Cape Peninsula
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LION (*PANTHERA LEO*), CATTLE AND WILDLIFE INTERACTIONS ON THE KUKU GROUP RANCH PASTORALIST AREA, KENYA

By

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A thesis submitted in fulfilment of the requirements for the degree

Master of Conservation Science: Nature Conservation

in the Faculty of Applied Sciences

at the Cape Peninsula University of Technology

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Cape Town
December 2021

DECLARATION

I, Iain Ralph Olivier, declare that the contents of this thesis represent my unaided work and that the thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions, not necessarily those of the Cape Peninsula University of Technology.

____________________ **Signed**

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ABSTRACT

Globally, large carnivores populations are declining with dramatic effects on lower trophic levels. As apex predators, large carnivores play critical roles in ecosystem processes, and unnatural declines in large carnivore populations can adversely affect their ecosystems. The reasons for declining carnivore numbers are numerous. However, one of the main threats to carnivores is human-wildlife conflict. Increases in human-wildlife interactions can pose significant threats to human safety and domestic livestock, causing conflict. Global human-wildlife conflicts have increased drastically over the last decade, and the countries of East Africa experience some of the highest rates of carnivore and other wildlife conflicts in the world. Lions are often the cause of conflict with livestock-owning people outside of formally protected areas when they often prey upon livestock, causing financial loss and negative perceptions, which frequently leads to their destruction. It is essential to understand why lions are involved in human-wildlife conflicts and the drivers of such conflict.

East Africa is home to three lion strongholds in Africa, including the study site within The Kuku Group Ranch (KGR). The KGR is a community-owned area covering 1 133 km², located near the Kenya-Tanzania border. The KGR is a wildlife corridor linking the Tsavo West, Amboseli, Chyulu Hills, and Kilimanjaro national parks. KGR is crucial for maintaining healthy wildlife populations, including a lion population, and preserving natural ecological processes in the area. However, lion populations are more frequently coming into contact with humans due to livestock and human expansion in the group ranch. Livestock expansion increases pressure on lion populations, and conflicts where lions are killed due to cattle depredations, are becoming commonplace. Viable lion populations present in the KGR suggest that lions can survive if the conflict rate between cattle owning people and lions is slowed. But the situation requires research as no formal, standardised investigations into the diets of lions and the drivers of cattle depredation have been conducted.

Therefore, the primary aim of this study was to investigate lion diet and prey preference in the KGR, a communal mixed-use area. The secondary aim was to understand how rainfall, lag rainfall (the average of the preceding two months and current months rainfall), Normalized Difference Vegetation Index (NDVI) and prey availability variables affected cattle depredation rates over 36 months in the KGR. Drivers that affected cattle depredation were investigated by modelling how variables influenced cattle depredation rates. Information on lions' diets was obtained from an investigation of predicted lion feeding sites obtained from location data of lions fitted with satellite collars (n = 7). Potential feeding sites were identified by analysing Global Positioning System (GPS) data points to identify positions where three or more consecutive GPS fixes were less than 100 m apart, and lions spent longer than 9 hours consecutively. Two data sources were used to estimate prey availability. Biannual aerial counts for overall prey availability, while community ranger patrol data provided continuous monthly data on prey availability in the form of monthly encounter rates per km. Data collected on lion diet and prey availability allowed preference calculations to discern which prey was most consumed and preferred. Prey preference was calculated using the Jacobs index for prey selectivity.

GPS cluster analysis resulted in 112 confirmed feeding events where large-bodied prey species (>50Kg) could be identified to species level. Cattle (*Bos taurus*), plains zebra (*Equus quagga*), Coke's hartebeest (*Alcelaphus cokeii*), Maasai giraffe (*Giraffa tippelskirchi*), blue wildebeest (*Connochaetes taurinus*), and eland (*Tragelaphus oryx),* made up 92% large-bodied prey consumed. The most common species consumed by lions were cattle (74%). The four most important wild prey species contributing to lion prey biomass were the Maasai giraffe, plains zebra, eland and Coke's hartebeest. These four species are also the most frequently encountered wild large prey species in the KGR.

An analysis of cattle depredation data for the KGR resulted in 330 cattle depredations sites. Field investigation of the 330 sites resulted in 176 negligent events and 154 non-negligent events. To identify drivers of cattle depredation, General Linear Modelling was used to compare rainfall, lag rainfall, NDVI and prey availability (predictor variables) to the number of cattle depredation events recorded every month over 36 months. The most important driver of cattle depredation was lag rainfall. During higher periods of lag rainfall, cattle depredation doubled. Although only displaying weak relationships, cattle depredations increased with increasing NDVI and decreased with a concurrent increase in wild prey availability.

Lions consumed high cattle numbers, and increases in lag rainfall drove rates of cattle depredation. The survival of lions in Africa and Kenya will be dependent on the ability of NGO's, governmental agencies, and local communities to prevent, mitigate, and address human-lion conflicts. Identifying the drivers of human-wildlife conflicts here can assist conservationists and communities in better understanding and minimising the risk of cattle depredations. Improving husbandry practices during the periods of higher lag rainfall and protecting large-bodied wild prey populations are management interventions likely to maintain lion populations and improve conservation in the KGR communal area. Improving these factors can preserve wildlife corridors and sustain diverse, ecologically functional mammal assemblages that can disperse to and from the surrounding national parks.

ACKNOWLEDGEMENTS

- Thank you to my supervisor, Dr Frans Radloff, for his patience, guidance and time invested in me and this project. I am privileged to have been able to work with and learn from him. His many trips to Kenya and the study site were always meaningful, where I enjoyed the off-road navigation and tracking lions and lion kills across the Tsavo-Amboseli landscape. Also, thank you for the many long, insightful conversations about the project and many other topics. I honestly could not have asked for a more dedicated supervisor over the length of this project. Thank you.

- Thank you to my co-supervisor, Dr Craig Tambling - His time, knowledge, patience, and expertise was generously given throughout this project, including field trips out to Kenya and many long sessions spent discussing methodology and analysis. Particularly for the discussions on chapters 3 and 4 and the fieldwork relating to GPS cluster follow-ups, data analysis and modelling in R. It was a genuine privilege to learn from him.

- Thank you to MWCT founder Luca Belpietro and MWCT president Samson Parashina, who supported the project and provided guidance at its inception. You are both visionaries, and the work you do for the communities in the Kuku Group Ranch changes lives every day. Thank you.

- Thanks to David Kanai, Simba Scout Coordinator, and his team of Simba scouts. My friend Kanai assisted me with most of the cluster follow-ups across the Kuku Group Ranch. Together we followed up on many kills on foot in the landscape. I could not have done this without his support and guidance in the field, and I will never forget our first close encounter with the sleeping lioness.

- Thank you to Robin Colyn. Robin assisted me with the NDVI calculations and Google Earth Engine scripts. I could not have done it without his guidance and expertise.

- Thank you to Jules, my wife, for the patience and support during this very long journey. You took one for the team throughout this process with a busy family and many sacrifices made along the way. You were always amazingly supportive, thank you.

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GLOSSARY

Acronyms & Abbreviations

GPS	Global Positioning System
GPS Cluster Point	A concentration of GPS coordinates within 100 meters from the previous locality
Group Ranch	A livestock production system and a community area where local Maasai people jointly own freehold title to land, maintain agreed stocking levels and herd their individually owned livestock collectively.
Ha	Hectares
KWS	Kenya Wildlife Service
KGR	The Kuku Group Ranch
Km	Kilometres
MWCT	Maasai Wilderness Conservation Trust
m	Meters
SD	Standard Deviation
SE	Standard Error

CHAPTER 1: GENERAL INTRODUCTION

1.1. Human-Carnivore Conflict

Apex carnivores, such as the African lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), and African wild dog (*Lycaon pictus*), have shown global declines in population numbers (Bauer & Van Der Merwe, 2004; Riggio *et al.,* 2013; LeFlore *et al.,* 2020). Primary threats to these large carnivores are habitat destruction, declining prey populations, and human-carnivore conflicts (Winterbach *et al.,* 2015; Bauer *et al.,* 2020). Human-carnivore conflicts occur frequently and constitute a global challenge (Ripple *et al.,* 2016; Broekhuis *et al.,* 2017; Montgomery *et al.,* 2018; Van Eeden *et al.,* 2018; Melzheimer *et al.,* 2020; Morehouse *et al.,* 2020; Jacobsen *et al.,* 2021). Human-carnivore conflicts are likely to increase in the future with increasing habitat fragmentation (Bauer *et al.,* 2020), as large predators require extensive, intact habitats and connected landscapes to survive (Sillero-Zubiri & Laurenson, 2001; Riggio *et al.,* 2013; Sargent *et al.,* 2021).

In addition to requiring large home ranges, large carnivores have specific biological characteristics, such as large body size, slow reproductive rates, and low population densities, that make them particularly vulnerable to human-carnivore conflicts (McKinney, 1997; Keinath *et al.*, 2017). Due to the extensive ranges required by large carnivores and their biological vulnerability, maintaining viable populations can be difficult without individuals from the population coming into contact with the ever-increasing human population (Estes *et al.,* 2011; Packer *et al.,* 2013; Ripple *et al.,* 2016; Melzheimer *et al.,* 2020). Human-carnivore interactions frequently occur as carnivores prey upon or are perceived to prey upon livestock and, in particular, cattle (Broekhuis *et al.,* 2017; Montgomery *et al.,* 2018; Melzheimer *et al.,* 2020; Morehouse *et al.,* 2020).

Increased negative human-wildlife interactions leading to livestock depredation can pose significant threats to human safety and domestic livestock, causing conflict between predators and humans (Estes *et al.,* 2011; Packer *et al.,* 2013; Broekhuis *et al.,* 2017). Due to these negative interactions, carnivore populations continue to decline principally due to retaliatory killing (Nowell & Jackson, 1996; Bauer & Van Der Merwe, 2004; Bauer *et al.,* 2020).

While large carnivore populations are declining, their distribution ranges are also reduced, which is evident when comparing their historical range with what remains. Lions have lost 75% (Riggio *et al.,* 2013), cheetahs 91% (Durant *et al.,* 2017), and leopards 63%–75% of their historical range in Africa (Jacobson *et al.,* 2016). Diminishing ranges and the decline of large carnivore populations can have adverse effects on lower trophic levels (Sinclair *et al.,* 2003; Estes *et al.,* 2011; Hopcraft *et al.,* 2010), as large carnivores play critical roles in ecosystem processes as apex predators (Estes *et al.* 2011; Packer *et al.,* 2013; Ripple *et al.* 2014; Wallach *et al.,* 2015). Due to the ecological importance of large carnivores, their extirpation due to conflicts and livestock depredation can negatively affect ecosystem structure and functioning (Ripple *et al.,* 2015).

As large carnivores are particularly vulnerable to human-wildlife conflict and have large spatial requirements, there has been an increase in the research of human-wildlife conflicts, where large carnivores have been prioritised (Ripple *et al.,* 2014; Trouwborst *et al.,* 2017). In large carnivore conservation projects and initiatives, the causal factors of population declines have been identified and researched extensively (Ripple *et al.,* 2014; Trouwborst *et al.,* 2017; Sargent *et al.,* 2021). However, studies have failed to improve carnivore conservation, despite the increased research efforts of the past 25-30 years (Montgomery *et al*., 2018), and global human-wildlife conflicts have been steadily increasing (Beck *et al.,* 2019). African countries experience some of the highest carnivore-related and other wildlife conflicts globally (Beck *et al.,* 2019). The high rates of human-wildlife conflicts in Africa demonstrate a failure to translate research and understanding of conflict into conservation action to improve carnivore conservation (Ripple *et al.,* 2016; Sargent *et al.,* 2021).

In Africa, lions are often the cause of conflict with livestock-owning people causing financial loss and negative perceptions, frequently leading to the destruction of lions (Kissui, 2008; MacLennan *et al*., 2009; Ontiri *et al.,* 2019; Bauer *et al.,* 2020). Conflict occurs both within and outside formally protected areas (PAs) (Dolrenry, 2013; Kissui, 2008; Okello, 2014), and approximately 44% of the remaining range of the African lion lies outside of PA's (Bauer *et al.,* 2018; IUCN, 2018; Sargent *et al.,* 2021). Lion-livestock conflicts become severe when cattle (*Bos taurus*) are involved (Mbise *et al*., 2018; Gebresenbet *et al*., 2018; Van Eeden *et al*., 2018). Cattle are highly prized and valued in pastoralist communities, and losses to lions can have significant financial impacts for pastoralists (Patterson *et al.,* 2004; Kissui, 2008; Mwakatobe *et al.,* 2013). Furthermore, within numerous pastoralist cultures, the keeping of cattle and cattle ownership is entrenched in both religious and cultural heritage (Galaty, 1982). Owning cattle in these pastoralist cultures and societies is a feature of communal identity and can indicate pride, wealth, and status (Hazzah, 2007; Nkiziibweki & Emmanuel, 2018).

Consequently, depredation of cattle by lions is viewed more severely than a loss of any other livestock and will frequently provoke a retaliatory response among affected communities (Everatt *et al.,* 2019). These retaliatory responses often result in the retributive killing of lions responsible or perceived responsible for these losses (De Iongh *et al.,* 2009; Loveridge *et al.,* 2010; Mponzi *et al.,* 2014; Kuiper *et al.,* 2015; Everatt *et al.,* 2019). Lion depredation of cattle and associated human retaliation is thus one of the most common and significant issues affecting lion conservation today (Bauer *et al.,* 2018; Cushman *et al.,* 2018; Beck *et al*., 2019; Bauer *et al*., 2020).

1.2. Lion Population Status

Lion numbers are declining rapidly outside of formally protected, and fenced areas (Bauer & Van Der Merwe, 2004; Bauer *et al.,* 2015; Lindsey *et al.,* 2017; Dures *et al.,* 2019), and approximately half the unfenced lion populations may decline to near extinction over the next 20-40 years (Packer *et al.,* 2013). Lions are thus considered vulnerable to extinction on the International Union for Conservation of Nature (IUCN) Red List (Bauer *et al.,* 2016). Lion population size estimates across Africa suggest that there are only 23 000 to 39 000 lions left on the African continent (Chardonnet, 2002; Bauer *et al.,* 2005; Bauer *et al.,* 2016; Dures *et al.,* 2019) spread across 65 different locations (Riggio *et al.,* 2013; Bauer *et al.,* 2016).

Lions were once common throughout Africa and occupied most of the continent's biomes except for tropical rainforests and the Sahara Desert (Nowell & Jackson, 1996; Bauer & Van Der Merwe 2004; Dolrenry *et al.,* 2014; Bauer *et al.,* 2018; Bauer *et al.,* 2020). Currently, lions are mostly restricted to formally protected areas in South and East Africa and to a lesser extent, in West Africa (Bauer *et al.,* 2018; Bauer *et al.,* 2020). The extent of free-ranging lion populations was estimated at 3.4 million km^2 or approximately 25% of the savannah biome in 2013 (Riggio *et al.,* 2013). Within the current free-ranging lion populations, there is evidence of population declines and local extinctions (Riggio *et al.,* 2013; Bauer *et al.,* 2015; Bauer *et al.,* 2018; Bauer *et al.,* 2020). The factors that threaten lion survival have led to an associated range decrease of up to 80%, with an approximate 30% decline in numbers in the last 20 years (Bauer *et al.,* 2005; Bauer *et al.,* 2015; Bauer *et al*., 2020).

Global lion assessments have shown that populations in West and Central Africa are small and fragmented, whereas, in East and southern Africa, the species occurs more widely over large inter-connected conservation areas or lion strongholds (Bauer & Van Der Merwe, 2004; Bauer *et al.,* 2005; Riggio *et al.,* 2013; Bauer *et al.,* 2020).

In their analysis of the current extent of free-ranging lion populations, researchers outlined ten areas that can be considered lion strongholds or areas of improved lion conservation, connectivity, and protection (Riggio *et al.,* 2013). Four of these lion strongholds are in East Africa, and six are in southern Africa. There are approximately 20 000 lions in these lion-stronghold areas and 4 000 in areas with lesser protection (Riggio *et al.,* 2013; Bauer *et al.,* 2018). However, over 6 000 lions are in populations of doubtful long-term viability outside of protected areas (Riggio *et al.,* 2013; Bauer *et al.,* 2018; Bauer *et al.,* 2020). In Kenya, these areas include the communally owned Maasai rangelands that frequently surround formally protected areas (Western *et al.,* 2021).

1.3. Human-Lion Conflict: Kenya

Livestock depredation has been reported throughout the distribution range of lions in southern, western, and East Africa, including Kenya (Patterson *et al.,* 2004; Tumenta *et al.,* 2013; Tuqa, 2015; Blackburn *et al.,* 2016; Lesilau, 2019), where the problem is particularly acute (Lesilau, 2019; Bauer *et al.,* 2020). In Kenya, 8% of the land has been declared national parks and a further 11% as community conservancies (Lesilau, 2019), but despite this, fewer than 2 000 lions remain in the country (Lesilau, 2019). Livestock depredation by lions and the consequent negative human-lion interactions are significant drivers of the decline of lion populations in Kenya (Lindsey *et al.,* 2017; Loveridge *et al.,* 2017; Bauer *et al.,* 2020). Human-lion conflicts occur in all areas adjacent to Kenyan national parks and other protected areas (Patterson *et al.,* 2004; Woodroffe & Frank, 2005; Tuqa, 2015) and present a challenge for effective lion conservation (Lindsey *et al.,* 2017; Lindsey *et al.,* 2018; Western *et al.,* 2021). The increased frequency of human-lion interactions needs further investigation as over 65% of Kenya's wildlife species are found on private and communal lands outside protected areas in human-dominated, pastoralist landscapes (Western *et al.,* 2009; Mukeka *et al.,* 2019; Western *et al.,* 2021).

Across Kenya's human-dominated, pastoralist landscapes, lion attacks on livestock occur frequently and can lead to retaliatory and preventative killings of lions in areas outside of protected reserves (Ontiri *et al.,* 2019; Western *et al.,* 2021). On privately and communally owned Kenyan ranches, predators (including lions) can kill and consume as much as 2–3% of the livestock annually (MacLennan *et al.,* 2009; Bauer *et al.,* 2017; Western *et al.,* 2021). Although other carnivores also attack and consume livestock, lions are often disproportionately persecuted (Kissui, 2008; Bauer *et al.,* 2017; Beattie *et al.,* 2020), and historical studies demonstrated that between 2001 and 2008 alone, over 130 lions were killed in the Tsavo-Amboseli Ecosystem (Hazzah *et al.,* 2009; Hazzah *et al.,* 2014).

Because the retaliatory killing of lions is common, significant efforts have been taken to reduce livestock depredations to enable coexistence between people and lions on private and communal lands (Creel *et al.,* 2013; Bauer *et al.,* 2017; Dolrenry *et al.,* 2020). However, lion numbers are still declining rapidly in the country's rangelands due to ongoing conflict with local Maasai communities, habitat loss, and associated livestock expansion (Ikanda & Packer, 2008; Hazzah *et al*., 2009; Bauer *et al.,* 2020).

Despite the ongoing conflicts, lions in southern Kenya still reside outside protected landscapes that provide connectivity between protected areas (Dolrenry *et al.,* 2020). Proven connectivity and movement among lion populations between protected areas in Kenya suggests that unprotected areas and their local communities can create corridors of tolerance, facilitating connectivity and long-term survival of lion populations within and outside PA's (Dolrenry *et al.,* 2020). One such area is the Tsavo- Amboseli landscape, considered a critical wildlife corridor in Kenya that includes three formally protected national parks, several informally protected communal group ranches, and other unprotected areas (Dolrenry *et al.,* 2020; Henschel *et al.,* 2020).

1.4. The Tsavo-Amboseli Landscape

The Tsavo-Amboseli landscape is approximately 21 000 km² in size and is one of four lion strongholds in East Africa (Riggio *et al.,* 2013). In the national parks (Tsavo West, Amboseli, Kilimanjaro & Chyulu Hills National Parks) that fall within this stronghold, lions are formally protected, but in the adjacent communal land and wildlife corridors, the conflict between pastoralist communities and lions persists (Riggio *et al.,* 2013; Henschel *et al.,* 2020). Land communally owned by the Maasai, known as Maasai group ranches, play an essential role in lion conservation within the Tsavo-Amboseli landscape, as they have historically supported viable lion populations and created connectivity between lion populations in the adjacent protected areas where lion numbers are stable (Okello, 2005; Okello, 2009; Bauer *et al.,* 2017; Dolrenry *et al.,* 2020; Henschel *et al.,* 2020).

In some areas of the Tsavo-Amboseli landscape, lion numbers are declining due to multiple factors, including rapid human population growth within the group ranches, increased dependence of pastoralists on livestock, and the associated livestock expansion (Bauer *et al.,* 2020). Lion predation on cattle is increasing in the Tsavo-Amboseli landscape due to the growing cattle numbers that increase lion-cattle encounter rates and competition with wild prey species for space and resources (Bauer *et al*., 2020; Mukeka *et al.,* 2020).

Within the Tsavo-Amboseli landscape, the expansion of livestock farming on the communal group ranches has placed considerable pressure on resources and contributes to the disappearance of native species and lions prey base (Bauer *et al.,* 2020; Long *et al.,* 2020; Mukeka *et al.,* 2020). Studies have found that lion populations are declining in the rangelands of southern Kenya, where Maasai pastoralists have been spearing and poisoning lions at a rate that will guarantee short-term local extinction (Hazzah *et al.,* 2014; Ontiri *et al.,* 2019).

The result of increased lion-livestock and, in particular, lion-cattle conflicts leads to retaliatory or preventative killing of lions (Dickman *et al.,* 2014; Bauer *et al.,* 2020). In most cases, lion killing is reported to be aimed at problem lions only. However, these threats affect all lions, as pastoralist communities within Kenyan group ranches in the Tsavo landscape frequently resort to indiscriminately killing many lions and even poisoning entire lion prides (Loveridge *et al.,* 2017; Ontiri *et al.,* 2019). Kenyan group ranches are the last remaining natural pastoral regions where humans and large wildlife populations exist outside protected areas in Kenya and are thus crucial for the landscape and lion-stronghold (Awere-Gyekye, 1996; Okello *et al.,* 2003).

Group ranch areas offer important connectivity through wildlife corridors and provide suitable habitats to many wildlife species (Ogada *et al.,* 2003; Bauer *et al.*, 2015), and in particular, group ranches benefit large carnivore species (Okello, 2005; Woodroffe, 2011; Dolrenry *et al.,* 2014; Dolrenry *et al.,* 2020). One such group ranch is the Kuku Group Ranch (KGR), which is particularly important as it borders both the Tsavo West and the Chyulu Hills National Parks and forms a critical migratory corridor for wildlife species linking Amboseli National Park to the Tsavo-Chyulu ecosystem (Kiringe, 2005; Okello, 2005; Dolrenry *et al.,* 2020; Henschel *et al.,* 2020) (Figure 1.1).

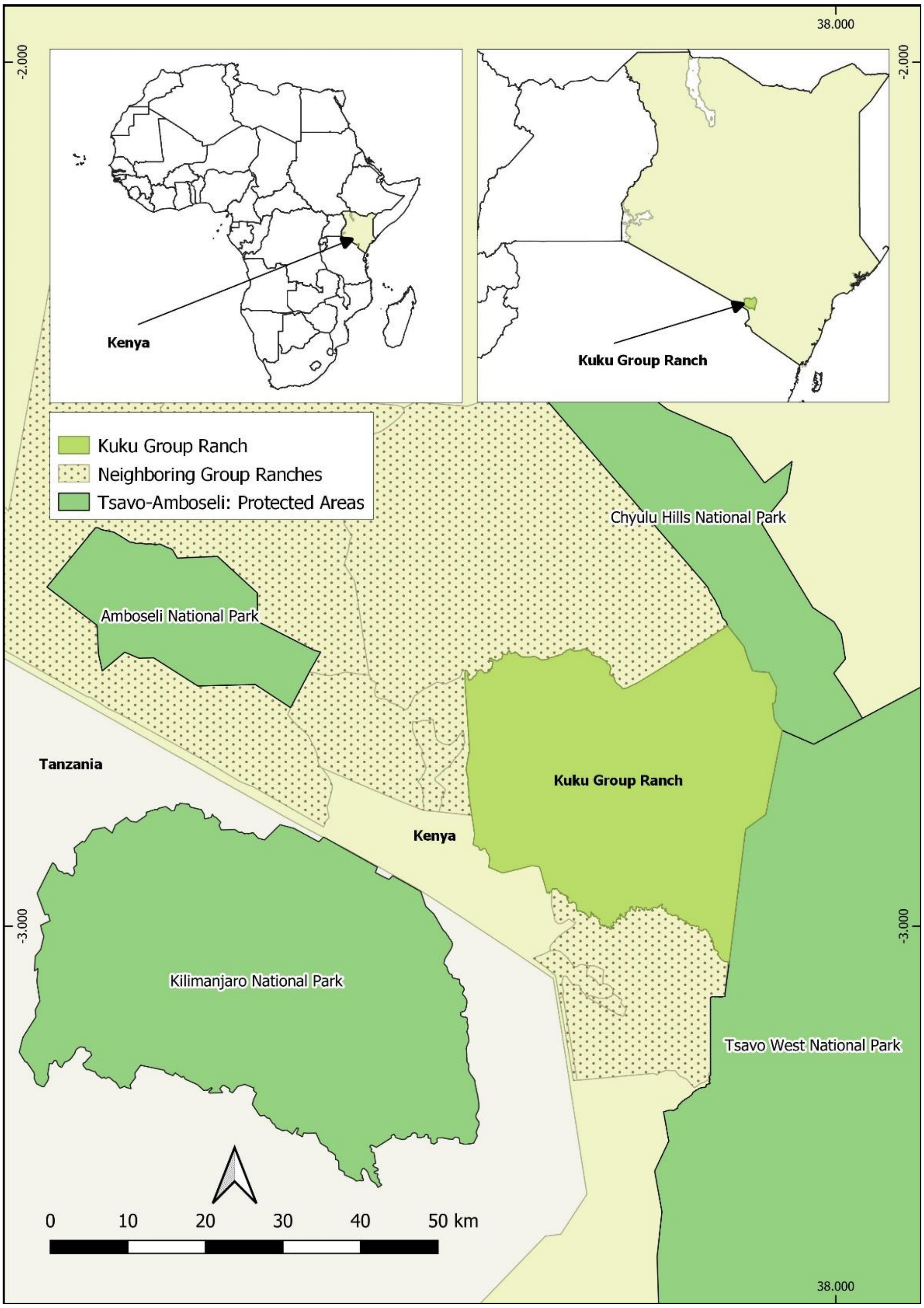

Figure 1.1: The Kuku Group Ranch, the Tsavo West National Park, Chyulu Hills National Park, Kilimanjaro National Park, Amboseli National Park, and neighbouring Group Ranches.

1.5. The Kuku Group Ranch

In Kenya, a group ranch is an area of communal land used as a joint livestock production system where communities jointly own freehold title to land, maintain agreed stocking levels, and herd their individually owned livestock collectively (Awere-Gyekye, 1996). Group ranches are located across Kenya, but there is a high concentration of these areas in the southern Maasai rangelands of the country (Awere-Gyekye, 1996), where the KGR is one of these ranches. The KGR was gazetted as a group ranch by the Kenyan Government in 1970 following the Kenya Group Ranches Act in 1968 (Awere-Gyekye, 1996; Okello, 2005). The KGR is a community-owned administrative area with internal conservancies covering 1 133 km^2 and is located in southern Kenya, near the Kenya-Tanzania border (Okello, 2005; Kiringe & Okello, 2005) (Figure 1.1).

The primary form of livelihood on the KGR is semi-nomadic pastoralism, with the primary source of income to local Maasai communities coming from the sale of large (cattle) and small (sheep, *Ovis aries*; goats, *Capra hircus*) livestock (Okello, 2005; Dolrenry, 2013). Within the KGR, there is also an alternative source of income through two community conservancy areas set aside as exclusive game viewing areas which house a lodge and tourism operation that partners directly with the local community (Bauer *et al.,* 2017). Tourists overnighting in the lodge pay a community conservation levy to finance conservation activities such as a predator compensation scheme compensating pastoralists for verified livestock losses to wild predators (Bauer *et al.,* 2017).

Tourist operators use the entire KGR area for game viewing, and lions are an important drawcard for tourists, thus playing an integral role in promoting tourism and contributing to ecosystem functioning (Ogutu, 2002; Okello *et al.,* 2014; Bauer *et al.,* 2015). The Maasai Wilderness Conservation Trust (MWCT) coordinates conservation, health, and education programs on the KGR, including the predator compensation scheme, environmental education, school programs, and rehabilitation. MWCT also runs a lion-specific conservation program with Simba Scouts (lion guardians) that monitor collared lions to warn pastoralists of lions near villages. Although the eco-tourism enterprise, predator compensation fund, and the lion conservation program effectively lower persecution levels, lion-cattle conflicts persist within the KGR (Bauer *et al*., 2017). Between 2011 and 2016, an average of 1.5 lions was killed per year in retaliatory action to cattle predation from local Maasai living within the KGR (MWCT: Unpublished data, 2016; Bauer *et al.,* 2017). Retaliatory killing, coupled with small lion population sizes, low wildlife densities, and a semi-arid environment, places considerable strain on the resident KGR lion population (Kissui, 2008; Hazzah *et al.,* 2017).

The depredation of cattle by lions within KGR is not evenly distributed throughout the year, with unpublished reports suggesting a peak in cattle predation coinciding with the annual peaks in rainfall during March to May and October to December (MWCT: Annual Reports, 2003 - 2016) (Figure 1.2). The seasonal spikes in depredation events may be related to husbandry practices, wild prey availability, or both. Good or bad cattle husbandry can affect lion predation, which has been found in Botswana (Wiese *et al.,* 2019; LeFlore *et al.,* 2020), Zimbabwe (Loveridge *et al.,* 2017), and Kenya (Western *et al.,* 2021). Jablonski *et al.* (2020) found that untended livestock accounts for > 80% of lion attacks, while Beattie *et al.* (2020) found wild prey availability a strong driver of lion-cattle conflict.

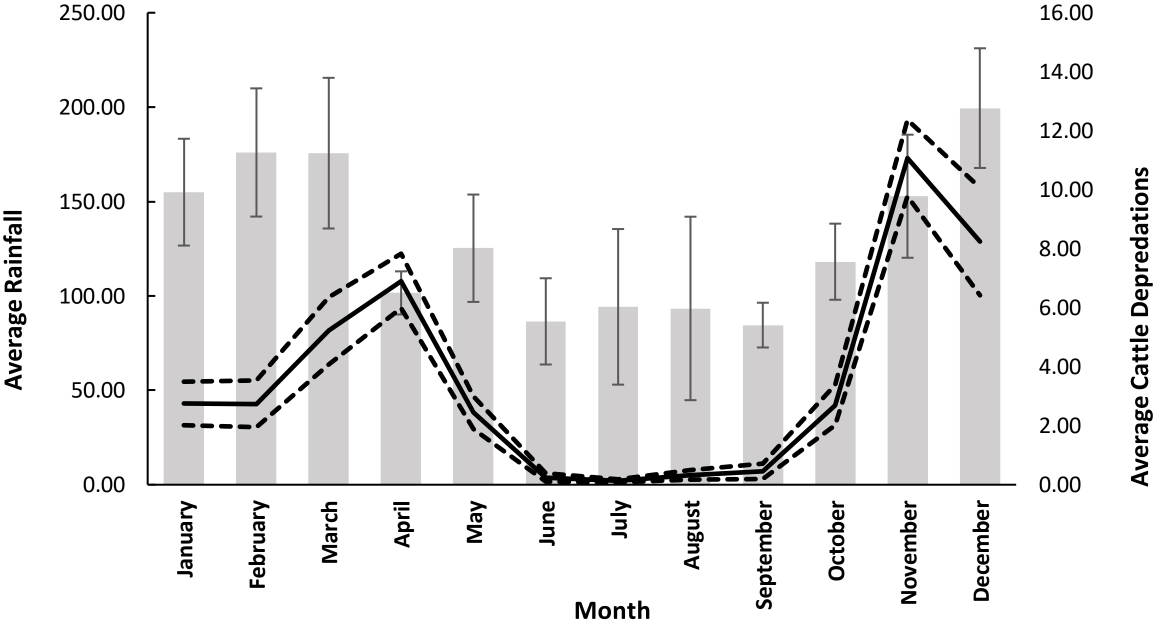

Figure 1.2: A graph indicating the average annual rainfall recorded at the Chyulu Conservation and Research Centre (CCRC) compared to the average number of monthly lion incidents recorded on the Kuku Group Ranch from 2003 to 2016 (MWCT 2011-2016, *Unpublished. Data*).

Not all wild prey are permanently resident within KGR, and the densities and distributions of species including plains zebra (*Equus quagga*), Coke's hartebeest (*Alcelaphus cokeii*), Maasai giraffe (*Giraffa tippelskirchi*), and blue wildebeest (*Connochaetes taurinus*) fluctuate within these types of areas depending on natural foraging resources and water availability (Schuette *et al.,* 2016). In other areas, the scarcity of wild prey has increased livestock consumption by lions, particularly cattle (Sundararaj *et al.,* 2012; Khorozyan *et al.,* 2015; Beattie *et al.,* 2020).

A better understanding of what drives the variation in cattle predation by lions throughout the year may guide mitigation strategies to not only reduce depredation events in months of peak cattle predation but might also help reduce lion-cattle killings across all months of the year. A first step in understanding the drivers of cattle predation is to identify what lions eat on the KGR. Knowledge of the most important prey species can be used to assess the temporal availability of key prey items, which can shed light on whether wild prey availability is a potential driver of elevated cattle predation events.

1.6. Research Problem Statement

African lions are endangered, and one of the last strongholds with viable populations is the Tsavo-Amboseli Ecosystem (Riggio *et al.,* 2013; Bauer *et al.,* 2020). At nearly 21 000 km^2, this stronghold area is one of only four lion strongholds in East Africa (Riggio *et al.,* 2013). The stronghold areas include the Tsavo West, Tsavo East, Amboseli, and Chyulu Hills National Parks, as well as several community Maasai group ranches within the area (Okello, 2005; Mbane *et al.,* 2019; Okello *et al.,* 2014; Bauer *et al*. 2015; Dolrenry *et al.,* 2020; Henschel *et al.,* 2020).

The Maasai group ranches play an essential role as wildlife corridors and refuges as there are still significant numbers of lions within these rangeland areas that are vital for gene flow and connectivity between the lions within the National Parks of Kenya (Okello *et al*., 2014; MacLennan *et al.,* 2009; Bauer *et al.,* 2017; Dolrenry *et al.,* 2020). The resident lion population is increasingly predating livestock, particularly cattle (Bauer *et al.,* 2017). On the KGR, MWCT has run a livestock compensation program, the Wildlife Pays (WP) program, since 2008 (Bauer *et al.,* 2017). The WP program records predator-related conflict incidents in the group ranch and compensates local communities monetarily for the loss of livestock to wildlife predation (Bauer *et al*., 2017).

Data from the WP program indicates an overall increase in lion-livestock conflicts over the last ten years (Bauer *et al*., 2017). If the upward lion-livestock conflicts trend persists, it could lead to an irreconcilable human-lion conflict situation with reduced lion numbers and even localised extinction in KGR. However, there is a lack of information about lion diet and the spatial and temporal variation of cattle depredation within the KGR. Studies have indicated that to manage Africa's changing landscapes effectively for lion populations; future research should be focussed on the analysis of habitat use outside protected areas, considering various abiotic factors, prey abundance, and anthropogenic risk (Montgomery *et al.,* 2018; Sargent *et al.,* 2021)

Investigation into the KGR's rainfall patterns, associated Normalized Difference Vegetation Index (NDVI) and cattle husbandry practices may shed further light on what creates the uneven cattle predation patterns. This study aims to identify the most important prey items of lions and use that information to investigate the drivers of cattle depredation within this area. A better understanding of the spatial and temporal interactions and the circumstances associated with cattle depredations can assist management in reducing livestock predation by lions and, in this way, prevent retribution killings of lions. Preventing lion killing will aid conservation efforts to ensure lion persistence outside the neighbouring national parks by implementing evidence-based management decisions.

1.7. Study Objectives

This study aimed to investigate lion, cattle, and wildlife interactions in the KGR pastoralist area, Kenya, by assessing the resident lion's utilisation of large prey (>50kg), the wild prey availability, and drivers of cattle depredation on the KGR.

The specific objectives were:

- To identify the primary large prey species (>50kg) of lions in the KGR using GPS (Global Positioning System) cluster analyses.
- To determine the seasonal variation in the availability of the most important lion prey species using aerial count and ranger patrol data.
- To assess the temporal variation in cattle depredation events by lions in the KGR and explore whether prey availability, environmental variables (rainfall, lag-rainfall, and normalised difference vegetation index), or husbandry practices can explain the temporal variation in cattle depredation patterns.

1.8. Structure of Thesis

The thesis consists of five chapters, of which Chapters 3 and 4 have been compiled as independent, stand-alone manuscripts to facilitate publication in peer-reviewed journals.

- **Chapter 2** contextualises the KGR and study site and focuses on the location, climate, topography, physical features, vegetation, land use, and general information.
- **Chapter 3** investigates the large-bodied prey (>50kg) of lions and the prey's availability in the KGR, using data obtained through GPS cluster analysis (investigating feeding locations), bi-annual aerial censuses, and wildlife sightings during ranger patrols.
- **Chapter 4** examines the patterns and drivers of temporal variation in cattle depredations in the KGR. Monthly cattle depredation rates were evaluated in relation to prey availability measures, rainfall, lag rainfall, NDVI and herding practices. Herding practices were categorised into both negligent and non-negligent practices.
- **Chapter 5** is a synthesis chapter that aims to relate the most important findings to conservation management action. Aspects in need of further research are also identified.

1.9. Permits and Ethical Considerations

Lion location information was obtained from lion collar data of the Maasai Wilderness Conservation Trust. The MWCT collars lions within KGR to reduce lion-human conflict through a lion guardian program (Bauer *et al.,* 2017), with the permission and participation of the Kenya Wildlife Service (KWS), permit number: KWS/BRM/5001 (2013-2017). Written permission for the use of the lion location data was obtained from the MWCT, and no lions were fitted with GPS collars for this study. Counts of wildlife and livestock were conducted non-invasively by the MWCT through total aerial counts and ranger observations on foot. Livestock depredation events were recorded and verified by trained verification offers of the MWCT on GPS-enabled smartphones and the information shared with the necessary written permission.

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CHAPTER 2: STUDY AREA

2.1. Introduction

The study was conducted in the eastern part of the Kuku Group Ranch (KGR), a community-owned administrative area with internal conservancies that covers 1 133 km^2 and is located in the southern part of Loitokitok District near the Kenya-Tanzania border (Kiringe *et al.,* 2005) (Figure 2.1). Group ranches have been defined as livestock production systems, where traditional occupants of the area jointly own a freehold title to land and continue to herd their livestock (Western *et al.,* 2009). The KGR conservancy is located at S 2.77554^{0}, E 37.85150^{0} and is one of six group ranches communally owned by the Maasai in the general area and is of critical importance as a wildlife corridor between the Tsavo West National Park (TWNP), the Amboseli National Park (ANP) and the Chyulu Hills National Park (CHNP) (Wilkie & Douglas-Hamilton, 2018; Dolrenry *et al.,* 2020; Mungo, 2021). This corridor is crucial for maintaining healthy wildlife populations and preserving natural ecological processes in the area (Kiringe *et al.,* 2005; Okello, 2009; Okello, 2012; Wilkie & Douglas-Hamilton, 2018) (Figure 2.2).

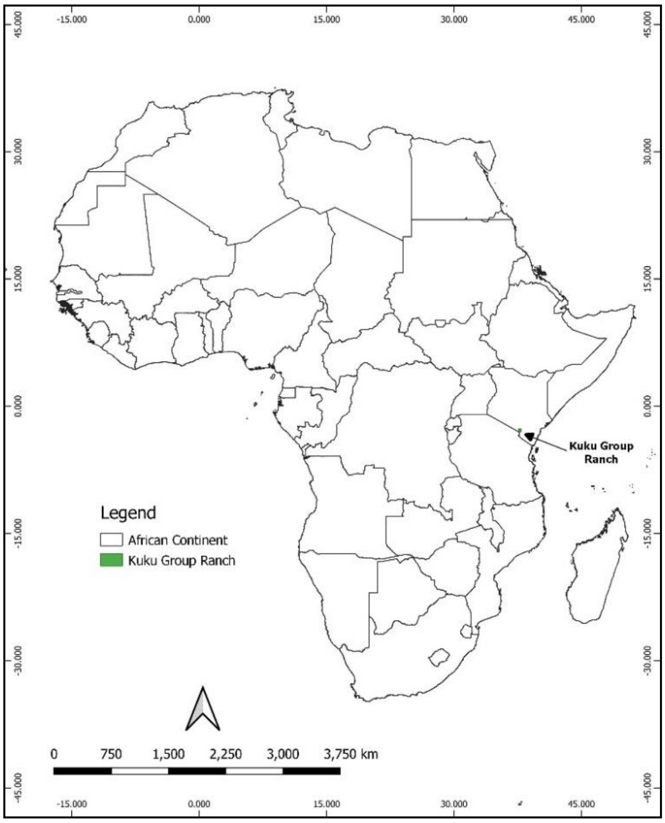

Figure 2.1: The location of the Kuku Group Ranch within the East African and continental African context.

The study site thus forms part of an essential corridor for wildlife, particularly for elephants (*Loxodonta africana*) and lions (*Panthera leo*) (Blanc *et al.,* 2007). The KGR is situated in the heart of the 9000 km² greater Amboseli-Tsavo ecosystem, and in addition to wildlife, the KGR also provides residence to approximately 17 000 Maasai and 90 000 livestock (Bauer *et al.,* 2017).

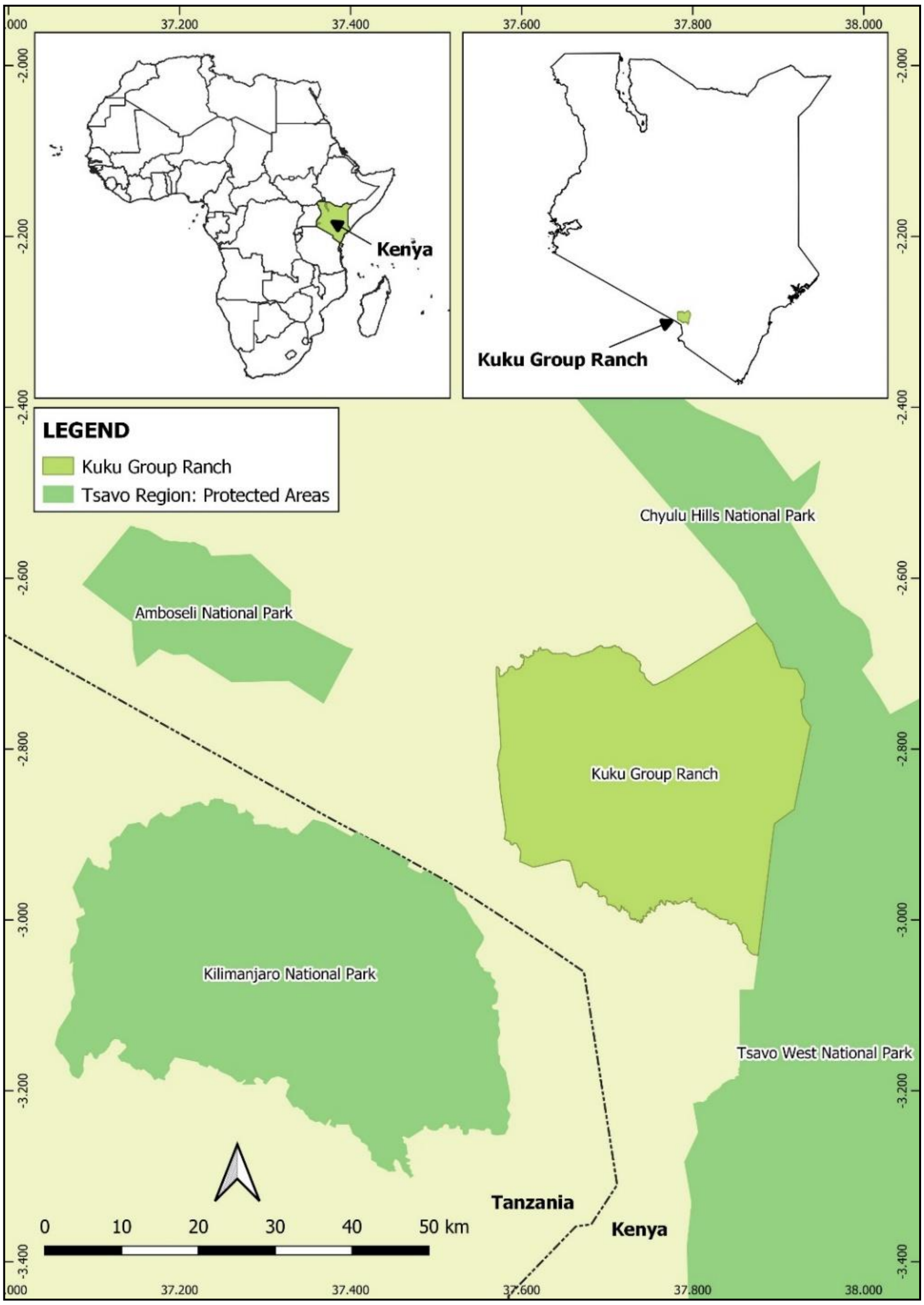

Figure 2.2: The location of the study site, the international boundary with Tanzania and other African countries (inset left) and the Kuku Group Ranch within Kenya (right inset) and the adjacent national parks of the Tsavo West Chyulu Hills, Amboseli and the Kilimanjaro National Park in Tanzania.

2.2. Climate

Rainfall in the lower regions of the KGR varies between 250–800mm annually and is unpredictable (Awere-Gyekye, 1996), whereas the Chyulu Hills to the north receives up to 700mm per year (Western *et al.,* 2009). Rainfall tends towards a bimodal distribution, with two rainy seasons a year and significant inter-year variation in quantity and timing (Phillipson, 1975; Altmann *et al.,* 2002) (Figure 2.3). A shorter rainfall period occurs over November and December, followed by a more extended period from March to May (Altmann *et al.,* 2002; Ntiati, 2002). In the ten years preceding this study, the average annual rainfall for the area was 670.9mm as measured at the Chyulu Hills Conservation & Research Centre (CCRC), 1 km West of the Chyulu Hills Gate of the TWNP (Figure 2.3). During the study period (2017 & 2018), the area received 369.0mm and 833.7mm of rainfall, respectively. Therefore, rainfall in 2017 was well below average and in 2018 much higher than the average.

The KGR is situated in an area considered to be arid to semi-arid, and like most dryland areas of Kenya, drought conditions are prevalent, with some droughts having devastating effects on the ecosystem and landscape (Kiringe 2005; Western *et al.,* 2009; Wangai *et al.,* 2013). In the study area, droughts have been recorded in 2001, 2006, and 2007 (Ojwang *et al.,* 2006). The most severe drought in recent history occurred in 2009. The area falls into the Agroclimatic Zones V and VI (Sombroek *et al.,* 1982) and is also referred to as the Lower Midland Ranching Zone, where rain-fed crops only succeed in good seasons (Nkedianye *et al.,* 2019). Mt Kilimanjaro, 5 898m in elevation, and the Chyulu Hills Range, 2 300m in elevation (at their hights points), have a significant influence on the climate and water distribution in this ecosystem and directly affect the rainfall gradient within the entire landscape (Altmann *et al.,* 2002; Kioko *et al.,* 2006; Dolrenry, 2013).

Temperatures range from annual highs in the mid-30s°C in February to temperature lows of approximately 20°C in July (Altmann *et al.,* 2002; Western *et al.,* 2009).

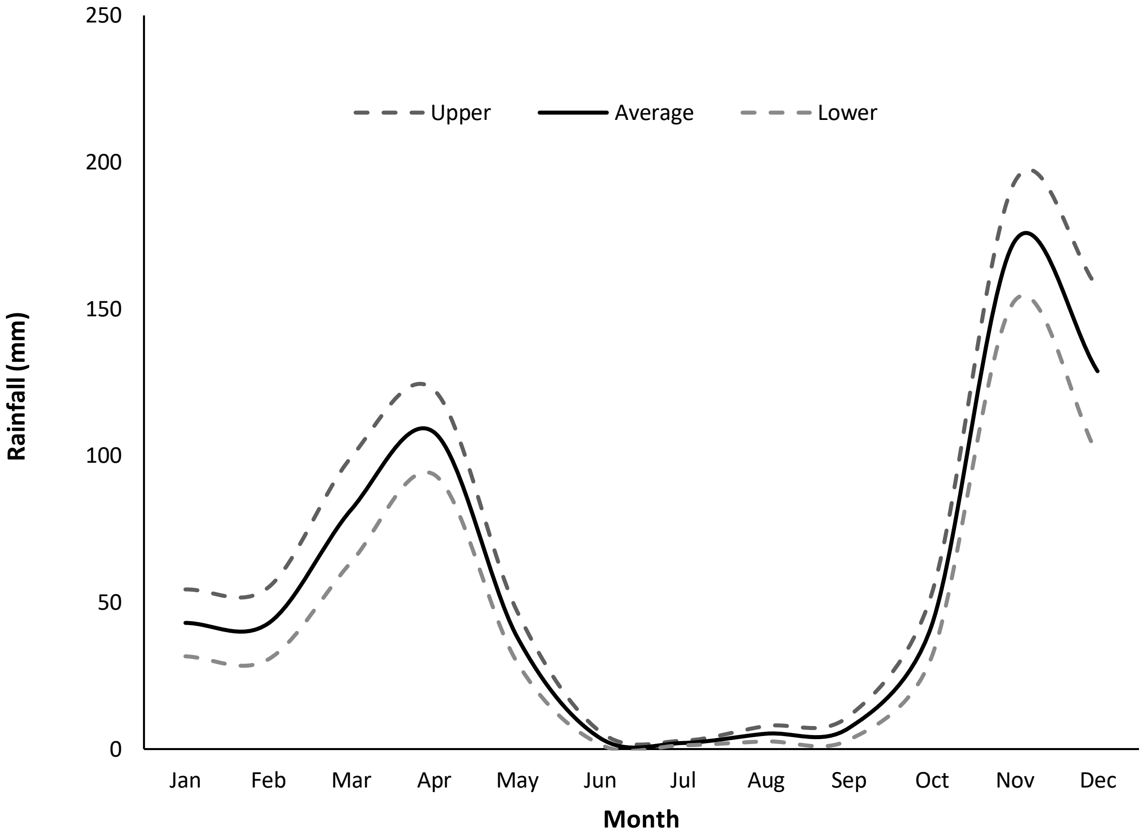

Figure 2.3: The average monthly rainfall for the 16-years rainfall has been recorded within the study area (2003-2018). The upper and lower estimates here show the standard error around the monthly values.

2.3. Topography

The altitude within the KGR ranges from 850m in the southeast to 2 175m at the peak of the Chyulu Hills in the northeast, which is the highest elevation in the study area (Kiringe *et al.,* 2005; Amin *et al.,* 2015). The eastern boundary of the KGR is mountainous at an average elevation of approximately 2 000m above seas level and adjoins the CHNP, whereas the western boundary of the KGR forms part of the low-lying Amboseli basin that stretches to the lower portions of Mt. Kilimanjaro (McLennan *et al.,* 2009). There are rocky outcrops, characteristic of the low-lying Amboseli basin in the south and east of the study area. Several old volcanic sites and cinder cones occur on the western side of the Chyulu Hills range and fall east of the KGR (Figure 2.4). The ridges and high lying areas of the Chyulu Hills on the eastern side of the study site are approximately 100 km in length and up to 30 km wide, covering an area of approximately 2 840 km² (Späth *et al.,* 2000).

2.4. Geology and Soils

The KGR can be divided according to the highland, hilly areas, and lowland areas. The Chyulu Hills are a young Quaternary volcanic field bordered by the Mozambique belt (Novak *et al.,* 1997; Sakkas *et al.,* 2002). The Chyulu Hills are located approximately 150 km southeast of the Kenyan rift valley (Novak *et al.,* 1997; Sakkas *et al.,* 2002). The lowlands comprise many coalesced volcanoes/cinder cones (Figure 2.4), and lava flows comprised of basalt rock (Figure 2.5) (Späth *et al.,* 2000; Wildlife Works, 2014).

Figure 2.4: An example of two old volcanic sites and cinder cones on the western side of the Chyulu Hills falls within the KGR and study site (Photo Credit: The Author, 2017).

Figure 2.5: A typical lava flow within the KGR and study site. These flows are characteristic of the lowland and Chyulu Hill areas associated with free-standing and coalesced volcanoes and cinder cones (Photo Credit: The Author, 2018).

The area can be further characterised by saline soils, with areas of interspersed deep, well-drained soils. In the Chyulu Hills, the primary soils are Lithosols on the lava flows, Andosols on coarse ash deposits, and deep Luvisols on the flatter plains in the west (Touber *et al.,* 1983; Wildlife Works, 2014) (Figure 2.6).

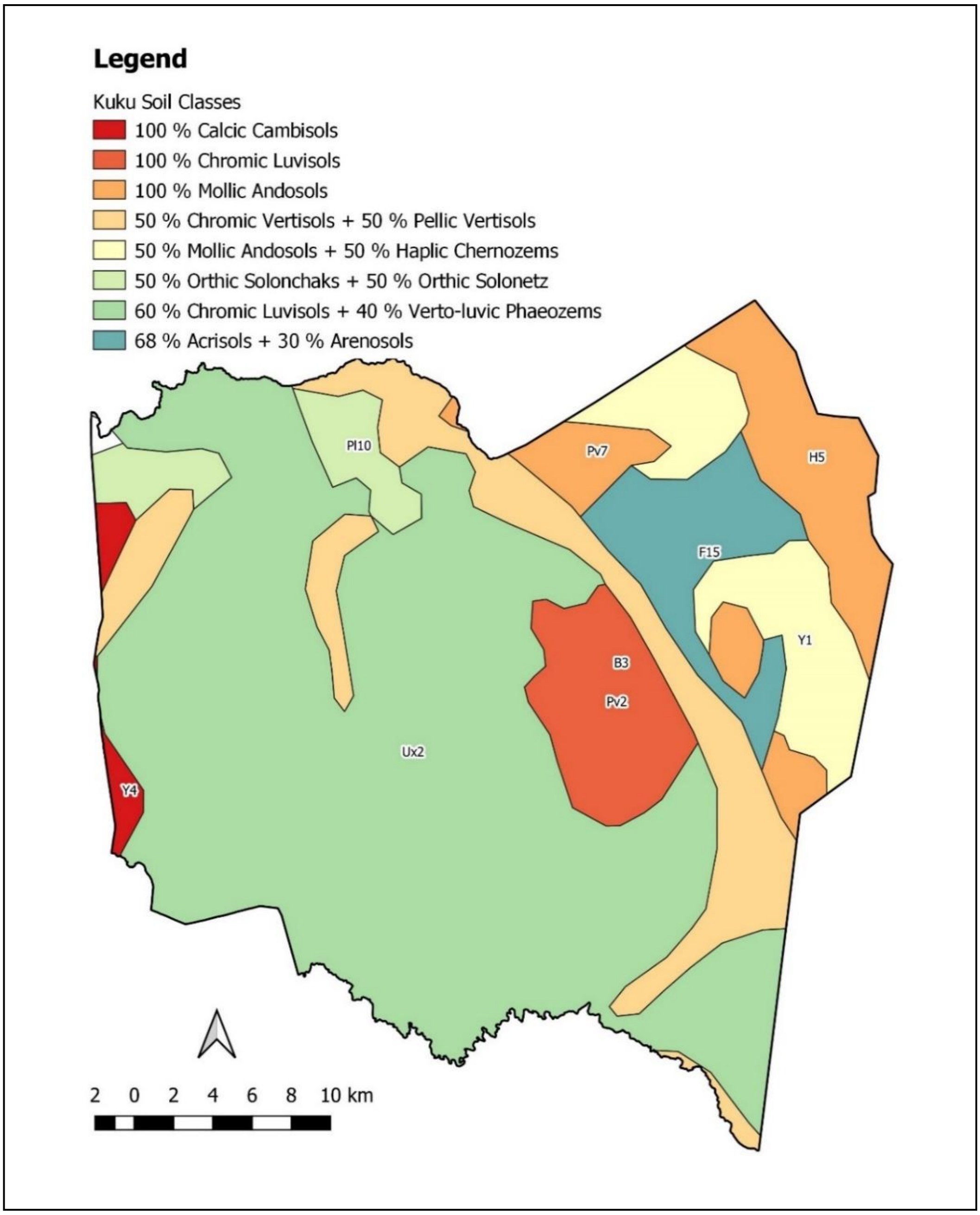

Figure 2.6: The different soil classes on the KGR (adapted from Wildlife Works, 2014).

2.5. Hydrology

Rivers and streams in the KGR only flow during the rainy season and are seasonal and not perennial. The main watercourses are the Mokoine River, the Nolturesh River, and several tributaries, such as Kikangorot (Figure 2.7). On the KGR, these river systems run south-westerly, and both serve as essential drainage channels for the group ranch during the two rainfall seasons (Wildlife Works, 2014).

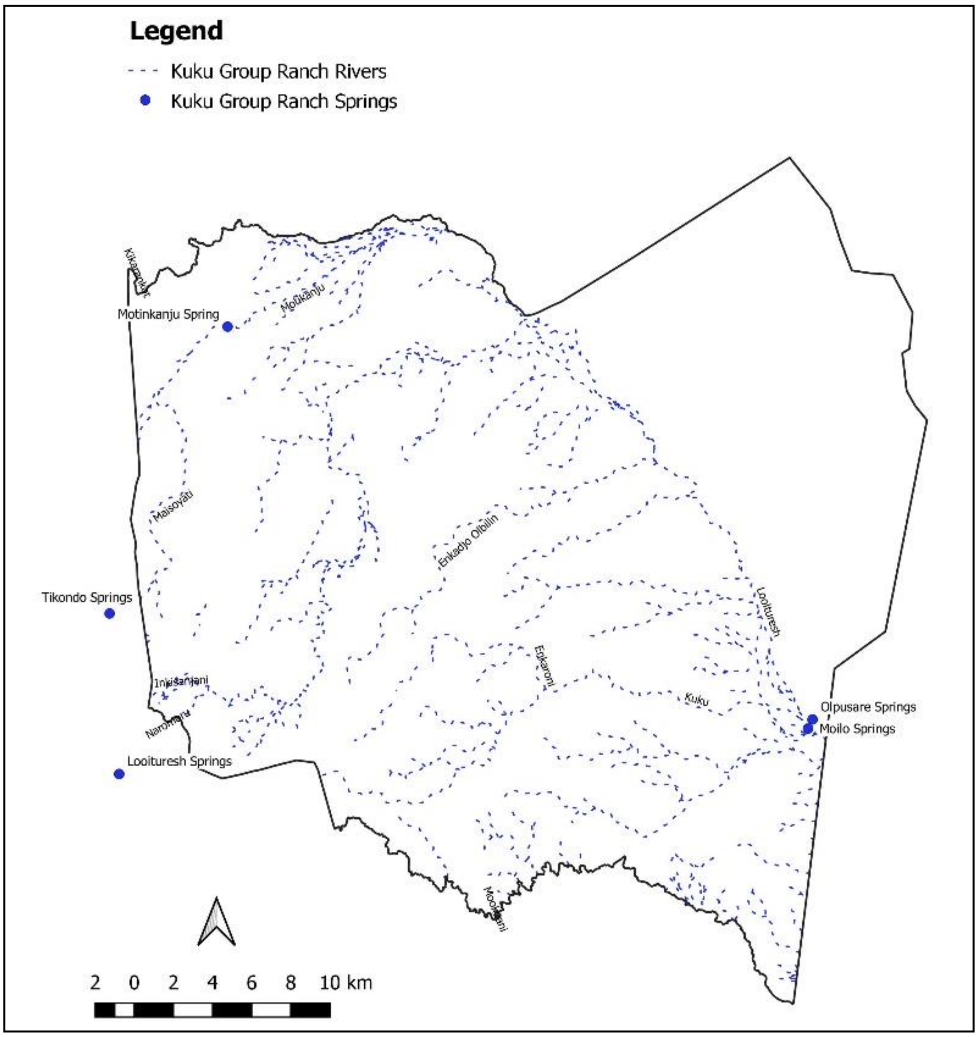

Figure 2.7: The distribution of the rivers, seasonal streams, natural springs within the KGR.

High levels of orographic rainfall are experienced only on the upper Chyulu Hills areas, and condensation from the mist belts in the cloud forest areas have led the Chyulu Hills area to become an important water catchment area providing critical ecosystem services to surrounding communities (Ertuna, 1979; Wildlife Works, 2014; Mwaura *et al.,* 2016b; Habel *et al.,* 2018). In the north-eastern areas of KGR, the rainfall seeps into the ground due to the porous nature of the rock and lava flows and emerges again at numerous springs (Ayeni, 1975; Ertuna, 1979; Kang'ethe, 2019).

The Mzima Springs to the southeast of the study site in Tsavo West National Park is an important water source that supplies water to towns and communities in South-eastern Kenya and the coastal region (Ertuna, 1979). In addition to Mzima Springs, the Chyulu Hills also feeds several springs within the KGR, most importantly Olpusare Springs (Figure 2.8) (Kiringe *et al.,* 2016). The Olpusare spring is situated east of the study area and is used by livestock and wildlife (*personal observation*, 2017). During the wet season, surface water increases across the KGR as the seasonal streams and rivers flow. Wetlands are present on the KGR, but following unsustainable water off-takes and increased agricultural activities, they have been drying up in recent years. Wells have been drilled in all villages to access the groundwater for people and livestock.

Figure 2.8: The Olpusare Springs on the KGR, due to abstraction for agriculture, no longer has permanent surface water during the dry season (Photo Credit: The Author, 2018).

2.6. Habitat Structure and Vegetation

The KGR is characterised by a heterogeneous landscape that features a transition in vegetation from lowland dry savannah grassland and *Vachelia-Commiphora* forest to areas dominated by a moist, dense cloud forest in the Chyulu Hills (Agnew, 1968; Jensen & Belsky, 1989; Kenya Wildlife Service, 2008; Wildlife Works, 2014). A general land cover classification of the KGR is provided in Figure 2.9, and a fine-scale vegetation map in Figure 2.10.

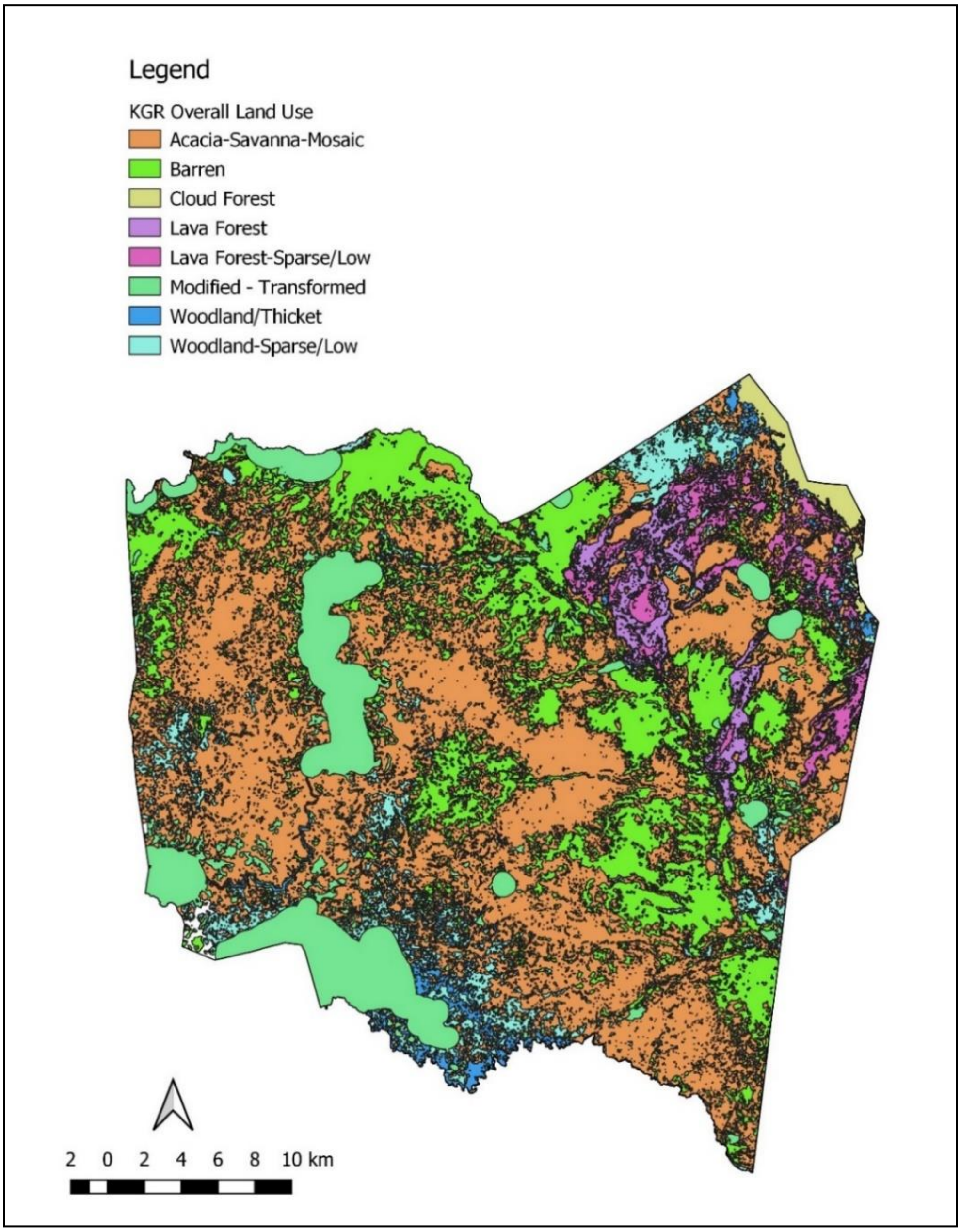

Figure 2.9: The general land cover classification of the KGR (Adapted from Wildlife Works, 2014).

Seven distinct vegetation types have been identified in the KGR and study area and have been defined as Grassland, *Vachelia*-Savannah Mosaic, Lava Forest, Lava Forest Sparse/Low, Cloud Forest, Woodland/Thicket and Woodland – Sparse/Low (Wildlife Works, 2014).

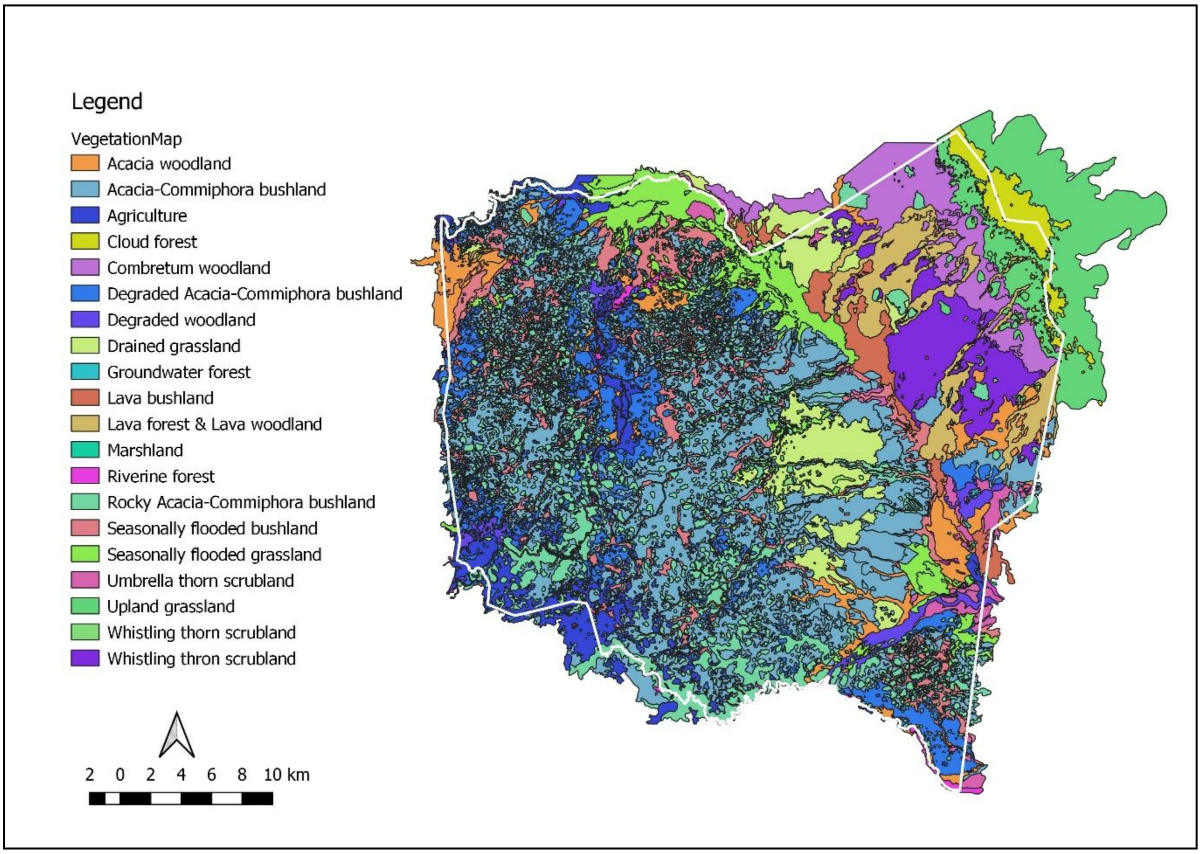

Figure 2.10: Vegetation types of the KGR (Adapted from Wildlife Works, 2014).

- **Grassland**

The grassland area is consistent with a typical lowland dry Kenyan savannah (Figure 2.11) (Edwards, 1940). The grassland vegetation types occur on the lower areas of the KGR and receive the lowest amount of rainfall (Boutton *et al.,* 1988). The stratum has very few surface water sources, and these are seasonal in nature. The grassland stratum is typified by large indigenous grasses dominated by *Pennisetum melianol*, *Cynodon dactylon*, *Cenchrus ciliarus* and *Themeda triandra*, with patches of low-density tree canopy cover only (Wildlife Works, 2014).

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Figure 2.11: This photograph, depicting the typical grassland cover stratum is consistent with a typical lowland dry Kenyan savannah. The picture was taken in the central part of the study site with Kilimanjaro visible in the background (Photo Credit: The Author, 2017).

- ***Vachelia*-Savannah Mosaic Forest**

Vachelia-Savannah mosaic forest is a *Vachelia-Commiphora* lowland dry forest characterised by a moderate tree canopy with an understory of herbaceous species (Figure 2.12). Thirty-eight tree species are within this vegetation type (Gemmill-Herren & Ochieng, 2008; Timberlake *et al*., 2010). The most common species include *Vachelia mellifera*, *Commiphora africana*, *Vachelia hockii* and *Vachelia tortilis*. Vegetation in this area is generally drought tolerant (Gathara *et al.,* 2014; Wildlife Works, 2014).

Figure 2.12: A photograph taken in the rainfall season depicting the *Vachelia*-Savannah mosaic Forest stratum in the study area. Cinder cones and old volcanic sites are also visible (Photo Credit: The Author, 2018).

- **Woodland/Thicket and Woodland-Sparse/Low Forest**

The Woodland-Sparse/Low and Woodland/Thicket vegetation types are similar in species composition and vegetation structure, with the main contrasts being the different species frequencies (Fenner, 1982; Kuria *et al.,* 2011). This stratum is typified by *Vachelia tortilis, Balanites aegyptiaca and Commiphora africana* with patches of low-density *Grewia bicolor* and *Vachelia mellifera.* These forest strata are also of a dryland forest type and contain drought-tolerant species. The tree canopy is denser than Vachelia-Savannah mosaic Forest (Wildlife Works, 2014; Musyoka, 2019) (Figure 2.13).

Figure 2.13: A photograph depicting the Woodland-Sparse/Low and Woodland/Thicket stratum in the study area (Photo Credit: The Author, 2018).

- **Lava Forest and Lava Forest Sparse/Low**

Lava Forest and Lava Forest Sparse/Low is a dry, upland forest with an open canopy mix of drought-tolerant species and a low-density understory (Figure 2.14). This vegetation is characteristic of the Chyulu Hills volcanic range areas (Novak *et al*., 1997; Sakkas *et al.,* 2002). The vegetation is primarily influenced by the rocky, shallow soils of volcanic rock and volcanic rock fragments (Figure 2.15) (Späth *et al.,* 2000). Despite dense lava on or near the surface, tree and shrub cover is significant on these historical lava flows (Meguro & Chalo, 2018). These two strata are similar in species composition and forest structure and can be distinguished by the forest canopy density, with the Lava Forest Sparse/Low being less dense. These differences are because the Lava Forest Sparse/Low stratum occurs on more recent lava flows, which have not degraded as much as the lava flows in the Lava Forest stratum (Wildlife Works, 2014; Mwaura *et al.,* 2016a).

Figure 2.14: A photograph depicting the Lava Forest in the background and Lava Forest Sparse/Low stratum in the foreground within the study site (Photo Credit: The Author, 2018).

Figure 2.15: A photograph depicting the lava flows in the Lava Forest, and Lava Forest Sparse/Low stratum has not yet had vegetation growth (Photo Credit: The Author, 2018).

- **Cloud Forest**

Cloud forest stratum is dominant in the Chyulu Hills range (Figure 2.16). This stratum is a montane forest, with a dense tree canopy and understory comprised of species dependent on moisture (Pringle & Quayle, 2014; Kiringe *et al.,* 2016). This forest has a high incidence of low-level cloud cover, often at the tree canopy height, resulting in high humidity with a high occurrence of mosses and thick understory vegetation (Pringle & Quayle, 2014; Musyoka, 2019). The dominant tree species observed in the Cloud Forest stratum are *Croton macrostachyus*, *Ficus sycomorus*, *Vepris nobilis*, *Mystroxylon aethiopicum* and *Strombosia scheffleri* (Pringle & Quayle, 2014; Wildlife Works, 2014; Musyoka, 2019).

Figure 2.16: A photograph depicting the cloud forest stratum in the study site on the Chyulu Hills (Photo Credit, Frans Radloff, 2017).

2.7. Large Herbivore Community

KGR is home to various medium and large herbivore species, and seventeen are larger than 5kg (Pringle & Quayle, 2014; Musyoka, 2019 (Table 2.1). Two of these species present are megaherbivores (Table 2.1). Six are of the species are comprised of grazers: buffalo (*Syncerus caffer),* plains zebra (*Equus quagga*), Coke's hartebeest (*Alcelaphus buselaphus cokii*), Maasai ostrich (*Struthio camelus massaicus),* mountain reedbuck (*Redunca fulvorufula*) and blue wildebeest (*Connochaetes taurinus*). Three are browsers; lesser kudu (*Tragelaphus imberbis*), gerenuk (*Litocranius walleri*) and Maasai giraffe (*Giraffa camelopardalis tippelskirchi)*, and eight are mixed feeders: Kirk's dik-dik (*Madoqua kirkii*), eland (*Tragelaphus oryx)*, the African elephant, fringe-eared oryx (*Oryx beisa callotis*), Grant's gazelle (*Nanger granti*), Thompson's gazelle (*Eudorcas thomso*nii) and impala (*Aepyceros melampus*).

Preying on these seventeen herbivore species are six large carnivore species that are typical of East African semi-arid ecosystems, including the wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*) and striped hyena (*Hyaena hyaena*), leopard (*Panthera pardus*) and lion. A portion of the mammals are believed to be residents in the area, but many use the area as a corridor to migrate back and forth between the adjacent National Parks, Conservancies, and the neighbouring group ranches of Mbirikani and Rombo (Wilkie & Douglas-Hamilton, 2018; Dolrenry *et al.,* 2020). There are four migration corridors in the Tsavo-Amboseli-Kilimanjaro ecosystem (Kioko & Ole Seno, 2011; Wilkie & Douglas-Hamilton, 2018). These critical corridors face threats due to anthropogenic disturbance, land conversion, and group ranch sub-division (Kioko & Ole Seno, 2011; Wilkie & Douglas-Hamilton, 2018; Dolrenry *et al.,* 2020; Mungo, 2021). Natural variation in census numbers is expected, with variations in wildlife numbers due to migrations (Henschel *et al.,* 2020).

The Tsavo-Amboseli-Kilimanjaro ecosystem is also a critical dispersal area for lions (Frank *et al.,* 2006; Dolrenry *et al.,* 2020; Henschel *et al.,* 2020). The estimated number of lions living in the Tsavo ecosystem is the second largest in Kenya (Frank *et al*., 2006; Henschel *et al.,* 2020). However, lion populations face severe pressure as they are still killed in retaliation for livestock (Dolrenry, 2013; Muriuki *et al.,* 2017; Henschel *et al.,* 2020). On the KGR, the lion population is estimated to be between 30–45 individuals, dependant on the season (Bauer *et al.,* 2017).

Table 2.1: The medium and large terrestrial wildlife species and their respective numbers recorded at KGR during the annual aerial censuses of 2010 to 2018. In the table below, "Gazelles" is used when it was not possible to differentiate Grants vs Thompson's gazelles during aerial census counts.

Year *Species*	*2010*	*2011*	*2012*	*2013*	*2014*	*2015*	*2016*	*2017*	*2018*
Buffalo	42	26	55	35	0	0	0	52	36
Plains zebra	1001	1109	2343	971	1383	784	1084	1812	1466
Coke's hartebeest	260	161	167	133	256	120	20	180	194
Dik-dik	0	0	0	0	11	11	20	6	4
Eland	411	379	659	131	336	70	87	336	228
Elephant	89	68	89	30	42	94	114	84	141
Fringe-eared oryx	14	6	0	0	0	0	1	0	10
Gazelles	515	706	1371	836	1454	469	327	610	191
Gerenuk	6	37	29	2	52	21	21	40	14
Maasai giraffe	658	513	598	374	666	327	553	1069	523
Grant's gazelle	0	0	921	782	470	428	347	321	343
Impala	233	150	316	234	515	93	199	184	158
Lesser kudu	10	43	5	6	43	17	47	12	12
Maasai ostrich	43	58	54	27	68	31	30	46	22
Mountain reedbuck	0	0	0	0	3	0	0	0	0
Thomson's gazelle	0	0	165	33	137	28	37	93	90
Warthog	4	3	0	6	15	12	4	12	4
Blue wildebeest	241	181	363	218	226	124	89	310	232

2.8. Infrastructure

There are no physical boundaries or fences on the KGR or surrounding group ranches. There are two conservancies on the KGR set aside to exclude grazing or any other forms of agriculture, and these are the Kanzi and Motikanju conservancies (Figure 2.17). The road network is limited, and only two main roads connect the nearby towns to the KGR. Other than these main roads, there are only 4x4 tracks concentrated in and around the village areas and within the conservancies used for game viewing and ecotourism operations. Within the Kanzi conservancy, there is one tourist lodge, Campi ya Kanzi, and on the Motikanju Conservancy, there is a "Fly-Camp "where guests are flown in for camping in the fixed safari tents. On the eastern edge of the KGR, the Maasai Wilderness Conservation Trust (MWCT) Research and Operational Headquarters are called the Chyulu Hills Conservation and Research Centre (CCRC). All operations, conservation, security, health, and education programs are run from this centre. All research for this study was conducted using CCRC as a base for operations. Roads on the KGR are used for management activities such as ranger and scout patrols, fire management, research, and livestock herders traversing the KGR in the dry season. The KGR is interspersed with 13 community ranger outposts that house 6-8 game scouts each. These outposts have been positioned to optimise patrol efficiency to prevent poaching, and the patrol boundaries for each ranger outpost is indicated in Figure 2.17.

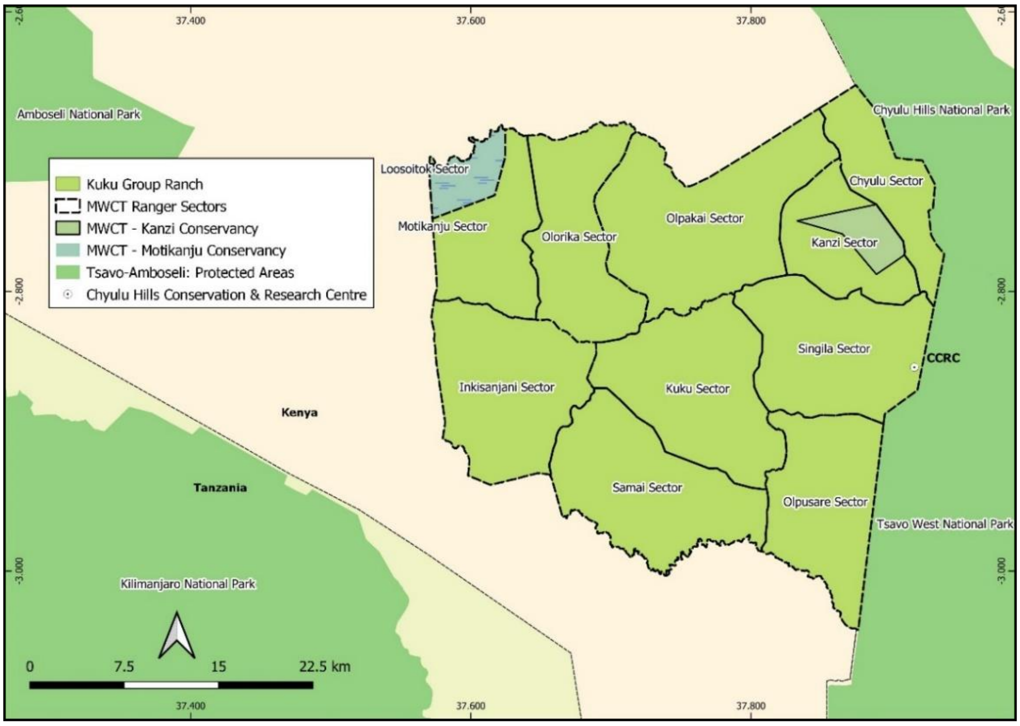

Figure 2.17: The KGR boundary, the KGR MWCT ranger sectors, the two conservancies, and critical structures within the KGR.

2.9. Surrounding Land Use and Human Influence

The KGR and the neighbouring land that excludes the proclaimed National Parks are divided into group ranches, collectively grazed by traditional Maasai pastoralists and their cattle, including cows, goats, sheep and camels (*Camelus dromedarius*). The landscape is interspersed with permanent and temporary (seasonal) Maasai manyattas (Figure 2.18). These manyattas (or kraals) combine thorn bush corrals (also called bomas) and Maasai dwellings traditionally used to keep livestock overnight in safety from predators.

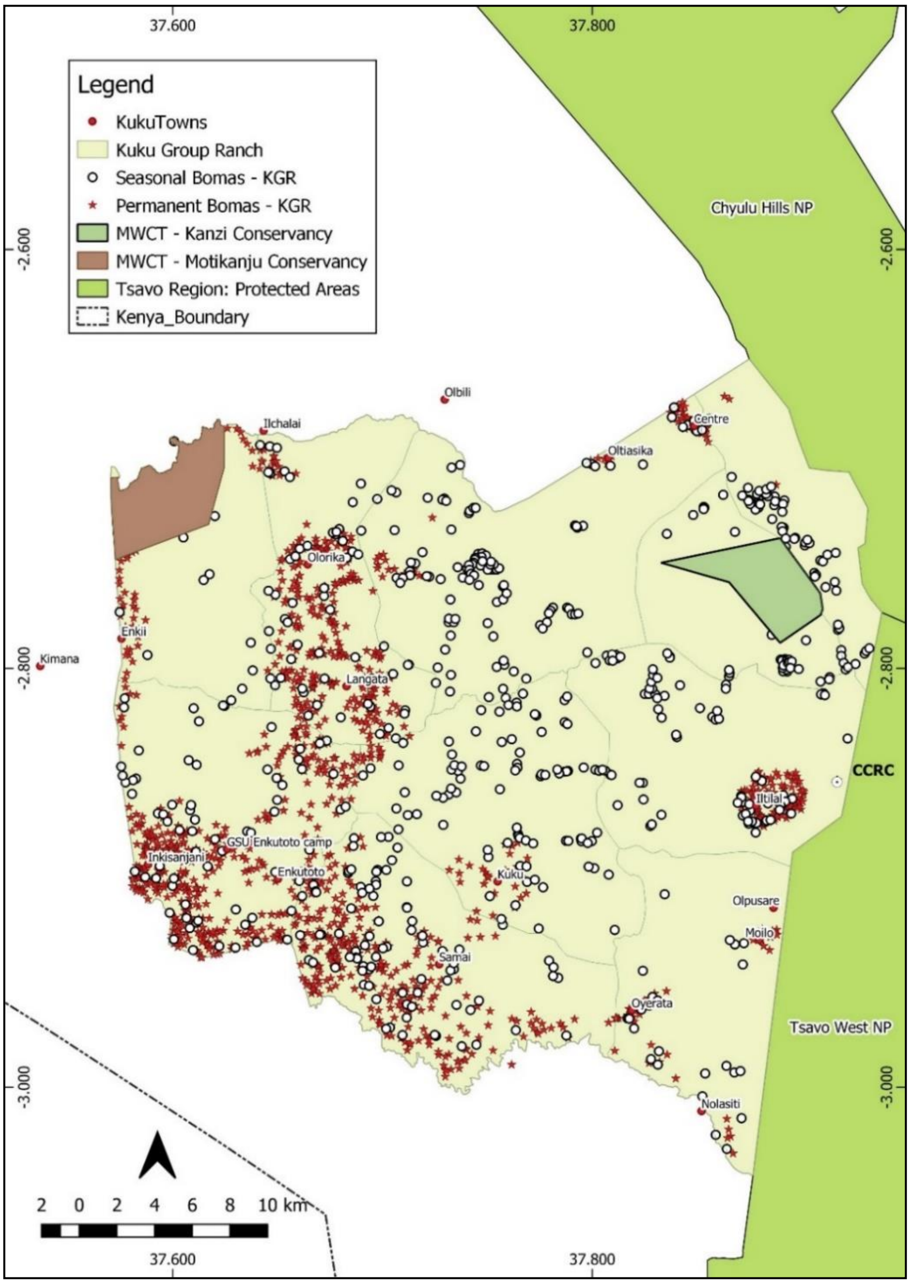

Figure 2.18: The permanent bomas, seasonal bomas, the surrounding protected areas, and neighbouring countries around the KGR (Adapted from Amin *et al.,* 2015)

Both permanent and temporary manyattas can be found in KGR. Permanent Maasai manyattas are those with more robust structures and cattle corrals, and these are used as home bases and are permanently occupied by livestock owners and their extended families. Conversely, temporary or seasonal Maasai manyattas are those that only consist of loosely constructed bomas that are used in the dry season where Maasai Warriors (herders armed with swords and spears that are the traditional caretakers of livestock) are required to travel further with their livestock to find suitable and sufficient quantities of forage.

The herders sleep out in the field with the livestock in these temporary bomas to protect their livestock from lions and other predators (Spear & Waller, 1993). Since 2010, excluding 2015, livestock numbers have been counted during aerial censuses, and the results suggest that livestock numbers have nearly tripled between 2010 and 2018 (Table 2.2). There has been a steady increase in overall livestock numbers from 8 286 in 2010 to 42 914 in 2014. The aerial census numbers fluctuate not only because of actual increase and decrease in livestock (and wildlife) numbers but also due to husbandry practices where herders move livestock into the neighbouring national parks during the dry season to obtain adequate grazing, and these then do not form part of the aerial census figures during that period (*personal obs*, 2016-2018).

Table 2.2: The medium and large terrestrial livestock species recorded on the KGR (2010-2018). In the table below, "Shoats" is used when it was not possible to differentiate goats and sheep. In 2015 there was no count of livestock conducted.

	Year							
Livestock Species	**2010**	**2011**	**2012**	**2013**	**2014**	**2016**	**2017**	**2018**
Cattle	3171	7481	9507	12731	12341	10020	12564	9581
Donkey	39	62	120	148	147	123	228	12
Shoats (Goat & Sheep)	5076	11611	19669	25124	30426	21916	28283	18708
Total	8286	19154	29296	38003	42914	32059	41075	28301

The dominant livelihood within the area is semi-nomadic pastoralism, and the majority of household income comes directly from the sale of livestock at designated markets (Groom & Harris, 2008). The KGR is densely populated with approximately 17 000 people.

2.10. Conservation and Research

MWCT is a community and conservation NGO that has been operating on the KGR for over 18 years. The organisation, established in 2002, pursues a holistic approach (Conservation, Health & Education programs) focusing on all large predators and specifically lions in the Tsavo-Amboseli ecosystem by working with the local Maasai community KGR to address human-lion conflict. Since 2015, to mitigate lion-livestock conflicts, MWCT has attempted to collar at least one lion from each known pride on the KGR (Amin *et al.,* 2015; Bauer *et al.,* 2017). MWCT has thus been interacting with lions and other predators regularly with a team of dedicated local Maasai called Simba Scouts and Wildlife Pays Verification officers (Bauer *et al.,* 2017).

The Simba Scouts continuously monitor these collared lions through Global Positioning Systems (GPS) and VHF (Very High Frequency) tracking. Scouts then use updated locations of lion prides to warn herders of potentially dangerous areas and avoid areas where females are denning. In addition, MWCT also funds and runs a Predator Conservation Fund (PCF) and compensation program called Wildlife Pays. Wildlife Pays Verification officers meticulously monitor and record all reported predator-livestock conflict incidents for compensation each quarter through this program (Bauer *et al.,* 2017). The lion movement information and compensation data allowed the MWCT to identify the ranger sections with the highest lion activity and human-lion conflict incidences. The seven ranger sections with high lion-human conflict are situated in the western part of KGR and formed the focus of this study (Figure 2.19)

During the study period, MWCT had seven collared lions (five collared lionesses and two collared male lions), frequenting the focal study area of 84 177 hectares whose spatial location data were used to locate feeding sites. It is important to note that the collaring of lions was not done for this study's purpose. The data from the collars were made available for research purposes by MWCT, which use the information daily to facilitate human-lion conflict mitigation actions.

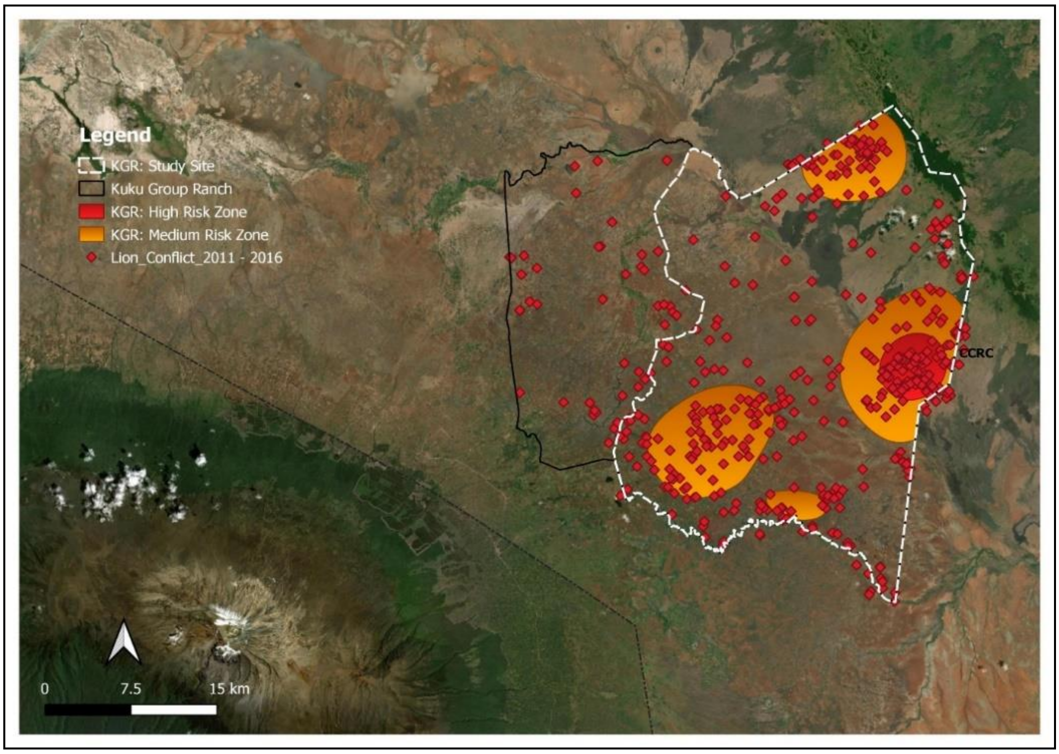

Figure 2. 19: The location of the focal study area within the KGR. The focal area is delineated by the boundaries of the seven ranger sections that experience the highest incidence of the lion – human conflict. The location where lions killed livestock between 2011–2016 is located with red diamonds. Zones of the highest lion-human conflict are depicted in the red and medium conflict in orange.

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CHAPTER 3: LION DIET AND PREY AVAILABILITY ON THE KUKU GROUP RANCH, KENYA

3.1. Introduction

The African lion (*Panthera leo*) is categorised as vulnerable on the International Union for Conservation of Nature (IUCN) Red List (Bauer *et al.,* 2016) and occupies only 8% of its historical range (Bauer *et al.*, 2016, Sargent *et al.,* 2021). Lion numbers are declining outside fenced areas (Bauer & Van Der Merwe, 2004; Bauer *et al.,* 2015), and approximately half the unfenced lion populations may drop to near extinction over the next 20-40 years (Packer *et al.,* 2013). Researchers have identified ten areas that are considered lion strongholds (Riggio *et al.,* 2013). Four of these lion strongholds are in East Africa, and six are in southern Africa (Riggio *et al.,* 2013; Henschel *et al.,* 2020).

The Tsavo-Amboseli landscape is one of the lion strongholds of East Africa, where lions have stable or increasing population numbers within the national parks (Riggio *et al.*, 2013; Henschel *et al.,* 2020). The land connecting the national parks within the Tsavo-Amboseli landscape, such as Maasai group ranches, plays an essential role in lion conservation as they support viable lion populations and create wildlife corridors (Okello, 2009; Okello, 2012). An exception is within the Tsavo-Mkomazi lion area, where decreases in lion population numbers are occurring due to livestock expansion, declining wildlife numbers and cattle depredation (Bauer *et al.,* 2017; Bauer *et al*., 2018; Bauer *et al.,* 2020).

Lion populations within conflict landscapes such as the Tsavo-Mkomazi lion area do not survive only on livestock but also select wild prey species (Schuette *et al.,* 2013; Beatie *et al.,* 2020). Wild prey populations are important, and the dynamics of wild prey populations have not always been considered when addressing human-lion conflicts (Montgomery *et al.,* 2018). For more effective lion conservation, researchers advocate for the problem of human-lion conflict to be looked at from five dimensions - lion, livestock, wild prey, human, and environmental (Montgomery *et al.,* 2018).

Since lion populations are under significant threats and are limited by their available food (Carbone & Gittleman, 2002), a significant consideration for lion conservation should be an adequate abundance of suitable prey (Karanth, 2004; Hayward *et al.,* 2007; Clements *et al.,* 2014). Ensuring suitable prey availability for lion populations is dependent on an understanding of which prey are killed by the predator and how this relates to prey availability (Clements *et al.,* 2014).

Understanding predator-prey interactions and lion diet are thus essential for managing lion populations in both formally and informally protected areas (Blackburn *et al.,* 2016; Montgomery *et al.,* 2018; Wilkinson *et al.*, 2020). Lion diet and prey preference can assist in understanding impacts on prey populations and how lion populations drive cattle depredation in pastoral communities (Beatie *et al.,* 2020; Wilkinson *et al.,* 2020). The concept of prey preference can thus be helpful for conservationists identifying which prey species are likely to be targeted by a predator, as it identifies prey that comprises a more significant proportion of a predator's diet than expected according to the prey item's relative abundance in the landscape (Hayward & Kerley, 2005). Researchers have described predator-prey interactions at finer scales and, in doing so, have identified accessible prey weight ranges for African carnivores (Clements *et al.,* 2014). The accessible prey weight range for lions is 32–632 kg (Clements *et al.,* 2014), and understanding prey availability will thus be important for larger-bodied prey (>50kg) that contribute more (76-98%) of the prey biomass consumed by lions (Hayward & Kerley, 2005; Hayward *et al.,* 2007; Davidson *et al.,* 2013). Prey profile information for larger-bodied prey can inform conservation programs and influence lion survival positively by identifying which species (domestic and wild) are likely to be targeted by predators.

Within the Tsavo-Mkomazi area, the Kuku Group Ranch (KGR) is a communal area that forms a part of the Tsavo-Amboseli lion-stronghold (Henschel *et al.,* 2020). Lions frequently kill and consume cattle on the KGR (Bauer *et al.,* 2017). In this chapter, the diet and prey preferences of lions are investigated in relation to cattle depredations. Based on Montgomery *et al.* (2018), four dimensions that include lions, livestock, wild prey and environmental (climate, seasonality, and land cover) that contribute to human-lion conflicts are investigated. Montgomery *et al.* (2018) recommend that research should prioritise the study of the lions' wild prey, as this, along with lion-livestock dynamics, are particularly relevant to Human-Lion conflict (Khorozyan *et al.,* 2015; Montgomery *et al.,* 2018; Miller & Schmitz, 2019; Wilkinson *et al.,* 2020).

This chapter aims to investigate the large-bodied (>50Kg) prey preference of lions through GPS cluster analysis and prey availability on the KGR. Specifically, we obtained prey abundance estimates for lion species using ground-based ranger counts and an aerial census for wildlife and livestock counts. We investigated lions' diet through ground investigation of predicted lion feeding locations from 7 lions fitted with GPS collars. Given that our study area is a human-wildlife conflict hotspot, we hypothesised that cattle would contribute considerably to the large-bodied prey profile of lions and that lions would show a preference for cattle since wildlife numbers have declined due to livestock expansion (Everatt *et al.,* 2019; Bauer *et al.,* 2020; Mukeka *et al.,* 2020).

3.2. Methodology

3.2.1 Study Site

The study was conducted in southern Kenya on the Kuku Group Ranch (KGR), a community-owned area covering 1 133 km² located in the district of Loitokitok at S 2.77554⁰, E 37.85150⁰ (Figure 3.1). Group ranches are livestock production systems, where traditional Maasai occupants of the land jointly own a freehold title to land and continue to herd and graze their livestock alongside wildlife species (Western, 1994; Western *et al.,* 2009). The KGR is situated within the 9 000 km² Amboseli-Tsavo ecosystems, and in addition to wildlife, provides residence to approximately 17 000 Maasai and 90 000 livestock (Groom & Harris, 2008). There are also two community conservancies covering a combined area of 45 km² within the KGR. Tourism operators use these conservancies for wildlife safaris, and cattle grazing is limited.

The KGR is situated in an arid to a semi-arid area (Kiringe & Okello, 2005; Western *et al.,* 2009). The KGR has a bimodal rainfall distribution, with two rainy seasons a year with significant inter-year variation in the quantity and timing of rainfall (Altmann *et al.,* 2002). Annual rainfall varies between 250mm to 800mm (Awere-Gyekye, 1996), with an average of 340mm (Moss *et al.,* 2011). In the Amboseli National Park and surrounding group ranches, temperatures range from highs in the mid - 30s°C in February to annual temperature lows of approximately 20°C in July (Altmann *et al.,* 2002; Western *et al.,* 2009).

The KGR is comprised of a heterogeneous landscape that features a transition in vegetation from lowland dry savannah grassland and *Vachelia-Commiphora* forest to an area dominated by a moist, dense cloud forest in the Chyulu Hills (Agnew, 1968; Jensen, 1989; Kenya Wildlife Service, 2008). Spatial information obtained from collared lion movement and data from lion livestock killing events obtained from a predator compensation scheme (Bauer *et al.,* 2017) identified the eastern section of the KGR as having the highest levels of lion activity which consequently formed the focus area of this study (Figure 3.1). A more detailed account of the biotic and abiotic features of the KGR and study area has been described in Chapter 2.

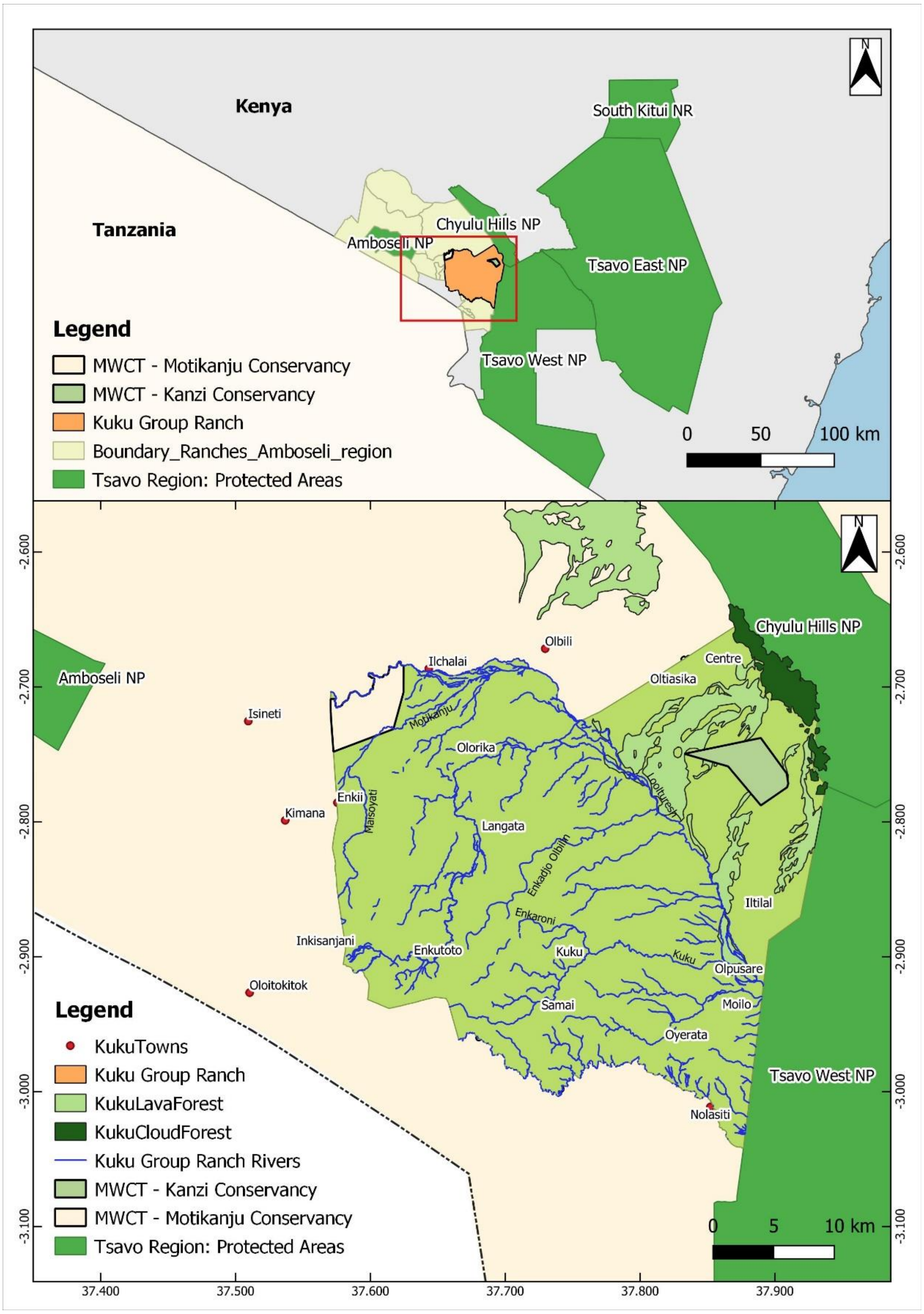

Figure 3.1: The Kuku Group Ranch in an East African context. The map shows the ranch in Kenya, its relation to Tanzania, and the surrounding protected areas of Tsavo West National Park, Chyulu Hills National Park, Amboseli National Park, and the neighbouring group ranches.

3.2.2 Data Collection

3.2.2.1 Lion Diet

As part of a livestock protection program called wildlife Pays under the KGR Lion Project (Amin *et al.,* 2015), the Maasai Wilderness Conservation Trust (MWCT) fitted seven lions (five adult lionesses and two adult male lions) holding territories across the KGR with GPS/ VHF and satellite transmitter collars (African Wildlife Tracking cc., Pretoria, South Africa). The collaring operations occurred between 2013 and 2018 and were conducted with the permission of the Kenya Wildlife Service (KWS). Permit numbers were KWS/BRM/5001 (*2013-2017*). All lion collaring and associated veterinary work was conducted exclusively by the KWS Veterinarian in the Tsavo Conservation Area (TCA). Information on lions' diets was obtained from the ground investigation of predicted lion feeding sites obtained from location data of the seven GPS collars. Global positioning system cluster investigation uses GPS technology that enables the collection of spatio-temporal movement data and locations from the field to construct a movement path of lions, from which locations of predicted feeding sites can be estimated (Tambling *et al.,* 2012). Lion movement paths then allow the prediction of a possible lion feeding site, which can be investigated for confirmation of a lion feeding event and to identify any prey species through their remains and other evidence (Anderson & Lindzey, 2003; Sand *et al.,* 2005; Tambling *et al.,* 2012).

Investigations took place between January 2017 and December 2018. Potential feeding sites (GPS Clusters) were identified by analysing the GPS data points to identify a position where three or more consecutive recorded GPS fixes were less than 100m apart (Tambling *et al.,* 2010; Tambling *et al.,* 2012; Davidson *et al.,* 2013). GPS collars recorded GPS positions every three hours, creating a movement pattern of all collared lions over time. Clusters were thus identified by investigating locations where lions spent longer than 9 hours consecutively. Tambling *et al*. (2012) found that the best indicators of potential lion feeding sites were those clusters where the distance ratio moved 24 hours before versus 24 hours after a cluster event was greater than 1. Other predictor variables used in the model to identify lion feeding sites were close-fitting clustering formed during the night when lions had higher success in the dark. These predictor variables were used to filter GPS clusters to only include the most likely feeding sites, which were then visited in the field to look for remains of prey species that were consumed (Tambling *et al*., 2012).

A consistent effort was made to visit and investigate all potential feeding sites within 30 days after cluster formation. However, due to the inaccessibility of certain areas due to flooding, not all clusters were checked within 30 days. Clusters were checked on average 33 days after formation, with the minimum being on the same day and the maximum number of more than 100 days. GPS clusters were located in the field by uploading all cluster points (x:y coordinates) onto a handheld GPS unit (Garmin GPS 64S, Garmin International, Olathe, KS, USA), and potential feeding sites were located in the field by vehicle and on foot and comprehensively searched for any positive evidence of a feeding site (Tambling *et al.* 2010; Tambling *et al*., 2012). A 100-meter radius around each point was searched at every cluster for signs of feeding and prey remains (Tambling *et al.,* 2010; Sand *et al.,* 2005). If no evidence was found at the first point, every consecutive point that made up that cluster was also located, and a new 100-meter radius was searched (Beukes, 2016; Beukes *et al.,* 2017).

A positive lion feeding site was recorded when there was evidence indicating that a feeding event had occurred (this included both predation and scavenging) and provided data to determine the dietary profile of the collard lion (Sand *et al.,* 2005; Tambling, 2010). Indicators of feeding sites were signs of a struggle (soil disturbance or trampled vegetation), rumen content, and any other biological signs including hair, bone, jaws, horns, blood, or whole carcasses (Pitman *et al.* 2014; Davidson *et al.,* 2013; Beukes *et al*., 2017). When a feeding site was positively identified, the species consumed was identified on-site if possible. If not possible, biological samples (hair, jaws, horns, and skulls) were collected for reference purposes and used to classify prey according to species at a later stage (Anderson & Lindzey, 2003). It has been shown that a sample size of between 65–69 lion feeding records can provide a representative description of lion diet (Beukes *et al.,* 2017), and the study aimed to exceed the recommended minimum sample size of 65–69 lion feeding records.

3.2.2.2 Prey Availability

Two data sources were used to estimate prey availability during 2017 and 2018. Biannual aerial counts provided a snapshot of overall prey availability in the wet and dry seasons, while MWCT community ranger patrol data provided more continuous information on prey availability in the form of monthly encounter rate scores. In most studies, prey availability is estimated only from aerial census data, which provides the absolute availability of prey items (Tambling, 2010). However, as opposed to absolute numbers, prey groups have been argued to be a better measure for assessing predator-prey interactions (Fryxell *et al*., 2007; Tambling *et al.,* 2010). Ideally, predator selection of prey should incorporate both encounter rates for different prey species groups and absolute abundances (Funston *et al*., 1998; Tambling, 2010). Aerial census results will be re-scaled to compare the aerial census as a percentage of wild prey (excluding cattle) to the encounter rate as a percentage of the wild prey encountered by rangers in the field.

- *Aerial Census*

Aerial counts were done in May and October of 2017 and in May and November of 2018 using the total aerial count technique of Norton-Griffiths (1978). Total count methodology requires parallel line transects in a north to south bearing across the study site spaced exactly 1 km apart. Line transects are flown systematically following north to south, bearing at the height of approximately 150 m above ground level and a speed of approximately 180 km/h. For each census, there was a total cumulative flight time of eight hours. Two Cessna 206 aircraft were used with four observers and four data recorders responsible for recording sightings (Norton-Griffiths, 1978; Amin *et al.,* 2015). All wildlife and livestock within a 500m strip on each aircraft side were counted during the census. Before carrying out each aerial census, distance estimates were calibrated on the aircraft wing struts in addition to running trial flights to standardise data collection among different observers (Norton-Griffiths, 1978; Amin *et al.,* 2015). Based on the methodology and work done by Redfern *et al.* (2002), no estimates of bias or precision error were obtained for the census data, and no adjustments for undercounting were applied.

- *Ranger Patrol Data*

MWCT has eleven sectors and ranger stations from which daily patrols are conducted for wildlife monitoring and anti-poaching purposes. In addition, there are seven ranger sectors within the study area from which daily foot patrols are conducted. Rangers collectively patrol a minimum of 100 km per day, and as part of the patrols, all wildlife sightings and threats to the areas are recorded (Figure 3.2). MWCT rangers use Cybertracker, a software system developed by a South African company, CyberTracker Conservation (Liebenberg, 2012). Cybertracker uses devices to allow handheld data capture in the field. The Cybertracker smartphone application and the Spatial Monitoring and Reporting Tool (SMART) are used by MWCT rangers while conducting their routine ranger patrols on the KGR. Data were collected by rangers between January 2017 and December 2018. During patrols, rangers recorded all mammal sightings across the study site (excluding livestock species) and wildlife groups identified to species level. All data are logged on the Cybertracker Application on cell phones, later downloaded to the MWCT SMART database. SMART ranger patrol data provided monthly accounts of large herbivore abundance across the study area. Through the Cybertracker system, wildlife counts are given a spatial reference by field rangers logging the x and y coordinates of every wildlife sighting observed in the field.

The observations made by the community rangers were used to calculate the relative abundance of prey based on encounter rates (number of wildlife detected per km walked) of groups of potential prey items. This approach corrected the count for ranger patrol effort to avoid higher encounters around the ranger posts located within the study site.

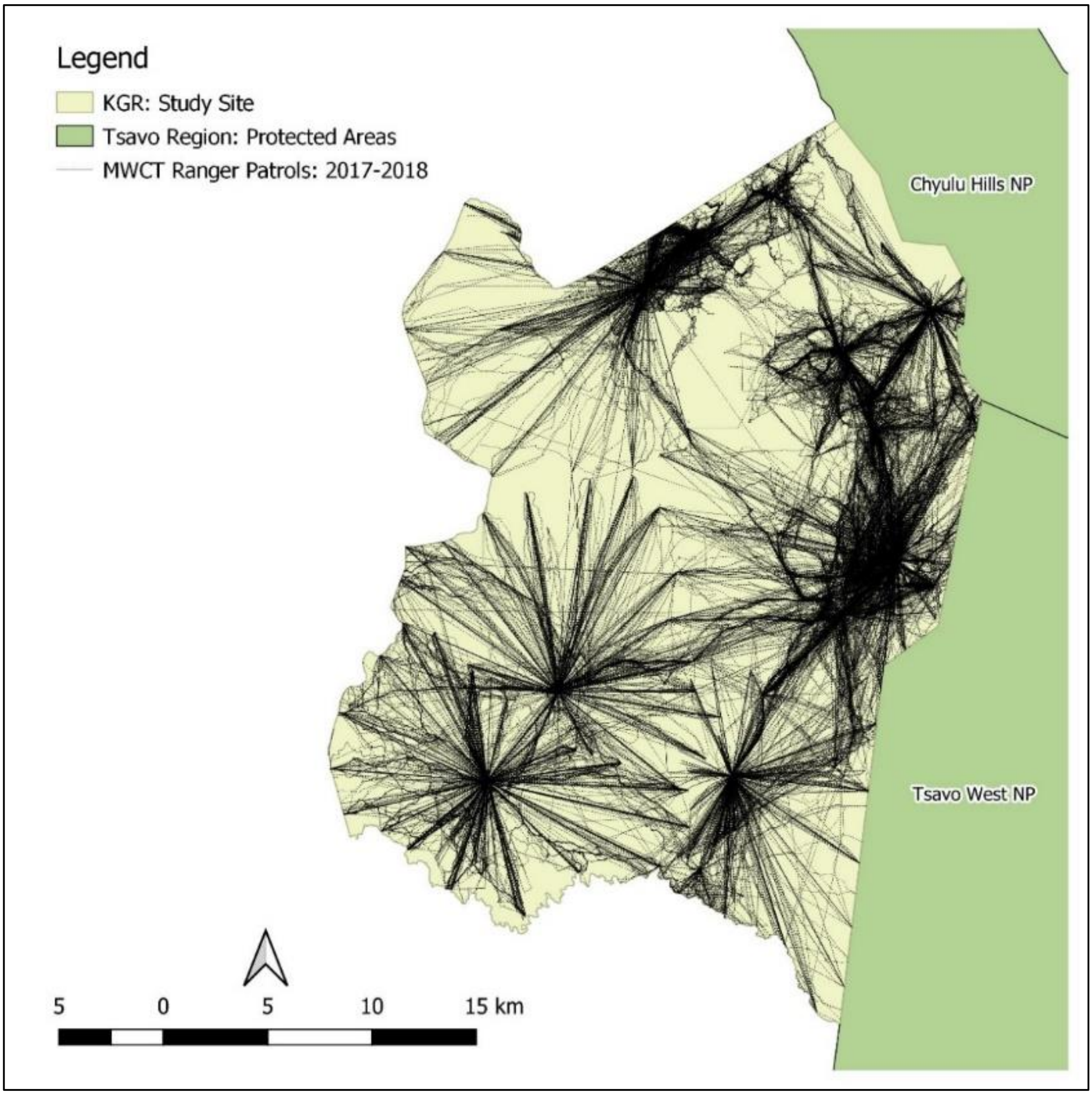

Figure 3.2: The SMART Ranger GPS patrol tracks recorded between January 2017 and December 2018. Black dotted lines indicate patrol tracks walked logged by MWCT rangers while on patrol in their respective ranger sectors within the study site.

3.2.3 Data Analysis

3.2.3.1 Lion Diet

Lion diet was expressed as relative proportions of the total number of prey species identified through GPS cluster investigation of large-bodied prey species (Tambling *et al.* 2010; Tambling *et al.,* 2012; Davidson *et al.,* 2013; Beukes, 2017). Due to the small sample size, a Fisher's Exact Test for count data was used to assess if male and female diets differed for prey species (> 50kg). For all confirmed feeding events, the relative contribution and frequency of occurrence of each prey species was calculated and then converted into biomass estimates using the average adult female body weight for each species (Radloff & du Toit, 2004; Cumming & Cumming, 2003; Davidson *et al.,* 2013).

3.2.3.2 Prey Availability

The absolute number of wildlife and livestock prey species (> 50kg) available to lions during the study period was estimated by calculating the average number of prey available per species using the values from the four uncorrected total aerial counts. The proportional prey species availability was then calculated from these average count values. Prey species encounter rates as a measure of prey availability were estimated by expressing ranger sightings of wildlife groups per month per 100 km walked. The monthly encounter rate of wildlife groups per 100 km was calculated by dividing the pooled number of groups encountered by all rangers during a month by the pooled kilometres patrolled and multiplying this by 100. Total ranger effort (km patrolled) was calculated per month by summing the total distance walked by all ranger patrol groups in any given month. For ranger patrols, the relative encounter rate value was estimated to calculate the proportion of all encounters.

The minimum daily and monthly patrol effort (distance walked on patrol) required to provide robust estimates of prey encounter rates was estimated. Minimum ranger effort to produce a robust prey encounter rate was determined by estimating the variance around average encounter rates per 100 kilometres and assessing at what distance the variance asymptotes. The analysis determines when variation levels off and estimates are no longer variable, thus impacting sampling effort. At the asymptote, the detection variance of wildlife groups per km walked was acceptable and represented the optimum level of effort required to include ranger patrol data in this study.

3.2.3.3 Prey Preference

Aerial count and encounter rate measures were analysed against all lion diet data pooled for the entire study area to estimate prey preference. Wild prey feeding events were thus compared to wild prey encounter rate data (SMART ranger sightings) and wild prey abundance data (aerial census counts) to estimate which wild prey is preferred. Prey selection and measurement of prey preference (*D*) were calculated using the Jacobs' index for all comparisons (Jacobs, 1974; Hayward & Kerley, 2005).

In Jacobs' index, *r* is the proportion of the overall number of prey consumed by lions in the dietary sample, and *p* is the proportional availability of that species for the study area (Jacobs, 1974; Hayward & Kerley 2005;). The Jacobs index allows for assessing prey selection when different relative abundances of prey are compared (Jacobs, 1974). The resulting value falls between +1 and -1, with zero indicating no selection, +1 indicating maximum preference, and -1 indicating maximum avoidance.

$$D = \frac{r - \mathrm{p}}{r + p - 2rp}$$

Using Jacobs'Index, it is possible to avoid non-linearity and bias to rare food items (Jacobs, 1974; Hayward & Kerley, 2005). Confirmed lion feeding events obtained from GPS cluster data provided *r,* and *p* were derived from the average of the aerial game counts and the encounter rates obtained from SMART patrol data.

Preferred lion prey were estimated only for large-bodied prey species (>50Kg), and given that the rangers did not count cattle in the field, the analysis was completed both including and excluding cattle in the analysis (including cattle: aerial census, excluding cattle, ranger counts). The importance of cattle in relation to wild prey was thus estimated by comparing cattle's absolute aerial census abundance data with all recorded lion feeding events.

3.3. Results

3.3.1 Lion Diet Estimates

Investigation of serial GPS locations from collared lion movement data resulted in 2386 clusters within the delineated study site, of which 205 (9%) were identified as high likelihood potential feeding sites and were investigated (Figure 3.3). Field investigation of the 205 sites resulted in the discovery of 119 sites with evidence of a feeding event that could be identified to species level, with 112 of these being large-bodied prey species (>50Kg).

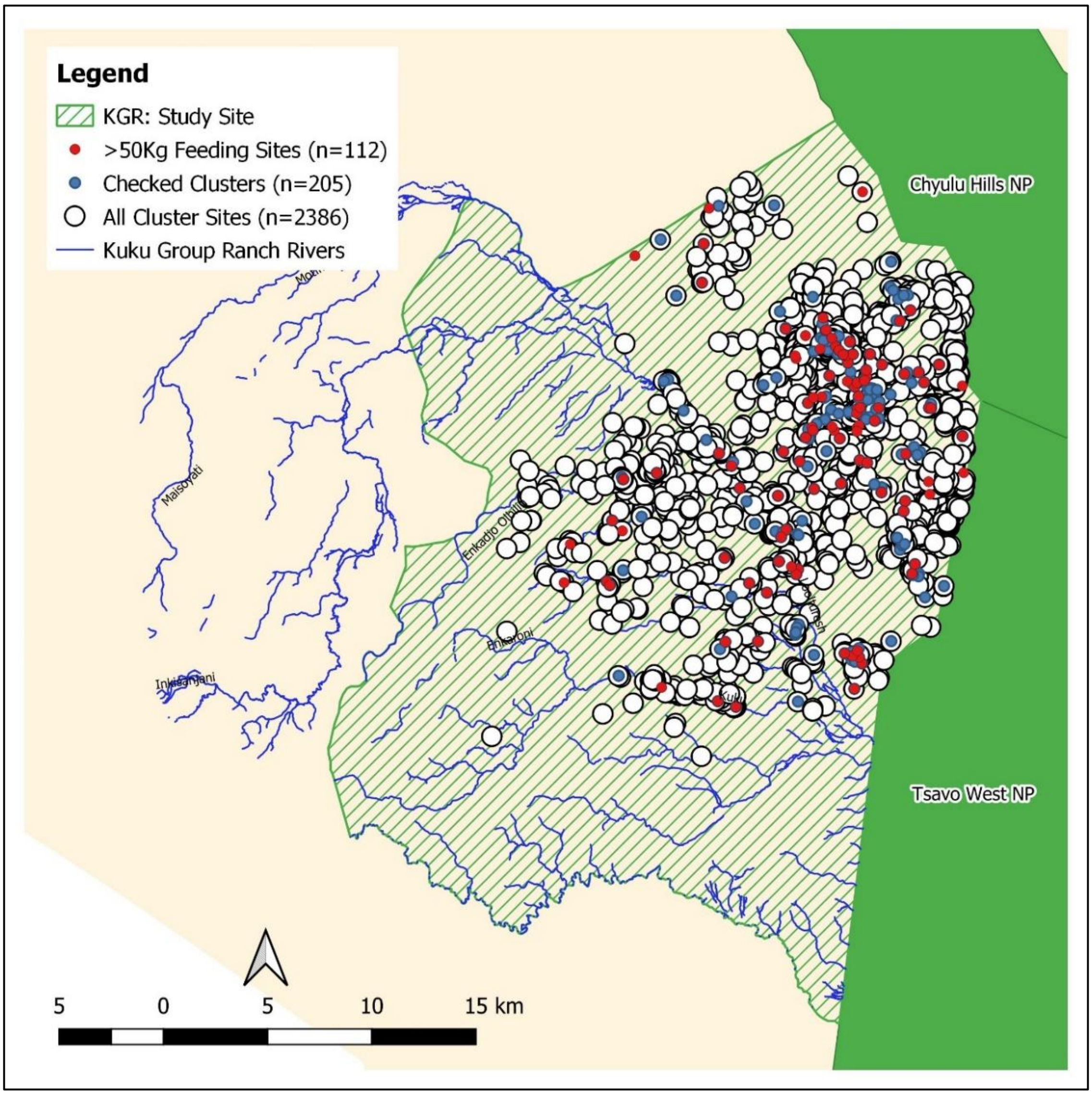

Figure 3.3: The study area in the Kuku Group Ranch shows the GPS cluster points identified from the seven collared lions' movement data. White dots indicate all cluster points (*n=2386*), blue dots are clusters identified as potential feeding sites (*n=205*), red dots are those clusters where prey remains were found of prey that was > 50Kg (*n=112*).

Nine different large-bodied prey species contributed to feeding events at GPS cluster sites (Table 3.1). Six species, namely cattle (*Bos taurus*), plains zebra (*Equus quagga*), Coke's hartebeest (*Alcelaphus cokeii),* Maasai giraffe (*Giraffa tippelskirchi*), blue wildebeest (*Connochaetes taurinus*), and eland (*Tragelaphus oryx*), made up 92% of all the identified prey consumed larger than 50kg (Table 3.1). The complete list of all species confirmed as consumed at feeding sites can be found in Appendix: A.

Table 3.1. Data collected at GPS Cluster feeding events provides the number and percentage contribution of large-bodied prey species to the lion diet and the proportional biomass contributing to the lion diet.

Prey Species	**No. of Times Identified**	**Percentage Contribution (%)**	**Adult Female Mass (Kg)**	**Total Biomass Consumed (Kg)**	**% Biomass Contribution to Diet (Kg)**
Cattle (*Bos taurus*)	27	24.11	306	8262	22.80
Plains zebra (*Equus quagga burchellii*)	23	20.54	302	6946	19.16
Cokes' hartebeest (*Alcelaphus cokeii*)	20	17.86	135	2700	7.45
Maasai giraffe (*Giraffa camelopardalis tippelskirchi*)	13	11.61	828	10764	29.70
Eland (*Tragelaphus oryx*)	11	9.82	450	4950	13.66
Blue wildebeest (*Connochaetes taurinus*)	9	8.04	180	1620	4.47
Warthog (*Phacochoerus africanus*)	5	4.46	57	285	0.79
Maasai ostrich (*Struthio camelus massaicus*)	3	2.68	68	204	0.56
Buffalo (*Syncerus caffer*)	1	0.89	513	513	1.42
Total	**112**			**36244**	

Thirty-four of the large-bodied prey species consumed and identified were obtained from clusters associated with the collared male lions, and 78 were associated with the collared female lions (Figure 3.4). Confirmed feeding events associated with male lions comprised 82% wild prey species and 17.65 % cattle, while those associated with female lions comprised 73% wild prey species and 26.92% cattle (Figure 3.4). Due to small sample sizes, a Fisher's Exact Test was used to test for differences between male and female diets, and the count data showed no significant differences between male and female diets for prey species larger than 50Kg (*p=0.9527*).

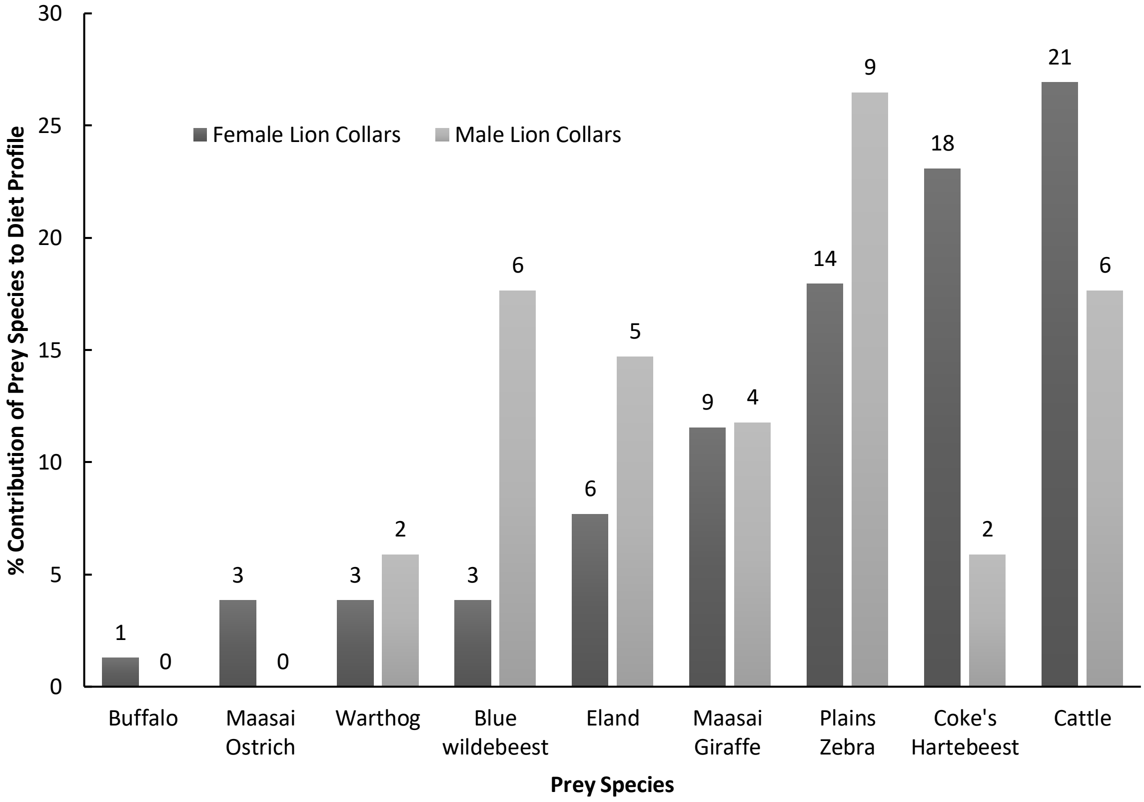

Figure 3.4: Female and male lion dietary proportions (%) were derived from GPS cluster investigations during 2017 and 2018 while investigating locations identified as possible lion feeding locations. Data labels above bars indicate the actual prey numbers consumed by lions.

3.3.2 Prey Availability

3.3.2.1 Aerial Census Data – Wildlife & Livestock

The most common large mammal species counted during the aerial census were cattle (74%). Wildlife only made up 26% of the large prey available, with plains zebra (11%) and Maasai giraffe (7%) the most common wild prey species recorded (Table 3.2). Please refer to Appendix: B for a complete and detailed account of all herbivore species recorded during the aerial counts.

Table 3.2: The large terrestrial wildlife and livestock species recorded in the Kuku Group Ranch study site during aerial census counts conducted in 2017 and 2018. Counts include both wildlife and livestock species.

Prey Species	May 2017	Oct 2017	Jun 2018	Nov 2018	Average	Average % Contribution
Buffalo	0	0	35	35	17.5	0.2
Eland	268	115	197	245	206.25	2.6
Maasai giraffe	750	343	427	814	583.5	7.2
Coke's hartebeest	180	61	194	390	206.25	2.5
Maasai ostrich	39	10	14	19	20.5	0.3
Warthog	3	0	4	4	2.75	0.0
Blue wildebeest	244	23	190	256	178.25	2.1
Plains zebra	1088	326	937	1340	922.75	11.3
Wildlife Totals	**2572**	**878**	**1998**	**3103**	**2137.75**	**26.2**
Cattle Totals	**6610**	**4668**	**5182**	**6340**	**5700**	**73.8**
Overall Total	**9182**	**5546**	**7180**	**9443**	**7837.8**	

3.3.2.2 SMART Ranger patrol data

A total of 49 780 km were walked on patrols over the two-year study period, with an average of 2074 km patrolled per month. The average number of encounters recorded by rangers per month across all prey species was 16 per km. The minimum daily patrol distance that could provide robust encounter rate data was more than 60 km collectively patrolled per day across all ranger patrol areas, and this daily figure tallied to a total of 1800 km per month. During the study period, the average daily patrol distance was 174 km, with a minimum being 114 km and a maximum of 242 km. We, therefore, included encounter rate data from all months in the analysis (Figure 3.5). For a complete account of MWCT community ranger distances patrolled per month, refer to Appendix 3C.

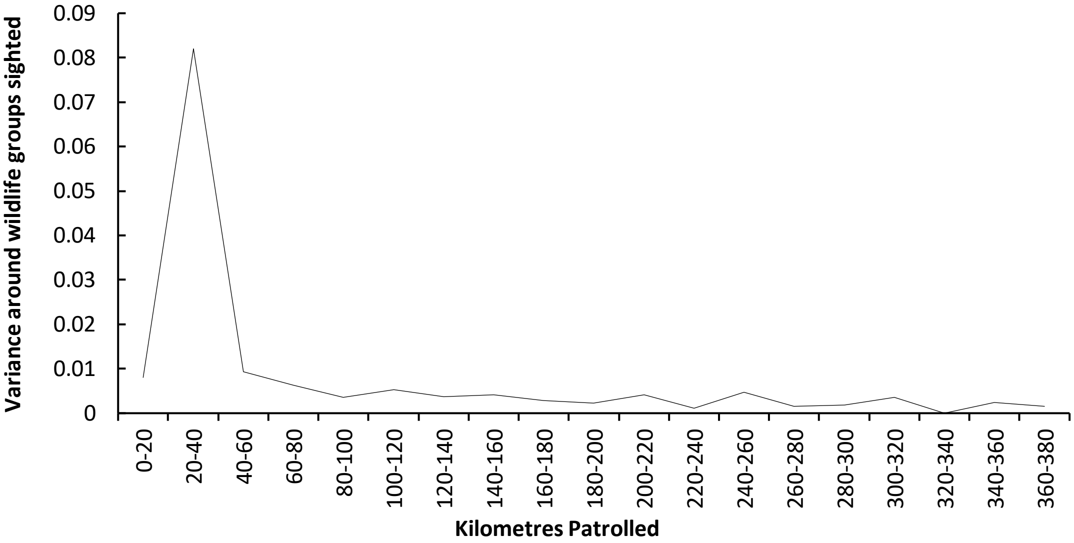

Figure 3.5: An analysis of the distance patrolled by field rangers within the study site compared to the variance around the mean of sightings of wildlife groups recorded.

The study site's large-bodied mammals recorded through SMART Ranger Patrols from 2017 to 2018 are presented as monthly encounter rates per kilometre patrolled. Maasai giraffe and plains zebra are encountered frequently, with average encounter rates above 1.5/km Coke's hartebeest and eland are also often encountered, with average encounter rates above 0.75/km. Buffalo, blue wildebeest, Maasai ostrich and warthog are seldom seen. For a complete account of specific species, encounter rates, including error and standard deviation calculated from MWCT community ranger distances patrolled per month, refer to Appendix: D.

3.3.2.3 Aerial Count Prey Availability & SMART Encounter Rates

When comparing total counts with percentages of encounters, the Maasai giraffe is the most encountered but not the most abundant as counted from the aerial census. Eland, Coke's hartebeest, and blue wildebeest occur at similar abundances, but blue wildebeest are encountered less than the former two species (Figure 3.6).

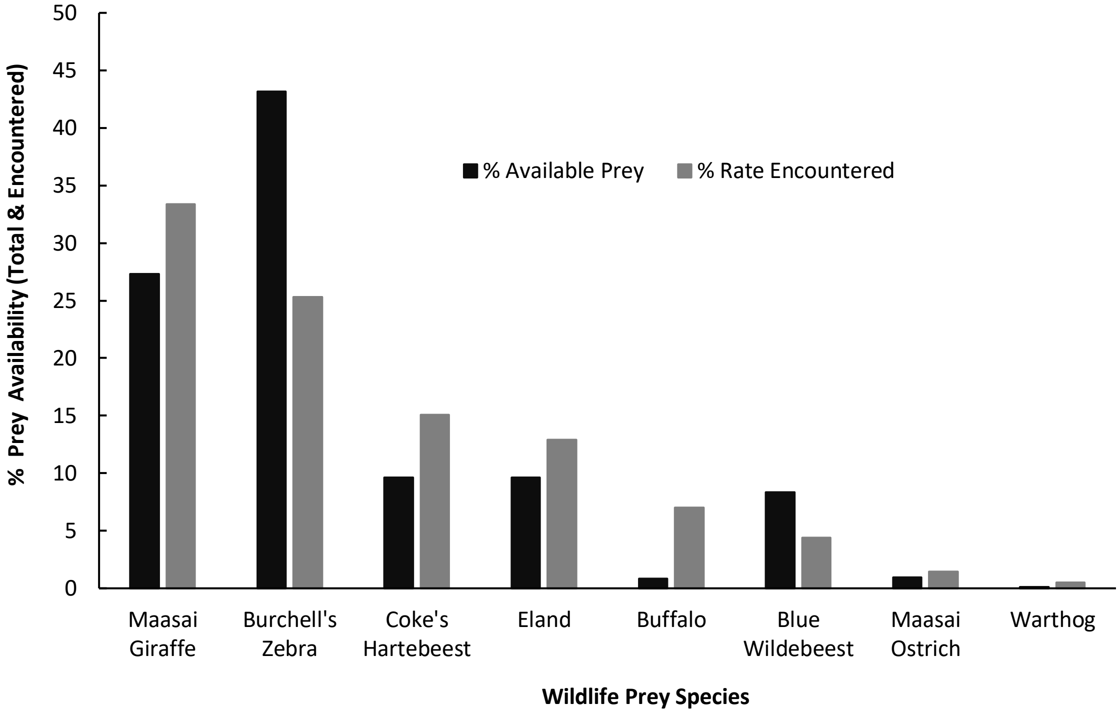

Figure 3.6: A comparison of the proportional large prey availability as calculated from total aerial count data and prey encounter rates recorded during ranger foot patrols conducted in the KGR study site during 2017 and 2018.

3.3.3 Prey Selection

3.3.3.1 Comparing Wildlife & Cattle Prey Preference

Although lions consumed more cattle than any other prey species during our study, they showed a greater preference for wild prey (Figure 3.7). Cattle were the least sought-after species of all the available large prey species despite their high numbers and biomass availability within the study site (Figure 3.8).

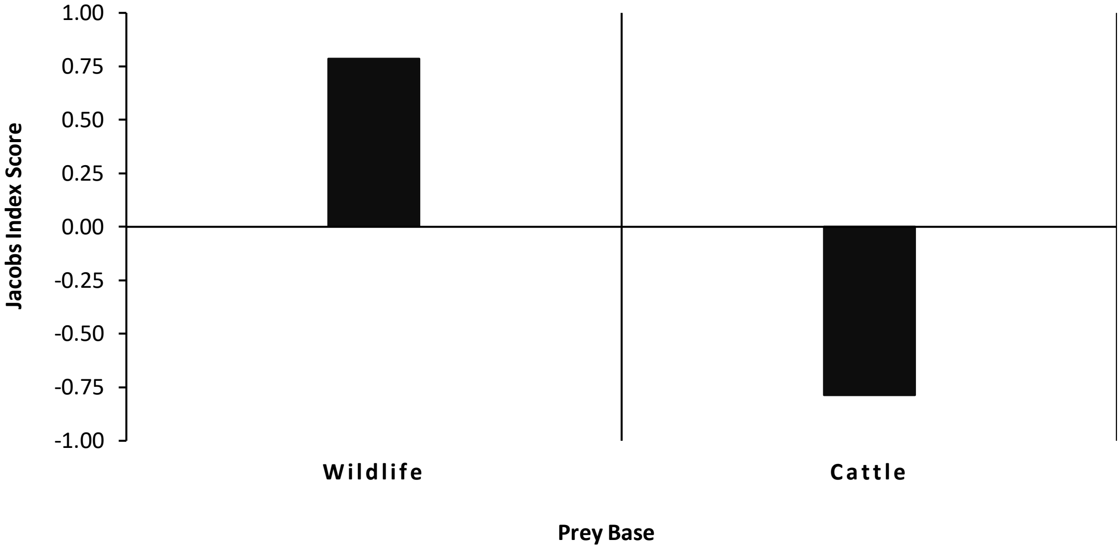

Figure 3.7: Wildlife prey preference and cattle prey preference calculated from aerial count data. The Jacobs' indices presented above indicate that lions preferred large-bodied wild prey over large-bodied domestic prey (cattle) within the study site.

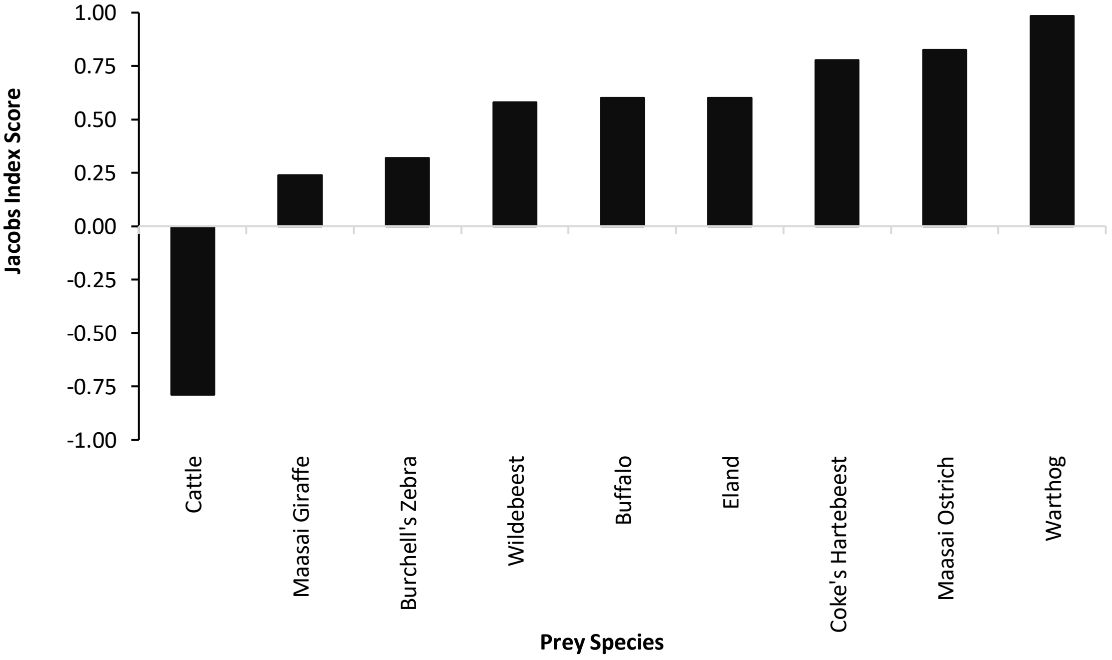

Figure 3.8: Prey preference was calculated using prey records obtained from GPS cluster analysis (confirmed feeding events) and aerial census data.

3.3.3.2 Wildlife Prey Preference

Warthog, blue wildebeest, Maasai ostrich, Coke's hartebeest, and eland were preferred prey species compared to prey availability measures from both encounter rate and aerial census data (Figure 3.8). According to ranger encounter rates, buffalo was the only preferred prey species but underutilised when tested against the aerial census data.

Eland is consumed relative to their availability in the landscape for ranger encounter rates but is preferred based on aerial census results. The Maasai giraffe was less preferred and underutilised by lions based on the encounter rate and aerial census availability data (Figure 3.9).

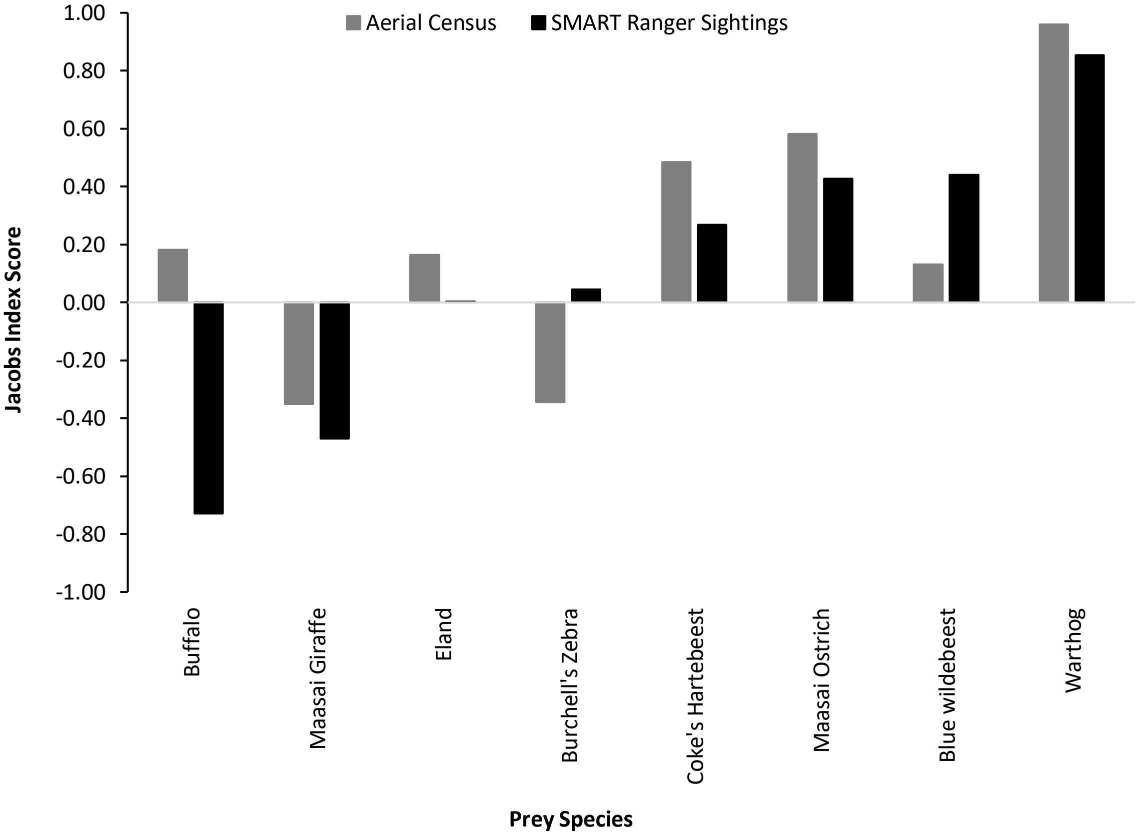

Figure 3.9: Prey preference calculated from both ranger encounter rates and aerial census data for wildlife prey only.

3.4. Discussion

Determining predator diet is essential in understanding predator ecology and the influence predators have on prey populations and significantly so for large carnivores that can influence other trophic levels (Radloff & du Toit, 2004; Hayward & Kerley, 2005; Owen-Smith & Mills, 2008). In African savannas, smaller species contribute little to the overall prey biomass consumed by lions, and large prey is important (Hayward & Kerley, 2005; Owen-Smith & Mills, 2008). Knowing which large prey species are preferred and utilised by lions is essential to ensure a sufficient prey base for lion populations (Davidson *et al.,* 2013; Montgomery *et al.,* 2018; Bauer *et al.,* 2020). The results presented in this study focus on the availability and consumption of large-bodied prey by lions in the KGR, where cattle are the most consumed species and contribute considerably to the prey biomass.

Cattle are significant contributors to lion diet, and this study has confirmed that cattle are an essential prey item for lions and are likely to affect the ecology of lions in the study site (Valeix *et al.,* 2012; Davidson *et al.,* 2013). However, cattle were the least preferred prey species, consumed by lions less frequently than expected, and underutilised by lions based on their overall abundance (Figure 3.8). Lower consumption rates of cattle allude to the unprofitability of cattle as a prey item in this landscape, possibly related to herder vigilance and the risk of retaliation by Maasai warriors (Frank *et al.,* 2006; Dolrenry, 2013; Ontiri *et al.,* 2019; Beattie *et al.,* 2020). Other studies have confirmed lions fear of retaliation and that lions balance the benefits of consuming cattle with the risks associated with doing so (Valeix *et al.,* 2012; Oriol-Cotterill *et al.,* 2015). Despite the risks, cattle are still consumed at frequencies that lead to increased human-wildlife conflicts in Africa (Bauer *et al.,* 2020) and on the KGR (Bauer *et al.,* 2017). Conflict levels are similar to those observed on neighbouring group ranches, where Maasai pastoralists frequently kill lions in retaliation (Western, 2018; Western *et al.,* 2021).

To our knowledge, although there are no comparative studies that evaluate the lion, livestock, and wild prey and environmental dimensions, the proportion of cattle depredation events appears to be similar to other studies (Banerjee *et al.,* 2013; Okemwa, 2015; Western, 2018; Ontiri *et al*., 2019; Beattie *et al.,* 2020). In the Gir Forests of India, cattle were estimated to contribute between 25 to 42% of lions' biomass consumptions (Banerjee *et al.,* 2013). Similarly, in two neighbouring group ranches, Kimana and Olgulului, the number of predatory incidences reported that lions contributed to 25% of all depredations and that lions attacked large livestock, particularly cattle (Okemwa, 2015). In the Olkiramatian–Shompole community in the South Rift Valley of Kenya, a total of 31 lion depredation incidents were verified, including 30 incidents where lions predated upon cattle (Western, 2018).

It is thus evident that cattle are commonly available, are the most abundant potential prey species and are consumed by lions in pastoral areas in Africa and on the KGR (Okemwa, 2015; Bauer *et al.,* 2017; Ontiri *et al*., 2019; Bauer *et al.,* 2020). Despite frequent utilisation, not all cattle are available to lions, and of the cattle recorded on the KGR, not all can be considered available, as well-protected cattle may be unavailable to lions (Lichtenfeld *et al*., 2015). The unavailability of all cattle has been illustrated because lions consume cattle less frequently than expected based on their abundances (Table 3.2). Although useful, total aerial counts cannot discern the level to which herders protect cattle. Further studies need to categorise cattle into two separate pools of availability, those that are well protected and those that are poorly protected and whether poorly protected cattle are preferred prey of lions.

Large prey species consumed on the KGR range from cattle to the Maasai giraffe, both are within the preferred prey weight range of lions (Hayward & Kerley, 2005; Owen-Smith & Mills, 2008). Results indicate that cattle are consumed frequently and contribute significantly to the overall biomass consumed by lions on the KGR. Prey populations such as the Maasai giraffe are characterised by high abundances in the KGR but are difficult for lions to hunt (Hayward & Kerley, 2005). Despite this, lions consume Maasai giraffe in this ecosystem, with the giraffe accounting for 11.61% of all prey consumed and nearly a third (29.7%) of the large prey biomass consumed on the KGR. We can thus conclude that Cattle are the primary prey for lions on KGR, followed by the Maasai giraffe.

According to their primary prey species abundances, other studies have shown that lions increase predation of secondary prey (giraffe) (Lee *et al.,* 2016). This increased predation reduced giraffe reproduction rates by 37% (Lee *et al.,* 2016), indicating variability in the preference for giraffes directly linked to the abundances of other preferred prey species populations consumed by lions. This shift in secondary prey consumption happens on the KGR, where Maasai giraffes are more frequently killed and consumed in the wet season when preferred prey is more dispersed and challenging for lions to find and kill. After the Maasai giraffe, plains zebra contributed 20.54% of the total diet and 19.16% to the overall biomass contribution. These results differ from lion diet estimates in Laikipia, Northern Kenya, where plains zebra was the top prey item (44.3% of all prey consumed, O'Brien *et al*. 2018).

In Laikipia, plains zebra consumption was followed by that of cattle, which contributed only to 13% of all prey consumed (O'Brien *et al.*, 2018) at a lower rate than the KGR (Table 3.1). Plains zebra was the most abundant prey species in this landscape (Groups at 1.98/km² and individual density at 15.94/km²) and was the primary prey species consumed by lions in the Laikipia landscape (O'Brien *et* *al.*, 2018; Ng'weno *et al.,* 2019). Similarly, in the Olkiramatian–Shompole community located in the southern Rift Valley of Kenya, lions frequently consumed zebra in addition to cattle (Creel *et al.,* 2014, Western, 2018). These comparisons indicate that cattle and zebra are import prey for lions and are consumed frequently in Kenya. Shifts from wild to domestic prey have been linked to reduced prey abundance, with lions switching to livestock predation when wild prey biomass falls below a threshold of 812 kg/km2 (Khorozyan *et al*., 2015). Plains zebra conservation should thus be prioritised as drop-in zebra biomass could drive livestock depredation in these pastoral communities and the KGR.

After plains zebra, Coke's hartebeest contributed the following highest percentage to the overall diet of lions (17.86%), although it only contributed 7.45% to the overall biomass consumed. In this instance, Coke's hartebeest can represent a bridging species utilised by lions in between accessing prey species of much higher biomass contribution, such as cattle or plains zebra (Beukes *et al.,* 2017) occur at higher abundances. Despite the lower contribution to biomass consumption, hartebeest was consumed frequently by lions on the KGR. The consumption of hartebeest is related to the spatial distribution of their primary prey (Ng'weno *et al.,* 2019). Coke’s hartebeest has previously been recorded as contributing similarly to lion prey diet contribution in other community areas of Kenya in Laikipia (O'Brien, 2018) and in the Ol Pejeta Conservancy in Northern Kenya, where hartebeest contributed to 13% of known lion kills; n=27 (Ng'weno *et al.,* 2019).

Lions consumed eland according to their abundance in the landscape on the KGR (Figure 3.9). Eland consumption on the KGR is thus similar to meta-analyses on the lion's diet (Hayward & Kerley, 2005). Eland contributed significantly to biomass consumed at 13.66%. In the Ol Pejeta Conservancy in Northern Kenya, eland was less preferred than expected (Ng'weno *et al.,* 2019). In the KGR, blue wildebeest and warthog contributed less to the lion's diet at 8% and 4.5% of the total diet, respectively, and only 4.5% and 0.75% to the overall biomass contribution of lions diet. The Maasai ostrich contributed 2.68% to the total items consumed and the 0.56% biomass consumed.

In summary, the prey item consumed most frequently by lions are cattle, and the prey species contributing most to prey biomass is the Maasai giraffe (Table 3.1). In comparison, the most preferred prey species was the warthog, which, as the smallest species consumed, is likely to be undercounted and thus inflate preference estimates (Figure 3.8). In addition to warthog, lions consumed blue wildebeest, warthog and Maasai ostrich more than expected based on their abundance in the study site. Preferences such as this are not uncommon, and other studies have confirmed that lions encounter preferred prey species more frequently than expected based on their abundance, and they consumed these species more frequently than expected based on this higher encounter rate (Hayward *et al.,* 2011). Conversely, plains zebra and eland were consumed in line with their abundance, while both cattle and Maasai giraffe were consumed less than expected based on their abundance. The consumption of zebra and blue wildebeest has relevance for this study as other research has demonstrated that predation by lions affected wildebeest more than zebra due to the sedentary behaviour of the wildebeest and semi-migratory behaviour of the zebra (Mills & Shenk, 1992). During seasonal shifts, wildebeests remain within the KGR while zebra move in and out and disperse in the wet season.

In African savannas, changes in the abundance of crucial large prey species can influence lions ecology (Hayward & Kerley, 2005; Valeix *et al.,* 2009; Valeix *et al.,* 2011; Beattie *et al.,* 2020). The results presented here provide vital information on the wildlife species that are most important for lions on the KGR, which may decline due to competition with livestock. Important wildlife species on the KGR include the plains zebra, eland, and Coke's hartebeest. Conversely, as a browser and non-competitor to domestic cattle, the Maasai giraffe can easily persist and provide necessary food for resident lion populations. However, the Maasai giraffe may only be more frequently utilised when cattle abundance and availability is reduced, forcing lions to shift from their primary prey species (cattle) to more frequent consumption of the Maasai giraffe (Lee *et al.,* 2016). A shift in lions primary prey availability would allow Maasai giraffe to be consumed following their availability (Hayward & Kerley, 2005). More frequent consumption of the Maasai giraffe by lions could reduce livestock predation and the associated human-carnivore conflict while lion populations would then remain, for the most part, regulated by a bottom-up process (Sinclair *et al.,* 2003).

The abundance of wild prey populations, particularly those of Maasai giraffe, and the protection of these populations can ensure that lions can survive in the KGR. The lion diet information is essential for the KGR as it can inform activities based on local circumstances, and conservation interventions based on local circumstances are most likely to be effective (Bauer *et al.,* 2020). The lion diet described here indicates that cattle are an important prey species for lions. The findings presented here will contribute to the discussions around the needs of livestock owners, wild prey, and lions in the multiple-use area of the KGR and other similar areas in East Africa (Schuette *et al.,* 2013; Bauer *et al.,* 2020; Wilkinson *et al.,* 2020). These discussions are essential for the long-term conservation and persistence of lions in the broader landscape (Kissui, 2008; Blackburn *et al.,* 2016; Montgomery *et al.,* 2018; Wilkinson *et al*., 2020; Sargent *et al.,* 2021).

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CHAPTER 4: DRIVERS OF TEMPORAL VARIATION IN CATTLE DEPREDATION BY LION ON THE KUKU GROUP RANCH, KENYA

4.1. Introduction

Lions (*Panthera leo*) have large space requirements, and as such, maintaining viable populations can be difficult without individuals from the population coming into contact with humans, often resulting in human-wildlife conflict (Estes *et al.,* 2011; Packer *et al.,* 2013; Hodgetts *et al.,* 2018; Bauer *et al*., 2020). Increased human-lion conflict can pose significant threats to human safety and livestock, causing conflict between lions and humans (Packer *et al*., 2013; Van Eeden *et al.,* 2018). Human conflicts with lions are driven by competition for natural resources between wild prey and domestic animals (Treves & Karanth, 2003; Inskip & Zimmermann, 2009). Lion attacks on livestock (further livestock depredation) can have significant social and economic impacts (Patterson *et al.,* 2004; Kissui, 2008; Hemson *et al.,* 2009; Beattie *et al.,* 2020) and often create negative attitudes toward carnivores if left unmanaged (Schuette *et al.,* 2013; Bencin *et al.,* 2016). Human-wildlife conflicts have led to populations of lions declining globally across their range (Bauer *et al*., 2018; Bauer *et al*., 2020).

Kenya experiences some of the highest human-carnivore conflicts in Africa (Beck *et al.,* 2019). Agonistic interactions are particularly severe when lions kill cattle (Gebresenbet *et al.,* 2018; Mbise *et al.,* 2018; Van Eeden *et al.,* 2018) and often leads to retaliatory killing of lions (Hazzah *et al*., 2009; Sundararaj *et al*., 2012; Meena *et al*., 2014; Ripple *et al.,* 2014; Everatt *et al.,* 2019). Human lion conflicts occur most frequently and are commonplace in the areas adjacent to national parks and other formally protected areas (Patterson *et al.,* 2004; Bauer *et al.,* 2020). Formally protected areas offer lion conservation solutions but may fail to provide this solution if they are too small or are surrounded by human populations (Woodroffe & Ginsberg, 1998). Kenya's largest protected area (PA) network, the Tsavo PA (Tsavo East National Park and Tsavo West National Park), forms a part of the Tsavo Amboseli landscape and includes approximately 20 000 km^2 of arid savanna, sustaining viable populations of wildlife species, including but not limited to elephants (*Loxodonta africana*) and lions (Armbruster & Lande, 1993). But because the PA boundaries within this landscape were regularised to exclude prior settlements, nearly 250,000 people now live on the PA's borders in villages and communal areas called group ranches (Patterson *et al.,* 2004). In the communal areas, human-carnivore conflicts and particular human-lion conflicts are commonplace (Patterson *et al.,* 2004)

Despite the high level of human-wildlife conflict, the land connecting the national parks within the Tsavo-Amboseli landscape, such as Maasai group ranches, plays an essential role in lion conservation. Maasai group ranches support viable lion populations and create wildlife corridors (Okello, 2005; Okello, 2019). Conflicts between humans and lions in the areas surrounding PA's, including the focal area and study site, are inevitable, given their geography and close proximity to wildlife.

Several variables are associated with human-carnivore conflicts (Montgomery *et al.,* 2018; Beatie *et al.,* 2020). For example, cattle depredation by lions may differ over time and be associated with rainfall, the abundance of wild prey and vegetative productivity (Beattie *et al.,* 2020). The depredation of cattle by lions within the focal study area is not evenly distributed throughout the year, with unpublished reports suggesting a peak in cattle predation coinciding with the annual peaks in rainfall during March to May and October to December (MWCT: Annual Reports, 2003 - 2016). These seasonal spikes in depredation events may be related to husbandry practices, rainfall, natural foraging resources for prey species, wild prey availability.

- ***Rainfall***

Both rainfall and lag rainfall is often used to explore the delayed effect of rainfall on vegetation and predation, and in this study, we will attempt to determine the link between cattle depredation and rainfall (Mills *et al.,* 1995; Ogutu & Owen-Smith, 2005). In the Kruger National Park, South Africa, the relationship between rainfall, lion predation and population trends in herbivores showed that herbivores reacted differently to rainfall cycles and that the driving force in the ecosystem was rainfall (Mills *et al.,* 1995). The distribution of wildlife as affected by rainfall, surface water availability, and natural foraging resources thus has the potential to affect how lions select prey, what prey is accessible and in the instance of mixed-use areas with cattle, how this can affect cattle depredation (Hopcraft *et al*., 2005; Davidson *et al*., 2012; Beatie *et al*., 2020)

The potential association between rainfall and cattle depredation requires further investigation, as it is essential to understand why cattle are killed more frequently during certain times of the year. Previous research has investigated rainfall concerning cattle depredation frequency with varied results, and Rudnai (1979) could not find any association at all. Other studies have found the highest depredation rates in the dry season (Butler, 2000; Patterson *et al*., 2004). Other recent studies have documented increases in depredation during the rains in Africa (Patterson *et al*., 2004; Woodroffe & Frank, 2005). Understanding this will help improve mitigation efforts and to developing strategies for conserving both carnivores and wildlife corridors (Polisar *et al.,* 2003).

In the dry season with low rainfall, large herbivore distribution is mainly limited to areas near water resources (Owen-Smith & Mills 2008a; Davidson *et al*., 2012), and lions often kill and consume large herbivore prey species (wild and domestic) closer to these sources (Hopcraft *et al.,* 2005; Davidson *et al.,* 2012). Contrastingly, surface water availability increases in the wet season, and wild prey disperses throughout the landscape, making it more difficult for lions to find, kill, and thus utilise wild prey (Owen-Smith & Mills, 2008b). Thus, year-round variation in rainfall can potentially affect cattle depredation by lions (Owen-Smith & Mills 2008b; Patterson *et al.,* 2004). However, rainfall's influence on food availability cannot be considered without taking predator-prey interactions into account, and the effects rainfall has on predation and depredation might not be immediately following a significant rainfall event (Ogutu & Owen-Smith, 2005), and can be measured by vegetative productivity, through Normalized Difference Vegetation Index (NDVI).

- ***NDVI***

The timing and amount of vegetation for herbivores is essential as it directly influences natural forage availability, wildlife distribution and cover (Mills *et al.,* 1995; Ogutu & Owen-Smith, 2005). Vegetation responds with a lagged effect to both the quantity and frequency of rainfall events, and the cumulative effect takes time to reflect itself in the vegetation. This change in vegetation then affects the susceptibility of the different wild and domestic prey species to predation (Ogutu & Owen-Smith, 2005; Owen-Smith & Mills, 2006). NDVI as a measure of vegetative productivity (quality of forage) and improved natural foraging also thus needs consideration. The potential influence of consistent higher NDVI measured in the study site can potentially improve the fitness of wild prey and reduce wild prey catchability increasing cattle depredation events (Owen-Smith & Mills, 2008b; Beatie *et al.,* 2020).

Furthermore, studies in Tanzania have indicated that large-bodied prey species are essential for lions (buffalo & hartebeest) (Hayward & Kerley, 2005), and migrants (plains zebra & blue wildebeest) tend to use and move across entire landscapes while avoiding areas of low NDVI (Anderson *et al.,* 2016). However, one must consider the potential difficulties linking satellite-derived data to the forage quantity/quality trade-off and that for this study, we did not ground truth the NDVI measurements in the field. The effect of NDVI may be underestimated using NDVI, where lag rainfall could prove more useful (Ogutu & Dublin, 2004). Nevertheless, NDVI can influence wild and domestic prey susceptibility to lion predation (Beatie *et al.,* 2020), and in areas with higher levels of NDVI recorded, there may be increased cattle predation risk as prey densities support lions by providing an increased overall prey base (Pettorelli *et al.,* 2009; Kissui *et al.,* 2019). Vegetative productivity can thus be used to track patterns of depredation (Owen-Smith, 1996; De Boer, 2010; Beatie *et al.,* 2020).

- ***Prey Availability***

Prey availability as a potential driver of depredation is also important as only a few species, such as impala (*Aepyceros melampus*) and Coke's hartebeest (*Alcelaphus cokeii*), remain sedentary near year-round water (Fryxell *et al.,* 1988; Owen-Smith, 1996). For example, In the landscape surrounding the study area in the Amboseli National Park and surrounding group ranches, it has been found that 90% of buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga burchellii*), Cokes' hartebeest, impala and elephant were within 4-6 km of water in the dry season. Conversely, 95% of fringe-eared oryx (*Oryx beisa callotis*) and all eland (*Tragelaphus oryx*) were found further than 4 km from permanent water (Western, 1975).

Elsewhere in Africa, in the Kruger National Park, South Africa, most large herbivores are migratory species and represent the bulk biomass of species, vital for lions and other large predators (Owen-Smith, 1996). While in the Amboseli National Park, the range of herbivore species was four times larger than the dry season concentration zone (Western, 1975), demonstrating that when prey fitness and condition improve during wet periods, migratory species disperse away from the heavily utilised areas close to surface water (Owen-Smith, 1996). Closer to the study site, in a study carried out in Tsavo, cattle depredation was higher when natural prey density was lowest, showing that wild prey variation has the potential to influence prey densities and cattle depredation (Mukeka *et al*., 2020). In the Koyake and Siana Group ranches, neighbouring the Maasai Mara National Reserve (1500 km^2), cattle depredations by lions were negatively correlated with a decline in natural prey abundance, which directly influenced depredation rates (Kolowski & Holekamp, 2006). In Manyara Ranch Conservancy, northern Tanzania, seasonal variation in vegetative productivity and proximity to surface water appeared to be strong predictors of livestock depredation risk (Beattie *et al*., 2020).

The tendency of cattle depredation varying throughout the year in other areas and within the Kuku Group Ranch (KGR) suggests that the driver of cattle depredation has a temporal variation that needs further investigation. In comparing rainfall, lagged rainfall, measures of range condition and prey availability, one can thus investigate how these interact and how each variable may be a potential driver of cattle depredation and human-wildlife conflicts. The potential drivers should also be considered in light of differences in cattle husbandry practices (Bauer *et al.,* 2017; Loveridge *et al.,* 2017). In this study's focal area, cattle are placed in predator-proof bomas at night, while a livestock compensation scheme aims to reduce retaliatory action against lions while improving cattle husbandry (Bauer *et al*., 2017).

Although these efforts aim to reduce lion killing, human population growth, livestock expansion, cattle depredation, and human-lion conflicts lead to frequent lion killings (Bauer *et al.,* 2018; Maclennan *et al.,* 2009; Bauer *et al.,* 2020). Cattle husbandry practices includes the sociological component of livestock husbandry and can aid the understanding of how intensely, when, and potentially why lions attack and consume cattle (Loveridge *et al.,* 2017). On the KGR, cattle husbandry includes various practices, including protective enclosures (permanent & seasonal bomas) and seasonal herding practices. Permanent bomas are better constructed, while seasonal bomas are used when grazing further from settlements and are less effective in preventing predation (Manoa & Mwaura, 2016).

Lion cattle conflict can thus be mitigated or exacerbated by the style of livestock husbandry, with some styles creating a far greater predation risk and intensity of attacks than others (Loveridge *et al.,* 2017; Sutton *et al.,* 2017). An example is the seasonal bomas constructed of poor fencing structures, such as traditional acacia fences, potentially affecting predation risk (Sutton *et al.,* 2017). In support of this, Loveridge *et al.* (2017) found that lion attacks on cattle were more frequent in the wet season, suggesting that seasonal herding practices may result in increased cattle vulnerability. This study aims to better understand the temporal variation in cattle depredation on the KGR over thirty-six months by examining variables that could influence cattle depredation events on the KGR. Variables include prey species availability, rainfall, lag-rainfall, and NDVI and how these affect husbandry practices.

I hypothesise that during the 36 months of 2016 -2018 that:

a) Cattle depredation by lions would be highest when wildlife and, in particular, critical prey species availability are low.

b) Cattle depredation by lions will be more common during periods of higher rainfall when surface water availability improves and wildlife disperses, reducing prey species numbers.

c) Cattle depredation by lions would be more common during periods with higher lag rainfall and NDVI values as the availability of foraging resources away from dry season water sources improves and wild prey disperse. The dispersed wildlife will reduce key prey species numbers leading to higher cattle predation.

4.2. Methodology

4.2.1 Study Site

This study examines lion-cattle depredation in the Kuku Group Ranch (KGR), a group ranch adjacent to the Tsavo West and Chyulu Hills National Parks in southern Kenya. The KGR is a community-owned rangeland area covering 1 133 km² at S 2.77554°, E 37.85150° (Figure 4.1). The KGR is situated within the 9,000 km² Amboseli-Tsavo ecosystems, and in addition to wildlife, provides residence to approximately 17,000 Maasai and 90,000 livestock (Groom & Harris, 2008). Group ranches are livestock production systems, where traditional Maasai occupants jointly own a freehold title to land and both herd and graze their livestock alongside wildlife (Western *et al*., 2009; Bauer *et al*., 2017).

The KGR is situated in an arid to a semi-arid area, and rainfall in the lower regions of the KGR varies between 250 – 800 mm annually, with an average of 340mm (Okello, 2005). The Chyulu Hills to the north receives up to 700 mm per year (Western *et al.,* 2009). Rainfall in the KGR varies significantly annually, is highly unpredictable, with two rainy seasons a year and significant inter-year variation in quantity and timing (Phillipson, 1975; Awere-Gyekye, 1996; Altmann *et al.,* 2002). In the Amboseli National Park and surrounding group ranches, temperatures range from highs in the mid-30s°C in February to annual temperature lows of approximately 20°C in July (Western *et al.,* 2009). The KGR is comprised of a heterogeneous landscape that features a transition in vegetation from lowland dry savannah grassland and *Vachelia-Commiphora* forest to an area dominated by a moist, dense cloud forest in the Chyulu Hills (Agnew, 1968; Jensen, 1989).

Spatial information obtained from collared lion movement and data from lion livestock killing events obtained from a predator compensation scheme (Bauer *et al.,* 2017) identified the eastern section of the KGR as having the highest levels of lion activity, which consequently formed the focus area of this study (Figure 4.1). The landscape is interspersed with permanent and temporary (seasonal) Maasai manyattas. These manyattas (or kraals) combine thorn bush corrals (also called bomas) and Maasai dwellings traditionally used to keep livestock overnight in safety from predators (Figure 4.1). A more detailed account of the biotic and abiotic features of the KGR and study area has been described in Chapter 2.

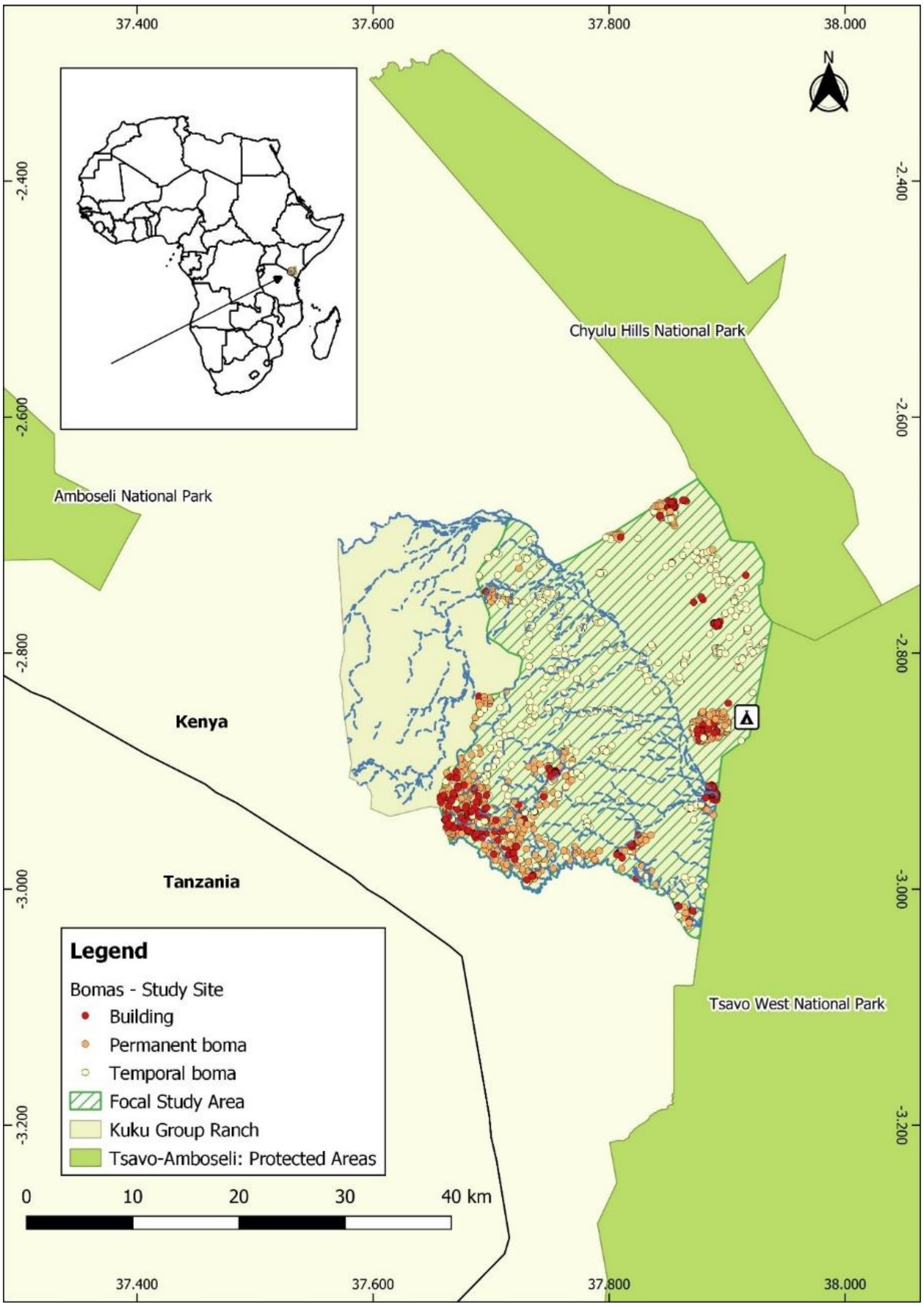

Figure 4.1: The Kuku Group Ranch in Kenya, its relation to Tanzania, and the surrounding protected areas of Tsavo West National Park, Chyulu Hills National Park, and the Amboseli National Park. The temporary and permanent bomas located on the Kuku Group Ranch, where cattle are kept in the area, are indicated on the map.

4.2.2 Data Collection

In this study, I compared cattle predation events at monthly intervals against a range of environmental variables, including the availability of key prey species, rainfall, lag rainfall, and NDVI for each month of 2016, 2017 and 2018, to identify the drivers of cattle depredation within the study area. The data came from the following sources.

4.2.2.1 Cattle Depredation Data

On the KGR, the Maasai Wilderness Conservation Trust (MWCT) has compensated livestock farmers for livestock losses due to wildlife since 2003 (Bauer *et al*., 2017). Although cattle depredation data have been available since 2003 (Chapter 1, Figure 1.2), reliable monthly prey availability data for the entire study area is only available from 2016 when ranger patrol station placement and associated patrols started to cover the whole area (Chapter 2, Figure 2.17). Details for lions' consumption of large key prey species are also only available for 2016 and, more specifically, 2017 and 2018 (Chapter 3). Due to this, cattle depredation data are only investigated from 2016 onwards. The predator compensation fund is commonly known as Wildlife Pays (WP). As part of the programme, verification officers (VO's) are employed by MWCT to respond to all livestock depredation events on a motorcycle and investigate each claim in detail by stating the livestock species lost in the husbandry context – commonly referred to as "loss type". Loss types include poor bomas, good bomas, negligent herding and non-negligent herding. The carcass condition and circumstances assist in the classification of a depredation event as either non-negligent or negligent husbandry (Bauer *et al*., 2017).

Non-negligent husbandry practises are generally recorded when appropriate defences are applied, such as keeping livestock in a boma of at least 1.2 m high and 1.2m wide at night and ensuring cattle are well attended to during the day. Good herding by livestock owners entails rapid response, which leads to the recovery of an intact carcass. Negligent husbandry is recorded when depredation occurs on livestock that is unattended by a herder during the day or night or where depredation occurs within sub-standard bomas. Lion depredation events recorded in the WP program on cattle in 2016, 2017 and 2018 were used for this study and included negligent and non-negligent cattle predation incidents. The WP program has been running for over ten years, and community members are aware of the compensation scheme and actively participate in it due to the monetary rewards. It is thus assumed that reporting levels, verification, and data capture in the field by VO's, have been constant over the study period (Bauer *et al.,* 2017). The actual number of reported cattle depredations for each month was used to investigate differences between months over the 36 months.

4.2.2.2 Lion Prey Availability Data

In chapter 3, a total of eight different large-bodied wild prey species (> 50kg) contributed to lion feeding events at GPS cluster locations. The species identified included plains zebra, Coke's hartebeest, Maasai giraffe (*Giraffa tippelskirchi*), blue wildebeest, eland, warthog (*Phacochoerus africanus*), Maasai ostrich (*Struthio camelus massaicus*) and buffalo. The complete list of all species confirmed as consumed at feeding sites can be found in Appendix: A. Four of the eight large wild prey species provided more than 70% of the wild prey biomass consumed by lions. The four species and their biomass contributions were as follows: Maasai giraffe (30%), plains zebra (19%), eland (14%) and Coke's hartebeest (7.5%). We used the encounter rate (number encountered per km patrolled) of these four wild prey species in the study area per month to establish whether their availability can potentially explain the temporal variation in cattle depredation events by lions.

The four large wild prey species' monthly availability was obtained from MWCT patrol data which provided continuous information on prey availability in monthly encounter rate. MWCT has 11 sectors and ranger stations from which daily patrols are conducted for wildlife monitoring and anti-poaching purposes. Rangers collectively patrol a minimum of 100 km per day, and as part of the patrols, all wildlife sightings (excluding livestock species) and poaching threats are recorded. Rangers use Cybertracker, a system developed CyberTracker Conservation (Liebenberg, 2012). Cybertracker uses devices to allow handheld data capture in the field wildlife where counts are given a spatial reference by field rangers logging the x and y coordinates of every wildlife sighting observed. Data were collected between January 2016 and December 2018.

These observations made by the community rangers are then used to calculate the relative abundance of prey based on encounter rates of groups of potential wild prey species. The reliability of encounter rate data was tested by evaluating patrol effort and the probability of varying levels of effort affecting the reliability of prey encounter rate calculations (See Chapter 3 for detailed methodology). The encounter rates for the four prey species contributing most to the prey biomass consumed were then pooled to provide a "large prey availability index" for each of the 36 months in the study site. The large prey availability index was used to test whether wild prey availability potentially drives cattle depredation rate by lions.

4.2.2.3 Monthly Rainfall and Lag-rainfall Data

Rainfall was recorded within the study area at the Chyulu Hills Conservation & Research Centre (CCRC), situated on the eastern border of the study area (Figure 4.1). The monthly rainfall for 2016 – 2018 was obtained from MWCT rainfall data records. The lag rainfall for any particular month was calculated by averaging the preceding two months' rainfall values and including the current month for recording (Ogutu & Owen-Smith, 2005). For example, the lagged rainfall for March 2016 was the average rainfall received during January, February, and March 2016.

4.2.2.4 Monthly Normalised Difference Vegetation Index (NDVI) values

The NDVI of the vegetation within the study site was assessed using geospatial techniques in Google Earth Engine (GEE) (Martín-Ortega *et al.,* 2020; Kumari *et al.,* 2021). Estimating the relative vegetative productivity in the study was done through GEE to extract individual NDVI values recorded at 911 points obtained from cattle depredation locations dating back to 2011. The NDVI values at these 911 sites between 2016–2018 were used to calculate an average NDVI value for each month over the 36 months. For each month from January 2016 through to December 2018, 911 NDVI point readings were used to calculate an average NDVI value per month for each of the 36 months. Effectively, this averaged NDVI data provided a proxy for relative vegetative productivity for each month across the study site (Kundu *et al.,* 2018).

4.2.3 Data Analysis

All statistical procedures were conducted in R software, version 3.1.2 (R Core Team, 2017). The frequency and occurrence of lion attacks on cattle within the KGR were summarised using the number of cattle depredation events per month from 2016-2018 (n = 330). Modelling the potential drivers of lion depredation on cattle (rainfall, lag rainfall, NDVI and prey availability), the number of cattle depredation events was compared against a combination of predictor variables. Due to the high variability in the quantity and timing of rainfall events, we explored the effect of the variables over three years in monthly intervals rather than as averaged effects over calendar months. We started the modelling process by developing a global model assuming a *Poisson* distribution that additively included all predictor variables and the interaction of NDVI and importamt prey. The Generalized linear model (glm) with a *Poisson* distribution identified which of the four variables best predicted cattle depredation. Model validity was assessed using diagnostic checks (Pearson's correlation investigated pairwise relationships between predictor variables), and the models showed no clear outliers and a relatively even spread of residuals. Thus, the *Poisson* model was used going forward.

Collinearity between our predictor variables was tested by investigating the variance inflation factors for all predictor variables (VIF) (Zuur *et al*., 2010, Davies *et al*., 2016; Western *et al*., 2021). Before model formulation, all variables resulting in VIF of more than three were determined, and no variables were excluded with variance inflation factors > 3 (Zuur *et al*., 2010, Western *et al*., 2021). Using the global model as a starting point, we investigated all possible additive combinations of the predator variables using the "dredge" function in the package "MuMin" (MuMIn, version 1.43.17).

We used a model selection approach to select the top model from our resulting candidate models, ranking models using Akaike Information Criterion (AICc) (Burnham, 1998; Davies *et al*., 2016). We considered a single top model if the delta AIC of the second model was greater than 2 (Mazerolle, 2006; Hazzah *et al.,* 2009). Otherwise, we employed a model averaging approach to investigate the top candidate models. The above modelling approach was conducted on three different datasets of depredation data. We investigated overall negligent and non-negligent cattle depredation and whether depredation events varied across husbandry practices and drivers.

To visually assess the influence of significant predictor variables on the probability of an increase or decrease in cattle depredation events for a given month, the median marginal probability of cattle depredation was plotted as a function of the range of observed predictor variables used in this study (Davies *et al*., 2016). These plots were constructed by fixing the predicted cattle depredation as a function of the variable that varied across its observed range and, for each value, predicting the observed probability of cattle depredation from the best candidate model while maintaining all other predictor variables (fixed) at their original input values (Elith *et al*., 2005).

4.3. Results

4.3.1 Cattle Depredation and Husbandry

Three hundred and thirty cattle depredation events were recorded through the Wildlife Pays scheme in the study area between 2016 and 2018 (Figure 4.2). Of the 330 events, 176 (141: Negligent herding; 35: Negligent Bomas) were categorised as negligent and 154 (126: non-negligent herding; 28: Non-negligent Bomas) as non-negligent depredation events. There was some variation in cattle depredations events during the study, with differences between and within years. The highest month of cattle depredation was recorded in July 2016 (n = 25 depredation events), but generally, January, May, and December have the highest incidences of cattle depredation (Figure 4.3).

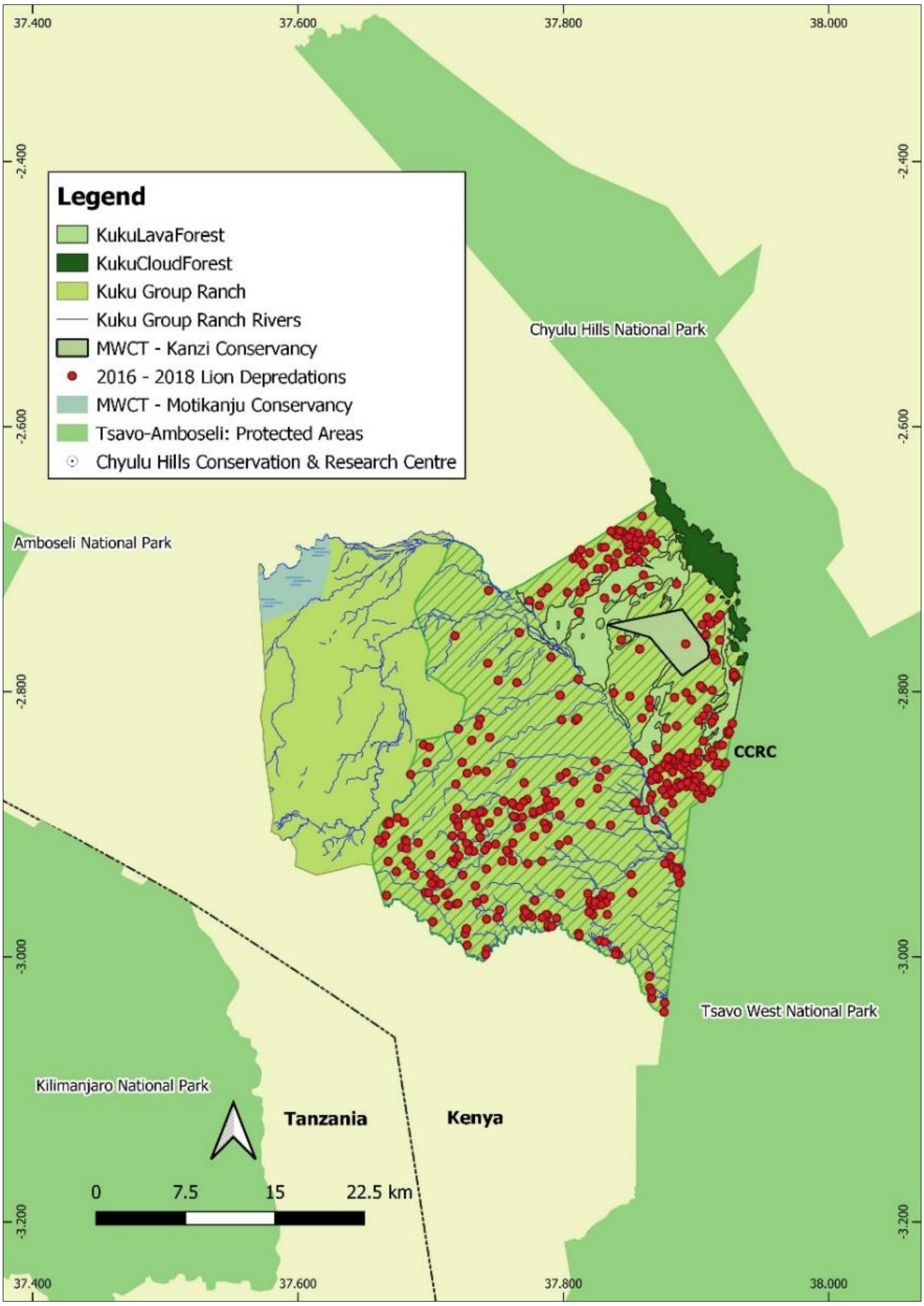

Figure 4.2: The study area on the KGR shows the location of all cattle depredation events recorded between 2016 and 2018 within the study site (n=330).

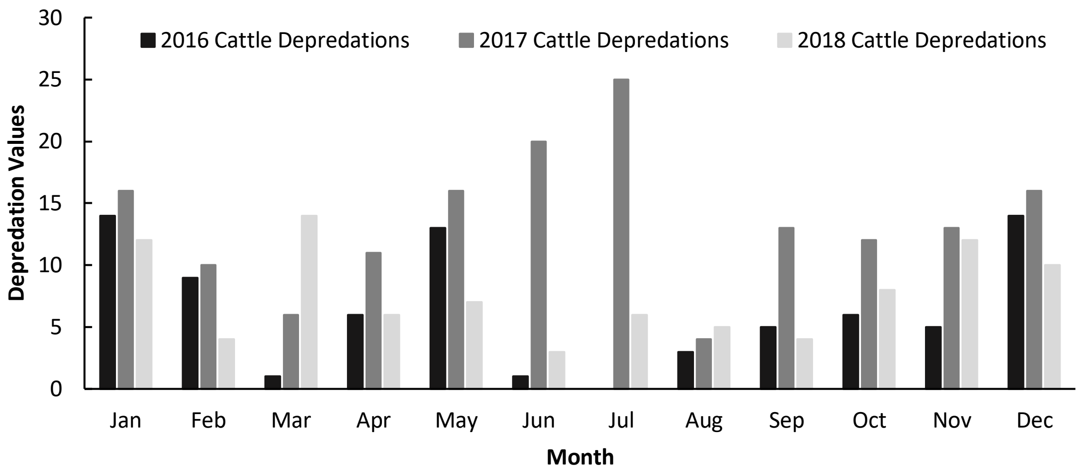

Figure 4.3: The number of cattle depredation events by lion per month for the 36 months between 2016 and 2018 (n=330)

4.3.2 Important wild prey availability

The four most important wild prey species contributing to lion prey biomass, namely Maasai giraffe, plains zebra, eland and Coke's hartebeest, are also the four most encountered wild large prey species by the ranger patrols (Fig 4.4). The Maasai giraffe is the most encountered animal, followed by plains zebra, while Coke's hartebeest and eland are encountered similarly across the study area (Figure 4.4). The combined encounter rate of the four species that contributed most to the lion diet in the study area also showed variation within and between the years (Figure 4.5).

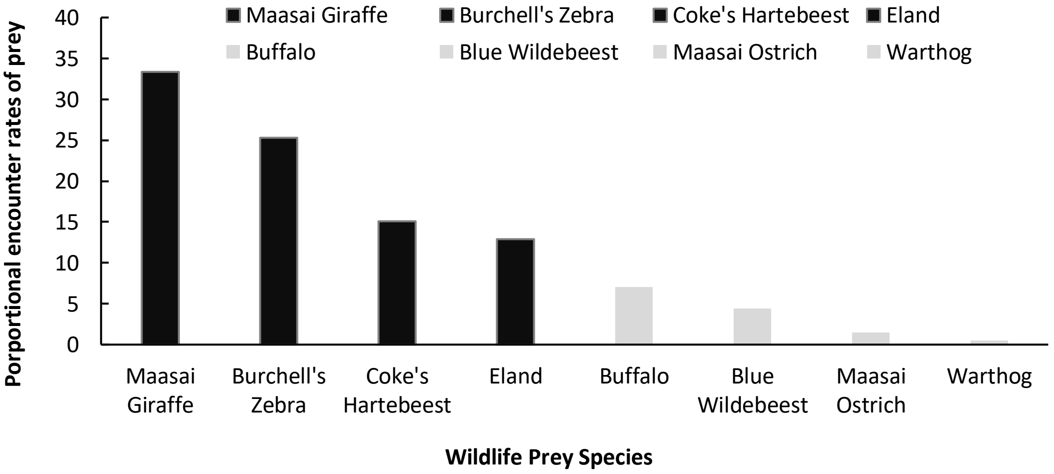

Figure 4.4: A comparison of the proportional encounter rate of the eight most common large prey items consumed by lions as recorded during ranger patrols conducted in the KGR study area between 2016 - 2018. The four wild prey species contributing the greatest portion of biomass to lions' diet are highlighted in dark grey.

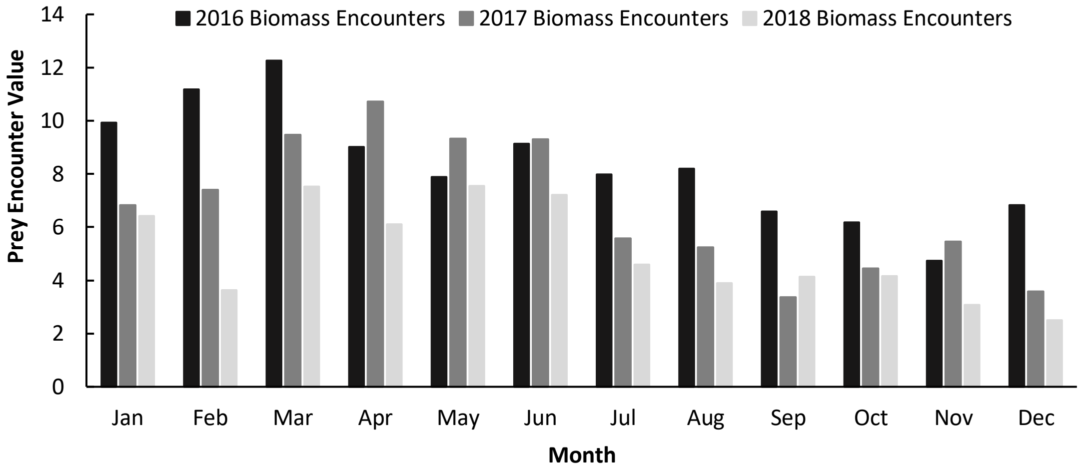

Figure 4.5: A monthly comparison of the encounter rates of the four wild prey species contributing most to the prey biomass consumed by lions at KGR for the period 2016-2018. The values depicted are the sum of the encounter rate of Maasai giraffe, plains zebra, eland and Coke's hartebeest.

4.3.3 Rainfall

Rainfall between 2016 and 2018 showed a broad bimodal distribution typical for this area with a shorter rainfall period over November and December, followed by a more extended period from March to May (Figure 4.6). The months of June to October were particularly dry across all three years. Variation in the quantity and timing of rain during the typical rainfall months is evident, with March 2018 experiencing nearly double the amount of rain than any other month over the 36-month study period (Figure 4.6).

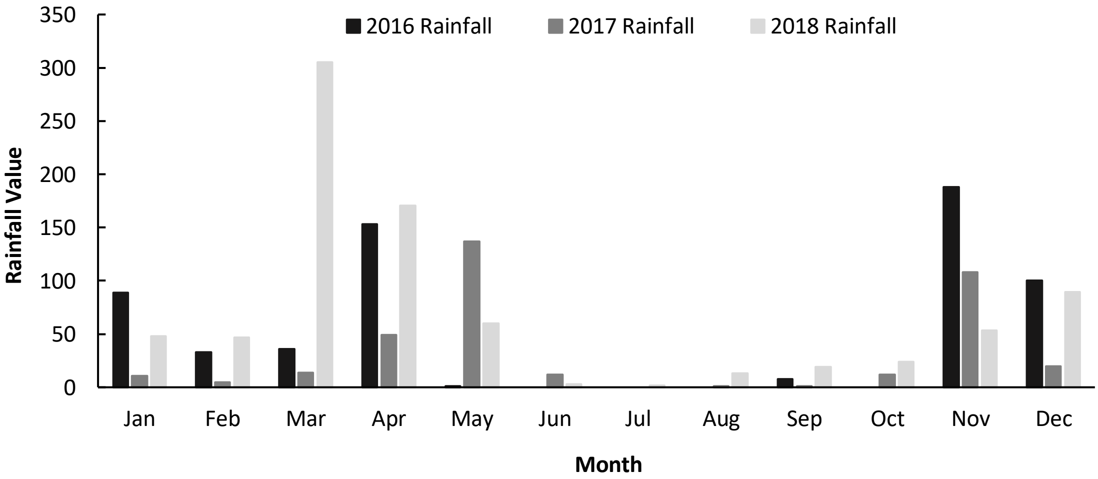

Figure 4.6: The monthly rainfall received in the KGR study area during 2016 – 2018.

4.3.4 Lag Rainfall

The lag rainfall from 2016 and 2018 was generally high from November to June, while lower cumulative figures were recorded for July, August, September, and October (Figure 4.7).

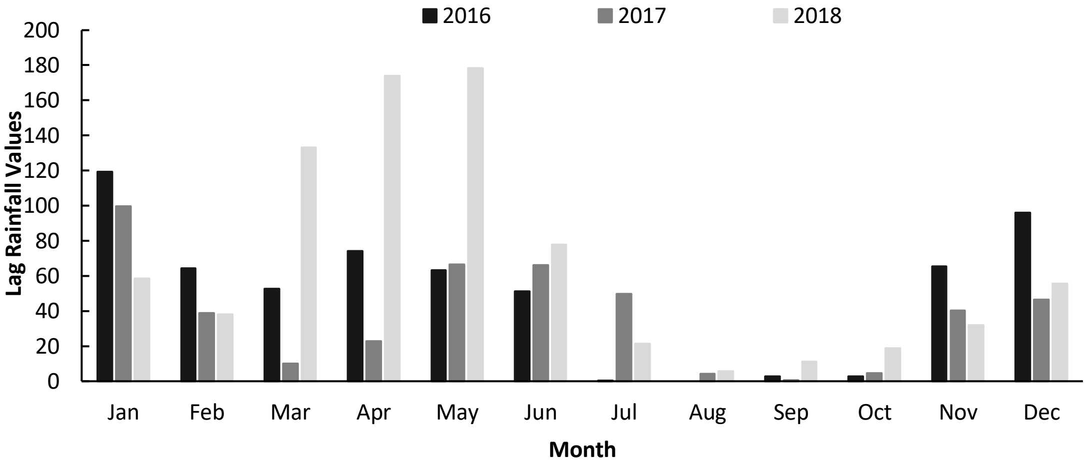

Figure 4.7: The calculated monthly lag rainfall values for each of the 36 months of the study from 2016 – 2018 for the KGR study site.

4.3.5 Normalised Difference Vegetation Index (NDVI)

Mean NDVI values recorded between 2016 and 2018 range from 0 - 0.5, with 0 representing low vegetation productivity and 0.5 representing higher vegetation productivity (Figure 4.8). Only in August were values recorded below 0.1 over the three years, suggesting that August is a period of extreme forage limitation. The higher NDVI reading of May 2018 results from the high rainfall received during March 2018.

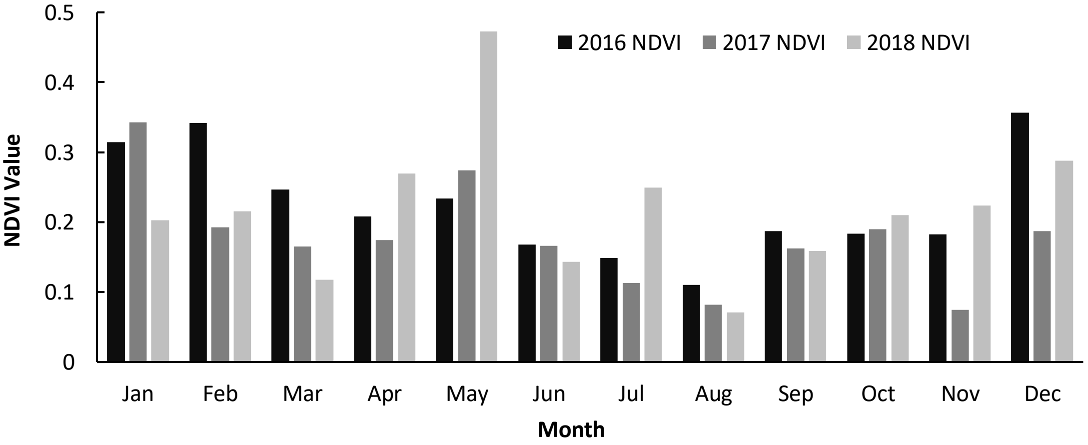

Figure 4.8: The monthly Normalised Difference Vegetation Index (NDVI) values calculated for the KGR study area for the 36 months of 2016 – 2018.

4.3.6 Modelling Predicted Effects

4.3.6.1 Overall Cattle Depredation

The top two models for overall predation included lag-rainfall and important prey (Table 4.1). An increase in lag-rainfall resulted in an increase in the levels of depredation (Table 4.2), with an increase in lag rainfall of 150 mm resulting in an almost doubling of the number of predicted depredation events per month (Figure 4.9). In contrast, the relative probability of cattle depredation declined with an increase in the availability of the most important prey (Table 4.2), but this effect was weak (Figure 4.10).

Table 4.1: The set of 13 regression models applied to **overall cattle depredation** events and ranked according to the frequency (Min AICc frequency and the Akaike weights (wi) of the models. The top-ranked models are in bold. Models are used to estimate the likelihood of livestock depredation risk year-round by African lions in the Kuku Group Ranch, Kenya.

Rank	*Form of regression model*	*Df*	*LogLik*	*AIC*	*Delta*	*Wi*
1	**Lag Rainfall**	**2**	**-131.0878**	**266.5392**	**0.0000000**	**0.252891534**
2	**Lag Rainfall + Important Prey**	**3**	**-129.9708**	**266.6917**	**0.1525289**	**0.234321995**
3	Lag Rainfall + NDVI	3	-130.9590	266.6917	2.1287511	0.087233214
4	Lag Rainfall + Rainfall	3	-130.9590	268.9158	2.3766212	0.077065064
5	Lag Rainfall + NDVI + Important Prey	4	-130.9590	269.0705	2.5313257	0.071328633
6	Lag Rainfall + Important Prey + Rainfall	4	-130.9590	269.1592	2.6200303	0.068234173
7	Null	1	-130.9590	270.9705	4.4313163	0.027585838
8	Lag Rainfall + NDVI + Rainfall	4	-130.9590	271.0819	4.5427394	0.026091014
9	Rainfall	2	-130.9590	271.1501	4.6109378	0.025216329
10	Lag Rainfall + NDVI + Important Prey + NDVI: Important Prey	5	-130.9590	271.2015	4.6623731	0.024576093
11	Lag Rainfall + NDVI + Important Prey + Rainfall	5	-130.9590	271.5381	4.9989711	0.020769284
12	NDVI	2	-130.9590	271.7785	5.2393116	0.018417566
13	NDVI + Rainfall	3	-130.9590	272.4304	5.8912460	5.8912460

Table 4.2 Model results for overall cattle predation at the Kuku Group Ranch, Kenya.

Variable	***B***	***SE β)***	***Z***	***P***
Lag Rainfall	0.16257	0.05556	2.828	0.00469
Important Prey	-0.09417	0.07936	1.166	0.24379

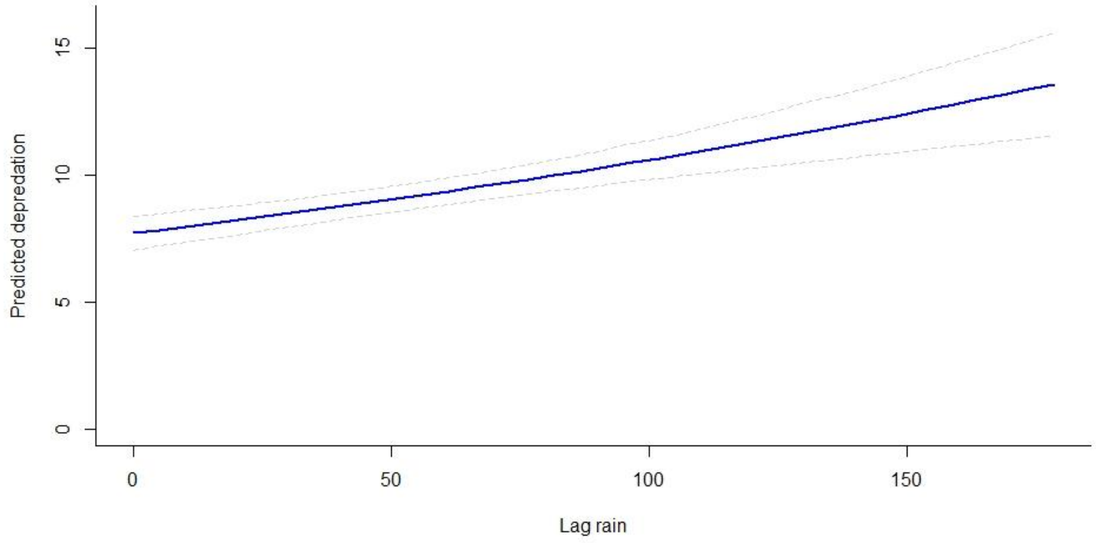

Figure 4.9: For overall depredation, General linear modelling indicated a positive relationship between monthly cattle predation effects by lions and the monthly lag rainfall recorded between 2016 and 2018.

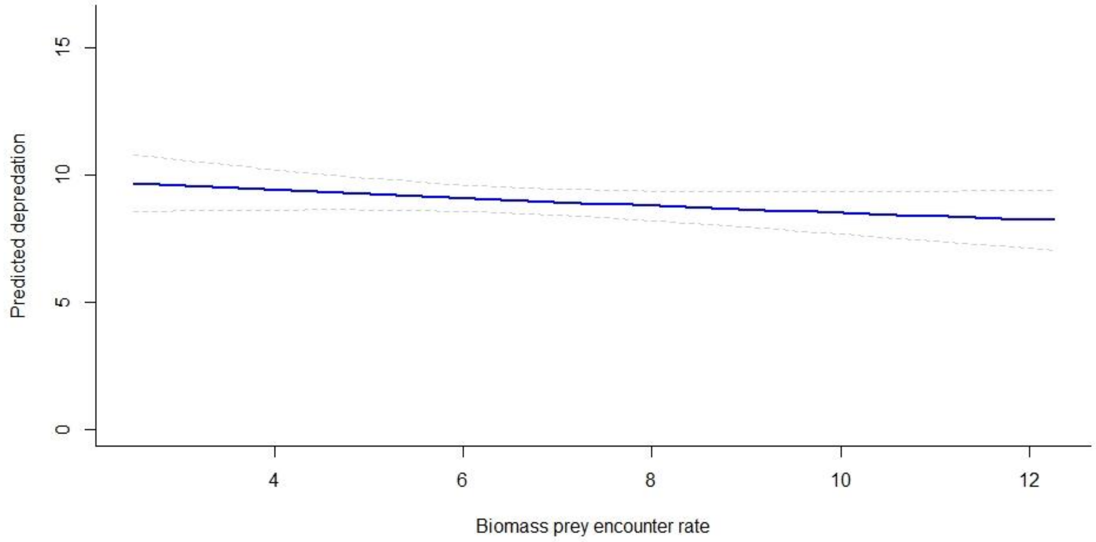

Figure 4.10: For overall depredation, General linear modelling indicated a negative relationship between monthly cattle predation effects by lions and the monthly encounter rate of the four prey species contributing most to lion diet, including Maasai giraffe, plains zebra, eland and Coke's hartebeest.

4.3.6.2 Negligent Cattle Depredation

None of the modelled predictor variables were present in the top models for negligent predation, and the null model was the best fit (Table 4.3).

Table 4.3: The set of 15 regression models applied to **negligent cattle depredation** events and ranked according to the frequency (Min AICc frequency and the Akaike weights (wi) of the models. The top-ranked model is in bold. Models are used to estimate the likelihood of livestock depredation risk year-round by African lions in the Kuku Group Ranch, Kenya.

Rank	*Form of regression model*	*Df*	*LogLik*	*AIC*	*Delta*	*Wi*
1	**Null**	**1**	**-121.1231**	**244.3638**	**0.000000**	**0.259453494**
2	Important Prey	2	-120.7844	245.9324	1.568673	0.118420417
3	NDVI	2	-120.8634	246.0905	1.726760	0.109420440
4	Lag Rainfall	2	-120.9748	246.3132	1.949404	0.097893043
5	Rainfall	2	-121.1151	246.5939	2.230149	0.085072406
6	NDVI + Important Prey	3	-120.3692	247.4883	3.124544	0.054396818
7	Lag Rainfall + Important Prey	3	-120.4786	247.7071	3.343354	0.048759532
8	Important Prey + Rainfall	3	-120.7816	248.3131	3.949341	0.036013979
9	Lag Rainfall + Rainfall	3	-120.8208	248.3917	4.027921	0.034626414
10	NDVI + Rainfall	3	-120.8385	248.4270	4.063189	0.034021169
11	Lag Rainfall + NDVI	3	-120.8561	248.4622	4.098473	0.033426237
12	Lag Rainfall + Important Prey + Rainfall	4	-120.2486	249.7876	5.423811	0.017230346
13	Lag Rainfall + NDVI + Important Prey	4	-120.3269	249.9441	5.580283	0.015933690
14	NDVI + Important Prey + NDVI: Important Prey	4	-120.3506	249.9914	5.627662	0.015560668
15	NDVI + Important Prey + Rainfall	4	-120.3507	249.9918	5.628028	0.015557821

4.3.6.3 Non-Negligent Cattle Depredation

The top three models for non-negligent predation included lag-rainfall, NDVI and important prey (Table 4.4). An increase in lag-rainfall resulted in an increase in the levels of cattle depredation on the KGR (Table 4.5), with an increase in lag rainfall of 150 mm resulting in an almost doubling of the number of predicted depredation events per month (Figure 4.11). NDVI showed a limited relationship with cattle depredation (Figure 4.12). In contrast, the relative probability of cattle depredation declined with an increase in the availability of the most important prey (Table 4.5), but this effect was weak (Figure 4.13).

Table 4.4: The set of 10 regression models applied to **non-negligent cattle depredation** events and ranked according to the frequency (Min AICc frequency) and the models' Akaike weights (wi). The top-ranked model is in bold. Models are used to estimate the likelihood of livestock depredation risk year-round by African lions in the Kuku Group Ranch, Kenya.

Rank	*Form of regression model*	*Df*	*LogLik*	*AIC*	*Delta*	*Wi*
1	**Lag Rainfall**	**2**	**88.00407**	**180.3718**	**0.0000000**	**0.282836384**
2	**Lag Rainfall + NDVI**	**3**	**87.29024**	**181.3305**	**0.9586981**	**0.175128424**
3	**Lag Rainfall + Important Prey**	**3**	**87.40993**	**181.5699**	**1.1980926**	**0.155372007**
4	Lag Rainfall + Rainfall	3	87.91794	182.5859	2.2140928	0.093486980
5	Lag Rainfall + NDVI + Important Prey	4	86.79234	182.8750	2.5032321	0.080903131
6	Lag Rainfall + NDVI + Rainfall	4	87.27167	183.8337	3.4618845	0.050095257
7	Lag Rainfall + Important Prey + Rainfall	4	87.36487	184.0201	3.6482824	0.045637391
8	Lag Rainfall + NDVI + Important Prey + NDVI: Important Prey	5	86.32846	184.6569	4.2851444	0.033191585
9	Lag Rainfall + NDVI + Important Prey + Rainfall + NDVI: Important Prey	5	86.75550	185.5110	5.1392134	0.021655553
10	Rainfall	2	90.60879	185.5812	5.2094384	0.020908366

Table 4.5 Model results for non-negligent cattle predation at the Kuku Group Ranch, Kenya.

Variable	***B***	***SE β)***	***Z***	***P***
Lag Rainfall	0.28070	0.08411	3.231	0.00123
Important Prey	0.13499	0.11593	1.141	0.25400
NDVI	-0.01818	0.05578	0.318	0.75037

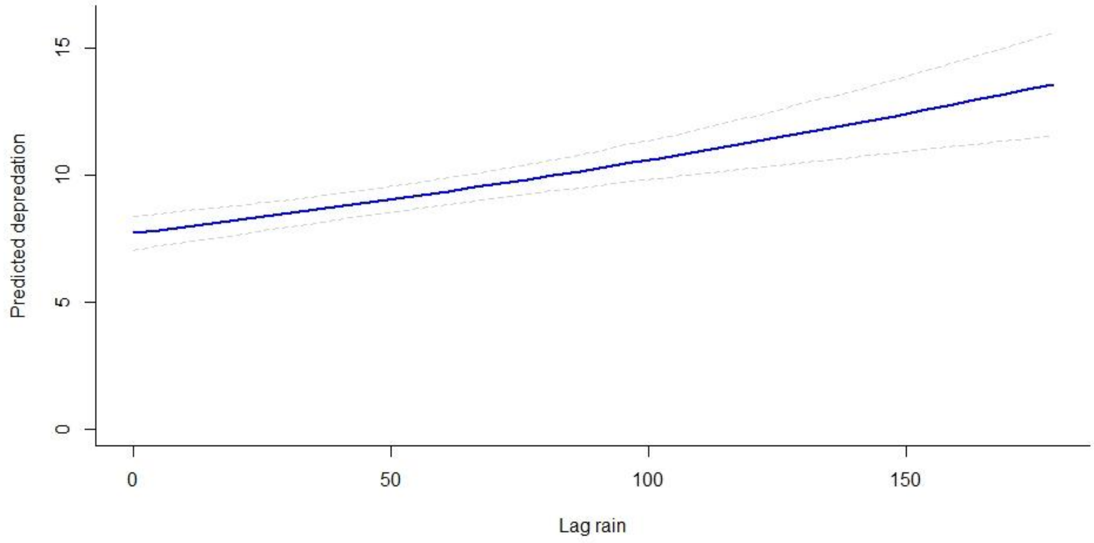

Figure 4.11: For monthly non-negligent cattle depredation, general linear modelling indicated a positive relationship between monthly cattle predation effects by lions and the monthly lag rainfall recorded between 2016 and 2018.

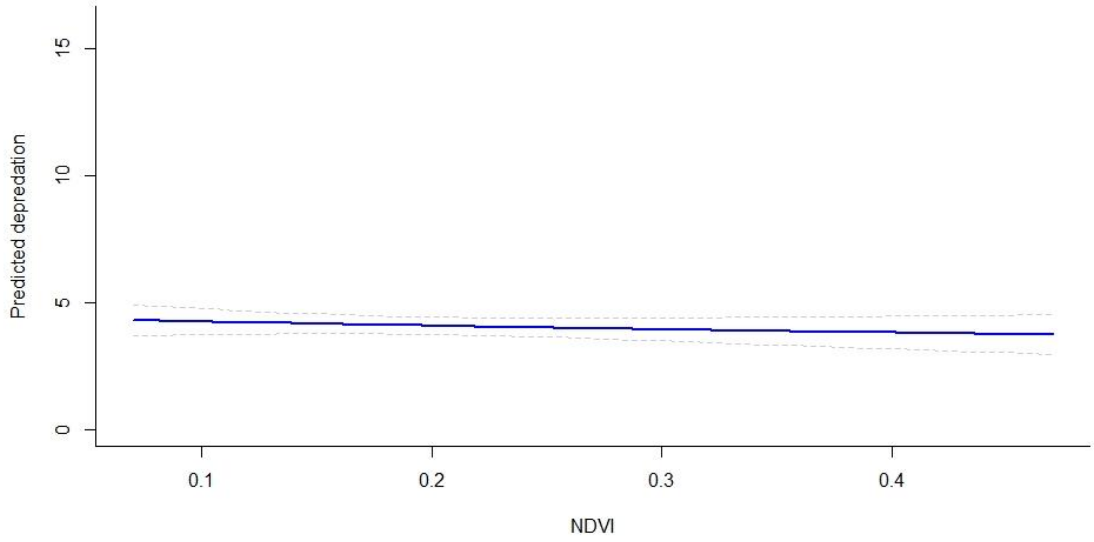

Figure 4.12: For monthly non-negligent cattle depredation, general linear modelling indicated a balanced relationship between monthly cattle predation effects by lions and the monthly NDVI recorded between 2016 and 2018.

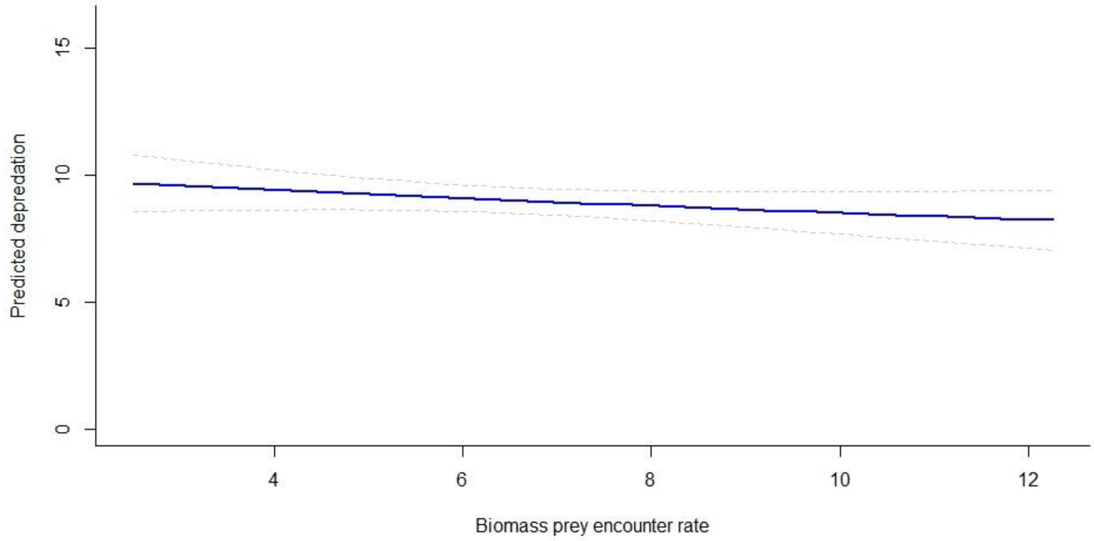

Figure 4.13: For Non-Negligent depredation, General linear modelling indicated a negative relationship between monthly cattle predation effects by lions and the monthly encounter rate of the four prey species contributing most to lion diet, including Maasai giraffe, plains zebra, eland and Coke's hartebeest.

4.4. Discussion

The survival of lions in Africa and Kenya will be dependent on the ability of NGO's, governmental agencies, and local communities to prevent, mitigate, and address human-lion conflicts. Identifying the drivers of human-wildlife conflicts will greatly assist conservationists and communities in better understanding and minimising the risk of cattle depredations. As cattle fall directly within the lion's preferred prey weight range (Radloff & Du Toit, 2004; Hayward & Kerley, 2005; Clements *et al*., 2014), it is not surprising that cattle predation by lions drives human-wildlife conflict in Africa (Weise *et al*., 2020). Pastoralists on the KGR protect their cattle by using herders and through the practice of placing cattle in bomas or corals at night (Bauer *et al*., 2017).

Despite these traditional defence practices, cattle depredation frequently occurred on the KGR, and between 2016-2018, there were 330 instances where lions killed and consumed cattle. Our findings indicate that lag rainfall seems to be the best predictor of cattle depredation, where cattle depredation by lions in the KGR varied over the 36 months and was partly explained by variation in lag rainfall, and to a much lesser extent, NDVI and wild prey availability.

- ***Effects of Lag Rainfall***

We found that lions were more likely to attack cattle after consistent high rainfall for an extended period (Figure 4.9). Lion attacks on cattle were least frequent during the lower lagged rainfall months and were most frequent during January, May, and December, which had the highest lag rainfall measurements for the study site (Figure 4.7). Lag rainfall is thus the most significant driver of cattle depredation identified in the study, supporting our hypothesis that cattle depredation by lions would be more common during these months. The influence of consistent high rainfall periods indicates that lions on the KGR target cattle during wet periods.

It is interesting to note that lions' overall and non-negligent cattle predation increases when the cumulative rainfall of the past three months increases, but there are no clear patterns for negligent herding (Table 4.3). This result may be driven by wild prey being in better condition and thus harder to catch (Mills *et al*., 1995; Owen-Smith & Mills, 2008) or due to the increased cover provided that assists lions in avoiding detection by Maasai herders while hunting (Ogutu & Dublin, 2004; Beatie *et al*., 2020). Cattle depredation associated with negligent herding is thus not influenced by lag rainfall, suggesting that herders do not adjust husbandry practices in times of increased rainfall despite increasing depredations. In contrast, herders do not become more negligent in their husbandry practices, but more cattle are killed during high rainfall periods despite this, indicating that the effects of lag rainfall on cattle depredation are not influenced by better husbandry. Thus, on the KGR, more cattle are killed despite reasonable herding practice during presumably better times for wildlife and lions (after three months of high rainfall).

Seasonal variation in the herding of cattle may play a role in the variation of cattle depredations over time (Kuiper *et al.,* 2015) and cattle on the KGR are sometimes herded seasonally, which relates to the lag rainfall. In dry periods mature warriors herd cattle into the Chyulu Hills and the neighbouring national parks. Although cattle are in seasonal bomas at night, cattle are well protected, and herder vigilance is high, reducing the vulnerability of cattle to predation in the dry season. In contrast, when sufficient rainfall has fallen, cattle are kept closer to settlements and tended by younger herders close to permanent settlements. However, although they are present and accurately detect attacks on cattle (According to Wildlife pays, a non-negligent practice), they may be less effective at discouraging attacks than the warriors. This shift in husbandry practice potentially explains the patterns for depredation related to negligence husbandry and highlights that cattle may be killed and consumed by lions on the KGR regardless of the level of herder vigilance.

The behaviour of lions regarding killing cattle on KGR underpins the fact that top-down, prey-predator interactions cannot be separated from the extraneous influences on prey population dynamics facilitated through natural resources (Owen-Smith & Mills, 2006). The potential influence of consistent high rainfall periods indicates that lions on the KGR target cattle during wet periods and do not do so opportunistically. Increased predation on cattle during higher rainfall periods is potentially thus driven by improved fitness of the most important wild prey (Mills *et al.,* 1995; Owen-Smith & Mills, 2008b) or increased cover assisting lions in ambush hunting (Ogutu & Dublin, 2004). A further possibility could be that increased lag rainfall allows the quantity of vegetation to respond, providing increased cover to obscure lions from herders and thus, they can get closer to cattle and herds without being detected while they also graze closer to well-shaded lion daytime resting areas.

- ***Effects of Prey Availability***

There was no strong relationship between prey availability and cattle depredations on the KGR, suggesting that lions on the KGR had sufficient wild prey over the 36 months. The results for prey availability are similar to the work done in the Olkiramatian and Shompole conservancies, Kenya, where no significant relationship between prey density and frequency of livestock predation was identified (Western *et al.,* 2021). However, it is worth noting that it has been shown elsewhere to be important in that cattle depredation increased when wildlife dispersed evenly into the landscape (Beatie *et al.,* 2020). Wild prey availability can thus affect a lion's predation on wild prey and directly influence cattle depredation (Beatie *et al.,* 2020). However, the weak relationship where cattle depredations were negatively associated with increased wild prey availability indicates that prey availability variation between months was not a driver of cattle depredation.

The migration of grazers (plains zebra and Coke's hartebeest) out of the KGR during the low rainfall months may reduce cattle depredation, while inward migrations of wild prey availability create a threshold enough to increase cattle depredation rates as lions are known to follow concentrations migratory prey (Schaller, 1972). It is thus possible that the movement of lions from the surrounding National Parks into the group ranch leads to increased opportunities for cattle predation by lions during high rainfall periods. Lions follow concentrations of migratory prey such as plains zebra, blue wildebeest, and Coke's hartebeest (Schaller, 1972). The movement of lions from the surrounding National Parks into the KGR grazing areas may thus lead to increased opportunities for cattle predation during high rainfall periods. This migratory behaviour has been documented in the Tsavo-Amboseli landscape when seasonal rains fill non-permanent waterholes, and wild prey species disperse into the previously dry areas and are followed by lions (Eltringham *et al.,* 1999; Patterson *et al.,* 2004)

In investigating prey availability as a potential driver of cattle depredation, there was a potential risk in evaluating cattle depredations against the availability of larger-bodied wild prey species only, as it is well-documented that lions also kill and consume small prey (Hayward & Kerley, 2005). Using the four prey species that contribute most to the lion diet in terms of biomass, the effect of small prey may have been overlooked. We assessed the possible impact of this by looking at other metrics of prey availability, including the most preferred prey and the most consumed prey. The predation variables were all colinear, and thus the results do not change when running the models with the other prey variables. Furthermore, it has been documented that although lions consume smaller prey items, smaller prey often represents bridging kills between larger species killed and are not driving predations patterns (Beukes *et al.,* 2020).

- ***Effects of NDVI***

Increased NDVI indicating high-quality foraging resources can allow wildlife to disperse in response to better foraging resources making it increasingly challenging for lions to encounter wild prey (Bhola *et al*., 2012; Beattie *et al.,* 2020). When modelling depredation as a function of NDVI, we thus expected that higher NDVI values would potentially lead to an increased incidence of cattle depredation. NDVI in the study area remained relatively constant across months and years compared to other variables measured (Figure 4.8). Although one would expect that cattle depredation by lions would increase in areas with high NDVI measures, no statistical relationship was found, and NDVI thus did not explain the monthly variation observed in the cattle depredation.

The results show that lag rainfall (Figure 4.7) shows much more variation between months than NDVI (Figure 4.8). Stable NDVI measured on the study site can be because browse availability remains relatively constant even in dry months and is influenced by the lava Forest, low forest, and other vegetation types. The lava forest type is characteristic of the KGR where perennial tree and shrub cover is significant on lava flows (Sakkas *et al.,* 2002; Meguro & Chalo, 2018), while the other forest types of strata are also of dryland forest types and contain drought-tolerant species (Musyoka, 2019). In this instance, the stability of tree and shrub NDVI (browse availability) may stabilise the overall NDVI figures during the high variation in rainfall between months. Thus, NDVI is not a true reflection of graze availability, leading to the weak relationship between cattle depredation and NDVI, as the NDVI values do not accurately capture dry periods during the dry months (Moleele *et al.,* 2001).

- ***Conclusion***

During the study, most cattle depredation occurred after the cumulative rainfall over three months was more than 50 mm and while cattle were outside of bomas grazing or moving between grazing areas. Lagged rainfall can potentially influence lion hunting behaviour by increasing cover for stalking and hunting, increasing wild prey fitness, and reducing wild prey catchability (Beatie *et al.,* 2020). This study demonstrates that cattle depredations and human-carnivore conflicts are multifaceted and complex. What may be driving cattle depredations in other areas cannot simply be inferred for other similar rangelands. Influences such as resident prey availability, rainfall, and foraging resources affect cattle depredation and are different for every area.

The importance of environmental variables (including for this study, rainfall, NDVI & wild prey availability), but most notably lag rainfall, has highlighted the importance of investigating all of these components on human-wildlife conflicts when attempting to mitigate these conflicts. Mitigating conflict on the KGR will depend upon the management and conservation entities being able to predict basic patterns of conflict and using lag rainfall as a guide to improve cattle husbandry during high-risk periods. Our findings can partly meet this need by providing researchers, conservationists, and pastoralists with a tool to predict high-risk periods and temporary periods of "more suitable lion habitat" for cattle depredation as an early warning for herders on the KGR.

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CHAPTER 5: RESEARCH FINDINGS AND MANAGEMENT IMPLICATIONS

5.1. Introduction

Wild spaces and the wildlife they conserve throughout Africa face numerous threats due to the rapidly expanding human population (Gerland *et al.,* 2014; Jones *et al.,* 2018). In such circumstance's competition frequently arises between wildlife and people for space and other resources, often leading to human-wildlife conflict. Carnivores are particularly susceptible to human-wildlife conflict due to their extensive home ranges and dietary requirements (Linnell *et al.,* 2001; Macdonald & Sillero-Zubiri, 2002; Inskip & Zimmermann, 2009). In East Africa and Kenya, the most well-known carnivore under threat is the African lion (*Panthera leo*). The most severe human-carnivore conflicts involve domestic cattle and lions (Franco *et al.,* 2018; Gebresenbet *et al.,* 2018; Van Eeden *et al.,* 2018; Bauer *et al.,* 2020). Lions predate upon cattle and attack people, resulting in affected communities responding by killing lions with subsequent lion population declines (Bauer *et al*., 2020).

Declining lion populations can have negative ecological impacts (Miller *et al.,* 2001; Sinclair, 2003; Ripple *et al.,* 2014) and can impact the tourism industry with financial implications (Fayissa *et al.,* 2007; Okello *et al.,* 2008). The negative impact on tourism is mainly caused by the fact that lions are both environmentally and commercially important, while for pastoralist communities, lions represent an ever-present threat to cattle (Gogoi *et al.,* 2020; Bauer *et al.,* 2020). Given the importance of lions for tourism and cattle's cultural and socio-economic significance for pastoralist communities, it is thus essential that sustainable solutions for human-lion conflict be developed and implemented (Trinkel & Angelici, 2016). Due to the ecological and socio-economic challenges faced by lion conservationists, the conservation of lions, and indeed all large carnivores, has been considered to only be realistically achievable by making use of the preservationist approach through setting aside large areas of suitable habitat away from human settlements (Packer *et al.,* 2013; Van Eeden *et al.,* 2018).

Coexistence between humans and large carnivores is possible, as demonstrated by increasing populations of large carnivores in parts of Europe (Chapron *et al.* 2014) and Asia (Athreya *et al*., 2013), where humans occur at high densities. Although coexistence poses challenges, it can be achieved and is increasingly vital to mitigate conflicts between humans and large carnivores by using management and legislative tools to ensure the effective conservation of these carnivore species (Ripple *et al.,* 2016). In improving the conservation of these carnivore species, it is possible to preserve their functions more broadly (Ritchie *et al.,* 2012; Ritchie *et al.,* 2014; Ripple *et al.,* 2014).

This higher-level management and legislative view of lion conservation have been proven possible when the management regime is favourable and can allow large carnivore populations to be increased after favourable legislation is introduced, despite further increases in human population density (Linnell *et al.,* 2001). The Kuku Group Ranch (KGR) is a vital lion conservation area and forms part of a critical wildlife corridor that connects not only the Tsavo and Amboseli National parks but also all of the neighbouring group ranches and the Chyulu Hills National Park to the north (Henschel *et al.,* 2020). Monitoring and understanding this system and the associated wildlife corridor are essential for the conservation and protection of the resident lion population into the future (Bauer *et al.,* 2017). Before this study, little was known about the area's lion, cattle, and wildlife interactions.

5.2. Prey Availability

Prey declines within lion ranges can negatively impact lion populations and reduce connectivity with protected areas (Bauer *et al.,* 2020). Prey populations are under threat from anthropogenic changes (poaching pressures and livestock expansion), and understanding which prey species are most important for lions requires repeated ongoing monitoring (Funston *et al.,* 1998; Tambling *et al.,* 2012). Aerial counts and ranger patrols provide excellent tools for conducting wildlife surveys in informally and formally protected areas (Funston *et al.,* 1998; Tambling *et al.,* 2012). Aerial counts and ranger patrols were used to collect the data used in this study.

My results suggest that specific wild prey species are important dietary choices for resident lions. These include, in particular, the Maasai giraffe (*Giraffa tippelskirchi*), eland (*Tragelaphus oryx*), Coke’s hartebeest (*Alcelaphus cokeii),* and plains zebra (*Equus quagga*). However, cattle (*Bos taurus*) occur in very high abundances throughout the year and are consumed frequently by lions. The aerial census method used in the study (see Chapter 3 for detailed methods and Appendix A for a complete account of all herbivore species recorded) and SMART Ranger patrols data collection should be repeated by management to monitor the changing trends in wildlife and cattle numbers accurately annually.

Only through continued monitoring with sound and repeatable methodology will KGR management detect fluctuations in prey numbers, and in the context of this study, both wildlife and cattle numbers should be monitored annually. Ongoing monitoring is essential as wild prey populations within the KGR and Tsavo-Amboseli landscape are threatened by bush-meat poaching (Okello *et al.,* 2015) and livestock expansion (Bauer *et al.,* 2020).

The Maasai giraffe is being targeted for the bush-meat trade by poachers from Tanzania, exacerbating the threat to prey base (Okello *et al.,* 2015). Maasai giraffe poaching is concerning as on the KGR, the Maasai giraffe is the most significant contributor to lion diet biomass and represents 12% and 30% of prey consumed and prey biomass, respectively. There is ongoing evidence of poaching in the Kenya/Tanzanian borderlands (Okello *et al.,* 2015), including KGR and should poaching reduce giraffe populations beyond the threshold at which the population is growing, the threat to lions could be exacerbated by this critical prey species decline (Bauer *et al.,* 2020).

Although we did not directly consider cattle competition with wild prey species due to livestock expansion, there are potential ecological effects on lion diets and resulting feedback loops with lions consuming cattle. Studies have shown that when there is sufficient wild prey, lions are less likely to kill livestock, but where prey biomass is not high enough, the probabilities of livestock predation are high (Khorozyan *et al.,* 2015). Competition between wild and domestic lion prey species thus requires further attention and research where the rangers on the KGR can provide a more fine-scale resolution of data on the ratios of cattle to wild prey abundance over time (through SMART ranger patrols). We did not measure wild-prey to cattle ratios for this study due to a cultural resistance of Maasai rangers counting cattle. Due to this cultural influence, measuring this ratio would require that social norms be challenged and that through Cybertracker, rangers start monitoring cattle during foot patrols. This finer-scale data could assist in better understanding the patterns of livestock depredation may be beneficial for future studies. Alternatively, cattle could be fitted with tracking collars (Kuiper *et al.,* 2015). In a study in the Tsholotsho Communal Land, it was found that seasonality in cattle herding practices influenced the vulnerability of cattle to depredation (Kuiper *et al.,* 2015). Fitting cattle with tracking collars on the KGR could provide further insights into cattle depredation.

5.3 Lion Diet

Knowing what lions eat is essential to understanding their behaviour and influence on prey populations (Barnardo *et al.,* 2020; Beukes *et al.,* 2020). In African savannas, smaller species contribute little to the overall prey biomass consumed by lions, and large prey is important (Radloff & du Toit, 2004; Hayward & Kerley, 2005; Owen-Smith & Mills, 2008). A recent study in drier Kgalagadi re-confirmed that large-bodied prey species are the primary food source for lions and constitute a key driver of lion population dynamics (Beukes *et al.,* 2020). Preference and importance for larger prey have also been confirmed in the more mesic Hluhluwe–iMfolozi Park (HiP), when the resident lion population preferred prey species larger than 50kg in body size (63–684 kg) and had consumed a more significant proportion of preferred prey than other prey items (Barnardo *et al.,* 2020).

The results presented in this study focus on the availability and consumption of large-bodied (> 50 kg) prey by lions in the KGR. However, it is important to stress that lions will maintain a degree of opportunism even when preferred large prey is abundant and that abundant, smaller prey is likely to be an essential resource for lion populations in addition to larger-bodied prey (Barnardo *et al.,* 2020). An investigation into the contribution of smaller prey to lions' diet should be considered for further studies within the study site and Tsavo-Amboseli landscape. Although we know large species are essential for lion populations, knowing which smaller prey species support their main diet is essential to guide conservation efforts to ensure a sufficient prey base for threatened lion populations (Montgomery *et al.,* 2018; Beck *et al.,* 2019 Bauer *et al.,* 2020).

By using GPS cluster follow-up to record confirmed feeding events, this study recorded a total of nine different large-bodied prey species contributing to confirmed feeding events at GPS cluster sites (Table 5.2). However, it could not provide reliable information on the utilisation of smaller prey given that GPS cluster approaches to diet estimation, in the absence of additional data sources like scats, are biased to large prey (Tambling *et al*., 2012). Of concern is that cattle are consumed frequently and contribute a large percentage to the overall biomass consumed by lions on the KGR. Despite this high utilisation of cattle, populations of the Maasai giraffe are characterised by high abundances, contributing 12% to all prey consumed by lions and approximately a third (30%) of the large prey biomass consumed on the KGR.

A better grasp of the dynamics of the important prey species populations is required to protect lion populations and their prey base. The potential drivers of cattle depredation indicate that lagged rainfall strongly influences cattle depredation, and with a sustained increase in rainfall, cattle depredation increases (Chapter 4). Furthermore, the higher numbers of cattle and their frequent consumption by lions accentuates the importance of understanding what drives current human-lion conflicts and adjusting herding and husbandry practices accordingly.

5.4. Drivers of Predation

Cattle depredation patterns were explored by comparing the number of cattle depredation events in a given month from 2016-2018 with rainfall, lag rainfall, NDVI, prey and wild prey availability (See Chapter 4). The General linear models suggest that lagged rainfall had the strongest association with cattle depredation. The results further suggested that it is essential to consider abiotic variations, as predation of cattle by lions can be linked to the variation in accumulated rainfall and the potential shift in conditions and grazing practices. Within KGR, lions consume more cattle during wetter periods.

However, it is not simply a matter of improving husbandry and protecting resident prey populations required. Even with a predator compensation fund in the KGR, current husbandry practices do not adequately prevent cattle-killing by lions even if strictly followed. Overall, both combined (overall depredation) and non-negligent depredation correlate with lagged rainfall, but this is not the case for negligent depredation. Thus, even when herding is good, cattle are still frequently killed on the KGR. NDVI and prey availability showed only weak relationships, despite being included in some of the top model combinations. Although not significant for this study, NDVI and prey availability may contribute to cattle depredations peaks by making wild prey increasingly challenging to locate due to more cover.

One also needs to consider that during elevated rainfall periods where the vegetation has recovered, it may be easier for lions to stalk and kill cattle as herders cannot see lions easily from a concealment perspective and can get closer to cattle during the day. Prey availability was similarly included in the top models, but subsequent investigations of the magnitude of the effects suggest a weak relationship with depredation. However, when important prey availability (Maasai giraffe, eland, Coke's hartebeest, and plains zebra) increases, cattle depredations are reduced slightly with the potential to reduce cattle depredations. During periods of lag rainfall, cattle depredation rates may be maintained at current levels or reduced if the proportion of wild prey to cattle increases.

The general linear models allowed a visual summary of how the predictor variables influenced cattle depredations in the landscape. Lag rainfall was the strongest predictor of cattle depredation, which has long term implications for lion conservation on the KGR. Climate models for the Horn of Africa, which experiences two rainfall periods or seasons per year, indicate that east Africa will experience increased rainfall during the shorter rains under future climate change predictions (Rowell *et al.,* 2015; Dunning *et al.,* 2018). More recent modelling has further predicted that short rains are projected to end over a week later, with a significant increase in seasonal rainfall (Wainwright *et al.,* 2021).

These climate change predictions indicate that the KGR can expect increased rainfall during the short rain periods with extended high-risk cattle depredation windows, and due to the relationship with lag rainfall, an increase in cattle depredation and human-lion conflicts. It will thus be essential to factor the impacts of climate change and predictive modelling into any mitigation strategy to plan for the long term on the KGR. Results and findings outlined in chapters 3 and 4 suggest that while preserving wild prey populations is critical, the actual availability of cattle available for lions (through husbandry) need to be reduced by improving husbandry practices to prevent high levels of human-lion conflict. Enhanced husbandry will ensure that fewer cattle depredation takes place on the KGR. Enhanced husbandry and herding practices should focus on the important times when cattle losses are greatest, namely during the wet months of the year when the focus should be placed on ensuring better supervision and protection of grazing cattle. Lastly is essential to note what we did not measure, and that is that none of the variables used to interrogate drivers of cattle depredations incorporated smaller-bodied prey, and this creates opportunities for further research into the role that both wild and domestic smaller-bodied prey (<50kg) play in modulating lion-cattle interactions. How smaller prey are utilised and the community perceptions of the loss of sheep and goats may be beneficial and interesting for further research.

5.5. Conclusions

Cattle depredation must be considered in a broader landscape with environmental variables, cattle husbandry, and lion behaviour. The importance of environmental variables (including for this study, rainfall, NDVI & wild prey availability), most notably lag rainfall, has highlighted the importance of understanding all components when attempting to mitigate human-wildlife conflicts. The results presented here suggest that strategies need to consider that the rate of cattle depredations is closely linked to lag rainfall and that this has the potential to drive cattle depredations and should thus directly influence both herding and husbandry practices. Pastoral communities on the KGR should put in place extra cattle guarding measures and increase herder vigilance and presence during periods of lagged rainfall to try to reduce conflict and depredation during this time. The owners of cattle also need to consider that east Africa will experience increased rainfall during the shorter rains under future climate change predictions and that this has the potential to increase the rate and incidence of high-risk cattle depredation periods and the associated human-lion conflicts.

Protecting all wildlife prey populations can contribute to lion survival in the KGR. The two primary threats affecting the number of lion populations and their numbers are cattle depredation, which leads to the retaliatory killing of lions, and the depletion of wild prey (Bauer *et al*., 2020; Western *et al*., 2021). Although wild prey availability was not identified as a strong driver of cattle depredation in this study, it is vital in the context of other areas in Kenya and the Tsavo- Amboseli landscape (Bauer *et al*., 2020; Dolrenry *et al*., 2020; Western *et al*., 2021). That wild prey availability was not a strong driver of cattle depredations may indicate that the KGR still has enough wild prey to support the resident lion population. Further research should, however, investigate other variables, such as the ratio of wild to domestic prey, as the interaction between the two prey bases may be more important than the absolute abundance of wild prey only. Despite this, it is clear that the already severe issues of cattle depredation and retaliatory killing of lions on KGR could be worsened with a further loss of wild prey and accentuate the already high cattle mortalities at the hand of lions.

Mitigating human-lion conflict on the KGR will depend upon conservation entities being able to predict the basic patterns of conflict. Cattle depredation and the confounding issues of bush-meat poaching, livestock expansion and poor husbandry are issues that need to be addressed in the KGR and broader Tsavo-Amboseli landscape (Bauer *et al.,* 2020; Dolrenry *et al.,* 2020). Increasing livestock expansion and poaching activities may significantly reduce lion populations due to dwindling prey bases and competition for resources between wild and domestic animals (Bauer *et al.,* 2020). Livestock expansion, twinned with the inevitable increase in human-lion conflicts and retaliatory killings, could thus potentially lead to the local extirpation of lions should the conflicts identified in this study not be addressed. There are few options to address these conflicts, but a common subject across all lion-livestock conflict situations is that improved cattle husbandry can limit the availability of livestock to lions, and the current husbandry regimen of the KGR can be improved in this regard.

The benchmark measures put in place for good husbandry practices outlined in the Wildlife Pays program (Chapter 4) still allow for negligent cattle depredation to take place (n=176 out of 330 incidents). Conserving important prey species may be confounded if cattle herding husbandry practices do not improve. This problem is because lions are opportunistic and consume what is frequently available and encountered (Hayward & Kerley, 2005; Barnardo *et al.,* 2020). Reducing cattle availability should thus be prioritised by providing predator-proof bomas, introducing better cattle husbandry, and increasing custodianship for the wild prey population. These measures can protect cattle better while concurrently increasing wild prey availability in the long term. For herders on the KGR, adapting to cyclic variation in lag rainfall and high-risk periods for cattle depredations during wet periods will assist in reducing the frequency of human-lion conflicts. Cattle herders in the KGR should be aware that the risk of predation increases at times of high lag rainfall and the end of the rainfall season, and they should be extra vigilant.

To improve vigilance levels and current cattle husbandry practices, cattle owners in the KGR should employ only adult, professional herders and engage with the Maasai warriors to guard cattle at all times, and not only when cattle need to be moved long distances. Even when range conditions improve, better herders should be maintained, even when cattle are closer to permanent settlements. The use of guard dogs can also deter lion predation on livestock both while grazing and in protective bomas, and the KGR community should also investigate this intervention (Treves & Karanth, 2003)

By using exclusively adult herders, engaging the Maasai warriors and the potential deployment of guard dogs, better husbandry can reduce cattle depredation on the KGR. The findings outlined in this study can provide insights into similar mixed-use areas where humans and wildlife coexist in Africa and contribute to the discussions around the requirements of cattle owners, wild prey populations, and lions in the Tsavo-Amboseli ecosystem and KGR. Protecting these multiple-use areas, often wildlife corridors will assist larger intact ecosystems to conserve prey species, lions, and other carnivore species in interconnected landscapes. Lastly, the findings outlined here can assist management in refining specific management actions for the KGR through an improved understanding of the drivers of the lion, cattle, wildlife interactions in the KGR pastoral area.

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APPENDICES

Appendix: A - The total number and percentage contributions of prey species to lion diet derived from GPS clusters on the KGR between 2017 and 2018.

Prey Species	**No. of Times Identified**	**Percentage Contribution (%)**
Buffalo	1	1
Goat	1	1
Grant's gazelle	1	1
Thompson's gazelle	2	2
Impala	3	3
Maasai ostrich	3	3
Warthog	5	4
Blue wildebeest	9	8
Eland	11	9
Maasai giraffe	13	11
Cokes' hartebeest	20	17
Plains zebra	23	19
Cattle	27	23
Total	**119**	**100 %**

Appendix: B - The results of the four aerial census counts (conducted in 2017 – 2018) within the KGR Study site show the total counts of all recorded herbivore species.

Prey Species	**May 2017**	**October 2017**	**June 2018**	**November 2018**
Buffalo	0	0	35	35
Dik-Dik	6	0	4	4
Eland	268	115	197	245
Elephant	38	00	137	120
Gazelle (Unidentified)	467	60	52	215
Gerenuk	34	44	14	28
Maasai giraffe	750	343	427	814
Grant's gazelle	4	329	30	506
Coke's hartebeest	180	61	194	390
Impala	110	124	275	345
Lesser kudu	12	0	11	17
Fringe-eared oryx	0	0	10	10
Maasai ostrich	39	10	14	19
Thompson's gazelle	21	21	0	4
Warthog	3	0	4	4
Blue wildebeest	244	23	190	256
Plains zebra	1088	326	937	1340
Wildlife Totals	**3264**	**1456**	**2531**	**4352**
Shoats (Sheep & Goat)	16857	12586	11874	19655
Cattle	6610	4668	5182	6340
Donkey	150	2	12	19
Livestock Totals	**23617**	**17256**	**17068**	**26014**

Appendix: C - The monthly ranger patrol distances walked by rangers on the Kuku Group Ranch study site from 2017 through to 2018 and used for prey preference analysis in Chapter three.

Month & Year	**Distance Patrolled (Km)**
Jan 2017	5561
Feb-17	6794
Mar-17	5943
Apr-17	5005
May-17	5621
Jun-17	3759
Jul-17	4827
Aug-17	5395
Sep-17	6170
Oct-17	5877
Nov-17	5724
Dec-17	5217
Jan-18	5873
Feb-18	5550
Mar-18	3935
Apr-18	3421
May-18	3865
Jun-18	4904
Jul-18	4532
Aug-18	6115
Sep-18	5805
Oct-18	4992
Nov-18	6647
Dec-18	5256
Average	**5283**

Appendix: D - Appendix D: The medium and large terrestrial mammals recorded through SMART Ranger Patrols on the KGR study site. These include only wildlife encounter rates calculated for groups of animals encountered at every 100 km walked by rangers. An average of these encounter rates is used for the preference analysis, presented at the end of this table

Species & Encounter Rates (wildlife groups/100 km)								
Date	**Coke's hartebeest**	**Blue wildebeest**	**Buffalo**	**Eland**	**Warthog**	**Maasai giraffe**	**Plains zebra**	**Maasai ostrich**
Jan-17	1.02	0.41	0.45	1.15	0.04	2.78	1.88	0.04
Feb-17	1.38	0.26	0.41	1.49	0.06	2.64	1.90	0.19
Mar-17	1.72	0.55	0.69	1.69	0.07	2.59	3.48	0.28
Apr-17	3.10	0.62	0.77	1.39	0.09	2.63	3.60	0.04
May-17	2.91	0.98	0.87	1.21	0.04	3.44	1.78	0.11
Jun-17	1.95	0.30	0.60	1.43	0.11	2.85	3.08	0.08
Jul-17	0.56	0.19	0.93	1.11	0.02	2.23	1.67	0.19
Aug-17	0.33	0.25	0.33	0.99	0.02	2.47	1.44	0.21
Sep-17	0.23	0.07	0.59	0.56	0.02	1.68	0.89	0.07
Oct-17	0.00	0.09	0.18	0.37	0.02	2.88	1.19	0.18
Nov-17	0.34	0.44	0.58	0.83	0.01	2.68	1.61	0.00
Dec-17	0.21	0.21	0.47	0.78	0.02	1.77	0.83	0.05
Jan-18	1.39	0.35	0.58	1.10	0.01	2.26	1.68	0.12
Feb-18	0.38	0.06	0.38	0.63	0.02	1.63	1.00	0.13
Mar-18	1.13	0.60	1.05	1.13	0.00	3.09	2.18	0.08
Apr-18	1.55	0.27	0.55	0.27	0.06	2.37	1.91	0.09
May-18	2.21	0.06	0.12	0.23	0.05	3.14	1.97	0.06
Jun-18	1.36	0.29	0.44	0.78	0.01	2.71	2.37	0.15
Jul-18	0.42	0.36	0.36	0.54	0.00	2.21	1.43	0.12
Aug-18	0.49	0.24	0.32	0.45	0.02	1.90	1.05	0.12
Sep-18	0.82	0.05	0.14	0.82	0.02	1.20	1.30	0.00
Oct-18	0.43	0.32	0.16	0.96	0.02	1.50	1.28	0.00
Nov-18	0.39	0.09	0.17	0.78	0.03	0.91	1.00	0.09
Dec-18	0.35	0.15	0.35	0.40	0.02	0.95	0.80	0.00
Average:	**1.03**	**0.30**	**0.48**	**0.88**	**0.03**	**2.27**	**1.72**	**0.10**
SE	**0.18**	**0.05**	**0.05**	**0.08**	**0.01**	**0.14**	**0.16**	**0.01**
SD	**0.86**	**0.22**	**0.25**	**0.40**	**0.03**	**0.69**	**0.78**	**0.07**