PROSPECTIVE REVIEW AND ANALYSIS OF THE ECOLOGY OF THE MOVEMENT OF THE AFRICAN ELEPHANT (*Loxodonta africana*). CASE OF THE SAVANA OF THE NIASSA RESERVE, NORTHEASTERN MOZAMBIQUE

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ABSTRACT - The objective of this work was to conduct a literature review on the perspective and analysis of African elephant movement ecology through case studies. The telemetry and spatial modeling used in this study aimed to understand how the method improves the perception of how animals use space and their interactions that affect conservation. Understanding the complexity of how animals use their lives has proven to be a new era and crucial for conservation planning. The review initially described the species' biology, followed by characterization and its role in ecosystem functioning, and the ecological analyses used. The case study was conducted in the protected area whose telemetry data were ethically made available for study of African elephant movement in this specific area, the Niassa Special Reserve. Regionally and internationally, the analyses performed constitute a viable alternative for conservation management decisions and support research because they contribute to biodiversity conservation. Specifically, and internationally, they reduce the knowledge gap regarding the conservation of this charismatic species, which is increasingly threatened by habitat loss and population decline due to illegal hunting in the region.

Keywords: Home range, spatial analysis, Protected area

REVISÃO PROSPECTIVA E ANÁLISE DA ECOLOGIA DO MOVIMENTO DO ELEFANTE AFRICANO (*Loxodonta africana*). CASO DA SAVANA DA RESERVA DO NIASSA, NORDESTE DE MOÇAMBIQUE

RESUMO – O objetivo deste trabalho foi realizar uma revisão bibliográfica sobre a perspetiva e análise da ecologia do movimento do elefante africano por meio de estudos de caso. A telemetria e modelagem espacial abordada visava compreender como o método melhora perceção de como os animais utilizam o espaço e suas interações que contribuem para a conservação. Compreensão da complexidade do uso do home range pelos animais mostrou nova era e crucial para o planeamento da conservação. A revisão descreveu a prior a biologia da espécie, seguido pela caraterização e seu papel no funcionamento do ecossistema e as análises ecológicas utilizadas. O estudo do caso foi na área protegida cujos dados telemétricos foram eticamente disponibilizados para estudo sobre movimento do elefante africano nesta área específica, a Reserva Especial de Niassa. No cenário regional e internacional as análises feitas constituem uma alternativa viável para decisões de gestão de conservação e apoiam a pesquisa porque ela contribui para a conservação da biodiversidade. Especificamente e internacionalmente, reduzindo a lacuna de conhecimento sobre a conservação desta espécie carismática, que está cada vez mais ameaçada pela perda de habitat e pelo declínio populacional devido à caça ilegal na região.

Palavras-chave: Home range, análise espacial, Protected área

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GENERAL INTRODUCTION

The ecology of wildlife movements is important because it provides key metrics to improve the formation and understanding of their population dynamics, in interaction with ecosystem structure for better biodiversity conservation (Dublin et al., 2001, Ngene et al., 2009). Currently, new approaches bring many technological innovations that have intervened to shape and improve elements that help explain spatial phenomena observed in the field by modeling movement captured at the finest scale. Their progress and structure have evolved to such an extent that the newly developed theories integrate the movement of organisms, relating them to their internal state, their capacity for movement, and their ability to cope with external factors. For this reason, these new concepts are recognized worldwide as a milestone in the field of ecology (Clauss et al., 2007). Conceptually, movement began to gain attention in modern ecology due to its implications for reproduction, gene flow, and metapopulation dynamics; as such, studies of animal and plant dispersal constituted a large part of the ecological literature on movement until twenty years ago. Initially, a frequently tested hypothesis in animal movement ecology was the inclusion of variables that determine home range size, based on body mass, feeding habits, and sociality levels. For example, ecologically testing the influence of habitat on productivity, or herd type on variation in food availability (Clauss et al., 2007; Bohrer et al., 2014).

Regardless of how movements affect the individual vital historical traits of populations of each species, with different landscape components in form and differences in home ranges, the influence of landscape heterogeneity and ecological factors on variation in individual home ranges is still incipient (Own-Smith 2014; Bohrer et al., 2024). Therefore, this review of studies addresses the importance and relevance of this technology as a contribution to improving conservation through estimates of sufficient sample sizes using robust methodologies that reinforce the understanding of the connection between individuals and environmental factors and home ranges (Seigle-Ferrand et al., 2021).

This was done through a case study in a protected area with one of the largest African elephant populations in sub-Saharan Africa. Justifying this fact, the approach to individual home range sizes, combined with factors influencing elephant population variation and distribution, and the spatial models used in spatial modeling of African elephant movement.

METHODOLOGY

The literature review was conducted using a descriptive bibliographic approach, based on technical and scientific publications relevant to the proposed topic. The bibliographic survey included books, academic articles, and doctoral theses from Asian elephant ecology study (Othman, 2017) and the case study on the ecology of African elephant movements (Manjate et al., 2023). The sources used in the text were selected based on relevance criteria for the topic in question. The bibliographic references prioritized publications from the last ten years, although there are also older relevant citations. The scientific quality of the material used was also taken into account. The main databases used were Google Scholar, the electronic library's journal portal. The following keywords were used in the searches: home range, NDVI, EVI, productivity modeling, telemetry data, BBMM, NSD, PHR index (tools used in spatial modeling); and GLMM and R (tools used in statistical analysis).

The case study was analyzed to identify the main methods used to study African elephant movement. The models discussed allowed us to understand the role of modern technology in supporting practical improvements in environmental quality, as well as the applicability of these tools in biodiversity conservation. Therefore, this study aimed to ensure a descriptive bibliographic survey related to the topic, including theoretical background, and enrichment of the movement ecology of the African elephant (*Loxodonta africana*) for the production of the doctoral dissertation.

REVIEW RESULTS

PROSPECTIVE REVIEW AND ANALYSIS OF THE ECOLOGY

Biological Classification of the African Elephants

Apart from Asian species *Elephas maximus* (Heffner and Heffner, 1980, Othman, 2017), The African elephant was previously considered a single species, and the other two known species were classified as subspecies. This influenced conservation strategies that followed this pattern for elephants in Africa. However, this changed when interventions aimed at genetic matching for replication and population growth, and new taxonomic evidence emerged based on the existence of large genetic distances. multiple differences in genetically fixed nucleotide sites, morphological distinctions, and differences in forest and savanna habitats. These differences therefore limited hybridization and gene flow between of african elephants, resulting in their reclassification and separation into two distinct species: forest (*Loxodonta cyclotis*) and savanna (*Loxodonta africana*) (Roth and Douglas-Hamilton 1991; Dublin et al. 2001; Roca et al. 2014) .The species studied here is the African elephant, belonging to the Domain: Eukaryota; Kingdom: Animalia; Phylum: Chordata; Subphylum: Vertebrata; Class: Mammalia; Infraclass: Placentalia; Order: Proboscidea; Family: Elephantidae; Genus: Loxodonta (Blumenbach, 1797) ilustated in Figure. 1.

Figure 1. African elephant (*Loxodonta africana,* Blumenbach, 1797)

Behavioral Patterns of African Elephant

Understanding behavioral patterns and peculiarities is fundamental to the movement and grouping of this species. Since then, they have defined their aptitude and ability to succeed in the subtlety of maintaining and preserving their populations in favorable ecosystems (Neumanned, et al. 2015 and Ngene et al 2009). These are, therefore, characteristics acquired during the evolutionary process of the species, as some of them define precision in leadership and behavioral coordination of the animals' movements. For example, the ability of males or bulls to remain in sync during long-distance movements. It is documented by the authors that the minimum distances established determine that, even if the animals are separated at certain distances from the group, cognitively, they maintain perfect communication with the other members of the clan, within a radius of one to three kilometers Huntley et al., 2010. Within this radius, for example, most of the time males wander alone, but achieve reproductive success, finding females that mature very quickly due to evolved auditory abilities (Heffner and Heffner, 1980; Langbauer, 1991). African elephants are considered large seasonal movers across home ranges that can vary greatly in size. Previous data have documented that individual elephants can range from 10 to 10,738 km2 (Huntley et al., 2010) and distance runner routes can reach approximately 450 km in a predictive seasonal movement because the animals' movements are repetitive in areas of perennial water availability in the arid African savannas (Douglas-Hamilton et al., 2005; Lindeque and Lindeque, 1991; Thouless et al., 1992; Whyte et al., 1993; Polansky et al., 2015). However, the predictability of seasonal repetitiveness and the timing of movement decisions are still recommended for subsequent studies focusing on the ecology of elephants movimentos dos elefantes. Entre estes fatores, pode-se mencionar a variabilidade sazonal das distâncias aos recursos de subsistência Huntley et al., 2010, elephant movements. Among these factors, we can mention the seasonal variability of distances to subsistence resources (Polansky et al., 2015; Wato et al., 2018; Purdon et al., 2018; Benitez et al., 2022), which normally accompanies the variation in the availability of water and food resources, such as vegetation (Huntley et al., 2010) Related to movements are densely dependent and densely independent intraspecific interactions within a given home range under different ecological and social contexts (Polansky et al., 2015; Wato et al., 2018; Purdon et al., 2018; Seigle-Ferrand et al., 2021).

Spatial Distribution Patterns of the African Elephant

African elephants are found in subsaara region (Figure. 2) occupying diverse habitats in social groups (clans) with random spatial distribution and varying sizes within their habitats. This randomness and dispersion make them vulnerable and threatened by poaching attacks along their movement corridors. For most of their lives, groups move steadily and predictably, in a certain number per unit of home range. Therefore, it is important to continually deepen research into their connectivity corridors, habitats, measurement sizes, and seasonal variability in order to protect them (Kerley et al., 2008; Owen-Smith, 2014). Combined with this is the dispersed distribution and occupation of these spaces. Cases of occurrence in agricultural habitats or multiple-use areas are frequent. However, they are reported and seen as crop destroyers and, in many cases, trigger human-wildlife conflicts (Hoare and DuToit, 1999; Douglas-Hamilton and Vollrath, 2005). Due to elephants' demand for food and water, whose availability follows seasonal cycles, they move extensively. However, decisions to confine the remaining and scattered African elephant populations within protected areas, using electrified fences for better control, become a major challenge due to increased recruitment and pressure on resources that quickly reach carrying capacity. Therefore, to the detriment of maintaining populations in the open and controlling them is more viable (Kerley et al., 2008; Loar et al., 2009; Huntley et al., 2010).

The authors describe that, at the African ecosystem level, the population distribution is documented as occupying spatially varying sizes of home ranges in savanna and forest habitats. The description of habitat configurations at the biome level in Sub-Saharan Africa is in the form of mosaics of metapopulations, defined by their organization and social structure within the ecosystem. The same authors report that habitat configuration is modified by habitat loss caused by deforestation, bush encroachment, the effects of climate change, and overgrazing. Some effects are reflected elephant populations have declined dramatically in recent times, linked to poaching, the main cause of which is human (Roth and Douglas-Hamilton, 1991). The current habitat configuration of African elephants is mosaics of savanna, riverine, herbaceous, and marshy areas, where they are preferred areas for aggregation in small, scattered populations with varying abundance over time (Roth and Douglas-Hamilton, 1991). They occur primarily in open savannas and marsh habitats, with variable occurrence, sometimes in relatively large groups. These observations have been an indication of abundant food and water, suggesting good habitat quality when large numbers aggregating in these habitats (Whyte et al., 1993; Roever et al., 2014; Owen-Smith, 2014). Therefore, they are attractive to both animals and to agriculture and itinerant livestock farming and become areas of multiple uses, triggering the so-called human-elephant conflict.

Figure 2. African elephant distribution in subsahara region (www.wcs.org).

Role of the African Elephant in Savanna Ecosystem Services

Elephants play an important role in providing various services and goods to savanna ecosystems, such as dispersing seeds, maintaining open wooded savanna grasslands, increasing habitat structural complexity, and facilitating local increases in the abundance and diversity of small vertebrates (Robson et al., 2017; Western, 1989; Pringle, 2008). The African elephant is a keystone and charismatic species that plays a crucial role in maintaining food web links in African ecosystems. Their lifestyle makes them charismatic, as it is intrinsically linked to feeding behavior with constant, long-distance movements that result in changes in the vegetation structure of ecosystems, modifying the savanna or forest landscape directly and indirectly in savanna vegetation. The rate of vegetation consumption is higher and variable between females and males. Compared to other herbivores, the elephant is the largest herbivore in Earth's terrestrial ecosystem (Roth and Douglas-Hamilton 1991; Dublin et al., 2001). Females can reach a maximum body mass of over three tons, less than males, which reach six tons. Therefore, elephants, along with other species that exceed one ton in adult body mass, such as rhinos and hippos, are categorized as "megaherbivores" (Owen-Smith, 2014). Despite its enormous size, it has a fairly simple digestive system, with most digestion occurring in the small intestine and colon, providing a relatively rapid digestion process, with an average retention time of about 24 hours, regardless of food intake (Clauss et al., 2007). This rapid digestion, compared to other large herbivores, results in very low digestive efficiency, with less than half of the ingested forage assimilated and the remainder eliminated in feces. Furthermore, large amounts of fiber are ingested without any digestion, unlike other herbivores. Thus, apparent daily food intake (in terms of dry mass) is also low, approximately 1–1.5% of body mass per day (e.g., compared to 2–3% for cattle). However, due to their large size, the absolute amount of vegetation consumed per day by each elephant is enormous, estimated at over 60 kg dry weight, or approximately 180 kg of wet vegetation consumed daily by an adult male (Owen-Smith, 2014). A portion of the plant biomass lost is in the form of feces, which serves as food for other taxonomic groups, such as invertebrates, which are nutrient recyclers, making soils productive for ecosystem dynamics (Sukumar 2003; Kerley et al., 2008; Roever et al., 2014; Owen-Smith, 2014).

Conservation Status of African Elephant Populations in the Region

Elephant populations are in constant decline due to ivory poaching, habitat loss, and retaliatory killing (Thouless et al., 2017). Due to this condition, the African elephant is categorized as Vulnerable on the IUCN Red List. Efforts are underway to maintain biodiversity in the Niassa landscape, which boasts a diverse fauna and flora, where elephants stand out in numbers and functions, and provide landscape services of great local and regional socioeconomic importance. Populations are experiencing significant decline due to mortality in the region. Data from the 2014 annual counts estimate approximately 4,441 animals, of which 450 are males and 3,991 are females. Mortality is estimated at 3,183 (1,340 recent carcasses and 1,843 old carcasses) (Grossmann et al., 2014; Booth and Dunham, 2014). The counts serve as a reference model for describing trends in the impact of poaching on populations, given the high human-caused mortality rate of elephants in the region (Benitez et al., 2022). Therefore, even current data collection and analysis trends may differ in recent years.

Theories/perspectives for ecology in elephants movements

In the context of developing this topic, some theoretical concepts help focus the study of movement ecology. In this context, authors have developed the following theory: Organisms such as African elephants move as a strategic evolutionary adaptive behavior. For example, Bradbury (1977) in the theory called "Leks Theory" states that to maximize chances in survival strategies, organisms adopt behavior that is economically viable, by males avoiding movement to the resources needed, females, and settle themself in suitable habitats (e.g., forage), where reproductive success is guaranteed (male-female pairings) and nesting sites (hazard shelters/refuges) to sustain their populations (Davis, 1991 in Sutherlands, 1996, Krebs, 1994, Odum and Barrett, 2007; Krebs and Davies, 1996). According to Dolman and Sutherland (1995) in "Theory of Evolutionary Strategies of Stable Migrations," the authors describe that organisms, throughout their movement, assume that the density of resources is the same in all locations. This implies that, in response to habitat loss, populations move, changing their usual routes to establish new areas (Evolutionary response to habitat loss). Krebs (1994) in the "Theory of Habitat Suitability (Fitness)" states that an individual, through random movements, moves differently (Speed) along a moisture gradient.

Therefore, it is faster in dry than in humid environments (e.g., bird migration). Furthermore, patches differ in quality along a landscape gradient. Thus, animals have evolved the ability to move differently to discriminate suitability as an inheritance. According to Odum and Barrett (2007) in their "Allee and Refuge Theory," the assumption is that animals move in aggregates in social groups as an evolutionary ability to: Overcome differences between locations or landscapes, Seasonal climate, Maximize the reproductive process, Social attractors, and increase the overlap of females and males. Together, this aims to increase individual advantages in terms of food and space used for the benefit of the group. The refuge theory, also previously defended by Sutherland (1997), states that spatial aggregation aims to allow better establishment of populations in places with suitable habitats. Associated with the refuge, some individuals tend to isolate themselves to increase their chances of survival.

History of conservation in the region

Authors describe biodiversity conservation in the region where the studied elephant is located as early as 1954. Therefore, the area has undergone several stages of development, with discontinuities lasting decades or more. In 1975, Mozambique gained independence from Portuguese colonialism and soon after experienced a long period of civil war that lasted until 2002, and with the end of hostilities. At this point, initiatives to reorganize and control the fauna dispersed throughout the forest were resumed. Subsequently, the restructuring process of this conservation area was challenging and required some adaptations. Conservation models need to adapt to local characteristics for the sustainable management of the region's fauna and flora (Craig, 2009; Grossmann et al., 2014; Booth and Dunham, 2014). In the case of the Niassa Reserve, one of the adaptations, for example, is the management of the buffer zone granted to private managers and nine blocks for "legal hunting," where the killing of males is permitted. It also includes six photo-tourism blocks and two key areas that are the core of the Special Reserve, with high biodiversity value and diverse fauna and flora. Since 2019, the Reserve has followed new criteria for reclassifying Conservation Areas in Mozambique, making it the Niassa Special Reserve (NSR) (Craig, 2009; Grossmann et al., 2014).

Elephant Movements

Elephant abundance is partially associated with productivity and water availability, while poaching is a major driver of this iconic animal's population decline (Robson et al., 2017). These factors, including anthropogenic actions, are general determinants of the animals' decisions and population dynamics. It is not surprising that they determine the spatial distribution of African savanna elephants on a large scale (De Boer et al., 2013). Compared to most vertebrates studied in different regions, understanding different aspects of their spatial ecology is difficult due to their long movements through inhospitable habitats.

Thus, spatial analysis details that the size of the home range during movement is influenced by precipitation, productivity, water availability, and human impacts (Benitez et al., 2022; Seigle Ferrant et al., 2021; Loarie et al., 2009, Atwood and Weeks-Jr, 2003), including the presence of fences, and activities related to agriculture and livestock should be highlighted due to their high potential to isolate disjunct populations (Benitez et al., 2022; Huang et al., 2022). Movement is a fundamental process that plays a critical role in determining an animal's fate, but it also has effects that extend to influence the structure and dynamics of the populations, communities, and ecosystems in which the individual lives, as well as to establish mitigation measures. Human actions can have a direct effect, altering animal movement patterns (e.g., Gara et al., 2021; Bohrer et al., 2014; Loarie et al., 2009; Nathan et al., 2008; de Leeuw et al., 2001), vement Data Analysis Models. Case Study in the Niassa Reserve

The movement ecology analysis model followed the example of modern technology used in a study recently conducted in the Niassa Special Reserve (REN) (Manjate et al., 2023) **(**Figure. 3) The studied area is a relatively low and flat protected area, with altitudes ranging from 8±1,000 m above mean sea level, with the Mecula mountain reaching >1,500 m in height at the center of the reserve (PRIN, 2014). Primary productivity, based on 2010 NDVI data, indicates an expansion of vegetation throughout the REN starting in February, and primary productivity remains high until June, when senescence begins at the eastern border of the plain, which is dominated by grasslands vSenescence vegetation advances westward and peaks in November, when only the wetter mountainous region in the open miombo woodland of the southwest remains green (PRIN, 2014). According to estimates from 2014 aerial wildlife surveys, approximately 50% (~5457) of Mozambique's elephants live in the REN and adjacent areas (Grossmann et al., 2014; Booth et al., 2016).

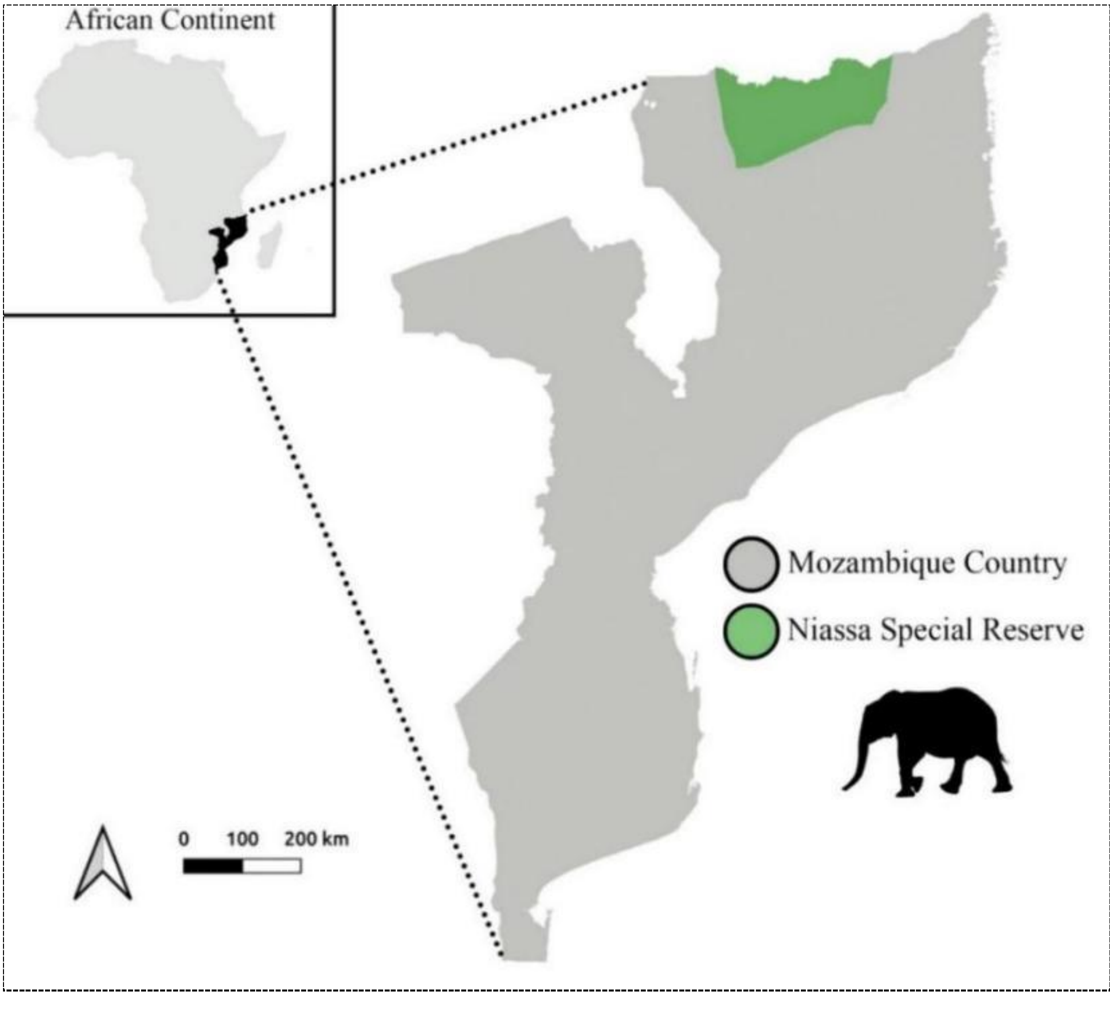

Figure 3. Study area showing the Niassa Special Reserve in northern Mozambique.

Anthropization in Niassa Special Reserve

In the Mozambique region, since the Reserve's existence, the districts within it, and districts in areas surrounding the Reserve, have consistently reported movements and situations of human-elephant conflict, which have been key areas of human disturbance (Figure. 4). The livelihoods of local communities are centered on agricultural production through shifting cultivation, which is one of the drivers of habitat degradation through slash-and-burn practices. The continued clearing of natural vegetation through this practice poses a significant threat to Niassa's conservation objectives. Communities also face considerable challenges in terms of remoteness and limited access to physical and social infrastructure, which exacerbates widespread poverty across the landscape. Therefore, this study is important as a contribution to conservation and inclusion in conflict mitigation strategies.

The existence of infrastructure and human settlements is a major challenge in African conservation areas, making it a mandatory variable in biodiversity management strategies as it interferes with the routine movements of wildlife. Within the Reserve, some areas are highly anthropized, containing infrastructure where approximately 35,000 people live (Craig, 2009; Grossmann et al., 2014) (Figure. 4). Like many global protected areas, local and regional encroachments consist of patches of community lands, housing, streets, and other infrastructure extending from the north of the Reserve, bordered by the Rovuma River in southern Tanzania, along the Selous-Niassa corridor (Booth and Dunham, 2014).

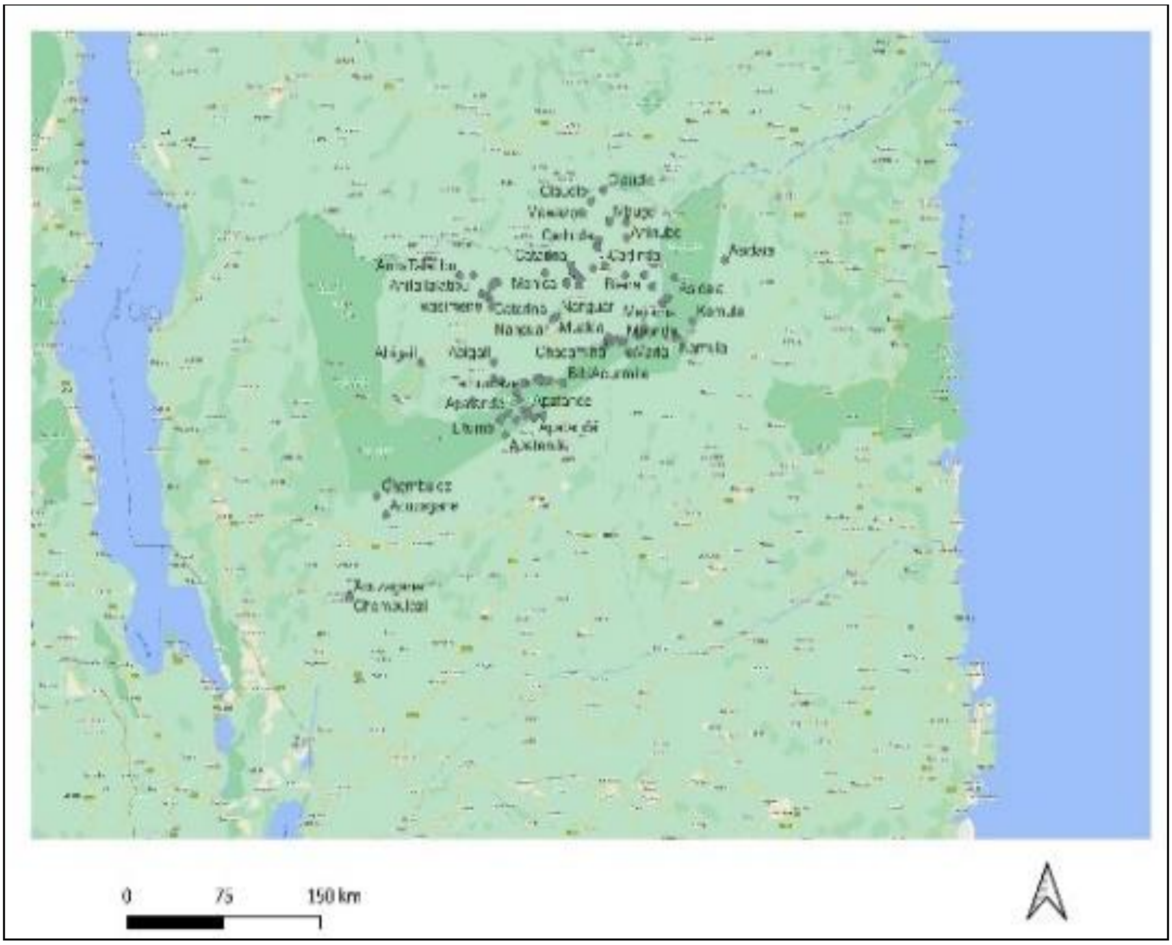

FIGURE. 4: Points in Black represent Elephants and areas highly anthropized, in green Protected Areas are containing infrastructure surrounding with yellow dots (GoogleEarth.image.)

Applying Modern Analysis to Movement Ecology

The data used in the research describe movements from 2019 and 2020, sourced from a database. Stakeholders recognize the need for new analytical elements missing in the movement ecology of African elephants (Joo et al., 2007; Meekan et al., 2017; Miller et al., 2018). In this context, there was a rapid response to the call for studies in this area, due to the availability of data (Shelved) for use in studies and to offer detailed analyses with more advanced models that contribute to the most up-to-date descriptions of the ecology of animal movements in this region (Miller et al., 2019; Joo et al., 2020; Demšar et al., 2021; Seigle-Ferrand et al., 2021).This marks the beginning of the current reduction of the knowledge gap or "bias" in the region, as other regions, such as Kenya, Tanzania and Namibia, already have advanced studies on movements (Leyequien et al., 2007; Joo et al., 2020; Benitez et al., 2022). According to Benitez et al. (2022), the study, through the analysis of telemetry data, aims to understand the home ranges; how animals use these areas; and aspects of interactions that contribute to the conservation of this species, which is increasingly vulnerable due to habitat loss and requires space for movement. Understanding the complexity of home range use by individuals marks a new era and is crucial for conservation planning that aims to balance regional interests for the benefit of the animals and humans that cohabit the region, which still constitutes a data gap on elephant movements (Seigle-Ferrand et al., 2021).

African elephant movement data in Niassa were collected by an animal management and tagging team consisting of four veterinarians experienced in collaring wild animals. Following appropriate animal welfare procedures in the area, they proceeded with the GPS collar implantation program for 45 elephants, led by the WCS multidisciplinary team in 2018 at the Reserve (Figure. 5, WCS, 2018). The process was well coordinated, consisting of flyovers of herds of female or male elephants. Each target was shot with an opioid-containing arrow, which was immediately immobilized. Following this, the necessary biological measurements were taken, following ethical protocols, and the corresponding GPS collar implantation for satellite locations. The entire process, including testing equipment, took at least 30 minutes. The animal was then injected with naltrexone (150mg) for recovery (Kock, 2018). All GPS-collared elephants followed the same protocol. They were organized in the database that, by agreement, was provided to us by the Wildlife Conservation Society (WCS) accessed under the license agreement and used for all analyses and production of the thesis in Niassa (Manjate et al., 2023),

Figure 5. Procedure for collaring an elephant in the Niassa Special Reserve area, northern Mozambique (WCS, 2018).

The 2019–2020 data consisted of 45 elephants (35 females and 10 males) equipped with GPS satellite transmitters placed from October to November 2018 (Kock, 2018). The GPS devices were assembled by African Wildlife Tracking – AWT (South Africa, Pretoria) and Vetronics (Germany, Berlin). The models were programmed to begin obtaining locations every hour from 01-01-2019 at 02:00:00 local time (Central Africa Time – CAT), with an expected battery life of approximately two years (Kock, 2018). Twenty of the 45 elephants were tracked for 676 days (range = 133–704 days), or 601 days on average (s.d. = 147.2 days). While twenty-five of the forty-five animals were tracked for 676 days, one adult female was tracked for only 133 days. On the other hand, two females were tracked for 704 days.

The database lacks previous information on the composition of the elephant group in the area. Therefore, this aspect was crucial to determine whether more than one tracked elephant belonged to the same group. A proximity analysis was performed between all "dyads" with home range overlaps greater than 90%. To do this, the original one-hour location dataset was first resampled to a one-day interval using the crawlWrap function of the momentuHMM package (McClintock & Michelot, 2018). Using the resampled dataset, we estimated home ranges with fixed kernels (kernelHR95%), and calculated the overlap between all dyads using the probability of home range overlap (PHRindex) method. This model calculates the probability of encountering a given animal in the other animal's home range and was one of the methods recommended by Fieberg and Kochanny (2005). Then, we used the original one-hour interval dataset to estimate the proximity between the two elephants in each dyad with PHR ≥ 50%. The two elephants were considered to belong to the same group if they were ≥ 88% of the time at locations ≤ 400 meters apart. Elephants in the same group and those without a full year of data, or those with a full year of data but with interruptions in monitoring during the period, were excluded from the analyses. By applying the criterion of analyzing the movements of one elephant per group, a sample was obtained that represents the dynamics of several herbivore groups that could impact the landscape (Coverdale et al., 2016). After applying these criteria, the final dataset in Niassa consisted of 32 elephants (25 females and 25 males). GLMM statistical analysis was applied in R, with a t-test for heterogeneous variance: $t = -0.48819$, $df = 25.175$, $p = 0.6296$; mean number of days monitored: F = 661.88 ± 50.71, M = 668.143 ± 20.8). Results showed no difference between males and females in the number of days monitored.

Spatial Analysis

Three methods were used to estimate the space utilization of Niassa elephants. Home ranges were estimated using the more conservative 95% Brownian Bridge Motion Model (95% fixed kernel HR). For comparison with other studies, the utilization distribution (UD) was also estimated using BBMM. While fixed kernels used individual location to estimate HRs, BBMM used movement paths that resolve temporal autocorrelation to estimate UDs (Kranstauber et al. 2012). Therefore, BBMM assumed that the animal moves randomly and diffusely. The 95% fixed kernel HR was also used to establish the relationship between seasonality and the effect of sex on home range size. To classify elephants as migratory or non-migratory, two procedures were used: the "Seasonal Overlap Home Ranges" (PHR index) (Cagnacci et al., 2016) and the "Net Square Displacement" (NSD) (Bunnefeld et al., 2011; Manjate et al., 2023).

Some previous studies report that elephant movements in Sub-Saharan Africa show convergent results, with movements occurring during the rainy season (e.g., Bohrer et al., 2014; Purdon et al., 2018). Based on these studies and characteristics, the study in Niassa (Manjate et al., 2023) compared the 50% HR of the three wettest months (January to March) with the 50% HR of the driest months (July to September). Therefore, the criterion to be considered migratory was that there should be a spatial separation between the seasonal HR50% (first seasonal interval and second seasonal interval), but a high degree of overlap between the HR50% of the same session (first seasonal interval and third seasonal interval) (Cagnacci et al., 2016; Purdon et al., 2018).

The probability of HR overlap index (PHR index), which estimates the probability of animal j being found within the home ranges of animal i (Fieberg and Kochanny 2005), was used to estimate the 50% overlap between seasonal home ranges. To be considered migratory by this criterion, an elephant had to have a PHR between its first and second 50% HR of BA ≤ 0.15 (Table S3), and a PHR between its first and third seasonal 50% HR of BA ≥ 0.5 (Table S3) (Cagnacci et al., 2016; Purdon et al., 2018; Manjate et al., 2023). Seasonal and sex differences in 95% HR were tested with a generalized linear mixed-effects model (GLMM) because seasonal HRs were estimated for the same set of individuals and were not independent (Zuur et al., 2009).

To run the model, the response (95% HR) was standardized and centered to the fixed-effect predictors (season and sex). We included individuals as a random effect to address pseudo-replication while incorporating individual variability in the size of HR into the model estimates. The HRs and UDs were estimated using the kernelHR95% and BBMMUD95% functions from the adehabitatHR library (Calenge & Fortmann-Roe, 2023). The Bhattacharyya affinity index was estimated using the kernaloverlaphr function (href = smoothing factor) from the adehabitat library (Calenge et al., 2006). The NSD was estimated using the ltraj function from the same adehabitat (Output R2n). The GLMM was implemented using the lmer function from the lme4 package (Bates et al., 2015) for all statistical analyses that were performed in the R environment (R Core Team 2023).

Prospective Review

This study is of great importance in modeling the movement ecology of African elephants. Applying current ecological indices to spatial analysis models adds value to our understanding of individual movement patterns of African elephants in one of the most important terrestrial systems for biodiversity. Furthermore, conducting ecological analyses of elephants using technologically advanced data collected from newly available remote sensing is timely in African elephant movement studies, as it places this specific area in the regional and international arena (Bartlam-Brooks et al., 2013; Bohrer et al., 2014; Dodge, 2014). Therefore, ecological analysis models are very recent and are indicative of the individual patterns of space use by African elephants in the region (Seigle-Ferrand et al., 2021; Goodheart et al., 2022). Major international conservation agencies, such as WWF and WCS, support the research because it contributes to biodiversity conservation in the region, both specifically and internationally. The study reduces the knowledge gap on the subject in this area. Consequently, the knowledge generated by answering this question is crucial for decision-making regarding the conservation of this charismatic species, which is increasingly threatened by habitat loss and population declines due to poaching, and for preventing escalating elephant mortality in the region. Therefore, it will constitute a science-based contribution to enrich the implementation of the evidence-based management plan for African elephant management and biodiversity. The study focuses on avoiding economic losses due to elephant depredation and preventing human activities from exacerbating human-elephant conflict (and becoming a growing socioeconomic and political problem), while also supporting existing plans in the development region and management blocks surrounding the Reserve with sustainable ecotourism focused on elephant observation and improving the protection of elephant movement corridors in the Niassa region. Thus, this study aims to provide a structured and objective response to the movement ecology of African elephants in Niassa, northeastern Mozambique, in the southern region of sub-Saharan Africa.

DISCUSSION AND CONCLUSIONS

According to the content presented in the literature review, it can be stated that movement ecology is a scientific tool...whose analysis models allow capturing biotic and abiotic factors of organisms, for example, as advocated by Odum and Barrett, (2007). The basis of population dynamics is the strategic evolutionary behavior of adaptation whose chance of survival is high by ad opting economically viable movements, increasing reproductive chances. For example, males, in energy conservation, reduce movements for females, always defending high-quality refuge habitat sites with sufficient resources for reproductive success (Sutherlands, 1996; Krebs, 1994; Odum and Barrett, 2007; Krebs and Davies, 1996). Therefore, the content reviewed in this work suggests that the "Allee and Refuge Theory" study in Niassa is more enlightening. The assumption is that African elephants move in aggregates in social groups to overcome differences between locations or landscapes (due to habitat loss) and seasonal climate variation, in abiotic terms. Clans appear to group together to maximize the reproductive process, social attractiveness, and increase the overlap of females and males. Both proceed as a group, aiming to increase individual advantages in terms of food and space used for the benefit of the group. As well as the refuge theory, also previously defended by Sutherland (1997), it appears that the spatial aggregation of the African elephant likely allows for improved population establishment in locations declined by illegal hunting. According to Thouless et al. (2017), illegal ivory hunting, habitat loss, and retaliatory killing cause high mortality of African elephants. And they also look for suitable habitats associated with the refuge, and some individuals tend to isolate themselves to increase their chances of survival.

According to Grossmann et al. (2014); Booth and Dunham (2014), the mortality rate of African elephant populations in Niassa is estimated at 3,183 (1,340 recent carcasses and 1,843 old carcasses). New counts are needed as a reference model to describe trends in the impact of poaching on populations, given the high human-caused mortality rate of elephants in the region (Benitez et al., 2022). Regarding the movements of elephants in the studied region and as a reference for this review, it is noted that elephant abundance is partially associated with productivity and water availability, while illegal hunting is one of the main drivers of the population decline of this iconic animal (Robson et al., 2017).

These factors, including anthropogenic actions, are general determinants of animal decisions and population dynamics. It is not surprising that they determine the spatial distribution of African savanna elephants on a large scale (De Boer et al., 2013). To understand different aspects of their spatial ecology, due to their long movements and inhospitable habitats, spatial analysis has shown that the size of the home range during movement is influenced by precipitation, productivity, water availability, and human impacts. These patterns are supported by the study by Benitez et al., 2022; Seigle Ferrant et al., 2021; Loarie et al., 2009), and patterns found by Manjate et al., (2023). The presence of agricultural and livestock activities appears to have a high potential to isolate disjunct populations (Benitez et al., 2022; Huang et al., 2022). Landscape configuration, combined with the level of anthropization, likely plays a critical role in determining the fate of African elephants, and likely has effects that influence the structure and dynamics of populations, communities, and ecosystems. Thus, human actions can have a direct effect, altering the animals' movement patterns (e.g., Gara et al., 2021; Bohrer et al., 2014; Loarie et al., 2009; Nathan et al., 2008; de Leeuw et al., 2001).

According to Benitez et al. (2022), telemetry data analysis aims to understand home ranges; how animals use these areas; and aspects of interactions that contribute to the conservation of this species, which is increasingly vulnerable due to habitat loss and requires space for movement. Understanding the complexity of individual home range use marks a new era and is crucial for African elephant conservation planning in general.

In the spatial analysis, the methods used to estimate space utilization by Niassa elephants were fundamental to estimating home ranges using the more conservative 95% Brownian Bridge Motion Model (95% fixed kernel HR). For comparison with other studies, the utilization distribution (UD) was also estimated using BBMM. While fixed kernels were used for individual location to estimate HRs, BBMM used movement paths that resolve temporal autocorrelation to estimate UDs (Kranstauber et al. 2012). Therefore, BBMM assumes that the animal moves randomly and diffusely. The fixed kernel HR95% was also used to establish the relationship between seasonality and the effect of sex on home range size. To classify elephants as migratory or non-migratory, two procedures were used: “Seasonal Overlap home ranges” (PHR index) (Cagnacci et al., 2016) and “Netsquared displacement” (NSD) (Bunnefeld et al., 2011; Manjate et al., 2023). Therefore, it has proven to be of great importance in modeling the movement ecology of African elephants. Applying current ecological indices to spatial analysis models adds value to our understanding of individual movement patterns of African elephants in one of the most important terrestrial systems for biodiversity. Furthermore, conducting ecological analyses of elephants using technologically advanced data collected from newly available remote sensing is timely in African elephant movement studies, as it places this specific area in the regional and international arena (Bartlam-Brooks et al., 2013; Bohrer et al., 2014; Dodge, 2014).

FINAL CONSIDERATIONS OF THE REVIEW

Movement Ecology

We realize that African elephant movement and the precursors measured here are important because they impact and shape wildlife dynamics, both in Miombo savanna vegetation and in the hierarchical dynamics of other species, gene flow, and metapopulation dynamics of animal and plant dispersal. Therefore, they constitute a large part of movement ecology studies (Joo et al., 2022). Except for the effect of sex, it is not significant. However, biologically, it is impactful from a management perspective. On the other hand, the buffer zone is described as granted to tourism where the removal of adult males is permitted (e.g., Grossman et al., 2014), so the male population likely affects the modeling. In this context and work, classical telemetry data, where estimators assume that movement data are independent and uniformly distributed (Joo et al., 2022), become important for wildlife management models, allowing them to apply an analysis model that addresses the challenges of autocorrelated data, overcoming the assumptions of contradiction (Fleming et al., 2015).

Results and conclusions can be contradictory in automation and ecological analysis during the preliminary analysis phase, which can be resolved by using an appropriate model to estimate DUs (e.g., BBMM, which handles autocorrelated data). For Conservation, we made better use of existing data, as well as greater use of expert knowledge (WCS key informant). For example, model parameter values and their uncertainty approaches were informed by expert knowledge gathered from conservation professionals at REN (Martin et al., 2012).

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In terms of drivers, the spaces used in the REN were influenced by water and temperature. Thus, water availability in the large rivers within the Reserve's boundaries conditions centralized movement in large, overlapping groups within the REN and surrounding areas. Our results demonstrated the intrinsic connection between environmental factors, such as water resources and availability, season, and animal movement, with partial migration (Purdon et al., 2018), confirmed in our results. This may also be associated with habitat loss caused by climatic and anthropogenic effects.

Does birth rate matter?

This ecological element should be included in the analysis. However, it is important because it is a factor that has a huge influence on wildlife movement, and the Reserve has sufficient data for future research. The implementation process showed that the population did not remain static, and most females were in good health and lactating (Kock, 2018). New groups emerged and determined the movement pattern (e.g., Purdon et al., 2018). So much so that the prediction of finding animals of both sexes combined was quantified (Kock, 2018). Therefore, the hypothesis is that weather variations could implicitly determine the activities of both sexes.

Does mortality matter?

Other factors that should be quantified, such as poaching, may have influenced these populations, a hypothesis that requires investigation, as these populations are not at their peak. The populations have declined, however, and it is important to consider senescence factors combined with biannual count data and carcass information in the region to fully explain mortality (e.g., Grossman et al., 2014).

Conservation

Effective elephant conservation requires a system that includes predictive information reviewed here to elucidate how to respond to environmental changes and how such responses can be implemented through effective conservation interventions (e.g., Cartwright et al., 2016). Environmental changes can create new environmental conditions; For example, climate change generates new extremes in temperature and precipitation patterns, while social or anthropogenic issues (e.g., infrastructure, fire, and shifting agriculture) have created new population groups and interactions between animals, requiring measurement of their effects. In the case of Niassa, many approaches and intervention forecasts are based on observed relationships between a biological property of conservation interest (e.g., the location of elephants competing with the action of forest rangers (WCS information). However, such relationships are typically measured for immediate practical actions. Thus, once immediate action is completed, the demands on ecological systems remain incipient because they are unpredictable and long-term (e.g., Stillman et al., 2015a).

Conservation decisions based on adaptive behavior are not guaranteed to change even if the simulated environment changes, because they are more likely to maintain their predictive power as environmental conditions change (e.g., Sutherland and Norris, 2002; Stillman et al., 2015a). This basis for prediction allows such models to produce accurate, robust predictions outside the range of environmental conditions for which they were parameterized (Stillman et al., 2015b).

Classical conservation predictive models need to be enhanced with current computational models found in NSR managers should be unafraid to release sensitive data for scientific use (Stillman et al., 2015b; Cartwright et al., 2016). Data limitations prevent the development of predictive models in conservation, as such models require relatively large amounts of testing data.

Impacts and Recommendations

In conclusion, the dataset contributes to identifying ecological elements to improve African elephant conservation in the sub-Saharan region and to address conservation issues related to NSR. A specific fund should be allocated to NSR to discuss, review, and implement policies regarding NSR resizing limits, as well as to nurture future generations of young people in conservation concepts and actions (i.e., empowerment) of communities, as they may be at the forefront of any development events and have an important voice that should be heard regarding elephant conservation in Mozambique. Therefore, this topic reviews further research stands out in this valuable merit of serving as a bridge between different stakeholders involved in elephant conservation and conflict resolution, in environmental policy and scientific and economic development.

However, there is a significant challenge posed by hunting tourism in the buffer zone and anthropization that requires a thorough understanding. It is recommended to study these groups so that multiple stakeholders are involved in sustainable conservation.

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