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Evidence from GPS collars reveal a novel movement pattern and site fidelity for wildebeest migratory population in the Serengeti-Mara Ecosystem

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Ungulate migrations in ecology encompass various aspects, including movement behavior and site fidelity among species. This study aimed to investigate whether the Loliondo/Pololeti and Laetoli/Kakesio wildebeest herds exhibited migratory behavior and site fidelity during both wet and dry seasons within the Serengeti-Mara Ecosystem. Six female wildebeest were immobilized by a wildlife veterinarian and fitted with GPS collars from Savannah Wildlife Tracking Ltd., Kenya. The results indicated that the wildebeest herds utilizing the Loliondo Game Controlled Area (LGCA) were not a resident population but rather a migratory sub-population moving between Angata Kheri (Tanzania side) and Keekorok (Kenya side) of the plains. Both herds showed a high degree of site fidelity during the wet season, primarily within the Angata Kheri and Laetoli/Kakesio areas, indicating distinct herd behaviors. Based on these findings, the study concludes that the two herds exhibited different movement behaviors, with the Loliondo/Pololeti herd showing linear movements and the Laetoli/Kakesio herd displaying circular movement patterns. The study recommends continuous monitoring of these wildebeest herds using GPS collars to better understand their large-scale movement behaviors.

Key words: GPS collars, Serengeti-Mara ecosystem, site fidelity, wildebeest migration.

INTRODUCTION

Across the globe, there are numerous wildlife migrations involving both vertebrates and invertebrates (Chapman et al., 2014). Documented migrations include birds, mammals, and fish. Animals participating in migrations may exhibit either high or low site fidelity ranges, depending on the status of specific habitats over time (Morrison et al., 2021). Grassland and forest ecosystems offer a diverse array of resources for their inhabitants (Gosain et al., 2015; Fartyal et al., 2023). Migration behavior is influenced by species' requirements such as feeding, mating, and calving, as well as factors like climate change and human activities (Morrison et al.,

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2021). Migratory species are particularly vulnerable to multiple threats including climate change, human settlement, and habitat loss. The overexploitation of natural habitats has created significant barriers for migratory species due to imbalances in resource availability (Pandey et al., 2023; Bisht et al., 2024). These effects are particularly pronounced as species move between ecosystems, potentially altering their site fidelity. Xu et al. (2021) demonstrated that both natural and human-induced factors can significantly impact migratory species.

Ungulate migrations play a crucial role in ecosystems by contributing to environmental health, serving as primary food sources for large carnivores and scavengers. The loss of major migrations could lead to reduced plant diversity and productivity, and alter patterns of plant phenology on a large spatial scale, which may also affect fire regimes and soil nutrient cycles (Kauffman et al., 2021). In ungulate migrations there is a variation in site fidelity especially in the case of caribou (*Rangifer tarandus*). The barren caribou was thought to have cohesive herds in the Alaskan population, however, with GPS collar tracking analysis, it was evident that female caribou switched their calving grounds and the Alaskan caribou herds were falsely established because of having a low site fidelity (Prichard et al., 2020). However, the woodland caribou (*Rangifers taradus caribou*) have a seasonal range in the spring and summer; and for the winter and autumn range, each of the females return to the same calving grounds (Dalziel et al., 2016). The two subspecies have displayed different site fidelity with barren caribou in Alaska showing lower site fidelity than woodland caribou. The study by Prichard et al. (2020) demonstrated that environmental changes can shift migratory routes and calving sites in a range of species and can lead to fraudulent population establishment.

In their study, Morrison et al. (2021) found that Moose (*Alces alces*) and Mule Deer (*Odocoileus hemionus*) maintain their migratory routes and have strong site fidelity in their summer and winter ranges, and this was in favor of the survival of the young moose and mule-deer despite increasing pressure from human settlements. The Western White Bearded Wildebeest (*Connochaetes taurinus mearnsi*) which dominates the Serengeti-Mara Ecosystem is known to migrate in a circular pattern allowing the herds to move in open corridors that have not been blocked (Boone et al., 2006). Some studies describe the presence of non-migratory sub-populations in the Serengeti-Mara including the Ndabaka in Western Serengeti National Park (Sinclair et al., 2019), the Loliondo in the Eastern part of the Serengeti National Park (Hopcraft, 2010), Mara-Loita in Kenya (Stabach, 2015), and the Crater floor in the Ngorongoro Conservation Area (Estes, 2014). The Mara-Loita migrants moved between Kenya's Loita Plains and Maasai Mara Game Reserve, but have recently shown more restricted movements in the Mara Conservancies due to blockages from fences erected within their corridors (Stabach et al., 2022). The Ndabaka sub-population have shown to be a resident population, forming a separate genetic cluster (Ernest et al., 2012) and only migrating between Ndabaka and Nyasirori (Owen-Smith et al., 2020). Estes (2014) described that both sedentary and migratory sub-populations differ in their herd compositions; and a further study showed a strong bias in females over males in resident populations, especially those in Western Serengeti's Ndabaka (Ndibalema, 2009).

Site Fidelity is quite common where a species has a long-term knowledge and experience of local conditions with a particular site that has an advantage over another. Animals that display strong site fidelity interact with drivers which include an experience memory on how to determine the spatial proximity of where to return to in a particular site each year. For most species site fidelity was strongest in areas where there is a high Normalized Difference Vegetation Index (NDVI), which is essentially a high-quality foraging and breeding habitat (Morrison et al., 2021; Shimada et al., 2020). In the Maasai steppes, wildebeest are known to have a strong wet season site fidelity, despite the increasing numbers of people living in their wet season range (Morrison and Bolger, 2012). While studies have well described the general wildebeest movements during the wet and dry seasons in the Serengeti-Mara ecosystem (Hopcraft, 2010), there is still a lack of information on the migratory sub-population site fidelity, especially in areas where there are high numbers of people using wildlife habitat for agricultural activities and human settlement (Veldhuis et al., 2019).

Site Fidelity can reflect stability in a location of an important resource. Studies have also shown that animals that have a high site fidelity in particular habitats that have a high NDVI (Morrison et al., 2021). Migratory animals, that display a high site fidelity indicate that the vegetation in the region, have important nutrients that are required for the animal's survival (Kauffman et al., 2021). Within home range variation, many of the ungulate disperse in large areas and have the ability to return to the original areas (Kauffman et al., 2021). Climatic effects such as rainfall and weather patterns can also affect a certain home range and the spatial memory of migrating ungulates to determine which locations to return to each year (Mahony, 2020). By selecting a particular location at a certain time of the year, this can help the animal's survival and it is also where animals can find the best nutrition for lactation and the survival of new offspring (Kauffman et al., 2021).

Animals with high site fidelity in their home range variation also have shown to have a social learning. Female mammals that are closely related to each other have established home ranges that are near to each other. This was the case for Bighorn Sheep (*Ovis canadensis*) that were grouped into existing herds that

were able to learn to migrate where an individual was able to learn to return to those same habitats (Kauffman et al., 2021). The home range variation of ungulate migrations and site fidelity is also determined by the sexes of the individuals. Females are more selective in finding the best quality habitat with the appropriate nutrients and minerals that can provide the best lactation for young animals and locating a habitat that provides the best protection against predators (Ruckstuhl, 2007). Evidence suggests that increasing anthropogenic activities that occur in migratory corridors cause disturbance to animal movement and their migratory ranges (Stabach, 2015). Knowledge gaps on whether a population is migratory or non-migratory are important for the long-term management of the region. Therefore, this study investigates whether the Loliondo herds exhibit migratory behavior and site fidelity. Furthermore, we investigate whether the known migratory herds in the main Serengeti population show site fidelity.

As grazers, and a significant proportion of the ungulate biomass, migratory wildebeest form the most impactful ungulates with significant effects on the vegetation turnover. Due to this wildebeest presence influences the movement and distribution of other species such as zebra (*Equus buchelii*), topi (*Damaliscus topi*), cokes hartebeest (*Alcelaphus buselaphus cokii*), Thomson gazelle (*Eudorcas thomsonii*) and large carnivores within the ecosystem. The wildebeest migration also plays an important part in the nutrient recycling by improving grass quality from their droppings and urine, trampling of seedling trees and tree horning which maintain open grasslands (Estes, 2014; Hopcraft et al., 2015). Consequently, the migration of the wildebeest has an enormous influence on the tourism industry that generates substantial income for the country and community livelihood (MNRT, 2023).

In recent years there has been an increase in the human population in migratory corridors which has blocked wildebeest from reaching their migratory ranges (Msoffe et al., 2019; Morrison et al., 2021). The causative factors include cultivation and demands for livestock grazing especially in African habitats (Riggio et al., 2023). Already in the Loliondo Game Controlled Area in northern Tanzania there is increasing numbers of settlements spreading in the Waso town and nearby villages, not far from the Loliondo/Pololeti herd's wet season range (Veldhuis et al., 2019). If this Loliondo/Pololeti migration's corridor is blocked this could potentially lead to the decline of the Serengeti migratory population.

MATERIALS AND METHODS

Study area

The study was conducted in the Serengeti-Mara Ecosystem located in northern Tanzania and south-western Kenya, between latitudes 1 and 3° S and longitudes 34 and 36° E which covers about 30,000 km^2. Within Tanzania, the study focused on the southern short grassland plains of the Serengeti National Park (SNP) the Ngorongoro Conservation Area (NCA), and the Eastern SNP in the Loliondo (currently Pololeti) Game Controlled Area (Figure 1). On the Kenyan side, the study concentrated on Kenya's Maasai Mara National Reserve in The Mara Triangle and the Keekorok Plains. The Serengeti-Mara Ecosystem exhibits a bimodal rainfall pattern, with annual average rainfall of 1100 mm for the north-west and 500 mm for the south-east. The dry season is typically from July to October and sometimes February and early March, with a short-rain period from November to January, and long-rain period from March to May (Holdo et al., 2009).

GPS collaring and data collection

Six animals were fitted with Iridium GPS collars from Savannah Wildlife Tracking Company (Kenya), involving three adult females from each area (Table 1), aged between 2 and 3 years, with a body-condition score of either 4 or 5 with a newborn calf or a yearling. Aging was done by dentition and identifying the horn structure as described by (Watson, 1969). Selection of the individual for collaring was based on the observation of the herds within specific sites whilst in open vehicles. Herd estimates were done by slowly driving through the herd in open vehicles whilst observers counted individuals. Immobilization and GPS-Collar-fixing protocols were carried out by an experienced wildlife veterinarian under TAWIRI protocol. Collaring was done between December and May (2021 and 2023) when the animals were on the short grassland plains at their respective sites. Collars were set to deliver hourly readings covering 24 readings a day; Laetoli/Kakesio for the Serengeti migratory individuals and Loliondo/Pololeti areas for the Loliondo/Pololeti herd (Figure 1). After fitting the collars, respective individuals were tracked by both GPS positions and VHF over the next day to assess their welfare, and to see if they had re-united with the calf and/or offspring. Our assumption was that by collaring individuals in the LGCA, this can indicate whether the Loliondo sub-population is a migratory or a resident population.

Data analysis

GPS data from collared wildebeest was gathered for a period ranging between 199 to 772 days. (January 2022 to April 2022; January 2023 to April 2023). Microsoft Excel for Window 2021 was used to handle the data. QGIS version 3.32.3 was used to analyze the movement behavior with daily displacement, home range sizes (using Minimum Convex Polygon 100%) and by using the measurement polygon tool for the study. The GPS readings appearing in the same areas in consecutive years were considered as indications of site fidelity. Site Fidelity was measured by the number of days the animal utilized the same range consecutively.

RESULTS

The results show that the wildebeest herd utilizing the LGCA is not a resident herd, but rather a migratory sub-population that moves between Angata Kheri (Tanzania side) and the Keekorok plains (Kenya side). Furthermore, results demonstrated that this migration phenomenon takes into consideration the seasonality; meaning that the herds move to Tanzania and Kenya during wet and dry seasons respectively by using specified routes (Figure 2). The results demonstrate that the GPS readings recorded the wildebeest migrating to the same locations over

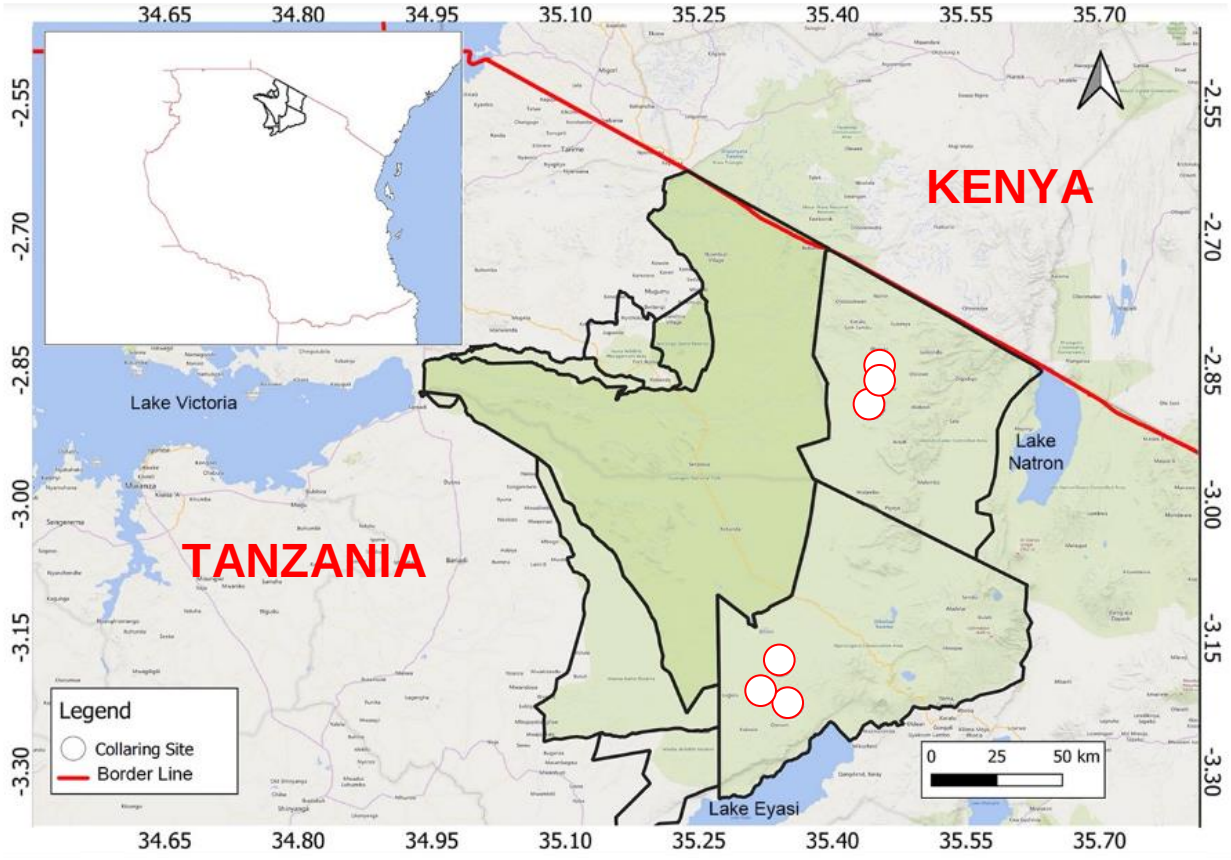

Figure 1. Map of the study area in the Serengeti-Mara Ecosystem showing a collaring site (circled white).

Table 1. The collared wildebeest indicating the collar ID, estimated age, estimated herd size, date of deployment, number of days recording locations and total number of GPS fixes.

S/N	Collar ID	Age (years)	Herd size, estimate	Date collar deployed	Days	Total No. of fixes
1	IRI12016_3708	4	20	31st January, 2021	772	16634
2	IRI12016_4161	3	200,000	31st March, 2022	348	6573
3	IRI12016_4160	4	200,000	31st March, 2022	347	6848
4	IRI12016_4134	3	20	12th December	438	9343
5	IRI2016_4680	3	1,000	26th March, 2023	199	5256
6	IRI2016_4135	3	1,000	26th March, 2023	199	5256

consecutive years indicating that the herds were exhibiting site fidelity, whereby the Loliondo/Pololeti Herds stayed for 5.5 months, whilst the Laetoli/Kakesio stayed for a shorter period (Table 2).

The identified herds use two regions for their wet season home range (Figure 3 and Table 3). For the Laetoli/Kakesio herd, they use the southern Ngorongoro Conservation Area which is in the Laetoli/Kakesio Region. The Loliondo/Pololeti herd uses the middle part of the Loliondo Game Controlled Area in the grasslands of the Angata Kheri. Since calving occurs during the wet season, the two migratory herds use the calving range as the feeding ground and spend approximately four months in the same home range.

DISCUSSION

The study findings reveal a novel movement pattern from collared wildebeest whereby the Loliondo/Pololeti herd shows a clear migratory movement covering wet and dry season and should no longer be considered a resident population. Both the Loliondo/Pololeti and the Laetoli/Kakesio herd exhibit high site fidelity during the wet

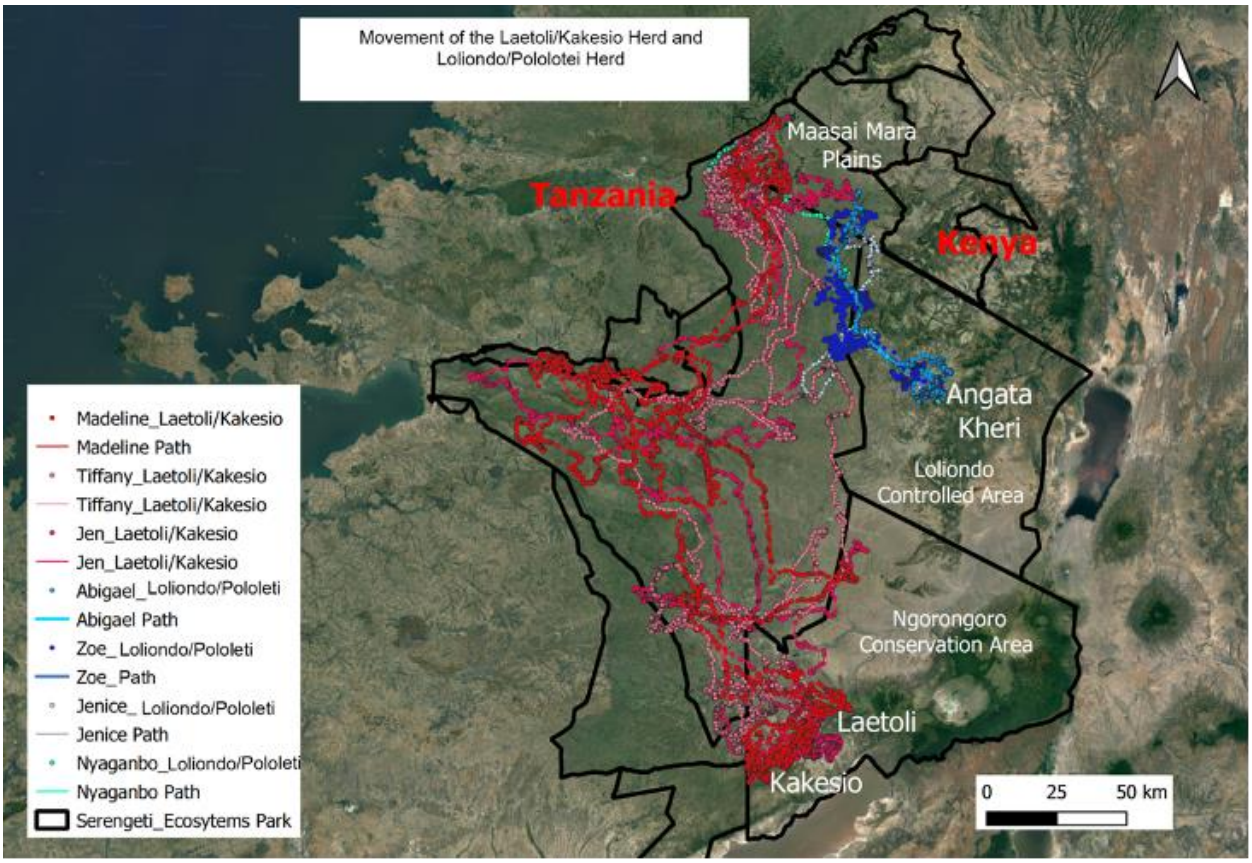

Figure 2. The Entire Movement (Wet and Dry Season) of the Loliondo/Pololeti (blue) and Laetoli/Kakesio (red) Herd. Female wildebeest named by the author for ease in tracking individuals.

Table 2. Total GPS fixes and Percentage of the Wet Season Home Range.

Animal ID	Total fixes of wet season home range		% fixes of wet season home range			
Name of animal and herd	Fixes for 2022	Fixes for 2023	% 2022	%2023	Days (2022)	Days (2023)
(IRI2016-4161)-Laetoli/Kakesio	N/A	1521	N/A	83.80	10	105
(IRI2016-3708)-Laetoli/Kakesio	1747	877	61.13	59.02	63	104
(IRI2016-4160)-Laetoli/Kakesio	N/A	1467	N/A	77.05	4	74
(IRI2016-4134)-Loliondo/Pololeti	3667	3234	95.64	89.63	167	208
(IRI2016-4180)-Loliondo/Pololeti	N/A	N/A	N/A	N/A	-	100
(IRI2016-4135)-Loliondo/Pololeti	N/A	N/A	N/A	N/A	-	72

season. The data shows clearly that the Loliondo/Pololeti and Laetoli/Kakesio herds are two distinct herds. The Loliondo/Pololeti herd showed a linear movement during the wet season ranging from the Angata Kheri Plains further towards the north covering wet-to-dry season and back again to the south during dry-to-wet season due to rainfall variation. The herd moves in short movements within Angata Kheri (Tanzania side), however during the dry season (June and July), it's clear that the Loliondo/Pololeti Herd migrates to Keekorok Plains (Kenya side). Furthermore, the Loliondo/Pololeti herd shows migration between Angata Kheri through Serengeti National Park's Lobo Valley and Bolongoja Springs and entering the Maasai Mara Plains in the dry season. When the wet season commences, the Loliondo/Pololeti herd uses the same corridor migrating southwards through Lobo Valley and into the Bolongoja Springs into Angata Kheri.

The observation from this study supports earlier observations by Cleaveland et al. (2001) as there were some significant numbers of wildebeest that were using the Angata Kheri grasslands Plains in Loliondo which

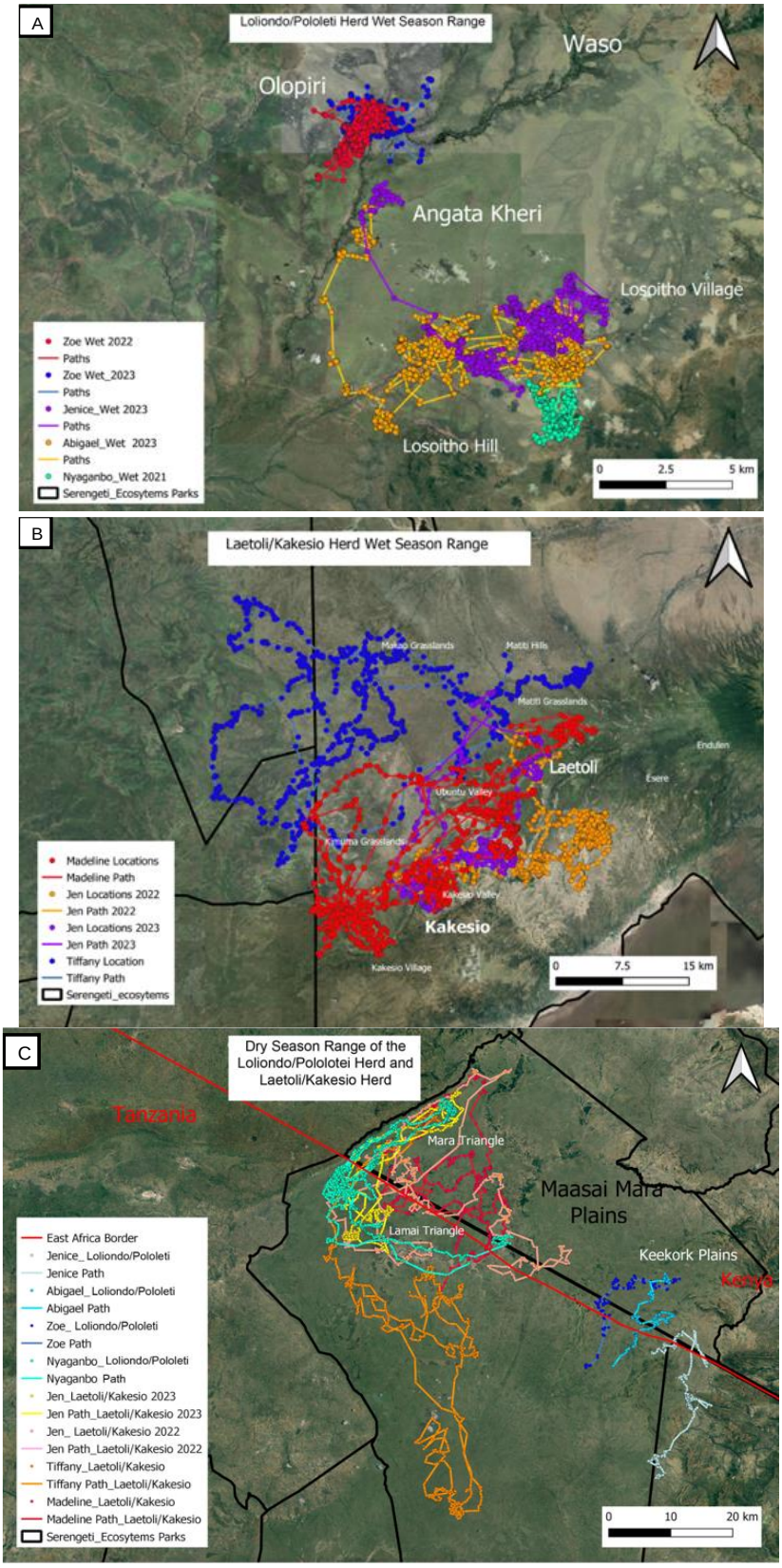

Figure 3. (a, b, c) The site fidelity of the two herds which includes Loliondo/Pololeti herd and the Laetoli/Kakesio herd in both wet and dry seasons. During the wet/calving season the two herds remained in their respective home ranges.

were not fitted with GPS Collars. Similar to our findings, evidence from previous studies indicates that two collared animals had moved from Kenya's Maasai Mara Plains towards the south during the commencement of the wet season and had utilized the Angata Kheri grasslands in the Loliondo Game Controlled Area (Stabach, 2015).

Contrary to our findings one collared animal had moved towards Ndutu area through Angata Kheri from Loita Plains whist the other animal moved from Loita Plains to Angata Kheri and into the Salei grasslands during the commencement of the wet season (Stabach, 2015). In this study, the Loliondo/Pololeti herd shows a significant movement between the southern part of Loliondo Game Controlled Area in Arash Village and Piaya Valley, and further south to the Ngorongoro Conservation Area. Moreover, the Loliondo/Pololeti herd had not moved into Lemuta Plains and beyond the Lemuta Plains including Ndutu, Laetoli and Kakesio areas within the Ngorongoro Conservation Area.

The Laetoli/Kakesio herd showed a circular migration moving from the Laetoli/Kakesio region to the western corridor and then into the Maasai Mara Plains and back through the Western Corridor into Laetoli/Kakesio region. This finding supports previous studies conducted by Hopcraft (2010). The Mule Deer had similar seasonal migratory pathways covering summer and winter ranges (Kauffman et al., 2023). In addition, the Laetoli/Kakesio herd's wet season range extends from Kimuma Grasslands to Ubuntu Valley and further east towards Matiti Grasslands and Laetoli Footprints region in southern Ngorongoro Conservation Area. These study results suggest that continued monitoring of the collared wildebeest will reveal whether the movement is stable and recurring, confirming these detailed findings that reveal the two herds are performing distinct migratory behavior.

The study demonstrates evidence that the Laetoli/Kakesio and Loliondo/Pololeti herds display a high percentage of wet season site fidelity which includes the two areas (Laetoli/Kakesio and Angata Kheri Plains) outside of the SNP. Reasons for this site fidelity include: presence of calving grounds, rainfall and grass quality in these areas. Our observations on the site fidelity behavior have also been reported in wildebeest populations utilizing the Tarangire-Manyara ecosystem (Morrison and Bolger, 2012). The finding from this study further described that the presence of wildebeest in a similar location was due to lactation, calving and quality of grazing. However, the observed increase of unpalatable grass species for wildebeest grazing have reduced the ranging pattern making the Laetoli/Kakesio herd remaining longer within the Laetoli and Kakesio region and less within the Lemuta and southern Serengeti National Park plains during the calving season.

Previous studies have shown that the wildebeest return to short grasslands in the Southern Serengeti but not always describing specifically the defined areas (Estes, 2014; Hopcraft, 2010; Sinclair et al., 2019; Torney et al., 2019). In this study we observed that the number of days of collared wildebeest returning to the same GPS location in the Serengeti provided accurate evidence. This pattern is well described by previous GPS tags using the satellite locations in the following species of Mule Deer (Ortega et al., 2023) and Elk (Morrison et al., 2021). However, in this study, none of the collared animals had shown any switching of the site fidelity between Angata Kheri and Laetoli/Kakesio areas. Similar home range sizes for both herds were limited within the site fidelity areas during the wet season; further evidence that the herds are distinct.

CONCLUSION AND RECOMMENDATIONS

The study concludes that the Loliondo/Pololeti herd is not a resident wildebeest population. The migratory behavior patterns reported from Laetoli/Kakesio herd and the Loliondo/Pololeti herd warrants that there are two distinct migratory herds occurring in the Serengeti Ecosystem. Furthermore, there was no observed switching of the site fidelity between the two herds; which justified that they exhibit linear and circular migratory movements. Lastly, the observed collared wildebeest show signs of avoiding areas with high unpalatable grass species (including invasive weed species) or human-dominated areas; this justifies the health of ecosystem in terms of wildebeest grazing. Based on these findings, the study recommends that the constant monitoring of wildebeest herds using GPS collars is important in determining the macro-scale movement of the wildebeest population within the Laetoli/Kakesio herd and Loliondo/Pololeti areas. The plan is to document whether the migratory movement pattern changes in the long term because of increasing human pressure in the migratory regions.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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