signature and date:**  **10 Dec 2024**