Conservation and management of lions in Kenya: an assessment of factors influencing Panthera leo melanochaita (Hamilton Smith, 1842) population dynamics

Chege, M.M.

1

Introduction

Africa is endowed with rich biodiversity and is home to one of the last remaining large carnivore fauna including lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*) (Bodasing, 2022). As apex predators, large carnivores play a critical role in ecosystem health and may contribute to people's livelihoods through tourism and ecosystem benefits (O'Bryan et al., 2018). However, large carnivore populations are declining rapidly and several species are locally extinct or predicted to soon be extirpated outside protected areas (PAs) (Packer et al., 2013). For instance, African lions are classified on the global IUCN Red List of threatened species as 'Vulnerable' due to dwindling populations (Bauer, et al., 2016). Their geographic range has dramatically declined in the last half century with 83% of lion range reportedly lost in the Congo basin, 90% in west-central and ~50% in the eastern and southern African regions (Bauer et al., 2015; Loveridge et al., 2022). The decline has been attributed to threats such as loss of habitat due to land use change, conflicts with humans as a result of livestock depredation, climate change and disease (Bauer et al., 2015; Nicholson et al., 2023; Ripple et al., 2014; Riggio et al, 2013). Habitat fragmentation in Africa has reduced connectivity between lion habitats resulting in small, isolated and less permeable habitat patches (Loveridge et al., 2022). Thus, to conserve the remaining habitats, PAs have been established and it has been proposed that long-term conservation of lions is pegged on fenced PAs that have adequate management budgets (Packer et al., 2013; Bauer et al., 2015; Lindsey et al., 2017, 2018).

Fencing of PAs has however been contested as it adversely affects movement, genetic connectivity and long-term viability of animal populations (Cushman et al., 2016; Durant et al., 2015; Frankham et al., 2019; Newmark, 2008; Woodroffe et al., 2014). Fencing may further increase the risk of extinction and reduce resilience in the face of climate change, especially for populations inhabiting arid ecosystems, where mobility is essential to access temporarily variable and spatially heterogeneous resources (Durant et al., 2015; Hoffmann & Sgro, 2011; Woodroffe et al., 2014). It is therefore imperative that management of lion populations is proactive to keep track of changes in resources. Furthermore, as human activities continue to intensify and encroach into wildlife habitats, PA boundaries, especially unfenced ones, are increasingly becoming conflict hotspots due to 'edge effects' (Loveridge et al., 2010; Woodroffe & Ginsberg, 1998). These conflict situations represent a major source of mortality for lions and may lead to local extinctions (Frank et al., 2006; Woodroffe & Ginsberg, 1998). Edge effects are more pronounced in small PAs, that may be disproportionately affected due to their limited size and higher boundary-to-core ratio (Woodroffe & Ginsberg, 1998). It is therefore critical that dispersal areas and corridors are maintained to ensure population viability and genetic diversity (Björklund, 2003; Pinto et al., 2023). Hence, establishing systems such as community-based conservancies, that create 'corridors of tolerance' are vital for facilitating connectivity through non-PAs (Dolrenry et al., 2014, 2020). These so-called landscape approaches, that allow for the creation of conservancies adjacent to PAs, combined with effective land use policies are crucial for the long term conservation of lions (Blackburn et al., 2016; Massey et al., 2014).

In Kenya, lions are distributed across government- run (national parks and reserves), group ranches, community and private conservation areas (Figure 1) (Elliot et al., 2021; Kenya Wildlife Service, 2020). The country is home to two of Africa's last lion strongholds (Riggio et al., 2013) and hosts a population of about 2,400 lions (Kenya Wildlife Service, 2020). Like the rest of Africa, the lion population in Kenya is declining due to human-lion conflicts, loss of wild prey, disease, habitat loss and fragmentation (Kenya Wildlife Service, 2016, 2020). Over the past few decades, the country has intensified infrastructural development both within and outside PAs driving the conversion of natural habitats and reducing connectivity between lion habitats and increasing the prevalence of lions killed by road and rail collisions (Kenya Wildlife Service, 2020). Currently, the lion population is characterised by a fragmented distribution with the largest populations being in the Maasai Mara national reserve, Tsavo national park (NP), the Laikipia conservation area, and Amboseli NP (Kenya Wildlife Service, 2020). Conflicts with humans account for most of the adult lion mortality in the country and populations outside PAs are diminishing at an alarming rate (Frank et al., 2010). Nationally, the lion population is considered threatened, prompting several strategic policy frameworks i.e., Wildlife Conservation and Management Act (WCMA), 2013 and the National Wildlife Strategy, 2030 to call for an ecosystem-based approach to conservation practice and policy. This approach is centred on restoring and maintaining viable lion populations and their wild prey, while minimising conflict and maximising benefits to communities. The Kenya Wildlife Service (KWS), a government institution with a mandate to conserve and protect all wildlife in Kenya, aside from promoting the establishment of community run conservancies (Ministry of Tourism and Wildlife, 2018), has over the years employed fencing and translocation of 'problem lions' among other conflict mitigation methods (Kenya Wildlife Service, 2018). However, while translocations aimed at resolving human lion conflicts have generally been reported to fail (Linnell et al., 1997; Morapedi et al., 2021), successful cases have also been reported (Briers-Louw et al., 2019; Thomas et al., 2023). In Kenya, the impacts of fencing and translocation on the genetic diversity of lions have not been assessed to date.

Additionally, in the last five decades, Kenya has experienced a sharp decline in wild herbivore populations both inside and outside PAs (Western et al., 2009), as a result of climate change, human wildlife conflicts, government land policies that have discouraged pastoralism and encouraged sedentarisation and diversification of livelihood options resulting in habitat degradation, fragmentation and loss (Bedelian & Ogutu, 2017; Ogutu et al., 2016). Also frequent droughts, driven by climate change, combined with livestock overstocking, have increased the frequency of livestock incursions into wildlife areas, leading to increased resource competition and habitat degradation (Ogutu et al., 2016; Waweru et al., 2021). Ogutu et al. (2016) attribute a ~68% decline in wild herbivore species between 1977 and 2016 to climate variability, among ther factors. These impacts continue to reduce the habitat for lions and heighten conflict between lions and people (Kenya Wildlife Service, 2020). Tuqa et al. (2014), in Amboseli NP, reported an increase in human lion conflicts, a decrease in the lion population, and changes in their social behaviour and diet after a severe drought period. Therefore, given the significant impacts of climate variability, it is crucial to prioritise studies that explore these effects. Moreover, because Kenya consists of a diverse range of ecological regions that are influenced by the distribution of rainfall (Obiero & Onyando, 2013), local conditions are bound to influence lion populations in varied ways. It is therefore imperative to look at factors that may lead to variation in natural resources and relate them to specific areas to inform lion conservation and management strategies. Therefore, this study examines the influence of management strategies, ecological and anthropogenic factors on lion population dynamics, i.e., their genetic diversity, grouping patterns, home range size and movement patterns in protected areas across Kenya. To ensure that management strategies are adaptive, it is essential to have proper monitoring systems that keep track of wildlife and ecosystem changes (Nichols & Williams, 2006). Therefore this study also explored how this can be carried out in the face of rapidly changing ecosystems and dwindling conservation funding through the application of Spatially Explicit Capture-Recapture (SECR) methods.

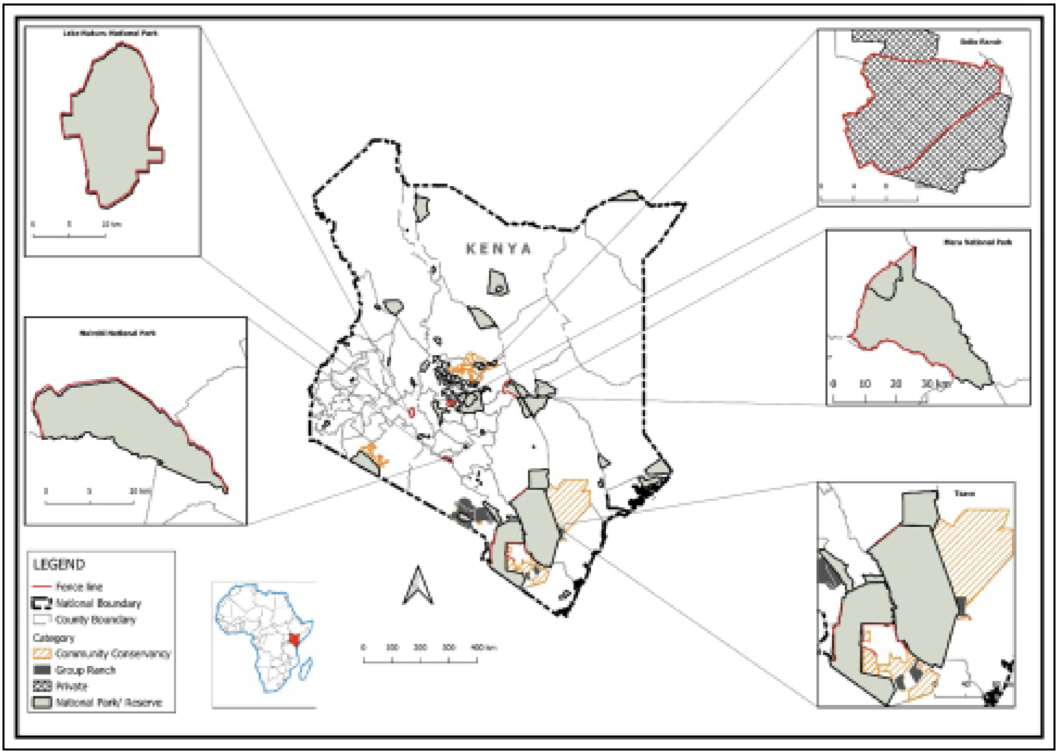

Figure 1. Map showing the study areas covered in this thesis. The excerpts show the fenced areas.

1.1 Lion genetic diversity

Recent molecular studies on lion populations have revealed two distinct subspecies of lions i.e., *Panthera leo leo* found in Asia, west and central Africa and *P. leo melanochaita* in east and south Africa (Bertola et al., 2011, 2015, 2016, 2022; Dubach et al., 2013). These have formally been adopted by the IUCN (Kitchener et al., 2017). Additionally, analyses of mitochondrial DNA have revealed six geographically distinct genetic clades in west, central, north east, east southern, south west Africa and India (Bertola et al., 2016). This differentiation is thought to have occurred during the late Pleistocene epoch as a result of natural geographical barriers and climatic fluctuations that led to shifts in vegetation distribution, which then formed temporary barriers for connectivity (Bertola et al., 2016). Further, habitat fragmentation caused by anthropogenic activities also resulted in geographic isolation of lion populations (Barnett et al., 2014; Bertola et al., 2016; Creel et al., 2019; Curry et al., 2020). For the lion, it is vital that large and connected populations are maintained through a system of core areas, linked by wildlife corridors that ensure habitat connectivity and gene flow (Björklund, 2003; Riggio et al., 2013). It is therefore essential that management actions for lion conservation take into account both the genetic diversity within lion populations as well as the connectivity between populations (Barnett et al., 2006; Dubach et al., 2013). Several studies have demonstrated that a species ability to adapt, survive and thrive is related to the level of genetic diversity and the loss of genetic diversity can be detrimental to long-term species survival (Packer et al., 1991; Pimm et al., 2006; Reed & Frankham, 2003). Thus, genetic variation data is paramount to the long-term conservation of lions (Frankham, 2005; Reed & Frankham, 2003).

In Kenya, land use changes resulting in loss and fragmentation of habitats that substantially reduce connectivity between lion habitats have led to two challenges: 1) managers must find solutions to reduce human-lion conflicts on the long term, e.g. by translocating lions which repeatedly attack livestock or fencing to separate wildlife from people and livestock, 2) managers must ensure that the remaining lion populations are connected, to avoid typical problems associated with small and isolated populations, such as inbreeding. However, although fencing plays a significant role in reducing conflict, it also increases isolation, as connectivity between populations may be reduced and/or terminated, thereby increasing the risk of inbreeding depression (Björklund, 2003; Creel et al., 2013; Trinkel et al., 2010). As well, translocation of 'problem' lions from their native territory to other areas in Kenya, has been used for several decades as a conflict mitigation tool, without taking into consideration the genetic properties of the translocated individuals or the target population release site and therefore may influence natural distribution patterns of lion diversity (Chege, Sewalt, et al., 2024). It may result in admixture of different genetic lineages, which is less desirable from the conservation point of view, as it may reduce resilience and adaptability to a particular environment (Bertola, Miller, et al., 2022), and ultimately lead to homogenization and loss of genetic diversity on a larger scale. This suggests that lion conservation can only be effectively tackled when genetic information is taken into account. Understanding the impact of translocation is important especially given that Bertola (2015) found indications of genetic divergence between the southern and northern Kenya populations (see also Armstrong et al., 2025).

Since the genetic makeup of the Kenyan lion population has not been studied in detail, there is need to establish a genetic baseline database for Kenyan lions that can be included into translocation efforts so as to avoid disrupting local adaptations and maintain genetic diversity. As several lion populations in Kenya are increasingly becoming isolated, and escalating conflicts are prompting frequent translocation events, it is expected that translocations will become an increasingly important conservation intervention. Therefore this study aimed to create a genetic baseline for lion populations in Kenya and to investigate population structure, differentiation between and genetic diversity within populations.

1.2 Social structure and group size

Lion behaviour is defined by a complex social system and vast home ranges than can span hundreds of kilometres (Funston, 2011; Snyman et al., 2018: Schaller, 1972). They live in family groups called prides that can consist of 2-18 adult females, their dependent offspring, together with male coalitions that are unrelated to the females and only transiently associated with the pride. A lion group is defined as lions observed together at a certain time and place (Schaller, 1972). Prides are characterised by fission-fusion dynamics and individuals are typically found in a range of sub-units referred to as groups, which may fragment further into smaller sub-groups depending on intrinsic or extrinsic factors (Caraco & Wolf, 1975; Mosser & Packer, 2009). Lion groups are constantly formed and altered, and pride members are infrequently together (Mosser & Packer, 2009; Packer et al., 2001). Benefits such as cooperative hunting (Stander, 1992), mutual defence of kills from spotted hyenas (Packer & Ruttan, 1988), and cooperative defence of territory and young (Packer et al., 1990) are some of the factors that influence grouping patterns. For instance, in Okavango Delta, Botswana the subgroup size of adult females was influenced by the number of cubs or the number of rival prides present (Kotze et al., 2018). Larger groups are formed to protect cubs and to have numerical advantage over rival prides, as larger groups can gain and maintain access to highest quality habitats with more prey (Mosser & Packer, 2009). For example, in Serengeti NP, Tanzania, territorial competition directly affects female fitness, with prides containing 3-6 resident females achieving the greatest per capita reproductive success (Packer et al., 1990; VanderWaal et al., 2009). The same is the case for males, the probability of nomadic male coalitions acquiring residency increases with age and coalition size, with larger coalitions having greater reproductive success (Borrego et al., 2018).

Several hypotheses have been proposed to explain the evolution of group living in lions, for example the resource dispersion hypothesis (RDH) that links theories of landscape ecology and animal behaviour (Carr & Macdonald, 1986; Valeix et al., 2012). RDH predicts that group size will increase as habitat patch richness increases i.e., prey, shelter and water (Mbizah et al., 2019; Valeix et al., 2012). Under optimal conditions i.e., resource rich areas, lions will form large groups (Carr & Macdonald, 1986; Donkin, 2000) and in areas with less resources, lions will form small groups (Dolrenry, 2013; Loveridge et al., 2010). Trinkel et al., (2007) in Hluhluwe-Umfolozi Park, South Africa, found that large lion groups occurred in open woodlands and small groups in dense forest, this was attributed to the densely vegetated area providing cover for ambush hunting and for concealment of cubs. This is because in the densely vegetated habitat there was less inter-group competition and higher hunting success, thus lions were not driven to form large groups. As well, areas close to water sources provide denser vegetation that shelters cubs and attracts water dependent herbivores (De Boer et al., 2010; Hopcraft et al., 2005; Snyman et al., 2018), factors that are associated with larger lion group sizes. Lion grouping patterns are also influenced by the availability and body mass of prey species, with larger lion groups being formed when prey is abundant and of large body mass, while smaller lion groups are formed when prey is scarce and of smaller body mass (Bauer et al., 2008; Van Orsdol et al., 1985). Bauer et al (2008) suggested that lion group size in West Africa was generally small due to low prey densities and low body mass of prey. Also in Kenya the decline in prey populations during droughts has been shown to influence lion sociality where lion group sizes reduced from an average of 3.5 to 1.35 in Amboseli NP, Kenya (Tuqa et al., 2014).

Anthropogenic activities also influence lion grouping patterns. In areas where lions live either on or in close proximity to communities, they suffer from persecution due to livestock depredation (Dolrenry, 2013; Harcourt et al., 2001). In these areas, lions form smaller social groups to avoid detection by humans (Bauer et al., 2003; Dolrenry, 2013). Social systems can influence population responses to environmental changes and ultimately shape population trends over time (Packer et al., 2005). This can in turn also have an influence on lion genetic diversity. Therefore, understanding how lions adapt their social organization to local conditions is crucial to any conservation planning process. Recognizing the social processes underpinning demography and behaviour provides key information required to enhance the success of wildlife management (Goldenberg et al., 2019). An investigation into changes in lion group size in response to ecological and anthropogenic conditions can provide insight into how local conditions are impacting lion populations and therefore may inform their management. This study covered eight sites in Kenya known to host resident lion populations with the aim of assessing the impact of type of management, ecological and anthropogenic factors on lion grouping patterns.

1.3 Lion home range size and movement

A home range is the area that an animal uses to secure resources for reproduction and survival (Burt, 1943) and is a reflection of its interaction with the environment (Nams et al., 2023). Therefore understanding how animals utilise their habitat can provide ecological insights valuable for conservation efforts (Broekman et al., 2022). This is especially true for arid and semi-arid ecosystems that are characterised by variable precipitation and thus seasonal fluctuations in availability of resources i.e., water and forage (Chesson et al., 2004). In these ecosystems, wild ungulates often migrate to areas with nutrient-rich and abundant forage, leading to dynamic shifts in resource distribution, requiring predators to adapt to the spatial and temporal variations in prey availability (Chesson et al., 2004; Hopcraft et al., 2010). This pattern is consistent with RDH which suggests that carnivores will increase their home range and movement as resources become more dispersed (Macdonald, 1983). For example, in Maasai Mara, Kenya, Broekhuis et al. (2021) observed that cheetahs exhibited larger movements during large herbivore migrations. Similarly, Laizer et al. (2014) observed that lions in Tarangire

NP, Tanzania had larger home ranges and covered larger distances during the wet season due to migration of prey species. Herbivore migratory movements are pivotal in shaping ecological dynamics by optimising the use of resources (Maher et al., 2023), buffering against negative effects of habitat/climate change (Jeltsch et al., 2013), and enhancing gene flow (Vergara et al., 2017). However, these movements are susceptible to habitat loss and fragmentation and often lead to conflicts as a result of competition with domestic livestock for pasture and depredation of livestock by carnivores when they follow wild herbivores out of PAs (Bauer et al., 2015; Maher et al., 2023). To reduce conflicts, fencing has been used to confine wildlife, however, fences impede movement, block migratory routes and often lead to isolation of populations (Newmark, 2008). While, migratory areas outside PAs in the country may experience conflicts, a majority of PAs are not fully fenced because they do not encompass whole ecosystems making migratory areas central for the survival of wildlife (Ottichilo et al., 2001). Thus, active monitoring programs that will aid in understanding the impact of rainfall variability on large carnivore movement are essential to inform their management.

Lion home ranges are known to change in size according to resource availability, a phenomenon influenced by variability of rainfall (Chege et al., 2025; Tuqa et al., 2014). Prey density and availability of water are considered to be the most important factors determining lion home range size and movement (Carr & Macdonald, 1986; Hopcraft et al., 2010; Nams et al, 2023.). In Amboseli NP, Kenya, Tuqa et al. (2014), found that lion home range and movement patterns were centred on perennial water sources and areas of high prey density. Similarly, in Waza NP, Cameroon, lions increased their home range and movement during the wet season and ventured outside the park in search of prey, while in the dry season they stayed within park boundaries (Tumenta et al., 2013). While Lesilau et al. (2021) found no difference between wet and dry season lion home range size in Nairobi NP, Kenya, they found seasonal variation in lion movements. All three studies suggested that when lions increased their movement, it correlated with an increase in human-lion conflicts during the wet seasons as lions ventured out of PAs and into community lands and depredated on livestock. Patterson et al. (2004) documented a direct association between livestock attacks on ranches outside Tsavo NP, Kenya, and rain events. With Kenya experiencing an increase in extreme weather conditions, characterised by unpredictable rainfall patterns and rising temperatures (Palmer et al., 2023), new challenges are expected to emerge for lion conservation. As extreme weather events such as drought and floods have an impact on prey availability and lion ranging patterns (Bhalla, 2017; Kotze et al., 2018; Tuqa et al., 2014). Further, ecological conditions such as rainfall influence cub survival, making this an important aspect for any population monitoring program (Funston, 2011).

Lions exhibit distinct inter-sexual ranging patterns, with males typically occupying larger home ranges and covering greater distances than females. This is because male ranging behaviour is mostly configured around the distribution of females, while females tend to maintain smaller home ranges influenced by the distribution of resources (Loveridge et al., 2009). This behaviour may imply that males are a higher risk of mortality as a result of conflict, especially for populations that live either close to or inside non-protected areas (Funston, 2011). Lions living in human dominated landscapes tend to have larger home ranges and movements particularly when such areas have low prey densities or limited water availability (Dolrenry, 2013). These lions also are at a higher risk of mortality as a result of conflict (Loveridge et al., 2010). To reduce conflict, fences have been constructed, however, fences influence lion home range size and movement (Lesilau et al,2021; Chege et al., 2025; Naha et al., 2023; Turner et al., 2022). This could potentially lead to broad scale modifications of community structure and ecosystem dynamics (Cozzi et al., 2013). Therefore, this study looked at the influence of rainfall of lion home range and movement in three national parks in Kenya that are characterised by different weather conditions, varying levels of fencing and anthropogenic pressures to determine space use and to provide site –specific recommendations for management of lion populations.

1.4 Monitoring and management of lions using spatial capture-recapture

Effective conservation and management of wildlife relies on robust estimates of key population parameters such as density and abundance (Buxton et al., 2021; Keiter et al., 2017). These parameters provide crucial insights into the dynamics of species and their ecosystems and are essential for the evaluation of past, current interventions and for informing future conservation actions (Buxton et al., 2021). Globally, several governments adhere to international and national frameworks that emphasize the need for systematic monitoring of wildlife status and trends (Tittensor et al., 2014). In Kenya, the National Recovery and Action Plan for lions (2020–2030) calls for regular population monitoring to assess trends and distribution so as to inform management interventions (Kenya Wildlife Service, 2020). As well, at the conclusion of most research studies is a call for regular long-term monitoring or further research so that the resulting recommendations and management actions can be evaluated. However, accurately estimating population size and density is often hindered by the substantial resource requirements and the logistical challenges involved, particularly for large carnivores, such as lions, that occur at low densities, are cryptic and have varying detection probabilities (Elliot et al., 2020; Gavin & Delahay, 2001). Moreover, lions being wide-ranging species, local conditions can significantly influence their local population densities, leading to variations in population density across different areas depending on specific environmental factors present within an ecosystem (Jacquier et al., 2021). This is because ecosystems are dynamic and prone to site-specific impacts of anthropogenic activities and seasonal variations that influence species abundance, distribution and movement patterns (Chege, Bertola, et al., 2024; Pettorelli et al., 2014).

Lions inhabiting ecosystems characterised by wild prey migrations have been reported to adjust their densities and space use in order to adapt to seasonal fluctuations in resource availability (Loveridge et al., 2009). In such ecosystems conservation and management of lions relies on monitoring programs that can provide accurate data on population status, trends and distribution (Braczkowski et al., 2020). Monitoring is particularly critical for areas where conflicts arise as a result of these seasonal movements. Over the years, a variety of approaches have been employed in Kenya to establish population status, including call-in surveys (Ogutu & Dublin, 1998), track/spoor surveys (Henschel et al., 2020), and total counts (Lesilau, 2019) among others. However, these approaches have been criticised because they violate population closure assumptions and do not account for variability and biases in detection probability, which may lead to inaccurate estimates with high uncertainty (Gopalaswamy et al., 2015; Elliot & Gopalaswamy, 2017). Additionally, estimates with large confidence intervals do not allow for assessment of lion population trends over time, which can negatively affect conservation planning (Braczkowski et al., 2020; Gopalaswamy et al., 2022). With most PAs being under funded (Lindsey et al., 2018), there is need to develop rigorous, appropriately scaled and cost-effective options for long-term monitoring of lion populations (Gopalaswamy et al., 2022). This calls for the use of robust frameworks such as spatially-explicit capture-recapture (SECR) models that simultaneously estimate abundance, density and space use. These hierarchical models distinguish between the observation process (manner in which individuals are detected) and the state process (density and distribution), while accounting for imperfect detection (Royle et al., 2013). SECR models are reliant on being able to identify individuals and can integrate multiple monitoring methods within the same modelling framework, making SECR models a flexible and versatile tool for effective monitoring across different habitats (Gopalaswamy et al., 2012). The models produce accurate estimates with high precision enabling future surveys to estimate population trends, rates of survival, recruitment and movement (Tourani, 2022). Therefore, SECR methods have the potential to both guide conservation interventions and provide crucial insights on lion population dynamics.

Hence, this study assessed the spatiotemporal variation in lion density in Nairobi national park (NNP), a small partially fenced peri-urban ecosystem where seasonal prey migrations occur through the unfenced southern section during the wet season (Reid et al., 2008). Three different approaches to data collection were used and were deployed within an SECR modelling framework, which explicitly accounts for the observation process, thus allowing for direct comparison (Royle et al., 2013). The first approach was carried out by professional field biologists during a dedicated survey, the second survey was conducted by wildlife enthusiasts, and the third was conducted by professional field biologists as part of a 10-day SECR training workshop. These surveys were designed to assess the following predictions: 1) lion density inside the park would be higher during the dry season; (2) during the wet season, lion activity centres would shift towards the southern boundary in response to seasonal migration of prey; and (3) lions would display larger movements during the wet season.

1.5 Research objectives and research questions

The main aim of this PhD research was to assess the interplay of genetic, ecological and anthropogenic factors on lion population dynamics in Kenya. Specifically, the study had the following objectives:

1. Assess the genetic population structure and within-population levels of diversity of lions in Kenya and the influence of management interventions on the genetic diversity.
2. Assess the impact of local ecological and anthropogenic factors on lion grouping patterns, home range and movement patterns across various protected areas in Kenya.
3. Use Spatially Explicit Capture Recapture models to optimise monitoring techniques and determine the spatiotemporal variation of lion population density and abundance.

The study covered the following main research questions:

1. What is the distribution of lion genetic diversity in Kenya and can impacts of past management interventions be observed on these patterns?
2. What is the influence of land management, ecological and anthropogenic factors on lion group size in Kenya?
3. What is the impact of rainfall on lion home range and movement across Meru, Nairobi and Lake Nakuru national parks in Kenya?
4. How can spatial capture-recapture models be applied to enhance long- term monitoring of lion population dynamics?

1.6 Structure of PhD thesis

This thesis provides a multifaceted examination of lion populations in Kenya, encompassing genetic diversity, grouping patterns, spatiotemporal variation of lion population density, home range and movement patterns across various landscapes. Through an integrated approach, this study aims to enhance our understanding of lion ecology and inform conservation strategies. It comprises of six chapters:

Chapter one provides a general introduction and review of the study topics. It presents the research questions and objectives of the study.

Chapter two covers 12 lion populations in Kenya and examines their genetic diversity, population structure and differentiation between and within populations, as well as the impact of management practices such as fencing and translocation on genetic diversity.

Chapter three focuses on eight study sites in Kenya known to host resident lion populations and examines the effects of ecological and anthropogenic factors on lion grouping patterns.

Chapter four assesses the influence of rainfall of lion home range and movement in three national parks in Kenya.

Chapter five uses the lion population in Nairobi national park as a case study to assess the spatiotemporal variation in lion population density and abundance using SECR. It provides a baseline for repeat surveys to monitor lion population trends and guide conservation strategies.

Chapter six discusses the holistic impacts of management practices and the influence of ecological and anthropogenic factors on the management of lion populations in Kenya. It draws conclusions from the research findings and provides recommendations for management.

References

Armstrong E.E., C. Curry, K.A. Solari, S. Morgan, B.D. Patterson, B. Agwanda et al. 2025. President Roosevelt's lions reveal a century of population fragmentation in Africa's largest carnivore. *bioRxiv* 2025.02.26.640359. DOI

Barnett, R., Yamaguchi, N., Barnes, I., & Cooper, A. (2006). *The origin , current diversity and future conservation of the modern lion (Panthera leo). May*, 2119–2125. https://doi.org/10.1098/rspb.2006.3555

Barnett, R., Yamaguchi, N., Shapiro, B., Ho, S. Y., Barnes, I., Sabin, R., Werdelin, L., Cuisin, J., & Larson, G. (2014). Revealing the maternal demographic history of *Panthera leo* using ancient DNA and a spatially explicit genealogical analysis. *BMC Evolutionary Biology*, *14*(1). https://doi.org/10.1186/1471-2148-14-70

Bauer, H., & Van der Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, *38*(1), 26–31. https://doi.org/10.1017/S0030605304000055

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., Macdonald, D. W., & Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(48), 14894–14899. https://doi.org/10.1073/pnas.1500664112

Bauer, H., De Iongh, H. H., & Di Silvestre, I. (2003). Lion (*Panthera leo*) social behaviour in the West and Central African savannah belt. *Mammalian Biology*, *68*(4), 239–243. https://doi.org/10.1078/1616-5047-00090

Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, K. 2016. *Panthera leo*. *The IUCN Red List of Threatened Species 2016*: e.T15951A115130419. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en

Bauer, H., Vanherle, N., Di Silvestre, I., & De Iongh, H. H. (2008). *Lion – prey relations in West and Central Africa*. *73*(1972), 70–73. https://doi.org/10.1016/j.mambio.2006.11.006

Bedelian, C., & Ogutu, J. O. (2017). Trade-offs for climate-resilient pastoral livelihoods in wildlife conservancies in the Mara ecosystem, Kenya. *Pastoralism*, *7*(1), 1–22. https://doi.org/10.1186/s13570-017-0085-1

Bertola, L. D. (2015). *Genetic Diversity in the lion (Panthera leo)*. PhD Thesis. Leiden University, Netherlands. https://doi.org/10.1017/CBO9781107415324.004

Bertola, L. D., Jongbloed, H., Van der Gaag, K. J., De Knijff, P., Yamaguchi, N., Hooghiemstra, H., Bauer, H., Henschel, P., White, P. A., Driscoll, C. A., Tende, T., Ottosson, U., Saidu, Y., Vrieling, K., & De Iongh, H. H. (2016). Phylogeographic Patterns in Africa and High Resolution Delineation of Genetic Clades in the Lion (*Panthera leo*). *Scientific Reports*, *6*(August 2016), 1–11. https://doi.org/10.1038/srep30807

Bertola, L. D., Miller, S. M., Williams, V. L., Naude, V. N., Coals, P., Dures, S. G., Henschel, P., Chege, M., Sogbohossou, E. A., Ndiaye, A., Kiki, M., Gaylard, A., Ikanda, D. K., Becker, M. S., & Lindsey, P. (2022). Genetic guidelines for translocations: Maintaining intraspecific diversity in the lion (Panthera leo). *Evolutionary Applications*, *15*(1), 22–39. https://doi.org/10.1111/eva.13318

Bertola, L. D., van Hooft, W. F., Vrieling, K., Uit de Weerd, D. R., York, D. S., Bauer, H., Prins, H. H. T., Funston, P. J., Udo de Haes, H. A., Leirs, H., van Haeringen, W. A., Sogbohossou, E., Tumenta, P. N., & De Iongh, H. H. (2011). Genetic diversity, evolutionary history and implications for conservation of the lion (*Panthera leo*) in West and Central Africa. *Journal of Biogeography*, *38*(7), 1356–1367. https://doi.org/10.1111/j.1365-2699.2011.02500.x

Bertola, L. D., Vermaat, M., Lesilau, F., Chege, M., Tumenta, P. N., Sogbohossou, E. A., Schaap, O. D., Bauer, H., Patterson, B. D., White, P. A., De Iongh, H. H., Laros, J. F. J., & Vrieling, K. (2022). Whole genome sequencing and the application of a SNP panel reveal primary evolutionary lineages and genomic variation in the lion (*Panthera leo*). *BMC Genomics*, *23*(1). https://doi.org/10.1186/s12864-022-08510-y

Bhalla, S. (2017). *Demography and ranging behaviour of lions (Panthera leo) within a human-occupied landscape in northern Kenya*. https://ewasolions.org/wp-content/uploads/2020/09/Shivani-Bhalla-Thesis-2017-compressed.pdf

Björklund, M. (2003). The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics*, *4*(4), 515–523. https://doi.org/10.1023/A:1024737317695

Blackburn, S., Hopcraft, J. G. C., Ogutu, J. O., Matthiopoulos, J., & Frank, L. (2016). Human–wildlife conflict, benefit sharing and the survival of lions in pastoralist community-based conservancies. *Journal of Applied Ecology*, *53*(4), 1195–1205. https://doi.org/10.1111/1365-2664.12632

Bodasing, T. (2022). The decline of large carnivores in Africa and opportunities for change. *Biological Conservation*, *274*(August), 109724. https://doi.org/10.1016/j.biocon.2022.109724

Borrego, N., Ozgul, A., Slotow, R., & Packer, C. (2018). Lion population dynamics: Do nomadic males matter? *Behavioral Ecology*, *29*(3), 660–666. https://doi.org/10.1093/beheco/ary018

Braczkowski, A., Gopalaswamy, A. M., Elliot, N. B., Possingham, H. P., Bezzina, A., Maron, M., Biggs, D., & Allan, J. R. (2020). Restoring Africa's Lions: Start With Good Counts. *Frontiers in Ecology and Evolution*, *8*. https://doi.org/10.3389/fevo.2020.00138

Briers-Louw, W. D., Verschueren, S., & Leslie, A. J. (2019). Big Cats Return to Majete Wildlife Reserve, Malawi: Evaluating Reintroduction Success. *African Journal of Wildlife Research*, *49*(1), 34–50. https://doi.org/10.3957/056.049.0034

Broekhuis, F., Elliot, N. B., Keiwua, K., Koinet, K., Macdonald, D. W., Mogensen, N., Thuo, D., & Gopalaswamy, A. M. (2021). Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography*, *44*(3), 358–369. https://doi.org/10.1111/ecog.05154

Broekman, M. J. E., Hoeks, S., Freriks, R., Langendoen, M. M., Runge, K. M., Savenco, E., ter Harmsel, R., Huijbregts, M. A. J., & Tucker, M. A. (2022). HomeRange: A global database of mammalian home ranges. *Global Ecology and Biogeography*, *32*(2), 198–205. https://doi.org/10.1111/geb.13625

Burt, W. H. (1943). Territoriality and Home Range Concepts as Applied to Mammals. *Journal of Mammalogy*, *24*(3), 346. https://doi.org/10.2307/1374834

Buxton, R. T., Bennett, J. R., Reid, A. J., Shulman, C., Cooke, S. J., Francis, C. M., Nyboer, E. A., Pritchard, G., Binley, A. D., Avery-Gomm, S., Ban, N. C., Beazley, K. F., Bennett, E., Blight, L. K., Bortolotti, L. E., Camfield, A. F., Gadallah, F., Jacob, A. L., Naujokaitis-Lewis, I., … Smith, P. A. (2021). Key information needs to move from knowledge to action for biodiversity conservation in Canada. *Biological Conservation*, *256*. https://doi.org/10.1016/j.biocon.2021.108983

Caraco, T., & Wolf, L. L. (1975). Ecological Determinants of Group Sizes of Foraging Lions. *The American Naturalist*, 109(967), 343–352. http://www.jstor.org/stable/2459698

Carr, G. M., & Macdonald, D. W. (1986). *The sociality of solitary foragers: a model based on resource dispersion*. *34*, 1540–1549.

Chardonnet, P. (2002) *Conservation of the African Lion: Contribution to a Status Survey*. International Foundation for the Conservation of Wildlife, France and Conservation Force, Washington DC, 171 p.

Chege, M., Bertola, L. D., De Snoo, G. R., Ngene, S., Otieno, T., Amoke, I., van 't Zelfde, M., Dolrenry, S., Broekhuis, F., Tamis, W., De Iongh, H. H., & Elliot, N. B. (2024). Effect of ecological and anthropogenic factors on grouping patterns in African lions across Kenya. *Ecology and Evolution*, *14*(2). https://doi.org/10.1002/ece3.10982

Chege, M., Sewalt, B., Lesilau, F., De Snoo, G.R., Patterson, B. D., Kariuki, L., Otiende, M., Omondi, P., De Iongh, H., Vrieling, K., & Bertola, L. D. (2024). Genetic diversity of lion populations in Kenya: Evaluating past management practices and recommendations for future conservation actions. *Evolutionary Applications*, *17*(3), 1–14. https://doi.org/10.1111/eva.13676

Chege, M., Torrents-, M., Bertola, L. D., De Snoo, G.R., van't Zelfde, M., Musters, C. J. M., & De Iongh, H. (2025). Rainfall variability shapes lion movement and home range dynamics in three Kenyan parks. *African Journal of Ecology*, *63*(e70003), 1–14. https://doi.org/10.1111/aje.70003

Chesson, P., Gebauer, R. L. E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M. S. K., Sher, A., Novoplansky, A., & Weltzin, J. F. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. In *Oecologia* (Vol. 141, Issue 2, pp. 236–253). https://doi.org/10.1007/s00442-004-1551-1

Cozzi, G., Broekhuis, F., Mcnutt, J. W., & Schmid, B. (2013). Comparison of the effects of artificial and natural barriers on large African carnivores: Implications for interspecific relationships and connectivity. *Journal of Animal Ecology*, *82*(3), 707–715. https://doi.org/10.1111/1365-2656.12039

Creel, S., Becker, M. S., Durant, S. M., M'Soka, J., Matandiko, W., Dickman, A. J., Christianson, D., Dröge, E., Mweetwa, T., Pettorelli, N., Rosenblatt, E., Schuette, P., Woodroffe, R., Bashir, S., Beudels-Jamar, R. C., Blake, S., Borner, M., Breitenmoser, C., Broekhuis, F., … Zimmermann, A. (2013). Conserving large populations of lions - the argument for fences has holes. *Ecology Letters*, *16*(11). https://doi.org/10.1111/ele.12145

Creel, S., Spong, G., Becker, M., Simukonda, C., Norman, A., Schiffthaler, B., & Chifunte, C. (2019). Carnivores, competition and genetic connectivity in the Anthropocene. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-52904-0

Curry, C. J., Davis, B. W., Bertola, L. D., White, P. A., Murphy, W. J., & Derr, J. N. (2020). Spatiotemporal Genetic Diversity of Lions Reveals the Influence of Habitat Fragmentation Across Africa. *Molecular Biology and Evolution*. https://doi.org/10.1093/molbev/msaa174

Cushman, S. A., Elliot, N. B., Macdonald, D. W., & Loveridge, A. J. (2016). A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. *Landscape Ecology*, *31*(6), 1337–1353. https://doi.org/10.1007/s10980-015-0292-3

De Boer, W. F., Vis, M. J. P., De Knegt, H. J., Rowles, C., Kohi, E. M., Van Langevelde, F., Peel, M., Pretorius, Y., Skidmore, A. K., Slotow, R., Van Wieren, S. E., & Prins, H. H. T. (2010). Spatial distribution of lion kills determined by the water dependency of prey species. *Journal of Mammalogy*, *91*(5), 1280–1286. https://doi.org/10.1644/09-MAMM-A-392.1

Dolrenry, S. (2013). *African lion (Panthera leo) behaviour, monitoring, and survival in human-dominated landscapes*. PhD thesis, University of Wisconsin-Madison, United States of America.

Dolrenry, S., Hazzah, L., & Frank, L. (2020). Corridors of tolerance through human-dominated landscapes facilitate dispersal and connectivity between populations of African lions *Panthera leo*. *Oryx*, 1–4. https://doi.org/10.1017/s0030605319000656

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, R. S., & Frank, L. (2014). A metapopulation approach to African lion (*Panthera leo*) conservation. *PLoS ONE*, *9*(2), 1–9. https://doi.org/10.1371/journal.pone.0088081

Donkin, D. A. (2000). *Lion spatial socio-ecology: the effect of habitat on lion group dynamics*. Masters thesis, University of Natal, Durban, South Africa.

Dubach, J. M., Briggs, M. B., White, P. A., Ament, B. A., & Patterson, B. D. (2013). Genetic perspectives on "Lion Conservation Units" in Eastern and Southern Africa. *Conservation Genetics*, *14*(4), 741–755. https://doi.org/10.1007/s10592-013-0453-3

Dubach, J. M., M. B. Briggs, P. A. White, B. A. Ament and B. D. Patterson (2013). "Genetic perspectives on "Lion Conservation Units" in Eastern and Southern Africa." *Conservation Genetics* 14: 741-755.

Durant, S. M., Becker, M. S., Creel, S., Bashir, S., Dickman, A. J., Beudels-Jamar, R. C., Lichtenfeld, L., Hilborn, R., Wall, J., Wittemyer, G., Badamjav, L., Blake, S., Boitani, L., Breitenmoser, C., Broekhuis, F., Christianson, D., Cozzi, G., Davenport, T. R. B., Deutsch, J., … Pettorelli, N. (2015). Developing fencing policies for dryland ecosystems. *Journal of Applied Ecology*, *52*(3), 544–551. https://doi.org/10.1111/1365-2664.12415

Elliot NB, Bett A, Chege M, et al. The importance of reliable monitoring methods for the management of small, isolated populations. *Conservation Science and Practice*. 2020;e217. https://doi.org/10.1111/ csp2.217

Elliot, N. B., & Gopalaswamy, A. M. (2017). Toward accurate and precise estimates of lion density. *Conservation Biology*, *31*(4), 934–943. https://doi.org/10.1111/cobi.12878

Elliot, N.B., Broekhuis, F., Omondi, P., Ngene, S., Kariuki, L., Sankan, K., Chege, M., Wato, Y., Amoke, I., Dolrenry, S., Kuloba, B., Gopalaswamy, A.M. (2021). *Report on the application of novel estimating methodologies to monitor lion abundance within source populations and large carnivore occupancy at a national scale*. Wildlife Research and Training Institute and Kenya Wildlife Service.

Frank, L., Gelber, L., Cotterill, A., Ekwanga, S., Hazzah, L., Dolrenry, S., Blackburn, S., Howard, A., Briggs, P., Napao, M., Nkiinti, L., Mamaai, L., & Kesoi, E. O. (2010). *Living with Lions annual report*. http://www.lionconservation.org/AnnualReports/2010-LWL-Annual-Report.pdf

Frank, L., Maclennan, S., Hazzah, L., Bonham, R., & Hill, T. (2006). *Lion Killing in the Amboseli -Tsavo Ecosystem, 2001-2006, and its Implications for Kenya's Lion Population Predator Compensation Fund and Masailand Preservation Trust*. Nairobi, *Kenya*. May, 2001–2006.

Frankham, R. (2005). Genetics and extinction. *Biological Conservation*, 126, 131–140. https://doi.org/10.1016/j.biocon.2005.05.002

Frankham, R., Ballou, J. D., Ralls, K., Eldridge, M., Dudash, M. R., Fenster, C. B., Lacy, R. C., & Sunnucks, P. (2019). *A Practical Guide for Genetic Management of Fragmented Animal and Plant Populations*. Oxford University Press. https://doi.org/10.1093/oso/9780198783411.001.0001

Funston, P. J. (2011). Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, *41*(1), 1–10. https://doi.org/10.3957/056.041.0108

Gavin J. Wilson and Richard J. Delahay. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research*, *28*, 151–164.

Goldenberg, S. Z., Owen, M. A., Brown, J. L., Wittemyer, G., Oo, Z. M., & Leimgruber, P. (2019). Increasing conservation translocation success by building social functionality in released populations. *Global Ecology and Conservation*, *18*. https://doi.org/10.1016/j.gecco.2019.e00604

Gopalaswamy, A. M., Elliot, N. B., Ngene, S., Broekhuis, F., Braczkowski, A., Lindsey, P., Packer, C., & Stenseth, N. C. (2022). How "science" can facilitate the politicization of charismatic megafauna counts. *Proceedings of the National Academy of Sciences of the United States of America*, 119(20), 1–4. https://doi.org/10.1073/pnas.2203244119

Gopalaswamy, A. M., Mohan, D., Karanth, K. U., Samba, K. N., & Macdonald, D. W. (2015). An examination of index-calibration experiments counting tigers at macroecological scales. *Methods in Ecology and Evolution*, *6*(9), 1055–1066. https://doi.org/https://doi.org/10.1111/2041-210X.12351

Gopalaswamy, A. M., Royle, J. A., Delampady, M., Nichols, J. D., Karanth, K. U., & Macdonald, D. W. (2012).

Density estimation in tiger populations: combining information for strong inference. *Ecology*, *93*(7), 1741–1751. https://doi.org/https://doi.org/10.1890/11-2110.1

Grant J. Hopcraft, C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, *74*(3), 559–566. https://doi.org/10.1111/j.1365-2656.2005.00955.x

Harcourt, A. H., Parks, S. A., & Woodroffe, R. (2001). Human density as an influence on species/area relationships: double jeopardy for small African reserves? *Biodiversity and Conservation*, 10, 1011–1026.

Henschel, P., Petracca, L. S., Ferreira, S. M., Ekwanga, S., Ryan, S. D., & Frank, L. G. (2020). Census and distribution of large carnivores in the Tsavo national parks, a critical east African wildlife corridor. *African Journal of Ecology*, *58*(3), 383–398. https://doi.org/10.1111/aje.12730

Hoffmann, A., & Sgro, C. (2011). Climate change and evolutionary adaptation. *Nature*, *470*(February), 479–485. https://doi.org/10.1038/nature09670

Hopcraft, J. G. C., Olff, H., & Sinclair, A. R. E. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Evolution*, 25(2), 119–128. https://doi.org/10.1016/j.tree.2009.08.001

Jacquier, M., Vandel, J. M., Léger, F., Duhayer, J., Pardonnet, S., Say, L., Devillard, S., & Ruette, S. (2021). Breaking down population density into different components to better understand its spatial variation. *BMC Ecology and Evolution*, *21*(1). https://doi.org/10.1186/s12862-021-01809-6

Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., Schröder, B., Buchmann, C. M., Mueller, T., Blaum, N., Zurell, D., Böhning-Gaese, K., Wiegand, T., Eccard, J. A., Hofer, H., Reeg, J., Eggers, U., & Bauer, S. (2013). Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology*, 1(6), 1–13. https://doi.org/10.1186/2051-3933-1-6

Keiter, D. A., Davis, A. J., Rhodes, O. E., Cunningham, F. L., Kilgo, J. C., Pepin, K. M., & Beasley, J. C. (2017). Effects of scale of movement, detection probability, and true population density on common methods of estimating population density. *Scientific Reports*, *7*(1). https://doi.org/10.1038/s41598-017-09746-5

Kenya Wildlife Service. (2016). *Conservation and Management Strategy for Lion and Spotted Hyena in Kenya_2009 - 2014*. Kenya Wildlife Service, Nairobi, Kenya. http://www.kws.go.ke/downloads.

Kenya Wildlife Service. (2018). *The National Wildlife Conservation Status Report 2015-2017*. Kenya Wildlife Service, Nairobi, Kenya. http://www.kws.go.ke/downloads

Kenya Wildlife Service. (2020). *National Recovery and Action Plan for Lion and Spotted Hyena in Kenya (2020-2030)*. (2nd Edition). Kenya Wildlife Service. Nairobi, Kenya

Kitchener, A., Breitenmoser, C., Eizirik, E., Gentry, A., Werdelin, L., Wilting, A., Yamaguchi, N., Abramov, A., Christiansen, P., Driscoll, C., Duckworth, W., Johnson, W., Luo, S.-J., Meijaard, E., O'Donoghue, P., Sanderson, J., Seymour, K., Bruford, M., Groves, C., & Tobe, S. (2017). A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN/SSC Cat Specialist Group. *Cat News Special Issue*, *May*, 80 pp.

Kotze, R., Keith, M., Winterbach, C. W., Winterbach, H. E. K., & Marshal, J. P. (2018). The influence of social and environmental factors on organization of African lion (*Panthera leo*) prides in the Okavango Delta. *Journal of Mammalogy*, *99*(4), 845–858. https://doi.org/10.1093/jmammal/gyy076

Laizer, H., Tarimo, T. M. C., & Kisui, B. (2014). Home Range and Movement Patterns of Lions (*Panthera Leo*) in Tarangire National Park, Tanzania. *American Journal of Research Communication*, *2*(1), 44–58. www.usa-journals.comwww.usa-journals.com,

Lesilau, F. L. (2019). *Human-Lion conflict around Nairobi National Park : Lion (Panthera leo melanochaita, Hamilton Smith, 1842) Population Structure, Landscape Use and Diet, in a Semi-Fenced Park*. PhD Thesis. Leiden University, Netherlands. https://hdl.handle.net/1887/81380

Lesilau, F., Verschueren, S., Zelfde, M. van 't., Musters, C. J. M., Snoo, G.R. de, & Iongh, H. H. de, (2021). Spatial ecology of lions in a small, semi-fenced park surrounded by dense human populations: The case study of

Nairobi National Park, Kenya. *Mammalia*, *85*(3), 198–207. https://doi.org/10.1515/mammalia-2020-0116

Lindsey, P. A., Miller, J. R. B., Petracca, L. S., Coad, L., DIckman, A. J., Fitzgerald, K. H., Flyman, M. V., Funston, P. J., Henschel, P., Kasiki, S., Knights, K., Loveridge, A. J., MacDonald, D. W., Mandisodza-Chikerema, R. L., Nazerali, S., Plumptre, A. J., Stevens, R., Van Zyl, H. W., & Hunter, L. T. B. (2018). More than $1 billion needed annually to secure Africa's protected areas with lions. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(45), E10788–E10796. https://doi.org/10.1073/pnas.1805048115

Lindsey, P. A., Petracca, L., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., Flyman, M., Henschel, P., Hinks, A., Kasiki, S., Loveridge, A., Macdonald, D. W., Mandisodza, R., Mgoola, W., Miller, S., Nazerali, S., Siege, L., Uiseb, K., & Hunter, L. (2017). The performance of African protected areas for lions and their prey, determinants of success and key conservation threats. *Biological Conservation*, *209*, 137–149. https://doi.org/https://doi.org/10.1016/j.biocon.2017.01.011

Linnell, J. D. C., Aanes, R., Swenson, J. E., Odden, J., & Smith, M. E. (1997). Translocation of carnivores as a method for managing problem animals: A review. *Biodiversity and Conservation*, 6(9), 1245–1257. https://doi.org/10.1023/B:BIOC.0000034011.05412.cd

Loveridge, A. J., Hemson, G., Davidson, Z., & Macdonald, D. W. (2010). African lions on the edge: reserve boundaries as 'attractive sinks.' *Biology and Conservation of Wild Felids*, *October 2021*, 283–304.

Loveridge, A. J., Sousa, L. L., Cushman, S., Kaszta, Ż., & Macdonald, D. W. (2022). Where have all the lions gone? Establishing realistic baselines to assess decline and recovery of African lions. *Diversity and Distributions*. https://doi.org/10.1111/ddi.13637

Loveridge, A. J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., & MacDonald, D. W. (2009). Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography*, *32*(6), 953–962. https://doi.org/10.1111/j.1600-0587.2009.05745.x

Maher, S. M. L., Barker, K. J., Kroetz, K., Butsic, V., Leonard, B., & Middleton, A. D. (2023). Assessing the ecosystem services and disservices provided by migratory wildlife across the Greater Yellowstone Ecosystem. *Biological Conservation*, *283*. https://doi.org/10.1016/j.biocon.2023.110090

Massey, A. L., King, A. A., & Foufopoulos, J. (2014). Fencing protected areas: A long-term assessment of the effects of reserve establishment and fencing on African mammalian diversity. *Biological Conservation*, 176, 162–171. https://doi.org/10.1016/j.biocon.2014.05.023

Mbizah, M. M., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2019). Applying the resource dispersion hypothesis to a fission–fusion society: A case study of the African lion (*Panthera leo*). *Ecology and Evolution*, *9*(16), 9111–9119. https://doi.org/10.1002/ece3.5456

Ministry of Tourism and Wildlife (2018) *National Wildlife Strategy 2030*. A bridge Version. Blueprint to transform wildlife conservation in Kenya. Nairobi, Kenya.

Morapedi, M., Reuben, M., Gadimang, P., Bradley, J., Given, W., Reading, R. P., Ngaka, K., Selebatso, M., & Maude, G. (2021). Outcomes of Lion, Panthera leo, Translocations to Reduce Conflict with Farmers in Botswana. *African Journal of Wildlife Research*, *51*(1), 6–12. https://doi.org/10.3957/056.051.0006

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, *78*(2), 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024

Naha, D., Périquet, S., Kilian, J. W., Kupferman, C. A., Hoth-Hanssen, T., & Beasley, J. C. (2023). Fencing affects movement patterns of two large carnivores in Southern Africa. *Frontiers in Ecology and Evolution*, *11*. https://doi.org/10.3389/fevo.2023.1031321

Nams, V. O., Parker, D. M., Weise, F. J., Patterson, B. D., Buij, R., Radloff, F. G. T., Vanak, A. T., Tumenta, P. N., Hayward, M. W., Swanepoel, L. H., Funston, P. J., Bauer, H., Power, R. J., O'Brien, J., O'Brien, T. G., Tambling, C. J., de Iongh, H. H., Ferreira, S. M., Owen-Smith, N., Beukes, M. (2023). Spatial patterns of large African cats: a large-scale study on density, home range size, and home range overlap of lions *Panthera leo* and leopards *Panthera pardus*. *Mammal Review*, *53*(2), 49–64. https://doi.org/10.1111/mam.12309

Newmark, W. D. (2008). Isolation of African protected areas. In *Frontiers in Ecology and the Environment* (Vol. 6, Issue 6, pp. 321–328). https://doi.org/10.1890/070003

Nichols, J. D., & Williams, B. K. (2006). Monitoring for conservation. *Trends in Ecology and Evolution*, *21*(12), 668–673. https://doi.org/10.1016/j.tree.2006.08.007

Nicholson, S. K., Dickman, A., Hinks, A., Riggio, J., Bauer, H., Loveridge, A., Becker, M., Begg, C., Bhalla, S., Burnham, D., Cotterill, A., Dolrenry, S., Dröge, E., Funston, P., Hazzah, L., Ikanda, D., Gebresenbet, F., Henschel, P., Mandisodza-Chikerema, R. L., … Jacobson, A. P. (2023). Socio-political and ecological fragility of threatened, free-ranging African lion populations. *Communications Earth and Environment*, *4*(1). https://doi.org/10.1038/s43247-023-00959-3

O'Bryan, C. J., Braczkowski, A. R., Beyer, H. L., Carter, N. H., Watson, J. E. M., & McDonald-Madden, E. (2018). The contribution of predators and scavengers to human well-being. *Nature Ecology and Evolution*, *2*(2), 229–236. https://doi.org/10.1038/s41559-017-0421-2

Obiero, J. P. O., & Onyando, J. O. (2013). Climate. *Developments in Earth Surface Processes*, *16*, 39–50. https://doi.org/10.1016/B978-0-444-59559-1.00005-0

Ogutu, J. O., & Dublin, H. T. (1998). The response of lions and spotted hyaenas to sound playbacks as a technique for estimating population size. *African Journal of Ecology*, *36*(1), 83–95. https://doi.org/10.1046/j.1365-2028.1998.113-89113.x

Ogutu, J. O., Piepho, H. P., Said, M. Y., Ojwang, G. O., Njino, L. W., Kifugo, S. C., & Wargute, P. W. (2016). Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: What are the causes? *PLoS ONE*, *11*(9). https://doi.org/10.1371/journal.pone.0163249

Ottichilo, W. K., De Leeuw, J., & Prins, H. H. T. (2001). Population trends of resident wildebeest [*Connochaetes taurinus hecki* (Neumann)] and factors influencing them in the Masai Mara ecosystem, Kenya. *Biological Conservation*, 97(3), 271–282.

Packer, C., & Ruttan, L. (1988). The Evolution of Cooperative Hunting. *The American Naturalist*, 132(2), 159–198.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., & Sinclair, A. R. E. (2005). Ecological Change, Group Territoriality, and Population Dynamics in Serengeti Lions. *Science*, *307*(January), 390–393. https://doi.org/10.1126/science.1105122

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., Zander, K. K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C. M., Begg, K. S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A. C., Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology Letters*, *16*(5), 635–641. https://doi.org/10.1111/ele.12091

Packer, C., Pusey, A. E., & Eberly, L. E. (2001). Egalitarianism in Female African Lions. *Science*, 293(5530), 690–693. https://www.jstor.org/stable/3084318

Packer, C., Pusey, A. E., Rowley, H., Gilbert, D. A., Martenson, J., & O'Brien, S. J. (1991). Case Study of a Population Bottleneck: Lions of the Ngorongoro Crater. *Conservation Biology*, *5*(2), 219–230. https://doi.org/10.1111/j.1523-1739.1991.tb00127.x

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups: food is not enough. *American Naturalist*, *136*(1), 1–19. https://doi.org/10.1086/285079

Palmer, P. I., Wainwright, C. M., Dong, B., Maidment, R. I., Wheeler, K. G., Gedney, N., Hickman, J. E., Madani, N., Folwell, S. S., Abdo, G., Allan, R. P., Black, E. C. L., Feng, L., Gudoshava, M., Haines, K., Huntingford, C., Kilavi, M., Lunt, M. F., Shaaban, A., & Turner, A. G. (2023). Drivers and impacts of Eastern African rainfall variability. *Nature Reviews Earth and Environment*, *4*(4), 254–270. https://doi.org/10.1038/s43017-023-00397-x

Patterson, B. D., S. M. Kasiki, E. Selempo and R. W. Kays (2004). "Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya." *Biological Conservation* 119: 507-516.

Pettorelli, N., Laurance, W. F., O'Brien, T. G., Wegmann, M., Nagendra, H., & Turner, W. (2014). Satellite remote sensing for applied ecologists: Opportunities and challenges. *Journal of Applied Ecology*, 51, 839–848. https://doi.org/10.1111/1365-2664.12261

Pimm, S. L., Dollar, L., & Bass, O. L. (2006). The genetic rescue of the Florida panther. *Animal Conservation*, *9*(2), 115–122. https://doi.org/10.1111/j.1469-1795.2005.00010.x

Pinto, A. V., Hansson, B., Patramanis, I., Morales, H. E., & van Oosterhout, C. (2023). The impact of habitat loss and population fragmentation on genomic erosion. *Conservation Genetics*, *25*(1), 49–57. https://doi.org/10.1007/s10592-023-01548-9

Reed, D. H., & Frankham, R. (2003). Correlation between Fitness and Genetic Diversity. *Conservation Biology*, 17(1), 230–237.

Reid, R. S., Gichohi, H., Said, M. Y., Nkedianye, D., Ogutu, J. O., Kshatriya, M., Kristjanson, P., Kifugo, S. C., Agatsiva, J. L., Adanje, S. A., & Bagine, R. (2008). *Fragmentation of a Peri-Urban Savanna, Athi-Kaputiei Plains, Kenya*. In Kathleen A. Galvin (Ed.), Springer (1st ed.). Springer Dordrecht. https://doi.org/https://doi.org/10.1007/978-1-4020-4906-4

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lichtenfeld, L., & Pimm, S. (2013). The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodiversity and Conservation*, *22*(1), 17–35. https://doi.org/10.1007/s10531-012-0381-4

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167). https://doi.org/10.1126/science.1241484

Royle, J. A., Chandler, R. B., Sun, C. C., & Fuller, A. K. (2013). Integrating resource selection information with spatial capture-recapture. *Methods in Ecology and Evolution*, *4*(6), 520–530. https://doi.org/10.1111/2041-210X.12039

Schaller, G. B. (1972). *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press. https://books.google.mw/books?id=rZP1MIJWiKsC

Snyman, A., Raynor, E., Chizinski, C., Powell, L., & Carroll, J. (2018). African Lion (*Panthera leo*) Space Use in the Greater Mapungubwe Transfrontier Conservation Area. *African Journal of Wildlife Research*, *48*(2). https://doi.org/10.3957/056.048.023001

Stander, P. E. (1992). Cooperative Hunting in Lions: The Role of the Individual. Behavioral Ecology and Sociobiology, 29(6), 445–454. http://www.jstor.org/stable/4600646

Thomas, S., van der Merwe, V., Carvalho, W. D., Macdonald, D. W., & Farhadinia, M. (2023). Evaluating the performance of conservation translocations in large carnivores across the world. *Biological Conservation*, 279. https://doi.org/10.1016/j.biocon.2023.109909

Tittensor, D. P., Walpole, M., Hill, S. L. L., Boyce, D. G., Britten, G. L., Burgess, N. D., Butchart, S. H. M., Leadley, P. W., Regan, E. C., Alkemade, R., Baumung, R., Bellard, C., Bouwman, L., Bowles-Newark, N. J., Chenery, A. M., Cheung, W. W. L., Christensen, V., Cooper, H. D., Crowther, A. R., … Ye, Y. (2014). A mid-term analysis of progress toward international biodiversity targets. *Science*, *346*(6206), 241–244. https://doi.org/10.1126/science.1257484

Tourani, M. (2022). A review of spatial capture–recapture: Ecological insights, limitations, and prospects. *Ecology and Evolution*, *12*(1), 1–13. https://doi.org/10.1002/ece3.8468

Trinkel, M., Fleischmann, P. H., Ferguson, N., & Slotow, R. (2007). The influence of vegetation on lion *Panthera leo* group sizes in Hluhluwe-Umfolozi Park, South Africa. *Acta Zoologica Sinica*, 53(1), 15–21. https://www.researchgate.net/publication/264044375

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C., & Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation*, 13, 374–382. https://doi.org/10.1111/j.1469-1795.2009.00344.x

Tumenta, P. N., Van 't Zelfde, M., Croes, B. M., Buij, R., Funston, P. J., Udo de Haes, H. A., & De Iongh, H. H. (2013). Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian*

Biology, *78*(6), 461–469. https://doi.org/10.1016/j.mambio.2013.08.006

Tuqa, J. H., Funston, P., Musyoki, C., Ojwang, G. O., Gichuki, N. N., Bauer, H. H., Tamis, W.L.M., Dolrenry, S., Van't Zelfde, M., De Snoo, G. R., & De Iongh, H. H. (2014). Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation*, *2*(August), 1–10. https://doi.org/10.1016/j.gecco.2014.07.006

Turner, J. A., Dunston-Clarke, E. J., Fabris-Rotelli, I., & de Iongh, H. H. (2022). Home Range and Movement Patterns of Reintroduced White Lions (Panthera leo melanochaita) in the Kruger to Canyons Biosphere Reserve, South Africa. *Animals*, *12*(15). https://doi.org/10.3390/ani12152003

Valeix, M., Loveridge, A. J., & Macdonald, D. W. (2012). Influence of prey dispersion on territory and group size of African lions: a test of the resource dispersion hypothesis. *Ecology*, 93(11), 2490–2496.

Van Orsdol, K., Hanby, J., & Bygott, J. D. (1985). Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology*, 206, 97–112. https://doi.org/10.1111/j.1469-7998.1985.tb05639.x

VanderWaal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, *77*(4), 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028

Vergara, M., Cushman, S. A., & Ruiz-González, A. (2017). Ecological differences and limiting factors in different regional contexts: landscape genetics of the stone marten in the Iberian Peninsula. *Landscape Ecology*, *32*(6), 1269–1283. https://doi.org/10.1007/s10980-017-0512-0

Waweru, J. B., Omondi, P., Ngene, S., Mukeka, J., Wanyonyi, E., Ngoru, B., Mwiu, S., Muteti, D., Lala, F., Kariuki, L., Ihwagi, F., Kiambi, S., Khyale, C., Bundotich, G., Omengo, F., Hongo, P., Maina, P., Muchiri, F., Omar, M., … Kanga, E. (2021). *National Wildlife Census 2021 Report_Abridged Version*. www.digimatt.co.ke

Western, D., Russell, S., & Cuthil, I. (2009). The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS ONE*, *4*(7). https://doi.org/10.1371/journal.pone.0006140

Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, 280(5372), 2126–2128. https://doi.org/10.1126/science.280.5372.2126.

Woodroffe, R., Hedges, S., & Durant, S. M. (2014). To fence or not to fence. *Science*, 344(6179), 46–48. https://doi.org/10.1126/science.1246251.