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Ecology and conservation of the African Lion (*Panthera leo)* in and around Meru National Park, Kenya

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DECLARATION

This thesis is developed within a framework of collaboration between the University of Antwerp, Institute of Environmental Sciences of the Leiden University in the Netherlands (CML), Kenya Wildlife Service (KWS), The Born Free foundation Kenya and the Leo Foundation, Netherlands.

LIST OF ABBREVIATIONS AND ACRONYMS

AUC – Area Under Curve

BNR – Bisanadi National Reserve

CAP 376, WCMA –Wildlife Conservation and Management Act, Chapter 376 of the Kenya constitution which was enacted in 2013.

FMD – Foot and Mouth Disease

IUCN – International Union for the Conservation of Nature

KEBS – Kenya Bureau of Standards

KNP – Kora National Park

KWS – Kenya Wildlife Service

LBL - Lewa Borana Landscape

MCA – Meru Conservation Area

MNP – Meru National Park

MNR – Mwingi National Reserve

PCF – Predator Compensation Fund

PSL – Project Snow Leopard

RNR – Rahole National Reserve

ROR – Relative Occurrence Rate

SDM – Species Distribution Model

TLU – Tropical Livestock Unit

UNESCO - The United Nations Educational, Scientific and Cultural Organization.

ABSTRACT

My research project covered a study on lion population size, pride structure, reproductive success, foraging success, distribution and factors influencing human-lion interactions in the MNP. Data on lion presence were collected during transect counts and through direct opportunistic searches and observations, while data on human-lion interactions were collected through a questionnaire survey that was administered in nine villages (sub-locations) around the park. Results show a lion density of 6.8 lions/km^2 and an estimated lion population size of 31 individuals. I identified four lion prides in the park. The pride structure seems to be influenced by prey availability and seasonal fluctuations of water and prey in and around the MNP. Attitudes towards carnivores are predominantly influenced by livestock ownership and level of education. Livestock husbandry practices, particularly the height of the boma fence and the type of livestock enclosure (boma) also influence livestock loss and mortality.

The questionnaire survey showed that human-lion conflicts mainly occur near the north-eastern boundary of the MCA, which is unfenced. The frequency of reported lion conflict incidences in the area peaks around August which is also the driest month of the year in the MCA and the month with the least number of lion observation sightings inside the park. Livestock raiding behaviour therefore seems to be mainly influenced by lion distribution in and around the park, the presence of livestock and livestock husbandry practices such as the type and height of the boma fence as well as the influence of seasonality. Other livestock husbandry practices (such as the use of flashlights, adult herders/guards and guard dogs) also reduce livestock depredation, although habituation to flashlights reduces the effectiveness of the flashlights and the Muslim pastoralists in the area (who also own the majority of livestock lost to carnivores) do not use guard dogs due to religious beliefs.

SUMMARY

The aim of this research is to study lion population size, pride structure, reproductive success, foraging success, lion distribution and factors influencing human-lion interactions of the African lion in and around Meru National Park in Kenya. Insights on the lion distribution range can help in indicating conflict hotspots and to warn and inform local people. Conflicts between humans and wildlife in Africa have increased during the last decades. Borders of National Parks become more and more densely inhabited by humans as a result of expanding human populations, which has led to the increase in conflicts between wildlife and humans. Meru National Park experiences low rainfall and is bordered by different ethnic groups which increases the complexity of the conflict. Consequently, there is human pressure on the borders of the park, thereby increasing conflicts between humans and wildlife. Only the western part of the park is fenced for 70 kms, enabling herbivore migration only from other non-fenced parts of the park boundary. This also makes it possible for lions and other carnivores to go outside of the park borders and to come in close contact with livestock, especially at watering points during the dry season. This increases the chances of human-lion conflict. The killings have a severe economic impact because most local farmers are financially dependent on their livestock for their livelihoods. In recent years, several lions have therefore already been killed in retaliation by the local population, to protect their own lives and their economically significant livestock, most of which go unreported. This research contributes to the PhD thesis of Luka Narisha and Kevin Groen and is supervised by the University of Antwerp, the University of Leiden and the Kenya Wildlife Service.

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CHAPTER ONE

1.0 INTRODUCTION

1.0.1 Lion population size, pride structure, reproductive success, foraging success and distribution

Large carnivores are keystone species in the African savannah ecosystem despite their relatively low densities (Kissui 2008; Croes *et al.,* 2011). They consist of carnivores larger than 20 kg such as the lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), brown hyena (*Hyena brunea*), striped hyena (*Hyaena hyaena*) and African wild dog (*Lycaon pictus*) (Mills, 1991). Removal of these predators may result in cascading effects on the ecosystem such as a surge in meso-predators and the overabundance of certain herbivore species (Ripple *et al,* 2013; Terborgh *et al.*, 2010). Furthermore, top predators are keystone species which interact with populations of herbivores and smaller carnivores at the lower trophic levels (Mills, 1991; Noss *et al.,* 1996). Generally, large carnivore populations are regulated by the availability of prey animals and not the other way around (Sinclair *et. al.,* 2010). However, large carnivores can also influence the abundance of certain vulnerable prey species (Caughley and Sinclair 1994, Ng'weno *et al* 2017) Competitive interactions between conspecifics as well as different carnivore species also exist when resources are limited, since a unit of food consumed by one individual cannot be consumed by another individual (Linnell and Strand, 2000). Predators can also have interspecific interactions and competition, even with an abundance of resources (Linnell and Strand, 2000). There is a relationship between predator size and prey size whereby the smaller a predator is, the smaller its preferred prey (Carbone et al 1999; Sinclair *et al.,* 2003; Owen-Smith and Mills, 2008). As a result of those different types of interactions in an ecosystem, it is submitted that large carnivores play significant roles in maintaining the balance and ecological functioning in an ecosystem (Terborgh, 1988; Ripple *et al.* 2014).

The habitat range of large carnivores in Africa is mainly savannah landscapes, which includes ecosystems that cover mosaics of grasslands, wetlands and dry woodlands (Kingdon, 1997; Riggio *et al.,* 2013). The size of these landscapes has however declined by 71% (from ~11.9 million km^2 in 1960 to ~3.5 million km^2 in 2012) (Riggio *et al.,* 2013). Lions survive in only 25% of the remaining savannah habitat in Africa (Riggio *et al.,* 2013). Populations of large carnivores have also declined rapidly with lion population estimates ranging between ~22,000 to ~38,000 in 2013, from ~200,000 in the beginning of the century (Chardonnet 2002; Bauer and Van Der Merwe 2004; Riggio *et al.,* 2013; Yirga *et al.* 2014). A major driver for this decline is the increasing level of human interference caused by an almost four-fold human population growth in the Sub-Saharan Africa since 1950 until 2000 which also plays a significant role in influencing large carnivore populations (Riggio *et al.,* 2013). The loss of savannah habitat due to human interference is one of the main reasons why populations of large carnivores are decreasing and becoming threatened (Yirga *et al.,* 2014; IUCN Red List, 2019). Large carnivores are vulnerable mainly because of their low abundance and large home ranges compared to prey species such as gazelles or zebras (Noss *et al.,* 1996).This often increases their interactions with humans which highlights the need for landscape-based approaches aimed at promoting coexistence between people and wildlife beyond protected areas and within socio-ecological systems (Tyrrell et al, 2020).

There has been a sharp decline in lion populations globally, more so in the East, West and Central African regions (Bauer *et al*., 2015). Recent taxonomic revision of Felidae describes the Asian lion sub-population as being closely related to the lion subspecies in the northern, western and central regions of Africa (*Panthera leo leo*) which is Regionally Critically Endangered on the global IUCN Red List while the southern and eastern African lions (*Panthera leo melanochaita*) which are Regionally Endangered have been classified as a distinct subspecies (Kitchener *et al.* 2017). In Kenya, the southern sub-species of the lion (*Panthera leo melanochaita;* Hamilton Smith (1842)) is listed as a protected animal in the Wildlife Conservation and Management Act .CAP376 (WCMA

2013). The lion population in Kenya has declined from 2700 individuals in 2000 to 2000 individuals in 2010 (KWS 2014). The current known permanent lion range in Kenya is 18% of the total land surface area of the country, with large populations being documented in the Maasai Mara and Tsavo complex protected areas (KWS 2008). In addition, there are important lion populations outside protected areas in Laikipia and Maasailand. Their status elsewhere is poorly known (KWS 2008).

This decline of lion populations during the past decades has been attributed to the loss of habitat due to human encroachment, decline of prey populations and human-lion conflict; leading to deliberate as well as retaliatory killing by livestock owners (Sillero-Zubiri & Laurenson 2001; Thirgood *et al.,* 2005). Substantial human-lion conflict cases have been shown to result from prey depletion and the fact that lion home ranges are often larger than the surface area of national parks which often results in an overlap with human dominated landscapes (Woodroffe 2000; Winterbach *et al.,* 2013). Local traditions and negative attitudes towards lions have also been noted to contribute to deliberate lion killing (Tuqa *et al.*, 2015; Hazzah *et al.,* 2017; Lesilau, 2019). Some studies suggest that the main factors influencing livestock predation patterns include the number of livestock in the village, distance to the park boundary from the village, seasonality, and the behaviour of individual lions (Van Bommel *et al.,* 2007; Tuqa *et al.,* 2015). Despite the highly complex nature of human-carnivore conflicts; perceived costs and damages may lead to lion persecution and retaliatory killing (Dickman 2010; Hazzah *et al.,* 2014). Lions are particularly vulnerable to retaliatory killing due to the ease of finding and approaching them compared to other predators (Tuqa *et al.,* 2015). Also, the prestige of killing a lion in some societies, like the Maasai and Samburu in Kenya, and the tendency of lions to return to a kill the following night contributes to increased mortality (Hazzah *et al.,* 2009).

Schaller (1972) grouped lions into four age classes for ease of studying their population and social structure which include small cubs (0-1 year), large cubs (1-2 years), sub-adults (2 – 4 years) and adults (4 years and above). Studies submit that the age of male lions can be estimated on the basis of mane size, mane colour and nose pigmentation, although these phenotypes have been shown to vary greatly across geographic range (West and Packer 2002). Whitman *et al.* 2004 found the extent of dark pigmentation in the tip of the nose to be the most efficient index in estimating the ages of both male and female lions in Serengeti and Ngorongoro conservation areas. The rhinarium of the lion becomes increasingly freckled with age (Whitman et al. 2004). Lions live in fission-fusion social units (prides) that allow pride members to form subgroups of differing sizes. These units are useful for group foraging as well as protection of young ones and long-term territories (Schaller 1972; Packer *et al.,* 1990). A pride of lions consists of 2-35 individuals, with 2-18 related adult females and 1-7 adult males, either related or unrelated, and their offspring (Rudnai 1973). There are indications that the larger prides encountered in some areas could be an adaptation to the presence of kleptoparasites such as spotted hyaenas, which occur in clans of large sizes (Rudnai 1973). Smaller prides take longer to consume a given prey animal and have less defence force thereby increasing their vulnerability to molestation by spotted hyaenas. In competition for a carcass, superiority depends on the relative number of lions to spotted hyaenas (Schaller, 1972). Spotted hyaenas in large clans have been identified as successful in driving lions off their kill on several occasions (Rudnai 1973).

Lions spend most of their time within a defined area usually known as the lion’s 'home range'. A lion’s home range is defined as “the area covered by an individual in its normal activities of foraging, mating and caring for the young” (Burt, 1943). This is different from the lion’s ‘territory’, which implies an area that is kept free of all, or a certain class of, conspecifics (Burt 1943). An animal's territory may include all of its home range, or, in most cases, constitute only a certain, part of it that it defends. Home range sizes vary in space and time, from 20km^2 to more than 1000km^2 (MCP 100%), as influenced by social interaction, seasonality, prey and resource availability (Schaller, 1972; Whitman *et al.* 2004; Sogbohossou *et al.* 2014). Home range size is generally related to pride size, individual age and sex; with home range size increasing relative to increase in group size (Packer *et al.*2005; Loveridge *et al.,* 2009; Tuqa *et al.*2014). Drought causes prey species to disperse, resulting in a temporary increase of lion home range sizes, which reduces with increased water supply and an influx of prey species (Bauer & de Iongh, 2005; Loveridge *et al.*, 2009). This is usually not always the case in parks such as Amboseli National park where there is a large permanent water body inside the park that causes wildlife to return to the park during the dry season and disperse during the wet season (Tuqa 2015). Measuring an animal's home-range dynamics is important for most ecological studies, particularly those concerned with the distribution of resources, habitat utilization by individuals and their interactions (Harris et al. 2010). Large carnivores living in human-dominated landscapes often exist in 'Landscapes of Fear' whereby they are faced with the challenge of spatio-temporally adapting their activity patterns in strategic ways that enhance their survival, while minimising the risk of human caused mortality (Oriol-Cotterill *et al*., 2015; Lesilau *et. al.,* 2018). This has led to the 'Landscapes of Coexistence' concept whereby the availability of valuable resources such as availability of pasture (which attracts prey), livestock (which is easy prey), and water resources during drought periods in human-dominated landscapes often introduce complexities which mean that the avoidance of these landscapes results in substantial foraging costs for large carnivores (Oriol-Cotterill *et al*., 2015; Lesilau *et. al.,* 2018).

1.0.2 Human dimensions of carnivore conservation

Due to the precarious conservation status of many felid species, there is a crucial need to develop effective human-felid conflict management strategies that aim to address the highly complex nature of the conflicts as well as reconcile human needs with those of felid populations (Inskip & Zimmermann, 2009; Ogada 2015). This will require the development of tailor-made solutions such as local revenue from photographic or trophy hunting based tourism for lions living in the periphery of protected areas (Nelson *et al.,* 2013) to fencing in order to keep lions inside protected areas (Packer *et al.* 2013; Pekor *et al.* 2019). Local communities living near protected areas often bear the costs of co-existing with large carnivores, which depend highly on prey living in human dominated landscapes (Dickman et. al.2011). Large carnivores are however valued highly by people living farther from these local areas; both for their intrinsic and touristic value (Dickman et al. 2011). Carnivore depredations on livestock can induce high costs to farmers as can be exemplified by data from Ruaha National Park in Tanzania (Dickman et. al.2011). A study in this protected area showed that livestock depredation by carnivores' costs farmers ~18% of their total annual income (Dickman et. al.2011). Villagers normally receive little to no benefits at all for living with carnivores to offset their losses, despite the presence of carnivores being a significant tourism revenue generator at the national level (Inskip & Zimmermann, 2009; Lindsey et al. 2012).

Economic loss due to carnivore depredation has been cited as the most common cause of human-lion conflict (Inskip & Zimmermann, 2009). Local communities often argue that they experience fewer personal benefits from living near protected areas relative to the costs incurred from wildlife roaming freely into their lands (Sillero-Zubiri and Laurenson, 2001). Antagonism towards the parks and park personnel often translates to conflict with wildlife as the locals feel as if their needs are being neglected in contrast to outsiders' needs (Naughton-Treves and Treves, 2005). Deep-rooted cultural and religious beliefs can also play a big role in influencing conflict (Hazzah, 2011; Kolipaka *et al.* 2018). This can be exacerbated by inter-tribal tension in areas with more than one ethnic group living close together such as the Meru Conservation Area (MCA) (Otuoma 2004). In such areas, depredation incidences can ignite conflicts in cases where neighbouring tribes accuse each other of using magical powers to control predators into causing damage on the opposite tribe (West, 2001; Dickman 2010). These beliefs bring about a human-human dimension of carnivore conflicts where for example a witch doctor could be targeted as a result of carnivore related conflict when an affected ethnic group believes that he/she is controlling the predators causing the damage (Redpath *et al.,* 2015). Emerging non-discriminatory methods of retaliatory killings on carnivores such as poisoning through the lacing of livestock carcasses with toxic pesticides like carbofuran have also been identified as significant factors leading to lion decline in Africa in recent times (Ogada 2014). KWS developed a wildlife poisoning incident protocol in 2018 to control poisoning incidences in the country in response to reported cases across the country (KWS 2018). There are indications however that much of this killing happens without government oversight (KWS 2018). Some suggestions for enhancing human-carnivore coexistence include consolation schemes, utilisation of bottom-up approaches in working with villagers to protect livestock from attacks, increasing positive interaction of locals with park personnel, as well as encouraging open inter-tribal discussion on carnivores (Bauer *et al. 2015;* Dickman, 2015; Redpath *et al.,* 2015; Tuqa, 2015).

1.0.2.1 Attitudes towards carnivores

Studies suggest that significant conflicts are still experienced even after the successful control of damage that is directly caused by wildlife (Dickman 2010; Marchini *et al.,* 2012). This highlights the importance of addressing underlying human–human conflicts, either between authorities and local people, or between people of different cultural backgrounds (Treves and Karanth 2003; Dickman 2010; Kolipaka *et al.,* 2015; Hazzah *et al.* 2017). Understanding the factors that influence the level of willingness by local farmers to tolerate carnivore presence helps to inform the development of effective human-carnivore conflict mitigation strategies (Mkonyi *et al.* 2017). People's attitudes towards wildlife are complex and often influenced by socio-economic and ecological factors as diverse as religious or political affiliation, ethnicity and cultural beliefs, access to natural resources, amount of livestock lost due to depredation, level of wealth/livestock owned, carnivore knowledge and education level, as well as distance from park boundary; all of which play a significant role in shaping the intensity of the conflict (Dickman 2010; Dickman *et al.* 2013; Kolipaka *et al.,* 2017; Gebresenbet *et al.* 2018a). Indigenous pastoralist groups generally adhere to many cultural norms and taboos that guide their behaviour towards the natural world and the wildlife in these areas (Dickman 2010; Kolipaka *et al.,* 2017). Moreover, large carnivores also trigger fear within people in some instances which often leads people to retaliate on carnivores and promoters of carnivore conservation programs (Chapron et al. 2014; Kolipaka *et al.,* 2017). This could potentially lead to human-induced mortality of large carnivores, indifference to their poaching or limited support to the efforts to conserve them which are all factors linked to large carnivore decline at the global scale (Inskip et al. 2013). However, there is also significant evidence showing that local people can coexist with large carnivores despite the threats posed to human interests by the carnivores which highlights the need for conservation planners to address the underlying factors that enable human-carnivore coexistence for more sustainable solutions (Kolipaka *et al.,* 2017). Developing a broader awareness of conflict drivers will improve understanding of the underlying factors that influence this critical conservation issue (Dickman 2010).

Studies show evidence that the lack of lion-related benefits for local people amplifies the notion that lions are conserved at the cost of the safety and economic subsistence of local communities (Bruner et al, 2001; Gebresenbet *et. al.* 2018b). For example, Romañach et al, (2007) reported during a study in Central Kenya that local people claimed they would be more tolerant of depredations if they benefited from carnivore conservation actions, and members of the community who received an income from tourism had positive attitudes towards predators. Hazzah et al (2014), also provided evidence that lion killing can be reduced by working within the cultural context of the Maasai. They argued that participatory approaches which engage locals from planning to implementation of conservation actions, promote legitimacy of proposed solutions to human-wildlife conflicts. However, if locals are passive participants, the participatory approach remains nominal and lacks power-sharing and partnership (Twyman 2000). Arnstein (1969) proposes that community participation and collaboration can become effective if guided through levels of participation ranging from a non-participatory stage (in which local populations are only be educated on the importance of carnivores) to a citizen empowerment stage (where individuals actively participate in the conservation process as well as hold governance and managerial positions). My study looks at how different factors influence farmers' attitudes towards carnivores in the MCA, and explores possibilities of incorporating increasingly innovative and interdisciplinary mitigation approaches that successfully facilitate the shift from conflict to coexistence in the MCA.

1.0.2.2 Livestock husbandry techniques

Livestock husbandry techniques influence the likelihood of conflict with carnivores whereby studies suggest that seasonality in cattle herding practices influences the vulnerability of cattle to depredation (Mishra, 1997, Ogada *et al.,* 2003, Wang and Macdonald, 2006, Tumenta *et al.,* 2013). Wang and Macdonald (2006) reported that herdsmen in Bhutan, who grazed their livestock closer to villages, suffered fewer losses to predators than those who grazed their animals in distant pastures. Other studies have also found that livestock which graze further away from villages (Mishra, 1997) and closer to protected/forested areas (Conforti and de Azevedo, 2003, Hemson *et al.,* 2009) are more vulnerable to predation by large carnivores (Kolipaka *et al.* 2017). Livestock depredation by lions and leopards has been reported to be higher in farmlands closer to the boundaries of their respective PAs than farther away in the Chirisa Safari Area in Zimbabwe and Khutse Game Reserve in Botswana (Butler, 2000, Schiess-Meier *et al.,* 2007). Wang and Macdonald (2006) also reported that traditional enclosures with sparse branches and the absence of enclosures in most cases increase predation prevalence in Benin's Pendjari National Reserve. Improved fences and walls are expensive but they are the most commonly used method to reduce predation frequency (Ogada *et al.*, 2003; Treves and Karanth 2003; Packer *et al.* 2013). Lesilau *et al* (2018) observed that lions take livestock during the day time when the opportunity to get them at night becomes difficult as a result of the installation of deterrent flashlights in bomas during a study at the Nairobi National Park in Kenya. This confirms the opportunistic adaptation of lion behaviour. In Botswana, livestock are frequently not herded and are often left to wander outside enclosures at night which results in increased predation (Hemson, 2003). While people did complain that lions raided their enclosures, the majority of livestock kills recorded were far away from the enclosures, indeed data from GPS collared cattle and interviews suggested that between 13-20% of livestock were wandering around untended at night, making depredation almost inevitable (Hemson, 2003).

1.0.2.3 Human-carnivore conflict intervention

Some notable initiatives that work to promote human-carnivore coexistence include the Lion Guardians model that empowers local communities by making use of local cultural values and carnivore knowledge with the aim of promoting human-lion coexistence and monitoring local lion populations (Hazzah et al 2014). Compensation or consolation schemes such as the Predator Conservation Fund (PCF) have been used for the purposes of better balancing the distribution of costs and benefits related to conserving large carnivores although their implementation is faced with a lot of challenges in comparison to insurance schemes (Hussain 2000; Naughton-Treves et al. 2003; Hazzah et al 2014). The PCF model involves incident verification, compensation payments, and penalties to ensure program rules are not violated; although such privately funded compensation programs still face challenges regarding their long-term financial sustainability and ability to potentially induce ethical conundrums such as reduced livestock guarding efforts or payments claimed for livestock lost through other causes (Hazzah *et al* 2014). The Project Snow Leopard (PSL) based in Baltistan, Pakistan provides a good example of the insurance scheme model. The project supports local farmers in ensuring every head of livestock owned is covered by the insurance scheme, and any financial balances are provided for by profits from trekking expeditions that focus on the snow leopard (Hussain 2000). The insurance scheme is jointly managed by a village management committee and PSL staff and is structured in such a way that villagers can monitor each other thereby creating incentives to avoid cheating the system. Insurance schemes therefore have a better potential of reducing costs by individual livestock farmers whereby, they encourage local farmers to set aside a collective pool of money or livestock equal to the value of the annual average depredation rate if designed appropriately (Hussain 2000).

1.1 RESEARCH OBJECTIVES

This master project contributes to the PhD research of Luka Narisha and Kevin Groen from the Institute of Environmental Sciences (CML) in the University of Leiden. The main aim of this study is to analyse how different environmental and anthropogenic factors influence lion ecology and status around the MNP in a spatio-temporal context. My study focusses on understanding lion population size, pride structure, reproductive success, foraging success, lion distribution in and around the MNP and factors that influence human-lion interactions in the area. Data used has been collected from lion populations and observed prey carcasses within the MNP as well as local farmers and other stakeholders who live around the MNP.

I hypothesise that lion distribution in the area is influenced by habitat characteristics and precipitation; as well as the distribution of households and livestock across the different villages (sub-locations) surrounding the MCA. I further hypothesise that variations in attitudes towards lions among the different villages (sub-locations) surrounding the MCA are influenced by distance to park boundary, cultural background, livestock ownership, as well as literacy and carnivore knowledge levels. Finally, I hypothesise that the amount of livestock depredated influences a farmer's willingness to seek compensation. The results obtained from my study may assist in informing strategies aimed at managing lion populations as well as human-carnivore interactions in the area in the future.

The research questions for the study include:

1. Lion population size, pride structure, reproductive success, foraging success and distribution:
    - 1.1. What is the current lion population size and density in the MNP?
    - 1.2. What is the male: female ratio?
    - 1.3. What is the adult: juvenile ratio?
    - 1.4. What is the influence of reproductive success on pride structure in the MNP?
    - 1.5. What is the frequency and location of feeding events by lions in the MNP based on observed carcasses?
    - 1.6. How does reproductive success and foraging success influence lion pride structure in the MNP?
    - 1.7. What is the potential distribution of lions in and around Meru National Park?
    - 1.8. Which environmental and anthropogenic factors influence lion distribution in and around MNP?
2. Carnivore knowledge and attitudes towards lions by different local stakeholders:
    - 2.1. What is the general knowledge on different carnivore species and their tracks by the different stakeholders?
    - 2.2. What is the general attitude towards lions and other carnivores in the area?
    - 2.3. What are the main factors influencing respondents' attitudes towards lions and other carnivores in the area?
3. Factors influencing livestock depredation patterns by lions in the area:
    - 3.1. What is the intensity of depredation incidences relative to livestock type and carnivore type?
    - 3.2. Where do majority of livestock depredation incidences occur?
    - 3.3. What is the frequency of carnivore attacks on humans in the area?
    - 3.4. What is the influence of different livestock husbandry practices on livestock survival rate in the area?
    - 3.5. What is the influence of livestock depredation on willingness by farmers to seek compensation?

CHAPTER TWO

2.0 METHODOLOGY

2.0.1 Study area

The Meru Conservation Area (MCA) is situated in the Somali-Maasai regional centre of endemism. It is the second largest conservation area in Kenya and is one of the remaining true wilderness areas in Kenya. It was made a UNESCO World Heritage Site in 2010 and hosts the lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocouta crocuta*), and herbivores like Grevy's Zebra (Equus *Grevyi)*, Black Rhinoceros (*Diceros Biconis*), and introduced southern White Rhinoceros (*Ceratotherium simum*). The MCA covers an area of ~4,000km^2 which includes (Figure 1):

I. Meru National Park (MNP) – Located in Meru North District, covering an area of 884km^2. Gazetted in 1967 and is one of the oldest parks in Kenya.
II. Kora National Park (KNP) – Covers an area of 1,787 km^2 making it the largest protected area in the MCA. Gazetted as a natural reserve in 1973, and as a park in 1990.
III. Bisanadi National Reserve (BNR) – Located North East of MNP, covering an area of 606km^2. It is an important dispersal area for many wildlife
IV. North Kitui/Mwingi National Reserve (MNR) – Located south of MNP and covers an area of 745km^2.
V. North Rahole Reserve (NRR) – Located north of KNP and covers an area of 1231km^2.

The four PAs have a high degree of ecological interdependence, especially with regards to large mammal movements. There are also significant synergistic benefits to be achieved by managing the area holistically, in particular regarding the promotion of human-carnivore conflict mitigation and security operations, and in the promotion and development of the MCA as a single visitor destination. For these reasons, the MCA has in recent years been managed by KWS as a single management unit, with a Headquarters at Murera in the north-west corner of Meru National Park. The MNP, established under legal notice 4756 of18/12/66, boundary plan number 204/37, covers an area of approximately 884 km^2 (Sitienei *et al.,* 2014). The MNP was established as a game reserve in 1957 by Meru County Council and gazetted as a National Park in 1967 (Narisha 2018). It is located in the Eastern Province, 0°20′∼0°10′S, 38°0′∼38°25′E (Fig. 1). It is situated between 300 m above sea level at the Tana River southern boundary and 1000 m above sea level at the base of the Nyambene Hills in the north (Sitienei, *et.al,* 2014). The MNP has been the main focus of tourism and management in the MCA, contains the highest concentrations of wildlife in the MCA, and currently contains the majority of the Protected Area (PA) infrastructure in the MCA such as roads and airstrips (Lala 2011). 70km of the protected area is fenced on the western boundary of MNP to reduce Human Wildlife Conflict (HWC), and it is the only PA in the MCA that is not seriously impacted by livestock incursions during the dry season (KWS 2006).

The rainfall regime in MNP is characterized by two rainy seasons. The long rains are experienced during the months of March–May and the short rains starting in October–December annually. However, the park experiences differential precipitation with strips around the north-western boundary receiving most precipitation which correlates with the area's elevation (Lala 2011). It is for this reason that the strips remain green throughout with the lowlands receiving low rainfall as they are on the leeward side. The southern half of the park, which lies on the equator, is dry. The annual rainfall can fluctuate considerably with wet years having more than double the mean annual rainfall and dry years less than half or quarter of the mean annual rainfall. Drought period in the park can last between 4 to 8 months (Meru National Park Annual Report, 2003–2004). The geology of MNP is divided into the northern and southern sections. The northern part is formed of Pleistocene lava flows from the Nyambene ridges and the Mount Kenya volcanic complex, while the southern part comprises of exposed pre-Cambrian rock basement (Lala 2011). The lava that flowed along pre-existing river valleys as a result of Nyambene hills' eruption diverted the watercourses thereby causing rivers that flowed along the edge of tongue-shaped lava flows, with their confluence uniting at tongue points as can be seen at the Kindani-Rojewero River confluence (Lala 2011). The olivine-basalt lava flows produce greyish brown soils on gentle slopes toward the Nyambene Ridges and greyish-black soils in swampy and river valleys (Lala 2011). Other areas in MNP have grey volcanic alluvial soils formed in pre-existing lakebeds from the Pleistocene Epoch. Fossiliferous Limestone, formed as a result of river damming by the lava flows, occurs on the banks of Rojewero River towards its confluence with the Murera River. Red sandy soil covers the basement rocks on the eastern park boundary as well as the north eastern side of the Murera river and its northern confluence with Rojewero river (Lala 2011). Metamorphic rocks occur in the south of Rojewero and Kiolu rivers while Pleistocene lava flows form ranges between the rivers and cover biotite gneiss of the basement systems. There are volcanic alluvial soils and exposed biotite gneiss covered by red soils on the Ura river at Ntoe Ndogo near the Ura gate (Lala 2011). The highest hill in the park is called Mugwongo (also known as the Elsa's Kopje) with a height of 660 feet, which is used by visitors as a viewpoint. Other hills include Ntoe Kubwa, Ntoe Ndogo and Leopard Rock that are composed of Precambrian rocks.

The Tana River, which marks the southern limit of the geomorphic area, is the largest river in Kenya and starts north of Nairobi, 250 km from the park. Fourteen rivers cross MNP including the Tana, Rojewero, Kiolu, Ura, Murera, Bisanadi, Bwatherongi, Mutundu, Makutano, Mulika, Njoru ya Kina, Kindani, Utambachago and Kachoradu (Fig. 1). The swamps include Mulika, Bwatherongi, Leopard, Mururi and Mungwongo (Fig. 3). The distribution of water resources is critical to understanding the MCA's ecosystems as it is the key to the natural plant life distribution and important to the habitats that attract the wild fauna in the area (Lala 2011). The vegetation in the park exists in three broad types of Acacia species, which occupy much of the park from the northern parts extending well past the central area. Combretum and Terminalia woodland dominate the western region, whereas the southern is densely occupied by the Commiphora species. Common fauna includes African elephants (Loxodonta africana africana) (Meru National Park Annual Report, 2003–2004).

The main ethnic communities inhabiting the areas around the MCA include Maasai, Borana, Somali, Meru, Kikuyu and Turkana (Otuoma 2004; Affognon *et al.* 2017). The Maasai, Borana and Somali are mainly transhumant pastoralists while the Turkana mainly practise nomadic pastoralism (Affognon *et al.* 2017). The Meru and Kikuyu ethnic groups mainly practise agro-pastoralism (Otuoma 2004). A survey done by the Kenya Central Bureau of Statistics in the six districts bordering the MCA demonstrated that ~70% of the households occupying the buffer zones that surround the MCA belong to migrant communities who moved to the area between 1980 and 2000 (Otuoma 2004). This led to an increase in human population density in the area from 50 people/km^2 to 125 people/km^2 in the southern Tharaka zone, and 126 people/km^2 to >500 people/km^2 in the western buffer zones bordering Nyambene Ranges. Pure pastoralists that settled in the MCA between 1980 and 2000, who constitute 12.5% of the total households, were found to have migrated from Isiolo, Garrisa, Marsabit and Mandera in northern Kenya (Otuoma 2004). 45% of the households in the area practise agro-pastoralism which is the main land use in the area (Otuoma 2004). The pastoralist communities mainly occupy the northern pastoral lands, although sometimes they are also spotted in the communal grazing lands and wildlife dispersal areas of the western Meru National Park boundary as well as towards the southern Tharaka areas, particularly in the dry season due to lack of formal boundaries in their grazing patterns (Otuoma 2004).

The MCA was gazetted as a protected area mainly for the purpose of wildlife management (KWS 2006). Main livestock species found in the area include cattle in the western boundary of the Meru National Park (MNP); and cattle, goats and donkeys in the southern Tharaka area; as well as cattle, goats, sheep and camel in the northern pastoral areas (KWS 1998; Otuoma 2004). Carnivore attacks on livestock have mostly been reported in the northern buffer zones that are generally occupied by pastoralists, with cattle being the most affected livestock species as well as occasional attacks on sheep and goats (Otuoma 2004). Human attacks by carnivores have also been reported in the area; particularly in Murera and Kindani in the West and Kinna and Rapsu in the North (Otuoma 2004). Reports indicate that attacks on humans and livestock have mainly been caused by lions and to a lesser extent by leopards (KWS 1998; Otuoma 2004). Meru NP has received a large number of translocated problem lions from other national parks over the past decades (Narisha 2018). To date, the fate of these translocated problem lions is not known, and there are indications that these lions are pushed out of Meru NP by resident lion populations in the area. This may lead to increased levels of conflict in the surrounding areas.

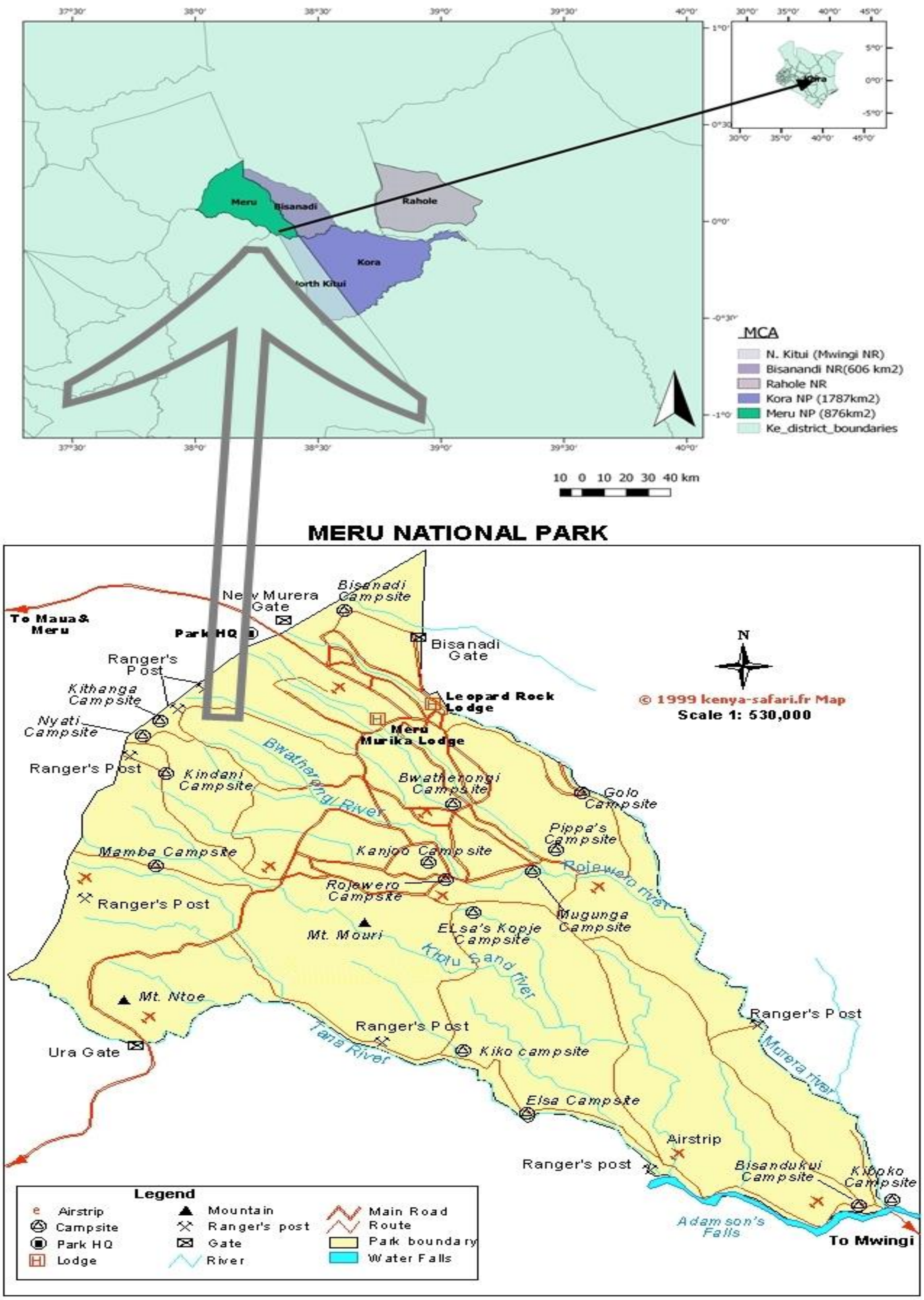

Figure 1: Map showing the position of Meru National Park within the Meru Conservation Area and Kenya (KWS 2014).

2.1 DATA COLLECTION

2.1.1 Lion population size, pride structure, reproductive success, foraging success and distribution

Fieldwork took place from 5th February, 2019 until 17th April, 2019. I collaborated with a team consisting of Master students Mateo Bal and Gert Jan Goeminne. I performed direct counts (Durant *et al.,* 2011) from direct opportunistic observations and call-up surveys (adapted according to Ogutu and Dublin, 1998) where different vocalisations were broadcasted to attract lions to a survey point to obtain data for population and social structure analyses. I also observed lions during regular prey transect counts. I applied the whisker spot method (Pennyquick & Rudnai, 1970) which uses photos of vibrissae patterns and other unique body markings to identify lions individually. The core survey area was c.a. 381km^2 which is approximately half size of the MNP (Fig. 2). We were only able to perform two call-up surveys with a total of six call up events due to logistical issues whereby we surveyed random points set up >25km apart (straight distance) from each other to avoid double counting (Mills et al. 2001). In cases of impenetrable vegetation, we relocated to a point of maximum 500m in either direction. We surveyed 3 points per night when lions are most active (Schaller 1972; Stander 1992) and an area was only surveyed once to avoid habituation of lions. We played recordings of a dying buffalo followed by laughing hyenas with each recording running for 5 minutes and then we would scan the area for five minutes to identify any carnivores present. The data was used to estimate the lion population structure and distribution as well as examine factors influencing the lion's distribution in and around MNP.

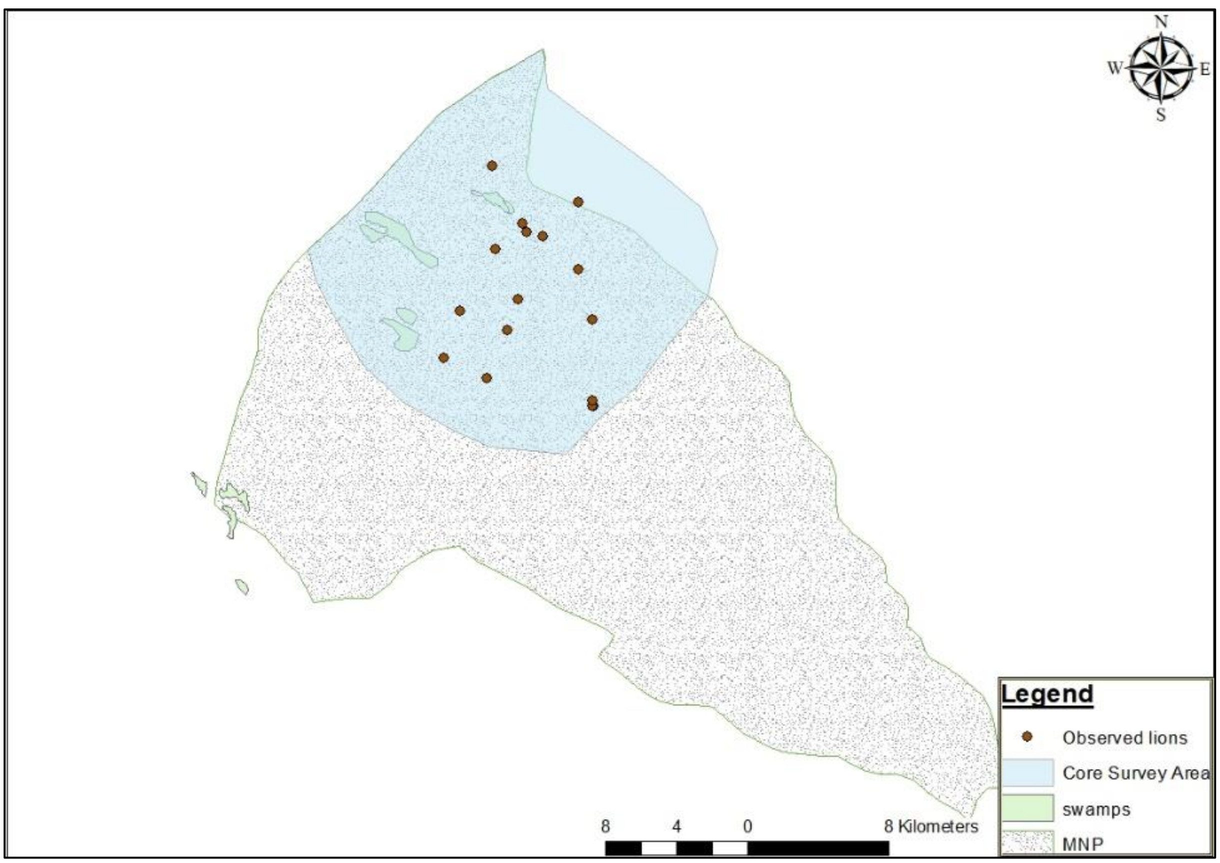

Figure 2: Map showing the core survey area for lion observation.

When a lion was encountered, the location was noted using a GPS unit (Garmin etrex). Lions were grouped into two main categories namely juveniles (cubs) and adults (sub-adults and adults) for purposes of increasing accuracy in age classification. This age classification was based on the approximation of the following age categories: small cubs (0 – 1 year), large cubs (1 - 2 year), sub-adults (2 - 4 year) and adults (> 4 year), following Schaller (1972). Additional notes were made on date, time, sex, health status, habitat characteristics, behaviour, and if the lion was in a group; the composition of that group (see form in Appendix 2). All lions were identified to the individual level by investigating typical characteristics such as unique marks, scars, ear notches and presence of scrotum allowing comparisons between individuals in order to examine the social structure.

I then collated lion observation data from the KWS/Born Free carnivore monitoring team collected from 2016-2019 that I used to develop pride histories to enable me to understand the reproductive success of lions in the MNP. I also recorded prey carcasses from lion kills that were observed around the MNP. Carcass data was collected through opportunistic searches during the lion observation exercises as well as through following up on reports from rangers and the KWS/Born Free carnivore monitoring team whenever a hunting incidence or lion kill carcass was sighted. Carcass data helps me to understand the frequency of lion feeding events per unit time which provides insights on foraging success of the MNP lions. Finally, I collated average monthly precipitation, river level and conflict data from the KWS research office that was collected from 2008-2018 to examine temporal and seasonal variations as well as complement the lion observation data I had collected.

2.1.2 Human dimensions of carnivore conservation

Data on human dimensions of lion conservation in the MCA was collected using semi-structured questionnaires which were conducted from households around the MNP. I conducted 120 semi-structured questionnaires (see form in appendix 3), on local pastoralist households from nine different villages (also referred to as sub-locations) around the MNP (Fig. 3) from 17th February to 17th April, 2019. Respondents were selected opportunistically all around the Meru National park buffer zone. A team consisting of the principal researcher and two research assistants conducted the survey. A printed description and survey form were offered to all participants who were required to give consent before taking part in the survey. The survey was then administered verbally in Swahili and the responses were translated by the principal researcher. Questions asked were based on previous survey questions (Otuoma 2004; Gebresenbet *et. al.* 2018b) that were refined following a pilot survey from 7th to 15th February. The questionnaire was divided into five sections (see appendix 3). The first two sections assessed the demographic and economic status of respondents. The third section assessed respondents' attitude, knowledge of, and coping with lion populations in and around MNP and was comprised of 15 questions using a Likert scale from 1 (strongly agree) to 5 (strongly disagree). The fourth section collected information on respondents' broad knowledge about carnivore species where they were asked to identify carnivores and their tracks by looking at photos of six carnivores, (Lion, spotted hyena, cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), striped hyena (*Hyaena hyaena*), and the African Wild dog (*Lycaon pictus*)). The last section of the questionnaire assessed the problem of lion attacks on humans and livestock, people's preventive actions, reasons for lion attacks, and the trend of these attacks in the past five years.

My data collection focused on: estimating the level of livestock depredation attributed to different carnivores; assessing local knowledge about carnivores; evaluating tolerance, husbandry practices and retaliatory actions towards lions; and documenting attitudes towards and cultural value of lions (see appendix 3). I also investigated how much livestock is lost to disease and theft in an effort to understand the finer details of livestock husbandry in the area. The nine different sub-locations neighbouring the MCA where the household surveys were conducted include: Korbesa, Kinna, Duse, Rapsu, Eskot, Mutuati, Baibiriu, Mauthini and Kaningo. (see Fig. 3). The first five sub-locations were from the Isiolo county, the side of the MCA where locals' livelihood is mainly based on pure pastoralism; two in Meru county, one in Tharaka and one in Mwingi counties, all of which practise mixed farming. For the survey, we opportunistically selected ~13 household heads (respondents hereafter) in each sub-location from the list of household head names provided by each location's chief office. If a household head was not present at the time of interview, household heads one door to the right of the selected one were interviewed. The questionnaire required about one hour to complete.

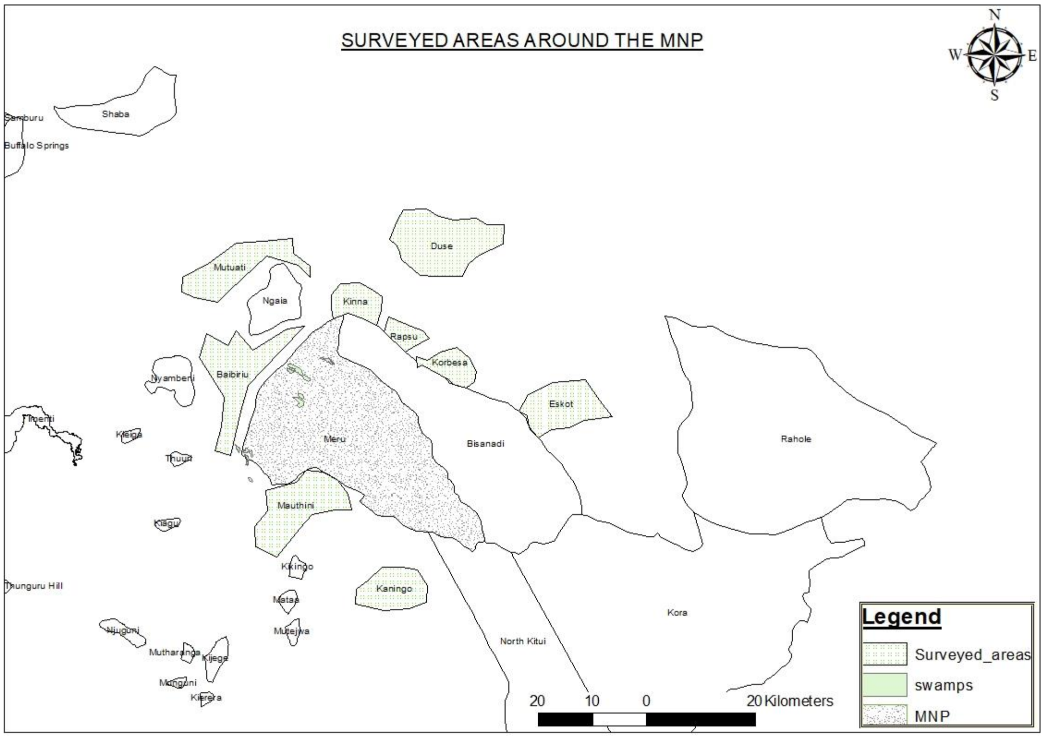

Figure 3: Map of areas around the MNP where the questionnaire survey was administered.

2.2 DATA ANALYSIS AND STATISTICS

2.2.1 Lion population size, pride structure, reproductive success, foraging success and distribution

Data obtained from opportunistic lion observations was used to analyse the lion population estimates and structure in the Meru National Park. Population density was estimated based on the core survey area (Fig. 2). The density estimate was calculated by dividing the total number of lions observed by the total core survey area (381km^2). Age-sex structure information obtained from the observation data was used to examine the population structure. I further recorded the frequency of observed pride sizes during our field work period. The Born Free lion monitoring data collected from 2016 – 2019, which was verified by interviewing Born Free and KWS staff involved in the lion monitoring process, was used to compile pride histories in order to understand the frequency of observed pride sizes in the park across a longer temporal scale. This information was then used to calculate reproductive success which was measured as the number of small cubs (≤1yr) per adult females per year. I further examined correlation between reproductive success and the preferred pride sizes in the area using a parabolic local regression as results from a Mann-U Whitney test indicated that the response variable is not normally distributed (McKnight *et al.* 2010).

The Locally Weighted Scatterplot Smoother, also known as a LOESS regression is the most common method used to smoothen a volatile data series (Cleveland 1979). It is a non-parametric method where least squares regression is performed in localized subsets, making it a suitable candidate for smoothing any numerical vector. It is therefore useful for investigating the behaviour of the response variable in more detail than would be possible when a simple linear model is used. In our case, we used 75% of the points in each localized subset to fit the curve. Data collected on confirmed carcasses of lion kills based on observations of successful lion hunts as well as reports from the KWS/Born Free carnivore monitoring team, park rangers and park visitors was used to examine foraging success of lions in the MNP by collating the relative abundance of captured prey biomass as well as the location of observed carcass sightings. This was further examined in relation to mean monthly observed lion pride sizes (sourced from the KWS/Born Free lion monitoring data 2016-2019); mean monthly precipitation in the MNP (sourced from KWS MNP rainfall data 2008-2018); mean monthly river levels (sourced from KWS MNP River Gauge data 2008-2018); and mean monthly reported conflict incidences per species for lions, hyenas and buffalos (sourced from KWS MNP PAC data 2008 – 2018) in order to gain further insights on the effect of seasonality on lion foraging success, distribution and human-lion conflict in the area.

Lion distribution range in the Meru National Park was modelled using a maximum entropy species distribution model (SDM; Merow *et al.* 2013). SDMs utilise presence points to estimate the similarity of the conditions at any site to the conditions at the locations of known occurrence (and perhaps of non-occurrence) of a phenomenon (Fourcade *et al.* 2014). This method predicts species ranges with environmental and anthropogenic data as predictors. Occurrence points were collated from the datasets collected through direct observation, call-up surveys and confirmed lion attacks from the questionnaire survey to model lion presence. Occurrence points from opportunistic lion observation data from the Born Free carnivore monitoring team collected from 2016 – 2019, and telemetry data (2016 -2018) were also incorporated. Predictor variables used to model potential lion distribution in the MNP include precipitation index (presented as the mean annual rainfall recorded from fourteen rain gauge stations spread across around the MCA from 2008 – 2018). This was calculated by finding the mean annual rainfall from daily rain gauge recordings at the rain stations and then finding the average annual rainfall level per station for the ten years.); habitat index (comprising of riverine forest, savannah woodland, savannah grasslands, agricultural land and pastoral land as recorded during the data collection period); livestock abundance index (calculated as the average number of livestock owned per household per sub-location around the MNP according to questionnaire responses as well as those recorded during the fieldwork period); and household abundance index (calculated as the average number of households per sub-location around the park; data sourced from KEBS 2009). The variables were standardized in the R statistical software with different values assigned to each occurrence point, then georeferenced and interpolated using the kriging tool in ArcMap 10.3 (ESRI Software, U.S.A.) to create maps at the scale of a 20 km buffer around the Meru National Park. The interpolation tool is useful in predicting unknown values for geographic point data, such as elevation, rainfall, chemical concentrations, and noise levels based on its ability to predict values for cells in a raster from a limited number of sample data points. The buffer radius was set based on the average radius of our questionnaire survey around the park. It was also assumed that a lion will be reported and controlled within an average of 20kms from the park boundary although telemetry data shows that collared translocated lions roam farther than 20kms from the park boundary (Goeminne 2020). A pairs plot was used to visually investigate collinearity in the variables (relative to the presence and background points). I then investigated the autocorrelation of the variables to reduce model overestimation as well as ensure no variables were left out while running the maxent model because I was interested in examining how each variable contributed to the distribution model (Boria et al. 2014). I used spatial jack-knifing analysis to evaluate the performance of spatially segregated and independent localities. I also selected background points to be used as pseudo-absence points for the model (Barve et al. 2011; Merow et al. 2013).

The use of maximum entropy for species distribution modelling relies on the Maxent program, which is an open source stand-alone Java software (http://biodiversityinformatics.amnh.org/open_source/maxent/).This package can be called in R via dismo. Maxent models can be tuned in several ways (Merow et al. 2013). Two common approaches are to: (1) adjust the regularization of the model (β) to specific thresholds; and (2) adjust the types of features considered. First, the regularization parameter can be changed manually. In this context, Maxent uses the lasso technique for regularization, such that coefficients that do not explain variation in presence locations are penalized and shrink toward zero. In this way, the default value for regulation is proportional to the number of presence locations and the variability in the environmental covariate at presence locations (Elith et al. 2011). The parameter, β, is a constant that is multiplied by the default regularization value. As β increases, a greater penalty is imposed.

We also evaluated the models with the evaluate function from the dismo package to get AUC statistics for ranking the models as well as estimate how the different variables influence the occurrence of lions across the Meru National Park. This function requires passing validation presence and absence points. The default approach in this function is the “logistic” output, whereas the underlying Maxent model output is termed “raw” output. In the raw output, probabilities across the region sum to 1, such that the probability in any given location is very low and is essentially a probability density, sometimes referred to as relative occurrence rate (ROR; Merow et al. 2013). The logistic output is a transformation of the raw output, aimed at providing probabilities that are more akin to probabilities of occurrence (Elith et al. 2011). In doing so, the average prediction for a location where a presence point occurrence with the logistic output approaches 0.5. Another alternative to the logistic and raw outputs is the cumulative log-log (cloglog) output (Fithian et al. 2015), which is better rooted in probability theory and is now the default output in the stand-alone Maxent software (Phillips et al. 2017). These different response outputs should not change the rank suitabilities from models, but they will change the absolute values such that care should be taken when implementing and interpreting output.

2.2.2 Human dimensions of carnivore conservation

Since households own different kinds of livestock, I used a conversion factor to calculate a standardized value of livestock ownership whereby the amount of a given livestock species is multiplied by its corresponding conversion factors (Table 1) to compute the Tropical Livestock Units (TLU) for that species that would be used in the analysis (Houerou and Hoste 1977; Njuki *et al.* 2011).

Table 1: Livestock conversion factors sourced from (Houerou and Hoste 1977).

LIVESTOCK TYPE	CONVERSION FACTOR
CAMELS	1.25
CATTLE	0.70
SHOATS	0.10
DONKEYS	0.50

I performed descriptive statistics to gain a basic understanding of the socio-economic background of the respondents as well as the attitude and livestock husbandry dynamics in the area. To compare the attitude of the respondents from different areas around MNP, I developed a composite attitude index by calculating the mean of responses for identical Likert Scale questions that measured attitude (Likert 1932). This was calculated by assigning values to responses (5: strongly agree, 4: agree, 3: neutral, 2: disagree, 1: strongly disagree) and multiplying the count of respondents for each question with its assigned value, summing the values, and dividing the sum by the total number of respondents. I fit a mixed effects logistic regression with an index of measuring attitude as the outcome variable to assess different factors influencing attitude towards lions around the MCA. I considered the question whether a respondent perceives any benefits related to the presence of lions in the area as the outcome variable whereby respondents who saw the benefits of co-existing with lions were presumed to have a positive attitude towards lions. Total number of livestock owned (as an index of wealth status), livestock depredated from 2008-2018, distance to park boundary, ethnic group, carnivore knowledge and education level of respondents as well as their interactions were considered as fixed effects. Respondent's sub-location was considered as a random effect. I then examined the distribution of the variables using jitter plots and violin plots which are useful for their ability to show skewness of the data. I further log transformed the scale to normalize the y axis which fairly improved the shape of the distributions. I then used the glmer command in the R statistical software to estimate a mixed effects logistic regression model based on an adaptive Gaussian Hermite approximation of the likelihood.

To understand how seasonality and different husbandry practices influence livestock loss in the area, I performed both principal component and linear discriminant analyses to explore the differences among the nine sub-locations as well as the two dominant economic activities (agro-pastoralism and pastoralism). I considered height of corral fence; livestock loss through depredation, theft and diseases; distance walked during both wet and dry seasons in search of pasture and water as well as the number of different husbandry methods used to prevent livestock depredation by carnivores to examine the similarities between different sub-locations. I then performed multivariate analyses in the R statistical software. Finally, I ran a Kruskas Wallis non-parametric test that compares the medians of ordinal variables with no definite distribution, to examine whether there were significant differences in amount of livestock depredated among those who were interested in receiving compensation and those who did not seek compensation.

CHAPTER THREE

3.0 RESULTS

3.0.1 Lion population size, pride structure, reproductive success, foraging success and distribution

I recorded a total of 20 lion observation incidences during 10 weeks of fieldwork, whereby the lion observation exercise took place for two days every week; with a total of 31 identified individual lions based on their whisker spot patterns, and other notable body features. The total density of lions in the park was calculated as 8.1 lions/100 km² including all ages and 6.8 lions/100 km² without cubs that are <1-year-old. I recorded 10 male and 11 female adult and sub-adult lions (>2 years old), which is a female: male sex ratio of 1.1:1. The recorded adult to juvenile ratio was 2.1:1 (15 adults, 6 sub-adults, 10 juveniles) (Fig. 4).

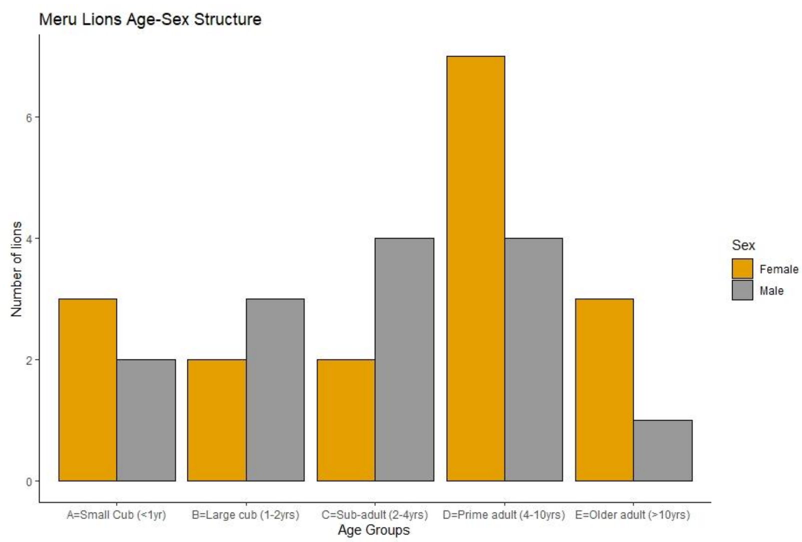

Figure 4: Detailed age structure classification of lions observed in the MNP from 7th February,2019 to 17th April, 2019.

We were not able to locate any of the collared lions, which includes translocated lions such as the Solio pride, despite getting a signal on the VHF telemetry device. This can be attributed to the nature of the thick vegetation in some parts of the park. Thus, these lions were not added in our population structure results. We however observed the so called 'Nairobi girls' pride' which currently includes a coalition of four sub-adult males that survived after their mothers who had been translocated into the park in 2012 died while hunting a buffalo in 2017 (pers. Comm. Peter Gitonga). Solitary adult lions (> 2 years-old) were observed 2 times. Groups of adult lions (≥ 2) were observed 16 times (Fig. 5). There was only one observation of solitary juveniles (Fig. 5).

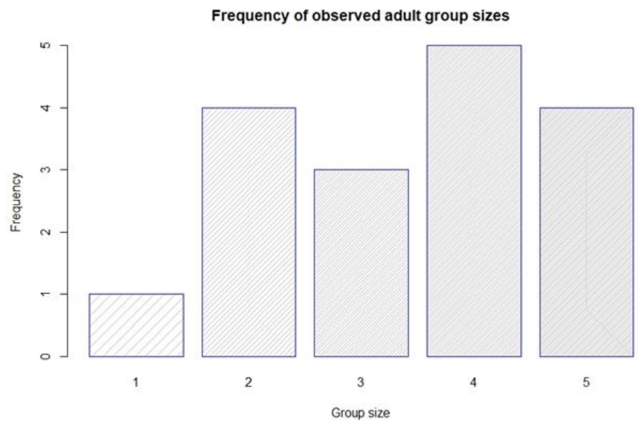

Figure 5: Frequency of observed group sizes of adult lions in the Meru National Park from 7th February, 2019 to 17th April, 2019.

The mean adult group size observed was 1.8 adult lions. I identified four main prides in the park, namely the "Mulika pride", "Elsa's pride", "Bisanadi pride" and "Nairobi girls' pride", which seem to separate and regroup together at different times in a fission-fusion organization. The Bisanadi pride which is situated in the Kinna triangle between Murera gate and leopard rock lodge (Fig. 6b) sometimes joins up with the two sanctuary females (also known as Virginia pride). The Mulika pride, which is situated between Mulika lodge, Bwatherongi and Kindani campsites (Fig. 1) also joins up with the G-coy pride at certain times (Fig. 6b). We also recorded two unknown sub-adult males in the area between Kindani and mamba campsites (Fig. 1) which we suspect could be part of the four Nairobi girls' coalition males as this is close to their territory. This can be seen in the dendrogram in (Fig. 6a). The Mulika pride consists of four pride females, one pride male, and six cubs. Elsa's pride consists of one pride male, two pride females and three cubs. Bisanadi pride consists of two pride males and two pride females but no cubs. Sanctuary pride also known as Virginia pride consists of two adult females while G-Coy consists of a female and male sub-adult. The 'Nairobi girls' is a coalition of four sub-adult males.

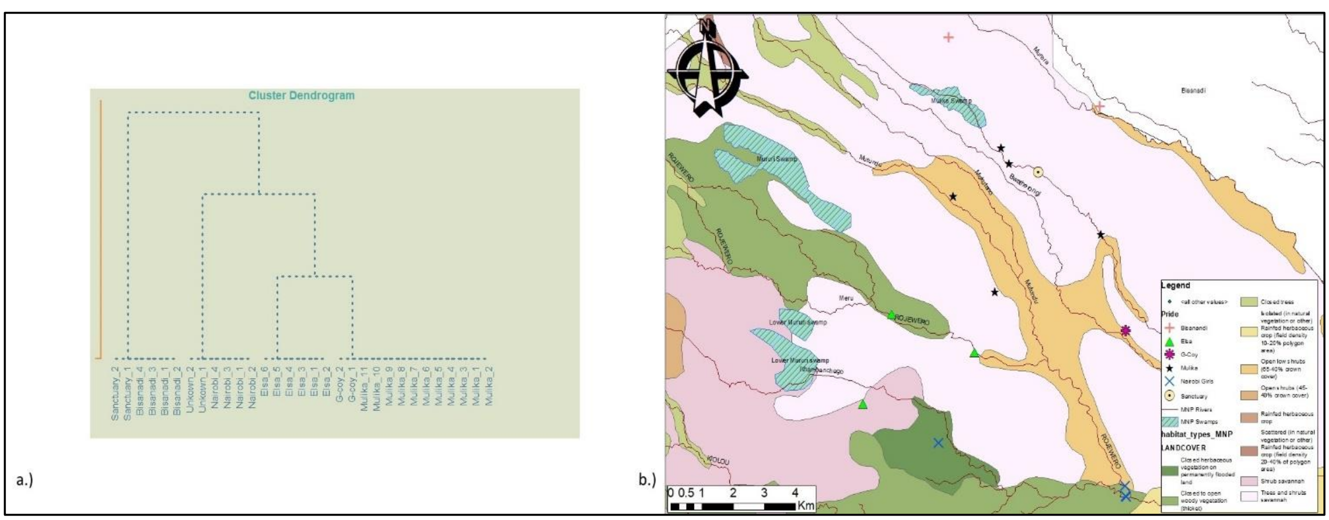

Figure 6: a.) A cluster dendrogram showing lion pride structure in the Meru National Park. b.) Map showing position of different lion prides and coalitions in the park.

Pride histories compiled from the Born Free lion monitoring data show that females in the MNP seem to prefer pride sizes of 8-11 lions although they have also been recorded to separate and form prides of 4-5 lions sometimes in a fission-fusion technique. This is mostly the case during dry periods. Prides of 4-7 lions seem to have the highest reproductive success while smaller and larger prides seem to have lower reproductive success in the park (Fig. 7a). There is no significant evidence of a positive correlation between preferred pride size and reproductive success in the area according to the local regression (Fig. 7b).

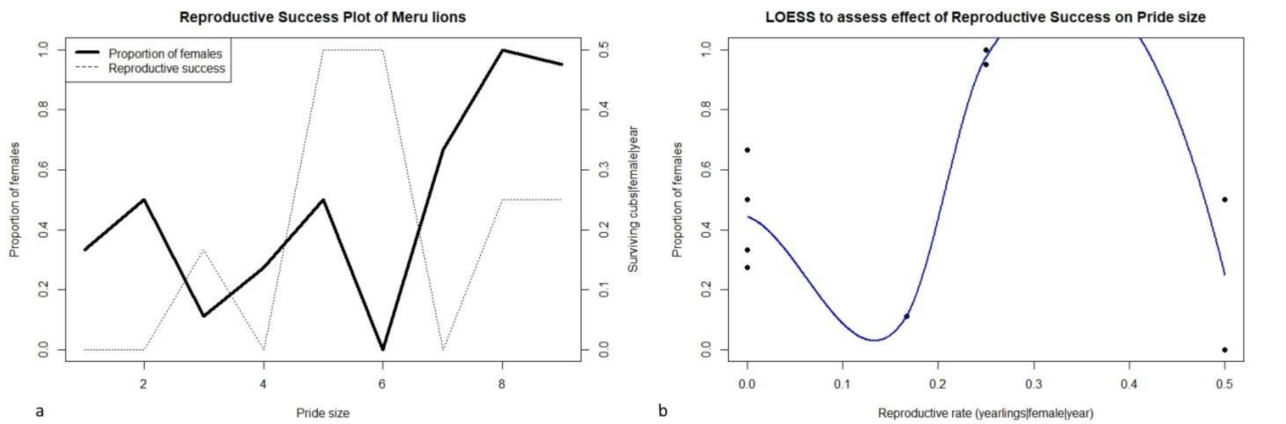

Figure 7: a). Line plot showing preferred pride sizes by female lions in the MNP in relation to reproductive success. b). Local regression examining the effect of reproductive success on proportion of females in the MNP lion prides.

Results from carcass counts suggest that Lions in the area prefer larger biomass, mainly buffalos (Fig. 8a). Most lion sighting locations (88%) and carcass sighting locations (74%) were recorded within 100m of waterways between River Murera and Rojewero (Fig. 8b), thereby highlighting the importance of hydrology in influencing both prey and lion distribution in the area.

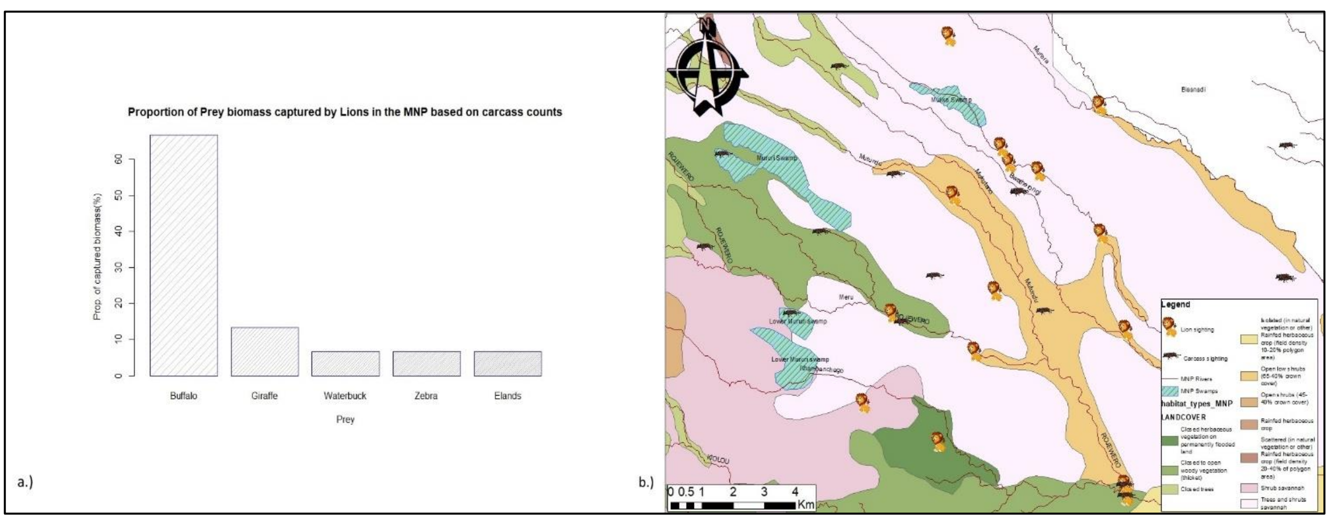

Figure 8:a.) Composition of kills by lions in the MNP based on carcass sightings data collected during the fieldwork period shows that lions in the park have the highest preference for the cape buffalo. b.) Position of recorded lion and carcass sightings in relation to rivers and swamps in the park.

Average monthly records of data collected from 2008 – 2018 by the KWS MNP research office indicate that rainfall in the area peaks in April and November with the driest period running from June to September (Fig. 9a). Apart from Murera river which is the main river in the park, the rest of the permanent rivers in the park such as Rojewero show a decline in water quantity during the driest periods in July and August (Fig. 9c). Records also indicate that reported incidences of both ungulate and carnivore related conflicts also peak during the driest periods in the area with a small temporal lag between the two peaks (Fig. 9b). Data from the Born Free lion monitoring team also shows a reduced number of lion sightings inside the park during the Driest months of the year (Fig. 9d).

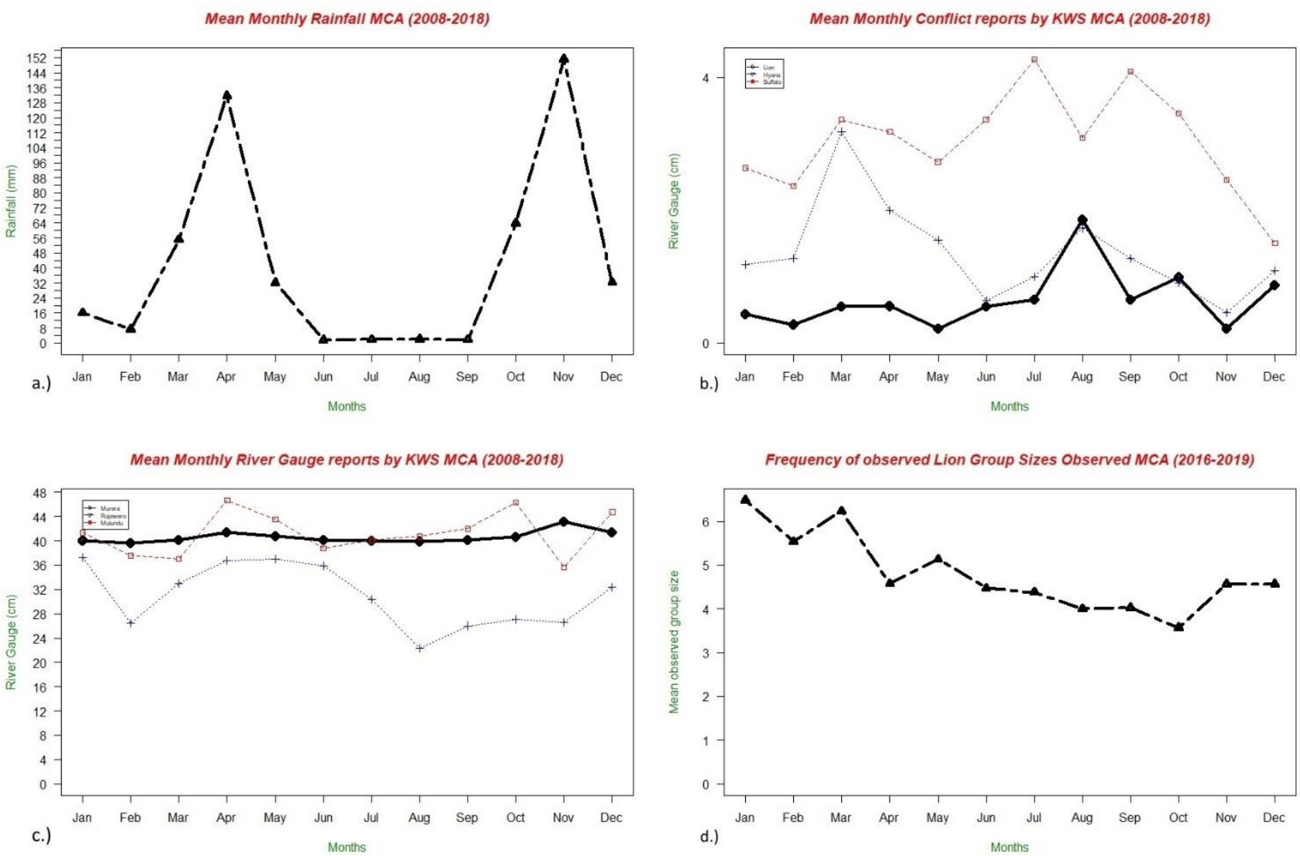

Figure 9: Graphs showing a.) Mean monthly rainfall in the MCA from 2008-2018; b.) Mean monthly river levels of River Murera, Rojewero and Mutundu from 2008 – 2018; c.) Mean monthly conflict reports in the MCA by Lions, hyenas and buffalos; and d.) Mean group sizes sighted per month based on the Born Free lion monitoring data (2016 – 2019).

A total of 12692 lion occurrence points was used to model lion presence while 20000 points were used as background points to model pseudo-absence. There were no significant correlations noted among the different variables (Fig. 11). Results from the jackknife analysis suggest that the household abundance index is the variable with the most influence on lion distribution around the park followed by precipitation, habitat type and livestock abundance respectively (see Appendix 5: Fig. 19).

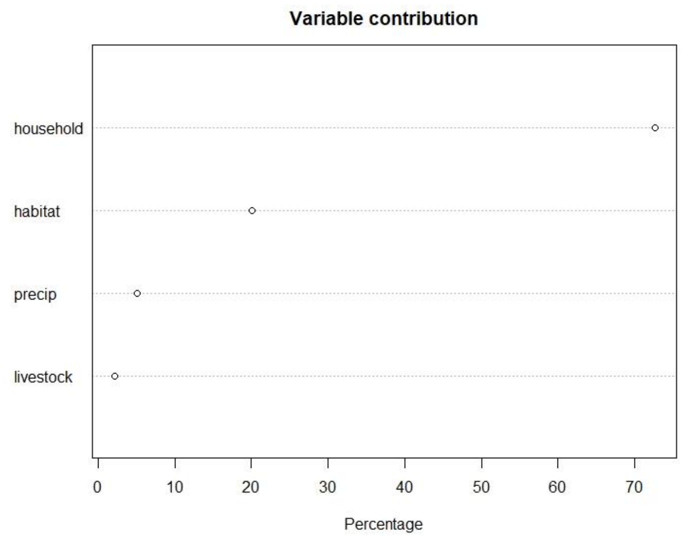

Figure 10:: plot showing the relative contribution of each of the variables to the species distribution model.

The comparison between different species distribution models used to model lion distribution suggests that each of these models are almost similar in terms of AUC (see Appendix 4: table 3). The raw maxent model had the highest AUC values and was thus chosen as the most robust model to explain distribution of lions in the area although all models generally show high AUC values (see Appendix 4: table 3). Results from the maxent model suggest that lions in MNP prefer the western side of MNP particularly the North western area of the park (Fig. 11)

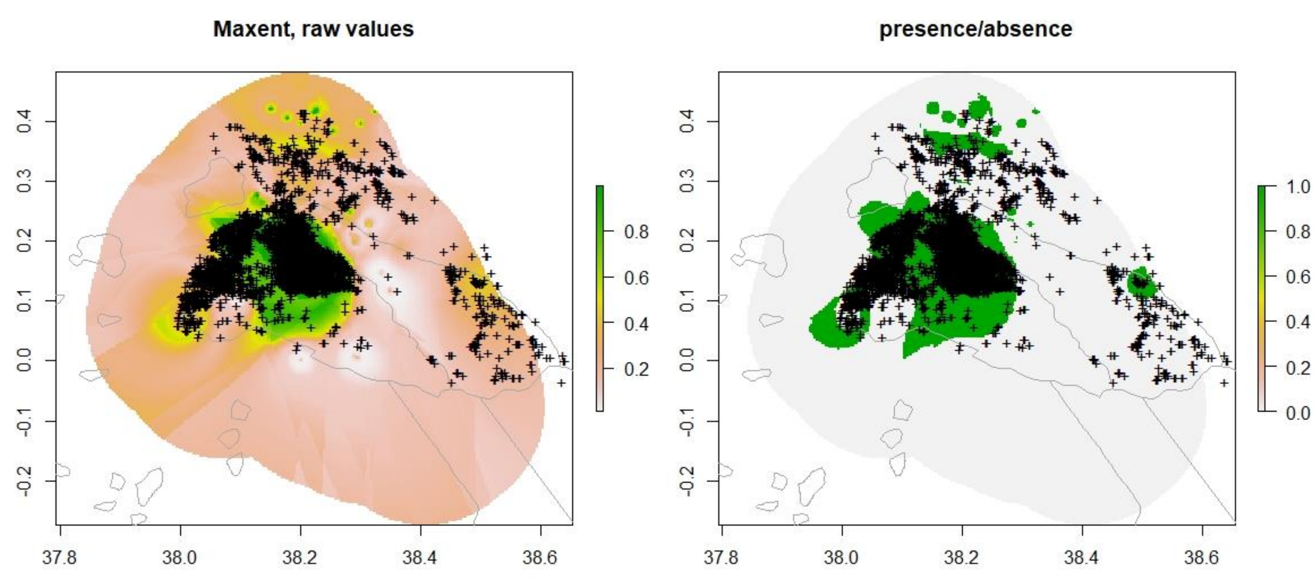

Figure 11: Output maps from the raw maxent model showing potential distribution of lions in the MNP.

3.0.2 Human dimensions of carnivore conservation

A total of 120 people responded to the questionnaire survey. A majority of the respondents were male (68.3%; (Appendix 6: Fig. 20 a)). Majority of the respondents (45.8%) had reached primary school education, while 33.3% were illiterate and 3.3% had a diploma and above (Appendix 6: Fig. 20b). Agro-pastoralists (62.5%) were more than pastoralists (37.5%; Appendix 6: Fig. 20c). Agro-pastoralists from the Meru tribe were the most abundant group. Akamba, Kikuyu and Meru were generally agro-pastoralists apart from a few respondents from the Meru tribe who had moved to the Eskot sub-location which is a predominantly Somali area and shifted to practise pure pastoralism (Appendix 6: Fig. 20c). The Borana tribe included both agro-pastoralists and pure pastoralists, while the Somalis were pure pastoralists (Appendix 6: Fig. 20c). Some respondents practiced other occupations on the side (41.7%; figure 20d). Religion and tribe of the respondents appear to be highly correlated (Appendix 6: Fig. 20e, f). The majority of the respondents (45%) owned more than one hectare while only (1.6%) of the respondents did not own land. Average total monthly household income ranged from <kshs 2000 (USD 20) to >kshs. 200,000 (USD 2000). Distance to park correlates negatively with height of fence whereby the farther the household from the park, the shorter the fence.

3.0.2.1 Carnivore knowledge and attitude towards carnivores

Only 20.8% of the respondents were able to recognize all the six carnivore species (based on photographs of Lions, Spotted Hyena, Striped Hyena Leopard, Cheetah, African wild dog). A majority (88%) of the respondents were able to recognize only lions and spotted hyenas while only (23%) recognized the African Wild dog (Appendix 7; Fig. 21a). A few (4.2%) of the respondents were able to recognize tracks of all species and slightly more respondents (21.3%) were able to recognize Lion and spotted hyena tracks efficiently (Appendix 7; Fig. 21b). Some respondents (35%) think that lions are the most destructive carnivores in the area, while the majority (54%) think Hyenas are the most destructive (Appendix 7: Fig. 21c). According to most of our respondents (73%), lions do not have any cultural value in Meru (Appendix 7: Fig. 21e). Additionally, the majority (57.6%) think that lion presence is not advantageous or does not benefit humans or the environment (Appendix 7; Fig. 21d).

The majority (59%) of our respondents answered that they like seeing lions in the wild, and when asked if lion killing should be allowed by law, only 6% of our respondents answered yes (Appendix 8; Fig. 22). Some (22%) of our respondents want to see lions extirpated from their community, while the majority (79%) believe that it is important to conserve lions. Most of our respondents (88%) prefer to have the lions confined within a restricted area, like MNP. Our index of internal reliability (Cronbach's α) was 0.678, slightly lower than the ideal cut-off value of 0.7. This suggests that 67.8% of the variability in our attitude data represents the true score of what we measured.

There does not seem to be any strong linear relations among our continuous predictors (Appendix 9: Fig. 23). Education level appears to be the most negatively correlated predictor in relation to number of carnivore species recognized from the pictures whereby respondents with higher literacy levels, particularly from Agro-pastoralist communities, seemed to have lower knowledge on carnivores. Number of livestock owned is also negatively correlated with distance from the park i.e. livestock owners with larger livestock herds seem to live closer to the park boundary. A bubble plot showing the distribution of the number of livestock depredated in relation to attitude suggests that respondents who lose more livestock generally have negative attitudes towards lions (Fig. 12).

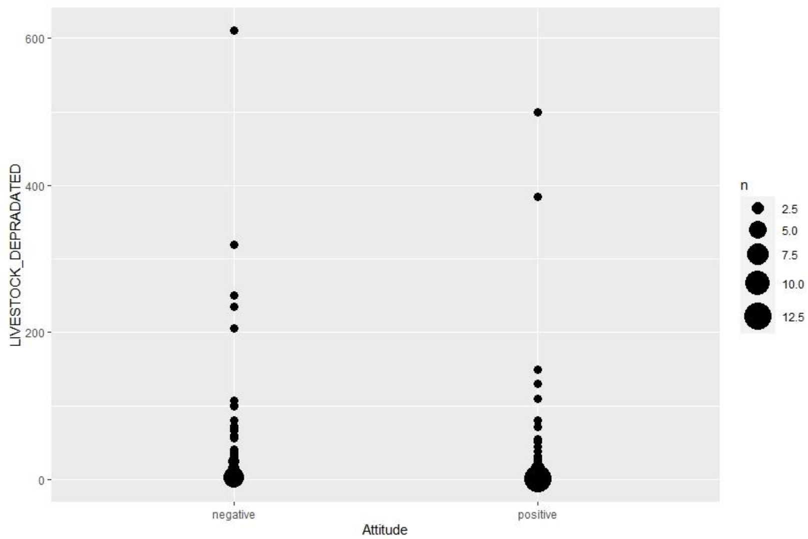

Figure 12: bubble plot showing the effect of livestock predation on attitudes towards carnivores.

Violin plots suggest that minimal differences between the different variables in relation to differences in attitude towards lions around the MCA (see Appendix 10: Fig. 24). Interactions were dropped from the model as they were not significant. Model output suggests an overall weak effect of livestock owned, livestock depredated, distance from park boundary, carnivore knowledge and education level on the respondents' attitude towards lions (table 2).

Table 2: Table showing the output of coefficient estimates from the logistic mixed model.

VARIABLE	COEFFICIENT	LOWER LIMIT (95% CI)	UPPER LIMIT (95% CI)
(INTERCEPT)	8.010787e-01	0.177889424	3.6074494
LIVESTOCK_DEPRADATED	1.006156e+00	0.999668313	1.0126863
LIVESTOCK OWNED	9.984292e-01	0.994317785	1.0025577
DISTANCE.TO.PARK	1.030141e+00	0.969966759	1.0940482
TRIBEBORANA	2.687925e-01	0.079898203	0.9042684
TRIBEKIKUYU	6.023126e+07	0.000000000	Inf
TRIBEMERU	3.983052e-01	0.133563998	1.1877979
TRIBESOMALI	3.566529e-02	0.001181769	1.0763637
EDUCATION LEVEL	1.228591e+00	0.832346709	1.8134707

Respondents from Eskot sub-location seem to have the most negative attitudes towards lions while participants from Baibairiu sub-location which is very close to the park's headquarters on the fenced western side seem to have a more positive attitude towards lions and understand the value of having lions in the protected area (Fig. 13).

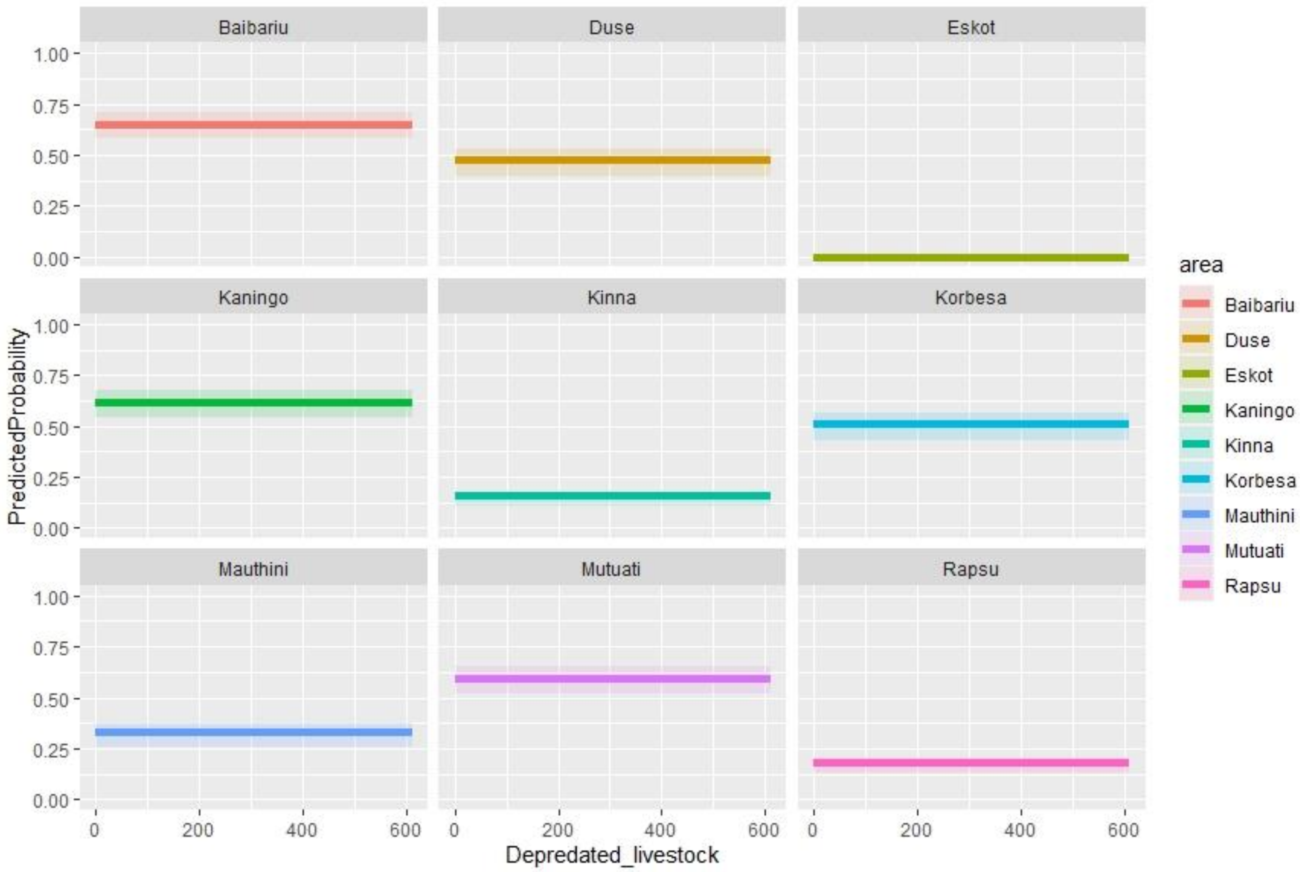

Figure 13: Plot output of the logistic mixed model.

3.0.2.2 Livestock loss and husbandry techniques

Livestock depredation numbers range from 0 to 611 in single depredation incidences with the last depredation incidence occurring in early 2019. (see Appendix 11: Fig. 25c). Majority (74.5%) of the cattle depredation incidences are caused by lions while others (25.4%) are caused by spotted hyenas (see Appendix 11: Fig. 25 a). Majority (65.5%) of the cattle depredation incidences happen inside the corral (boma) while others (34.5%) happen away from the homestead (see Appendix 11: Fig. 25 b). Spotted hyenas are responsible for the majority (69.2%) of donkey depredation incidences, while lions are responsible for some (23%) and leopards are responsible for a few (7.7%) incidences (see Appendix 11: Fig. 25a). Majority (53%) of donkey depredation incidences occur away from the homestead while others (46%) occur inside the homestead (see Appendix 11: Fig. 25b). Majority (53.7%) of shoats' depredation incidences are caused by spotted hyenas while others (18.3%) are caused by Leopards and others (10.8%) are caused by Lions (see Appendix 11: Fig. 25a). Baboons (2.2%), crocodiles (2.2%) and Wild dogs (1.1%) also contribute to a few shoats' depredation incidences. Majority (58%) of shoats' depredation incidences happen inside the corral while some (33.3%) happen away from the homestead. Some (38%) of the respondents revealed that lions do attack people while some respondents (44%) answered that lion attack trends have increased in the last five years. Results from the Kruskas Wallis test suggest that depredation incidences differ significantly among the different sub-locations (Chi square = 69.18, p <0.0001, df = 8). From the PCA analysis, we see that the first three components combine about 67% of all variation and each of them has an eigenvalue of >1 which means that they each account for more variance than is accounted for by each of the original variables after being standardized (Fig. 14).

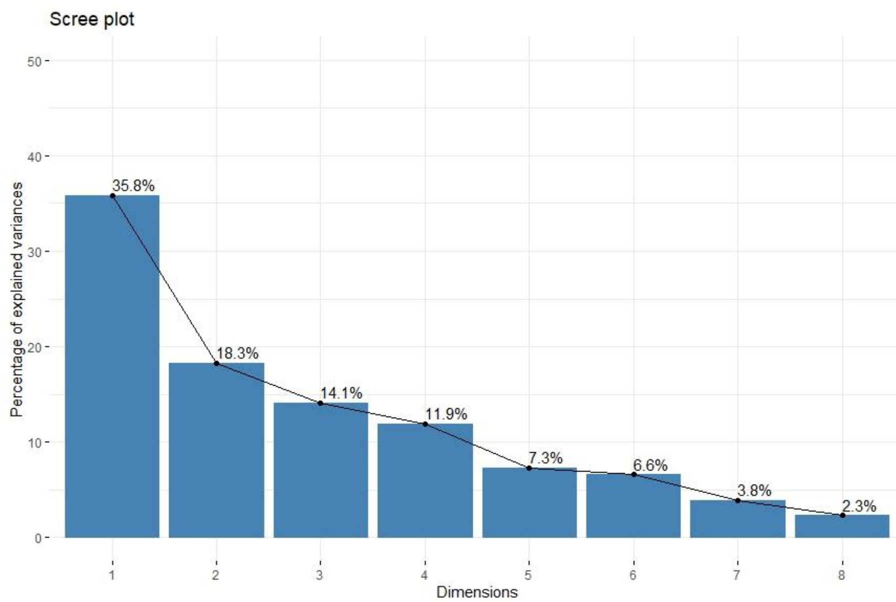

Figure 14: Graph output from the PCA showing the variation explained by the different Principal Components (PCs) in our dataset.

From the factor loadings table (which shows the correlations between the variables and principal components) we see that the first PC has positive loadings for all variables except height of fence. Therefore, we conclude that the first PC is a measure of husbandry practices across the different sub-locations. The second PC shows a contrast between numbers of livestock loss between the two major occupations in the area (agro-pastoralism and pastoralism). The arrows suggest a strong positive correlation among distance covered during grazing, methods used to prevent livestock depredation and livestock loss while all these appear weakly correlated with height of corral fence. The PCA suggests that the more the distance covered in search of pasture, the higher the livestock loss and the lower the height of the corral fence (Fig. 15). The PCA also suggests that livestock theft is particularly higher in Baibariu sub-location while respondents from Eskot sub-location own the largest herds of livestock and in turn experience the highest losses through disease and depredation, although theft of livestock is fairly low. Results from the multivariate analysis suggest a significant difference between the different sites and occupations in the area (P<0.0001). The interaction between sub-location and tribe is however not significant.

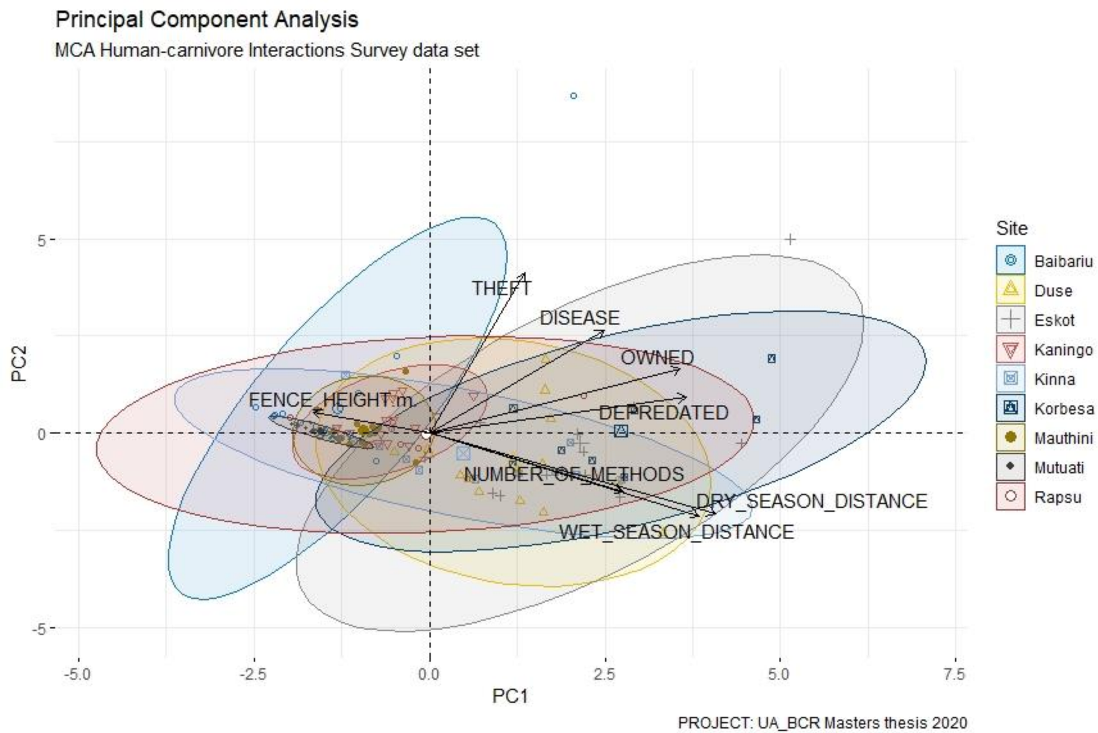

Figure 15: Biplot of the PCA output showing similarities in husbandry practices and causes of livestock loss among the different sub-locations.

However, we see three components in our output with an eigenvalue of >1 (Fig. 14) which means that the PCs do not summarise the dataset with its correlations fully. We therefore performed a linear discriminant analysis to confirm the differences and the results suggest a difference between the two major sources of livelihood in the area i.e. Pastoralism and Agro-pastoralism (Fig. 16). I also noted that locations with similar tribesmen seem to have almost similar livestock husbandry practices.

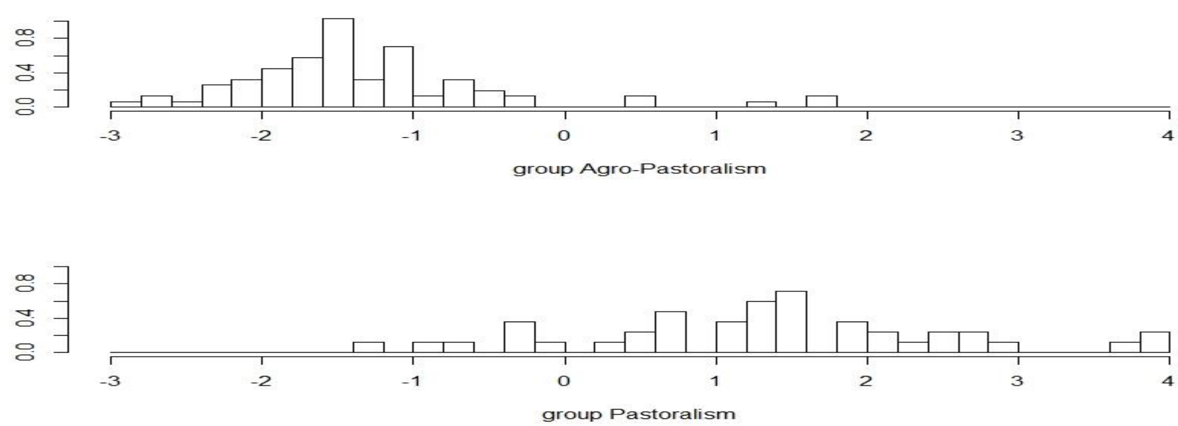

Figure 16: LDA outputs showing the differences between the two main sources of livelihood in the area.

3.0.2.3 Human-carnivore conflict intervention

Some (67.5%) of the respondents believe that depredation can be avoided. Some (36.75%) of the respondents answered that the fence is the most suitable mitigation measure against livestock depredation, others (31.62%) think the flashlight is the most suitable while a few (7.69%) think Dogs are the most useful (Fig. 17a). Majority (87.5%) of the respondents wish to seek compensation (Fig. 17b). Majority of the respondents (35%) said that lions attack livestock because they are violent in nature while others (26.7%) said that competition for water resources and pasture is the reason why lions attack livestock when they meet at common watering points. Results from the Kruskas Wallis test suggests no significant differences in amount of livestock depredated among the respondents who seek compensation and those who do not (Chi square = 0.18, p = 0.67, df = 1).

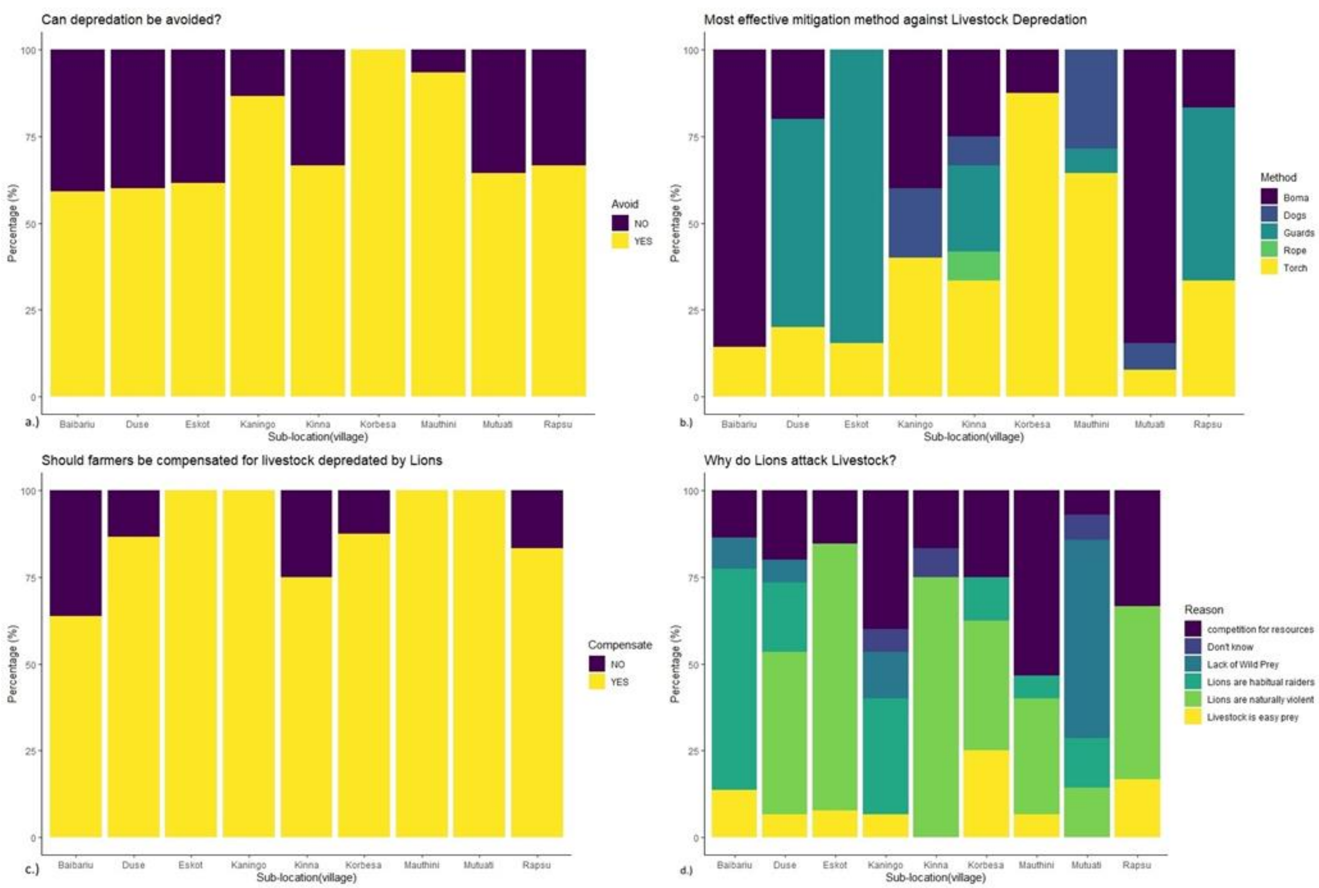

Figure 17: Graph showing a.) Whether depredation can be avoided; b.) the most effective methods of mitigating against livestock depredation and b.) The willingness of respondents to seek compensation; and d.) the reason why Lions attack livestock based on questionnaire responses.

CHAPTER FOUR

4.0 DISCUSSION

4.0.1 Lion population size, pride structure, reproductive success, foraging success and distribution

My results indicate support for the hypothesis that lion distribution in the area is influenced by habitat characteristics and precipitation; as well as the distribution of households and livestock across the different villages (sub-locations) surrounding the MCA. I also found support for the hypothesis that variations in attitudes towards lions among the different villages (sub-locations) surrounding the MCA are influenced by distance to park boundary, cultural background, livestock ownership, as well as literacy and carnivore knowledge levels. I however did not find support for the hypothesis that the amount of livestock depredated influences a farmer's willingness to seek compensation.

With an adult lion density of 6.8 lions/100km², the lion density in MNP is similar to recent lion densities in the Amboseli ecosystem with 6.8 lions/100km^2 (Lion Guardians, 2019, p. 8). This is still lower than the average density of lions in East Africa (16.2 lions/100km² - Woodroffe & Ginsberg, 1998), despite being higher than the mean lion density of West Africa (1 – 3 lions/100 km2 - Bauer & van Der Merwe, 2004). Higher estimates have been recorded in other parks in East Africa such as the Masai Mara National park, Kenya (37 lions/100km² - Ogutu *et al*., 2005) and the Ngorongoro Crater, Tanzania (38.8 lions/100km² - Hanby *et al*., 1995). The low lion density in the park could be attributed to the low prey biomass present in Meru National park, compared to other lion areas in the region which could be as a result of both anthropogenic-induced changes in the area as well as natural population oscillations related to rainfall and other ecological factors (Western *et al*., 2009). Another possible reason could be the large size of the park and thick impenetrable vegetation in most parts of the park which reduces the probability of detecting the lions. Prey availability has been found to have both a direct effect on the number of individuals a pride can maintain, and an indirect effect on the number of prides that can occur in the same area (Ogutu and Dublin, 2002). This seems to be the case in the MNP based on our data. In addition, the low density of lions can also be caused by the high density of competitors such as spotted hyenas (*Crocuta crocuta*) who have been reported to cause the highest number of livestock depredations all around the MCA based on the questionnaire results. The spotted hyena (*Crocuta crocuta*) is known to be a serious food competitor for lions, especially for middle-sized prey (Trinkel et al., 2005; Bauer et al, 2008; Yirga *et al.,* 2014). The ratio of spotted hyena clan sizes to lion pride sizes at a kill as well as the presence of pride males has been found to influence kleptoparasitism activities by lions as well as mobbing behaviors by hyenas which could ultimately cause displacement of lions from an area (Kruuk 1972; Trinkel et al., 2005).

It is worth noting that the wildlife population in the Meru Conservation Area had reduced to very low numbers due to increased poaching and bushmeat hunting levels in the area in the last couple decades of the 20th Century. This together with management issues led to a dissipation of wildlife numbers until the beginning of the new century when restoration efforts commenced in the conservation area. The last census by Kenya Wildlife Service in the MNP suggests a density of 4 lions/100km^2 (Meru national park annual report 2016-2017) which shows a relatively stable population relative to our results although it definitely needs to be monitored for a longer period in order to come up with robust results. The observed sex ratio in the MNP is above what is described in the literature, which ranges between 0.3-0.5 male per female (Schaller, 1972; Ogutu & Dublin, 2002; Bauer, 2003, Tuqa et al., 2015). Van Orsdol et al. (1985) suggested that the skewness towards females may be accentuated in small isolated reserves, where sub-adult males are driven away, and where immigration by new males is unlikely. This is not observed in Meru National Park. Solio pride was not taken into account in the observed population size (n=31), despite having indications of their presence (pers. Comm. with Newton Simiyu). However, the adult male lion from the pride was observed again after my fieldwork period, having taken over the second largest pride in the park when his collar was being serviced. Therefore, the observed number of lions is a close representation, but still an underestimate of the true number of lions in the park. There is always the possibility that some lions have not been spotted, this is especially so with newly born cubs.

My study showed that pride structure in the MNP is influenced by foraging success and seasonality. Five different prides have been identified by my research in line with reports from the carnivore monitoring team in the park. Pride structure differs from what is described in literature (Schaller, 1972), in the sense that, apart from the Mulika and Elsa's prides, the other two prides are rather small and without permanent pride males and the Nairobi pride is now reduced to a coalition of four sub-adult males. This is a direct result of retaliatory killing of several pride males who have wandered out of the park in the recent past as well as the death of the mother of the four males from Nairobi pride which was translocated from Nairobi National park in 2012. The female adult lion died in 2017 during a buffalo hunt (pers. Comm. with Peter Gitonga). Anthropogenic activities around and within protected areas are known to affect lions' social structure (Loveridge et al., 2007; Loveridge et al., 2009). I found the mean adult group size of MNP lions to be rather small. Bauer et al. (2003) suggested that a small group size of lions in West Africa may be a result of disturbance. The lack of a clear pride structure in the MNP can have an influence as well. In the Serengeti, where fully developed pride structures are present, an average group size of 2.8 lions is observed (Schaller, 1972), and in Kruger National Park, South Africa, the average group size is 4 (Funston, 2003). Recent changes in the social structure of MNP lions have had their effects on the pride structure. There is an old male lion known as Kenmare who is reported to have been pushed towards the community land adjacent to Bisanadi National Reserve which is mainly pastoralist land as well as members of the Bisanadi pride who are also approaching old age and gradually being pushed off to the pastoralist lands in the north eastern boundary (pers. Comm. with Newton Simiyu). Most of the older lions in the park seem to be pushed towards community land where they eventually disappear (pers. Comm. with Newton Simiyu). This highlights the importance of intensive monitoring to better understand the fate of the older lions.

Female lions in the park have been observed to maximize foraging success during the season of prey scarcity by separating into either group of two females or groups of four to five females in line with other literature (Fig. 5a). Foraging success does not vary significantly with group size when prey is abundant. Seasonal shifts in the hydrology of the area appear to influence lion foraging success and reproductive success which in turn influences lion pride structure and distribution in the area. Diversion of surface waters of the main rivers in MNP by farmers in the Nyambene hills upstream most likely plays a role in the hydrological dynamics of the park. This ultimately has an impact on human-wildlife conflict in the area (Fig. 9). Female lions live in fission-fusion social units (prides) and forage only with members of their own pride (Packer 1990). If lion grouping patterns were primarily related to group-size-specific feeding efficiency, females in prides containing fewer than four females should forage in twos when prey is scarce, whereas females in larger prides should forage in groups of two or four to five (Mosser and Packer 2009). Females in large prides most often forage in intermediate group sizes of four or five (Mosser and Packer 2009). Moreover, mothers keep their cubs in a creche and form highly stable maternity groups that are effective in defending the cubs against infanticidal males (Mosser and Packer 2009). Most large prides contain a creche involving three or four mothers, and in the absence of a creche, large prides show no preference for any group size (Mosser and Packer 2009). Females also compete aggressively against neighbouring prides, and larger groups successfully repel smaller ones in territorial disputes. Small prides appear to be excessively gregarious in order to compete against larger neighbouring prides.

Results from the maxent model suggest that presence of households with livestock also influence lion distribution, especially during the driest periods of the year when both pastoralists and wildlife increase their distribution range and come into contact with each other. This is particularly the case around the Ngaya Forest, Kinna, Rapsu and Korbesa areas in the north as well as Eskot in the eastern boundaries. These areas seem to be key exit points and corridors for wildlife distribution. Most pastoralists have also been noted to encroach the park during the driest periods in search of water and pasture which could attract predators who could easily attack the livestock or follow the herdsmen back to their household and consequently attack the livestock. Highlighting the ecological mechanisms that drive carnivore distribution and predation on livestock has been noted to broaden insights on the success or failure of conflict mitigation tools as well as broaden contexts on how and why intervention effectiveness changes over space and time. Such knowledge could be used to develop a framework that will be useful in informing research and management of carnivore–livestock conflict (Graham et al. 2005; Goswami 2015; Miller 2015).

4.0.2 Human dimensions of carnivore conservation

The abundance of households as an index of human presence has been shown as the most influential predictor of lion distribution in the area according to the maxent SDM which is in line with previous studies that have mentioned conflict with humans over livestock depredation as the single most important factor causing the decline in African lion populations. With growing numbers of people and livestock throughout the continent, lions will become entirely restricted to very large or intensively-managed protected areas if conflict mitigation cannot be implemented on a wide scale. Ancient methods of livestock husbandry are remarkably effective at minimizing conflict, but these are rapidly being lost to modernization. Building good bomas and conscientiously tending livestock require time and effort at a time when poison is readily available (Frank et, al. 2006). Carnivore density is often higher in small fenced areas owing to protection from anthropogenic related conflict whereby fences can cause carrying capacity to be reached quickly by impeding dispersal (Miller et al., 2013; Davidson et, al., 2019). Exit points designed to guide wildlife movement and dispersal into safe areas (away from communities) have been shown to be effective on the LBL (Dupuis-Desormeaux et al., 2016). However, exit points into conservancies are bi-directional and provide a way for predators and prey to return to a conservancy in times of insecurity or poor foraging outside its boundaries. When predator numbers swell due to immigration into a small conservancy, this can destabilize predator socio-spatial behaviour and potentially impact the predator–prey dynamic (Davidson et al.,2011). Determining the dietary habits of carnivores is thus essential to allow informed management decisions at the species level (Kamler et al.,2015). Carnivores that are in the same guild coexist through resource partitioning, with dietary separation being an important factor in facilitating niche separation (Vieira & Port, 2007; Kamler et al., 2012). Behavioral and spatial separation may also facilitate coexistence (Kushata et al., 2018) via different activity peaks (Kamler et al., 2012), foraging behavior (Périquet et al., 2016), selection for different prey size classes (Purchase, 2004), and segregation of generalist and specialist feeding strategies (Périquet, Fritz & Revilla, 2015). Understanding the relative impacts of carnivores on prey species would help to prioritize management interventions to mitigate population declines.

Spotted hyenas were reported to cause the more livestock predation than lions in the surroundings of MNP since 2009, and they are the main species attacking camels, cattle and donkeys, which are the most expensive livestock species. Leopards also follow lions closely and have been mentioned to prefer mid-sized livestock species such as sheep and goats. Hyenas and Leopards have been mentioned to kill livestock indiscriminately therein killing more than they can consume. Tuqa (2015) reported that lions predate on livestock more than leopards, but below the level of hyenas, jackals and cheetahs in Amboseli National Park, whereas Ogada et al (2003) and Patterson et al (2004) found lions to be the main carnivore species attacking livestock in Nairobi National Park. Reports on livestock predation by lions show a small peak around March, followed by the highest peak in reported conflicts from July to September (Fig. 9). This is in tandem with previous research that has found seasonal differences between attacks, with a higher proportion of livestock attacks when wild prey availability is lowest (Hemson 2003; Patterson et al. 2004, Huqa 2015; Khorozyan et al. 2015). During the questionnaire administered in my study, of all the attacks recalled by the respondents, 38% went unreported. Beattie et. al., (2020) recommend minimizing spatiotemporal overlap between livestock and abundant wild prey by developing alternative livestock water and feeding locations and increasing caution near surface water areas which has also been seen as a major driver of carnivore depredation on livestock in the MCA.

4.0.2.1 Carnivore knowledge and Attitudes towards carnivores

There is generally a low positive attitude towards carnivores in the MCA. According to the survey results, Eskot, Rapsu and Kinna sub-locations which are predominantly pastoralist areas experience the least benefits of coexisting with lions. Rural Africans continue to lose their tolerance of predators as a cash economy has become increasingly relevant to them and are therefore likely to continue eliminating lions and other large carnivores unless they bring in financial benefits that outweigh costs. In many areas, tourism ventures are encouraged with unrealistic promises of wealth creation and/or employment in areas where tourism is unlikely to be sustainable or without sufficient investment in local skills development (Walpole and Thouless, 2005, Hemson, 2003). In these circumstances (which might easily be extended to hunting) the potential for wealth generation should not be overstated when setting up a new venture. Having encouraged a community to view lions and wildlife as their own private economic resource, conserving the local lion population might no longer make sense should the economy change (e.g. Zimbabwe) or the venture fail to live up to economic expectations of a growing population. That's not to say that encouraging sport hunting and tourism is bad, but an enormous amount of work remains to identify the components of a successful venture.

Our results show an overall weak effect of livestock owned, livestock depredated, distance from park boundary, carnivore knowledge and education level on the respondents' attitude towards lions in the area. Education levels seem to have a higher effect on influencing respondents' attitudes towards carnivores in the MCA which illuminates the need for introducing programs that will engage all relevant stakeholders with a focus on improving literacy levels of local residents, carnivore knowledge as well as increasing the benefits received from co-existing with carnivores, particularly in the Eskot sub-location and surrounding areas. Previous studies within the Amboseli-Tsavo ecosystem also show that high levels of local participation in conservation and a greater sense of ownership of their environment, increases tolerance for lions by local communities (Okello, 2009; Hazzah et al., 2014; Dolrenry et al., 2016). Site-specific human–wildlife conflict issues such as crop-foraging by wild ungulates and variation in attitudes towards different species should also be considered when deciding possible intervention measures. Our results generally indicate a negative attitude towards Hyenas, Lions and Leopards all around the park, although respondents also mentioned other species of concern such as crocodiles in Mauthini and Kaningo. Baboons, Buffalos, Elephants and snakes were also mentioned all around the park. Respondents in Eskot also mention the lack of an early response system dedicated to human-carnivore conflict issues and request for the setting up of a ranger outpost or conflict response team in the vicinity of the sub-location. Specifically, improved livestock management, motivation of local youth and their participation in awareness campaigns could all further strengthen the prevalent positive attitudes towards lions. Dolrenry et. al., (2020) reported that although Maasai pastoralists of the Amboseli region had decimated the lion population by the early years of the 21st century (Chardonnet, 2002), current tolerance of lions by the human communities, presumably because of conservation initiatives (Hazzah et al., 2014),has seemingly allowed these lions to survive to adulthood, breed and successfully disperse (Packer et al., 1991; Björklund, 2003; Trinkel et al., 2008; Dolrenry et al., 2016).

4.0.2.2 Livestock loss and husbandry techniques

Results from the questionnaire survey indicate that livestock loss in the area is mainly due to carnivore predation, livestock diseases and livestock theft. Cattle raiding among pastoralist communities in Northern Kenya, Sudan, Ethiopia, Uganda and Somalia is an ancient cultural practice that has evolved over the years from a sport to a dangerous affair that involves the losing of human lives (KNHRC, 2010). Cattle raiding was traditionally practiced for the purposes of restocking livestock herds after droughts, generating bride price and as a rite of passage by young pastoralist warriors into adulthood. This has since evolved into a commercialized and politically motivated activity; thus it is crucial to design and implement mitigation approaches that are sensitive to the political implications of cattle raiding and view the pastoralist areas more in the context of the struggles over democratization, decentralization, and nation building that are currently happening in Kenya (Greiner 2013). Main livestock diseases in the area include foot and mouth disease (FMD) which is a highly contagious viral-based disease and trypanosomiasis which is transmitted by tsetse flies. Both of these diseases lead to high economic losses and thus need to be regulated for better livestock yields. Main causes of livestock loss in Ogada et al. (2003) assessed the efficacy of traditional African methods of livestock husbandry practices in protecting livestock from predators on commercial ranches. These practices evolved in response to the twin threats of both predators and livestock-stealing humans, and are thought to have remained relatively unchanged for thousands of years (Marshall, 1990). Not surprisingly, Ogada et al. (2003) found that ranchers kill significantly more predators on ranches where predators kill more livestock. Thus, implementation of any practice that reduces the vulnerability of livestock is critically important for reducing retaliatory killing of predators. (Frank et. al., 2006) reported that seventy-five percent of depredation on cattle, sheep and goats took place at night, and lions were responsible for over 75% of the total; predation in East African ranches was reported to occur largely at the boma.

Results from my survey indicate that height of corral fence is the most significant predictor of livestock loss in the area and is negatively correlated with livestock loss through depredation, disease or theft. Well-built bomas effectively constrain cattle and keep predators out. Bomas in Meru are made from native thorn bush, stone walls, wooden posts or wire mesh (which is used for goats and sheep); of these, thick strong thorn bush with a high height was most effective at keeping lions out and panicked cattle in. Stone is an excellent building material if there is a fence on top to prevent lions from leaping onto the wall and into the boma. Although most expensive to build; stone bomas last essentially forever and need no maintenance. Frank L. (2006), suggests that wire mesh is a very poor barrier if not well-supported, but one Laikipia ranch has developed a modular, moveable fence made of 8x4x4 foot panels of mesh welded into interconnecting angle iron frames that is highly resistant to predators and easily transported. This would most likely work well for the pastoralist communities living around the MCA due to their nomadic lifestyle. Thorn bush bomas are most effective if divided into inner 'rooms' that make it harder for cattle to reach the main gate, and the gate must be very strong, preferably made from strong timber. The normal practice of using a tree or bush as a gate is ineffective, as it does not contain panicked cattle and allows hyenas to enter. Frank L. (2006), found that lions are reluctant to approach bomas that are located in close proximity to large numbers of people. However, for security and environmental reasons, some ranches do not allow herders to have their families at the bomas. Of course, in traditional societies bomas usually have large numbers of people and dogs. Dogs are also highly effective deterrents; they do not chase predators, but warn of their approach, waking the herders who then chase the lions. Dogs can also carry lethal carnivore diseases, but they are such an effective deterrent that vaccinated dogs are an essential component of livestock husbandry. In the case of the MCA however, Dogs may not be very popular as the main pastoralist groups in the area who own majority of the livestock do not keep dogs as they are Muslims and it is a religious taboo. A bright light or noise-making device like a shotgun or thunderflash is also very helpful at discouraging loitering lions and respondents also mentioned flashlights to be useful although carnivores get habituated to the light after sometime if there is no human presence to scare them away. The presence of adult herders/guards who can efficiently scare the predators away is also a useful way of reducing carnivore attacks on livestock.

4.0.2.3: Human – carnivore conflict intervention

I did not find support for the hypothesis that livestock depredation motivates the willingness to seek compensation in the MNP. It appears as if farmers in the area are generally interested in seeking compensation regardless of whether their livestock have been depredated or not. This raises the issue of ethical conundrums when administering compensation schemes (Hazzah *et. al.* 2014). Finally, I developed a mechanistic framework following Wilkinson et. al. 2020, that will be handy for exploring a summary of the drivers of lion–livestock interaction dynamics in the area by integrating both biological and socio-economic mechanisms that fundamentally underlie human–lion conflict in a holistic perspective (Fig. 18). This framework also helps to determine how current conflict–intervention tools act through specific ecological pathways to prevent or reduce livestock predation, highlight the importance of implementing management interventions on an ecological basis, and the value of combining intervention strategies to target the diverse ecological drivers of livestock predation in a given system (see table in Appendix 12). The applications of this framework will be significant in informing future research, management, and policy making regarding the ecology and management of lions in the area and could also be rolled out to other similar areas.

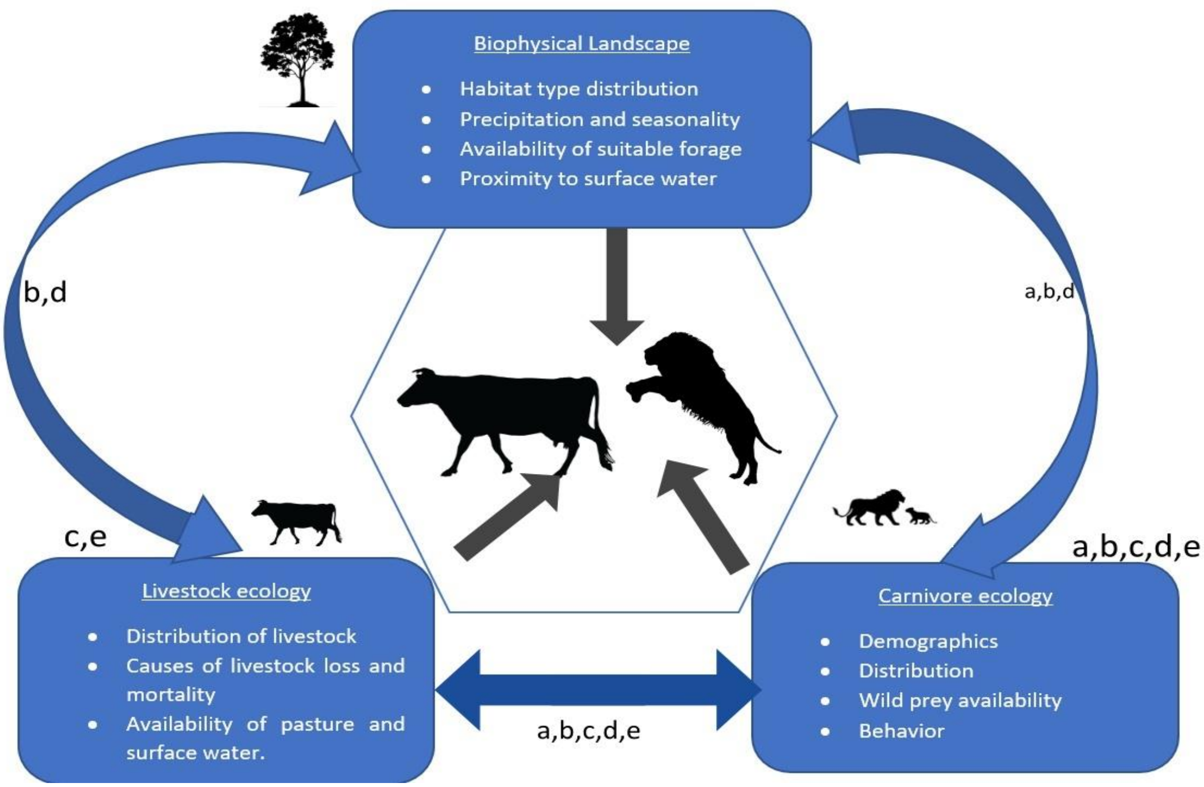

Figure 18: Scheme showing ecological interactions between aspects of the biophysical landscape, carnivore ecology, and livestock ecology that influence livestock predation events in the MCA: (a) density-mediated trophic cascades; (b) landscape of fear for carnivores and behaviourally mediated trophic cascades; (c) optimal foraging theory (as applies to carnivore–livestock interactions), which includes the real or perceived cost of hunting livestock; (d) inter and intra-species interactions; and (e) predator–prey shell games and response races including humans serving as the response on behalf of the livestock prey.

CHAPTER FIVE

5.0 CONCLUSION

Meru National Park and its surroundings experiences complex human-lion interactions and is highly susceptible to carnivore related conflict. I found support for my hypothesis that lion distribution in the area depends on habitat characteristics, precipitation, household distribution and livestock density across the area. Furthermore, I found support for my hypothesis that differences in attitudes towards lions and knowledge of the relevance of lions variations in attitudes towards lions among the different villages (sub-locations) surrounding the MCA are influenced by distance to park boundary, cultural background, livestock ownership, as well as literacy and carnivore knowledge levels. However, I did not find support for the hypothesis that livestock depredation motivates the willingness to seek compensation in the MNP. It appears as if farmers in the area are generally interested in seeking compensation regardless of whether their livestock have been depredated or not.

Extended drought periods cause ungulates to disperse in search of water and pasture. This in turn causes the lion prides to separate and disperse all over the park, and even outside. Results indicate that the disturbed lion pride structure in the MNP is likely due to seasonal fluctuations in water and forage availability which could be influenced by water usage upstream of main rivers of the park. The lions seem to adapt to these seasonal shifts by separating into smaller prides and increasing their distribution range into community lands which leads to an increase in conflict incidences. Predicting species' distributions based on associations between environmental variables, anthropogenic variables and known species' occurrence records to identify conditions which influence lion population and distribution has been identified as an important component of conservation planning in recent years, and a wide variety of modeling techniques have been developed for this purpose. Livestock raiding behavior seems to be influenced by a lion's location, its respective group size and seasons. Attitudes towards carnivores seem to be influenced by the livestock ownership, whereby livestock farmers generally have negative attitudes towards carnivores regardless of the number of livestock depredated, and level of academic education. Effective livestock husbandry practices may reduce livestock depredation and are therefore recommended to be implemented by the farmers around the Meru National Park. This would prevent further predation by lions, and would reduce the reliance on livestock by lions as an alternative food source in the long term. Further investigation on the impact of lion translocation to the MNP on human-lion interactions would be of high interest.

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APPENDICES

MERU NATIONAL PARK LION PROJECT

Appendix 1: Data sheet for Observation with vocalisation

Name of Data Recorder: _____________ Date: _____________

Observation Time: Start _______ Finish _______ Team left _______

Calling Station GPS: _______

Location:

GPS: _____ Habitat: _______ Weather / Wind Conditions: ___________

Broadcast 1: 1 – 30 min

Vocalization: __________

Time Start: ________ Time Stop: ________

Remarks:

……

……

Species Observed	Number (Responding[1])	Cub / Sub-adult / Adult	Male / Female
Lion [1]	( )	/ /	/
Hyena [2]	( )	/ /	/
Leopard [3]	( )	/ /	/
Cheetah [4]	( )	/ /	/
Wild dog [5]	( )	/ /	/
Other	( )	/ /	/

Other: ___________

Turn 180 Degrees

Broadcast 2: 31 - 60 min

Vocalization: ________

____

Time Start: _______ **Time Stop: ________**

Remarks:

……

……

Species Observed	**Number (Responding)**	**Cub / Sub-adult / Adult**	**Male / Female**
Lion [1]	**( )**	**/ /**	**/**
Hyena [2]	**( )**	**/ /**	**/**
Leopard [3]	**( )**	**/ /**	**/**
Cheetah [4]	**( )**	**/ /**	**/**
Wild dog [5]	**( )**	**/ /**	**/**
Other	**( )**	**/ /**	**/**

Other: ___________

Appendix 2 : Data sheet for observation without vocalisation

Date………………..TIME OBS…………………….Name of the recorder………………………

Name of The collared lion

Insight…………….

Not seen…………..

Group Composition total…………………

Adults: Total………Males members……………..Females members…………………………

Juveniles total……Male members …………… Female Members……………………….

Cubs less than 2years Total…………………..

GPS location: E……………………………..S………………………………………….

Behavior of collared and uncolored lions during observation

Resting/sleeping

Playing

Walking

Courting or Mating

Territorial behavior (roaring/Scent Marking)

Aggression/fighting

Feeding

Hunting

Health Status

Very poor

Very Poor (ribs visible)

Average

Good

Very Good (Fat)

Area Name:……………………………GPS Location………………………

Habitat Type Where observation was Made

Swaps

Riverine Forest

Savannah Grassland

Savannah Woodland

Observation of behavior of translocated lions to the resident Pride……………………………

Appendix 3: Data Sheet for Questionnaire survey to the local community

Questionnaire no…………….

I am Kennedy Kariuki From University of Antwerp. I am conducting a research on **Factors influencing human-lion interactions within and around Meru National Park, Kenya.** The information you provide in this questionnaire will be treated with outmost confidentiality and used for academic purposes only.

Date:____________________ Interviewer Name: ____

Socio-economic characteristics of the respondent

1. Location name: ________________________
   - X coordinates
   - Y coordinates
2. Sex:______________
3. Date of birth:______________________________
4. Place of birth:______________________________
5. How long have you lived in Meru?_____________________________________
6. Education level: A. Illiterate B. Read and write C. Primary/middle school D. High school E. Diploma and above
7. What is the family composition of your household? Spouse___________Children_______(M)_______(F) Relatives_________Others____________
8. Occupation:
9. Ethnic tribe:
10. Religion:

Economic level of the household

9. Average land holding in hectares?

   a. < 0.25 b. 0.26-0.5 c. 0.51-0.75 d. 0.76-1 e. >1 f. I don't have a land

   (If you said you do not have land, please pass to question 13)

10. Do you produce crops? a. Yes b. No.

11. If yes, is your harvest usually enough to feed your family?

    a. Yes b. No

12. How long do you generally consume your harvest before you start buying food?

13. What is the estimated average total household monthly income in KSHs?

    a. ≤2000 b. 2001-4000 c. 4001-8000 d. 8001-12000 d. >12000

Lion management, knowledge and perception

14. Pleas tick the alternative that the best describes your opinion
(Key: 1-Strongly agree, 2-Agree, 3- Neutral, 4- Disagree and 5- Strongly disagree)

No.	Questions	1	2	3	4	5
1	Lion is bad animal					
2	The presence of lions is a sign of a healthy environment					
3	Depredation by lions is a very concerning issue in Meru					
4	Lions are known for attacking and injuring people					
5	I would be afraid to go into the forest/filed if there are lions					
6	Lion is dangerous to humans					
7	It is important to conserve lions in Meru					
8	I like seeing lions in the wild					
9	I want lions extirpated from Meru					
10	Lions should only live in restricted places in Meru					
11	Killing of lions should be strictly regulated by law					
12	Killing of lions should be allowed by law					
13	Lions have ample prey in the wild					
14	The number of lions in Meru has notably increased in the past ten years					
15	Lions habitat destruction is a problem in Meru					

Carnivore knowledge

15. Which carnivore species do you recognize from the pictures?
1.___________2. ___________3. __________ 4. _____________5. ______6. ______________
16. Which species (from the pictures in Qn #15) have you ever seen?
1.___________2. ___________3. ___________ 4. _____________5. _______6. ________
17. Which of the tracks can you identify (from the provided picture of tracks)?
1.___________2. ___________3. _____ 4. _________5. ____6. ___________
18. According to you, among the above given carnivores (in Qn #15) which are the most dangerous? (Give a score: 1: extremely dangerous, 2: very dangerous and 3: dangerous)
1.________________________2._______________________3. ___________________________

Why do you think these carnivores are dangerous?

____

19. Do you want lion numbers to increase in Meru? a. Yes b. No
Why? ____

20. Do you think lions have any advantages? a. Yes b. No
If yes, please mention some of their benefits?

____

21. Do lions have a special meaning/importance in your culture? a. Yes b. No
If yes, please explain in detail:

____

22. Do you know any carnivore body parts that are used for preparing traditional medicines?
a. Yes b. No; If yes, please explain in detail: Which animal? ____________

Which part of its body?_____________________________________

For which disease? ____

23. What are the common prey types for lions in Meru?

____

24. Do people kill lions in Meru? a. Yes b. No
If yes, please explain why

____

Livestock depredation

25. Do you have livestock? a. Yes b. No
If yes, please fill the table below. If No, please move to question 33.

Livestock species	Sex		Age level		
	Male	Female	Young	Adult	Old
Cow					
Donkey					

Sheep					
Goat					
Camel					
Others					

26. Did you lose livestock as a result of wild carnivore depredation? If yes, please fill the table below.

Species	Sex	Age	Number	Depredation place	Carnivore species responsible for depredation	Year
Cattle						
Donkey						
Sheep						
Goat						
Others						

27. Do you think you can avoid depredation? a. Yes b. No

28. What method you use to limit/avoid livestock depredation?

a. Dog
b. Enclosures/Fences
c. Guard/Shepherd
d. Fire
e. Others; please specify: ______________________________

29. According to you, among the above given depredation mitigation options, which are effective? Give a score of 1 to 3: from the most effective to effective)

1. 2. 3.

30. How far away is your livestock grazing area from your house?

Dry season____________________Wet season ____________________

31. Have you ever lost livestock due to disease? a. Yes b. No

If yes, please give details:

a. Which animals did you lose? How many?______________ __________
b. Which disease? ______________________________
c. When? Month________________Year ________________

32. Have you ever lost livestock due to theft? a. Yes b. No

If yes, please give details:

a. Which animals did you lose? How many? ______________________
b. Where were they stolen from and how? ______________________
c. When were they stolen? Month____________Year ____________

33. What can be a suitable remedial measure to reduce depredation by lions?

a. Killing all lions
b. Killing the problem causing individual lions
c. Relocating all the lions
d. Keeping livestock in a strongly fenced area
e. Better protection of livestock
f. Others; please explain ______________________________

34. In your opinion; what is the trend of livestock attacks by lions these last five years?

a. It has increased
b. It has decreased
c. It has not changed
d. I do not know

35. Do you think people who lost livestock to lion attacks should be compensated?

    a. Yes b. No

    Why?____

36. When do you think the livestock predation by lions takes place? a. Mornings (6:00-12:00)

    b. Afternoons (12:00-18:00)

    c. Nights (18:00-23:00)

    d. Around and past midnight to Dawn (23:00-6:00)

    e. I do not know

37. In your opinion, why do lions attack livestock?

    a. Lack of wild prey
    b. Because livestock graze close to (and inside) lion habitats
    c. Because they are violent in nature
    d. Because they are habitual raiders
    e. I do not know
    f. Other reasons; please explain:____

38. Do lions attack people? a. Yes b. No

39. If yes, what preventive techniques do you use to avoid being attacked by a lion?

    ____

40. Has anyone from your immediate family been attacked by a lion?

    ____

    a. Yes b. No

    If yes:

    a. What type of attack was it?_______________________

    b. Where did it happen?

    c. How did it happen?

    d. When did it happen? Month _________________ Year

41. Do you have any comments, observations or recommendations about livestock production, lion conservation, and the problem of depredation?

    ____

    ____

    ____

    ____

    ____

Appendix 4: Table showing the model evaluation of lion distribution maxent models

Table 3: Model evaluation of the maxent models used to analyse lion distribution in the MNP

MODEL	MODEL DESCRITPTION	AUC	COR	MAX TPR+TNR
Raw	The default approach in this function is the “logistic” output, whereas the underlying Maxent model output is termed “raw” output. In the raw output, probabilities across the region sum to 1, such that the probability in any given location is very low and is essentially a probability density, sometimes referred to as relative occurrence rate (ROR; Merow et al. 2013).	0.9689022	0.7124632	0.1775978
Beta (3)	a beta multiplier of 3 (the default setting is 1) is set. Typically, this multiplier is altered to be > 1 because of concerns regarding potential overfitting of environmental relationships.	0.9563502	0.6656124	0.2641403
Unhinged	product (interactions), hinge, or threshold features are not used. This reduces the model complexity to only consider linear and quadratic features, similar to a simple GLM.	0.9101014	0.6213049	0.3293226

Appendix 5: Correlation graph for predictor variables used in the lion distribution maxent model

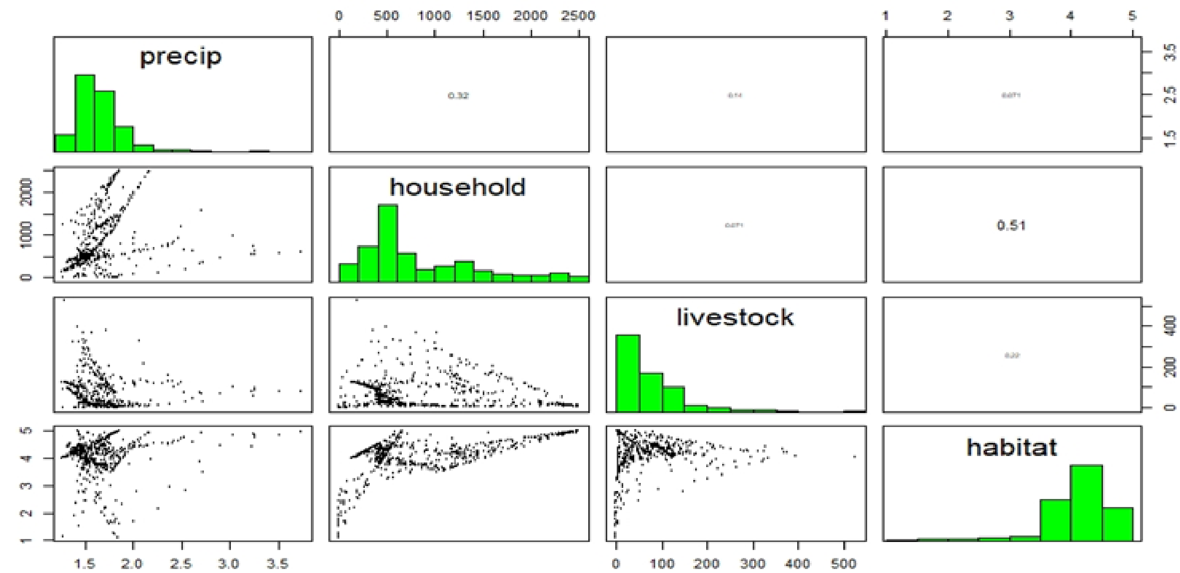

Figure 19: Pairs plot output showing collinearity of the variables used in the maxent model.

Appendix 6: Graph output showing socio-economic descriptions of the questionnaire survey respondents

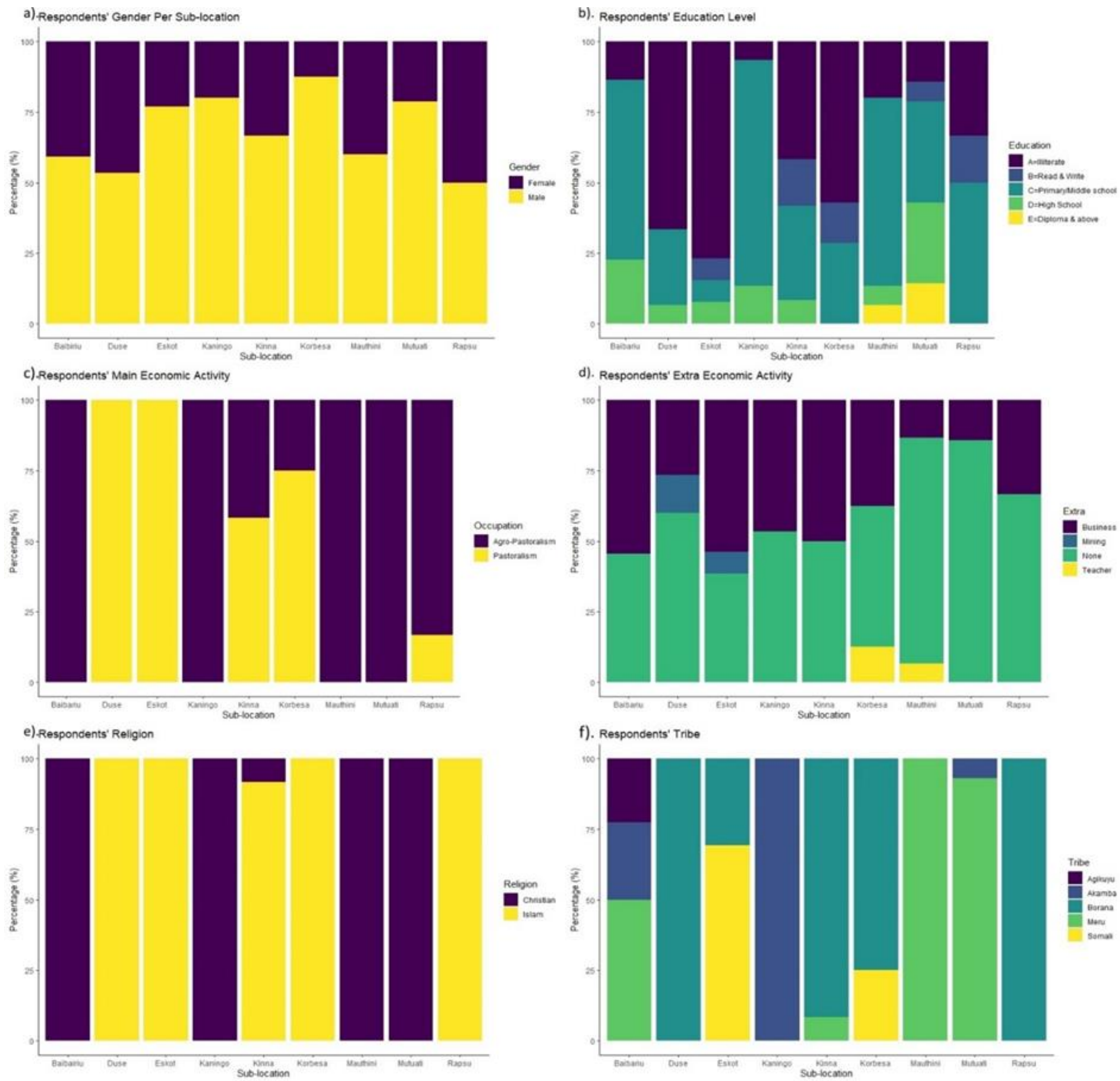

Figure 20: Stacked bar graphs summarising the socio-economic characteristics of the respondents.

Appendix 7: Graph output showing descriptions of carnivore knowledge and attitudes towards carnivores by the questionnaire survey respondents

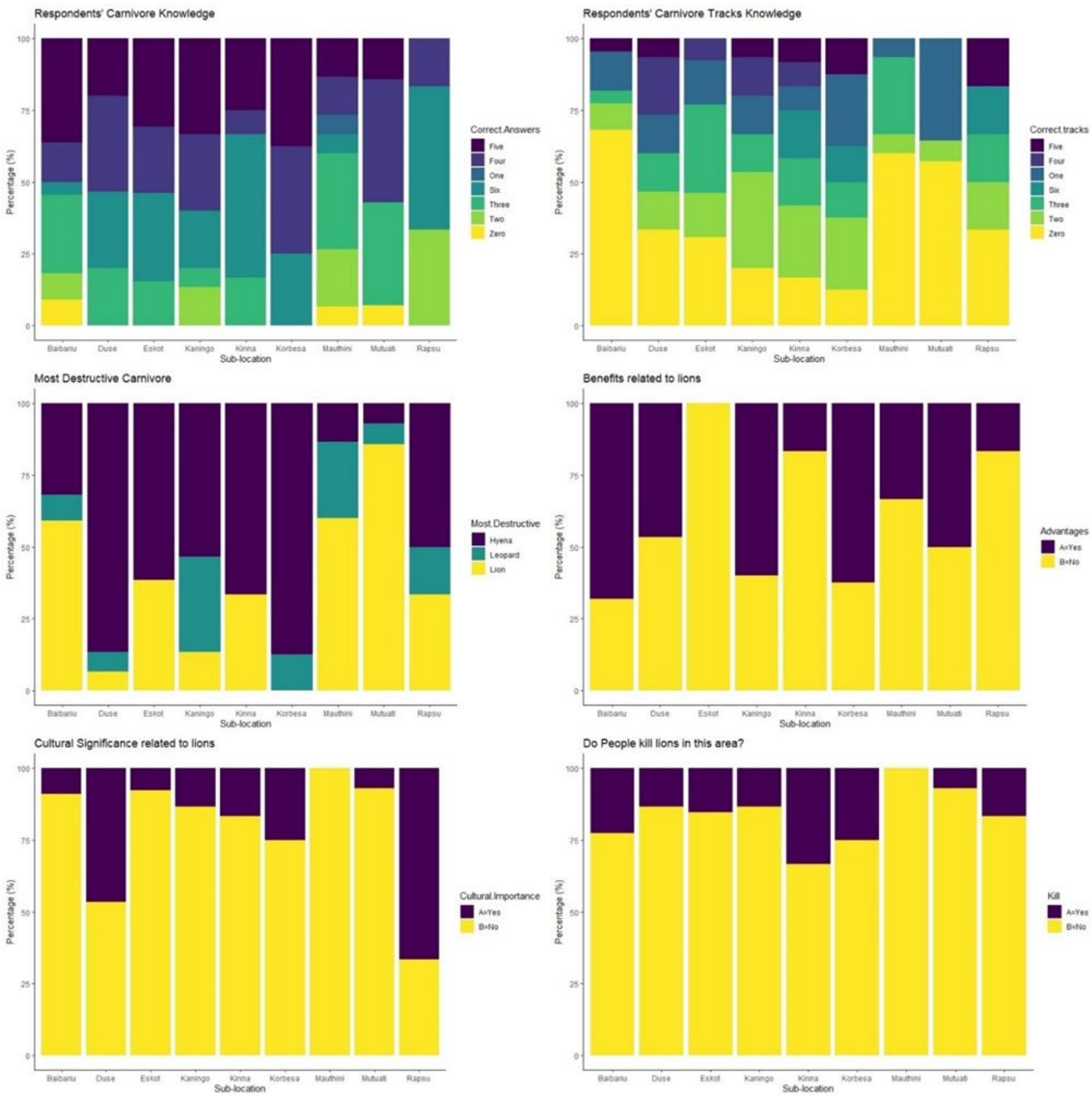

Figure 21: Stacked bar graph showing carnivore knowledge and attitude towards carnivore in the area.

Appendix 8: Graph output showing results from the likert scale used test attitude levels of the questionnaire survey respondents

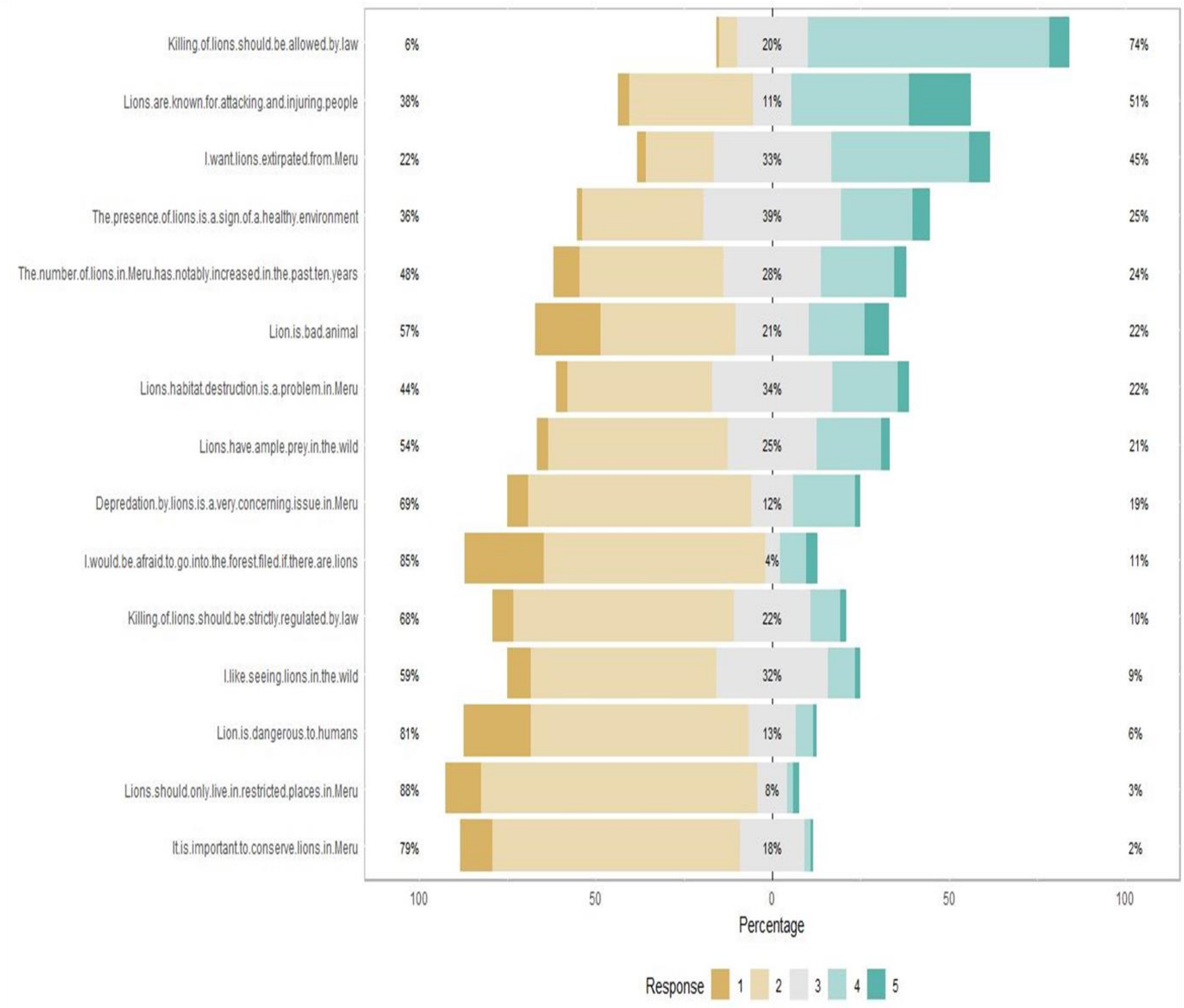

Figure 22: Graph showing outputs from the likert scale questions that measured attitude. To do this, we assigned values to responses (1: strongly agree, 2: agree, 3: neutral, 4: disagree, 5: strongly disagree) and multiplied the count of respondents for each question with its assigned value, summed the values, and divided the sum by the total number of respondents.

Appendix 9: Graph output showing correlation structure of factors influencing attitudes towards carnivores based on responses from the questionnaire survey.

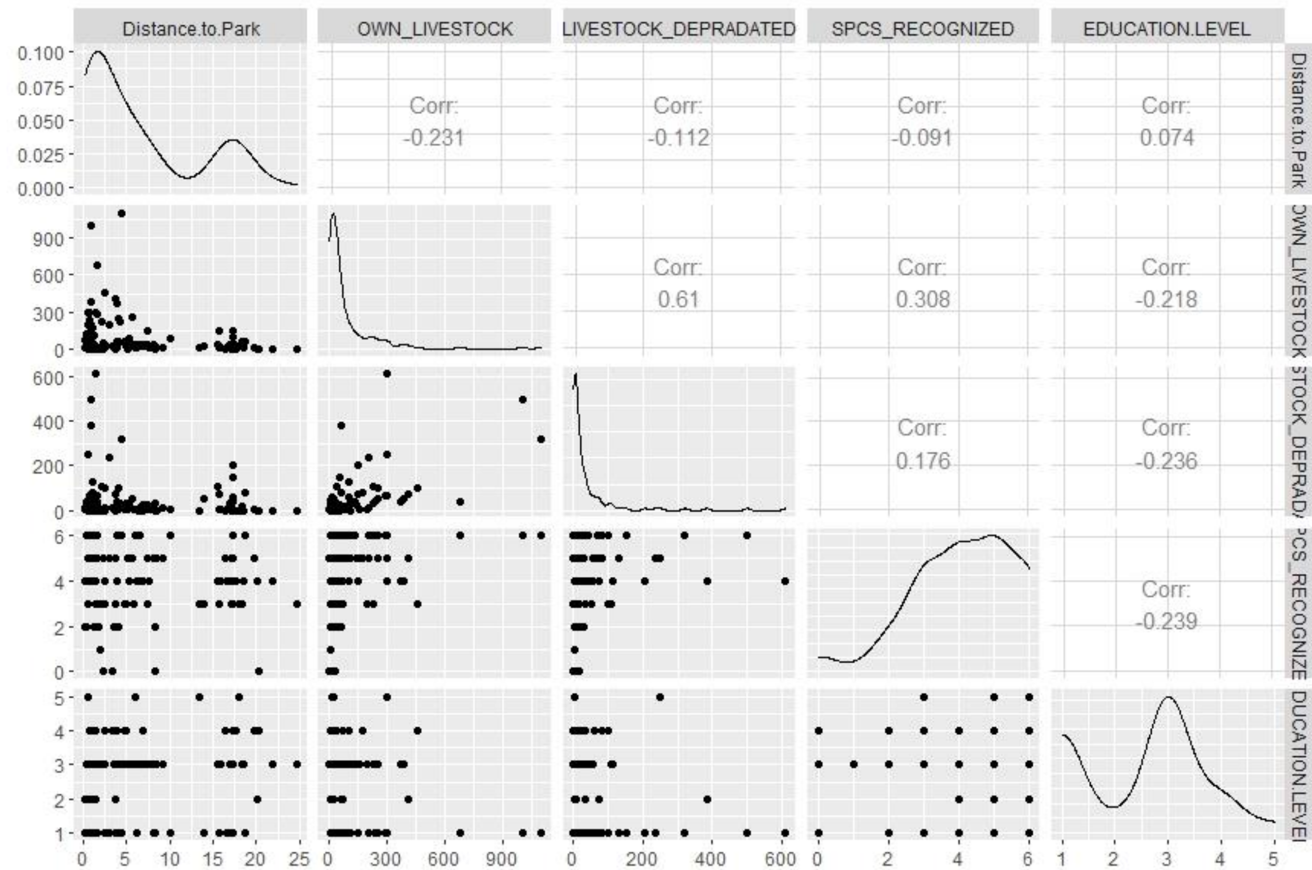

Figure 23: Graph showing correlation structure of the most important predictors of attitudes towards carnivores in the area.

Appendix 10: Graph output showing data distribution of factors influencing attitudes towards carnivores based on responses from the questionnaire survey.

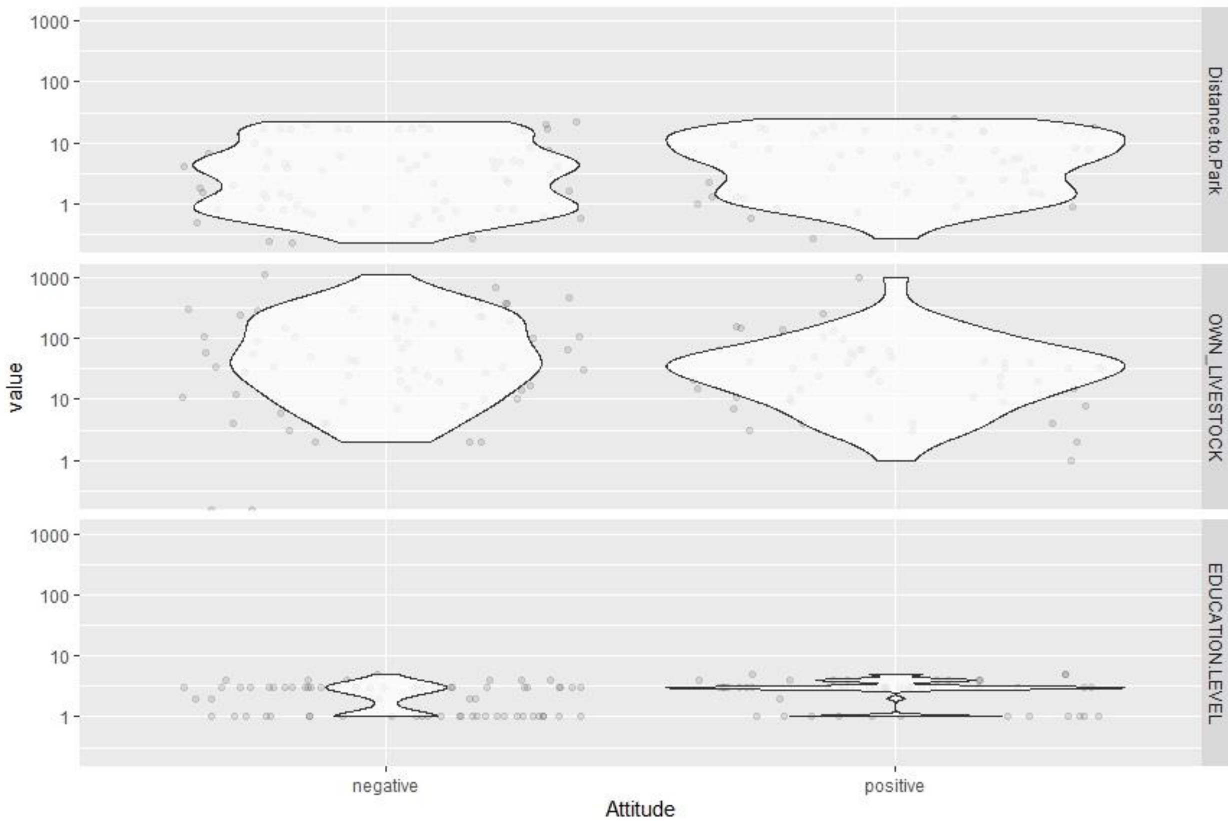

Figure 24: Violin plots showing how distance to park, livestock ownership and education level influence attitudes towards carnivores in the area.

Appendix 11: Graph showing factors influencing livestock depredation around the MCA based on responses from the questionnaire survey.

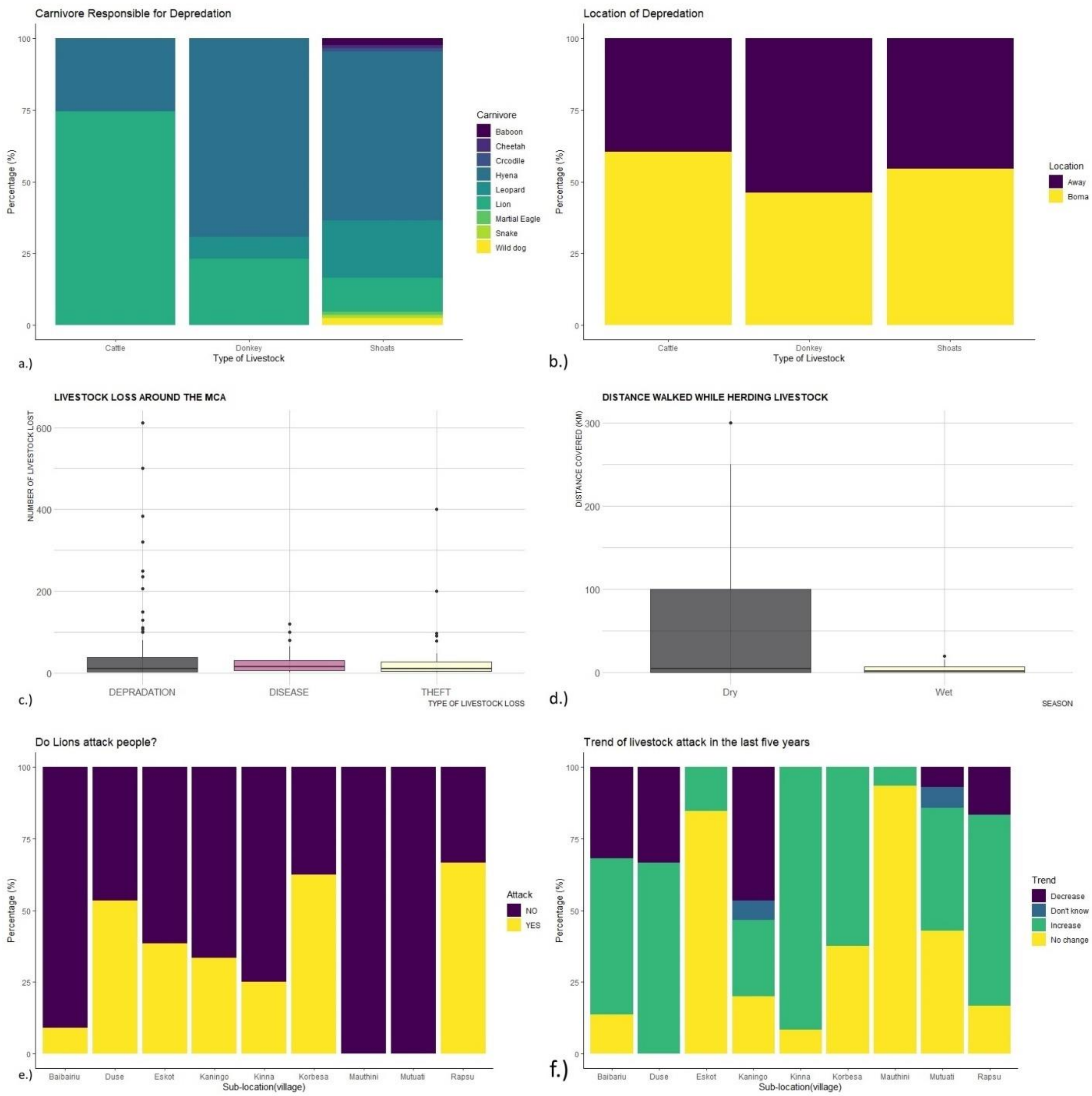

Figure 25: Graph showing a.) the proportions of different carnivores responsible for depredation of different livestock types; b.) proportions of depredation incidences occurring inside the boma or away from the boma; c.) livestock lost through different causes; d.) distance walked while herding livestock during wet and dry seasons; e.) responses on whether lions attack people; and the trends of livestock attacks in the area for the last five years based on responses from the questionnaire survey.

Appendix 12: Table summarizing the ecology and conservation of lions in the MNP with suggestions of possible conflict intervention measures.

Table 4: A typology of livestock–carnivore conflict intervention techniques that links specific tools with ecological concepts considered within the study.

Ecological category	Intervention classification	Description	Example	Ecological concept
Livestock ecology	Livestock management	Animal husbandry Approaches governing Livestock management and species or breed Biological characteristics that influence space use and behaviour of livestock	Stocking rate (Blaum et. Al., 2009) Rotational grazing (Boitani & Powell 2012) Breed selection (Landa et al. 1999) Guarding (Andelt 1992; Woodroffe et al. 2007; Gehring et al. 2011; Rigg et al. 2011) Calving barns (Pimenta et al. 2017) Livestock enclosures (Rigg et al. 2011; Mazzoli et al. 2002; Kolowski & Holekamp 2006) Space use (Boitani & Powell 2012; Pimenta et al. 2017) Fencing (Boitani & Powell 2012; Pimenta et al. 2017)	Optimal foraging theory Prey switching Landscape of fear Predator–prey interactions
Carnivore ecology	Carnivore deterrent	Physical objects and sensory stimuli that target and disrupt specific elements of carnivore behaviour or ecology	Guarding (Andelt 1992; Woodroffe et al. 2007; Gehring et al. 2011; Rigg et al. 2011) Fladry (Musiani et al. 2003; Davidson-Nelson & Gehring 2010) Flashing lights (Shivik et al. 2003) Audio	Landscape of fear Behaviourally mediated trophic cascades Habituation

			recordings (Shivik et al. 2003) Chemical deterrents (Smith et al. 2000) Turbo fladry (Lance et al. 2011)	
Carnivore ecology	Carnivore removal	Techniques that reduce the number or change the demographics of carnivores in a given area	Hunting (Wagner & Conover 1999) Targeted removal (Blejwas et al. 2002) Translocation (Bradley & Pletscher 2005; Milligan et al. 2018) Sterilization or contraception (Boitani & Powell 2012; Bromley & Gese 2001)	Landscape of fear Optimal foraging theory Prey switching Population ecology
Biophysical environment Livestock ecology Carnivore ecology	Indirect land and wild prey management	Management approaches that separate carnivores and livestock by altering wild prey habitat use and behaviour and land management in and around the grazing area		Inter and intra-species interactions Optimal foraging theory